

**Canopy Arthropods and Herbivory
on the Tasmanian Southern Beeches,
Nothofagus cunninghamii and *Nothofagus gunnii***

Volume 1

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DECLARATION

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ABSTRACT

The Gondwanan relict tree genus *Nothofagus* has generated much research due to its biogeographical significance in understanding the biota of the Southern Temperate Zone. However, the southern temperate forest arthropod fauna, including that of *Nothofagus*, has received less attention than northern temperate forest and tropical rainforest. The extant Tasmanian *Nothofagus* canopy arthropod fauna has been considered depauperate. Yet with a palaeohistory of long persistence, high diversity and widespread distribution of the genus within Australia, the endemic Tasmanian Nothofagaceae – the evergreen *Nothofagus cunninghamii* and winter deciduous *N. gunnii* – could be expected to have accreted a large and diverse arthropod fauna, as have its sister Fagalean families in the northern hemisphere. Conversely, range contraction of Tasmanian *Nothofagus* in the increasingly arid conditions of the late Tertiary, and its cyclical isolation from the Australian mainland during the glacial cycles of the Pleistocene, could have depleted the associated arthropod fauna.

Thus the aims of this project were to document in detail the diversity and structure of the invertebrate communities associated with both species of Tasmanian *Nothofagus*; to build an inventory of canopy arthropod fauna according to feeding guild; and to measure the levels of herbivory, as an indication of herbivore activity, on these host species. These data enabled comparison of the arthropod communities on the two hostplants, and comparison with similar studies on closely related tree species (*Nothofagus* elsewhere, northern temperate Fagales) and other Australian tree taxa, now widespread (*Acacia* and *Eucalyptus*).

A cross section of survey sites was chosen, 17 for *N. cunninghamii*, and 12 for *N. gunnii*, including three where the host plants were sympatric. Canopy arthropods were sampled by branch beating, and leaves were collected from, or examined in situ on marked branches. The sampling schedule from March 1998 until March 2002 yielded data sets by *Nothofagus* species, site, sampling aspect, season, region, and between years. Priority was given to arthropod orders containing herbivorous taxa or scavenging taxa known to forage on trees. These were sorted to family, then genus and species where possible, otherwise to morphospecies; and allocated to feeding

guilds. The leaves were designated 'chewed' or 'intact' and the leaf area lost from the chewed leaves was estimated. Mean percentage leaf area loss was calculated as a measure of herbivory.

The main finding from these investigations was that there existed a strong contrast in the diversity and taxonomic profile of the arthropod fauna between the two *Nothofagus* species. For *N. cunninghamii*, the associated fauna was relatively rich in taxa and comparable with other temperate zone trees in both its diversity and guild structure. Similarly the *N. cunninghamii* herbivory levels were within the range of those found on temperate and subtropical tree taxa. *N. gunnii* in contrast was clearly depauperate, particularly lacking many important folivorous groups such as chrysomelid beetles, leaf miners and aphids. However there was, for the two *Nothofagus* species, considerable local variation in the arthropod communities and levels of herbivory - between regions; between sites within a region; and within a site, seasonal variation and also differences between consecutive sampling years - insights which have significance for effective biodiversity surveys and conservation strategies.

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‘Without curiosity, without a passion for discovery, nature cannot endure. And without nature, curiosity will fade ... I cannot help feeling that, ultimately, curiosity will be sustained. It is so fundamentally human to thirst for knowledge and to turn to nature for visions of the unknown.’

Thomas Eisner, 2003, *For the Love of Insects*, p.404.

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Chapter 1 INTRODUCTION

There is widespread interest in the Gondwanan relict genus *Nothofagus* because of its biogeographical significance in understanding the biota of the Southern Temperate Zone (Veblen *et al.*, 1996a), however knowledge of the biogeography and evolution of a host plant and its ecosystem is enhanced by an appreciation of its invertebrate fauna (McQuillan, 1993). Research into the interactions between arthropods and plants has its foundation in Southwood's (1961) observation that a greater distribution of the host plant species was associated with a more diverse arthropod fauna, as was a longer history of host presence, and the topic was enlarged on during subsequent decades. However, much of this work was based on the British insect fauna, which is largely post-glacial and may not be typical of phytophagous groups elsewhere. Although northern temperate forest and more recently, tropical rainforest invertebrate fauna has been frequently researched, southern cool temperate rainforest and subalpine canopies have received less attention (Lowman & Wittman, 1996). In particular, there have been few studies of the arthropod fauna on the tree genus *Nothofagus*, once widespread and highly diverse in Australia (Hill, 2001) but now restricted to three species, two of which occur in Tasmania - the evergreen *N. cunninghamii* and the Tasmanian endemic, winter-deciduous, *N. gunnii*.

The forests and woodlands of Australia are now dominated by genera better adapted to warm, dry conditions, notably *Eucalyptus* and *Acacia*. These plants have been found to support distinctive profiles of invertebrates which have diversified across the continent (Majer *et al.*, 1997; 2000). Some beetle (e.g. Paropsini) and homopteran (Psylloidea) taxa number hundreds of species on these hostplants. Although evidence is limited, the characteristic "Australian" profile of this fauna appears to be different from that associated with the more restricted cool temperate forest tree genera of the south east of the continent.

1.1 RESEARCH RATIONALE

The long history and widespread distribution of *Nothofagus* would suggest, following Southwood (1961), that the genus would have a diverse arthropod fauna. Despite fragmentation across the Southern hemisphere during the breakup of Gondwana, the genus maintained extensive distributions within the separating landmasses (Veblen *et al.*, 1996a).

As the Australian landmass drifted northward during the Tertiary, conditions became drier and the rainforests retreated to the eastern mesic margins of the continent. In mainland Australia and Tasmania, *Nothofagus* underwent further contraction in response to cold and aridity during the last ice age until 10,000 years ago, resulting in the current pattern of small residual populations in the remaining wet temperate regions (Hill, 2001). This range reduction and separation into small isolated communities would be expected to have reduced faunal diversity on the extant *Nothofagus* species, both overall and within each region; and to create differences in diversity between the host species with larger (*N. cunninghamii*) or smaller (*N. gunnii*) ranges.

Available records suggest that Tasmanian *Nothofagus* canopies are depauperate compared with their counterparts in New Zealand and South America (McQuillan, 1993) or with wet *Eucalyptus* forest in their home state (Richardson *et al.*, 1997). Albeit likely to have a reduced fauna, a paucity of data could also be contributing to the perception of such a low level of diversity on Tasmanian *Nothofagus*.

1.2 RESEARCH QUESTIONS

With the above points in mind, the purpose of this study has been to gather baseline data on the canopy arthropods and levels of herbivory on *N. cunninghamii* and *N. gunnii*, at sites representative of their distribution in Tasmania, with the aim of answering the following research questions:

1. Is the Tasmanian *Nothofagus* arthropod fauna truly depauperate?
2. Within that fauna, do *N. cunninghamii* and *N. gunnii* have characteristic, but different, core species organised in similar way?
3. Do the herbivorous taxa attack the two *Nothofagus* species to the same degree?
4. Are there regional characteristics to the fauna and levels of herbivory?

1.3 RESEARCH APPROACH

The study was based on seasonally-structured surveys, with a representative regional coverage. Samples were collected systematically from *N. cunninghamii* and/or *N. gunnii* at sites around Tasmania, at intervals to allow comparisons within and between seasons. At selected sites, a finer degree of variation was sampled for: from opposite aspects (north or south facing) of the same tree canopy, or from adjacent trees of both *Nothofagus* species.

Sampling was conducted for canopy arthropods and levels of herbivory. Within the arthropods samples, the major taxa were identified, assigned to feeding guilds, and ordination used to explore the data. Herbivory, in the form of both chewing and non-chewing leaf damage, was recorded from discrete samples, and also from labelled branches examined in situ at consecutive visits. Finally, the statistical analyses of arthropod and herbivory sampling were brought together into a synthesis of the results and a comparison with other tree species, followed by a discussion and the conclusions of the research. This research approach is summarised below (figure1).

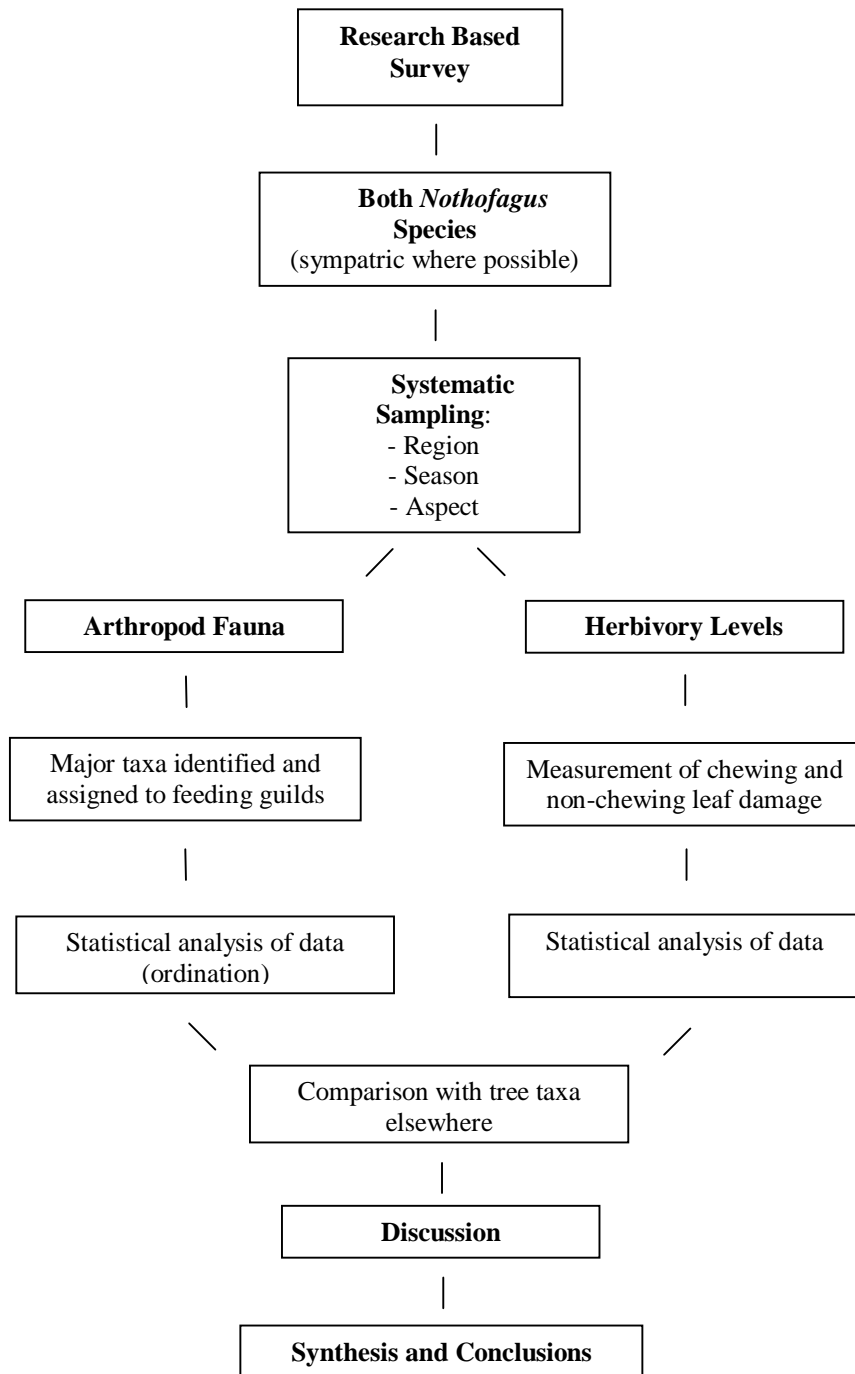


Figure 1. Flow diagram summarising the research approach used in this study.

1.4 THESIS OUTLINE

The broad structure of this thesis flows from an initial brief introduction to the research topic, the rationale behind the study, and its objectives, to a literature review providing a background to both the genus *Nothofagus* and the discipline of arthropod – plant research, including a discussion of sampling methods. There follows a description of the methods used and research limitations, results obtained, and subsequent analysis of that data. Finally, the various strands of the research are drawn together to lead to the thesis conclusions. Expanding on this précis, the chapters are outlined below.

Chapter 1 introduces the research topic, gives the rationale for the formulation of the research questions, then summarises the research approach and thesis structure. In the next two chapters this research is placed in context. Chapter 2 explores the taxonomy, phylogeny, palaeohistory and biogeography of the genus *Nothofagus*, its current distribution in the Southern Hemisphere, and focuses on the extant species in Tasmania. Then as a prelude to the next chapter, the evolutionary history of *Nothofagus* is set beside that of its arthropods. Chapter 3 discusses the foundations of arthropod – plant research, host-plant – herbivore interactions, and the significance of host-plant history and area of distribution. The remainder of the chapter reviews methods of sampling, highlights factors to take into consideration in such investigations, and documents the parlous state of research into Tasmanian *Nothofagus* canopy arthropods.

The following three chapters form the core of the research investigations undertaken and present the results therefrom. Chapter 4 describes the research schedule, sites, materials and methods employed, and indicates the limitations of the project. Chapters 5 and 6 document the results of the specimen collection and processing, and the statistical analysis of that data, for arthropods and herbivory respectively. Chapter 7 compares these results with the arthropod fauna and herbivory levels found on *Nothofagus* elsewhere, as well as northern temperate Fagales, *Acacia* and *Eucalyptus* in Australia, and with tree taxa from the Tropics. Finally, Chapter 8 encompasses the discussion, and conclusions of the research.

Chapter 2 NOTHOFAGUS

Nothofagus (literally ‘false beech’) has been called the ‘Southern Beech’ because of its Southern Hemisphere distribution and in recognition by nineteenth century explorers and botanists of its resemblance to the familiar Beech (*Fagus*) trees of northern climes (Poole, 1987). Evaluation of morphological characters of extant and fossil species together with molecular data has progressively clarified the phylogeny of the genus, establishing the relationships between the four extant subgenera: *Brassospora*, *Fuscospora*, *Lophozonia* and *Nothofagus*. However, their disjunct distribution across the Pacific Ocean still gives rise to debate as to their biogeographical history. Two extant species, from different subgenera, remain in Tasmania, *N. cunninghamii* (*Lophozonia*) and *N. gunnii* (*Fuscospora*), and their history and distribution, with that of the genus as a whole, is described in this chapter.

2.1 NOTHOFAGUS, FAGUS AND THE ORDER FAGALES

The genus *Nothofagus* sits in the monogeneric family Nothofagaceae, relatively recently distinguished from its sister family Fagaceae (Kuprianova, 1962 in Jones, 1986; Nixon, 1989; Hill & Jordan, 1993; Manos & Steele, 1997; AGPII, 2003; AGPIII, 2009) which includes the familiar northern hemisphere genera *Fagus* (beech) and *Quercus* (oak). Both Nothofagaceae and Fagaceae are members of the order Fagales, and phylogenetic studies establishing their separation have suggested that within this order, Nothofagaceae could be more closely related to Betulaceae (Birch, *Betula*; Alder, *Alnus*) than Fagaceae (Crane, 1989; Nixon, 1989). However, subsequent molecular sequencing studies have refuted this (Herbert, *et al.*, 2006; Li, *et al.*, 2004; Manos & Steele, 1997; Stevens, 2001 onwards) and although the three families remain firmly within the order Fagales, Nothofagaceae is currently placed closer to Fagaceae (figure 2.1).

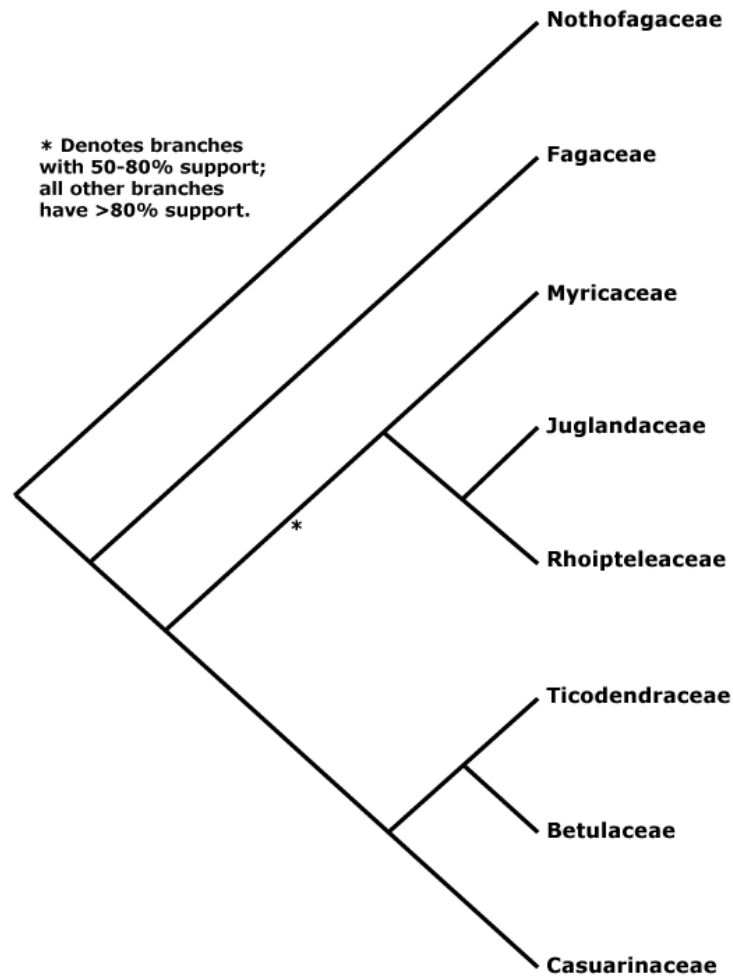
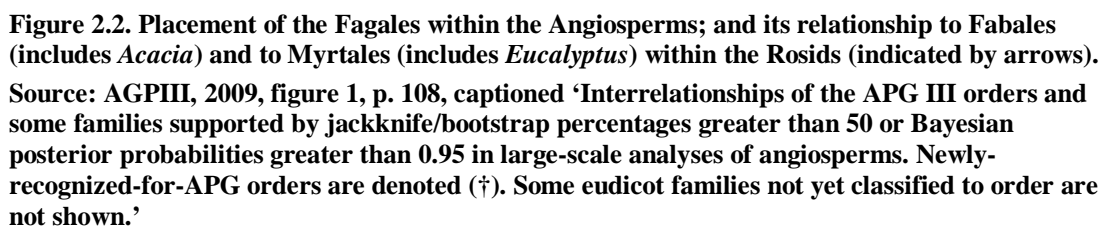


Figure 2.1. Relationships of the families within the plant order Fagales. Source: Stevens, P. F. (2001 onwards), <http://www.mobot.org/MOBOT/research/APweb/> (page updated: 19/03/2011).

Recent molecular phylogenies for the Angiosperms place the order Fagales in the Rosids clad (figure 2.2), together with the Fabales and Myrtales (AGPIII, 2009; Burleigh *et al.*, 2009; Wang *et al.*, 2009). Within the Rosids, Fagales and Fabales are grouped in the Fabids, while Myrtales belong to the sister group, the Malvids (AGPIII, 2009; Wang *et al.*, 2009). These latter two orders are of relevance because they both contain genera which are widespread and highly diverse in Australia: *Acacia* (family Fabaceae) in Fabales; and *Eucalyptus* (family Myrtaceae) in Myrtales.



2.2 BIOGEOGRAPHY AND PALAEOHISTORY

The origin and distribution of *Nothofagus*, and its relationship to the Fagaceae, had taxed botanists and biogeographers since European exploration of the Southern hemisphere during the eighteenth and nineteenth centuries. Joseph Banks, botanist on Cook's first voyage (1768-71), noted in Tierra del Fuego that "trees here are chiefly of one sort, a kind of birch *Betula antarctica* with very small leaves" (Banks, in Hooker, 1896: 49) and also that there was "a beech (*Fagus antarctica*)" (Banks, in Hooker, 1896: 57). Over a century later, Joseph Hooker edited and published Banks' journal of that voyage and added footnotes qualifying Banks' observations of South American *Nothofagus* with then-current understanding of the species, such as

"Both the beech and birch [of Banks] are species of beech (*Fagus*): one, *F. betuloides*, Mirb., is an evergreen; the other, *F. antarctica*, Forst, is deciduous-leaved."
(Hooker, 1896: 57)

Hooker still placed the southern beeches in the genus *Fagus* although his contemporary, the Dutch botanist and taxonomist Carl Ludwig Blume had placed them in a separate genus, *Nothofagus*, a decision supported by further evidence from Anders Sandoe Oersted (Poole, 1987).

Assistant director of the Royal Botanic Gardens at Kew from 1855, and its director from 1865, Hooker, like Banks, had been a naturalist-explorer in younger days and his writings reflect his curiosity about the distributions of the plants he observed, including the southern beeches. Both his *Flora of New Zealand* (Hooker, 1853) and *The Flora of Australia* (Hooker, 1859), as well as documenting their respective plant life, also explore the concept of 'species' (in the latter work with reference to the recently formulated ideas of Charles Darwin and Alfred Russel Wallace (Darwin & Wallace 1858); and how the same or closely related species can occur on such widely separated landmasses as South America, Antarctica, mainland Australia, Tasmania and New Zealand. He was perhaps the first to suggest, on the basis of the similarities in their floras, that these regions had once been connected. Rodway (1912) too, proposed a land connection between South America and Tasmania given the similarity of their floras but at that time there still was no accepted mechanism to explain the separation of the landmasses.

2.2.1 Plate Tectonics and the demise of Gondwana

In Hooker's day there was only speculation as to the means of connection and separation of these regions, such as sea-level variation exposing or inundating chains of volcanic islands or other land bridges. Wegener's theory of Continental Drift (first published in 1912) provided a possible explanation, but gained little credence for over half a century, until, with stronger geological supporting evidence, it was revived as the theory of plate tectonics and sea-floor spreading, and was embraced as the most credible mechanism for the break up of the southern supercontinent, Gondwana; and consequently for the occurrence of similar biota on the fragments (Raven & Axelrod, 1972; Schlinger, 1974; Gill, 1975).

There is now a generally accepted sequence of separation for the austral landmasses, although the exact timings remain uncertain (see Wilford & Brown, 1994; McLoughlin, 2001; Smith *et al.*, 2004) and for the changes in climate associated with such geological upheaval see (Quilty, 1994). In summary (with reference to distribution maps of *Nothofagus* from the Late Cretaceous: figure 2.3):

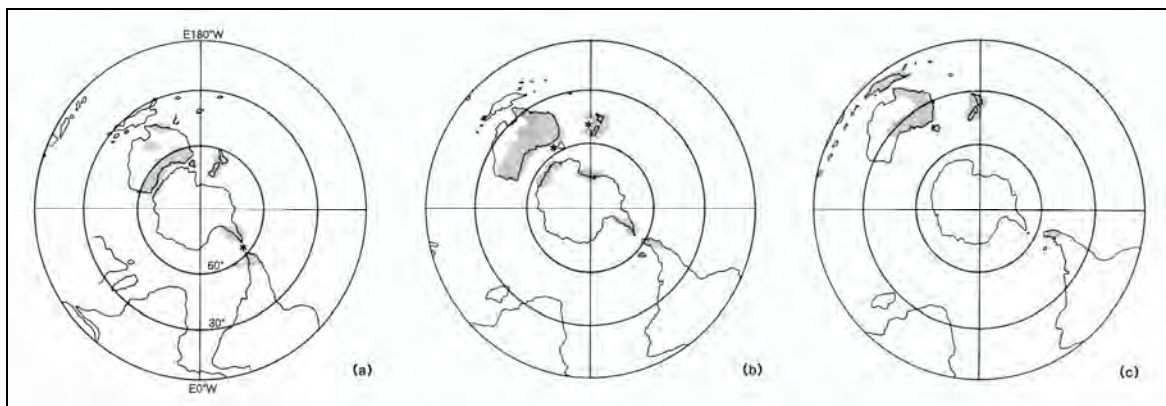


Figure 2.3. *Nothofagus* Distribution, Late Cretaceous to Late Tertiary. (a) Late Cretaceous, ~70mya; (b) Early-Middle Tertiary, ~35mya; (c) Late Tertiary, ~5mya. Modified from Humphries (1981) and Dettman *et al.* (1990) in Veblen *et al.* (1996a).

Mya (million years ago) indicates approximate timescale in 10^6 years before present.

Late Jurassic (~150mya)

Pangaea fragments into Gondwana (south) and Laurasia (north). Rifting occurs between East and West Gondwana (~152 mya).

Early - Mid Cretaceous (~100mya)

Africa splits off and moves north (~100 mya), South America remains attached to East Gondwana.

Late Cretaceous (~70mya: figure 2.3a)

East Gondwana starts to divide (90-80mya), the Tasman Sea starts to form (~83mya) as New Zealand and New Caledonia break off, separating from each other 70-40mya.

Early-Middle Tertiary (~35mya: figure 2.3b)

Eocene (~60-35mya): Australia separates from Antarctica; the Southern Ocean breaks through between Tasmania and Antarctica by about 35mya, and from this time there is rapid northward movement of Australia.

The early Eocene was a period of marked warming, while from the late Eocene onward (~36mya) the Australian climate became cooler and drier.

South America separates from Antarctica with the opening of Drake Passage (timing uncertain, either during Eocene or Oligocene).

Oligocene (~35-25mya): The Southern Ocean circumpolar current becomes established and in Antarctica, now thermally isolated, there is large-scale ice sheet development.

Late Tertiary (~5mya: figure 2.3c)

Miocene/Pliocene (~20-5mya): The expansion of the Antarctic ice sheet causes increasing aridity. Australia continues to move northward to mid latitudes.

2.2.2 *Nothofagus* Lineage: Origins, Palynology, Phylogeny and Cladistics

The exact site of origin of *Nothofagus*, within the great southern landmass, remains uncertain: the weight of palynological (fossil pollen) and macrofossil evidence points to the late Cretaceous on the South America-Antarctic Peninsula (Hill & Dettman, 1996; Poole, 2002; Li & Zhou, 2007) and this has been supported

by cladistic analysis: of extant *Nothofagus* examining both morphological (Hill & Jordan, 1993) and molecular characters; and of modern areas of endemism (Swenson *et al.*, 2000). An alternative theory, unsupported by such evidence, suggested a Cretaceous fagalean pollen complex in the southeast Asian-Australian region, which subsequently divided into northern (Fagaceae, Betulaceae) and southern (Nothofagaceae) populations (Hill & Dettman, 1996; Swenson *et al.*, 2000).

2.2.2.1 The Pollen Record

Wind pollinated *Nothofagus* and the Beeches of the northern hemisphere produce copious amounts of pollen, especially in mast years, and from the abundance and widespread distribution of fossil pollen this appears to be so for *Nothofagidites*, the extinct forerunner of the genus *Nothofagus*. Pollen grains are encased within a protective coat, the surface sculpting of which varies between species, providing a highly resistant, readily identifiable taxon marker which fossilises well. Pollen recognisable as *Nothofagidites* has been found on the Antarctic Peninsula, in southern South America, southeastern Australia, including Tasmania, and in New Zealand. Palynological examination has divided the species of *Nothofagidites* into eight pollen types (Dettmann *et al.*, 1990): Ancestral (a), 1 species; Ancestral (b), 2 species; *N. brassii* (a), 9 species; *N. brassii* (b), 7 species; *N. brassii* (c), 4 species; *N. fusca* (a), 3 species; *N. fusca* (b), 7 species; *N. menziesii*, 1 species. Of these fossil pollen groups two, as suggested by their names, are regarded as ancestral. However they appear significantly earlier in the pollen record than the other types and although related, they are not necessarily precursors of the later subgenera (Hill, 2001). Ancestral (a) is related to *N. fusca* type (a), which corresponds with extant subgenus *Fuscospora*; while Ancestral (b) is related to *N. fusca* type (b) which corresponds with extant subgenus *Nothofagus*; *N. menziesii* and *N. brassii* (a) pollen types correspond with extant subgenera *Lophozonia* and *Brassospora* respectively; *N. brassii* types (b) and (c) have no extant equivalents (Dettmann *et al.*, 1990; Hill & Dettmann, 1996) (Table 2.1).

Location	First appearance	~mya	<i>Nothofagitides</i> pollen group	Pollen type	<i>Nothofagus</i> subgenus	Extant subgenera
Southern Gondwana	Campanian	82	Ancestral (a)	<i>N. fusca</i> type (a)	<i>Fuscospora</i>	SSA, Tas, NZ
		76	Ancestral (b)	<i>N. fusca</i> type (b)	<i>Nothofagus</i>	SSA
Antarctic Peninsula	Late Campanian	72	<i>N. fusca</i> type (a)	<i>N. fusca</i> type (a)	<i>Fuscospora</i>	SSA, Tas, NZ
		72	<i>N. fusca</i> type (b)	<i>N. fusca</i> type (b)	<i>Nothofagus</i>	SSA
		72	<i>N. menziesii</i>	<i>N. menziesii</i> type	<i>Lophozonia</i>	SSA, SEA, Tas, NZ
		72	<i>N. brassii</i> (a)	<i>N. brassii</i> type	<i>Brassospora</i>	NC & NG
		72	<i>N. brassii</i> (b)		No extant type	
		72	<i>N. brassii</i> (c)		No extant type	
Southern South America	Maastrichtian	70	<i>N. fusca</i> type (a)	<i>N. fusca</i> type (a)	<i>Fuscospora</i>	SSA, Tas, NZ
		70	<i>N. fusca</i> type (b)	<i>N. fusca</i> type (b)	<i>Nothofagus</i>	SSA
		70	<i>N. menziesii</i>	<i>N. menziesii</i> type	<i>Lophozonia</i>	SSA, SEA, Tas, NZ
		70	<i>N. brassii</i> (a)	<i>N. brassii</i> type	<i>Brassospora</i>	NC & NG
		70	<i>N. brassii</i> (b)		No extant type	
		70	<i>N. brassii</i> (c)		No extant type	
Southeast Australia	Late Campanian	72	<i>N. fusca</i> type (b)	<i>N. fusca</i> type (b)	<i>Nothofagus</i>	SSA
	Maastrichtian	70	<i>N. fusca</i> type (a)	<i>N. fusca</i> type (a)	<i>Fuscospora</i>	SSA, Tas, NZ
		67	<i>N. brassii</i> (a)	<i>N. brassii</i> type	<i>Brassospora</i>	NC & NG
	Palaeocene	60	<i>N. menziesii</i>	<i>N. menziesii</i> type	<i>Lophozonia</i>	SSA, SEA, Tas, NZ
New Zealand	Late Campanian	72	<i>N. fusca</i> type (b)	<i>N. fusca</i> type (b)	<i>Nothofagus</i>	SSA
	Palaeocene	60	<i>N. menziesii</i>	<i>N. menziesii</i> type	<i>Lophozonia</i>	SSA, SEA, Tas, NZ
	Palaeocene	60	<i>N. fusca</i> type (a)	<i>N. fusca</i> type (a)	<i>Fuscospora</i>	SSA, Tas, NZ
	Eocene	45	<i>N. brassii</i> (a)	<i>N. brassii</i> type	<i>Brassospora</i>	NC & NG

Table 2.1. Times of earliest fossils, *Nothofagitides* pollen groups, *Nothofagus* pollen types, subgenera and extant distribution. Abbreviations: NC & NG, New Caledonia and New Guinea; NZ, New Zealand; SEA, South-eastern Mainland Australia; SSA, Southern South America; Tas, Tasmania. Sources: Dettmann et al. (1990); Hill (2001); Hill & Dettmann (1996); MacPhail et al. (1994).

In his review of the origins of *Nothofagus*, Hill (2001) concurs with the above groupings but questions the use of the term '*Nothofagidites*' for the fossil pollen genus. The term is confusing and would appear to be redundant if, as is acknowledged, this fossil pollen is the 'parental source' (Dettman *et al.*, 1990 in Hill, 2001 p.322) of the genus *Nothofagus*. However for now at least, '*Nothofagidites*' remains in the taxonomic lexicon distinguishing the fossil from extant *Nothofagus* taxa.

Given the prominence of palynology in *Nothofagus* research, Hill (2001) examines the value of fossil pollen in determining the origins and diversification of the genus and gives three reasons as to its importance:

- “(1) It is relatively extensive.
- (2) It provides a general indication of past diversity.
- (3) It provides broad times of arrival on different landmasses and distribution patterns for the genus, the subgenera and species.” (Hill, 2001: 322)

Hill (2001) also remarks upon the significance of the absence of fossil *Nothofagus* pollen from regions such as Africa and India: given its abundance and diversity elsewhere in the Southern Hemisphere, this suggests that these earlier migrants from Gondwana were never home to the genus.

Thus, the fossil pollen record suggests the times of appearance and disappearance of *Nothofagus* taxa giving an indication of the longevity of the genus, its diversity and changing distribution during the break up of East Gondwana (Figure 2.3). However, identifying a plant to species level requires comparison of more distinct morphological features than are found on pollen grains and thus, the fossil pollen ‘types’ may include multiple taxa. Fossilised leaf fragments, wood and other plant parts - macrofossils with organic preservation – have more reliable diagnostic features than either fossil pollen grains or simple impression fossils (Hill, 1993; Hill, 2001). Such specimens are rare, with few having been found outside Tasmania, and care is needed in their interpretation; but they can augment the palynological data and in some cases allow a high level of taxonomic identification. Table 2.2 lists leaf macrofossils specimens, current to 2001, with organic preservation sufficiently good for identification with reasonable confidence. The Tasmanian macrofossils are discussed more fully in section 2.2.1.

Li and Zhou (2007) dispute Hill’s (1993; 2001) assertion that impression fossils are of less value than those with organic preservation, but their results from Antarctic impression fossils agree with the suggestion that the origin and early diversification of *Nothofagus* occurred in the Southern Hemisphere. Well-preserved fossil wood fragments have also been found in Antarctica, and Poole (2002) reassessed all previous records in the light of new finds. She identified six species that could be assigned to the organ genus *Nothofagoxolon* on cluster analysis and concluded that

the temporal and distribution patterns support an Antarctic Peninsula - South America origin for the genus.

Nothofagus species	Subgenus	Age	Location	Source
<i>N. cethanica</i> [△]	<i>Fuscospora</i> *	Early Oligocene	Tasmania	Hill (1984)
<i>N. gunnii</i> [△]	<i>Fuscospora</i>	Oligocene	Tasmania, Antarctica	Hill (1984, 1991)
<i>N. lobata</i>	<i>Nothofagus</i> *	Early Oligocene	Tasmania	Hill (1991)
<i>N. maidenii</i>	<i>Lophozonia</i>	Late Oligocene – Early Miocene	Tasmania, Victoria	Pole <i>et al.</i> (1993)
<i>N. microphylla</i>	<i>Nothofagus</i> ?	Late Oligocene – Early Miocene	Tasmania	Scriven and Hill (1996)
<i>N. mucronata</i>	<i>Brassospora</i> *	Early Oligocene	Tasmania	Hill (1991)
<i>N. muelleri</i>	<i>Lophozonia</i>	Late Eocene	New South Wales	Hill (1988)
<i>N. novaezealandiae</i>	<i>Lophozonia</i>	mid–Late Miocene	New Zealand	Pole (1993b)
<i>N. pachyphylla</i>	<i>Lophozonia</i>	Early Pleistocene	Tasmania	Jordan (1999)
<i>N. serrata</i>	<i>Brassospora</i> *	Early Oligocene	Tasmania	Hill (1991)
<i>N. tasmanica</i>	<i>Lophozonia</i> *	Eocene–Early Oligocene	Tasmania, SW Australia	Hill (1991), Hill and Merrifield (1993), Carpenter and Pole (1995)

Table 2.2. *Nothofagus* leaf macrofossils with sufficiently good organic preservation to allow identification to species. [△]Leaves share autapomorphies with extant *Nothofagus* species. *All four extant subgenera were present in the Early Oligocene. Modified from Hill (2001): 326, table 3.

2.2.2.2 *Phylogeny and Cladistics*

Traditionally the phylogeny of *Nothofagus*, as with other plant groups, had been constructed by comparison of morphological features of plant parts of fossil and/or extant lineages. In the case of *Nothofagus*, the occurrence of deciduous or evergreen habit originally formed the basis of classification of extant species, together with cupule morphology and leaf vernation, but these results conflicted with studies of fossil and extant pollen in that the only pollen group and subgenus to correspond consistently was *N. brassii* with *Brassospora*, (Hill & Read, 1991). In their reassessment of extant *Nothofagus*, Hill and Read (1991) examined in fine detail cupule and cuticular morphology and leaf architecture, resulting in a revision of the phylogeny of the genus in which their proposed subgenera closely coincide with the old pollen groups (as in table 2.2 above). Of the taxonomic indicators employed previously, they refuted the use of the evergreen/deciduous dichotomy, suggesting that the deciduous form is the more primitive and concluding that

“The character which has dominated the infrageneric classification of the genus for so long, the presence of deciduous or evergreen foliage, almost certainly arose independently at least three times in the genus and is therefore not a useful primary character”. (Hill & Read, 1991, p.70)

For their analysis, Hill and Read (1991) used numerical taxonomy (in particular with regard to cupule morphology and leaf cuticular pattern) rather than cladistic analysis, citing the need for detailed examination of a broad range of morphological data prior to using the latter method; and the difficulty in choosing an outgroup for such an ancient taxon as *Nothofagus*.

In a subsequent study, the stated aim of Hill & Jordan (1993) was to

“...produce a comprehensive data set for cladistic analysis to test the infrageneric classifications of *Nothofagus*. ... The philosophy behind our approach is that the data set must be accurate, thorough and substantial before any analysis of relationships is attempted.” (Hill & Jordan, 1993: 112)

To that end, they amassed data from past publications (details in Hill & Jordan, 1993) together with examination of specimens in the reference collection at the University of Tasmania; and subjected the data to cladistic analysis, using *Fagus* and Betulaceae as outgroups. Their results lent support for the four extant subgenera and pollen groups proposed above; and added weight to the dismissal of the deciduous vs. evergreen habit as a primary character in assessment of *Nothofagus* phylogeny.

During the 1990s, advances in molecular biology allowed comparison between biochemical characters, augmenting the traditional morphological approach to phylogeny. Martin and Dowd (1993) applied such methods to the *rbcL* chloroplast gene in 23 extant species of *Nothofagus* and 3 of *Fagus*, using parsimony-based analysis to establish phylogeny. Their closely results matched the subgenera of Hill & Read's (1991) revised phylogeny. Manos (1997) further refined the phylogeny of extant *Nothofagus* with cladistic analysis combining ribosomal DNA results with the data of Martin and Dowd (1993) together with a morphological survey; and again confirmed the relationships between the four subgenera (figure 2.4). Setoguchi *et al.* (1997) examined sequences of the *atpB-rbcL* intergenic spacer of chloroplast DNA in extant *Nothofagus* and their results concurred with the above analyses, namely that the subgenus *Lophozonia* predates the other subgenera and that *Nothofagus* and *Brassospora* are more closely related to each other than either is to *Fuscospora*; and

that this phylogeny is consistent with diversification into subgenera prior to the break up of East Gondwana.

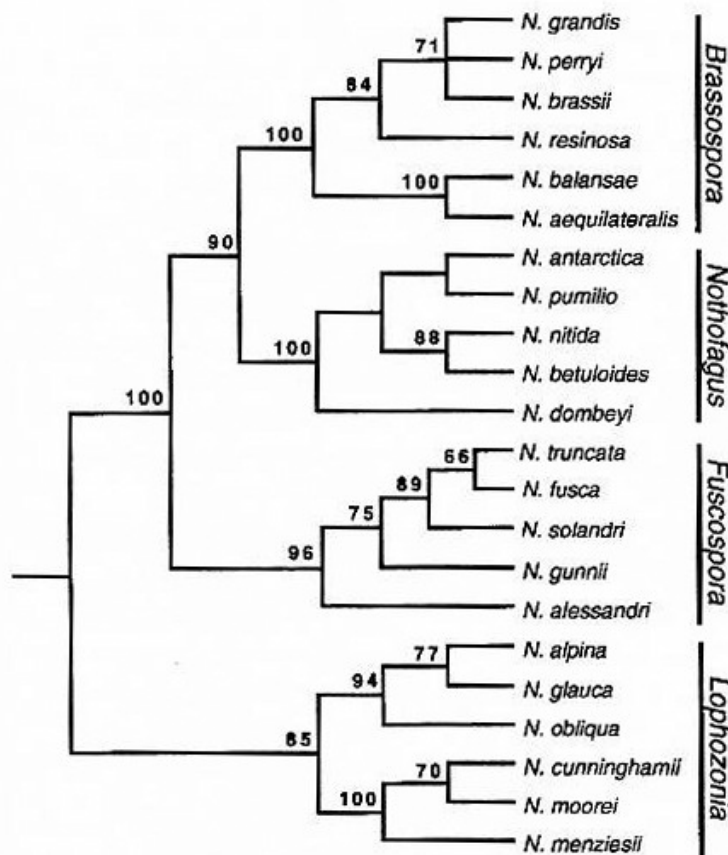


Figure 2.4. Extant *Nothofagus* cladogram produced by parsimony analysis of combined molecular and morphological datasets. Source: Manos (1997: 1143, fig. 5).

Building on their earlier work on fossil *Nothofagus* (Hill, 1991; Jordan, 1999), Jordan and Hill (1999) were able to place six fossil taxa within the *Nothofagus* phylogeny (with one more of ambiguous placement) using parsimony analysis of molecular data (the *rbcL* chloroplast gene results of Martin and Dowd (1993); and Manos' (1997) ribosomal DNA data) combined with morphological fossil leaf data and extant *Nothofagus* morphological data. Despite the difficulty of interpreting leaf fossils, even those few with good organic preservation (particularly of the cuticle), this analysis differed from those confined to extant species only in the placement of the evergreen *Lophozonia* and led Jordan and Hill to suggest

“... the combined morphological and molecular data provide a strong framework for the classification of fossils ... phylogenetic placement of *Nothofagus* leaf fossils is dependant on incorporating molecular and morphological data from extant species” (Jordan & Hill, 1999: 1186).

Thus the evolutionary history of *Nothofagus* has been pieced together using fossil pollen and macrofossils providing an indication of past diversity and distribution and an approximate chronology for the taxa; a phylogeny based on morphological features of extant species; and latterly, molecular analysis of extant species. When the results of these individual methods are compared, or when subjected to combined cladistic analysis there is consensus about classification into the four extant subgenera - *Lophozonia*, *Nothofagus*, *Brassospora* and *Fuscospora* – although detailed placement of species within them is less certain. There is also consensus that diversification into these subgenera occurred before East Gondwana fragmented.

However, the subsequent distribution and diversification into today's pattern of *Nothofagus* species strewn across the Southern Hemisphere, is subject to debate. Has vicariance alone been responsible? Or has trans-oceanic dispersal played a minor (or even a major) role in the spread of the genus?

2.2.3 Vicariance or Dispersal?

Given the extensive pollen and macrofossil record, *Nothofagus* has been proclaimed a model genus for biogeographical study, exemplifying vicariance events in its speciation as Gondwana broke up (Van Steenis, 1971; Raven & Axelrod, 1972). This argument was strengthened by the easy digestibility of the seeds, their poor wind dispersal and non-viability after submersion: all suggesting the improbability of long distance dispersal of *Nothofagus* by wind or sea (Rodway, 1912; Preest, 1963). However in recent years, a reappraisal of the role of long distance dispersal within the Southern hemisphere has been undertaken for many taxa (Nelson & Ladiges, 2001; de Queiroz, 2005); while other authors have considered the possibility that such dispersal may not always be West to East, the prevailing wind direction (Sanmartin *et al.*, 2007; Winkworth *et al.*, 2002). In particular, long distance dispersal has been invoked to account for the biota of New Zealand as there is mounting geological evidence suggesting that its islands were either partially or entirely inundated during the Oligocene (Goldberg *et al.*, 2008; Knapp *et al.*, 2007; Landis *et al.*, 2008).

In recent decades, with more information at their disposal from fossil pollen, macrofossils, extant taxonomic and molecular data, and geological evidence,

researchers are less emphatic about vicariance as the only explanation for the distribution of extant *Nothofagus*, particularly with regard to subgenus *Brassospora* in New Caledonia and subgenera *Fuscospora* and *Lophozonia* in New Zealand (Hill & Jordan, 1993; MacPhail *et al.*, 1994; Cook & Crisp, 2005; Waters & Craw, 2006). Some have supported vicariance but have advised caution in the interpretation of their results (Linder & Crisp, 1995; Swenson *et al.*, 2001; McLoughlin, 2001; Swenson & Hill, 2001; Ladiges & Cantrill, 2007); others regard both mechanisms as possible (Cook & Crisp, 2005) or at least, not mutually exclusive (Waters & Craw, 2006), while acknowledging that more research is needed. Few go so far as Pole (1994, 2001) or McGlone (2001), who suggest, given the degree of endemism, that long distance dispersal must be wholly responsible for the extant woody flora of New Zealand, including *Nothofagus*; or conversely take the view of Heads (2006) that vicariance must explain the distribution of the *Brassospora*.

One of the relationships most under contention is that between the New Zealand endemic *N. menziesii*, and its closest relatives within the subgenus *Lophozonia*, *N. cunninghamii* and *N. moorei*, both endemic to south-eastern Australia. The Australian species are closely related (Hill, 1983), the larger leaved *N. moorei* being closer to the ancestral type (Hill, 1991); and consistent with a vicariance event during their speciation, New Zealand having broken off from the South America-Antarctica-Australia landmass in the Late Cretaceous, they had been considered to be more closely related to each other than either was to *N. menziesii* (Hill & Jordan, 1993).

Doubt has been cast upon the traditional vicariance view by McGlone, Mildenhall and Pole (1996) and Pole (2001) who emphasise that the oldest *N. menziesii* fossil pollen found in New Zealand is from the Oligocene, by far postdating the split from Gondwana and therefore necessitating trans-Tasman dispersal from Australia. Analyses such as those of Martin and Dowd (1988), Hill and Jordan (1993), Manos (1997), Jordan and Hill (1999) show that *N. cunninghamii* arose earlier and is less closely related to *N. moorei* than is *N. menziesii*. This could indicate that a precursor to the latter two species reached New Zealand by long distance dispersal and gave rise to *N. menziesii*, while in Australia it speciated into *N. moorei* (Hill & Jordan, 1993; Macphail *et al.*, 1994). Furthermore, Knapp *et al.* (2005) using molecular dating, posit that relationships between the Australian and New Zealand species

within subgenera *Lophozonia* and *Fuscospora* are too young to have come about prior to the separation of New Zealand from Gondwana; although their analysis suggests a different relationship between the *Lophozonia* species: that *N. menziesii* arose from a common precursor before *N. cunninghamii* and *N. moorei* speciated. Heads (2006) meanwhile, throws doubt on the use of molecular methods in distinguishing between vicariance or dispersal in the distribution of *Nothofagus*, particularly questioning current dating techniques.

In summary, although vicariance biogeography can explain much of the distribution of extant *Nothofagus*, few researchers would rule out rare occurrences of long distance dispersal and most agree that more research is required. However, whether vicariance biogeography, with or without long distance dispersal, is responsible for the spread of *Nothofagus*, the extant patterns of distribution of the subgenera and species within the separating land masses has depended upon the changes in latitude, climate and environment as each fragment reached its current position in the Southern hemisphere. The next section looks at those changes in Australia.

2.2.4 *Palaeoecology of Nothofagus in Australia*

Hill has commented that *Nothofagus* was ‘more widely distributed in the past than today’ and ‘now occurs in spatially widespread localities’ (Hill, 2001: 325). The spatial spread due to the rifting of Gondwana has been described above, but the contraction of the genus over time has depended upon regionally adverse conditions for a genus which thrives in areas of reliable rainfall. The following brief chronological summary of those changes in Australia since the Late Cretaceous has been drawn from several detailed sources (McKenzie & Busby, 1992; Frakes, 1999; Hill, 1990, 1992, 1994a, 2001, 2004; Hill *et al.*, 1996; Hope, 1994; Jackson, 1999a, 1999b; Kershaw *et al.*, 1994; Macphail *et al.*, 1994; McKenzie, 1997; Quilty, 1994).

Late Cretaceous (from ~90mya)

By the Late Cretaceous, New Zealand and New Caledonia had already broken away from the Southern landmass which itself remained at polar latitudes. Although beginning to separate from East Gondwana, southern Australia, including Tasmania, would have been within what is now regarded as the Antarctic Circle, latitude 66° 33'S (Figure 2.3). Oceanic circulation between low and high latitudes carried warmer water to the latter, the accompanying warm moist air bringing high humidity and rainfall. These currents resulted in a low temperature differential between the equator and Polar Regions. As yet unexplained high levels of atmospheric CO₂ also contributed to warming.

The high latitudes would have experienced marked seasonality: mild summers of near perpetual daylight, but low sun angle, alternating with winters of interminable darkness. However, the warm currents and high humidity would have moderated cooling in the winter months and ensured relatively even rainfall throughout the year.

The early Cretaceous coniferous forests of Araucariaceae and Podocarpaceae were composed of conical and widely spaced trees, to expose the maximum surface to the low sun, with an understorey including cycads, ferns, horsetails and bryophytes. Angiosperms first appeared in Australia ~120 mya and rapidly diversified, particularly the Proteaceae. By the time of the arrival of *Nothofagus* ~84mya, angiosperms were present in both canopy and understorey and the conifers gradually gave way to an angiosperm dominated flora. Conifer genera from this time surviving to the present include: *Lagarostrobos*, *Dacrydium* and *Dacrycarpus* (Podocarpaceae).

Palaeocene (from ~65mya)

Australia split from Antarctica in a rift from west to east, creating between the two continents an elongated, warm, marine inlet bounded at its eastern end by the land connection of Tasmania, and the South Tasman Rise, with the Antarctic mainland. The growing warm oceanic inlet together with equator-polar currents maintained high temperatures and humidity and year-round rainfall.

Fossil evidence of the Australian Palaeocene vegetation is meagre. In the south-eastern highlands conifers were dominant and there is also evidence of broad-leaved angiosperms.

Eocene (from ~60mya)

Australia continued its separation from Antarctica throughout the Eocene culminating in a final rifting in the late Eocene (~37mya). Global warming ensured continuation of high temperatures and humidity in the mid to high latitudes until the end-Eocene global cooling, associated with lowered atmospheric CO₂.

During the Eocene South-eastern Australia was covered in megathermal rainforest requiring warm, damp conditions similar to extant forest in lowland tropical regions. Angiosperms had diversified and become dominant and included winter deciduous species which would have been well adapted to the long winter darkness. Around 49mya there was a significant increase in *Nothofagus* pollen, especially of the subgenus *Brassospora* which is now confined to the tropics in New Caledonia and New Guinea. By the Middle to Late Eocene, Tasmania had a more temperate flora in which conifer diversity remained higher and angiosperm diversity lower than further north.

Oligocene (from ~35mya)

Rupture of the land connection between Antarctica and Tasmania allowed the seas to break through establishing the circumpolar circulation of the Southern Ocean. Temperatures fell during the Oligocene due to a combination of the circumpolar current impeding the equator-polar flow, together with the lowered levels of atmospheric CO₂. Tasmania experienced a brief glaciation. Despite the cooling, humidity and rainfall remained high throughout the year.

The Oligocene saw a marked diversity of deciduous *Nothofagus* species in Southern Australia. As cooling continued there was a decrease in leaf size, particularly in the *Nothofagus* subgenera *Lophozonia* and *Nothofagus*. The fossil record provides the first evidence for cool temperate rainforest in Tasmania in which conifers were abundant and, among the angiosperms, all four extant *Nothofagus* subgenera were present. By the late Oligocene there appears macrofossil evidence of

alpine vegetation in Tasmania, comprising a wide diversity of conifers and small leaved angiosperms, including *N. gunnii*. In contrast with Tasmania, conifers in other parts of Australia were in decline.

Once free of Antarctica, Australia began rapidly moving equator-wards; this continued to the end of the Tertiary and through the Quaternary. Consequently, Australia is now 20° of latitude more northerly than during the Oligocene.

Miocene (from ~25mya), Pliocene (from ~5mya)

During the Miocene and Pliocene, the migration to lower latitudes was accompanied by alteration in ocean currents and weather patterns causing a trend towards lower humidity and rainfall. Australia experienced continent-wide cooling and drying interspersed with episodes of increased but more seasonal rainfall. At lower latitudes sun angle increased and daylight hours became more evenly distributed through the year with diurnal variation more marked than seasonal variation.

The Miocene saw the rise of dry rainforest dominated by *Acacia*; Myrtaceae, including the appearance and rapid spread of *Eucalyptus*; and Fagalean sister family to *Nothofagus*, Casuarinaceae. Meanwhile, the mesotherm rainforests dominated by *Nothofagus* were in retreat, becoming restricted to Tasmania, south-east Victoria and parts of New South Wales. By the late Miocene, the tropical subgenus *Brassospora* had undergone severe decline. Despite a brief recovery of rainforest in the South-eastern highlands during the Pliocene, overall the closed, wet rainforests increasingly gave way to more open dry sclerophyll vegetation.

Quaternary (from ~1.6mya - present)

The alternating glacial-interglacial cycles of the Quaternary resulted in widely oscillating temperatures, rainfall and sea level as well as fluctuating exposure and inundation of the continental shelf and land bridges. The Quaternary glacial-interglacial cycles caused the climate to fluctuate between long (100,000 year) cold, dry phases interspersed with short (10,000 year) warmer, wetter interludes. This in turn led to cyclical changes in vegetation: from woodland to steppe in the eastern highlands; compared with rainforest to montane/alpine vegetation in Tasmania. The

strongest trend was towards aridity and *Nothofagus* became restricted to the remaining the cooler, wetter regions, leading to its extant distribution in Tasmania and highland areas of the eastern Australian mainland.

2.3 NOTHOFAGUS IN TASMANIA

The two surviving *Nothofagus* species in Tasmania differ in their subgenera, appearance, habit and distribution. *N. cunninghamii*, subgenus *Lophozonia*, is evergreen; has small, rigid, dark green leaves (figure 2.5); and exists as a tall rainforest dominant, a co-dominant or understorey species of wet *Eucalyptus* forest, or in shrub form in Alpine areas.



Figure 2.5. *Nothofagus cunninghamii*, mature ('old') leaves.

N. gunnii, subgenus *Fuscospora*, is winter deciduous; its leaves, deep veined and pale green in spring, yellow-orange in autumn, are larger and softer than those of its cousin (figure 2.6); it is extremely fire-sensitive and occurs in subalpine rainforest or in alpine heath (Curtis, 1967: 646, 647; Kirkpatrick, 1997: 38, 40; Kirkpatrick & Backhouse, 1997: 121, 122)



Figure 2.6. *Nothofagus gunnii* leaves, early autumn (*Richea scoparia* foliage behind).

2.3.1 Palaeohistory

The palaeohistory of *Nothofagus* in Tasmania has been extensively researched and described via palynology and macrofossils (for example: Hill, 1983, 1984, 1991, 1994b, 2001; Hill *et al.*, 1999; Jackson, 1999a; Jordan, 1999; Jordan *et al.*, 1995; Jordan & Hill, 1995; Scriven & Hill, 1996). As described above, well-preserved leaf macrofossils are a rare but valuable adjunct to palynological data when reconstructing past vegetation patterns and phylogenies. Serendipitously, environmental conditions in Tasmania during the Tertiary were perfect for the laying down of fossils with organic preservation so that the *Nothofagus* macrofossil record in Tasmania, of leaves, cupules and wood, is exceptional in both its diversity and degree of preservation, in some cases allowing identification to subgenus or even to species (Hill, 2001). Thus taxa can be confidently differentiated morphologically and placed chronologically according to their times of appearance and disappearance

within the fossil record, giving an indication of the changes over time in diversity of *Nothofagus* in Tasmania.

There is evidence from the Early Oligocene that each of the four extant *Nothofagus* subgenera were present in Tasmania (table 2.2). This is significant to the biogeography of *Nothofagus* across the Southern Hemisphere since two of these subgenera, once present in Tasmania, are now restricted to their own localities: *Brassospora* to New Caledonia and New Guinea; and *Nothofagus* to South America. The absence of the large leaved, tropical subgenus *Brassospora* from the extant Tasmanian flora may be explained by its inability to adapt to the cooling climate during the remainder of the Tertiary and through the Quaternary, so that the subgenus became confined to the more northern, warmer, wetter regions within its range. Subgenus *Nothofagus* proves more puzzling since in Southern Chile and Argentina, species of the subgenus occur in cool temperate rainforest at latitudes and altitudes similar to those found in Tasmania (Donoso, 1996; Veblen *et al.*, 1996b). Scriven and Hill (1996) point out that in subgenus *Lophozonia* regeneration is by continual small scale replacement taking advantage of canopy gaps, whereas subgenus *Nothofagus* relies on large scale disturbance such as that caused by volcanic eruption, earthquake or landslide. Unlike South America, Tasmania does not have the history of cataclysmic events required to create the extensive clear areas needed by subgenus *Nothofagus*.

The macrofossil record is not restricted to single representatives of each subgenus, but reveals marked species diversity in Tasmanian *Nothofagus* during the Tertiary. One site, Little Rapid River, has yielded nine contemporaneous species and other sites contain four or more species; these include macrofossil leaves of at least two deciduous species, one of which is recognisable as the extant *N. gunnii* dating from the early Oligocene at Lea River and from the Late Oligocene/Early Miocene at Monpeelyata (Scriven & Hill, 1996). Leaf macrofossils of *N. gunnii* were first described, and subsequently their identity confirmed, by Hill (1984, 1991) from Oligocene deposits at Cethana (figure 2.7) and he suggests that the deciduous habit aided its survival during the later cycles of glaciation and in its current subalpine environment.

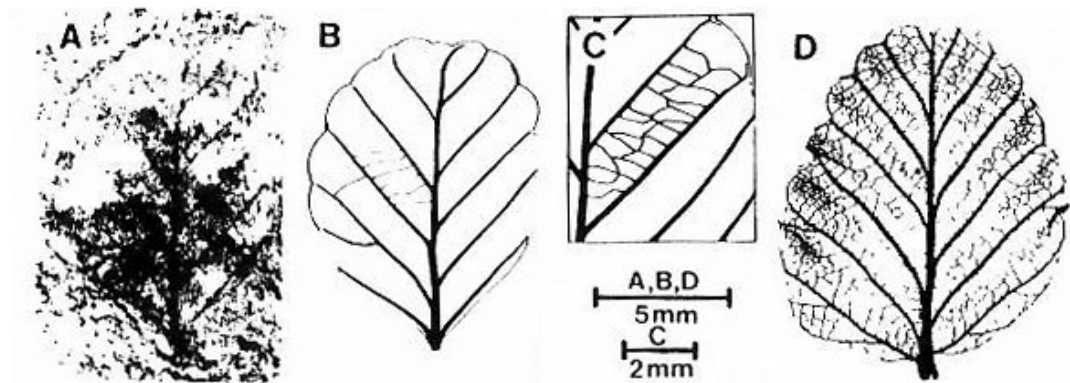
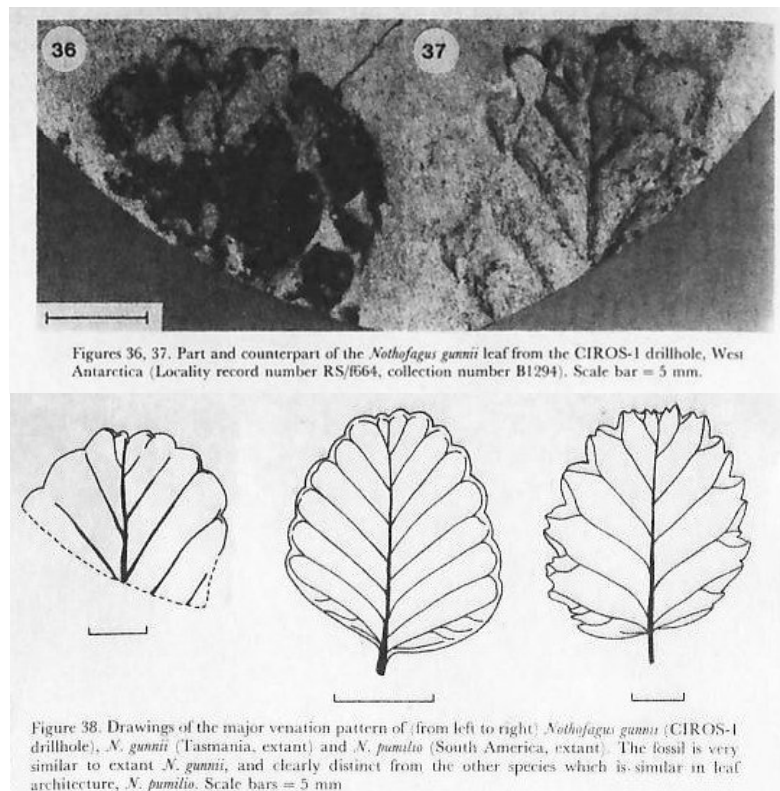
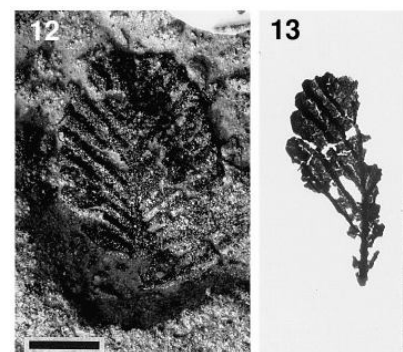


Fig. 4 A, fossil leaf of *Nothofagus gunnii* from Cethana B, drawing of the specimen shown in A. C, drawing of part of the specimen shown in A, highlighting the tertiary venation D, cleared leaf of extant *N. gunnii*
 a. Source: Fig 4, p. 85, Hill, R. S. (1984). Tertiary *Nothofagus* macrofossils from Cethana, Tasmania, *Alcheringa*, 8: 81-86.



b. Source: Figs 36-38, pp 88-89, Hill, R. S. (1991). Tertiary *Nothofagus* (Fagaceae) Macrofossils from Tasmania and Antarctica and Their Bearing on the Evolution of the Genus, *Botanical Journal of the Linnean Society*, 105 (1): 73-112.



c. Source: Figs 12, 13, Specimens M-800, Lea-001, p.352 Lea River Site, Scriven, L.J. and Hill, R.S., 1996: Relationships among Tasmanian Tertiary *Nothofagus* (Nothofagaceae) populations, *Botanical Journal of the Linnean Society*, 121: 345-364.

Figure 2.7. Tertiary *Nothofagus gunnii* macrofossils from Cethana (a) and Lea River (b) in Tasmania; and from West Antarctica (c). Sources as indicated in captions.

During the Early Oligocene, newly rifted from East Antarctica, Tasmania was still close to the Antarctic Circle and would have been experiencing long dark winters and summers of near twenty-four hours of daylight, favouring the winter deciduous species. The climate would have remained wet and humid but was cooling and drying as Tasmania moved north. Changes in *Nothofagus* leaf macrofossil morphology can be tracked against the changes in climate through the Tertiary and into the Quaternary. Although leaf sizes differed greatly within and between species during the Tertiary, there is a clear trend towards smaller leaves in the evergreen *N. cunninghamii* through the glaciations of the Pleistocene (Jordan, 1999; Scriven & Hill, 1996) and this corresponds with the extant taxon having smaller leaves at higher, and colder, altitudes (Hovenden & Vander Schoor, 2003).

Through increasing aridity and the climatic turmoil of the Pleistocene glaciations, *Nothofagus* in Tasmania underwent marked contraction. Two subgenera persisted, each represented by a single species, so that the extant Tasmanian *Nothofagus* taxa are more closely related to species elsewhere than they are to each other: *N. cunninghamii* to *N. moorei* on the Australian mainland and other *Lophozonia* in New Zealand and South America; *N. gunnii* to the *Fuscospora* of New Zealand and South America (figure 2.8). What they do share however, and which aided their survival, is tolerance to frost, and photosynthetic resilience in the face of wide temperature fluctuations (Read & Brown, 1996; Read & Busby, 1990). Yet Kirkpatrick and Fowler (1998) have calculated that at the height of the last glacial, alpine (above treeline) vegetation was widespread and *Nothofagus* would have been severely restricted, surviving only in scattered, sheltered valleys in the west, south and northeast, and that the extant distribution is due to recolonisation from these refugia.

2.3.2 Distribution and Floristic Associations

Compared with the vast contiguous regions covered by *Nothofagus* in the past, even within the small area of Tasmania the extant species have disjunct distributions (figure 2.9). *N. cunninghamii* occurs in the western half of the island, with a small population in the northeast and in pockets of rainforest along the east coast. *N. gunnii* is found exclusively in a few highland areas of the west and southwest where it has been spared from fire.

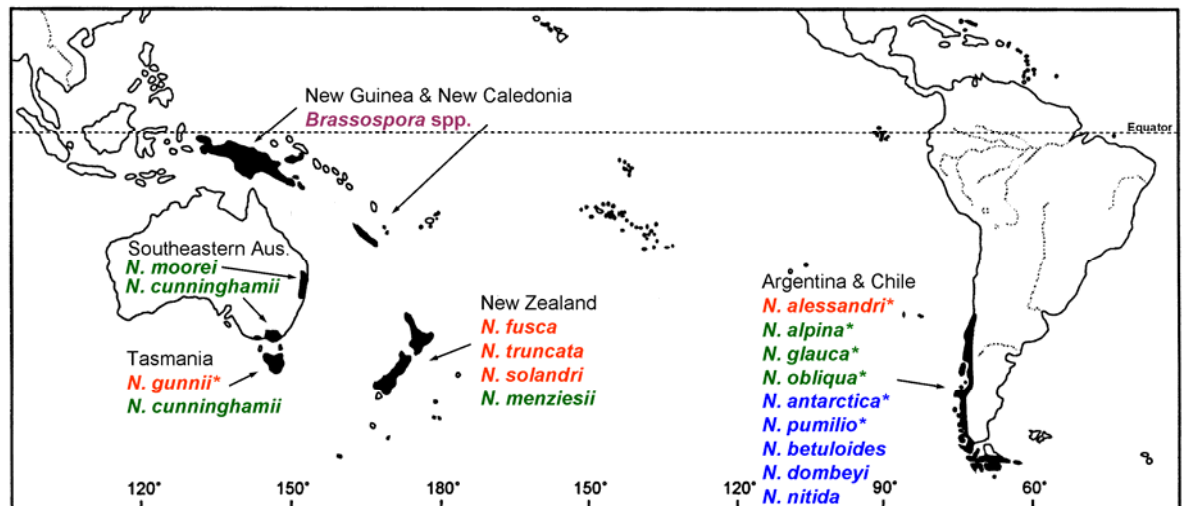


Figure 2.8. Extant distribution of *Nothofagus* subgenera and species (* denotes deciduous species). Key to subgenera: *Brassospora*: violet; *Fuscospora*: orange; *Lophozonia*: green; *Nothofagus*: blue. Modified from Knapp et al. (2005) and Swenson et al. (2001).

Within these distributions, the floristic associations of the two *Nothofagus* species vary with soils and altitude (for detailed vegetation descriptions see: Crowden, 1999; Harris & Kitchener, 2005; Jarman *et al.*, 1999; Kirkpatrick, 1997, 1999; Read & Brown, 1996). *N. cunninghamii* thrives on Tertiary basalt and dolerite soils and occurs along an altitude gradient from sea level to over 1200m. At lower altitudes the trees can attain heights of 30-40m and dominate the rainforest canopy. With increasing altitude tree size diminishes and canopy dominance is shared with other Gondwanic relicts such as *Atherosperma*, *Eucryphia*, *Lagarostrobos*, *Phyllocladus*, *Diselma* or *Athrotaxis* until, in *Athrotaxis cupressoides*-dominated montane forests, *N. cunninghamii* coexists with *N. gunnii* in the shrubby understorey. Mixed communities of *N. cunninghamii* and *Eucalyptus* species are common, either where eucalypts have invaded after fire, or by rainforest species encroaching on wet Eucalypt forest. In subalpine regions, the endemic *E. coccifera* frequently occurs with *N. cunninghamii* and/or *N. gunnii*.

Nothofagus gunnii can tolerate a range of substrates, but freely drained sites such as those on Jurassic dolerite are most common and at altitudes of 1000m or higher. In subalpine areas *N. gunnii*, with or without *N. cunninghamii*, is part of the understorey in short conifer (*A. cupressoides* or *A. selaginoides*) forest or *E. coccifera* woodland; and in alpine areas becomes the dominant species of deciduous heath.

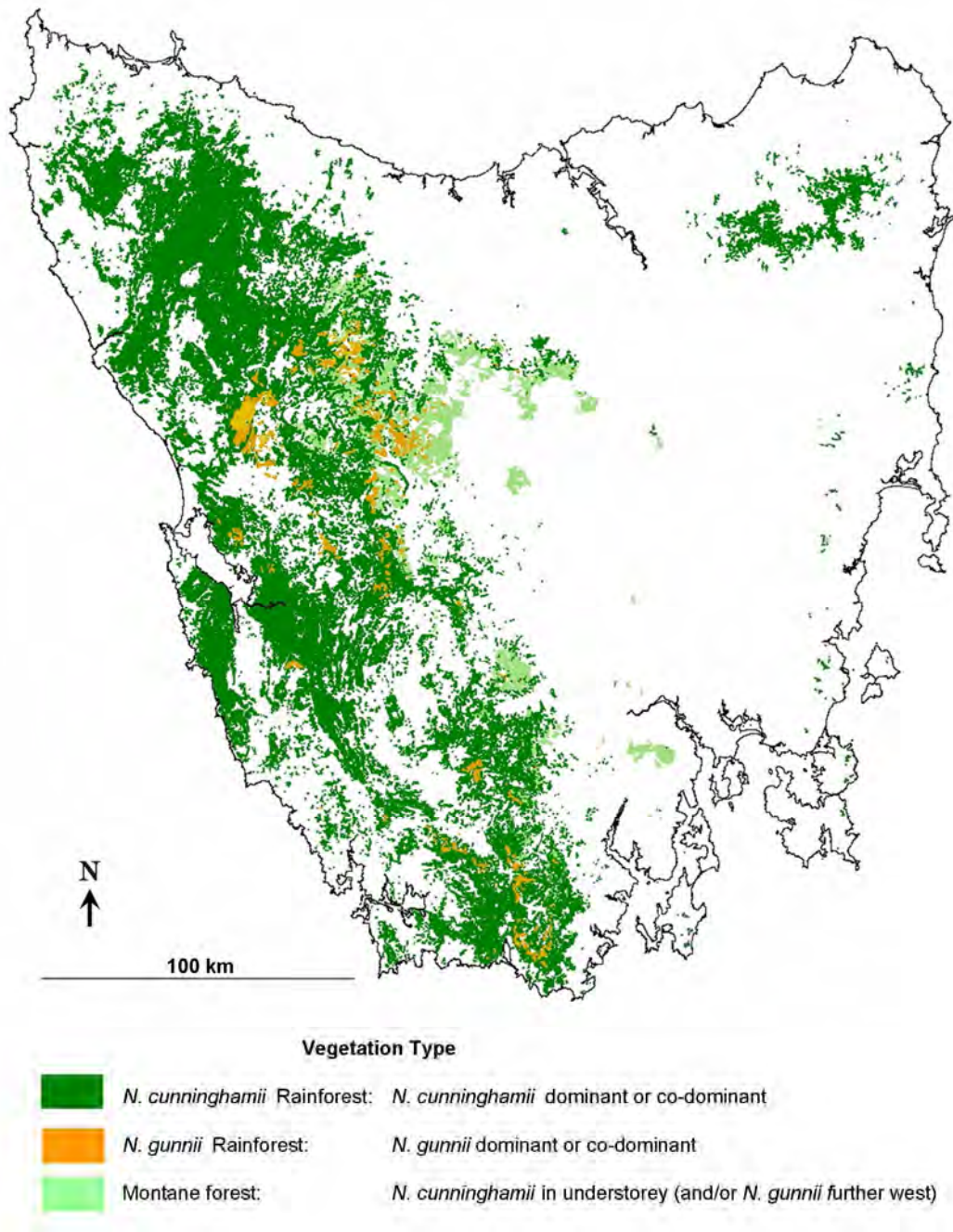


Figure 2.9. Extant distribution of Tasmanian *Nothofagus*. Vegetation types associated with *N. cunninghamii* and *N. gunnii*.

Data Source: TASVEG Version 1.0; Data collection: 1998-2003; Projection: Grid of Australia 1994 (MGA94); MGA zone 55 (GDA94); Original data scale: 1:25,000 across the whole State. ©Tasmanian Vegetation Mapping Program, DPIWE.

Further Information: Harris, S and Kitchener, A (2005). From Forest to Fjaeldmark: Descriptions of Tasmania's Vegetation, Department of Primary Industries, Water and Environment, Printing Authority of Tasmania, Hobart. Text © Government of Tasmania 2005.

2.3.3 Climate Profiles and Adaptations

Regardless of geology or altitude, the extant distribution of *Nothofagus*, as in its palaeohistory, is highly dependant upon climatic variables, particularly rainfall. The Tasmanian species require wet conditions and but both have adaptations for cold temperatures, including frost resistance and photosynthetic flexibility, enabling them to survive in temperate latitudes and in subalpine or alpine regions.

Based on combined data from Tasmania and Victoria, Busby (1986) estimated that *N. cunninghamii* requires a mean annual precipitation greater than 930mm and tolerates a mean annual temperature range of 4.7-13.9 °C. This profile is similar to that reported by Read and Brown (1996) using BIOCLIM-derived data; their profile for Tasmanian *N. cunninghamii* suggests a mean annual precipitation of 2028 mm, with a mean minimum of at least 40mm in the driest month, and mean annual temperature range of 4.7 - 12.2 °C (table 2.3).

N. gunnii requires cooler, wetter climate averages than *N. cunninghamii*. This is demonstrated by Read and Brown's climate profile for *N. gunnii*: mean annual temperature range 4.3 - 8.8°C, and mean annual precipitation of at least 1458mm, with at least 83mm in the driest month (table 2.3). As a result, *N. gunnii* is restricted to subalpine and alpine regions.

	Species	<i>N. cunninghamii</i> ¹	<i>N. cunninghamii</i> ²	<i>N. gunnii</i> ²
Annual Precipitation (mm)	Mean		2028 ± 574	2453 ± 468
	Min.	930	937	1458
	Max.	3523	3563	3125
Driest month (mm)	Mean		98 ± 29	113 ± 14
	Range	51 - 188	42 - 187	83 - 151
Wettest month (mm)	Mean		224 ± 56	258 ± 54
	Range	92 - 353	94 - 361	144 - 321
Annual Temperature (°C)	Mean		8.8 ± 2.0	6.0 ± 1.0
	Min.	4.7	4.7	4.3
	Max.	13.9	12.2	8.8
Min. Temp. (°C) of coldest month	Mean		1.6 ± 1.9	-2.9 ± 1.9
	Range	-2.9 - +6.4	-2.9 - +5.6	-2.9 - +1.9
Max. Temp. (°C) of warmest month	Mean		19.0 ± 1.9	16.5 ± 1.0
	Range	14.8 - 26.8	18.4 - 22.3	14.5 - 19.2

Table 2.3. Climate Profile Summary for *N. cunninghamii* and *N. gunnii*.

Means ± Standard Deviation. Sources: ¹Busby (combined data: Tasmania and Victoria), 1986;

²Read et al. (unpub.) in Read and Brown, 1996 (Tasmanian data): 149, table 5.5.

Physiological adaptations favouring both species in colder climes include frost resistance and photosynthetic flexibility. The leaves of *N. cunninghamii* are frost resistant to -16.5°C as compared with -8.5°C for its close relative, *N. moorei* (Read & Hill, 1989). In keeping with its more southerly distribution, as well as greater frost tolerance (Read & Hill, 1988, 1989; Read & Hope, 1989), *N. cunninghamii* also has a lower optimum temperature for photosynthesis than *N. moorei*: $17 - 22^{\circ}\text{C}$ and 23°C respectively (Hill *et al.*, 1988; Read, 1990). In addition, Read and Busby (1990) have demonstrated that the evergreen *N. cunninghamii* can tolerate a wide range of temperature while maintaining photosynthetic activity, and so can do so for much of the year.

In contrast, winter deciduous *N. gunnii*, is frost resistant to -17°C for its buds, cortex and xylem (Sakai *et al.*, 1981), but its leaves have an optimum photosynthetic temperature of 23°C (Read & Busby, 1990), enabling it to maximise photosynthesis during the Tasmanian Summer. However, they are more vulnerable to summer frost than the leaves of *N. cunninghamii* (Hill & Read, 1988).

As their extant distributions would suggest, minimum temperature is the major factor influencing *N. gunnii*'s lower limit, while minimum precipitation is more important in the occurrence of *N. cunninghamii* (Read & Busby, 1990). However both species, adapted to cold wet environments, have small disjunct populations which may face severe challenges in the coming decades, as will their associated arthropod fauna, in the face of a rapidly changing climate.

To end this review of the palaeohistory and biogeography of *Nothofagus*, and its extant representatives in Tasmania, the following section aims to place *Nothofagus* within the evolutionary history of its arthropods.

2.4 NOTHOFAGUS AND ITS ARTHROPODS: EVOLUTIONARY HISTORY

While flowering plants did not evolve until the Cretaceous (Crane *et al.*, 2004; Soltis & Soltis, 2004), the phytophagous insects and their associated arthropod communities now found on Tasmanian *Nothofagus* have a considerably longer history. The ferns, gymnosperms and bryophytes date from the Devonian and there is evidence of Oribatid mites, Collembola and spiders from this period; Coleoptera,

Psocoptera, Thysanoptera, Plecoptera, Hemiptera and Neuroptera evolved in the early Permian, the time of the appearance of the Southern conifers; Diptera and Hymenoptera date from the late Permian and early Triassic respectively, and Lepidoptera from the early Jurassic; only the Protura and Mesostigmata have a relatively recent history (table 2.4). Thus the majority of the orders composing the suite of arthropods associated with the canopy of extant Tasmanian *Nothofagus* were well established before the appearance of their host species and also before the break-up of the Gondwanan supercontinent.

Reviewing the Phytophagous Insect Data Bank, Ward *et al.* (2003) conclude that extant host plant preferences of British insects and mites reflect their evolutionary history, and that diversity of both plants and arthropods increases from gymnosperms to flowering plants. They note that specialist plant feeders predominate, that is those with a small number of host plant species; while in a previous paper they state that within plant families, those with a similar life form, e.g. a tree, support the most similar populations of phytophagous arthropods (Ward *et al.*, 1995).

Ward *et al.* (2003) categorise both plant and arthropod taxa as basal, intermediate or advanced. Basal taxa are known to have pre-Palaeocene origins, they form the more basal branches of their phylogeny and their morphological characteristics are considered to be primitive or ancestral. Advanced taxa in contrast, are considered to be derived species, advanced in both phylogeny and morphology. Correspondence analysis of plant and arthropod families revealed that the more ancient plant clades, ferns, conifers and Eurosids I, are associated with a greater number of the basal insect families. However, on all flowering plant clades, including Eurosids I, advanced insect species are most numerous and Ward *et al.* (2003) suggest that this is indicative of later colonisations.

Although these findings are restricted to British taxa, they have relevance for *Nothofagus* in that the flowering plant clade Eurosids I includes the order Fagales. Indeed, Ward *et al.* (2003) highlight the fact that the Fagales are associated with the basal insect families and also (Ward *et al.*, 1995) that families within the Fagales (especially Fagaceae, Betulaceae, Salicaceae, Corylaceae) have similar profiles of phytophages. Similar findings come from Japan (Imada *et al.*, 2011), where members of the Fagales have been found to support the most basal family of glossatan moths

(Eriocraniidae). The arthropod data from these northern temperate Fagales suggest that members of the order to which *Nothofagus* belongs have had the opportunity for accumulating herbivores since the Cretaceous, and they provide a source for comparison the with the extant arthropod fauna of Tasmanian *Nothofagus*.

Era	Period/Epoch		Mya	Insects, Spiders, Mites		Plants	Palaeo-geography
Cainozoic	Quaternary	Holocene	0.01	Zoraptera, Phthiraptera, Protura			
		Pleistocene	1.6				Last Glacial Maximum
	Tertiary	Pliocene	5				
		Miocene	25				
		Oligocene	35		Mesostigmata		S. America and Australia separate from Antarctica
		Eocene	60	Mantodea			
		Palaeocene	65				
Mesozoic	Cretaceous		145	Isoptera, Siphonaptera, Strepsiptera		<i>Nothofagus</i> Angiosperms	Gondwana starts to divide
	Jurassic		210	Dermaptera Lepidoptera, Raphidioptera			
	Triassic		245	Odonata Grylloblattodea Phasmatodea, Trichoptera, Hymenoptera, (+1)			Pangaea Divides
				Megaloptera, Mecoptera, Diptera			
Palaeozoic	Permian		285	Coleoptera, Psocoptera, Thysanoptera, Plecoptera, (+5) Embiopoda, Hemiptera, Neuroptera		Southern Conifers	
	Carboniferous		360	Diplura, Thysanura, Blattodea Ephemeroptera, Orthoptera, (+9)			
	Devonian		410	Archaeognatha	Endeostigmata	Bryophytes	
	Silurian		440	Collembola	Oribatida	Gymnosperms	
	Ordovician		500	Spiders		Ferns	
	Cambrian		545				
	Precambrian		>545				

Table 2.4. Geological history of insects, spiders, mites and plants, and significant palaeogeographical events. Mya (million years ago) indicates approximate timescale in 106 years before present.

Extant insect orders named in figure; numbers of extinct orders indicated (+ X): (+1) Titanoptera; (+5) Permothemistida, Protelyoptera, Glosselytrodea, Antliophora, Amphiesmenoptera; (+9) Monura, Diaphanoptera, Palaeodictyoptera, Megasecoptera, Protodonata, Paraplecoptera, Caloneurodea, Blattinopsodea, Miomoptera.

Adapted from New (1988 fig. 1.2, 1992 fig 27), Gullan and Cranston (2000:180 fig 7.3), data after Kukalova-Peck (1991), Labandiera (1998); Arachnida: Walter & Proctor (1999 fig 2.1).

Chapter 3 CANOPY ARTHROPODS AND HERBIVORY

3.1 ‘INSECTS AND PLANTS’

Biologists and amateur naturalists, particularly in the northern hemisphere, have a long history of describing and documenting both arthropod and plant taxa. However, until the middle of last century there had been little formal research into the interactions between arthropods and their host plants (Schoonhoven, 2006). This chapter outlines the foundations of current research into arthropod-plant interactions; looks at spatial and temporal variation and host specificity; reviews methods of sampling and processing both the arthropods and the impact of insect herbivores; and concludes with canopy arthropods in relation to *Nothofagus* in Tasmania.

3.1.1 ‘Insects and Plants’: History

In their review of the development of research into the ecology of insect-plant relationships, Lewinsohn *et al.* (2005) trace the foundation of such research to Southwood’s (1961) seminal paper in which he reviewed data from four countries documenting the numbers of insect species on a variety of trees. Comparing data from Britain with that from similar host trees in Cyprus, Russia and Sweden, he noted that the greater the host distribution the greater the number of insect species. Using the geological record of the presence of the British trees in the Quaternary he drew the conclusion that a longer history of host presence also resulted in greater numbers of insect species associated with that host. Such conclusions formed the basis for subsequent studies into species-area relationships and into insect-plant interactions and evolution.

In the same decade Ehrlich and Raven (1964) outlined the theory of coevolution whereby host plants and their herbivores are seen to reciprocally develop defences and the means to circumvent them; Beck (1965) examined means by which plants defend themselves; and Janzen (1968) applied to trees and their invertebrate communities McArthur’s and Wilson’s (1967) ‘Island Theory of Biogeography’, suggesting that the insect species richness of a tree is proportional to its size, its area of distribution or to the proximity of an individual, or a small population, to a larger

population of that tree species. In the following decades, Feeny (1970, 1976) was investigating plant chemical defences, particularly their variation with season (Feeny, 1970) and with the ‘apparency’, the chance of detection, of a plant by its potential consumers (Feeny, 1976); and Lawton (1983) began exploring the effect of plant architecture on insect diversity.

Meanwhile, Root (1967, 1973) had introduced the concept of feeding guilds which he described as ‘... groups of species that exploit the same class of environmental resources in the same way’ (Root, 1967: 346). Other researchers then explored and extended the idea (e.g.: Adams, 1985; Claridge & Wilson, 1981, 1982; Moran & Southwood, 1982; Rathcke, 1976; Terborgh & Robinson, 1986; Stork, 1987) and while it was accepted as a useful means of classification, so was the need for caution in how such guilds be defined (Hawkins & MacMahon, 1989; Simberloff & Dayan, 1991).

In 1972, the Royal Entomological Society of London reviewed the current trends in its symposium “*Insect/Plant Relationships*” (van Emden (ed.) 1973). These ideas were enlarged upon by Southwood (1973, 1984), Southwood and Kennedy (1983), Southwood *et al.* (1982) and other authors, such as Jermy (1984). The subject was further defined in “*Insects and Plants*” (Strong *et al.*, 1984), which drew together the various aspects of the topic, outlining the importance and abundance of insect herbivores, insect/plant evolution, guilds, community structures, co-evolution and host specificity. Other synopses followed, e.g. New (1988), and more recently Schoonhoven *et al.* (2006).

3.1.2 *'Insects and Plants': Summary*

The following summary draws heavily upon the above sources (especially Schoonhoven *et al.*, 2006 and Strong *et al.*, 1984) in addition to those cited specifically in the text.

3.1.2.1 *Feeding Guilds on Plants*

As indicated in Section 2.2.3, there has been a long association between insects, and other arthropods, and plants: ~ 400 million years for Collembola, spiders and Oribatid mites; ~ 300 million years for insects; and ~ 100 million years between arthropods and angiosperms. These arthropod communities were divided by Moran & Southwood (1982) into seven broad categories – 'major guilds' - each of which was open to further subclassification:

- Herbivores/phytophages: the largest group, which are dealt with below.
- Predators: prey on live arthropods on the plant, e.g. spiders, adult Coccinellid beetles, Mesostigmatid mites.
- Scavengers: feed on dead organic matter, animal or plant, which has collected on the plant (saprophages), but may also include consumers of bacteria, protozoa, algae, or fungal spores and hyphae, e.g. Leiodid beetles, Oribatid mites, Collembola.
- Parasitoids: parasites of the other taxa, e.g. the parasitiform mites.
- Tourists: more a non-feeding guild in that they are incidental visitors using the plant as, for example, a brief resting place.
- Ants
- Epiphyte fauna

Comparing invertebrate fauna from trees in Britain and South Africa, Moran and Southwood (1982) found consistent proportions of predator species between the different tree species, and of phytophage species on the broad-leaved trees. These trends, particularly the constancy of proportions of phytophage species numbers,

persist within tree types and biogeographical regions (Southwood, 1996). (Figure 3.1).

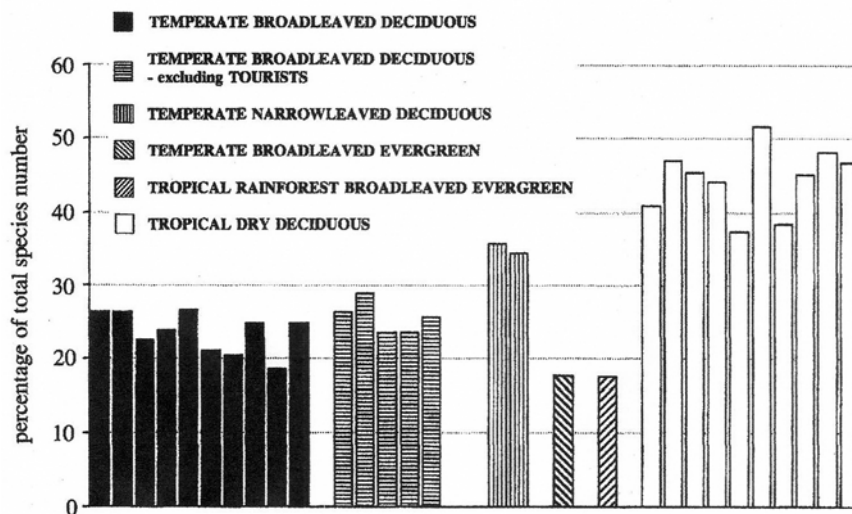


Figure 3.1. Phytophages as a proportion of overall species richness on different tree types and in different biogeographical regions. Source: Southwood, 1996, Figure 5, p. 1119, with data from Moran & Southwood, 1982 and Southwood *et al.*, unpublished (temperate forests in UK and South Africa); Stork, 1987 (tropical rainforest in Borneo); West, 1986 (tropical dry forest).

However, while the species richness of the feeding guilds remained fairly constant, the relative proportions of predator abundance to phytophage abundance were found to vary with season (Southwood, 1996). In addition, Southwood *et al.* (1982) noted that the amount of defoliation correlated with the biomass of phytophages i.e. the quantity of foliage eaten can give a measure of the numbers of phytophages active on a tree.

3.1.2.2 *Herbivory/Phytophagy*

As their food source is so abundant, plant eaters large and small are numerous. The Shorter Oxford English Dictionary defines ‘herbivorous’ as ‘Of an animal, esp. a mammal, that feeds naturally on plants’ (OED1, 1993: 1237). The term ‘phytophagous’, although often used interchangeably with ‘herbivorous’, is more specific to arthropods, being defined as ‘Esp. of an insect or other invertebrate: feeding on plants’ (OED2, 1993: 2197), and encompasses leaf chewers, leaf miners, sap suckers (of xylem or phloem), gall formers, and consumers of fruit, wood, bark, or roots.

Phytophages account for nearly half of all insect species. They occur in eight orders, three of which are exclusively plant feeding (Table 3.1), and they display varying degrees of host specificity.

Order	Total Species	Phytophagous Species	
		Total	%
Coleoptera*	349 000	122 000	35
Lepidoptera*	119 000	119 000	100
Diptera	119 000	35 700	30
Hymenoptera	95 000	10 500	11
Hemiptera*	59 000	53 000	90
Orthoptera	20 000	19 900	100
Thysanoptera*	5 000	4 500	90
Phasmida	2 000	2 000	100

Table 3.1. The plant-eating insects: total species per order, and the number and proportion of phytophagous species per order. *orders most relevant to this research on Tasmanian *Nothofagus*. Modified from Schoonhoven *et al.*, 2006: page 6 table 2.1.

The descriptive terminology of phytophagous insect feeding preferences is open to interpretation. Those insects that feed on a single species of host plant are monophagous in the strictest sense, but some authors extend the meaning to the generic level. The term oligophagy refers to feeding on several host species, usually within the same plant family, while polyphagy refers to feeding on a variety of plants from different families. However, insect preference may be for similarity of plant chemicals regardless of plant taxonomic proximity, or feeding preference can vary depending on host plant availability or the presence of predators (Jaenike, 1990).

In an attempt to circumvent these difficulties, the terms specialist and generalist have been introduced, whereby the former encompasses monophagy and oligophagy and the latter term corresponds with polyphagy.

3.1.2.3 Coevolution, Plant Defences, Arthropod Adaptations

Coevolution, the proposition that plant/phytophage species pairs undergo reciprocal evolution, has been much debated since it was first suggested by Ehrlich and Raven (1964). But whether it is accepted in its original form or on larger scales as a more diffuse community interaction or at a geographical level, there is agreement that plants and phytophages have evolved in parallel.

To guard against the attentions of phytophages, plants have evolved a formidable range of defences: temporal e.g. timing of leaf flush, mast years of pollen release; physical e.g. spines, hairs, leaf toughness; and chemical, the production of secondary metabolites noxious to consumers, e.g. tannins, phenolics and glycosides. The soft, nutritious, newly expanding leaves are most vulnerable to attack (Read *et al.*, 2003) and tend to have higher levels of chemical defences, such as phenolics and cyanogenic glycosides, than do mature leaves which have increased leaf toughness (Brunt *et al.*, 2006).

In response to these measures, arthropods have developed modifications to life cycle or behaviour, structural changes e.g. to mouthparts, and tolerance, or even storage for their own defence, of plant defensive chemicals. Insect specialisation is highest amongst Coleoptera, adults and larvae, Hemiptera, and Lepidoptera larvae; and especially in the internal feeders, the leaf miners, gall formers and sapsuckers. Specialists tend to target young leaves, while generalists are more likely to be external feeders and can tolerate ingestion of older leaves. Herbaceous plants tend to host more specialised insect populations than shrubs or trees, possibly because herbaceous taxa are themselves more diverse, in form, chemicals and life cycle, than woody species.

Colonisation of a new host plant depends upon its area of distribution and ‘the taxonomic, phenological, biochemical and morphological match’ (Strong *et al.*, 1984: 109) between the potential host and an insect’s feeding preferences: polyphagy and external feeding are common among colonisers.

3.1.2.4 *Summing up: Diversity of Arthropods on Plants*

Thus, between the early 1960s and mid 1980s, a number of factors were found to influence the diversity of the arthropod population on a given plant species. There is opportunity for accumulation of a diverse arthropod community if the species is abundant, has a long history or wide geographical range; the larger the area occupied by any population of a plant species and its proximity to sister populations can both help maintain the species richness of its associated arthropods (e.g.: Kelly & Southwood, 1999 – a re-analysis of Southwood’s earlier work; Lawton & Schroder, 1977; Leather, 1986; Kennedy & Southwood, 1984; Southwood, 1961; Southwood *et*

al., 1982; Strong, 1974; Strong *et al.*, 1977). Plant architecture and size, level of defences, physical and chemical, and seasonal changes can all have a bearing on the diversity of arthropods on a tree species (e.g.: Feeny, 1970, 1976; Lawton, 1983; Leather, 1986; New, 1979).

Since the formulation of the ‘insect-plant’ theories above, the topic has generated a vast amount of research. Initially most data came from northern temperate zones, with modest input from Southern temperate regions, but increasingly the focus shifted to large-scale projects in the tropics (Erwin, 1995; Lewinsohn *et al.*, 2005), while the study of plant secondary metabolites and chemical defence has become a research area in its own right. Much of this research and sampling explores the diversity and distribution of arthropods and herbivory in forest canopies, as will be discussed in section 3.2. More recently, attention has turned to the degree of host specificity within the tropical forest canopy, a subject previously dominated by work on northern temperate taxa. There follows a very brief digression into this subject.

3.1.3 Host Specificity

Following on from the earlier work into host specificity as described by Strong *et al.* (1984), research interest, particularly in the tropical regions, is shifting from diversity and distribution of canopy arthropods to studies of feeding patterns and host-plant preference (Novotny & Basset, 2005). In Papua New Guinean lowland rainforest increased host specificity has been associated with the overall species richness of a tree’s fauna, its altitudinal range and the ready availability of young leaves (Basset, 1996). Small body size of the herbivores, especially sap suckers and leaf chewers, was found to correspond with increased host specificity in Panama and New Guinea (Lindstrom *et al.*, 1994; Novotny & Basset, 1999). However, few herbivores are strictly monophagous, most feed within congeneric, or more rarely confamilial, groups of hosts (Novotny & Basset, 2000, 2005; Odegaard *et al.*, 2005; Weiblen *et al.*, 2006). Thus specificity is most often within a group of related host taxa, whose chemical composition is often similar (Becerra, 1997).

While these are just a few examples, Novotny & Basset (2005) in their review of insect herbivore specificity in tropical forests indicate that patterns of host specificity in the tropics have been found to mirror those in temperate regions. They draw the

conclusion that although comparison between tropical and temperate data is hampered by differences in methodology, there is little evidence of a marked increase in host specificity from high to low latitudes.

3.2 *INVESTIGATING DIVERSITY AND DISTRIBUTION IN CANOPY ARTHROPODS AND HERBIVORY*

The increasing interest in forest canopies, notably rainforest, resulted in ever more elaborate sampling techniques, enabling research into aspects of the canopy which were previously inaccessible. Such studies reveal the complexity and diversity within forest canopies, in overall species richness and abundance and their variation in space and time.

However, there is also variability in results obtained with different sampling techniques (Basset *et al.*, 1997), many of which e.g. chemical knockdown, canopy rafts and fixed towers are expensive and invasive. By contrast, less elaborate methods e.g. branch clipping, sweep netting and branch beating are simpler to carry out, cheap and less invasive, but may yield a narrower sample of the total arthropod population at a given site. In their review of non-fogging methods, Basset *et al.* (1997: 45) point out that no one method is a “panacea”, instead a combination of methods will be most effective to cover different facets of forest canopy systems. Meanwhile, assessing levels of defoliation presents another set of challenges, both in sampling schedules and in calculating the amount of leaf damage incurred.

3.2.1 *Spatial Variation*

Southwood and other authors (e.g. Basset, 1997; Gibb, 1963; Morris, 1960; Southwood, 1987) have recognised the need in canopy research to consider spatial variation in herbivory and faunal distribution. Lowman and Heatwole (1992) found that among Australian eucalypts, upper canopy leaves were most heavily defoliated. However, they describe considerable variability in rates of herbivory between sites, species, individuals of the same species and, within an individual, between branches and canopy heights.

In an earlier paper, Lowman (1985b) discusses the high degree of variability in herbivory at small spatial scales within five Australian rainforest tree species. However, she emphasises the similarity of results between individual canopies or sites at larger scales, where results from hundreds of leaves were pooled. In Australian rainforest canopies, leaves of the lower canopy and shade leaves are most heavily defoliated (Lowman, 1985b; Lowman and Heatwole, 1992). As lower canopy leaves are the most shaded, light intensity may be as important as height *per se* in influencing level of herbivory in Australian rainforest (Lowman, 1992). Nielsen and Ejlersen (1977), assessed arthropod herbivory on a mature beech stand, they too found that the lower, shaded canopy was more heavily grazed. They suggest that this pattern of herbivory is less stressful for the tree as shade leaves are least active in photosynthesis. However, in a study of twenty-five species of North Queensland mangroves, Robertson and Duke (1987) found little variation in herbivory at different levels in the canopy, although they report small but significant differences between sites for some species.

Basset (1991a, 1991c, 1992) discusses the distribution of canopy arthropods in tropical rainforest trees and like Lowman (1985b; Lowman and Heatwole, 1992), he reports that young leaves are eaten in preference to mature leaves, but also in preference to very young leaves (Basset, 1991c). He suggests that leaf age contributes to the spatial distribution of arthropods within a canopy, while other factors are arthropod specific – their aggregation patterns, activity and mobility (Basset, 1992).

3.2.2 *Temporal variation*

Besides spatial variation, temporal variation is another factor to consider when investigating arboreal arthropod populations (Basset, 1991b, 1997; Lowman & Wittman, 1996; Morris, 1960; Southwood, 1987). The population composition can vary with the time of day of collection: Lowman (1982b) compared tropical, subtropical and cool temperate rainforest and found an increase in nocturnal species during the cool temperate spring, coinciding with leaf flush. However, Costa and Crossley (1991) discuss patterns of arthropod activity and state that while some species are either diurnal or nocturnal, others show no clear division. These latter

species may be active for periods of the day and night, their activity being triggered by dawn or dusk.

Seasonality of canopy arthropod populations can be marked (Lowman & Heatwole, 1992), with highest numbers coinciding with leaf flush (Lowman, 1982b) and lowest numbers occurring in the coolest months, with minimum temperature being the limiting factor (Basset, 1991b). Lowman (1985b, 1992) has demonstrated seasonality in herbivory for five Australian rainforest tree species. She found that defoliation was highest during spring and summer and lowest during autumn and winter. Recher *et al.* (1996a, 1996b) describe seasonal and annual variation in arthropod abundance, biomass and species richness on four *Eucalyptus* species, two each in Eastern and Western Australia. They suggest that these differences reflect temporal variation in rainfall or temperature, affecting tree productivity and phenological events such as growth of new leaves. In their study of seasonality of activity patterns in geometrid moths in Tasmania, McQuillan *et al.* (1998) found that minimum temperatures at a given site determined seasonal moth activity at that site, whether highland or lowland.

Leaf age is also another aspect of temporal variation. The seasonality in phytophagous arthropod populations appears to reflect the greater palatability of young leaves over old leaves (Coley, 1980; Lowman, 1982, 1985b, 1992; Basset 1991d, 1992). Lowman and Box (1983) examined leaf toughness and phenolic content of the leaves of five Australian rainforest trees. They found that leaf toughness and toxicity increase with increasing leaf age. Basset (1992) established a food quality index for the leaves of the Australian rainforest tree, *Argyrodendron actinophyllum* Edlin (Sterculiaceae) and found that the preferred young leaves had higher nitrogen and water content than old leaves.

3.2.3 Canopy Arthropods: Collection methods

Numerous techniques have been developed for sampling arboreal arthropods (Table 3.2) and, as in the case of measurement of herbivory (section 3.2.6), it is difficult to draw direct comparisons between studies using different methods. Traditionally, early collectors held an upturned umbrella under the branch of a tree, to catch animals dislodged when the branch was struck with a stick (New, 1988;

Southwood, 1987). Since then, arthropod collection methods have advanced somewhat. Concomitantly, canopy access is tending away from ground-based sampling to increasingly complex and expensive within-canopy sampling, by means of adaptations of climbing techniques; canopy rafts and dirigible apparatus; canopy cranes and other fixed structures (Lowman & Wittman, 1996). Rather than canopy access, this section examines collection methods, particularly chemical knockdown (fogging or gassing), branch clipping and branch beating.

Chemical Fogging

For chemical knockdown, a fogging machine releases into the tree canopy a rapid knockdown insecticide, commonly a pyrethroid, as a mist or aerosol. The machine may be either placed on the ground, or drawn into the canopy with a pulley system or other device. Arthropods falling from the fogged tree are collected on trays on the ground beneath the canopy. Stork and Hammond (1997) describe the use of fogging in a study of oak tree beetle assemblages in Richmond Park, U.K. They summarise the advantages and disadvantages of this method:

Advantages

1. Relatively unselective – selectivity can be estimated by visual searches.
2. Not dependent on activity of arthropods.
3. No ‘attractants’ involved.
4. Not influenced by ‘trap behaviour’, unlike activity-based traps.
5. Sample composition not directly influenced by weather.
6. Collects some species difficult to sample by other means.
7. Fairly precise origin of specimens known.
8. Understorey species can be avoided if required.
9. No need to climb or disturb trees, particularly during sampling.
10. No servicing or maintenance problems on long-term sites.
11. Largely non-destructive to trees and surrounding habitat.
12. Samples are usually exceptionally clean and easy to sort.
13. Insecticide is non-residual and of limited toxicity.
14. Fogging (as opposed to spraying) can sample the high canopy.

Disadvantages

1. Labour intensive.
2. Equipment costly and bulky.
3. Limited by weather conditions, i.e. cannot be done when windy.
4. Not effective in sampling some externally feeding groups, e.g. phloem feeders and leaf-miners, and some internal feeders(e.g. wood borers).
5. The insecticide fog may be difficult to control, causing unnecessary fogging of other trees.

(Stork & Hammond, 1997: 19 & 20)

Collection Method Author(s)	Chemical Fogging	Branch Clipping	Branch Beating	Hand Collection	Flight Intercept Trap	Sweep Netting	Light Trap	Vacuum/ Aspirator	Trap Plants	Branch Shaking
Allison <i>et al.</i> , 1997	+									
Arias <i>et al.</i> , 2008	+									
Basset, 1991a, 1992	+									
Basset, 1991b	+				+					
Basset, 1991d	+			+	+					
Basset, 1996	+	+	+	+						
Basset, 1997	+	+	+	+	+					
Basset & Novotny, 1999				+				+		
Basset, Samuelson & Miller, 1996	+	+	+	+	+					
Costa & Crossley, 1991		+								
Davies <i>et al.</i> , 1997	+									
Didham, 1997					+					
Diehl <i>et al.</i> , 1997						+		+	+	
Elliott <i>et al.</i> , 2002			+	+		+	+			
Elton, 1973			+	+		+				
Gibb & Betts, 1963		+								
Hammond, Kitching & Stork, 1996	+									
Harris <i>et al.</i> , 1972			+							
Kitching <i>et al.</i> , 1993	+									
Lanfranco <i>et al.</i> , 2001		+								
Lowman, 1982a,b						+	+			
Majer & Recher, 1988*	+	+								
Majer, Recher & Ganesh, 2000	+									
Majer, Recher & Keals, 1996*	+									+
New 1979*	+		+							
Ohmart <i>et al.</i> , 1983b		+								
Peeters <i>et al.</i> , 2001		+								
Recher <i>et al.</i> , 1996a,b	+									
Russel <i>et al.</i> , 2000										+
Southwood <i>et al.</i> , 2004, 2005	+	+								
Stork, 1987	+									
Stork & Hammond, 1997	+									
White, 1975			+							
Wotherspoon, 1996		+		+						

Table 3.2 Examples of Collection Methods used in Canopy Arthropod Studies. * denotes studies comparing methods.

Thus fogging has a number of advantages including, comprehensive sampling of the canopy, with a clean sample, selectivity, and little disturbance of the tree. However, it has the disadvantages of being weather, particularly wind, dependent; sampling is not restricted to the tree under investigation; it misses some external and internal feeders; and it is labour intensive and expensive. In addition, Southwood (1987) points out that destroying the fauna from a sampling unit as big as a tree is rarely desirable in long-term ecological work.

Branchlet Clipping

Branchlet clipping involves enclosing the branchlet within a plastic bag, into which may be sprayed rapid knockdown insecticide. The bag is sealed around the branch stem until the contents can be examined in the lab. Majer and Recher (1988) compare branchlet clipping with chemical knockdown in a study of invertebrate communities on Western Australian eucalypts. They suggest that the two procedures sample different populations: knockdown samples contained a wider variety of invertebrates, including bark-dwellers; the clipped samples contained sessile or webspinning individuals but no mobile invertebrates or bark-dwellers. The authors conclude that the two procedures complement each other and may be used together with little extra effort in the field.

Branch Beating

Branch beating is a modern version of the naturalist's upturned umbrella. A plastic collecting tray, or net tray with a funnel into a collecting jar, is held under the branch to be sampled. The branch is struck firmly with a stick and the invertebrates that fall onto the tray are collected, either by picking them off the tray, or by emptying them through the funnel. White (1975) describes this method as longstanding for collecting Lepidoptera larvae, as it is simple and independent operators can produce uniform results. It gives a measure of relative rather than absolute abundance (Southwood, 1987; White, 1975). However as Southwood (1987) indicates, very small taxa e.g. mites may be overlooked, and the more mobile individuals may escape by flying or running off the collecting surface.

Branch beating, like chemical knockdown is weather dependent. Harris *et al.* (1972) evaluated the effect of weather on branch beating as a method of sampling

two species of Lepidoptera larvae, *Acleris gloverana* (Walsingham) and *Melanolophia imitata* (Walker), on Western Hemlock, *Tsuga heterophylla* (Rafinesque-Schmaltz) Sargent, on Vancouver Island, British Columbia. They found that wet foliage resulted in lower numbers of larvae collected, especially *A. gloverana*, whereas *M. imitata* counts were much reduced on clear, compared with overcast, days. Thus, the weather had an effect on the total population collected, and its composition. They also concluded that branch beating was suitable for identifying broad rather than minute changes in populations of forest defoliators, agreeing with White's (1975) conclusion that branch beating gives a relative, rather than absolute, measure of canopy invertebrate populations.

However, branch beating is inexpensive and easy to execute. Elton (1973) used branch beating in conjunction with sweep netting and hand collecting with a brush, for an extensive study of Neotropical rainforest invertebrate populations. He describes his sampling methods as "kept as simple as possible" in the field (Elton, 1973: 56). Similarly, New (1979) used branch beating as his method of choice in a study of Coleoptera on Australian acacias. He monitored the emerging tendencies from the beating samples with intermittent pyrethrum-mist fogging of trees outside the study, and found no significant difference between the two methods.

Majer *et al.* (1996) describe what appears to be a variation of branch beating - branchlet shaking - in which branches are shaken over appropriate collecting apparatus. The authors compared this with chemical knockdown. They conclude that the two procedures yield similar information about the canopy fauna but the branchlet shaking method, although resulting in a smaller sample, is a useful alternative method in windy weather.

Basset *et al.* (1997) review non-fogging methods of canopy arthropod sampling. They consider that, while branch clipping is inexpensive, it is also destructive and biased towards sedentary taxa. Whereas, they state that branch beating results in variable sample size depending on the type of foliage and it is effective for sampling free living caterpillars, but is less efficient for active or small individuals. However they emphasise that no single sampling method will provide a complete general arthropod survey. Complementary methods will take better account of spatial, temporal and behavioural variation arthropod populations. Indeed, Basset uses

combinations of methods in his extensive studies of canopy arthropods e.g. chemical knockdown, branch clipping, branch beating, hand collection and flight intercept traps (Basset, 1996, 1997; Basset *et al.*, 1996); while in smaller studies he has used a modified, more discrete form of chemical fogging (Basset, 1991a, b, d).

3.2.4 *Canopy Arthropods: Identification and Categorisation*

Classification is preferably to species, but exact identification may not be possible and so classification is often to morphospecies, in which identification is based on differences in morphological characteristics, as described by Basset (1997). However, depending on the study, classification to order may be sufficient. This may be for brevity, for example Lowman classifies to morphospecies in her Ph.D. thesis (Lowman, 1982a), but includes only ordinal totals in her paper using the same data (Lowman, 1982b). Elton (1973) classified to order and by size, for simplicity in the field. Where taxa are classified to morphospecies, categorisation into feeding guilds, or functional groups, is frequently used in the subsequent data analysis (table 3.3).

3.2.5 *Herbivory: Sampling*

A variety of techniques have been used to estimate levels of herbivory, ranging from visual estimates, to meters, to scanning and imaging. Each is a means of recording the amount of a leaf eaten, but direct comparison between studies of herbivory may be misleading due to the differing methods of data collection and their analysis.

Visual estimates allow rapid assessment in the field by categorising leaf damage into increments of the proportion of leaf eaten. Carne *et al.* (1974) chose 20% increments for their assessment of damage to plantation eucalypts by Christmas beetles. Fox and Morrow (1983), estimating insect herbivory for forty-four species of eucalypts, initially used four categories: 0%, <33%, <67%, <100%. They later revised this to seven categories for greater resolution: 0%, <1%, <10%, <25%, <50%, <75%, <100%; reflecting the greater proportion of leaves in the lower damage categories.

Author	Degree of Classification (Study of single Order)		Categorisation into Feeding Guilds?
Allison <i>et al.</i> , 1997	morphospecies	(Coleoptera)	yes
Arias <i>et al.</i> , 2008	morphospecies	(Coleoptera)	yes
Basset, Samuelson & Miller, 1996	morphospecies		yes
Basset, & Novotny, 1999	morphospecies		yes
Basset, 1991a,b,d, 1992, 1996, 1997	morphospecies		yes
Costa & Crossly, 1991	Insects to Superfamily/family, Non-insects to Order		no
Davies <i>et al.</i> , 1997	morphospecies	(Coleoptera)	yes
Didham, 1997	species (Diptera only)	(Diptera)	no
Diehl <i>et al.</i> , 1997	morphospecies		yes
Elliott <i>et al.</i> , 2002	species or genus		yes
Elton, 1973	Order		no
Gibb & Betts, 1963	species or genus	(Lepidoptera)	N/A
Hammond <i>et al.</i> , 1996	morphospecies	(Coleoptera)	yes
Harris <i>et al.</i> , 1972	species	(Lepidoptera)	N/A
Kitching <i>et al.</i> , 1993	Order		N/A
Lanfranco <i>et al.</i> , 2001	morphospecies		yes
Lowman, 1982a	morphospecies		no
Lowman, 1982b	Order		no
Majer & Recher, 1988	Order		N/A
Majer, Recher & Ganesh, 2000	morphospecies		no
Majer, Recher & Keals, 1996	Order		N/A
New, 1979	morphospecies	(Coleoptera)	yes
Novotny & Basset, 1999	morphospecies		yes
Ohmart <i>et al.</i> , 1983b	Insects to species, non-insects to Order		Gp
Peeters <i>et al.</i> , 2001	morphospecies		yes
Recher, Majer & Ganesh, 1996a	morphospecies		Gp
Recher, Majer & Ganesh, 1996b	Order		Gp
Russell <i>et al.</i> , 2000	morphospecies		yes
Stork & Hammond, 1997	Order		N/A
Stork, 1987	morphospecies		yes
White, 1975	species	(Lepidoptera)	N/A
Wotherspoon, 1996	morphospecies		yes

Table 3.3 Examples of Degree of Classification of Canopy Arthropods and Categorisation into Feeding Guilds, by Author. ‘Gp’ denotes functional group.

Benjamin *et al.* (1968) emphasise the difficulty in measuring the irregularly shaped areas of chewed leaves and they experimented with a dot-grid. They found that diagonal or vertical orientation affected accuracy and that, although it was adequate for larger areas, it was inaccurate for small areas. Tracing the leaves onto graph paper, although laborious gives a more detailed measure. Brown and Ewel (1987), investigating rainforest ecosystems, made initial manual estimates with graph paper and used an area meter when harvesting the leaves 3-7 weeks later. Similarly, Lowman and Heatwole (1992) used a combination of manual and digital estimates when investigating defoliation in eucalypts.

Use of an area meter requires representation of actual and potential leaf area. This may be achieved by tracing the actual area onto graph or other paper (Lowman, 1985b; Stone & Bacon, 1995) or by exposure of photographic paper (Reichle *et al.*, 1973), and then estimating potential area. Alternatively, Lowman (1985a) taped the leaf holes to measure the potential area. Wotherspoon (1996) taped damaged eucalypt leaves to plain paper, scanned them, and then used imaging software to measure area. Williams (1990) measured the actual area with a leaf area meter and found good correlation with the total leaf area estimated using a digitiser.

The choice of method often depends upon available time and facilities for measurement. Comparing visual against leaf area meter measurements, Robertson and Duke (1987) found a close correlation. However, Landsberg (1989) found her visual assessment consistently overestimated damage to a leaf when compared with its measurement on a digitising board. Landsberg and Gillieson (1995) suggest that visual estimates, using a chart of known areas of damaged leaves of different damage classes, calibrates visual with area meter measurements. Data can be compared within a study if the same procedure is used throughout, as any bias will be consistent within that study. However between studies, different methods of measuring herbivory may make direct comparison difficult. Lowman (1985a) suggests that this contributes to the variability in estimates of levels of herbivory in rainforest canopies.

3.2.6 *Herbivory: Damage Estimation*

Having measured the amount eaten per leaf, there is differing opinion as to how to extrapolate this to overall defoliation rates, most often referred to as either mean percentage damage or leaf area loss. Wotherspoon (1996: Appendix 2) reviewed twenty-nine studies of herbivory on eucalypts and he points out that many authors omit a description of how this was derived, while only 56% used the method considered most accurate. This, together with the question of the rate of expansion of the hole as the leaf grows, can be another source of inconsistency in estimates of herbivory.

Mean percentage damage

One approach to determining the mean percentage damage is to take the average proportion of damage per leaf in a given sample. Alternatively, mean percentage damage can be expressed as the ratio of total proportion of damage from all leaves in the sample, to total potential leaf area available in the sample (Williams & Abbott, 1991). Landsberg (1989) indicates that the two measures are equivalent only if all leaves are of similar size and have similar levels of defoliation: where there are many small leaves in the sample the average proportion of damage per leaf yields an overestimate of defoliation. In addition, this measure assumes a normal distribution in percentage damage per leaf, yet this rarely occurs (Landsberg, 1989). For these reasons Landsberg (1989) and Williams and Abbott (1991) favour the ratio of total proportion damage to total area potentially available as the more accurate measure of defoliation, a view also supported by Lowman and Heatwole (1992).

Hole Growth

Rate of hole growth compared with total leaf growth poses a puzzle for which the evidence is inconclusive. This has important implications since, if holes and leaves grow at different rates, the ratio of total proportion damage to total potential area will not be a true representation of the mean percentage defoliation.

Reichle *et al.* (1973) measured the expansion rate of leaves, and of the holes punched in them, in *Liriodendron tulipifera* forest for the 1967 growing season. They found that hole growth matched leaf growth except for rapidly expanding young leaves in which the holes enlarged at a faster rate than their corresponding leaves. They derived the equations for an insect grazing model to account for this. Nielsen (1978) followed the progress of punched holes in beech (*Fagus silvatica* L.) leaves. He states that height in the canopy, proximity to the stem and position of the tree in the stand did not influence leaf hole expansion. However, the position of the hole on the leaf blade led to considerable variation in rate of hole expansion. He suggests that taking average leaf hole expansion is an acceptable compromise if correcting for the differences of individual holes is impractical.

Coley (1980) concluded that there was no significant distortion in the estimated proportion of leaf area eaten as the leaves grew. Similarly, Lowman (1987) found

that the leaf holes expanded proportionally with leaf growth throughout the life of the leaves, for five rainforest species, including *Nothofagus moorei* (F. Muell.). In contrast to this, Landsberg (1989) documents hole growth as slower than leaf expansion in *Eucalyptus blakelyi* and formulates a correction equation to compensate.

3.2.7 *Herbivory: Discrete or long-term sampling?*

Discrete sampling is invasive, requiring the removal of plant material for later examination in the lab, but has the advantage that a larger number of leaves can be examined than would be possible in the field. Wotherspoon (1996) found this to be the most common method of sampling among the studies he reviewed. Branches may be clipped (e.g. Fox & Morrow 1983; Costa & Crossley 1991; Landsberg and Gillieson, 1995), shot out of trees (Ohmart *et al.*, 1983a), or individual leaves removed (Robertson & Duke, 1987). Discrete sampling gives a static picture of the extent of defoliation on a given branchlet at one moment. As rates of defoliation vary during the season and with leaves of different ages, a single sample can give an inaccurate estimate of overall defoliation. To mitigate this, some researchers took the sample at the end of the growing season (Fox, 1983), while others divided the leaves into age classes (Journet, 1981; Lowman, 1982a, 1985a).

For long-term monitoring, a branch and/or individual leaves are labelled, left in situ and measured at intervals during the sampling period. For example, Coley (1980) measured and marked leaves at two-weekly intervals over three months; Stone and Bacon (1995) marked leaves on labelled shoots and marked and recorded any new leaves each month between September 1991 and March 1992. Long-term recording provides a measure of change in patterns of defoliation, however it is not necessarily more accurate than repeated discrete sampling.

Lowman has used a combination of discrete and long-term sampling (Lowman, 1982a, 1985a, 1985b, 1992; Lowman & Heatwole, 1992). She compared the two methods and found 2-3 fold difference in measured leaf area loss: the discrete samples underestimated defoliation (Lowman, 1985a, 1985b). However, Lowman points out that long-term sampling is more time consuming, and she states that

“Discrete sampling is useful, however, to measure relative differences between leaf samples, and it may even approach the accuracy of long term samples when discrete collections are made repetitively and extensively” (Lowman, 1985b: 17).

Landsberg (1989) also compared the two methods: she sampled at regular intervals over one year and took discrete samples coinciding with the first and last of the long-term samples. Landsberg found that the results were closest for the earlier discrete sample, taken before new growth and leaf abscission created patchiness in the distributions of the long-term samples. Landsberg emphasises that long-term sampling is time consuming and that any measurement of herbivory is labour intensive. She suggests that

“Inevitably a compromise is reached between gaining detailed knowledge about a limited sample and increasing sample size at the expense of detail” (Landsberg, 1989: 432).

Thus, long-term sampling and repeated discrete sampling both have their merits. However, the fate of missing leaves is one question that would appear to be more readily addressed by long-term sampling. Missing leaves may have been eaten entirely, or dehiscence through senescence or in response to physical disturbance. The plight of missing leaves, as with rate of hole growth, may distort estimates of defoliation (Lowman, 1985a). Long-term monitoring allows direct observation of a younger leaf’s gradual demise by herbivory in contrast to the abrupt disappearance of older leaves by senescence (Lowman, 1982a). Lowman and Heatwole (1992) document that of 5623 marked eucalypt leaves followed over one year, nearly 80% senesced; only about 20% of leaves were fully eaten by herbivores, indicating that herbivory was not the major cause of missing leaves in their study. Not all reports are so straightforward, even with long-term monitoring the fate of missing leaves can be unclear. Landsberg (1989) states that in her long-term samples she was unable to distinguish between leaves lost to herbivory and those lost for other reasons.

3.2.8 *Herbivory: Non-chewing Damage*

Leaf chewing may be the most common form of foliage damage but not all damage is due to chewing insects (Landsberg, 1989). As Fox and Morrow (1983) and Lowman (1985b) point out, leaf area measurement underestimates total damage caused by folivorous arthropods. Sap-suckers, leaf miners and stem borers all

contribute to foliage depletion, while secondary viral and fungal infections exacerbate their effects. To take account of this, some authors categorize and document non-chewing damage in addition to damage due to leaf chewers (e.g. Lowman & Heatwole 1992; Nielsen & Ejlersen, 1977; Wotherspoon, 1996).

Leaf mines and galls have their own patterns of spatial and temporal variation. Basset (1991c) found that leaf mines in the Australian subtropical rainforest canopy species *Argyrodendron actinophyllum* were most common not in very young leaves, as targeted by the leaf chewers, but in leaves more than two months old, especially in the shady lower canopy; while galls occurred on larger leaves and in sunnier aspects. Mazia *et al.* (2004), studying variation in herbivory in *Nothofagus pumilio* forests across a rainfall gradient in northern Patagonia, observed that leaf chewers were most active in the wetter sites, but leaf miners caused more damage in the drier sites, while gall former activity showed little difference between sites.

Thus, a variety of methods have been adopted in the investigation of canopy arthropods and herbivory and, echoing the comments of Basset *et al.* (1997), none is perfect. In sampling and subsequent processing of specimens the choice of technique may depend upon the nature, scale and duration of the research, or the availability of expertise, equipment or funds.

This review of methods has an Australian bias, but data on *Nothofagus* is most often an incidental part of a more general study into Australian rainforest taxa rather than from research with the genus as its focus. The majority of these studies are based in mainland Australian rainforest with *N. moorei* as part of the data set (e.g. Iddles *et al.*, 2003; Kitching *et al.*, 1993; Lowman, 1982a, 1982b, 1985a, 1985b, 1992; Lowman & Box, 1983; Read *et al.*, 2003). The following section (3.3) considers research into Tasmanian *Nothofagus* and its canopy arthropods and herbivory.

3.3 CANOPY ARTHROPODS AND HERBIVORY: TASMANIAN *NOTHOFAGUS*

The arthropod fauna of Tasmanian *Nothofagus* has been little researched other than the pinhole borer *Platypus subgranosus*, considered a pest species because of its predilection for living trees which are then susceptible to infection by the pathogenic fungus (*Chalara australis*) causing Myrtle wilt (Elliott & deLittle, 1984). The canopy invertebrate fauna has received scant attention. In their survey of rainforest fauna, Richardson *et al.* (1997) suggest that rainforest (*Nothofagus* canopy dominant) has a less diverse invertebrate fauna than wet sclerophyll (*Eucalyptus* canopy dominant) forest. Indeed, based on these conclusions, *Nothofagus* herbivores were omitted from an extensive survey of Tasmanian rainforest invertebrates, the authors stating that “the herbivorous fauna was ... excluded from the main survey because it is believed to be impoverished (Richardson [*et al.*], 1991) on *Nothofagus* in Tasmania.” (Coy *et al.*, 1993: vii).

McQuillan (1993) drew together cumulative data for invertebrate herbivores recorded from all *Nothofagus* hosts (Appendix: 346-354, 388 entries). These data suggest that Tasmanian *Nothofagus* species are depauperate compared with their counterparts in New Zealand and South America, and that much of the evidence for Tasmania is anecdotal (table 3.4).

Although works by Reid (1991, 1992, 1994, 2002) and Hardy *et al.* (2008) have augmented the list (table 3.5), the opportunity for further research is evident.

Given the background of the palaeohistory and biogeography of the tree genus *Nothofagus*, and the relationship between a plant host and its associated arthropod fauna, the next two chapters discuss the rationale behind the research questions this study seeks to answer, and the methods employed in their investigation.

Host	Order	Family	Species	Guild
<i>N. cunninghamii</i>	Acari	Eriophyidae	Genus and species undetermined ¹	Gall former
	Coleoptera	Buprestidae	<i>Nasciodes quadrinotata</i> (Van de Poll) ²	Callus feeder
		Chrysomelidae	<i>Microdonacia</i> spp ³	Leaf chewer
		Curculionidae	<i>Merimnetes fagi</i> Lea ¹	Leaf chewer
			<i>Platypus subgranosus</i> Schedl ⁴	Pinhole borer
	Hemiptera	Aphididae	<i>Sensoriaphis tasmaniae</i> Carver & Martyn ⁵	Sap sucker
		Pseudococcidae	<i>Paracoccus nothofagi</i> Williams ⁶	Sap sucker
		Margarodidae	Genus and species undetermined ¹	Sap sucker
		Eriococcidae	<i>Eriococcus</i> sp.A undescribed ¹	Sap sucker
			<i>Eriococcus</i> sp.B undescribed ¹	Sap sucker
			<i>Madarococcus</i> sp.B undescribed ¹	Sap sucker
	Lepidoptera	Gracillariidae	<i>Cyphosticha ostracodes</i> Turner ¹	Leaf miner
			<i>Cyphosticha zophonota</i> Turner ¹	Leaf miner
			<i>Stigmella</i> sp. Undescribed ¹	Leaf miner
		Geometridae	<i>Chlenias</i> sp. ¹	Leaf chewer
			<i>Ennominae</i> sp. Undetermined ¹	Leaf chewer
			<i>Euloxia leucochorda</i> Meyrick ¹	Leaf chewer
		Roeslerstammiidae	<i>Chalcoteuches phlogera</i> Turner ¹	Leaf chewer
		Tortricidae	<i>Epiphyas xyloides</i> (Meyrick) ¹	Leaf chewer
			' <i>Tortrix</i> ' <i>incompta</i> Turner ¹	Leaf chewer
		Hepialidae	<i>Aenetus ligniveren</i> (Lewin) ¹	Callus feeder
<i>N. gunnii</i>	Acari	Eriophyidae	Genus and species undetermined ¹	Gall former
	Coleoptera	Curculionidae	<i>Merimnetes</i> sp. ¹	Leaf chewer
	Lepidoptera	Tortricidae	<i>Epiphyas xyloides</i> (Meyrick) ¹	Leaf chewer

Table 3.4 Invertebrate herbivores recorded from Tasmanian *Nothofagus* hosts, adapted from McQuillan (1993: 346-354, Appendix). References: ¹McQuillan, 1993, personal observation; ²Elliott & de Little 1984; ³Reid, C. personal communication, in McQuillan, 1993; ⁴Elliott et al., 1983; ⁵Carver & Martyn, 1962; ⁶Williams, 1985.

Taxon	Reference	Host
Coleoptera - Chrysomelidae: leaf chewers		
<i>Ewanius nothofagi</i> Reid	Reid, 2002	<i>N. cunninghamii</i> , <i>N. gunnii</i>
<i>Microdonacia octodentata</i> Reid	Reid, 1992	<i>N. cunninghamii</i> *
<i>Microdonacia incurva</i> Reid	Reid, 1992	<i>N. cunninghamii</i> *
<i>Platycolaspis mcquillani</i> Reid	Reid, 1994	<i>N. cunninghamii</i> , <i>N. gunnii</i>
<i>Platycolaspis pubescens</i> Reid	Reid, 1994	<i>N. cunninghamii</i>
<i>Semelvillea tasmaniae</i> Reid	Reid, 1991	<i>N. cunninghamii</i>
Hemiptera – Coccoidea – Eriococcidae: sap suckers		
<i>Madarococcus cunninghamii</i> Hardy & Gullan	Hardy <i>et al.</i> 2008	<i>N. cunninghamii</i>
<i>Madarococcus meander</i> Hardy & Gullan	Hardy <i>et al.</i> 2008	<i>N. cunninghamii</i>
<i>Madarococcus occultus</i> Hardy & Gullan	Hardy <i>et al.</i> 2008	<i>N. cunninghamii</i>
<i>Madarococcus osculus</i> Hardy & Gullan [^]	Hardy <i>et al.</i> 2008	<i>N. cunninghamii</i> , <i>N. gunnii</i>

Table 3.5. Six leaf chewing beetle species (Coleoptera Chrysomelidae) described by Reid (1991, 1992, 1994, 2002) and four felt scales (Hemiptera Coccoidea Eriococcidae) described by Hardy and Gullan (Hardy *et al.* 2008), recorded on Tasmania *Nothofagus* hosts.

[^] possibly a geographical variant of *M. osculus* (found on *N. moorei*) or a new species (Hardy *et al.* 2008: 397). * denotes that the specimen was labelled '*Nothofagus*' only, but the site and/or altitude suggest that the host was *N. cunninghamii* rather than *N. gunnii*.

Chapter 4 SITES, SCHEDULE AND SAMPLING METHODS

The selection of research sites and methods of collecting arthropod and herbivory specimens from *N. cunninghamii* and *N. gunnii* in Tasmania presented potentially conflicting requirements. Sites were to be representative of *Nothofagus* throughout Tasmania yet possible to reach, often on several occasions within a given sampling season. Specimen collection should be comprehensive, but the field materials and methods needed to be easy to use in the field, amenable to comparison between samples and to be portable, often to sites some distance away from vehicular access. The selected sites enabled study of a range of host populations, but also allowed accessibility, particularly of those sites visited repeatedly. The methods of specimen collection were determined by their simplicity and ease of replication, minimal invasiveness and budget.

4.1 SITES AND SAMPLING SCHEDULE

A total of twenty-nine sites were visited, spread across four regions representative of the distribution of *Nothofagus* in Tasmania. In the South and West/Central regions both *Nothofagus* species occur, while in the North West and North East only *N. cunninghamii* is found (figure 4.1). Details of all the sites are tabulated in Appendix 1: Site Details, with images in Appendix 2, Plates 1-4: Site Images; and climate profiles for weather stations representative of each region are presented in Appendix 3: Climate Data. The more accessible sites received multiple visits, with sampling in the spring, summer and autumn to give a measure of seasonal variation, in addition to regional variation, in arthropod populations and levels of herbivory. At seven sites (table 4.1; figure 4.2, plates 1 & 2) a more detailed investigation was carried out, sampling for a finer degree of variation: from opposite aspects (north or south facing) of the same tree, or from adjacent trees of both *Nothofagus* species and also between-year comparisons. These seven sites account for three-quarters of all arthropods collected and identified; and two-thirds of all leaves sampled and examined.

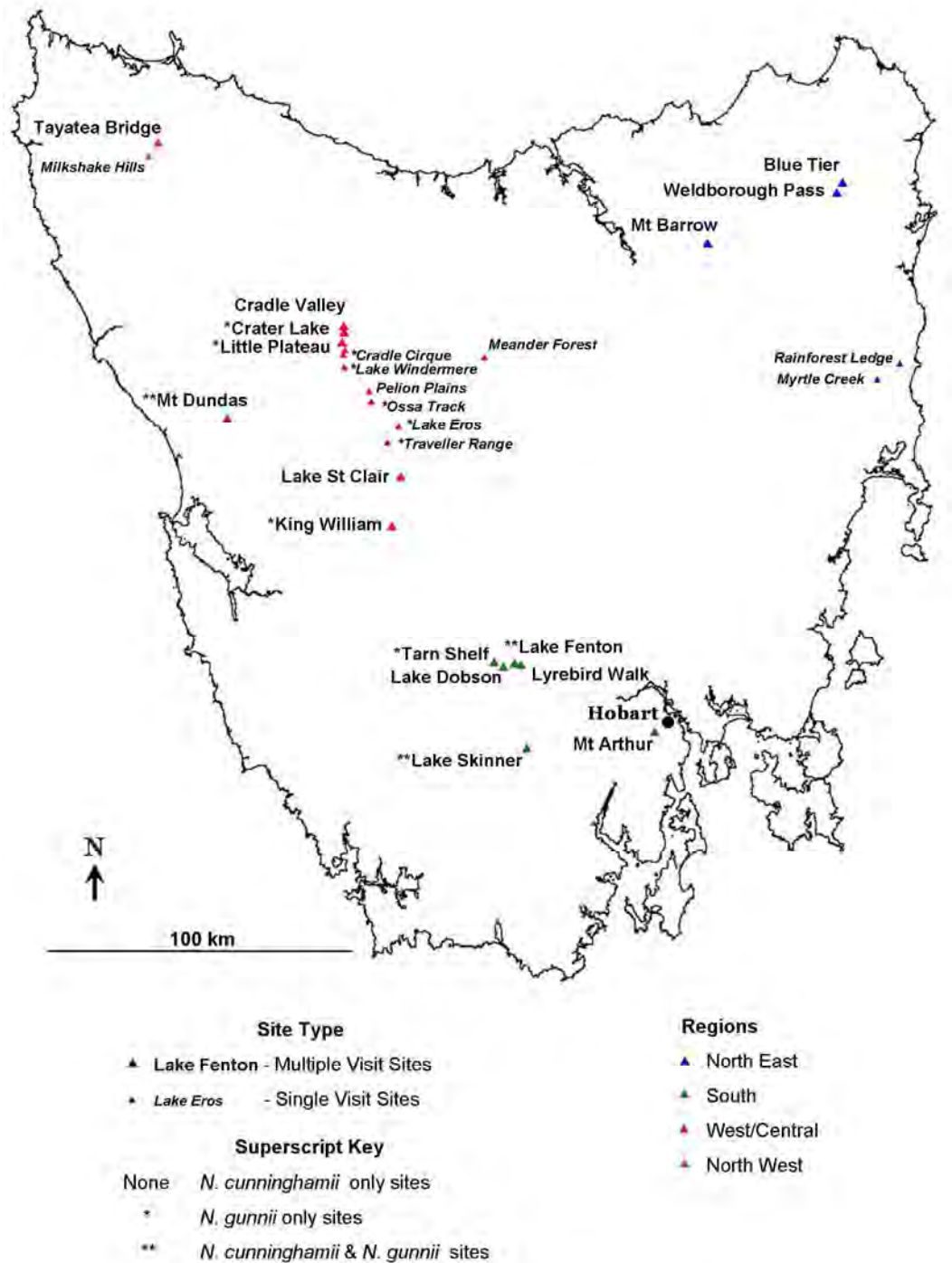
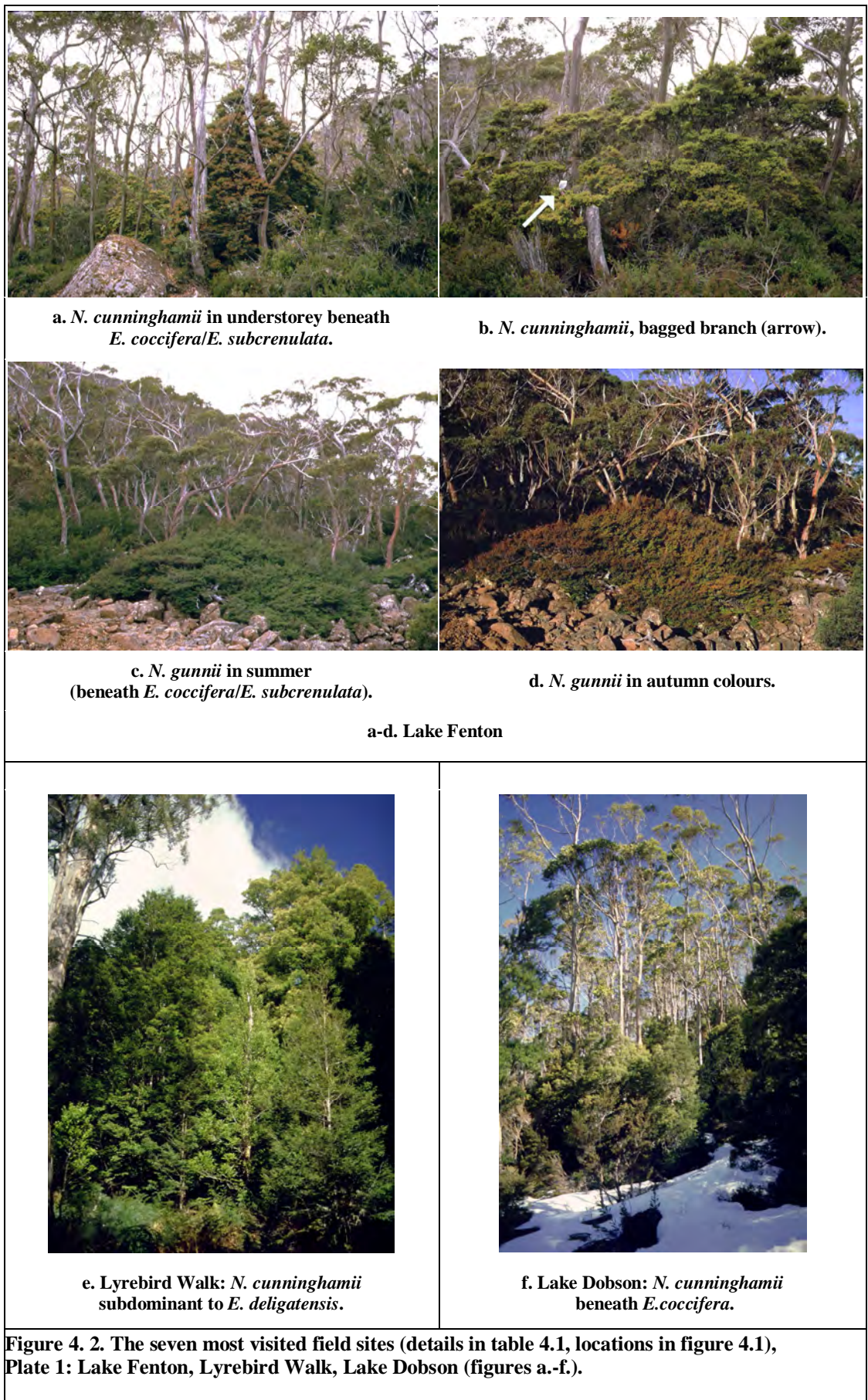


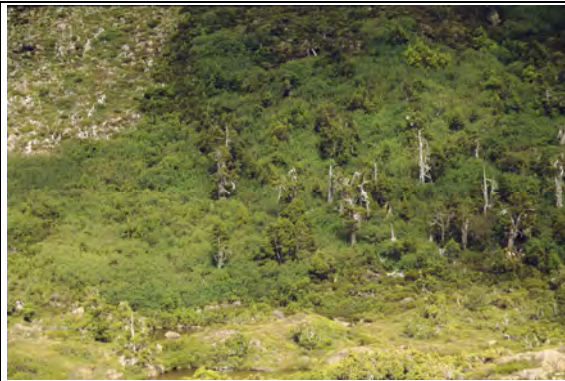
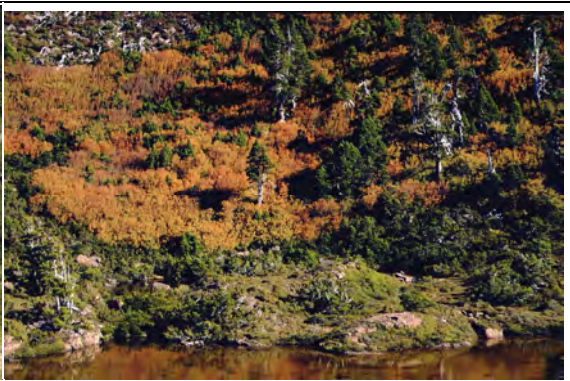

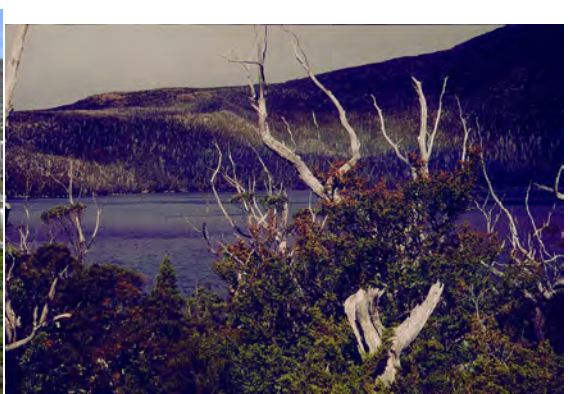
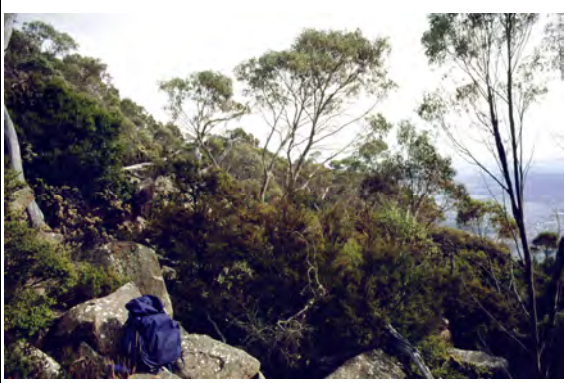

Figure 4.1. Location in Tasmania of field sites visited 1998-2002. Multiple visit sites are labelled in larger font, single visit sites in smaller font and italicised. The *Nothofagus* species at a site is indicated by presence or absence of the superscripts: none, *N. cunninghamii* only; * *N. gunnii* only; ** *N. gunnii* and *N. cunninghamii*. Regions are denoted by the colour of the site markers: blue, North East; green, South; red, West/Central; pink, North West.

Site	Mt Arthur	Lake Dobson	Lyrebird Walk	Lake Fenton	Lake Skinner	Tarn Shelf	King William
Site Code	ma	ld	lw	lf	ls	ts	kw
Location	Wellington Range	Mt Field N.P.	Mt Field N.P.	Mt Field N.P.	Snowy Range	Mt Field N.P.	Mt King William I
Region	South	South	South	South	South	South	West/Central
Universal Grid Ref. ^a	55GEN182520	55GDN662743	55GDN728746	55GDN692748	55GDN737456	55GDN639758	55GDP283226
Latitude ^b (°decimal N)	-42.88388	-42.68097	-42.67906	-42.67633	-42.93977	-42.66738	-42.24351
Longitude ^b (°decimal E)	147.22342	146.58900	146.67040	146.62558	146.67944	146.56095	146.13287
Altitude ^a (m)	1110	1080	690	1020	980	1165	1090
Substrate ^c	Jurassic Dolerite	Jurassic Dolerite	Jurassic Dolerite	Jurassic Dolerite	Jurassic Dolerite	Jurassic Dolerite	Jurassic dolerite and Pleistocene glacial deposits.
Ave. Ann. Ppt. ^d (mm)	1000	1200	1200	1200	1100	1200	1900
<i>Nothofagus</i> sp.	<i>N. cunninghamii</i>	<i>N. cunninghamii</i>	<i>N. cunninghamii</i>	both spp.	both spp.	<i>N. gunnii</i>	<i>N. gunnii</i>
TASVEG code ^e	DCO	DCO	WDR	WSU / RFK	RPF	RPF	RPF
Vegetation Community ^e	<i>Eucalyptus coccifera</i> forest and woodland	<i>Eucalyptus coccifera</i> forest and woodland	<i>Eucalyptus delegatensis</i> forest over rainforest	<i>E. subcrenulata</i> forest and woodland / <i>A. selaginoides</i> – <i>N. gunnii</i> short rainforest	<i>Athrotaxis cupressoides</i> – <i>N. gunnii</i> short rainforest	<i>Athrotaxis cupressoides</i> – <i>N. gunnii</i> short rainforest	<i>Athrotaxis cupressoides</i> – <i>N. gunnii</i> short rainforest
Canopy Dominant: and Associations ^e	<i>E. coccifera</i> : Subalpine community with <i>N. cunninghamii</i> and/or <i>N. gunnii</i>	<i>E. coccifera</i> : Subalpine community with <i>N. cunninghamii</i> and/or <i>N. gunnii</i>	<i>E. delegatensis</i> : Subdominants <i>N. cunninghamii</i> , <i>Atherosperma moschatum</i>	<i>E. subcrenulata</i> , <i>E. coccifera</i> : <i>N. cunninghamii</i> in understorey / <i>N. gunnii</i> , <i>A. selaginoides</i>	<i>A. cupressoides</i> in canopy: <i>N. gunnii</i> , and possibly <i>N. cunninghamii</i> , in dense understorey	<i>A. cupressoides</i> in canopy: <i>N. gunnii</i> , and possibly <i>N. cunninghamii</i> , in dense understorey	<i>A. cupressoides</i> in canopy: <i>N. gunnii</i> , and possibly <i>N. cunninghamii</i> , in dense understorey

Table 4.1. Details of the seven most visited field sites.

Sources: ^a Tasmaps, Geodata Services Branch; Department of Primary Industries, Water and Environment (DPIWE) © Tasmanian Government; ^b Google Earth data: Lat./Long.: downloaded 21/04/2010; ^c Land Systems of Tasmania: Regions 3, 4, 5, 6 (Davies, 1988; Pemberton, 1986; Pinkard, 1980; Richley, 1978); ^d data from Australian Government Bureau of Meteorology, Rainfall Contour Map based on a standard 30-year climatology, 1961-1990, © Commonwealth of Australia 2005; and Weather Station data for Mt. Wellington, Maydena P.O.; ^e Harris and Kitchener (2005) and TASVEG Version 1.0 Data collection: 1998-2003, Projection: Grid of Australia 1994 (MGA94); MGA zone 55 (GDA94), Original data scale: 1:25,000 across the whole State; © Tasmanian Vegetation Mapping Program, DPIWE. N.B. The site name is a label only, denoting the grid referenced location where sampling was carried out, it does not refer to the whole geographical area of that name.



	
<p>g. Tarn Shelf in summer: <i>N. gunnii</i> and the co-dominant <i>Athrotaxis cupressoides</i> (Pencil Pine) are difficult to distinguish.</p>	<p>h. Tarn Shelf in April: <i>A. cupressoides</i> stands out against the autumnal <i>N. gunnii</i>.</p>
	
<p>i. Lake Skinner: <i>N. cunninghamii</i> and <i>N. gunnii</i> in summer.</p>	<p>j. Lake Skinner: Autumn.</p>
	
<p>k. Mt. Arthur: <i>N. cunninghamii</i> with <i>E. coccifera</i>.</p>	<p>l. King William: <i>N. gunnii</i> in late summer.</p>
<p>Figure 4. 2 contd. The seven most visited field sites (details in table 4.1, locations in figure 4.1), Plate 2: Tarn Shelf, Lake Skinner, King William, Mt. Arthur (figures g.-l.).</p>	

In all, the sampling schedule comprised a total of ninety five site visits between March 1998 and March 2002, during which arthropod and/or leaf specimens were collected (Appendix 4: Fieldtrip Schedule). On twenty-six occasions both *Nothofagus* species were sampled at a single site visit, thus bringing the number of sample sets collected to a total of one hundred and twenty-one.

In data recording, site visits ('fieldtrips'), were denoted by a code comprising the lower case initials of the site name in conjunction with a fieldtrip number and the initials of the *Nothofagus* species sampled. Where both *Nothofagus* species occurred at the same site, each sample set was treated as a separate fieldtrip e.g. the fifth visit to Lake Fenton, sampling both *N. cunninghamii* and *N. gunnii*, becomes fieldtrips lf5Nc. and lf5Ng. With expert help, a database was set up in Microsoft Access to track and record sampling details; and the results of field and lab examination of specimens were entered into the same database.

4.2 ARTHROPOD METHODS

At each visit arthropods were collected by branch beating, from *Nothofagus cunninghamii* and/or *Nothofagus gunnii* as appropriate to the site. The sampling was restricted to areas of the canopy within reach from the ground or local means of elevation. Branches were beaten sharply with a stick, over a 38 x 29cm plastic tray, in multiples of ten haphazardly placed beats per host species. After each set of ten beats, all fallen arthropods were collected from the tray with forceps, or a paintbrush dipped in 80% ethanol, and then transferred to a collecting pot containing 80% ethanol. This method has specific limitations: mining or burrowing arthropods may not be dislodged; the more numerous the arthropods on the tray, the increased possibility of overlooking the more discrete individuals, so requiring higher vigilance on these occasions; and occasionally mobile individuals would escape from the tray, but the majority were stunned enough for collection.

In the lab, priority was given to arthropod orders containing herbivorous taxa or scavenging taxa known to forage on trees: Coleoptera, Lepidoptera, Hemiptera, Thysanoptera in the former category; Acarina, Collembola, Plecoptera, Psocoptera in the latter category. All were sorted to family, then genus and species where possible,

otherwise to morphospecies; except for Collembola, which were sorted to suborder. In addition, total counts were taken for Araneae, being natural predators of the other taxa; and more detailed identification was undertaken for twenty-one sample sets.

With few relevant identification keys or other descriptions of the individual families or species, a reference voucher collection was assembled with a type specimen, and photoplates of each morphotaxon labelled and archived to museum standard (Appendix 5: Archiving). Given the poor state of taxonomy of these groups, once recognised, morphotaxa were allotted a four letter code denoting order and family (suborder for the Acarina), plus a morphospecies number. Where expertise in further identification was not available locally, samples were sent to specialists interstate or overseas as necessary.

Specimen identifications and counts were entered into the fieldtrip database. The sampling schedule enabled the arthropod fauna data to be divided into six sets (table 4.1) for further interrogation. However, since the preliminary fieldtrips (Appendix 4: Fieldtrip Schedule) did not follow the protocol used throughout the rest of the study, this data has been used only in Sampling Set 1 and has been omitted from the quantitative analyses of Sampling Sets 2-6.

Details of the statistical methods employed in the subsequent data analyses are described in sub-chapter 4.5 and with the arthropod fauna results in Chapter 5.

Comparative community structure among arthropods on host tree species was investigated at the level of feeding guilds (e.g. Southwood 1996). Individuals were assigned to one of six feeding guilds according to that most likely for their order, suborder or family, and life stage based upon the literature (appendix). Herbivores accounted for four feeding guilds: nectivores; and three folivore guilds – leaf chewers, leaf miners and sap-suckers. Predators and fungivore/detritivores comprised the remaining guilds.

Set	Data	Sampling Windows	Sites
1. Arthropod Overview	<ul style="list-style-type: none"> · All sites all visits · Totals and presence/absence 	03 Mar 1998 - 24 Mar 2002	Nc 17 Ng 12
2. All sites host and regional variation	<ul style="list-style-type: none"> · All sites (less preliminary visits for Arthropods) · Quantitative 	27 Mar 1998 - 24 Mar 2002	Nc 17 Ng 12
3. Regional, between site, and seasonal variation	<ul style="list-style-type: none"> · 4 regions: South, West/Central, North West, North East · 3 visits to each site: early, mid, late · Quantitative 	early: 02 Nov 1999 - 22 Dec 1999 mid: 18 Jan 2000 - 15 Feb 2000 late: 25 Mar 2000 - 23 May 2000	Nc 12 Ng 7
4. Between site, between host variation	<ul style="list-style-type: none"> · ~6 weekly visits to each site (herbivory data cumulative) · Quantitative 	16 Oct 1999 - 11 Apr 2000	Nc 5 Ng 3
5. Aspect	<ul style="list-style-type: none"> · North & south facing, adjacent* · Quantitative 	27 Mar 1998 - 17 Apr 1999	Nc 2 Ng 3
6. Between year	<ul style="list-style-type: none"> · Sampling in consecutive years (herbivory data cumulative) · Quantitative 	27 Mar 1998 - 18 Mar 1999 16 Oct 1999 - 25 Sep 2000	Nc 3 Ng 3

Table 4.1. Sampling Sets: data type, sampling windows and number of sites visited for *N. cunninghamii* (Nc) and *N. gunnii* (Ng) 1998 – 2002. *Adjacent refers to neighbouring, and overlapping, trees of either *Nothofagus* species with the other species. For site locations, refer to map in Figure 4.1.

4.3 HERBIVORY METHODS

4.3.1 Leaf-Chewing Herbivory

Herbivory assessment entailed identifying a sample of leaves from which the amount of leaf chewed could be measured, or other herbivore damage noted. As with the branch beating, herbivory samples were collected from areas of the canopy within safe reach of the author i.e. from lower and middle canopy except for the smallest and more prostrate trees. Each sample comprised three haphazardly selected ‘branches’ – in reality a section of branch holding from tens to hundreds of leaves depending on the species of *Nothofagus* and the objective of the sampling.

The majority of the leaf collection involved encasing the selected branch in a plastic bag, to catch any leaves which might fall off during the procedure, then cutting and removing it and sealing the bag. In the lab, for each branch, the numbers of intact leaves, and those damaged by chewing were counted. Leaf age in the *N. cunninghamii* leaves was estimated by comparing the colour of the leaves and stem, the texture of the leaves and their position between nodes on the branch. Leaves were assessed as either ‘young’ (the soft pale green leaves emerging with leaf flush, figure 4.3, above centre) or ‘old’ (the tough dark green leaves of previous years’ growth, figure 4.3, below right) and they were numerically coded by year of spring emergence (Leaf Year 1, leaf flush spring 1995, having been judged as the oldest leaves in the preliminary samples of autumn 1998).

Numbers of young and old intact and chewed leaves were counted at the initial and subsequent site visits in 1998-1999, but in 1999-2000 the old leaves were noted only at the initial and final site visits. The numbers of missing leaves were more difficult to estimate. For the evergreen *N. cunninghamii*, leaf scars gave an indication of missing leaves, although not the cause of loss and for the deciduous *N. gunnii* the leaf scars were more likely to be from previous years’ foliage. Therefore “missing leaves” were not recorded.



Figure 4.3. *Nothofagus cunninghamii* leaves in April. The youngest leaves (above centre) are still considerably paler than the older leaves (below right), even in early autumn.

As with the arthropods, the majority of the herbivory sampling took place between autumn 1998 and autumn 2000, with seven additional single visit sites during 2001 and 2002. This allowed comparison between the two *Nothofagus* species; and regional, seasonal, between-year and sampling aspect comparisons within each *Nothofagus* species. Additionally at several sites, in an attempt to monitor the cumulative pattern of leaf chewing and to account for missing leaves, selected branches were tagged with pink flagging tape so that they could be easily found for reassessment at subsequent visits.

Cumulative Sampling

N. cunninghamii, was sampled cumulatively at five sites in 1999-2000 and sites in 1998-1999. At each site, three pairs of neighbouring branches were tagged, one of each pair being sealed in a light- permeable bag made from bridal veil (figure 4.4).



Figure 4.4. *Nothofagus cunninghamii* at Lake Fenton showing branches ‘bagged’ with bridal veil and labelled with pink flagging tape (above); and ‘tagged’ with pink flagging tape (below). The young leaves are markedly paler than the underlying old leaves.

The bags served several functions: to assess the amount of damage to new shoots prior to and during leaf flush and hopefully to trap herbivores which attack from within the leaf bud; to be a comparison with the branches to which herbivores had free access after leaf flush; and to catch leaves lost to senescence. At the first visit, prior to bagging, the numbers of intact, chewed or missing older leaves distal to the flagging tape were counted on both branches of each pair. The leaves were too small and too numerous to accurately mark or map and so on the follow-up visits the total numbers of chewed leaves and the areas lost were documented. In 2000, on the final visit an extra three ‘control’ branchlets, which had been neither tagged nor bagged, were collected at each site and all the branchlets were enclosed in plastic bags and removed for examination in the lab.

The cumulative sampling on *N. gunnii* occurred at three sites in both 1999-2000 (Lake Fenton, Lake Skinner and Tarn Shelf) and 1998-1999 (Lake Fenton, Lake Skinner and King William). Again, the branchlets were tagged with pink flagging tape and the leaves distal to the tape were assessed for chewing damage at the first and subsequent visits. As there were fewer and larger leaves than on *N. cunninghamii*, individual leaves could be numbered: in 1998-1999 the chewed leaves were labelled directly with a waterproof marker pen, but this often led to further damage or detachment of the leaf, so in 1999-2000 each branchlet was mapped at the first site visit (figure 4.5.). No branchlets were bagged; and as *N. gunnii* is deciduous, there was no need to take account of leaf age. At the final visit to each site, the branchlets were enclosed in plastic bags and removed for examination in the lab.

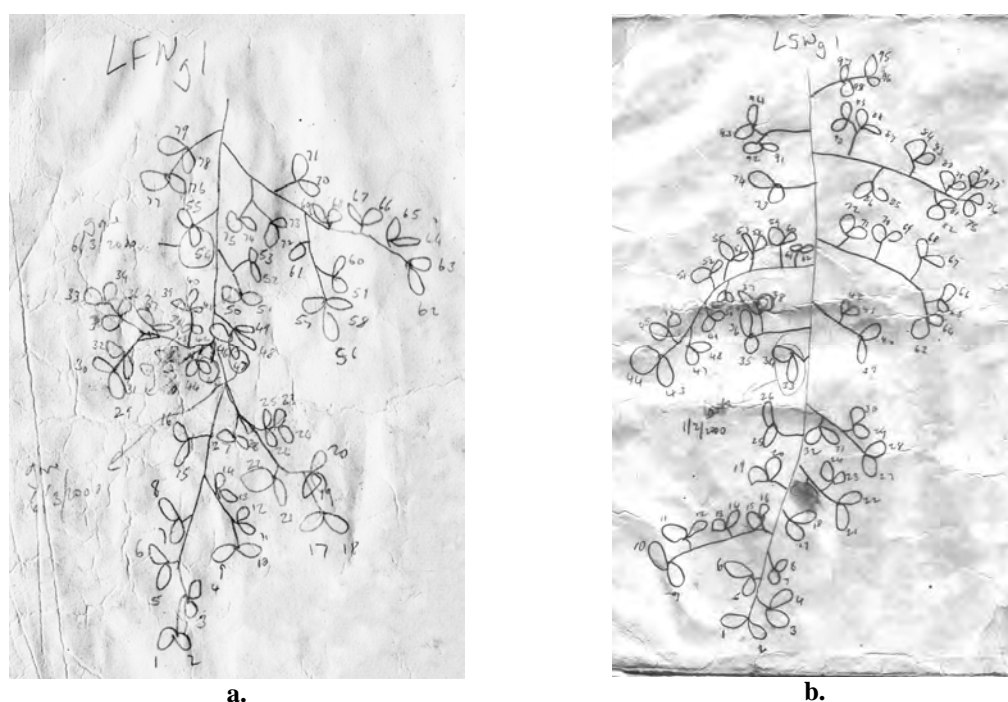


Figure 4.5. Examples of *Nothofagus gunnii* leaf maps: Lake Fenton branchlet lfNg1 (a) and Lake Skinner branchlet lsNg1 (b), both numbered proximally from the most distal leaf to the pink flagging tape. Annotations indicate: (a) leaves lost between site visits ('gone' at the visit of 6/3/2000 to L. Fenton); and (b) lost during mapping ('lost' at the visit of 1/2/2000 to L. Skinner).

In 1999-2000, at the final visit to Lake Skinner, the intact leaf count from one branchlet was not recorded, and so for the cumulative data analysis, the combined leaf total from the Lake Skinner was taken from the two branches with complete records. The 3-branch data were included for October 1999, December 1999 and January/February 2000 in the overall intact or chewed leaf counts and proportions graphs; and in the Lake Skinner 1999-2000 graphs for comparison with the 2-branch

data for the appropriate months. In 1998-1999, there were only two visits to King William, so these data were omitted from the cumulative combined leaf totals.

Data Sets and Analysis

The herbivory data was summarised into the Sampling Sets below (table 4.2).

Set	Data	Sampling Windows	Sites
1. All sites, between host and regional variation	· All sites	27 Mar 1998 - 24 Mar 2002	Nc 17 Ng 12
2. Regional, and seasonal variation	· 4 regions: North East, North West, South, West/Central · 3 visits to each site: spring, summer, autumn	early: 02 Nov 1999 - 22 Dec 1999 mid: 18 Jan 2000 - 15 Feb 2000 late: 25 Mar 2000 - 23 May 2000	Nc 12 Ng 7
3. Aspect	· North-facing, South facing, · Adjacent*	27 Mar 1998 - 17 Apr 1999	Nc 2 Ng 3
4. Cumulative Sampling and Yearly variation	· ~6 weekly visits to each site, tagged and bagged branches	16 Oct 1999 - 11 Apr 2000	Nc 5 Ng 3
	· Tagged branches	24 Nov 1998 – 17 Apr 1999	Nc 3 Ng 3
5. 3 year Autumn Comparison	· Sampling in consecutive years	Autumn 2000, 1999, 1998	Nc 3 Ng 3

Table 4.2. Herbivory Sampling Sets: data type, sampling windows and number of sites visited for *Nothofagus cunninghamii* (Nc) and *N. gunnii* (Ng) 1998 – 2002. . *Adjacent refers to neighbouring, and overlapping, trees of either *Nothofagus* species with the other species. For site locations, refer to map in Figure 4.1.

The leaf-chewing herbivory was documented for each sampling set, as for the arthropods in Chapter 5. Firstly, the counts and ratios of intact leaves and those with evidence of chewing damage were described and represented as bar graphs. Then, an estimate was made of the area of leaf tissue lost from the chewed leaves.

Leaf Area Assessment

As a leaf area meter was unavailable, two alternative methods of measuring leaf area were tried and compared using leaves from the preliminary samples: scanning software versus manual estimates using millimetre-square graph paper (Appendix 6: Manual versus Digitally Scanned Measurement of Leaf Area and Proportion of Leaf Damage). The two methods were comparable, however the manual approach was quicker, cheaper, freely available, portable and easier to perform, and so was adopted for the duration of the study. This method entails matching a chewed leaf with an intact one of similar size. The outline of the intact leaf is traced onto millimetre square graph paper, the chewed leaf is then placed upon the outline and the number of squares left exposed is counted, rounding up or down for incomplete squares as appropriate (figure 4.6). The leaves almost entirely consumed presented a potential difficulty, but this was overcome by measuring the area of an immediately neighbouring leaf, the author having observed that intact, or partially chewed leaves, of similar age and in close proximity, have similar areas.

Estimation of Percentage Leaf Area Loss (%LAL)

Following the examples of Landsberg (1989), Williams and Abbott (1991) and Lowman and Heatwole (1992), the leaf area lost to chewing damage was calculated from the ratio of the total of the areas removed from a set of chewed leaves (Leaf Area Loss: LAL): to the total of the potentially available areas of those leaves had they remained intact (Total Potential Area: TPA). Expressed as a percentage, this ratio becomes the Percentage Leaf Area Loss: %LAL.

i.e.
$$\%LAL = (LAL / TPA) \times 100$$

The results were then depicted as % bar graphs, Percentage Leaf Area Loss against the percentage of leaf area remaining intact.

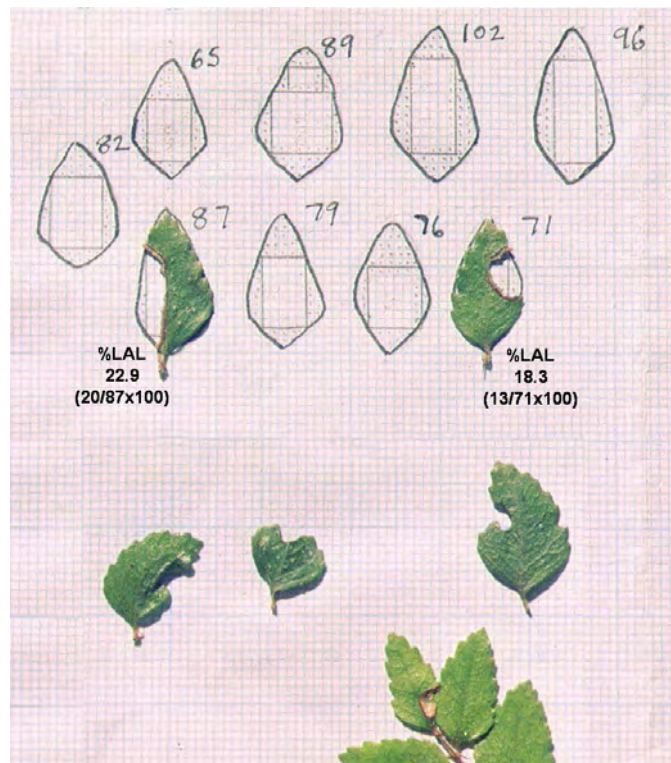


Figure 4.6. Estimation of Percentage Leaf Area Loss (%LAL) using leaf outlines on mm² graph paper.

Leaf outlines were traced around intact leaves, their area being estimated to the nearest 0.5 mm² and thus forming silhouettes of Total Potential Area (TPA) of intact leaves for comparison with those chewed. The chewed leaves were then placed over the tracings and the area chewed away/‘lost’ was similarly estimated, to give the Leaf Area Lost (LAL). The %LAL was calculated by the formula $\%LAL = (LAL / TPA) \times 100$, as superimposed on the image above.

4.3.2 Leaf Areas, Hole Growth and Non Leaf-Chewing Features

Leaf Areas

Between 1998 and 2002, haphazard samples of multiples of 100 intact leaves were collected from thirteen sites for *N. cunninghamii* and from ten sites for *N. gunnii* and their areas were recorded in order to explore the range of leaf areas which occurred at these sites, and the variation in leaf area with region and aspect. In addition for *N. cunninghamii*, the areas of young and old leaves were compared; at one site (Meander Forest) the effect of chewing damage on the potential area of the leaves was examined; while at Lake Skinner the sampling years (1998 and 2000) were compared; and at Mt. Dundas, samples were collected at low (260m), mid (615m) and high (900m) altitude. For *N. gunnii* at King William, an additional litter sample was collected for comparison with leaves removed directly from branches.

The leaf area data were analysed using JMP 8 (SAS Institute, 2008) statistical software. One Way Analysis of Variance (ANOVA) was applied to the data sets, with t-Test and Tukey-Kramer HSD means comparisons being used where appropriate.

Hole Growth

Following the example of Lowman (1982a), in order to compare the rate of growth of a hole with that of its leaf, single holes of uniform size were punched in up to six labelled leaves of *N. cunninghamii* (at 5 sites in 1999-2000; 2 sites in 1998-1999) and *N. gunnii* (at 3 sites in both sampling years). At the first visit, the leaves were tagged and labelled with pink flagging tape, a 1mm diameter hole was punched in the leaf lamina avoiding the mid-rib and the leaf length (and leaf area in 1999-2000) were measured. Changes in hole diameter, leaf length (and area) were noted at succeeding visits, fine measuring callipers being used to determine leaf length and hole diameter. In addition in 1999-2000, the length and area of unpunched control leaves were followed at Lyrebird Walk (*N. cunninghamii*) and Lake Fenton (*N. gunnii*). The results were plotted as stacked graphs with mean site values of the measurements, or hole/leaf ratios, against sampling month.

Non Leaf-Chewing Features (NCF)

In addition to the record of chewing-damaged leaves, non-chewing features (NCF) were also documented. These included leaves on both *N. cunninghamii* and *N. gunnii* with erineum (evidence of eriophiid mites), whereas the other non-chewing features occurred only on *N. cunninghamii* leaves: single arthropod eggs, leaf galls, leaf mines, leaf ties (excluding the leaf capsules of Roeslerstammiidae, which were dealt with in the arthropod data), scales (both lerps and solitary females), and sooty mould. Incidence of the non-chewing features was recorded as the number of leaves per sample on which the feature occurred. The data were analysed following a modified version of the Sampling Sets in table 4.2 and the incidence of the non-chewing features was expressed as a percentage of all leaves for those Sampling Sets. For *N. cunninghamii*, the relative proportions of the NCF types on the affective leaves was also calculated.

The percentages of leaves with erineum were plotted as bar graphs for each *Nothofagus* species, examining variation with region, season, sampling aspect (*N. gunnii* only) and sampling year. In 1999 on *N. cunninghamii*, non-chewing features including erineum were not documented, so that the sampling year comparison for *N. cunninghamii* is for two years (autumn 2000 and autumn 1998), while that for erineum on *N. gunnii* is for three years (autumn 2000, autumn 1999 and autumn 1998). In spring 2000, an additional 100 leaves were collected from the leaf litter at each of three sites (Lake Fenton, Lake Skinner, Tarn Shelf) and were examined for erineum. At the sites where both *Nothofagus* species occurred (Lake Fenton, Lake Skinner and Mt Dundas), the levels of erineum on the two species were compared.

The percentages of *N. cunninghamii* leaves with non-chewing features (NCF) and the relative proportions of the NCF types on these leaves were represented by bar graphs and pie charts respectively. The variation by leaf age, region, season, sampling aspect, and the 2-year comparison were documented for the *N. cunninghamii* non-chewing leaf features.

4.4 LIMITATIONS IN SAMPLING AND PROCESSING SPECIMENS

As noted above, the data used in this research results from specimens collected and examined from *N. cunninghamii* and/or *N. gunnii* at 29 sites, between March 1998 and March 2002, with a total of 121 fieldtrip records. This was within the constraints of accessibility to the field sites, ease of replication of the sampling and processing of specimens and least invasive methods. The limitations in this data collection and the specimen processing are outlined as follows:

Site Accessibility

Due to logistical constraints, the remote south-west of Tasmania was omitted from the survey; the north-west only briefly visited, and several sites visited only once.

Weather

Exact timing of site visits was dependant upon a promising weather forecast as rain would render sampling difficult and immobilise flying insects. On only three occasions was sampling affected by bad weather: at Lake Skinner (1s7, 5/12/1999) the weather deteriorated during sampling and the arthropod branch beating was

carried out first in drizzle and finally in heavy rain. Similarly at Weldborough Pass (wp3, 23/05/2000) deteriorating weather resulted in wet foliage for the final set of beats. One visit to Little Plateau was abandoned completely (5/02/2000), high winds and driving rain preventing safe access. A close but more sheltered site, Crater Lake, was sampled the following day and both sites were subsequently revisited.

Arthropod Specimen Collection

Only the lower canopy (within reach of operator) was sampled. Operator errors included probably missing some of the smallest specimens (<0.5mm) or occasionally, losing the more mobile individuals which quickly escaped from the tray. However, these errors are likely to be relatively constant across sites, seasons and trees.

Arthropod Processing

The original intention was to assess all specimens, but this aim was precluded by the volume of specimens collected. As a result, priority was given to herbivorous taxa and where relevant, to other non-herbivorous taxa in the same order. Within these major orders, taxa were identified to 'morphospecies' as a surrogate for species diversity (Oliver & Beattie, 1996), although the concept is not without some controversy (e.g. Goldstein, 1997). In addition, more taxonomically obscure groups such as Collembola were identified to suborder, and a subsample of Araneae were identified to family.

Herbivory

Affordable, effective and portable electronic means of assessing leaf area loss was not available at start of study so to maintain consistency, all leaf samples were assessed manually, and by the same person (the author) to minimise discrepancies in operator error. On-site leaf assessment was more prone to error due to sampling conditions, particularly when marked branchlets were lost or broken between & during fieldtrips. The difficulty of determining the number of leaves lost, and individual leaf area consumed, is discussed in Chapter 6.

4.5 STATISTICAL ISSUES

The study was designed to distribute sampling locations and times such that the geographical spread of the host trees was adequately represented and the seasonality of the fauna was accounted for.

Community patterns were explored with multivariate methods, notably non-metric ordination (nMDS) in PC-ORD4 software (McCune & Mefford, 1999). This method generates a simplified graphical representation of complex multidimensional community-type data in fewer dimensions. The Bray-Curtis (=Sorensen) measure was used to construct the dissimilarity matrix and solutions were sought in either 2 or 3 dimensions, subject to the stress level (a measure of badness of fit) remaining below 20% and preferably below 15%. For some analyses, count data were transformed as $\log(x+1)$ in order to downweight the influence of a few extremely abundant species. Taxa most influential in determining community patterns were displayed as vectors fitted in the same ordination space; in most cases a cutoff r^2 value of 0.2 was used; if too many taxa were selected by this criterion, the r^2 value was set higher until a more manageable number of taxa were fitted.

Contrasts between host species, regions and seasons were investigated using the Multiple Response Permutation Procedure (MRPP) in PC-ORD4 software (McCune & Mefford, 1999) using the default settings. This provides a test of whether there is a significant difference between two or more groups of sampling units. This difference may be one of location (differences in mean) or one of spread (differences in within-group distance). The method is philosophically and mathematically allied with analysis of variance, in that it compares dissimilarities within and among groups. If two groups of sampling units are really different (e.g. in their species composition), then average of the within-group compositional dissimilarities ought to be less than the average of the dissimilarities between two random collections of sampling units drawn from the entire population. The MRPP statistic δ is the overall weighted mean of within-group means of the pairwise dissimilarities among sampling units.

The MRPP algorithm first calculates all pairwise Euclidean distances in the entire dataset, then calculates δ . It then permutes the sampling units and their associated

pairwise distances, and recalculates δ based on the permuted data. It repeats the permutation step 1000 times. The significance test is the fraction of permuted deltas that are less than the observed delta, with a small sample correction. The function also calculates the change-corrected within-group agreement $A = 1 - \delta/E(\delta)$, where $E(\delta)$ is the expected δ assessed as the average of dissimilarities.

When separate groupings were discovered, indicator taxa were sought using the IndVal method of Dufrene & Legendre (1997) as supported in PC-ORD4. This method is used to identify the indicator value of a specific taxon. Relative abundance is compared to frequency in order to find a percentile that gives the best idea of this taxon as an indicator

Comparisons of herbivory, measured as Leaf Area Loss, were conducted using Analysis of Variance in JMP statistical software.

Chapter 5 RESULTS I: ARTHROPOD FAUNA

This chapter documents the results of examination of the main orders of arthropod fauna sampled from *N. cunninghamii* (17 sites) and *N. gunnii* (12 sites) between March 1998 and March 2002. The first section of this chapter provides a general overview of the data from all fieldtrips (Sampling Set 1, table 4.1), the morphotaxa identified and overall taxa occurrence, richness and abundance. Sub-chapters 5.2 and 5.3 document more detailed analyses of the main orders, and feeding guilds, respectively and use the quantitative data of Sampling Sets 2-5 (table 4.1). The arthropod fauna results are then summed-up in sub-chapter 5.4.

5.1 OVERVIEW

In total 15,155 specimens were identified at order level (table 5.1), Acarina being the most abundant with more than half of the total, and the three non-insect orders, Acarina, Araneae and Collembola, together accounting for more than 80% of specimens. Of the insect orders, Psocoptera were the most abundant but occurred almost exclusively on *N. cunninghamii*. Coleoptera were the next most abundant followed by the herbivore orders Hemiptera, Lepidoptera and Thysanoptera, each of which also had greater abundance on *N. cunninghamii* than on *N. gunnii*. Only Plecoptera, the least abundant order overall, occurred more on *N. gunnii* than on *N. cunninghamii*.

Order	<i>N. cunninghamii</i>		<i>N. gunnii</i>		Total	
	Count	%	Count	%	Count	%
Coleoptera	745	6.9	128	3.0	873	5.8
Lepidoptera	235	2.2	14	0.3	249	1.6
Hemiptera	257	2.4	32	0.7	289	1.9
Thysanoptera	165	1.5	31	0.7	196	1.3
Psocoptera	1083	10.0	14	0.3	1097	7.2
Plecoptera	15	0.1	32	0.7	47	0.3
Collembola	833	7.7	802	18.7	1635	10.8
Acarina	5857	54.0	3023	70.6	8880	58.7
Araneae	1680	15.5	209	4.9	1889	12.5
Overall Total	10870	100	4285	100	15155	100

Table 5.1. *Nothofagus* arthropod fauna, taxa abundance. All fieldtrips, all taxa (adults, larvae and miscellaneous immatures): total specimen counts and percentages by order and host plant.

Nearly two thirds of the specimens were assigned to one of 310 morphotaxa within the seven main orders (8861 adults to 258 morphotaxa; 720 larvae or other immatures to 52 morphotaxa) as tabulated in Appendix 7: Morphotaxon List). Collembola and Araneae (combined total: 3524) were not identified to morphotaxon, while the remaining 2050 specimens were unidentifiable beyond the level of order.

Nearly a quarter of morphotaxa (83) occurred on both *N. cunninghamii* and *N. gunnii*, Coleoptera having the greatest taxon richness (table 5.2). Even given the differences in numbers of sites (*N. cunninghamii* 17; *N. gunnii* 12), considerably more morphotaxa were found only on *N. cunninghamii* than only on *N. gunnii*.

Morphotaxa	Order	<i>N. cunninghamii</i> and <i>N. gunnii</i>	<i>N. cunninghamii</i> only	<i>N. gunnii</i> only	Total Morphotaxa per Order
Adult	Coleoptera	21	69	11	101
	Lepidoptera	1	32	4	37
	Hemiptera	7	14	5	26
	Thysanoptera	5	7	2	14
	Psocoptera	2	6	0	8
	Plecoptera	2	4	7	13
	Acarina	35	21	3	59
Adult Morphotaxa Total		73	153	32	258
Larva/ other immatures	Coleoptera	0	8	0	8
	Lepidoptera	3	23	2	28
	Hemiptera	2	3	0	5
	Thysanoptera	1	2	0	3
	Psocoptera	4	4	0	8
Immature Morphotaxa Total		10	40	2	52
Overall Morphotaxa Total		83	193	34	310

Table 5.2. *Nothofagus* arthropod fauna taxon richness: Adults, larvae and other immature life stages identifiable to morphotaxa, associated with either or both *Nothofagus* host species.

Of the fifteen most abundant morphotaxa (top 5%) twelve were Acarina (table 5.3 overleaf), with the Oribatid AcOr26 (Acarina: Oribatida: Brachypilina: Parakalummatae sp.1) the most abundant morphotaxon of all, numbering 2454 individuals (table 5.3). Counts rapidly decrease so that the most abundant non-Acarina morphotaxa within the top fifteen, the brachypterous Psocoptera PsBr7 and PsBr4 (Psocoptera: Psocomorpha: Ectopsocidae spp.1 and 4) and the leaf beetle CpCh3 (Coleoptera: Chrysomelidae: Chrysomelinae: Goniocetini: *Ewanius nothofagi* Reid) each number less than 150 individuals; and numbers continue to rapidly fall so that only 77 morphotaxa (25%) have an overall total of ten or more individuals, while 129 (41.6%) occur only as singletons (table 5.4). This pattern reflects the counts for *N. cunninghamii* and *N. gunnii* individually (table 5.4, figure 5.1).

Morphotaxa	<i>Overall Total N. cunninghamii + N. gunnii</i>	<i>N. cunninghamii only</i>	<i>N. gunnii only</i>
Total	310	276	117
Singletons	129	118	49
% Singletons	41.6	42.8	41.9

Table 5.4. Singletons as a percentage of all morphotaxa: overall, *N. cunninghamii* only and *N. gunnii* only.

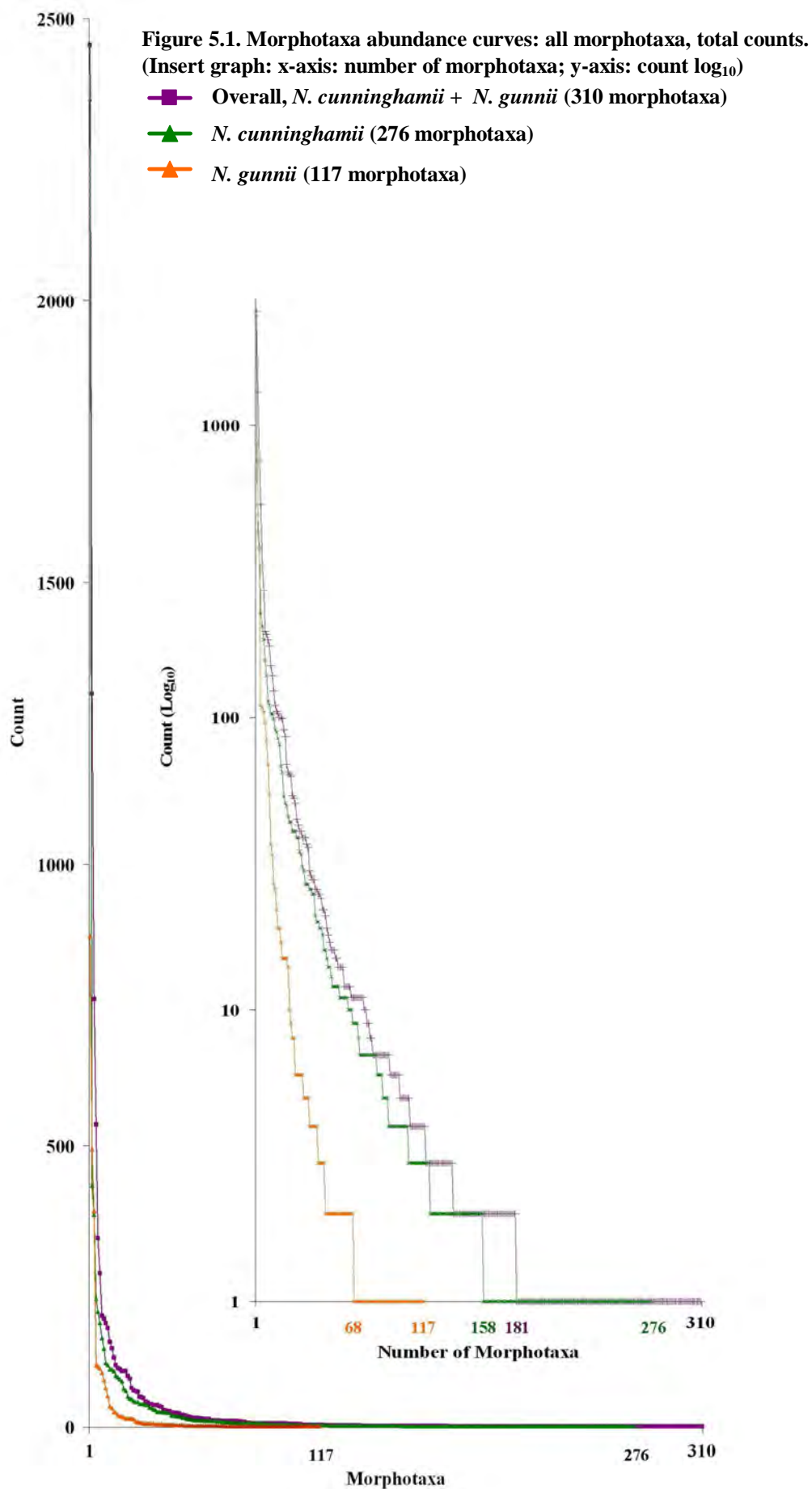
One hundred and sixty-two morphotaxa were found at only one site, while no morphotaxon was found at all the sampling sites (table 5.5 overleaf). The Mesostigmatid mite AcMe01 (Acarina: Mesostigmata: Dermanyssina sp.1) was the most widespread taxon overall and occurred on both *N. cunninghamii* (at 15 of 17 sites) and *N. gunnii* (at 10 of 12 sites). Other morphotaxa widespread on *N. cunninghamii* were: AcPr01 (Acarina: Prostigmata: Eupodina: Bdellidae sp.1), HeAp1 (Hemiptera: Sternorrhyncha: Aphididae: *Taiwanaphis tasmaniae*), ThTh2 (Thysanoptera: Terebrantia: Thripidae: Thripinae: *Pseudanaphothrips pallidus*) and LePsL1 (Lepidoptera: Glossata: Psychidae: Taleporiinae: *Narycia* sp.1), at 15, 14, 13 and 12 sites respectively. On *N. gunnii*, the next most widespread morphotaxa were AcOr05 (Acarina: Oribatida: Brachypilina: sp.1) and ThTh2 (as above) at 8 and 7 sites respectively. At Lake Fenton, Lake Skinner and Mt. Dundas, the mite AcMe01 and the thrip ThTh2 occurred on both *N. cunninghamii* and *N. gunnii*.

Mtx	Total	Nc	Ng
AcOr26	2454	2358	96
AcOr05	1302	429	873
AcMe01	760	377	383
AcOr10	538	44	494
AcOr20	335	227	108
AcOr2	273	204	69
AcPr24	197	114	83
AcOr1	192	184	8
AcPr1	184	157	27
AcPr7	175	65	110
AcOr3	150	46	104
PsBr7	139	139	0
AcOr9	123	68	55
PsBr4	110	110	0
CpCh3	105	103	2
CpChL1	103	103	0
PsCc1	100	99	1
ThTh2	100	81	19
AcPr8	99	89	10
PsPd1	91	91	0
HeAp1	86	85	1
CpCh1	69	35	34
AcMe3	65	50	15
AcOr24	64	27	37
AcOr11	63	41	22
CpCh8	54	54	0
AcOr12	53	34	19
AcOr4	51	51	0
LePsL1	45	44	1
CpCh10	43	26	17
CpChL2	41	41	0
LeGrL1	41	41	0
AcOr16	39	39	0
CpCo2	39	39	0
AcPr5	39	31	8
AcOr23	37	11	26
CpMe2	36	27	9
PsPp2	30	30	0
PsCc2	29	27	2

Mtx	Total	Nc	Ng
CpCo01	28	26	2
CpCu02	28	13	15
CpLa01	26	25	1
AcOr06	26	20	6
ThPhL1	25	25	0
AcPr17	25	21	4
AcMe5	24	9	15
PsBr5	22	20	2
LeGeL1	22	18	4
HeMeJ3	21	19	2
AcMe10	19	19	0
AcPr11	18	14	4
AcOr7	17	15	2
AcPr16	16	16	0
LeToL5	16	16	0
AcPr25	16	2	14
CpCh4	15	12	3
PcGr1	15	0	15
CpCh12	14	14	0
AcPr2	14	12	2
CpSa1	14	11	3
CpCh9	14	9	5
AcOr21	12	12	0
ThPh3	12	12	0
CpCoL1	12	12	0
CpSr2	12	11	1
ThTh3	12	7	5
CpCh7	11	11	0
LeGr1	11	11	0
LeGeL4	11	11	0
AcMe4	11	10	1
AcPr15	11	10	1
ThTh4	11	9	2
HePc1	11	7	4
CpLa2	11	6	5
AcOr13	11	5	6
CpChL3	10	10	0
HeAcJ1	10	4	6

Table 5.3. Most abundant morphotaxa: 77 morphotaxa (25%) have an overall total of 10 or more individuals. Mtx: Morphotaxon; Total: overall total, sum of both *Nothofagus* species; Nc: *N. cunninghamii* total; Ng: *N. gunnii* total.

Key to orders and families (for further detail see Appendix 7: Tasmanian *Nothofagus* Arthropod Fauna: Morphotaxa, Host Plant, Feeding Guilds): Ac, Acarina: AcMe, Mesostigmata; AcOr, Oribatida; AcPr, Prostigmata. Cp, Coleoptera: CpCh, Chrysomelidae; CpCo, Coccinellidae; CpCu, Curculionidae; CpLa, Lathridiidae; CpMe, Melandryidae; CpSa, Salpingidae; CpSr, Scirtidae. He, Hemiptera: HeAc, Acanthosomatidae; HeAp, Aphididae; HeMe, Membracidae; HePc, Pseudococcidae. Le, Lepidoptera: LeGe, Geometridae; LeGr, Gracillariidae; LePs, Psychidae; LeTo, Tortricidae. Pc, Plecoptera: PcGr, Gripopterygidae; Ps, Psocoptera: PsBr, brachypterous morphotaxa; PsCc, Caeciliusidae; PsPd, Pseudocaeciliidae; PsPp, Peripsocidae. Th, Thysanoptera: ThPh, Phlaeothripidae; ThTh, Thripidae. J and L preceding taxon number denote immatures: Juvenile and Larva.



Mtx code	All Sites			Occurrence at NcNg Sites		
	Total	Nc	Ng	L. Fenton	L. Skinner	Mt. Dundas
AcMe01	25	15	10	Nc & Ng	Nc & Ng	Nc & Ng
ThTh2	20	13	7	Nc & Ng	Nc & Ng	Nc & Ng
AcPr01	18	15	3	Nc & Ng	Nc & Ng	Nc only
AcOr05	17	9	8	Nc & Ng	Nc & Ng	Nc & Ng
AcOr02	15	11	4	Nc & Ng	Nc & Ng	Nc & Ng
HeAp1	15	14	1	Nc only	Nc & Ng	Nc only
AcMe03	14	9	5	Nc & Ng	Nc & Ng	Nc only
AcOr11	13	8	5	Nc & Ng	Nc & Ng	Ng only
AcOr20	13	10	3	Nc & Ng	Nc & Ng	0
AcOr26	13	9	4	Nc & Ng	Nc & Ng	Nc only
LePsL1	13	12	1	Nc only	Nc only	Nc only
AcOr03	12	7	5	Nc & Ng	Nc & Ng	Nc & Ng
PsCc1	12	11	1	Nc only	0	Nc only
AcOr24	11	7	4	Nc & Ng	Nc & Ng	Nc & Ng
AcPr08	11	7	4	Nc & Ng	Nc & Ng	Nc & Ng
LeGeL1	11	8	3	Nc only	Nc only	Nc & Ng
AcPr07	10	8	2	Nc & Ng	Nc & Ng	Nc only
AcPr24	10	8	2	Nc & Ng	Nc & Ng	0
PsBr7	10	10	0	Nc only	0	0
AcMe05	9	5	4	Nc & Ng	Nc & Ng	0
AcOr06	9	7	2	Nc & Ng	Nc & Ng	Nc only
AcOr09	9	5	4	Nc & Ng	Nc & Ng	0
AcPr16	9	9	0	0	0	Nc only
CpCh01	9	6	3	Nc & Ng	Nc only	Nc only
CpCo02	9	9	0	Nc only	Nc only	Nc only
HeMeJ3	9	7	2	Nc & Ng	Nc only	0
LeGrL1	9	9	0	Nc only	0	0
AcOr01	8	6	2	Nc & Ng	Nc & Ng	Nc only
AcOr12	8	6	2	Ng only	Nc & Ng	0
AcOr23	8	5	3	Nc & Ng	Nc & Ng	0
CpLa01	8	7	1	Nc only	0	Nc only
CpMe02	8	6	2	Nc & Ng	Nc & Ng	Nc only
LeToL05	8	8	0	0	Nc only	Nc only
PsBr4	8	8	0	Nc only	0	0
ThPhL1	8	8	0	0	0	Nc only

Table 5.5. Most widespread morphotaxa: 35 morphotaxa (11%) were found at 8 or more sampling sites. Mtx: Morphotaxon; Total: all sites (of 29); Nc: *N. cunninghamii* sites (of 17); Ng: *N. gunnii* sites (of 12); NcNg Sites: sites at which both *N. cunninghamii* and *N. gunnii* were sampled.

Key to orders and families (for further detail see Appendix 7: Tasmanian *Nothofagus*

Arthropod Fauna: Morphotaxa Host Plant, Feeding Guilds): **Ac**, Acarina: AcMe, Mesostigmata; AcOr, Oribatida; AcPr, Prostigmata. **Cp**, Coleoptera: CpCh, Chrysomelidae; CpCo, Coccinellidae; CpLa, Lathridiidae; CpMe, Melandryidae. **He**, Hemiptera: HeAp, Aphididae; HeMe, Membracidae. **Le**, Lepidoptera: LeGe, Geometridae; LeGr, Gracillariidae; LePs, Psychidae; LeTo, Tortricidae. **Ps**, Psocoptera: PsBr, brachypterous morphotaxa; PsCc, Caeciliusidae. **Th**, Thysanoptera: ThPh, Phlaeothripidae; ThTh, Thripidae. J and L preceding taxon number denote immatures: Juvenile and Larva.

5.1.1 Main Orders

5.1.1.1 Coleoptera

Coleoptera was the most biodiverse order, with 101 adult and 8 immature morphospecies being identified, comprising 29 families (appendices: taxon list & overall abundance). Nearly one fifth of these (21 morphotaxa, from ten families) occurred on both *N. cunninghamii* and *N. gunnii*; approaching three-quarters (77 morphotaxa, from 23 families) were found only on *N. cunninghamii*; and just one tenth (11 morphotaxa, from seven families) was found only on *N. gunnii*.

Curculionidae was the most taxon rich family overall (22 morphotaxa), followed by Chrysomelidae (14 morphotaxa) and Coccinellidae and Scirtidae (9 morphotaxa each); and these four families were the most taxon rich on both *N. cunninghamii* and *N. gunnii* (table 5.6). Overall, nearly half of the morphotaxa (47 adult, 2 larva) occurred as singletons (table 5.6).

Chrysomelidae had the highest taxon abundance (table 5.7) on both *N. cunninghamii* (424 individuals) and *N. gunnii* (62 individuals), but while Coccinellidae ranked second on *N. cunninghamii* (112 individuals), there were markedly fewer coccinellids on *N. gunnii* (6 individuals); Curculionidae were relatively more evenly spread (*N. cunninghamii*: 40 individuals, *N. gunnii*: 27 individuals).

The most abundant morphotaxa were the adult (CpCh03) and larva (CpChL1) of the Chrysomelidae beetle, *Ewanius nothofagi* Reid (figure 5.2.a), with 103 individuals each on *N. cunninghamii*, although only two adults and no larvae on *N. gunnii*. Most abundant on *N. gunnii*, with 34 individuals, was the adult Chrysomelidae beetle (CpCh01) *Platycolaspis mcquillani* Reid (figure 5.2.b), 35 individuals of which were also found on *N. cunninghamii*.

The most widespread morphotaxon on *N. cunninghamii* (9 sites) was the adult Coccinellidae beetle (CpCo02) *Rhizobius* sp.2 (figure 5.2.d) which was absent from *N. gunnii* at all its sites. Most widespread on *N. gunnii* (4 sites) was the adult Chrysomelidae beetle (CpCh10) *Microdonacia truganina* Monros (figure 5.2.c), which was also found on *N. cunninghamii* (2 sites).

Morphotaxa	Family	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall	
		Total	Total	Total	Singletons
Adult	Curculionidae	17	6	22	10
	Chrysomelidae	13	6	14	6
	Coccinellidae	9	4	9	1
	Scirtidae	8	4	9	4
	Lathridiidae	5	2	4	0
	Elateridae	4	0	4	4
	Staphylinidae	4	0	4	3
	Corylophidae	3	0	3	2
	Scydmaenidae	2	1	2	1
	Aderidae	1	0	2	1
	Apionidae	1	1	1	0
	Anthribidae	1	0	1	1
	Buprestidae	1	0	1	1
	Carabidae	1	0	1	1
	Clambidae	1	0	1	0
	Cleridae	1	0	1	1
	Leiodidae	1	0	1	1
	Melandryidae	1	2	6	1
	Melyridae	1	0	3	2
	Nitidulidae	1	1	3	3
	Pselaphidae	1	0	1	1
	Rhynchitidae	1	1	1	0
	Salpingidae	1	1	1	0
	Scarabaeidae	1	0	1	1
	Silvanidae	1	0	1	0
	Unknown	1	0	1	0
	Mordellidae	0	1	1	1
	Phalacridae	0	1	1	0
	Tenebrionidae	0	1	1	1
Adult Morphotaxa Total		82	32	101	47
Larva	CpChL	4	0	4	1
	CpCoL	4	0	4	1
Immature Morphotaxa Total		8	0	8	2
Overall Morphotaxa Total		90	32	109	49

Table 5.6. Coleoptera morphotaxon richness by family, *Nothofagus* species and overall totals; and number of singleton taxa per family.

Family	<i>N. cunninghamii</i> Total	<i>N. gunnii</i> Total	Overall Total
Chrysomelidae	424	62	486
Coccinellidae	112	6	118
Curculionidae	40	27	67
Melandryidae	39	10	49
Lathridiidae	37	6	43
Scirtidae	25	5	30
Salpingidae	11	3	14
Clambidae	7	0	7
Melyridae	6	0	6
Staphylinidae	5	0	5
Aderidae	4	0	4
Corylophidae	4	0	4
Elateridae	4	0	4
Unknown	4	0	4
Scydmaenidae	3	1	4
Silvanidae	3	0	3
Nitidulidae	2	1	3
Apionidae	1	2	3
Anthribidae	1	0	1
Buprestidae	1	0	1
Carabidae	1	0	1
Cleridae	1	0	1
Leiodidae	1	0	1
Pselaphidae	1	0	1
Rhynchitidae	1	1	2
Scarabaeidae	1	0	1
Mordellidae	0	1	1
Phalacridae	0	2	2
Tenebrionidae	0	1	1
Morphotaxa Abundance	739	128	867
Miscellaneous immatures	6	0	6
Overall Total Abundance	745	128	873

Table 5.7. Coleoptera morphotaxon abundance per family, *Nothofagus* species and total; and overall abundance including miscellaneous unidentified immatures.

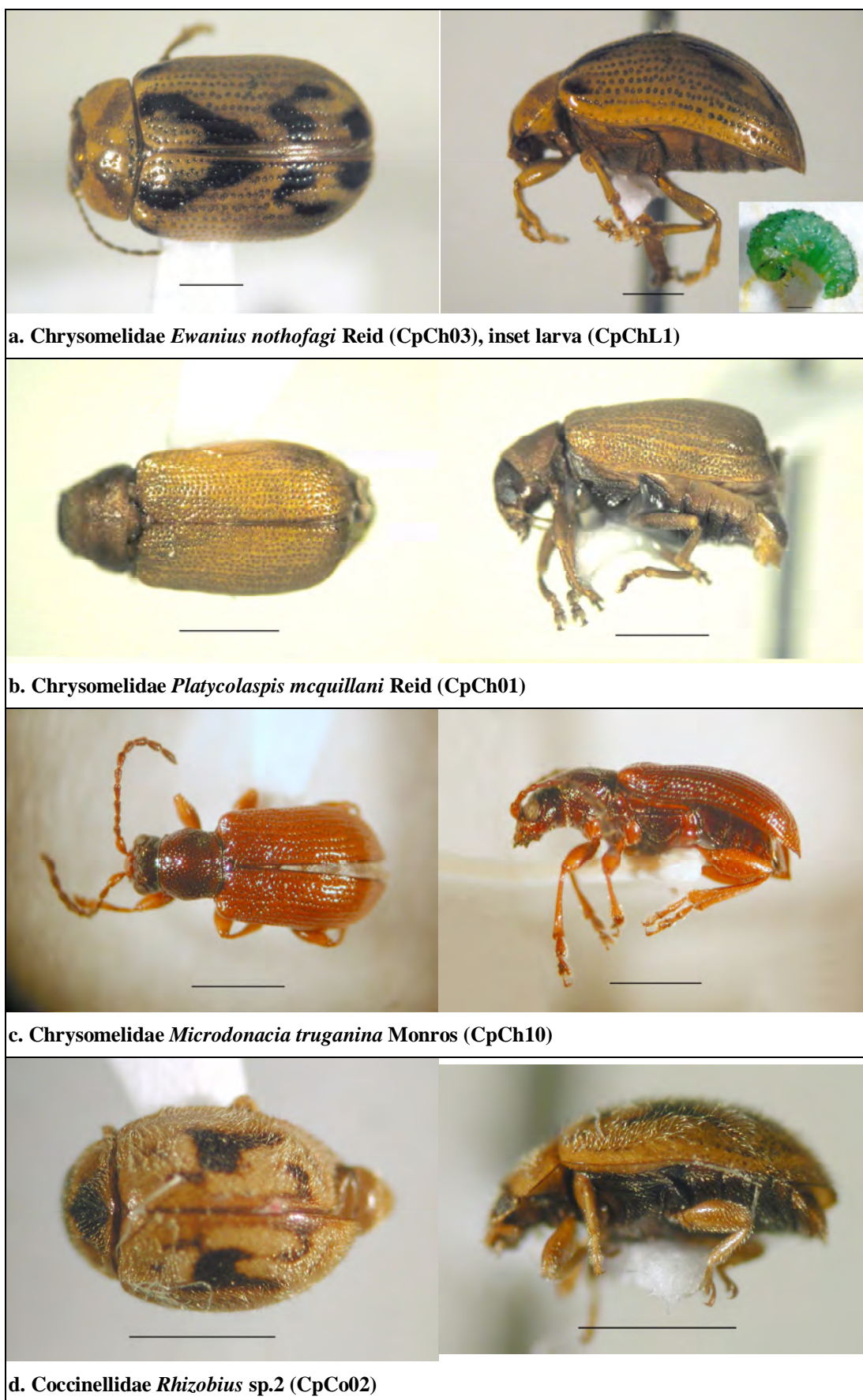


Figure 5.2. a-d. Most abundant and widespread Coleoptera morphotaxa. Scale Bar 1mm.

5.1.1.2 *Lepidoptera*

Overall, fourteen families of Lepidoptera were found, with eight adult and nine immature morphotaxa being identified, in addition two individual adults and one larva were of uncertain family (appendices: taxon list & overall abundance). Just 6% (4 morphotaxa, from 3 families) occurred on both *N. cunninghamii* and *N. gunnii*; nearly 85% (55 morphotaxa, from 12 families) were found only on *N. cunninghamii*; while less than 10% (6 morphotaxa, from 4 families) were found only on *N. gunnii*.

Oecophoridae was the most taxon rich family overall (20 adult morphotaxa), followed by Tortricidae (6 adult and 8 larval morphotaxa), Arctiidae (8 larval morphotaxa) and Geometridae (6 larval morphotaxa); and these four families were the most taxon rich on *N. cunninghamii*, while the most taxon rich families on *N. gunnii* were Oecophoridae (3 adult taxa, two of which only occurred on *N. gunnii*) and Geometridae (3 adult taxa, each of which only occurred on *N. gunnii*) (table 5.8). Overall, two thirds of the morphotaxa (31 adult, 12 larvae) occurred as singletons (table 5.8).

Lepidoptera larva morphotaxa were more abundant than adult morphotaxa (table 5.9). Overall the most abundant morphotaxon was the Psychidae larva (LePsL1) *Narycia* sp.1 (figure 5.3.a), with 44 individuals on *N. cunninghamii*, but just one on *N. gunnii*; next most abundant was Gracillariidae larva (LeGrL1) *Caloptilia ostracodes* (figure 5.3.b) with 41 individuals on *N. cunninghamii* but none on *N. gunnii*. The Geometridae larva (LeGeL1) Ennominae Nacophorini *sp. novum* (figure 5.3.c) was most abundant on *N. gunnii* with 4 individuals, although 18 individuals of the same morphotaxon occurred on *N. cunninghamii*.

The Lepidoptera were considerably more abundant on *N. cunninghamii* than on *N. gunnii* (table 5.9), with Gracillariidae having the highest taxon abundance (52 individuals), followed by Psychidae (44 individuals), Tortricidae (39 individuals) and Geometridae (33 individuals), whereas most taxon abundant on *N. gunnii* was Geometridae with a meagre seven individuals.

Morphotaxa	Family	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall	
		Total	Total	Total	Singleton Taxa
Adult	Oecophoridae	18	3	20	15
	Tortricidae	5	1	6	6
	Heliozelidae	3	1	4	4
	Gelechiidae	1	0	1	1
	Geometridae	1	0	1	1
	Gracillariidae	1	0	1	0
	Opostegidae	1	0	1	1
	Yponomeutidae	1	0	1	1
	?Anthelidae/ ?Lasiocampidae	1	0	1	1
	?Gracillariidae/ ?Tortricidae	1	0	1	1
Adult Morphotaxa Total		33	5	37	31
Larva	Arctiidae	8	0	8	3
	Tortricidae	8	0	8	4
	Geometridae	5	3	6	3
	Anthelidae	1	0	1	0
	Gracillariidae	1	0	1	0
	Noctuidae	1	0	1	1
	Psychidae	1	1	1	0
	Roeslerstammiidae	1	0	1	0
	Unknown	0	1	1	1
Immature Morphotaxa Total		26	5	28	12
Overall Morphotaxa Total		59	10	65	43

Table 5.8. Lepidoptera morphotaxon richness by family, *Nothofagus* species and overall totals; and number of singleton taxa per family.

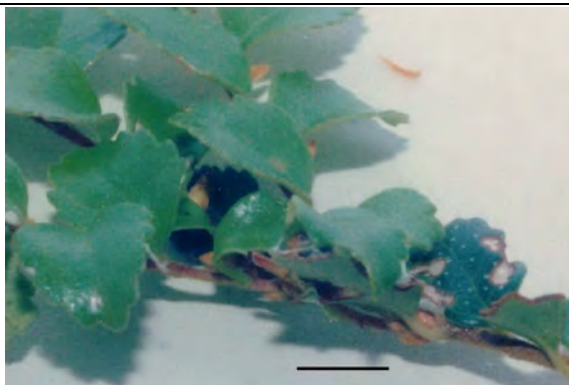
Family	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall
	Total	Total	Total
Gracillariidae	52	0	52
Psychidae	44	1	45
Tortricidae	39	1	40
Geometridae	33	7	40
Oecophoridae	26	3	29
Arctiidae	21	0	21
Roeslerstammiidae	7	0	7
Anthelidae	4	0	4
Heliozelidae	3	1	4
Yponomeutidae	1	0	1
Opostegidae	1	0	1
Noctuidae	1	0	1
Gelechiidae	1	0	1
?Anthelidae ?Lasiocampidae	1	0	1
?Gracillariidae / ?Tortricidae	1	0	1
Unknown	0	1	1
Overall Morphotaxa Abundance	235	14	249

Table 5.9. Lepidoptera morphotaxon abundance per family, *Nothofagus* species and overall abundance.

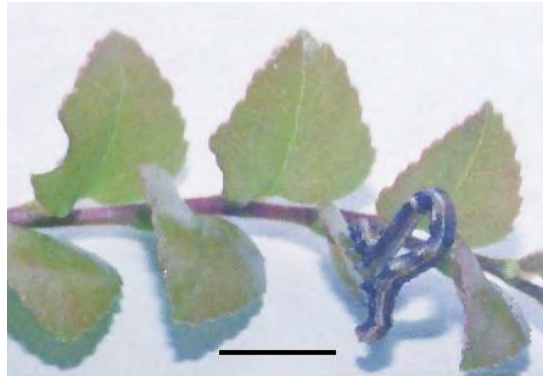
As well as being the most abundant morphotaxon, the Psychidae larva (LePsL1) *Narycia* sp.1 (figure 5.3a.) was also the most widespread, occurring on *N. cunninghamii* at twelve sites and on *N. gunnii* at one site. Next most widespread was the Geometridae larva (LeGeL1) Ennominae Nacophorini *sp. novum* (figure 5.3.c), occurring on *N. cunninghamii* and *N. gunnii* at eight and three sites respectively; followed by the Gracillariidae larva (LeGrL1) *Caloptilia ostracodes* (figure 5.3.b) found, on *N. cunninghamii* only, at nine sites.



a. Psychidae *Narycia* sp.1 (LePsL1)



b. Gracillariidae *Caloptilia ostracodes* (LeGrL1), leaf tie.



c. Geometridae Ennominae Nacophorini *sp. novum* (LeGeL1)

Figure 5.3. a-c. Most abundant and widespread Lepidoptera morphotaxa. Scale Bar 5mm.

5.1.1.3 Hemiptera

Overall eight families of Hemiptera were found, with 26 adult and 5 immature morphotaxa being identified (appendices: taxon list & overall abundance). Nearly a third (9 morphotaxa, from 8 families) occurred on both *N. cunninghamii* and *N. gunnii*; over half (17 morphotaxa, from 9 families) were found only on *N. cunninghamii*; while about a sixth (5 morphotaxa, from 4 families) were found only on *N. gunnii*.

Aphrophoridae and Membracidae were the most taxon rich families on *N. cunninghamii* with three morphotaxa each, although neither family was found on *N. gunnii*. Most taxon rich on *N. gunnii*, with three morphotaxa, was Aphididae, which also had one morphotaxon on *N. cunninghamii*. Overall, just over half of the morphotaxa (14 adult, 2 larva) occurred as singletons (table 5.10).

Morphotaxa	Family	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall	
		Total	Total	Total	Singleton Taxa
Adult	Aphrophoridae	3	0	3	1
	Membracidae	3	0	3	2
	Cicadellidae	2	2	3	2
	Cixiidae	2	2	2	0
	Eriococcidae	2	1	2	0
	Lygaeidae	2	1	2	1
	Tingidae	2	1	3	3
	Acanthosomatidae	1	0	1	0
	Aphididae	1	3	3	2
	Miridae	1	1	2	2
	Pentatomidae	1	0	1	1
	Pseudococcidae	1	1	1	0
Adult Morphotaxa Total		21	12	26	14
Larva	Cicadellidae	2	0	2	2
	Membracidae	2	1	2	0
	Acanthosomatidae	1	1	1	0
Immature Morphotaxa Total		5	2	5	2
Overall Morphotaxa Total		26	14	31	16

Table 5.10. Hemiptera morphotaxon richness by family, *Nothofagus* species and overall totals; and number of singleton taxa per family.

Aphididae had the highest taxon abundance (table 5.11) on *N. cunninghamii* with 163 individuals, the majority of these being immatures not identifiable beyond the level of family; just four aphid individuals were found on *N. gunnii*. Next most abundant were Membracidae (29 individuals on *N. cunninghamii*; 4 on *N. gunnii*). The most abundant families on *N. gunnii*, with 6 individuals each, were

Acanthosomatidae (10 individuals on *N. cunninghamii*) and Lygaeidae (5 individuals on *N. cunninghamii*).

The most abundant morphotaxa on *N. cunninghamii* were the adult Aphid (HeAp1) *Taiwanaphis tasmaniae* (figure 5.4.a), with 85 individuals, although only a single individual on *N. gunnii*; and the Membracidae immature (HeMeJ3) *Acanthuchus* sp.1 (figure 5.4.d) with 19 individuals (2 individuals on *N. gunnii*). Most abundant on *N. gunnii*, with 6 individuals each, were the Acanthosomatidae immature (HeAcJ1) Acanthosomatidae sp.1 (figure 5.4.c) and the Lygaeidae adult (HeLy2) *Nysius* sp.1 (figure 5.4.b), (4 and 3 individuals respectively were found on *N. cunninghamii*).

Family	<i>N. cunninghamii</i> Total	<i>N. gunnii</i> Total	Overall Total
Aphididae	163	4	167
Membracidae	29	2	31
Acanthosomatidae	10	6	16
Aphrophoridae	10	0	10
Cixiidae	8	3	11
Pseudococcidae	7	4	11
Eriococcidae	6	2	8
Lygaeidae	5	6	11
Miridae	5	2	7
Cicadellidae	4	2	6
Tingidae	2	1	3
Pentatomidae	1	0	1
Morphotaxa Abundance	139	22	161
Miscellaneous immatures	7	0	7
Overall Total Abundance	257	32	289

Table 5.11. Hemiptera morphotaxon abundance per family, *Nothofagus* species and total; and overall abundance including miscellaneous unidentified immatures.

The most widespread morphotaxon on *N. cunninghamii* was the adult Aphid (HeAp1) *Taiwanaphis tasmaniae* (figure 5.4.a), found at 15 sites (*N. gunnii*: 1 site); followed by the Membracidae immature (HeMeJ3) *Acanthuchus* sp.1 (figure 5.4.d), found at 7 sites (*N. gunnii*: 2 sites). Most widespread on *N. gunnii* was the Acanthosomatidae immature (HeAcJ1) Acanthosomatidae sp.1 (figure 5.4.c), which occurred at three sites (*N. cunninghamii*: 2 sites).

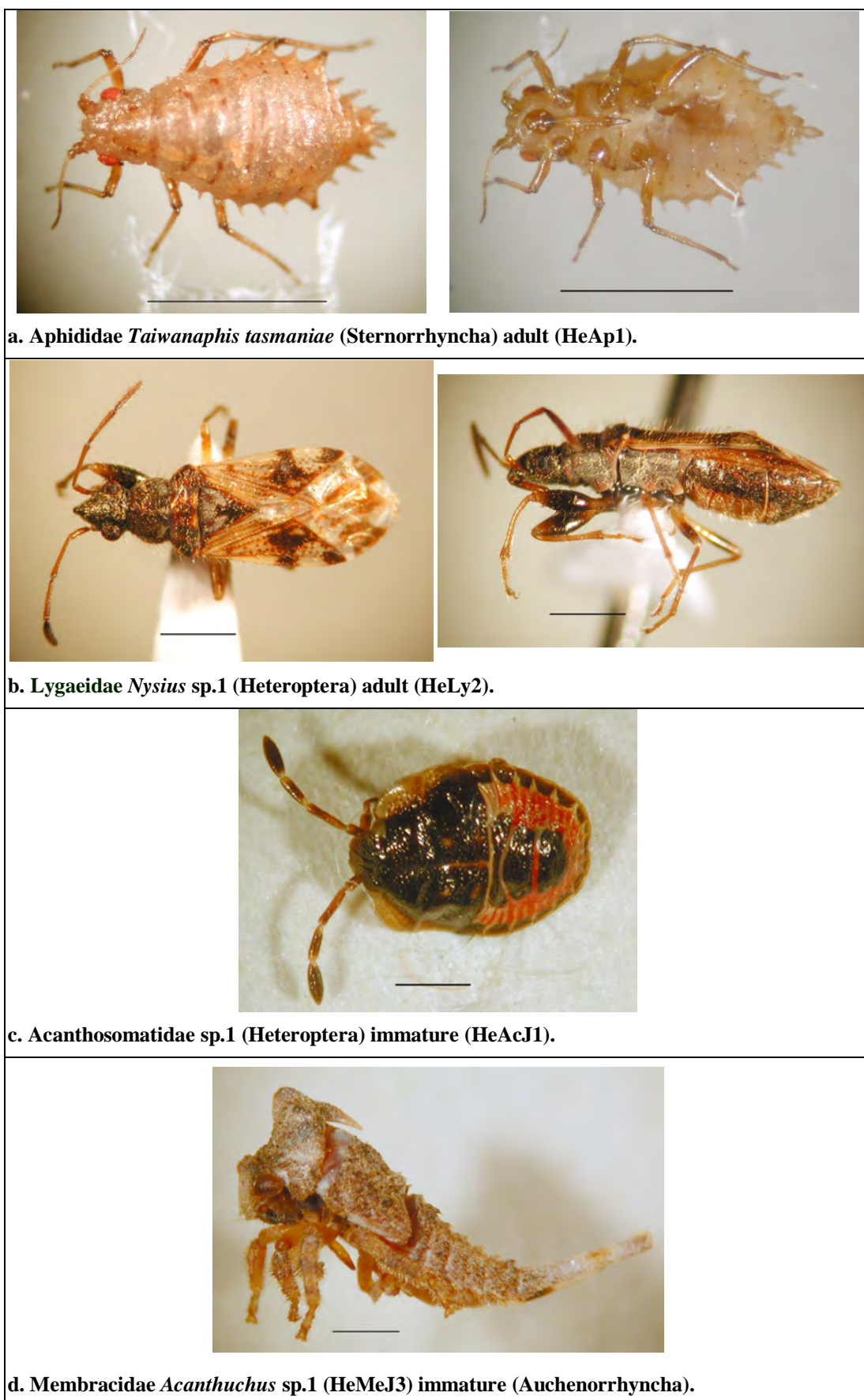


Figure 5.4. a-d. Most abundant and widespread Hemiptera morphotaxa. Scale Bar 1mm.

5.1.1.4 *Thysanoptera*

Between the two Thysanoptera families, fourteen adult and three immature morphotaxa were identified. Of these, six Thripidae morphotaxa (5 adult; 1 immature) occurred on both *Nothofagus* species; seven Phlaeothripidae morphotaxa, (5 adult; 2 immatures) together with two adult Thripidae morphotaxa were found only on *N. cunninghamii*; and one adult morphotaxon from each family was found only on *N. gunnii*.

Although unevenly distributed between the two *Nothofagus* hosts, the two Thysanoptera families had comparable morphotaxon richness (table 5.12): Thripidae having eight adult and one immature morphotaxa and Phlaeothripidae six adult and two immature morphotaxa. Overall, nearly half the morphotaxa (6 adult, 1 larva) occurred as singletons (table 5.12).

Morphotaxa	Family	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall	
		Total	Total	Total	Singleton Taxa
Adult	Thripidae	7	6	8	2
	Phlaeothripidae	5	1	6	4
Adult Morphotaxa Total		12	7	14	6
Larva	Phlaeothripidae	2	0	2	1
	Thripidae	1	1	1	0
Immature Morphotaxa Total		3	1	3	1
Overall Morphotaxa Total		15	8	17	7

Table 5.12. Thysanoptera morphotaxon richness by family, *Nothofagus* species and overall totals; and number of singleton taxa per family.

Thripidae had a markedly higher taxon abundance than Phlaeothripidae (table 5.13) on both *N. cunninghamii* (Thripidae: 114 individuals; Phlaeothripidae 51 individuals) and on *N. gunnii* (Thripidae: 30 individuals; Phlaeothripidae: 1 individual). The most abundant morphotaxa were the Thripidae adult (ThTh2) *Pseudanaphothrips pallidus* (figure 5.5), with 81 individuals on *N. cunninghamii* and 19 individuals on *N. gunnii*; and the Phlaeothripidae larva (ThPhL1) *Haplothrips ?victoriensis*, with 25 individuals on *N. cunninghamii* and none on *N. gunnii*. These two morphotaxa were also the most widespread: ThTh2 occurring on *N. cunninghamii* at 13 sites and on *N. gunnii* at 7 sites; and ThPhL1 occurring only on *N. cunninghamii* at 8 sites.

	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall
Family	Total	Total	Total
Thripidae	114	30	144
Phlaeothripidae	51	1	52
Overall Abundance	165	31	196

Table 5. 13. Thysanoptera abundance per family, *Nothofagus* species and overall total.

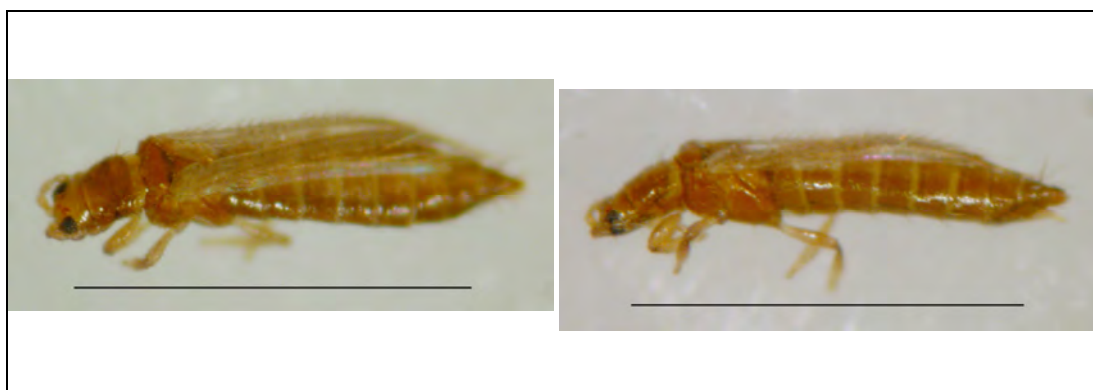


Figure 5.5. Most abundant and widespread Thysanoptera morphotaxon, Thripidae *Pseudanaphothrips pallidus* (ThTh2). Scale Bar 1mm.

5.1.1.5 Psocoptera

Five families of Psocoptera were found, with 8 fully-winged adult and 8 brachypterous morphotaxa being identified, in addition one brachypterous morphotaxon was of uncertain family (appendices: taxon list & overall abundance). Nearly two fifths (6 morphotaxa, from 3 families) occurred on both *N. cunninghamii* and *N. gunnii*; two thirds (10 morphotaxa, from 4 families) were found only on *N. cunninghamii*; while no morphotaxon was found only on *N. gunnii*.

Ectopsocidae was the most taxon rich family on *N. cunninghamii* with one fully-winged and five brachypterous morphotaxa (*N. gunnii*: 2 brachypterous morphotaxa); while two fully-winged Caeciliusidae morphotaxa occurred on both *N. cunninghamii* and *N. gunnii* (table 5.14). Overall, a fifth of the morphotaxa (1 fully-winged, 2 brachypterous) occurred as singletons (table 5.14). Ectopsocidae had the highest taxon abundance (table 5.15) with 274 individuals on *N. cunninghamii* and 3 individuals on *N. gunnii*; followed by Caeciliusidae with 126 individuals on *N. cunninghamii* and 3 individuals on *N. gunnii*. Two Ectopsocidae brachypterous morphotaxa PsBr7 (Ectopsocidae sp.4) (figure 5.6.b) and PsBr4 (Ectopsocidae sp.1) (figure 5.6.a), occurring only on *N. cunninghamii*, were the most abundant morphotaxa, with 139 and 110 individuals respectively.

Morphotaxa	Family	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall	
		Total	Total	Total	Singleton Taxa
Fully-Winged Adult	Peripsocidae	4	0	4	1
	Caeciliusidae	2	2	2	0
	Ectopsocidae	1	0	1	0
	Pseudocaeciliidae	1	0	1	0
Adult Morphotaxa Total		8	2	8	1
Brachypterous Morphotaxa	Ectopsocidae	5	2	5	2
	Elipsocidae	2	1	2	0
	Elipsocidae/ Peripsocidae	1	1	1	0
	Brachypterous Morphotaxa Total	8	4	8	2
Overall Morphotaxa Total		16	6	16	3

Table 5.14. Psocoptera morphotaxon richness by family, *Nothofagus* species and overall totals; and number of singleton taxa per family.

These were followed by the fully winged Caeciliusidae morphotaxon PsCc1 (Caeciliusidae sp.1) (figure 5.6.d), with 99 individuals on *N. cunninghamii* and a single individual on *N. gunnii*; and the fully-winged Pseudocaeciliidae morphotaxon PsPd1 (Pseudocaeciliidae sp.1) (figure 5.6.e) with 91 individuals on *N. cunninghamii* alone. Most abundant on *N. gunnii*, with 3 individuals, was the brachypterous morphotaxon PsBr3 (Elipsocidae/Peripsocidae sp.1 (figure 5.6.c), 4 individuals of which were found on *N. cunninghamii*.

The most widespread morphotaxon on *N. cunninghamii* was the fully winged Caeciliusidae morphotaxon (PsCc1) (figure 5.6.d) at 11 sites, followed by Ectopsocidae brachypterous morphotaxa (figure 5.6.b) and (PsBr4) (figure 5.6.a) found at 10 and 8 sites respectively. None of the morphotaxa found on *N. gunnii* occurred at more than one site.

Family	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall
	Total	Total	Total
Ectopsocidae	274	3	277
Caeciliusidae	126	3	129
Pseudocaeciliidae	91	0	91
Peripsocidae	36	0	36
?Elipsocidae / ?Peripsocidae	4	3	7
Elipsocidae	2	1	3
Morphotaxa Abundance	533	10	543
Miscellaneous immatures	550	4	554
Overall Total Abundance	1083	14	1097

Table 5.15. Psocoptera morphotaxon abundance per family, *Nothofagus* species and total; and overall abundance including miscellaneous unidentified immatures.

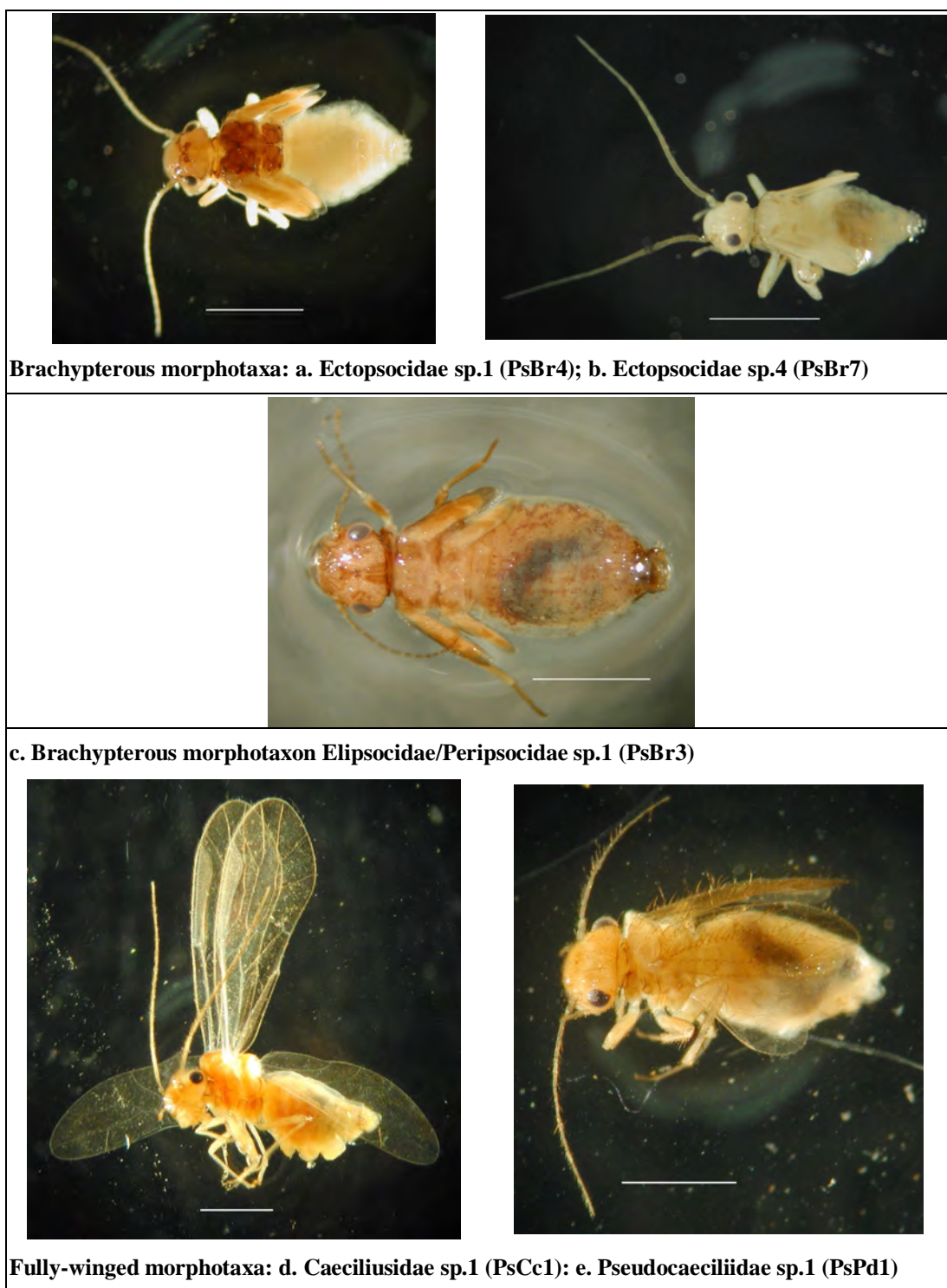


Figure 5.6. a-e. Most abundant and widespread Psocoptera morphotaxa. Scale Bar 1mm.

5.1.1.6 *Plecoptera*

The two Plecoptera (stonefly) families were found on both species of *Nothofagus*. Of the thirteen adult morphotaxa collected, two occurred on *N. cunninghamii* and *N. gunnii*, four occurred on *N. cunninghamii* alone and seven were found only on *N. gunnii*.

Gripopterygidae was the more taxon rich family (table 5.16) with seven morphotaxa found on *N. gunnii* and three on *N. cunninghamii*; Notonemouridae was more evenly distributed with two morphotaxa on *N. gunnii* and three on *N. cunninghamii*. Five morphotaxa, all Gripopterygidae on *N. gunnii*, occurred as singletons (table 5.16).

Morphotaxa	Family	<i>N. cunninghamii</i> Total	<i>N. gunnii</i> Total	Overall	
				Total	Singleton Taxa
Adult	Gripopterygidae	3	7	9	5
	Notonemouridae	3	2	4	0
Morphotaxa Total		6	9	13	5

Table 5.16. Plecoptera morphotaxon richness by family, *Nothofagus* species and overall totals; and number of singleton taxa per family.

The Plecoptera had a modest taxon abundance with 47 individuals overall, but of these, two thirds (30 individuals) were from the family Gripopterygidae, the majority of which were found on *N. gunnii* (table 5.17). The most abundant morphotaxon was the Gripopterygidae stonefly (PcGr1) (figure 5.7.a), with 15 individuals, all found on *N. gunnii*; followed by the Notonemouridae stonefly (PcNo3) (figure 5.7.c), found only on *N. cunninghamii*, with 7 individuals. The Gripopterygidae stonefly (PcGr1) was the most widespread, being found at five *N. gunnii* sites, while another Gripopterygidae stonefly (PcGr2) (figure 5.7.b) was found at three *N. gunnii* and one *N. cunninghamii* site. Most widespread on *N. cunninghamii* was the Notonemouridae stonefly (PcNo3), found at 3 sites.

Family	<i>N. cunninghamii</i> Total	<i>N. gunnii</i> Total	Overall Total
Gripopterygidae	4	26	30
Notonemouridae	11	6	17
Overall Abundance	15	32	47

Table 5.17. Plecoptera morphotaxon abundance per family, *Nothofagus* species and total.



a. Gripopterygidae *Leptoperla varia* Kimmins (PcGr1)



b. Gripopterygidae *Riekoperla pulchra* Hynes (PcGr2)



c. Notonemouridae *Kimminsoperla albomacula* Kimmins (PcNo3)

Figure 5.7. a-c. Most abundant and widespread Plecoptera: morphotaxa and wing venation. Scale Bar 1mm.

5.1.1.7 *Collembola*

Collembola were sorted only to suborder (table 5.18), overall taxon abundance being relatively evenly distributed between *N. cunninghamii* and *N. gunnii*, however suborder abundance has a different pattern. Of the three suborders, Symphypleona was the most abundant with 982 individuals, 68% of these being found on *N. gunnii*; Entomobryomorpha was the next most abundant suborder, 90% occurring on *N. cunninghamii*; and of the Poduromorpha, 70% were found on *N. gunnii*.

Suborder	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall
	Total	Total	Total
Symphypleona	313	669	982
Entomobryomorpha	488	54	542
Poduromorpha	32	79	111
Total Abundance	833	802	1635

Table 5.18. Collembola abundance per suborder, *Nothofagus* species and overall totals.

5.1.1.8 *Acarina*

Acarina was the most abundant of the orders. In total, 7499 adult individuals were collected representing three suborders, nine cohorts, twenty superfamilies and fifty-nine adult morphotaxa. Of the morphotaxa, nearly two thirds (36) occurred on both *N. cunninghamii* and *N. gunnii*; just over one third (21) were found only on *N. cunninghamii*; and just three morphotaxa (5%) were found only on *N. gunnii*.

Oribatida was the most taxon rich suborder overall (29 morphotaxa) and on both *N. cunninghamii* (28 morphotaxa) and *N. gunnii* (17 morphotaxa); Prostigmata was represented by 21 morphotaxa and Mesostigmata by 9 morphotaxa; and each suborder was more taxon rich on *N. cunninghamii* than *N. gunnii* (table 5.19). Overall, 10% of the morphotaxa (6) occurred as singletons (table 5.19).

Morphotaxa	Suborder	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall	
		Total	Total	Total	Singleton Taxa
Adult	Oribatida	28	17	29	3
	Prostigmata	20	15	21	3
	Mesostigmata	8	6	9	0
Adult Morphotaxa Total		56	38	59	6

Table 5.19. Acarina morphotaxon richness by suborder, *Nothofagus* species and overall totals; and number of singleton taxa per family.

Oribatida had significantly higher taxon abundance than the other suborders (table 5.20) on both *N. cunninghamii* (3854 individuals) and *N. gunnii* (1927 individuals). Prostigmata was also more abundant on *N. cunninghamii* (549 individuals) than on *N. gunnii* (280 individuals), but Mesostigmata was relatively more evenly distributed (*N. cunninghamii*: 472 individuals, *N. gunnii*: 417 individuals).

Suborder	<i>N. cunninghamii</i> Total	<i>N. gunnii</i> Total	Overall Total
Oribatida	4569	2301	6870
Prostigmata	728	288	1016
Mesostigmata	490	430	920
Suborders Abundance	5787	3019	8806
Miscellaneous Others Abundance	70	4	74
Overall Total Abundance	5857	3023	8880

Table 5.20. Acarina abundance per suborder (including immatures identified to suborder but not to morphotaxon), *Nothofagus* species and overall totals; and abundance including miscellaneous others not identified to suborder.

By far the most abundant morphotaxon was the Oribatida mite AcOr26 (Brachypilina Galumnoidea Parakalummatidae sp.1, figure 5.8.a), with 2358 individuals found on *N. cunninghamii* (*N. gunnii*: 96 individuals). Most abundant on *N. gunnii* was the Oribatida morphotaxon AcOr05 (Brachypilina Tectocephoidea sp.1, figure 5.8.c), with 873 individuals (*N. cunninghamii*: 429 individuals).

The most widespread morphotaxon on *N. cunninghamii* (15 sites) and on *N. gunnii* (10 sites) was the Mesostigmata mite AcMe01 (Dermanyssina Monogynaspida sp.1, figure 5.8.b). Most widespread of the Prostigmata was AcPr01 (Eupodina Bdelloidea Bdellidae sp.1, figure 5.8.d) found on *N. cunninghamii* at 15 sites (*N. gunnii*: 3 sites); and that of the Oribatida was AcOr05, found on *N. cunninghamii* at 9 sites and on *N. gunnii* at 8 sites.

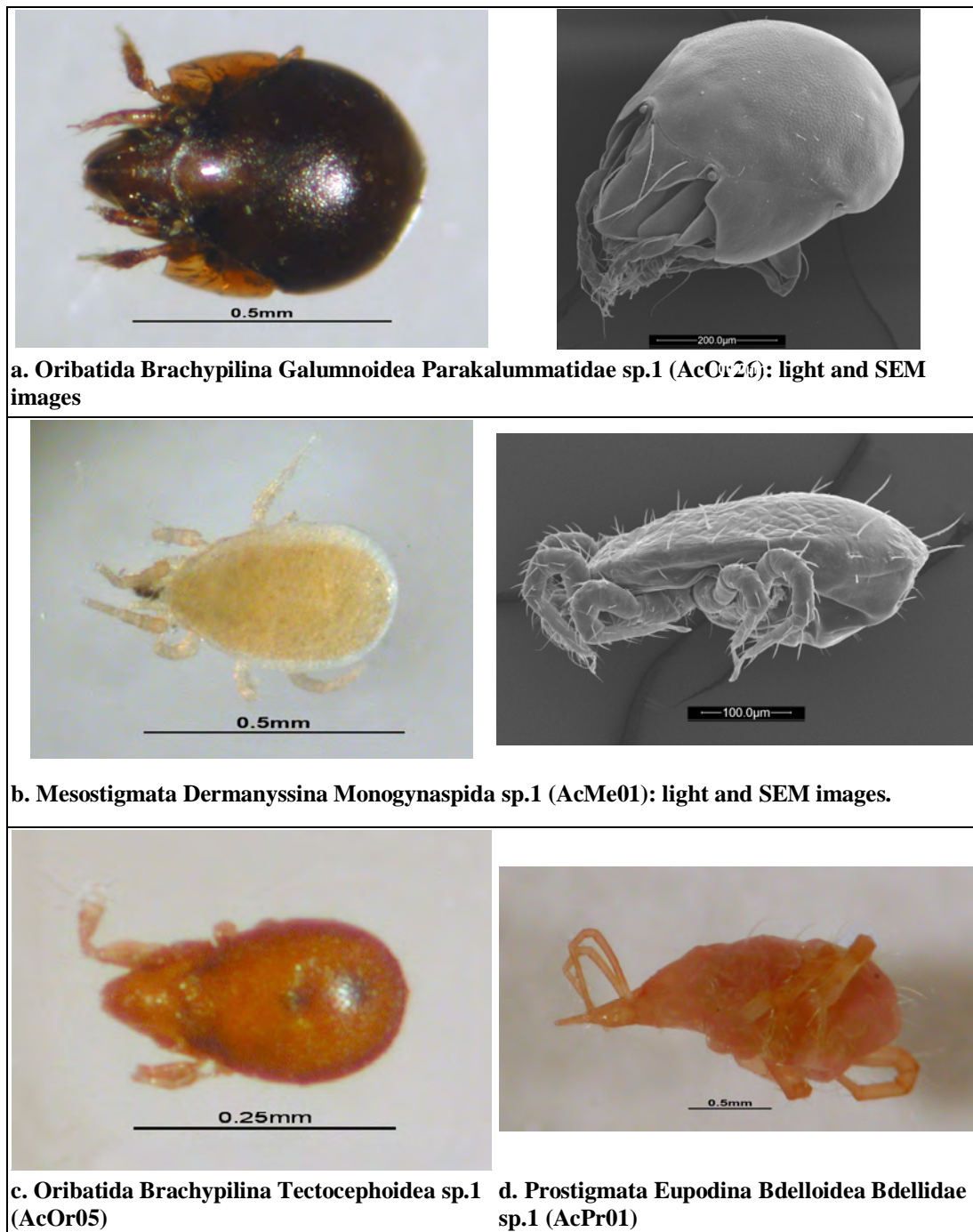


Figure 5.8. a. Most abundant Acarina morphotaxon; b-d. Most widespread morphotaxa from each Acarina suborder. Scale bars as indicated.
Scanning Electron Microscope (SEM) images c/o David Green, University of Tasmania.

5.1.1.9 Araneae

The total abundance of Acarina was 1889 individuals, 1680 being found on *N. cunninghamii* and 209 on *N. gunnii* (table 5.21). However, only a small subset (258 individuals, 13.6% of total, table 5.21) has been sorted and identified to the level of family and morphotaxon. These were collected from both *N. cunninghamii* and *N. gunnii* at Lake Fenton and Lake Skinner between 16/10/1999 and 25/09/2000 (sampling set 3 of table 4.1). The higher proportion on *N. gunnii* in the subset may reflect the parity of sampling effort on the two *Nothofagus* species at the two sites.

	<i>N. cunninghamii</i> Total	<i>N. gunnii</i> Total	Overall Total
Overall Abundance	1680	209	1889
Subset Abundance	198	60	258
Subset %	11.79	28.71	13.66

Table 5.21. Araneae: total abundance and Lake Fenton/Lake Skinner (16/10/1999 - 25/09/2000) subset, abundance as a percentage of the total.

Within the subset, eight families were found, from which 26 adult and 29 immature morphospecies were identified (table 5.22). Just over one fifth (15 morphotaxa, from 4 families) occurred on both *N. cunninghamii* and *N. gunnii*; nearly two thirds (35 morphotaxa, from 8 families) were found only on *N. cunninghamii*; and one seventh (8 morphotaxa, from 3 families) were found only on *N. gunnii*.

The most abundant morphotaxa was the immature Linyphiidae sp.2 (ArLnJ2, figure 5.9.b), with 19 individuals on *N. cunninghamii*, but only one individual on *N. gunnii* (table 5.23). The immatures Clubionidae sp.1 (ArCbJ01, figure 5.9.d) and Linyphiidae sp.1 (ArLnJ1, figure 5.9.a) were next most abundant on *N. cunninghamii* with 17 and 15 individuals respectively (*N. gunnii*: 0 and 1 individual). Most abundant on *N. gunnii*, with 11 individuals, was the immature Linyphiidae sp.10 (ArLnJ10, figure 5.9.c) (*N. cunninghamii*: 2 individuals), followed by immature Araneidae *Eriophora* sp.1 (ArArJ01, figure 5.9.e) with 9 individuals (*N. cunninghamii*: 5 individuals).

Morphotaxa	Family	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall	
		Total	Total	Total	Singleton Taxa
Adult	Linyphiidae	7	3	8	5
	Araneidae	3	4	6	3
	Theridiidae	4	1	5	5
	Clubionidae	2	0	2	1
	Theridosomatidae	2	0	2	1
	Orsolobidae	1	0	1	1
	Salticidae	1	0	1	1
	Thomisiidae	1	0	1	1
Adult Morphotaxa Total		21	8	26	18
Juveniles	Linyphiidae	10	6	11	2
	Theridiidae	6	0	6	2
	Araneidae	2	4	4	1
	Salticidae	3	1	3	1
	Clubionidae	2	1	2	0
	Orsolobidae	1	0	1	0
	Theridosomatidae	1	0	1	1
	Thomisiidae	1	0	1	1
Immature Morphotaxa Total		26	12	29	8
Overall Morphotaxa Total		47	20	55	26

Table 5.22. Araneae (Lake Fenton/Lake Skinner 1999-2000 subset) morphotaxon richness by family, *Nothofagus* species and overall totals; and number of singleton taxa per family.

Family	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall
	Total	Total	Total
Linyphiidae	95	27	122
Araneidae	11	26	37
Theridiidae	24	1	25
Clubionidae	21	3	24
Salticidae	5	1	6
Orsolobidae	4	1	5
Theridosomatidae	4	0	4
Thomisiidae	2	0	2
Morphotaxa Abundance	166	59	225
Miscellaneous immatures	32	1	33
Total Abundance	198	60	258

Table 5.23. Araneae (Lake Fenton/Lake Skinner 1999-2000 subset) morphotaxon abundance per family, *Nothofagus* species and total; and overall abundance including miscellaneous unidentified immatures.

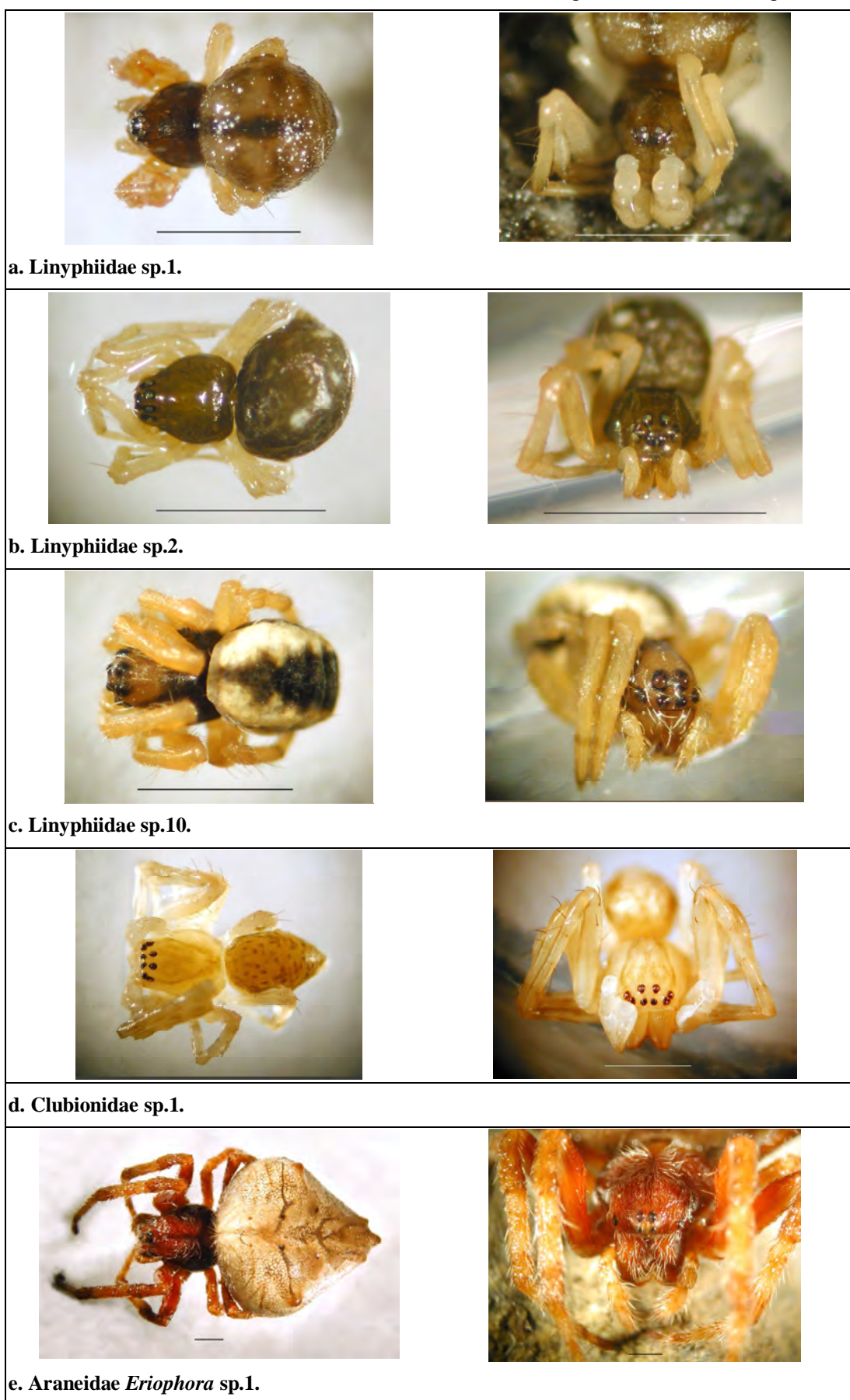
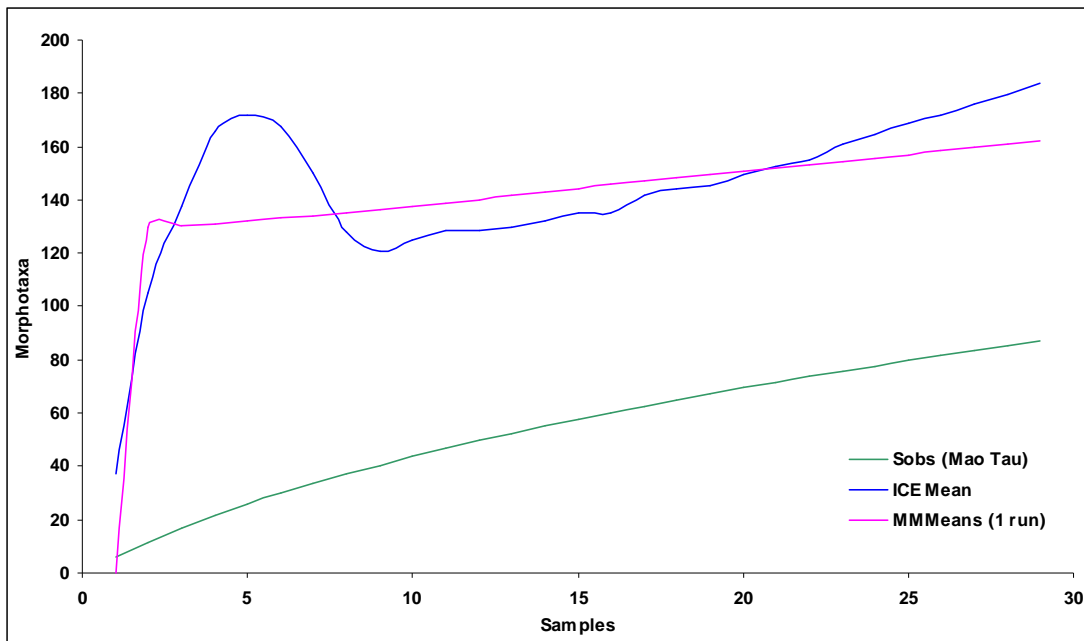


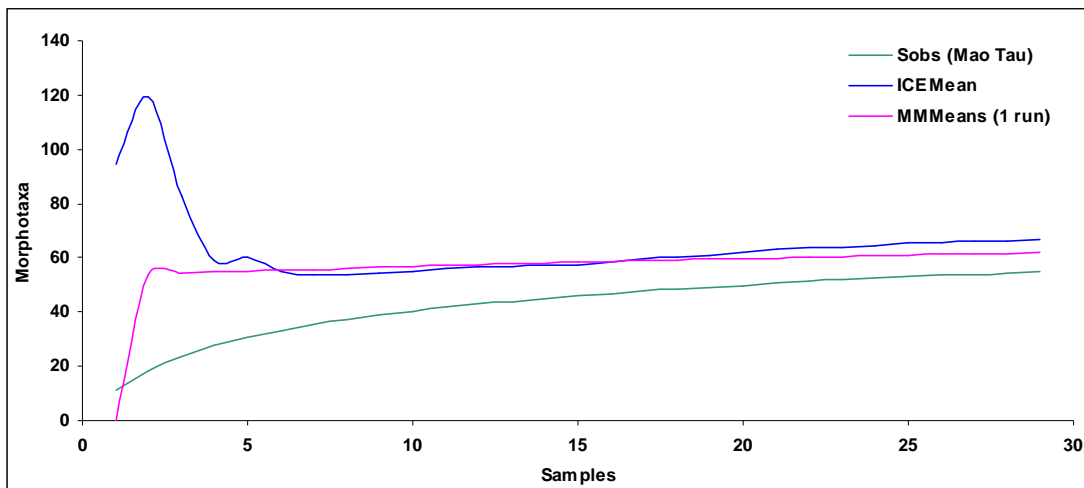
Figure 5.9. a-e. Most abundant Araneae (adults of the immature morphotaxa). Scale Bar 1 mm.

5.1.2 Morphotaxon Diversity: Sample-based Rarefaction Curves

Sample-based rarefaction curves were computed for the most taxon rich orders - Acarina and Coleoptera - using the combined *N. cunninghamii* and *N. gunnii* data, corrected for sampling effort per site and *Nothofagus* species (figure 5.10). The three curves, Sobs (Mao Tau, ICE Mean, MM Means) level off for Acarina, but not for Coleoptera.



a. Coleoptera



b. Acarina

Data Set	Samples (site/host)	Individuals Raw	Ind. Corrected (means per 10 beats)	Ind. Computed (converted to integers)	Sobs (Mao Tau)	ICE Mean	MM Means (1 run)
Acarina	29	7463	412.48	4113	55	66.47	61.94
Coleoptera	29	854	53.45	517	87	183.86	161.94

Figure 5.10. Sample-based rarefaction curves (Sobs MaoTau, ICE Mean, MM Means), combined data (*N. cunninghamii* plus *N. gunnii*): a. Coleoptera, b. Acarina. Computed using EstimateS (Version 7.5, R. K. Colwell, <http://purl.oclc.org/estimates>).

5.2 BETWEEN HOST AND REGIONAL VARIATION, ALL SITES

In order to explore general trends of variation in the arthropod fauna between the two *Nothofagus* species and between different regions within Tasmania, data from seventeen sites for *N. cunninghamii* and twelve sites for *N. gunnii* were corrected for sampling effort (to the equivalent of 1 x 10 beats per site) and singletons removed, before being subjected to multivariate analysis using the software package PC_ORD for Windows Version 4.7 (McCune & Mefford, 1999). The sample set excludes the preliminary visits and corresponds with Sampling Set 2, table 4.1.

5.2.1 Between Host, Between Region Variation

Between-host difference was found to be greater than differences between sites within each host group, as revealed by MRPP (Multi-Response Permutation Procedures) (table 5.24).

MRPP by Host	A	p	Average Euclidean Distance (Group size)	
			<i>N. cunninghamii</i>	<i>N. gunnii</i>
All sites	0.027	0.049	16.028 (17)	8.495 (12)

Table 5.24. MRPP results: data grouped by host.

Similarly, between-region difference was found to be greater than differences between sites within each region, but this was more strongly influenced by *N. cunninghamii* than *N. gunnii* (table 5.25).

MRPP by region	A	p	Average Euclidean Distance (Group size)					
			NE/Nc	NW/Nc	S/Nc	WC/Nc	S/Ng	WC/Ng
All sites	0.165	0.003	4.313 (5)	5.262 (2)	24.435 (5)	13.286 (5)	12.568 (3)	6.975 (9)
Nc sites	0.190	0.014	4.311 (5)	5.26 (2)	24.434 (5)	13.285 (5)	-	-
Ng sites	0.014	0.293	-	-	-	-	12.565 (3)	6.97 (9)

Table 5.25. MRPP results: data grouped by region. Nc: *N. cunninghamii*; Ng: *N. gunnii*; NE: North East; NW: North West; S: South; WC: West/Central.

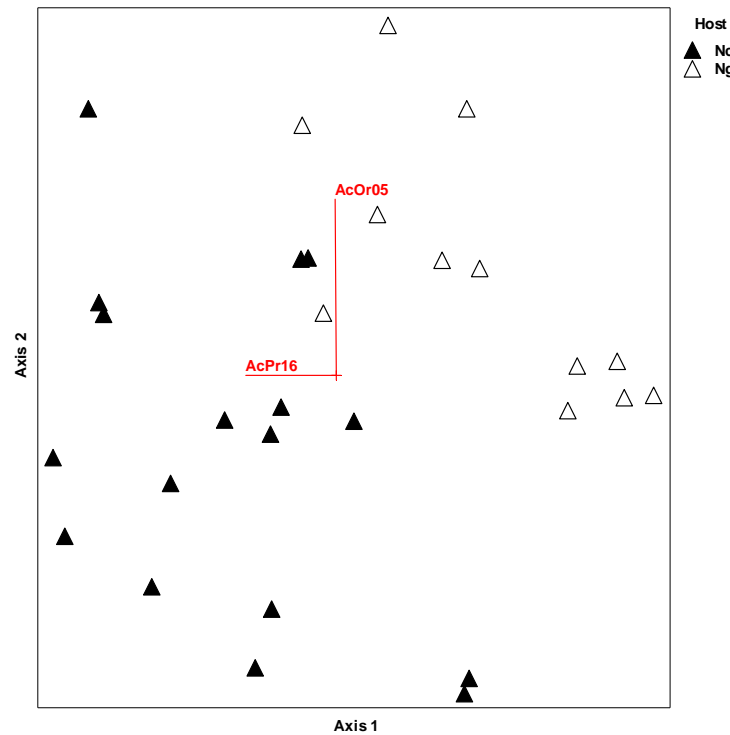
5.2.1.1 Between Host Variation: Indicator Values and Ordination

Indicator Species Analysis of all sites, grouped by host, revealed two morphotaxa, both on *N. cunninghamii*, with indicator values (IV) significant at $p = 0.001$: prostigmatid mite AcPr01, IV = 81.5; and aphid *Taiwanaphis tasmaniae* (HeAp1), IV = 81.8. Fourteen further morphotaxa, all on *N. cunninghamii*, had indicator values significant at $p < 0.05$, including the psocid PsCc1 (IV = 64, $p = 0.004$) (table 5.26).

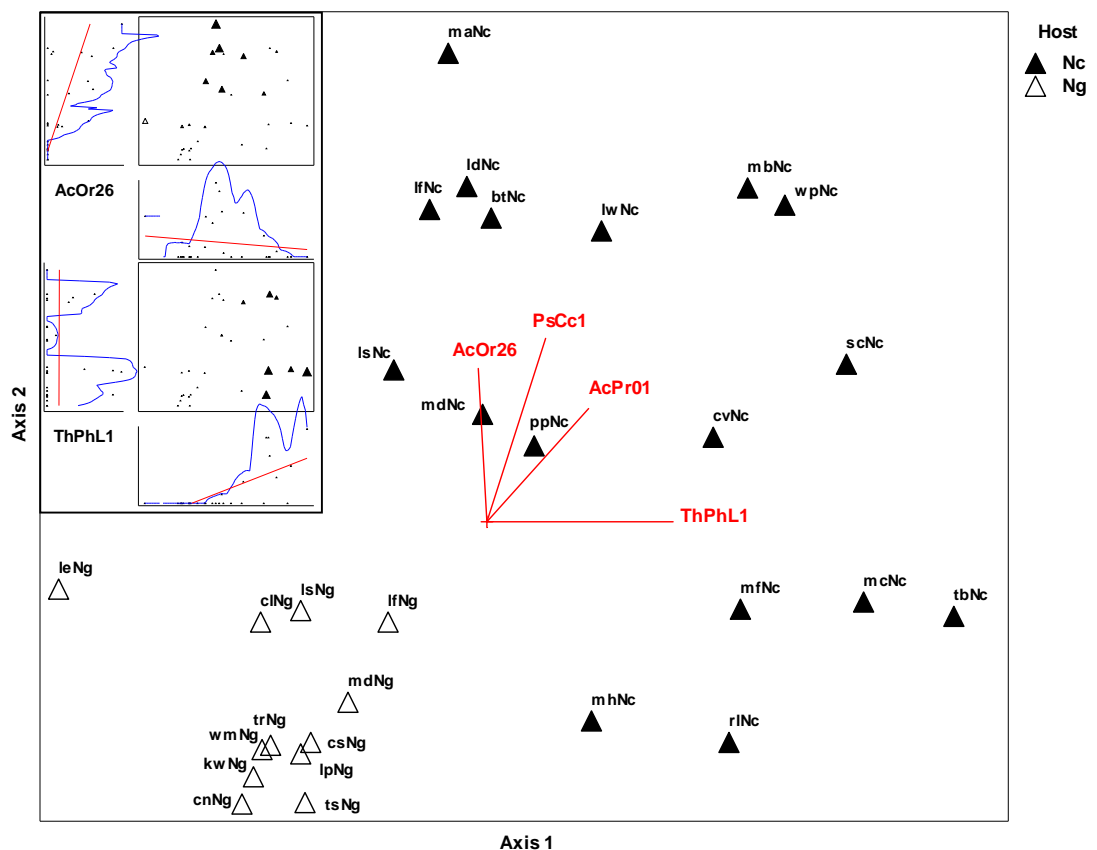
Morphotaxon	Host	IV	Mean	SD	p
AcPr01	Nc	81.5	41.7	8.79	0.001
HeAp1	Nc	81.8	36.8	8.75	0.001
LePsL1	Nc	66.8	32	8.05	0.002
PsBr7	Nc	58.8	28.4	8.94	0.003
PsCc1	Nc	64	30.8	8.93	0.004
CpCo02	Nc	52.9	25.5	8.33	0.006
LeGrL1	Nc	52.9	25.8	8.25	0.007
PcGr1	Ng	41.7	19.1	6.82	0.01
AcPr16	Nc	52.9	24.8	8.19	0.012
LeToL05	Nc	47.1	22.7	7.41	0.012
PsBr4	Nc	47.1	23.4	7.85	0.012
ThPhL1	Nc	47.1	22.6	7.3	0.012
AcOr16	Nc	41.2	20.6	7.28	0.018
AcOr02	Nc	55.3	35.9	8.73	0.036
CpLa01	Nc	39.5	24.3	8.24	0.036
CpCo07	Nc	35.3	18.5	6.82	0.043

Table 5.26. Indicator Values (IV): data grouped by host (All Sites, sample set 2). Significance at: $p = 0.001$ in red, $p < 0.05$ in blue. Nc: *N. cunninghamii*; Ng: *N. gunnii*. Ac, Acarina: AcOr, Oribatida; AcPr, Prostigmata. Cp, Coleoptera: CpCo, Coccinellidae; CpLa, Lathridiidae. He, Hemiptera: HeAp, Aphididae. Le, Lepidoptera: LeGr, Gracillariidae; LePs, Psychidae; LeTo, Tortricidae. Pc, Plecoptera: PcGr, Gripopterygidae. Ps, Psocoptera: PsBr, brachypterous morphotaxa; PsCc, Caeciliusidae. Th, Thysanoptera: ThPh, Phlaeothripidae. L preceding taxon number denotes immatures (Larva).

On ordination by host, the *Nothofagus* species separate (figure 5.11), the trend being more marked on ordination with the data transformed by $\log x + 1$. The morphotaxa joint plot (cutoff $r^2 = 0.4$) and main matrix overlays of the latter ordination reveal oribatid mite AcOr26 to have a positive correlation with axis 2 ($r = 0.634$, $\tau = 0.511$) and Phlaeothripidae larva ThPhL1 to be strongly correlated with axis 1 ($r = 0.702$, $\tau = 0.558$) (insets, figure 5.11).



a. Untransformed data: minimum stress 3 axes = 12.776, $p = 0.0323$, $r^2 = 0.3$.



b. Data transformed by Log X + 1. Minimum stress 3 axes = 12.057, $p = 0.0323$, cutoff $r^2 = 0.4$. Insert: main matrix overlay for AcOr26 and ThPhL1.

Figure 5.11. a, b. Ordinations by Host and morphotaxa joint plot (N = 147): all sites, morphotaxa trimmed of singletons. Nc: *N. cunninghamii*; Ng: *N. gunnii*. AcOr: Acarina, Oribatidae; AcPr: Acarina, Prostigmata; PsCc: Psocoptera, Caeciliusidae; ThPhL: Thripidae, Phlaeothripidae, larva.

5.2.1.2 Between Region Variation: Indicator Values and Ordination

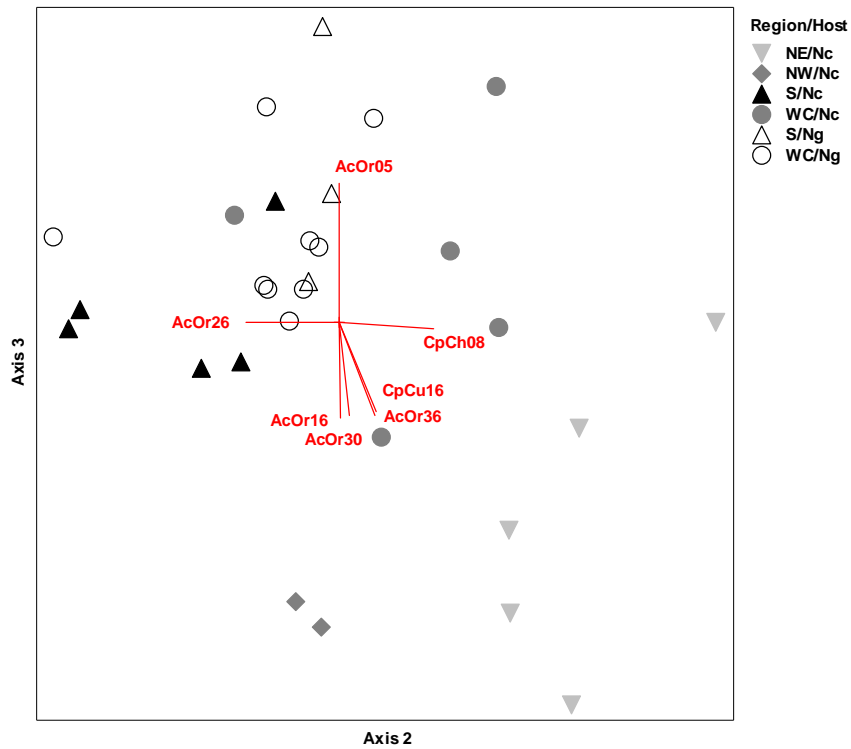
When all sites were grouped by region, two different morphotaxa had indicator values significant at $p = 0.001$: oribatid mite AcOr26, IV = 83.8, on southern *N. cunninghamii*; and stonefly PcGr2, IV = 91.9 on southern *N. gunnii*; and a further sixteen morphotaxa, most on southern *N. cunninghamii*, had indicator values significant at $p < 0.05$ (table 5.27), possibly reflecting the increased sampling effort in the South compared with the other regions in this sample set.

Morphotaxon	Region/Host	IV	Mean	SD	p
AcOr26	S/Nc	83.8	32.3	13.92	0.001
PcGr2	S/Ng	91.9	22	12.19	0.001
AcOr16	NW/Nc	80.5	23.7	11.64	0.002
ThTh2	WC/Nc	50.6	27.3	7.7	0.007
CpCu10	S/Ng	66.7	20.5	10.77	0.009
CpCm01	NE/Nc	57.6	22.9	12.22	0.017
CpSr02	NE/Nc	58.5	22.8	13.06	0.021
AcMe05	S/Ng	54.4	24.2	11.66	0.03
LeToL07	NE	51.4	21.5	12.43	0.03
CpCo01	S/Nc	55.6	22.8	13.23	0.032
CpCh03	S/Nc	55.8	23.7	12.56	0.033
HeCx1	S/Nc	51.7	22.4	12.75	0.037
LeGeL4	S/Nc	50.3	23.1	12.32	0.037
CpCh08	NE/Nc	56.8	25.5	13.53	0.038
AcOr05	S/Ng	49	28.7	9.86	0.041
CpChL1	S/Nc	48.9	21.4	12.13	0.042
HeLy2	S/Ng	45	20.7	11.04	0.043
PsPd1	S/Nc	54.5	24.2	13.65	0.045

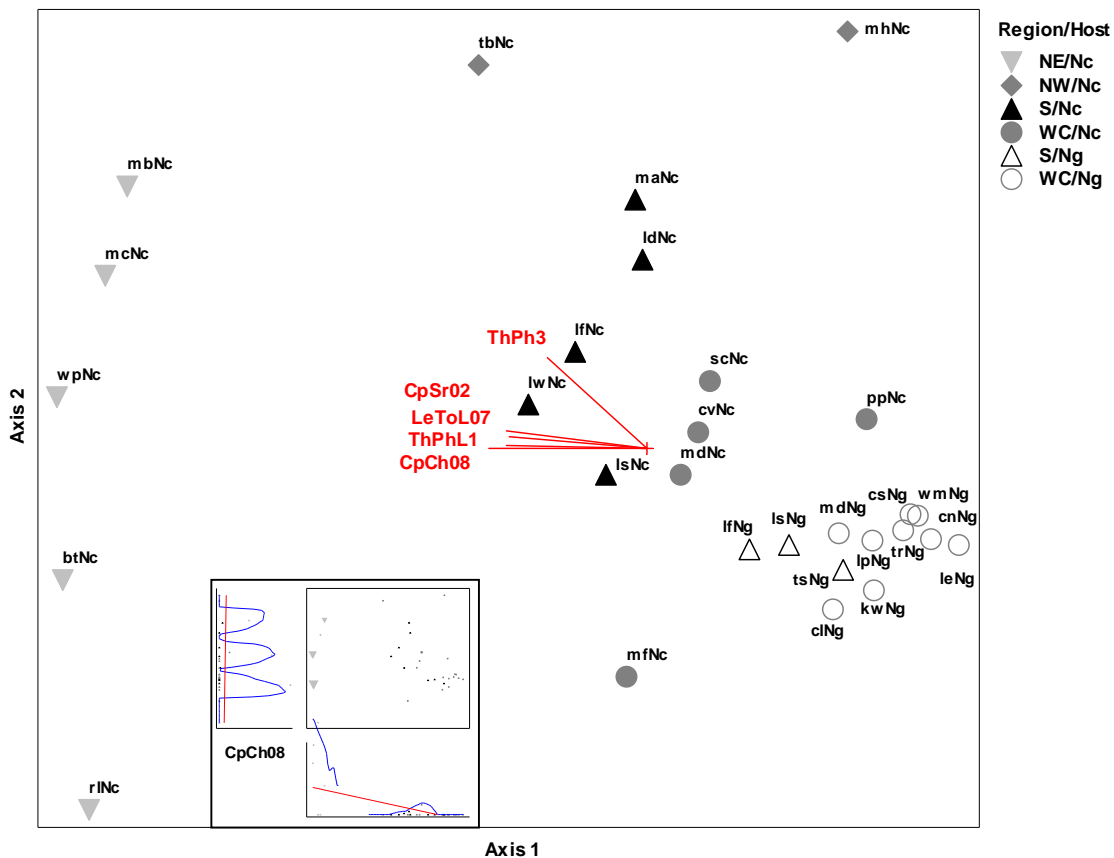
Table 5.27. Indicator Values (IV): data grouped by region (All Sites, sample set 2). Significance at: $p = 0.001$ in red, $p < 0.05$ in blue. Nc: *N. cunninghamii*; Ng: *N. gunnii*. NE: North East; NW: North West; S: South; WC: West/Central. Ac, Acarina: AcMe, Mesostigmata; AcOr, Oribatida. Cp, Coleoptera: CpCh, Chrysomelidae; CpCm, Clambidae; CpCo, Coccinellidae; CpSr, Scirtidae; CpCu, Curculionidae. He, Hemiptera: HeCx, Cixiidae; HeLy, Lygaeidae. Le, Lepidoptera: LeGe, Geometridae; LeTo, Tortricidae. Pc, Plecoptera: PcGr, Gripopterygidae. Ps, Psocoptera: PsPd, Pseudocaeciliidae. Th, Thysanoptera: ThTh, Thripidae. L preceding taxon number denotes immatures (larva).

Ordination by region showed the sites to separate into region/host groups (figure 5.12) and, as with the ordination by host, the trend was again more pronounced when the data was transformed by $\log x + 1$; the North East *N. cunninghamii* sites separating from the others, being constrained within low values on axis 1; the North West *N. cunninghamii* sites separated out on axis 2, at the top of the graph; the

remaining site/host groups are clumped but less clearly defined. Morphotaxa joint plot (cutoff $r^2 = 0.35$, fig) and main matrix overlays of the transformed ordination showed all five taxa correlated negatively with axis 1 and hence biased to the north-eastern sites, the effect being most marked for the chrysomelid beetle CpCh08 ($r = -0.664$, $\tau = -0.405$) (inset, figure 5.12).



a. Untransformed data: minimum stress 3 axes = 10.887, $p = 0.0323$, $r^2 = 0.3$.



b. Data transformed by Log X + 1. Minimum stress 3 axes = 7.032, $p = 0.0323$, cutoff $r^2 = 0.35$. Insert: main matrix overlay for CpCh08.

Figure 5.12. a, b. Ordinations by Region and morphotaxa joint plot (N = 147): all sites, morphotaxa trimmed of singletons. Nc: *N. cunninghamii*; Ng: *N. gunnii*; NE: North East; NW: North West; S: South; WC: West/Central.

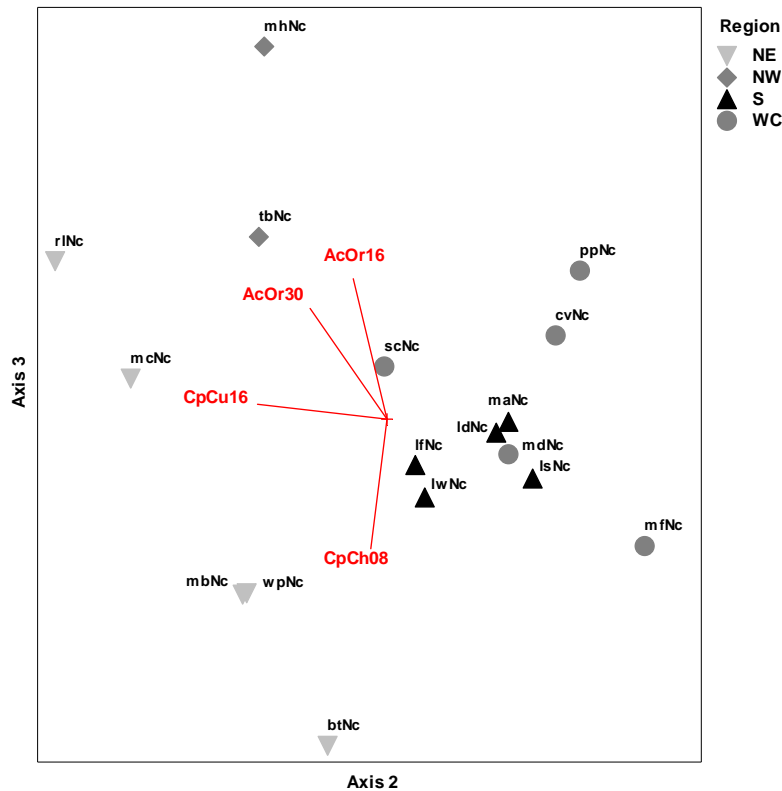
5.2.1.3 *Between Region Variation: Indicator Values and Ordination, N. cunninghamii*

When Indicator Species Analysis, grouped by region, was applied to *N. cunninghamii*, two morphotaxa, both in the South, had indicator values significant at $p = 0.005$: chrysomelid beetle CpCh01, $IV = 95.7$, $p = 0.003$; and oribatid mite AcOr26, $IV = 89$, $p = 0.005$; and a further four morphotaxa (from, West/Central, Northwest and South) had indicator values significant at $p < 0.05$ (table 5.28).

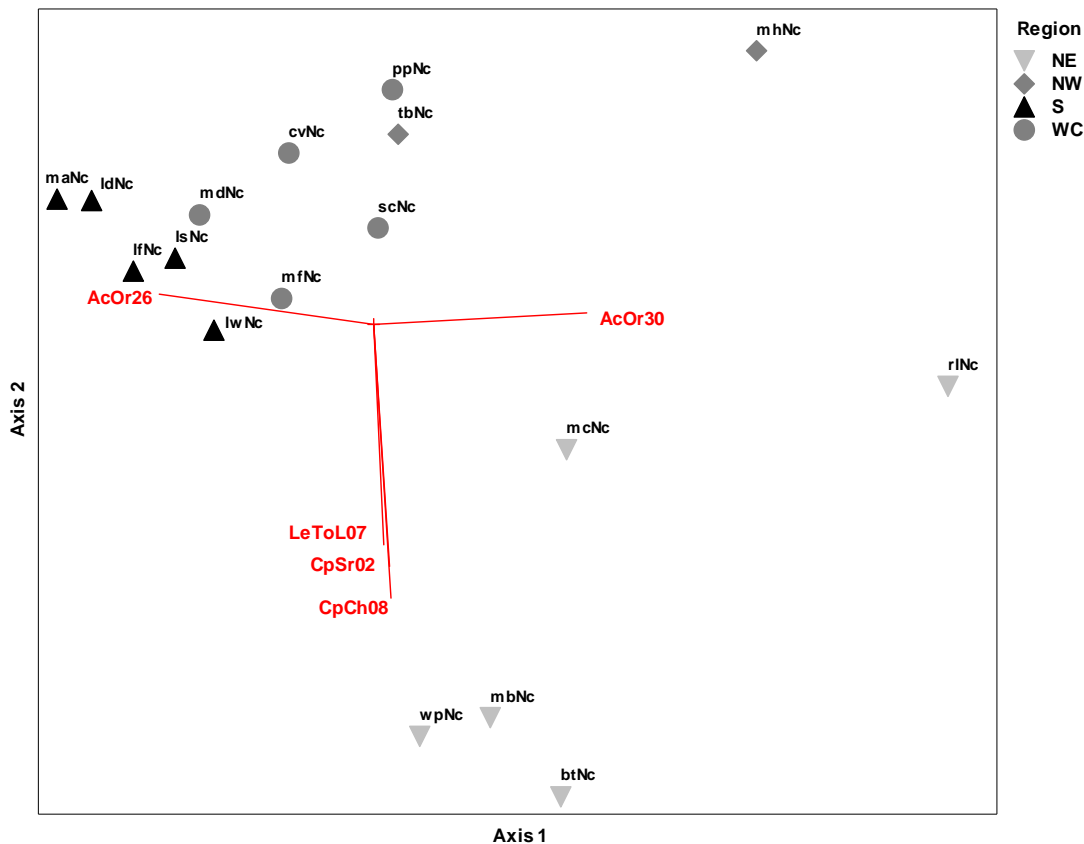
Morphotaxon	Region	IV	Mean	SD	p
CpCh01	S	95.7	37.4	17.27	0.003
AcOr26	S	89	39.1	15.6	0.005
ThTh2	WC	60.6	37.4	9.57	0.007
AcOr16	NW	80.5	33.1	14.19	0.014
AcOr10	S	80	28.7	15.28	0.023
ThTh3	S	80	31.6	16.36	0.032

Table 5.28. Indicator Values (IV): data grouped by region (All Sites, sample set 2), *N. cunninghamii*. Significance at: $p < 0.05$. NW: North West; S: South; WC: West/Central. Ac, Acarina: AcOr, Oribatida. Cp, Coleoptera: CpCh, Chrysomelidae. Th, Thysanoptera: ThTh, Thripidae.

Ordination of the *N. cunninghamii* sites showed separation of the regions (figure 5.13.a), this being more clearly defined on the ordination of the Log $x + 1$ transformed data (figure 5.13.b). Morphotaxa joint plot (cutoff $r^2 = 0.5$, figure 5.13.a) and main matrix overlays of the *N. cunninghamii* Log $x+1$ transformed ordination revealed three taxa heavily biased towards the north-eastern sites and strongly negatively correlated with axis 2: chrysomelid beetle CpCh08 ($r = -0.852$, $\tau = -0.410$), scirtid beetle CpSr02 ($r = -0.801$, $\tau = -0.499$) and tortricid moth larva LeToL07 ($r = -0.766$, $\tau = -0.466$); oribatid mite AcOr30 ($r = 0.753$, $\tau = 0.470$) has a strong positive correlation with axis 1, but is heavily biased by the sites rlNc (Rainforest Ledge, North East) and mhNc (Milkshake Hills, North West), both of which are single visit sites; finally, oribatid mite AcOr26 ($r = -0.754$, $\tau = -0.644$) has a strong negative correlation with axis 1, being skewed by the multi-visit southern sites, especially maNc (Mt. Arthur) and ldNc (Lake Dobson).



a. Untransformed data: minimum stress 3 axes = 6.627, $p = 0.0323$, cutoff $r^2 = 0.4$.



b. Data transformed by Log $x + 1$. Minimum stress 3 axes = 5.838, $p = 0.0323$, cutoff $r^2 = 0.5$.

Figure 5.13. a, b. Ordinations by Region and morphotaxa joint plot for *N. cunninghamii*: all sites, morphotaxa trimmed of singletons ($N = 128$). NE: North East; NW: North West; S: South; WC: West/Central.

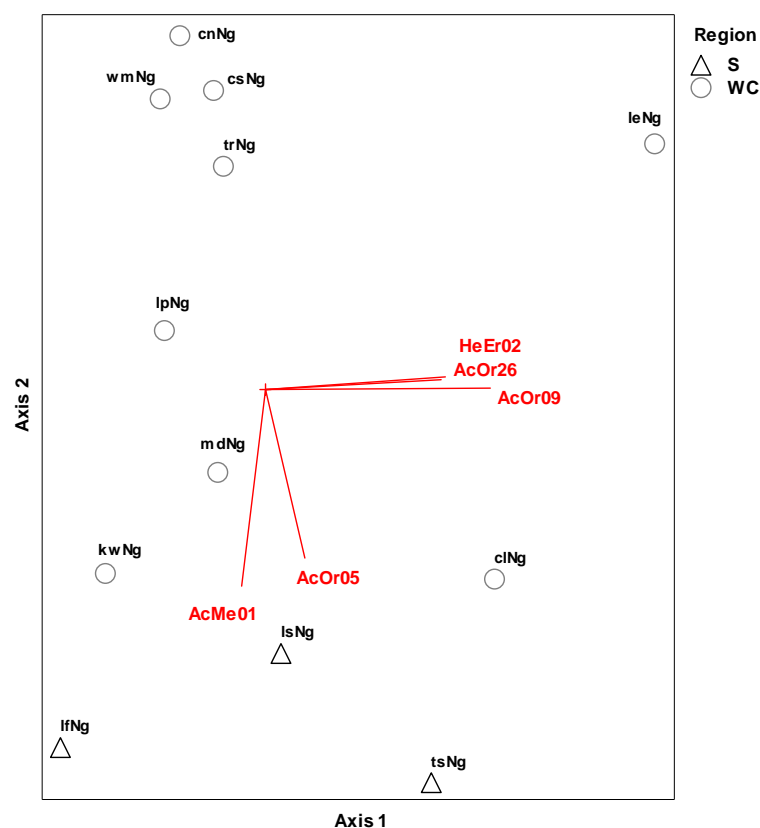
5.2.1.4 Between Region Variation: Indicator Values and Ordination, *N. gunnii*

Regional analysis of *N. gunnii* revealed one morphotaxon, in the South, with an indicator value significant at $p < 0.005$: stonefly PcGr2, IV = 100, $p = 0.004$. Five further morphotaxa, all in the South, had indicator values significant at $p < 0.05$ (table 5.29).

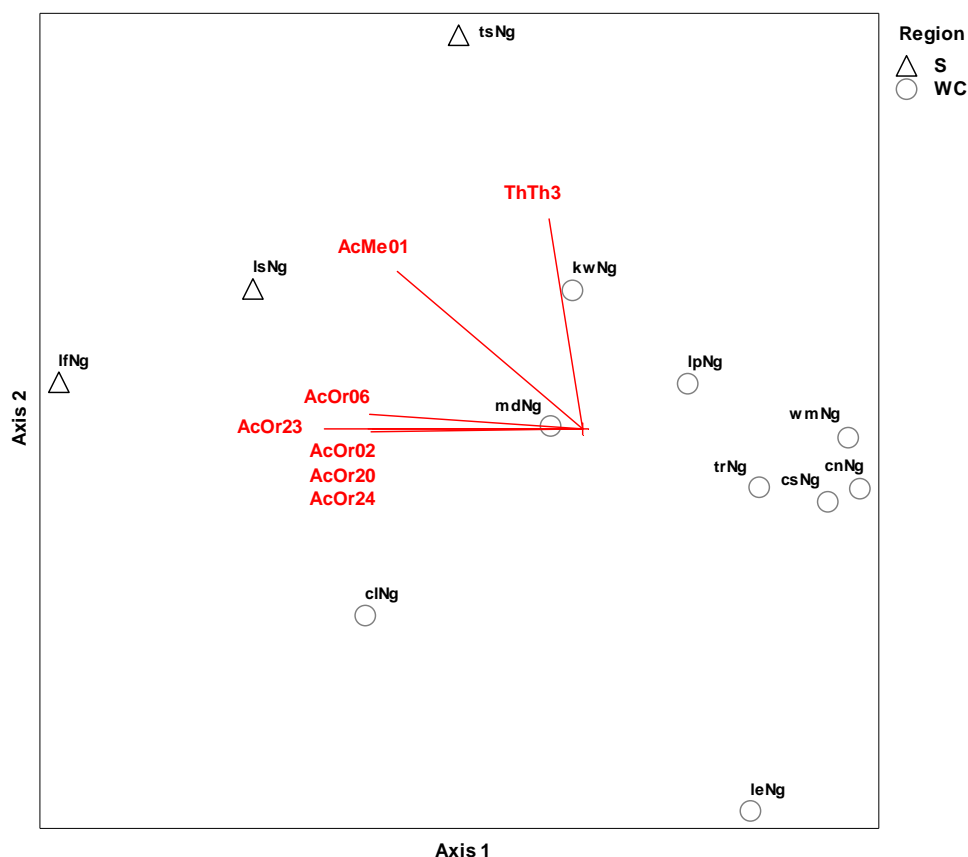
Morphotaxon	Region	IV	Mean	SD	p
PcGr2	1(S)	100	29.2	13.19	0.004
AcMe05	1(S)	91	34.3	14.09	0.009
ThTh3	1(S)	61.6	28.9	13.4	0.035
CpCu10	1(S)	66.7	25	9.15	0.044
HeLy2	1(S)	66.7	25.1	9	0.044
ThTh4	1(S)	66.7	24.6	9.89	0.044

Table 5.29. Indicator Values (IV): data grouped by region (All Sites, sample set 2), *N. gunnii*. Significance at $p < 0.05$. S: South. Ac, Acarina: AcOr, Oribatida. Cp, Coleoptera: CpCu, Curculionidae. He, Hemiptera: HeLy, Lygaeidae. Pc, Plecoptera: PcGr, Gripopterygidae. Th, Thysanoptera: ThTh, Thripidae.

On ordination, the two regions, South and West/Central separate with untransformed and Log $x+1$ transformed data (figures 5.14.a, b). The untransformed ordination (figure 5.14.a) is heavily biased by the sites leNg (Lake Eros, West/Central, single visit) and clNg (Cater Lake, West/Central, two visits) as shown by the morphotaxa joint plot (cutoff $r^2 = 0.5$) and main matrix overlays. The Log $x + 1$ ordination overlays (cutoff $r^2 = 0.6$, figure 5.14.b) show a strong bias of morphotaxa to the southern sites with five morphotaxa negatively correlating with axis1, oribatid mite AcOr23 ($r = -0.873$, $\tau = -0.674$) having the strongest correlation; thrip ThTh3 positively correlates with axis 2 ($r = 0.788$, $\tau = 0.674$), with a heavy bias to tsNg (Tarn Shelf); mesostigmatid mite AcMe01 has weaker correlation with either axis (axis 1: $r = -0.739$, $\tau = -0.625$; axis 2: $r = 0.682$, $\tau = 0.53$) and is more strongly biased by the West/Central sites, particularly mdNg (Mt Dundas).



a. Untransformed data: minimum stress 3 axes = 1.815, $p = 0.0323$, cutoff $r^2 = 0.5$.



b. Data transformed by $\text{Log } x + 1$. Minimum stress 3 axes = 1.892, $p = 0.0323$, cutoff $r^2 = 0.6$.

Figure 5.14. a, b. Ordinations by region and morphotaxa joint plot for *N. gunnii*: all sites, morphotaxa trimmed of singletons ($N = 11$). S: South; WC: West/Central.

5.3 REGIONAL AND SEASONAL VARIATION, REGION/SEASON SITES

Sampling set 3 (table 4.1), from twelve sites for *N. cunninghamii* and seven sites for *N. gunnii* visited in spring, summer and autumn enables a closer examination of regional variation, and also gives an indication of seasonal variation, in the arthropod fauna. The data were corrected for sampling effort to that used at the majority of sites (the equivalent of 9 x 10 beats per site for regional variation; and 3 x 10 beats for seasonal variation) and singletons removed, before being subjected to multivariate analysis using the software package PC_ORD for Windows Version 4.7 (McCune & Mefford, 1999). In the regional analysis, data from the single multi-visit North West *N. cunninghamii* site (Tayatea Bridge) were added to its closest neighbours, the West/Central *N. cunninghamii* sites, because grouped data analyses (MRPP and Indicator Values) require the groups to contain more than one member.

5.3.1 Regional Variation

Overall, the regional variation data set comprised 246 morphotaxa (107 singletons) with a total abundance of 4401 individuals. After beat correction and removal of singletons this became a total abundance of 4232 individuals and morphotaxon richness of 139.

5.3.1.1 Between Host, Between Region Variation

In this subset of the data, between-host difference was again found to be greater than differences between sites within each host group, as revealed by MRPP (table 5.30).

MRPP by Host	A	p	Average Euclidean Distance (Group size)	
			<i>N. cunninghamii</i>	<i>N. gunnii</i>
All sites	0.08	0.006	141.521 (12)	70.422 (7)

Table 5.30. MRPP results: data grouped by host (sampling set 3).

Between-region difference was found to be greater than differences between sites within each region overall and for *N. cunninghamii*, but not for *N. gunnii* (table 5.31).

MRPP by region	A	P	Average Euclidean Distance (Group size)				
			NE/Nc	S/Nc	WC/Nc	S/Ng	WC/Ng
All sites	0.186	0.005	36.91 (3)	174.872 (5)	109.45 (4)	69.183 (3)	77.077 (4)
Nc sites	0.162	0.032	36.892 (3)	174.865 (5)	109.44 (4)	-	-
Ng sites	-0.046	0.827	-	-	-	69.085 (3)	77.074 (4)

Table 5.31. MRPP results: data grouped by region (sampling set 3). Nc: *N. cunninghamii*; Ng: *N. gunnii*; NE: North East; S: South; WC: West/Central.

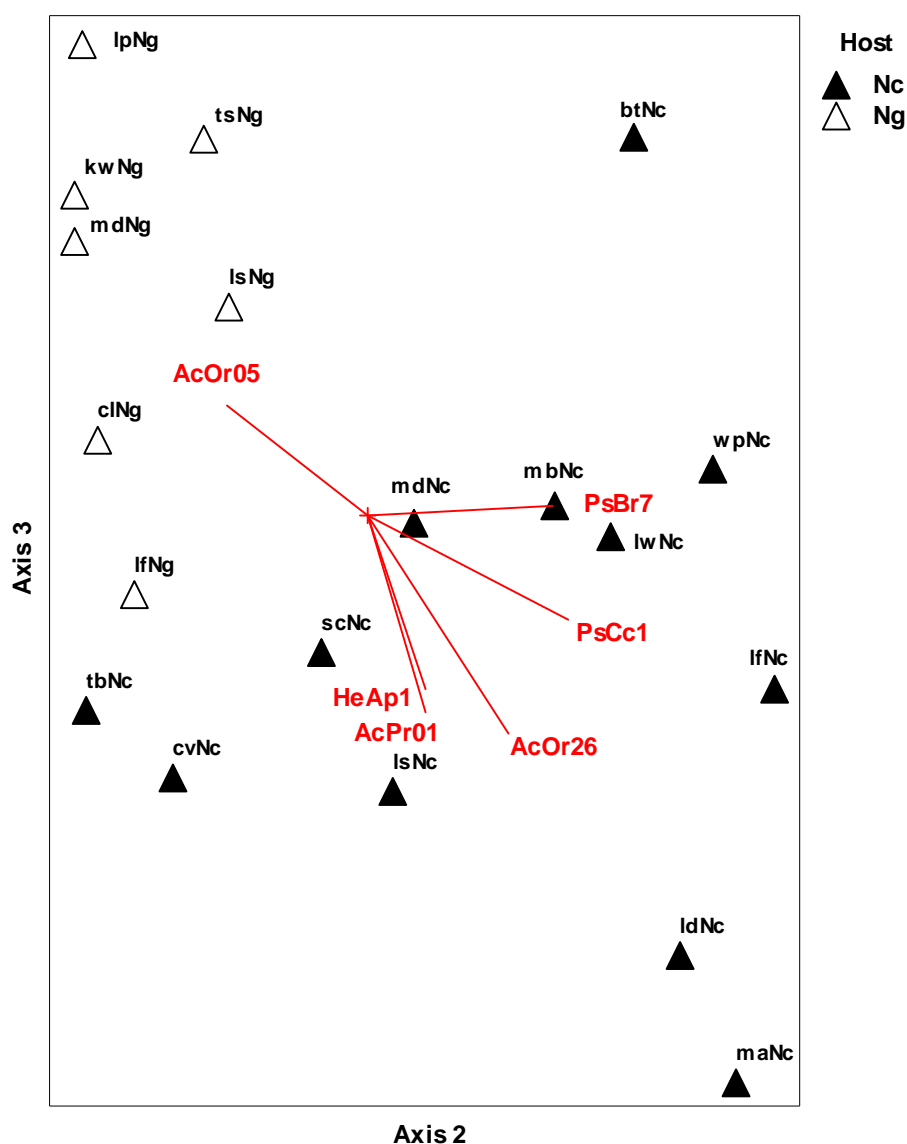
5.3.1.2 Between Host Variation: Indicator Values and Ordination

Indicator Species Analysis grouped by host, revealed two morphotaxa with indicator values (IV) significant at $p = 0.002$: on *N. cunninghamii* the aphid HeAp1, $IV = 100$; and on *N. gunnii* the small oribatid mite AcOr05, $IV = 83.4$. Eight further morphotaxa on *N. cunninghamii*, and one on *N. gunnii* had indicator values significant at $p = 0.05$ (table 5.32).

Morphotaxon	Host	IV	Mean	SD	p
HeAp1	Nc	100	43.7	10.17	0.001
PsCc1	Nc	81.6	42.4	10.54	0.003
PsBr7	Nc	75	36.5	10.76	0.008
CpCo02	Nc	58.3	30.2	9.6	0.025
AcPr01	Nc	75.6	49.8	11.05	0.026
PsBr4	Nc	58.3	32.2	10.65	0.033
LeToL05	Nc	58.3	30	10.08	0.036
LePsL1	Nc	61.5	36.7	10.64	0.042
AcOr06	Nc	50	27.2	9.65	0.046
AcOr05	Ng	83.4	48.8	9.81	0.002
AcMe01	Ng	68.8	57.3	5.57	0.037

Table 5.32. Indicator Values (IV): data grouped by host (sample set 3). Significance at: $p \leq 0.002$ in red, $p < 0.05$ in blue. Nc: *N. cunninghamii*; Ng: *N. gunnii* (shaded rows). Ac, Acarina: AcMe, Mesostigmata; AcOr, Oribatida; AcPr, Prostigmata. Cp, Coleoptera: CpCo, Coccinellidae. He, Hemiptera: HeAp, Aphididae. Le, Lepidoptera: LePs, Psychidae; LeTo, Tortricidae. Ps, Psocoptera: PsBr, brachypterous morphotaxa; PsCc, Caeciliusidae. L preceding taxon number denotes immatures (larva).

On ordination by host, the *Nothofagus* species separate on axes 2 and 3 (figure 5.15), *N. gunnii* being confined to low values on axis 2 and mid to high values on axis 3, whereas *N. cunninghamii* is spread across low to high values on both axes.



Morphotaxon	Axis2			Axis3		
	r	r-sq	τ	r	r-sq	τ
AcOr05	-0.569	0.323	-0.399	0.505	0.255	0.339
AcOr26	0.565	0.319	0.507	-0.702	0.493	-0.507
AcPr01	0.365	0.133	0.278	-0.669	0.448	-0.662
HeAp1	0.367	0.135	0.464	-0.631	0.398	-0.591
PsBr7	0.652	0.425	0.536	0.144	0.021	-0.096
PsCc1	0.675	0.456	0.62	-0.486	0.237	-0.233

Figure 5.15. Ordination by Host, with morphotaxa joint plot and main matrix correlations (sampling set 3), morphotaxa trimmed of singletons (N = 139). Minimum stress 3 axes = 9.679, $p = 0.0323$, cutoff $r^2 = 0.4$. Nc: *N. cunninghamii*; Ng: *N. gunnii*. Ac, Acarina: AcOr, Oribatida; AcPr, Prostigmata. He, Hemiptera: HeAp, Aphididae. Ps, Psocoptera: PsBr, brachypterous morphotaxa; PsCc, Caeciliusidae.

On morphotaxa joint plot (cutoff $r^2 = 0.4$) and main matrix correlation (figure 5.15) five morphotaxa are strongly biased to *N. cunninghamii*: two showing a strong positive correlation with axis 2: Psocids PsBr7 and PsCc1; and three showing strong negative correlation with axis 3: aphid HeAp1, oribatid mite AcOr26 and prostigmatid mite AcPr01; while one morphotaxon, the oribatid mite AcOr05, is biased towards *N. gunnii*.

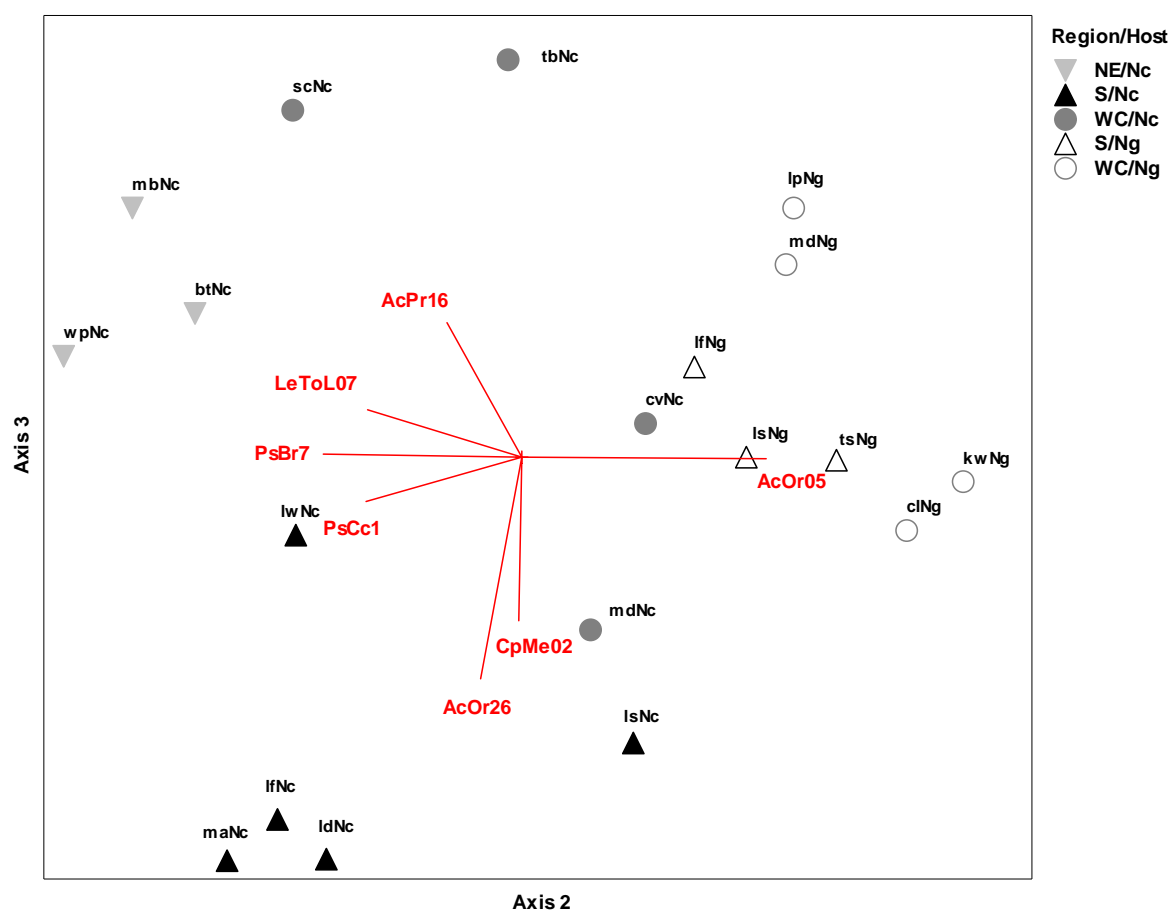
5.3.1.3 *Between Region Variation: Indicator Values and Ordination*

With the region/host data grouped by region, three morphotaxa, all on North East *N. cunninghamii*, had indicator values significant at $p = 0.005$: scirtid beetle CpSr02 (IV = 91.7, $p = 0.004$); chrysomelid beetle CpCh08 (IV = 94.9, $p = 0.005$); and brachypterous psocid PsBr7 (IV = 70.7, $p = 0.005$). A further twelve morphotaxa had indicator values significant at $p = 0.05$ (table 5.33) and reveal a different profile from the host-grouped data above, only five morphotaxa (on *N. cunninghamii*: AcOr26, CpCh08, LeGrL1, PsBr7; on *N. gunnii*: AcMe01) having indicator values significant at $p < 0.05$ in both analyses.

On ordination by region/host, the North East *N. cunninghamii* sites are confined within low values on axis, the South and West Central *N. cunninghamii* sites are constrained within low to mid values on axis 2, while the *N. gunnii* sites (South and West Central) occupy higher values on the same axis. Morphotaxa joint plot (cutoff $r^2 = 0.4$) and correlation with the main matrix (figure 5.16) show: two morphotaxa with strong negative correlation with axis 2 and strong bias toward the North East *N. cunninghamii* sites (PsBr7, LeToL07); two morphotaxa with strong negative correlation with axis 3 and strong bias toward the Southern *N. cunninghamii* sites (AcOr26, CpMe02); one morphotaxon with strong positive correlation with axis 2 and bias towards the Southern *N. gunnii* sites (AcOr05); and two morphotaxa strongly skewed by bias toward more than one region (AcPr16 to North East and West/Central *N. cunninghamii*, PsCc1 to North East and Southern *N. cunninghamii*).

Morphotaxon	Region/Host	IV	Mean	SD	p
CpSr02	NE/Nc	91.7	25.9	13.66	0.004
CpCh08	NE/Nc	94.9	30.8	15.13	0.005
PsBr7	NE/Nc	70.7	30.5	11.79	0.005
LeToL07	NE/Nc	88.9	25.4	13.85	0.006
CpSr07	NE/Nc	66.7	24.3	13.01	0.038
AcOr26	S/Nc	76.6	36.6	12.55	0.006
HeCx1	S/Nc	60	25.5	13.85	0.018
CpCh03	S/Nc	60.2	28.9	13.32	0.027
CpCo01	S/Nc	60	24.7	13.67	0.043
AcOr36	WC/Nc	75	23.1	13.47	0.008
LeGrL1	WC/Nc	67.9	31	14.51	0.023
ThThL1	WC/Nc	49.9	23.6	12.62	0.032
AcMe01	S/Ng	37.7	29.3	3.97	0.035
CpCu10	S/Ng	66.7	22.4	13.18	0.039
PcGr2	S/Ng	55.6	23.8	14.02	0.039

Table 5.33 Indicator Values (IV): data grouped by region (sample set 3) and sorted by region/host. Significance at: $p \leq 0.005$ in red, $p < 0.05$ in blue. Nc: *N. cunninghamii*; Ng: *N. gunnii*; NE: North East; S: South; WC: West/Central. Ac, Acarina: AcMe, Mesostigmata; AcOr, Oribatida. Cp, Coleoptera: CpCh, Chrysomelidae; CpCo, Coccinellidae; CpCu, Curculionidae; CpMe, Melandryidae. He, Hemiptera: HeCx, Cixiidae. Le, Lepidoptera: LeGr, Gracillariidae; LeTo, Tortricidae. Pc, Plecoptera: PcGr, Gripopterygidae. Ps, Psocoptera: PsBr, brachypterous morphotaxa. Th, Thysanoptera: ThTh, Thripidae. L preceding taxon number denotes immatures (larva).



Morphotaxon	Axis2			Axis3		
	r	r-sq	τ	r	r-sq	τ
AcOr05	0.803	0.644	0.653	-0.087	0.008	-0.157
AcOr26	-0.328	0.107	-0.269	-0.762	0.581	-0.733
AcPr16	-0.445	0.198	-0.361	0.595	0.354	0.441
CpMe02	-0.108	0.012	-0.168	-0.655	0.429	-0.521
LeToL07	-0.637	0.406	-0.579	0.356	0.127	0.37
PsBr7	-0.725	0.525	-0.673	0.107	0.011	0.014
PsCc1	-0.641	0.411	-0.659	-0.345	0.119	-0.142

Figure 5.16. Ordination by Region, with morphotaxa joint plot and main matrix correlations (sampling set 3), morphotaxa trimmed of singletons (N = 139). Minimum stress 3 axes = 9.635, $p = 0.0323$, cutoff $r^2 = 0.4$. Nc: *N. cunninghamii*; Ng: *N. gunnii*; NE: North East; S: South; WC: West/Central. Ac, Acarina: AcOr, Oribatida; AcPr, Prostigmata. Cp, Coleoptera: CpMe, Melandryidae. Le, Lepidoptera: LeTo, Tortricidae. Ps, Psocoptera: PsBr, brachypterous morphotaxa; PsCc, Caeciliusidae. L preceding taxon number denotes immatures (larva).

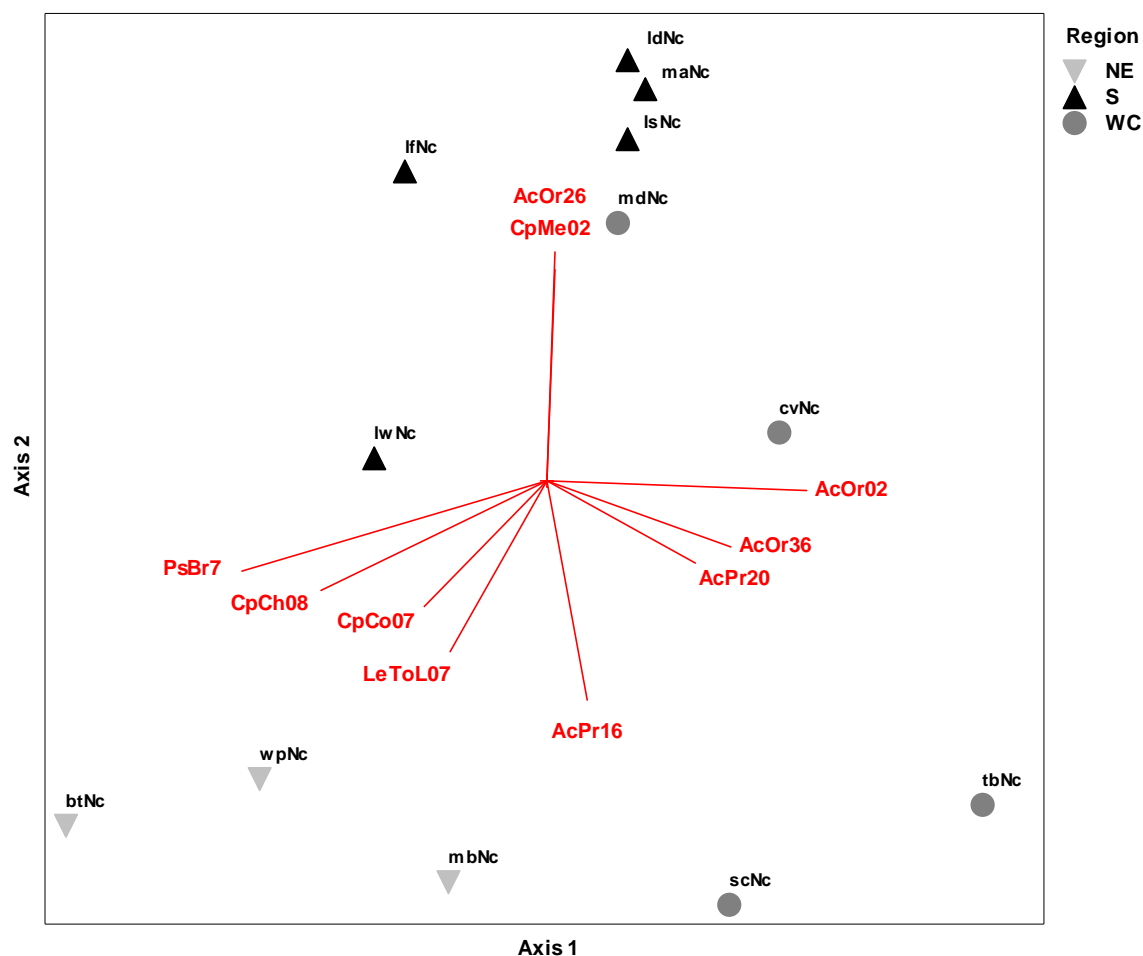
5.3.1.4 *Between Region Variation: Indicator Values and Ordination, N. cunninghamii*

Indicator Species Analysis, grouped by region, applied to *N. cunninghamii* Sample Set 3 sites, revealed one morphotaxon with an indicator value significant at $p = 0.005$: the scirtid beetle CpSr02 (IV 100) for the North East. Eight morphotaxa had indicator values significant at $p < 0.05$, four for the North East and two apiece for the South and West/Central (table 5.34).

Morphotaxon	Region	IV	Mean	SD	p
CpSr02	NE	100	30.2	15.95	0.005
CpCh08	NE	94.9	42.2	17.16	0.008
LeToL07	NE	88.9	33.7	15.32	0.009
PsBr7	NE	70.7	44.2	11.54	0.022
CpSr07	NE	66.7	26.8	14.59	0.048
AcOr26	S	83.1	48.1	13.84	0.01
CpCh01	S	77.8	39.9	17.37	0.044
AcOr36	WC	75	29.3	14.57	0.014
AcOr02	WC	69.1	43.6	11.26	0.017

Table 5.34 Indicator Values: *N. cunninghamii* data grouped by region (sample set 3). NE: North East; S: South; WC: West/Central. Table 5. Indicator Values (IV): data grouped by region (sample set 3) and sorted by region/host. Significance at: $p = 0.005$ in red, $p < 0.05$ in blue. Nc: *N. cunninghamii*; Ng: *N. gunnii*; NE: North East; S: South; WC: West/Central. Ac, Acarina: AcOr, Oribatida. Cp, Coleoptera: CpCh, Chrysomelidae; CpSr, Scirtidae. Le, Lepidoptera: LeTo, Tortricidae. Ps, Psocoptera: PsBr, brachypterous morphotaxa. L preceding taxon number denotes immatures (larva).

Ordination (figure 5.17), showed the North East sites to be constrained within lower values on both axes 1 and 2, separating from West/Central on axis 1 and from the South on axis 2. On joint plot (cutoff $r^2 = 0.4$), the morphotaxa fan out (figure 5.17). Two morphotaxa (oribatid mite AcOr26, melandryid beetle CpMe02) with positive correlation on axis 2 are biased towards the South, but with an additional influence from mdNc (Mt Dundas, West/Central). Three mite morphotaxa (oribatids AcOr02 and AcOr36, prostigmatid AcPr20) have strong positive correlation with axis 1 and are biased towards West/Central, while prostigmatid mite AcPr19 has strong negative correlation with axis 2 and is biased by both West/Central and the North East. Four morphotaxa are strongly biased towards the North East (tortricid moth larva LeToL07, coccinellid beetle CpCo07, chrysomelid beetle CpCh08, brachypterous psocid PsBr7), with negative correlations on both axes.



Morphotaxon	Axis 1			Axis 2		
	r	r-sq	τ	r	r-sq	τ
AcOr26	0.156	0.024	0.078	0.77	0.593	0.791
CpMe02	0.149	0.022	0.037	0.738	0.545	0.557
AcOr02	0.819	0.671	0.698	-0.168	0.028	-0.047
AcOr36	0.688	0.474	0.64	-0.415	0.172	-0.355
AcPr20	0.62	0.384	0.51	-0.462	0.213	-0.403
AcPr16	0.327	0.107	0.264	-0.754	0.568	-0.58
LeToL07	-0.498	0.248	-0.344	-0.663	0.44	-0.546
CpCo07	-0.564	0.318	-0.435	-0.568	0.323	-0.479
CpCh08	-0.763	0.582	-0.348	-0.536	0.287	-0.313
PsBr7	-0.887	0.786	-0.552	-0.481	0.232	-0.299

Figure 5.17. Ordination of *N. cunninghamii* site by Region, with morphotaxa joint plot and main matrix correlations (sampling set 3), morphotaxa trimmed of singletons (N = 139). Minimum stress 3 axes 4.545, $p = 0.0323$, cutoff $r^2 = 0.4$. NE: North East; S: South; WC: West/Central. Ac, Acarina: AcOr, Oribatida; AcPr, Prostigmata. Cp, Coleoptera: CpCh, Chrysomelidae; CpCo, Coccinellidae; CpMe, Melandryidae. Le, Lepidoptera: LeTo, Tortricidae. Ps, Psocoptera: PsBr, brachypterous morphotaxa; PsCc, Caeciliusidae. L preceding taxon number denotes immatures (larva).

5.3.1.5 Between Region Variation: Indicator Values and Ordination, *N. gunnii*

Meanwhile, indicator species analysis and ordination grouped by region for *N. gunnii* confirm the morphotaxa homogeneity of the two regions demonstrated by the MRPP values above (table 5.31). No morphotaxon had significant indicator values between the two regions, and ordination (figure 5.18) suggests that the arthropod profile of the sites in the South is a subset of that of West/Central sites.

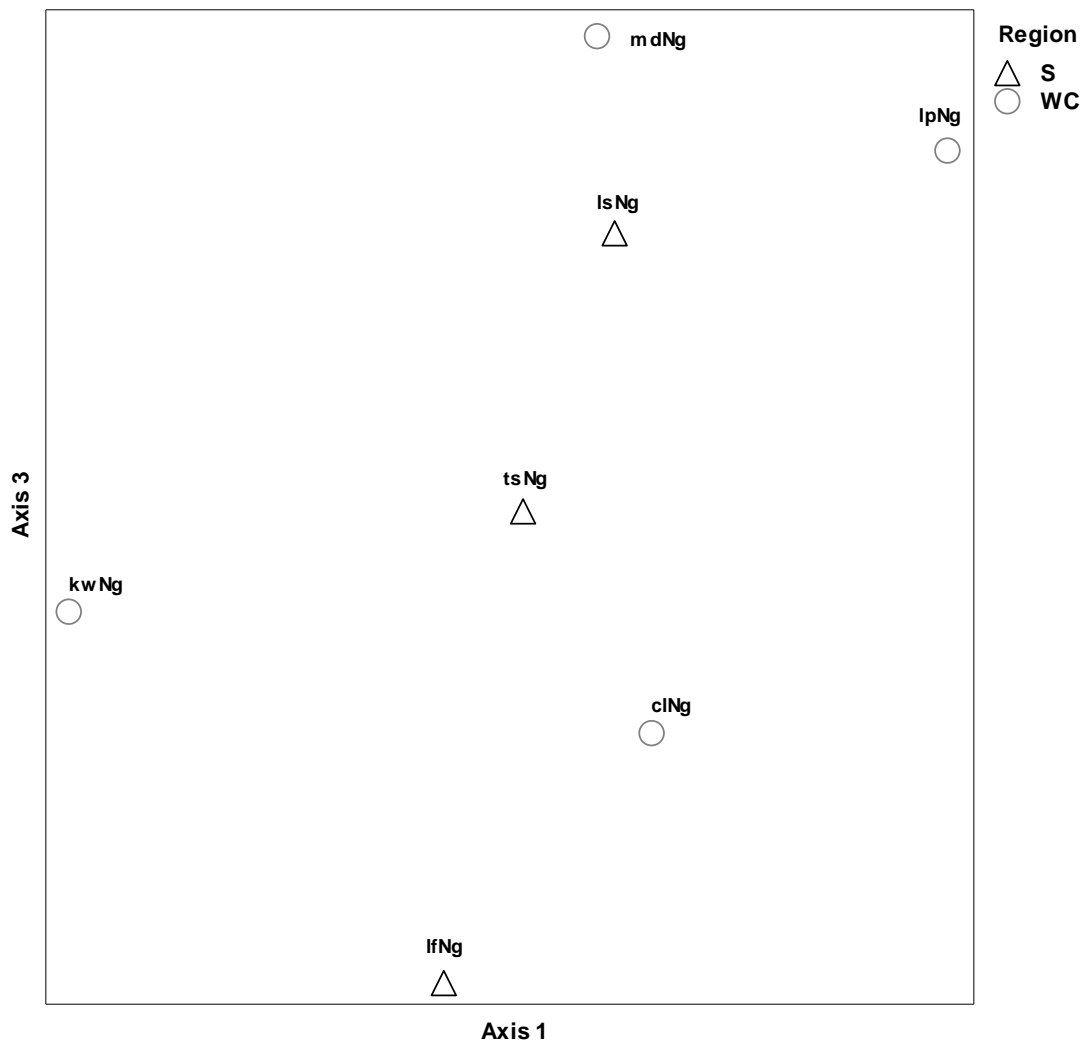


Figure 5.18. *N. gunnii* ordination by region (sampling set 3), morphotaxa trimmed of singletons (N = 42). Minimum stress 3 axes = 0.000, p = 0.0645. S: South; WC: West/Central.

5.3.2 Seasonal Variation

The beat-corrected data from the nineteen sites was grouped by season and singleton morphotaxa removed, resulting in a morphotaxon total of 118, and abundance of 3979.75 individuals. MRPP applied to this data showed between-season variation to be greater than that within each season (table 5.35).

A	p	Average Euclidean Distance (Group size)		
		Spring	Summer	Autumn
0.002	0.335	42.025 (18)	52.392 (18)	54.634 (19)

Table 5.35 MRPP results: data grouped by season (sampling set 3)

Indicator Species Analysis grouped by season (table 5.36) revealed two morphotaxa to have indicator values significant at $p \leq 0.01$: chrysomelid beetle CpCh08 (IV = 30.2) in Spring; and oribatid mite AcOr 03 (IV = 37.6) in Autumn; while a further five morphotaxa had indicator values significant at $p < 0.05$: tortricid moth larva, LeToL07 (IV = 22.2) in Spring; aphid HeAp1 (IV = 39), scirtid beetle CpSr01 (IV = 16.7), thrip ThTh2 (IV = 27.4) in Summer; and oribatid mite AcOr24 (IV = 32.1) in Autumn.

Morphotaxon	Season	IV	Mean	SD	p
CpCh08	1(Spring)	30.2	12.5	5.34	0.008
LeToL07	1(Spring)	22.2	7.8	3.73	0.016
HeAp1	2(Summer)	39	24.2	6.38	0.031
CpSd01	2(Summer)	16.7	6.9	3.85	0.047
ThTh2	2(Summer)	27.4	17.1	5.5	0.049
AcOr03	3(Autumn)	37.6	19.7	5.92	0.01
AcOr24	3(Autumn)	32.1	17.7	5.37	0.023

Table 5.36 Indicator Values (IV): data grouped and sorted by season (sample set 3).

Significance at: $p \leq 0.01$ in red, $p < 0.05$ in blue. **Ac**, Acarina: AcOr, Oribatida. **Cp**, Coleoptera: CpCh, Chrysomelidae; CpSd, Scydmaenidae. **He**, Hemiptera: HeAp, Aphididae. **Le**, Lepidoptera: LeTo, Tortricidae. **Th**, Thysanoptera: ThTh, Thripidae. L preceding taxon number denotes immatures: Larva.

However, on ordination (figure 5.19) there was no clear axis separation of the morphotaxa grouped by season; and although the oribatid mite AcOr26 has a strong negative correlation on axis 1 ($r = -0.689$, $\tau = -0.56$) it is heavily biased, in all three seasons, by the *N. cunninghamii* sites Mt. Arthur (maNc) and Lake Dobson (ldNc).

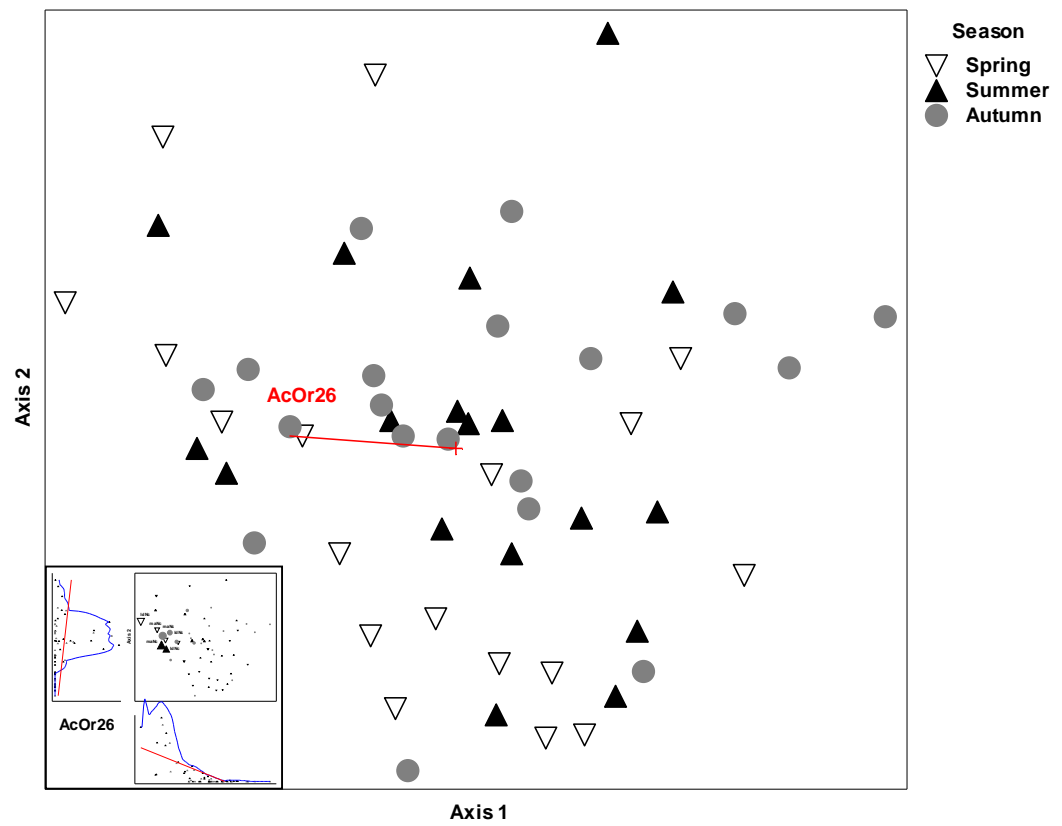


Figure 5.19. Ordination by Season (sampling set 3), morphotaxa trimmed of singletons ($N = 118$). Minimum stress 3 axes = 17.754, $p = 0.0323$, cutoff $r^2 = 0.3$. Insert: main matrix overlay for AcOr26.

5.3.2.1 Seasonal Variation: Host Comparison

With the data grouped by season and host, MRPP showed between-group variation to be greater than that within the groups (table 5.37).

A	p	Average Euclidean Distance (Group size)					
		Spring/ Nc	Spring/ Ng	Summer/ Nc	Summer/ Ng	Autum n/Nc	Autum n/Ng
0.046	0.28	191.74 (3)	23.216 (2)	191.426 (3)	23.791 (2)	183.597 (3)	101.568 (2)

Table 5.37. MRPP results: data grouped by season and host (sampling set 3).

Nc: *N. cunninghamii*; **Ng:** *N. gunnii*.

On Indicator Species Analysis (table 5.38), grouped by season and host, three morphotaxa were found to have indicator values significant at $p < 0.01$: plecopteran PcNo3 (IV = 100) on *N. cunninghamii* in spring; psychid moth larva LePsL1 (IV = 69.2) on *N. cunninghamii* in summer; and oribatid mite AcOr24 (IV = 45.8). A further six morphotaxa had indicator values significant at $p < 0.05$: thrip ThTh2 (IV = 50.7) and aphid HeAp1 (IV = 57.6) on *N. cunninghamii* in summer; juvenile acanthosomatid sucking bug, HeAcJ1 (IV = 100) on *N. gunnii* in summer; and prostigmatid and oribatid mites, AcPr25 (IV = 100) and AcOr10 (IV = 63.5) respectively, on *N. gunnii* in autumn.

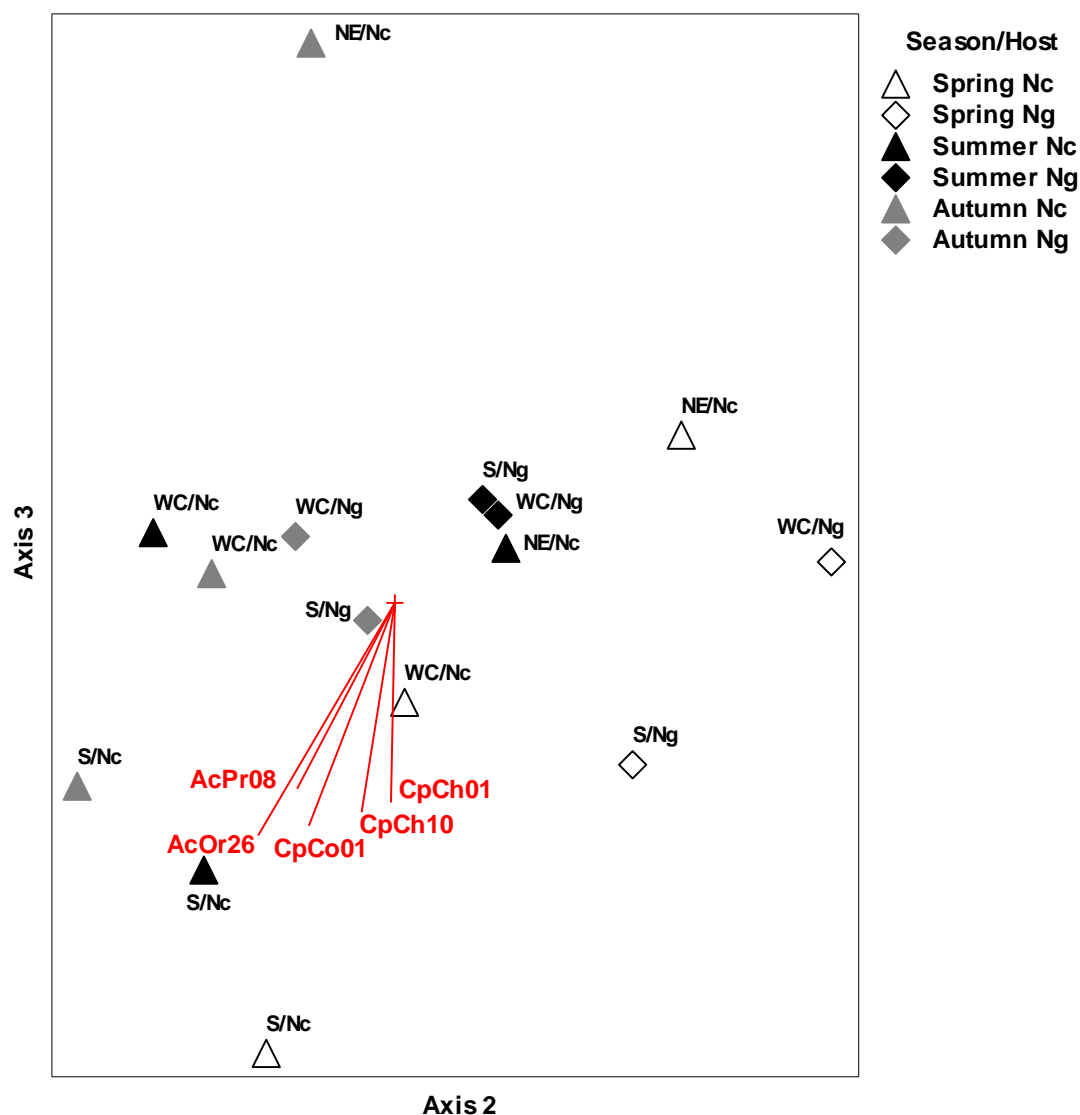
Ordination separates the *N. gunnii* sites by season along axis 2; while the *N. cunninghamii* sites separate by season diagonally, along a line from low values on axes 2 and 3 to high values on both axes, and with summer overlapping the other two seasons (figure 5.20).

Morphotaxon	Season/Host	IV	Mean	SD	p
PcNo3	Spring /Nc	100	34.1	18.8	0.009
LePsL1	Summer /Nc	69.2	32.7	13.77	0.001
ThTh2	Summer /Nc	50.7	32	9.98	0.015
HeAp1	Summer /Nc	57.6	34.9	12.44	0.043
HeAcJ1	Summer /Ng	100	36.9	16.07	0.028
AcOr24	Autumn /Ng	45.8	30.2	6.44	0.008
AcPr25	Autumn /Ng	100	30.7	16.37	0.021
AcOr10	Autumn /Ng	63.5	37.4	12.95	0.036

Table 5.38. Indicator Values (IV): data grouped and sorted by season and host (sample set 3).

Significance at: $p < 0.01$ in red, $p < 0.05$ in blue. **Nc:** *N. cunninghamii*; **Ng:** *N. gunnii*.

Ac, Acarina: AcOr, Oribatida; AcPr, Prostigmata. **He,** Hemiptera: HeAp, Aphididae; HeAc, Acanthosomatidae. **Le,** Lepidoptera: LePs, Psychidae. **Pc,** Plecoptera: PcNo, Notonemouridae. **Th,** Thysanoptera: ThTh, Thripidae; J or L preceding taxon number denotes immatures: Juvenile or Larva.



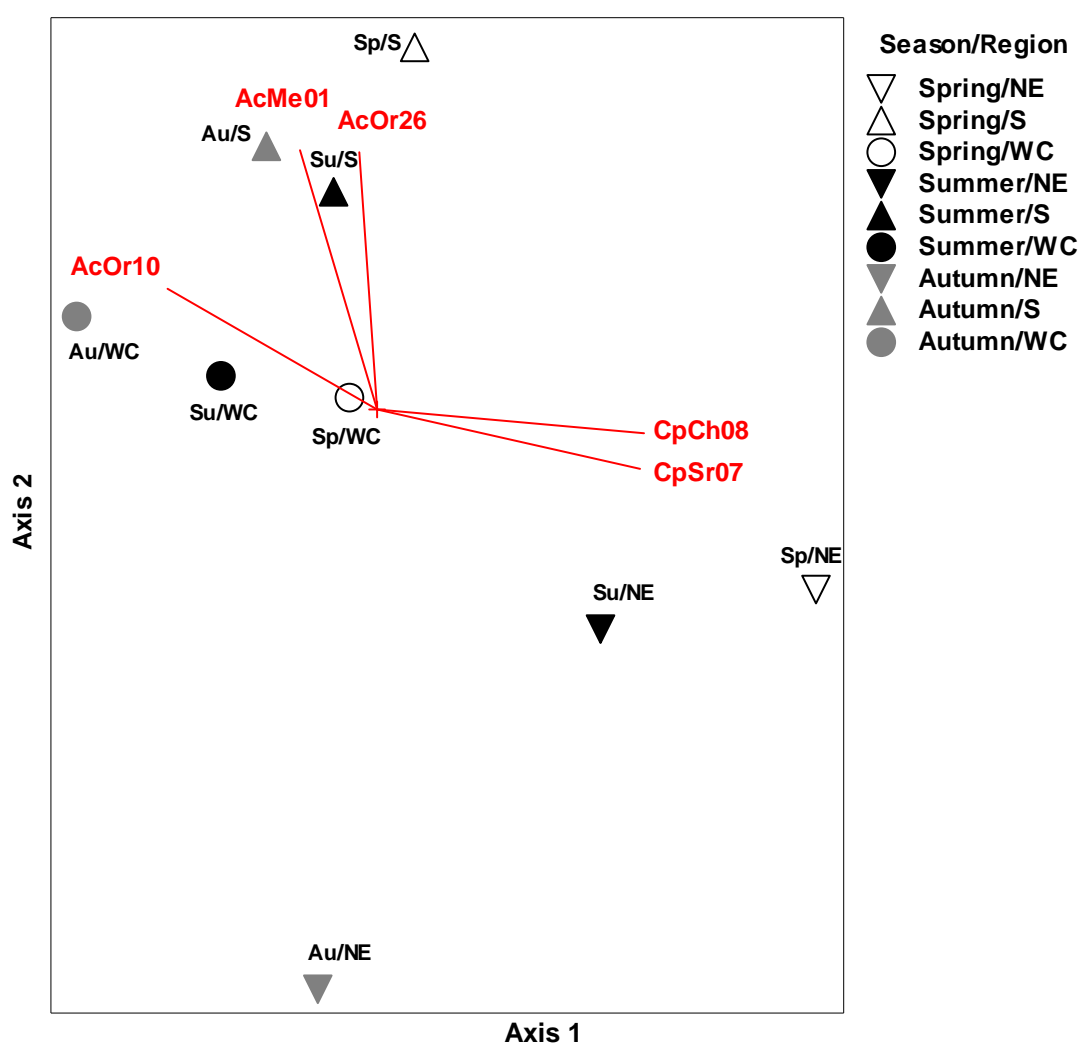
Morphotaxon	Axis2			Axis3		
	R	r-sq	τ	r	r-sq	τ
AcOr26	-0.567	0.322	-0.49	-0.736	0.541	-0.567
AcPr08	-0.477	0.228	-0.311	-0.656	0.431	-0.525
CpCh01	-0.099	0.01	-0.126	-0.682	0.465	-0.302
CpCh10	-0.285	0.081	-0.126	-0.697	0.485	-0.63
CpCo01	-0.45	0.202	-0.422	-0.721	0.52	-0.609

Figure 5.20. Ordination by Season and Host (sampling set 3) with morphotaxa joint plot and main matrix correlations, morphotaxa trimmed of singletons (N = 117). Minimum stress 3 axes = 5.253, $p = 0.0323$, cutoff $r^2 = 0.45$. Nc: *N. cunninghamii*; Ng: *N. gunnii*. Ac, Acarina: AcOr, Oribatida; AcPr, Prostigmata. Cp, Coleoptera: CpCh, Chrysomelidae; CpCo, Coccinellidae.

Morphotaxon joint plot at cutoff $r^2 = 0.45$, and main matrix correlations (figure 5.20, above), showed five taxa to have strong negative correlation with axis 3, corresponding with a bias to the *N. cunninghamii* southern sites. On axis 2 they have a range of negative correlation: the chrysomelid beetles CpCh01 and CpCh10 are biased towards Spring at these sites; oribatid mite AcOr26 and coccinellid beetle CpCo01 show a slight bias towards Spring and Summer at the *N. cunninghamii* southern sites; and the prostigmatid mite AcPr08 is biased towards Summer and Autumn at these sites, but also towards Spring on *N. cunninghamii* at the West/Central sites.

5.3.2.2 *Seasonal Variation: Region Comparison*

With the data grouped by season and region totals, each group had a single member so that MRPP and Indicator Species Analysis were precluded. However ordination (figure 5.21) revealed the regions to be separated on axis 2 and the seasons within those regions to be separated on axis 1. On morphotaxon joint plot at cutoff $r^2 = 0.6$, and main matrix correlations: two beetles, chrysomelid CpCh08 and scirtid CpSr07 were strongly positively correlated with axis 1, with a bias towards Spring, and Spring and Summer, respectively; two mites, mesostigmatid AcMe01 and oribatid AcOr26 have strongly positive correlations with axis 2, the former being towards South and West/Central sites in all seasons, and the latter biased towards southern sites regardless of season; oribatid AcOr10 has a strong negative correlation with axis 1 and is heavily biased by the Autumn West/Central sites.



Morphotaxon	Axis 1			Axis 2		
	r	r-sq	τ	r	r-sq	τ
AcMe01	-0.442	0.195	-0.056	0.806	0.65	0.444
AcOr10	-0.726	0.527	-0.609	0.551	0.304	0.609
AcOr26	-0.218	0.048	0	0.801	0.641	0.833
CpCh08	0.816	0.666	0.833	-0.248	0.061	-0.233
CpSr07	0.813	0.661	0.559	-0.391	0.153	-0.473

Figure .5.21. Ordination by Season and Region (sampling set 3) with morphotaxa joint plot and main matrix correlations, morphotaxa trimmed of singletons (N = 117). Minimum stress 3 axes = 0.155, $p = 0.0323$, cutoff $r^2 = 0.6$. Sp: Spring; Su: Summer; Au: Autumn. NE: North East; S: South; WC: West/Central. Ac, Acarina: AcMe, Mesostigmata; AcOr, Oribatida. Cp, Coleoptera: CpCh, Chrysomelidae; CpSr, Scirtidae.

5.4 ASPECT VARIATION

Variation in arthropod fauna by aspect, North-facing or South-facing sides of a tree (sampling set 4, table 4.1), was explored at two sites for *N. cunninghamii* (IfNc: Lake Fenton; IsNc: Lake Skinner) and at three sites for *N. gunnii* (IfNg: Lake Fenton; IsNg: Lake Skinner; kwNg: King William). In addition, the effect of close proximity of trees from each *Nothofagus* species (adjacent trees) was also sampled for at Lake Fenton and Lake Skinner. The data were corrected for sampling effort to that used at the majority of sites (the equivalent of 8 x 10 beats per site per aspect) and singletons removed, before being subjected to multivariate analysis using the software package PC_ORD for Windows Version 4.7 (McCune & Mefford, 1999).

5.4.1 North-facing or South-facing Aspect:

The north/south aspect data set comprised 77 morphotaxa (29 singletons) with a total abundance of 1253 individuals. After beat correction and removal of singletons this became a total abundance of 1031 individuals and morphotaxon richness of 48.

On MRPP analysis, within group variation was found to be greater than between group variation with the data grouped by aspect or by host and aspect (table 5.39).

Data Grouped by	A	p	Average Euclidean Distance (Group size)			
			North		South	
			NcN	NgN	NcS	NgS
Aspect	-0.065	0.96	64.953 (5)		71.324 (5)	
Host and Aspect	-0.081	0.847	62.042 (2)	72.17 (3)	95.304 (2)	53.592 (3)

Table 5.39. MRPP results: data grouped by aspect (North-facing or South-facing) or by host and aspect (sampling set 4). *N. cunninghamii*; Ng: *N. gunnii*. N: North-facing; S: South-facing.

5.4.1.1 North-facing or South-facing Aspect: Indicator Species Analysis and Ordination

Indicator Species Analysis grouped by aspect, revealed one morphotaxon with indicator values (IV) significant at $p = 0.05$: mesostigmatid mite, AcMe03, North-facing, IV = 80, $p = 0.047$; but no other morphotaxa had indicator values significant at $p < 0.1$. With the data grouped by host and aspect four morphotaxa had indicator values significant at $p < 0.1$ (table 5.40): on north-facing *N. cunninghamii*, juvenile membracid treehopper HeMeJ (IV = 80.5); on north-facing *N. gunnii*, mesostigmatid

mite AcMe03 (IV = 85.2); and on south-facing *N. cunninghamii*, oribatid mites AcOr01 (IV = 82.2) and AcOr11 (IV = 61.7).

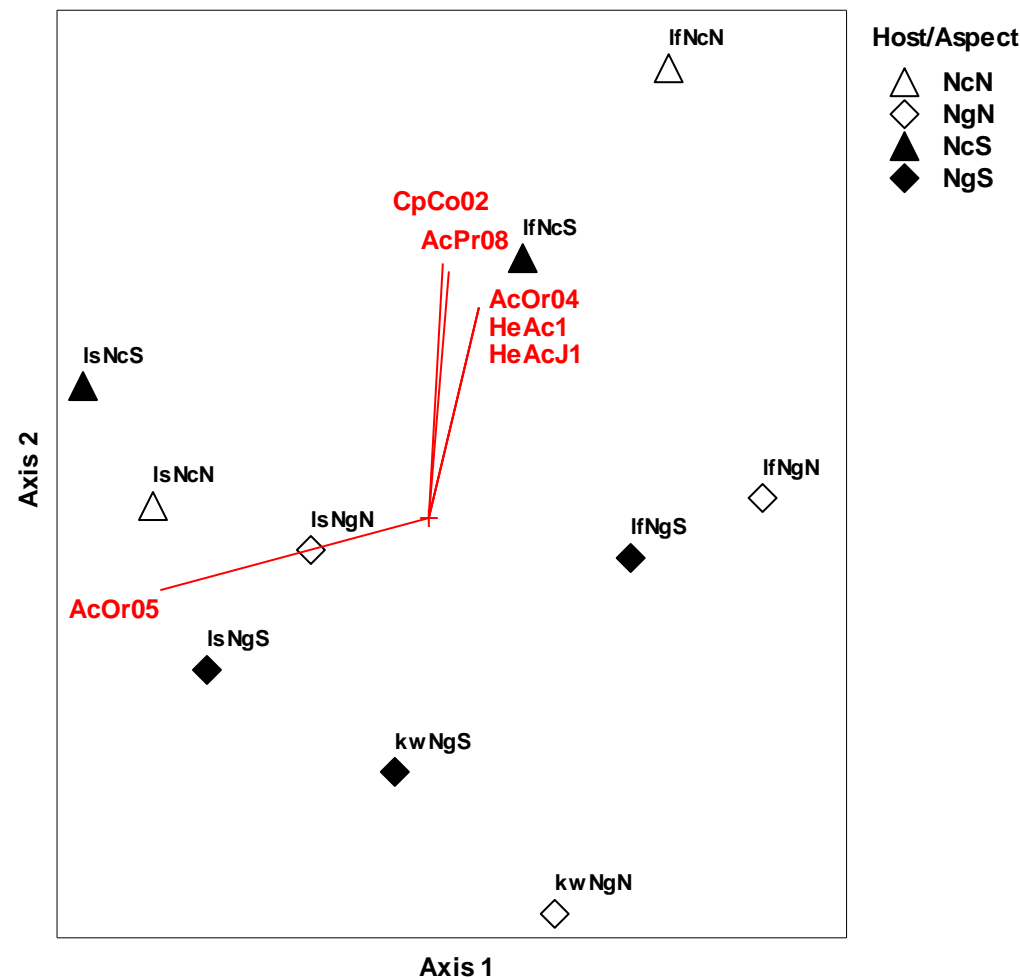
Morphotaxon	Host	IV	Mean	SD	p
HeMeJ3	NcN	80.5	36.3	19.98	0.069
AcMe03	NgN	85.2	40	19.48	0.069
AcOr01	NcS	82.2	37.9	20.1	0.068
AcOr11	NcS	61.7	42.1	12.81	0.069

Table 5.40. Indicator Values (IV): data grouped by host and aspect (sample set 3). Significance at: $p = 0.1$. Nc: *N. cunninghamii*; Ng: *N. gunnii*. N: North-facing; S: South-facing. Ac, Acarina: AcMe, Mesostigmata; AcOr, Oribatida. He, Hemiptera: HeMe, Membracidae. J preceding taxon number denotes immatures (Juvenile).

On ordination by aspect (figure 5.22), there is no overall separation between north and south, however for each site and host, the north facing aspect has a higher value on axis 1 than its south-facing counterpart. The *Nothofagus* species separate, with *N. cunninghamii* tending to lower values on axis1 and higher values on axis 2 compared with *N. gunnii*. Morphotaxa joint plot (cutoff $r^2 = 0.6$) and main matrix correlation (fig) shows five morphotaxa to be biased towards *N. cunninghamii* at Lake Fenton with coccinellid beetle CpCo02 and prostigmatid mite AcPr08 having a stronger correlation with axis 2. Oribatid mite AcOr05 is biased towards *N. gunnii* at Lake Skinner and has a strong negative correlation with axis1.

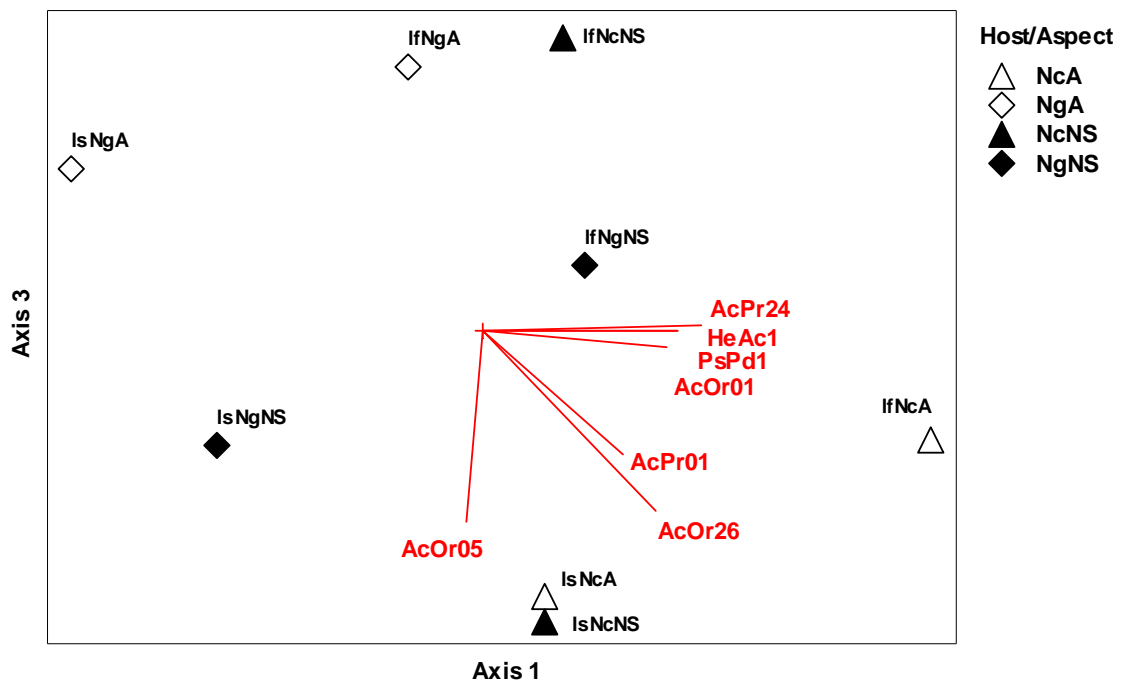
5.4.2 Proximity of Trees As a Factor Among The Two *Nothofagus* species

The above data was from samples taken from trees of one *Nothofagus* species located at least five metres from trees of the other *Nothofagus* species. The ‘adjacent’ trees were close enough for some of the branches of the two species to be touching (e.g. Appendix 2, Plate A.1.e) and were sampled, at the same visits as the north-and south facing sampling, to explore any effect of this proximity on the arthropod fauna. In this comparison (figure 5.23), the north- and south-facing data, per site and host, were combined and beat-corrected to match the ‘adjacent’ data (8 x 10 beats per site per host).



Morphotaxon	Axis 1			Axis 2		
	r	r-sq	τ	r	r-sq	τ
AcOr04	0.377	0.142	0.298	0.766	0.587	0.596
AcOr05	-0.866	0.75	-0.733	-0.45	0.202	-0.289
AcPr08	0.24	0.058	0.061	0.828	0.685	0.73
CpCo02	0.204	0.042	0.061	0.843	0.711	0.73
HeAc1	0.377	0.142	0.298	0.766	0.587	0.596
HeAcJ1	0.377	0.142	0.298	0.766	0.587	0.596

Figure 5.22. Ordination by Aspect (sampling set 4) with morphotaxa joint plot and main matrix correlations, morphotaxa trimmed of singletons (N = 48). Minimum stress 3 axes = 0.760, $p = 0.0323$, cutoff $r^2 = 0.6$. Nc: *N. cunninghamii*; Ng: *N. gunnii*. N: North-facing; S: South-facing. Ac, Acarina: AcOr, Oribatida; AcPr, Prostigmata. Cp, Coleoptera: CpCo, Coccinellidae. He, Hemiptera: HeAc, Acanthosomatidae. J preceding taxon number denotes immatures: Juvenile.



Morphotaxon	Axis 3			Axis 1		
	r	r-sq	τ	r	r-sq	τ
AcOr01	0.711	0.505	0.143	-0.22	0.048	0.071
AcOr05	-0.218	0.047	-0.327	-0.726	0.527	-0.618
AcOr26	0.689	0.475	0.286	-0.705	0.497	-0.214
AcPr01	0.62	0.385	0.473	-0.583	0.34	-0.4
AcPr24	0.775	0.6	0.691	0.136	0.018	0.255
HeAc1	0.732	0.535	0.577	0.005	0	0.262
PsPd1	0.731	0.534	0.577	-0.075	0.006	0.262

Figure 5.23. Ordination comparing adjacent (A) and non-adjacent trees (NS: north- and south-facing data combined and beat-corrected) (sampling set 4) with morphotaxa joint plot and main matrix correlations, morphotaxa trimmed of singletons (N = 50). Minimum stress 3 axes = 1.103, $p = 0.2903$, cutoff $r^2 = 0.5$. Nc: *N. cunninghamii*; Ng: *N. gunnii*. Ac, Acarina: AcOr, Oribatida; AcPr, Prostigmata. He, Hemiptera: HeAc, Acanthosomatidae. Ps, Psocoptera: PsPd, Pseudocaeciliidae.

MRPP was not used to compare groups as none had more than two members. No morphotaxon had an indicator value significant at $p = 0.1$ on Indicator Species Analysis, nor did ordination reveal separation of the adjacent and non-adjacent groups (figure 5.23), although five morphotaxa (hemipteran HeAc1, psocopteran PsPd1; and mites AcPr24, AcOr01 and AcOr26) were strongly correlated with axis 1 and biased towards the adjacent *N. cunninghamii* tree at Lake Fenton (IfNcA).

5.5 YEARLY VARIATION

Year to year variation in arthropod fauna (Sampling Set 6, table 4.1) was compared between 1998-1999 (Year 1) samples and 1999-2000 (Year 2) samples, at three sites each for *N. cunninghamii* (Lake Fenton, lfNc; Lake Skinner, lsNc; Lyrebird Walk, lwNc) and *N. gunnii* (Lake Fenton, lfNg; Lake Skinner, lsNg; and King William, kwNg). The raw data set comprised a total abundance of 7258 individuals and 118 morphotaxa were identified. Although sampling effort was less in the year 1999-2000, overall arthropod fauna abundance (table 5.41) and both morphotaxon richness and abundance were greater than in the previous year (table 5.42).

Host \ Year		1998-1999		1999-2000		2-Year Total
		Year 1	% 2-Yr Total	Year 2	% 2-Yr Total	
<i>N. cunninghamii</i>	Abundance	1982	43.71	2552	56.29	4534
	% Abundance	60.85	-	63.78	-	62.47
	Beats x 10	75	59.52	51	40.48	126
<i>N. gunnii</i>	Abundance	1275	46.81	1449	53.19	2724
	% Abundance	39.15	-	36.22	-	37.53
	Beats x 10	76	64.41	42.00	35.59	118
<i>N. cunninghamii</i> & <i>N. gunnii</i>	Abundance	3257	44.87	4001	55.13	7258
	Beats x 10	151	61.89	93	38.11	244

Table 5.41. Between-year comparison (Sampling Set 5): arthropod fauna abundance and sampling effort at three sites each for *N. cunninghamii* and *N. gunnii*. Total abundance and percentage abundance per host per year; and abundance and sampling effort per year as a percentage of the 2-year totals.

Host \ Year		1998-1999	1999-2000	2-Year Total
<i>N. cunninghamii</i>	Mtx Richness	90	119	152
	Mtx Abundance	1260	1504	2764
<i>N. gunnii</i>	Mtx Richness	58	67	87
	Mtx Abundance	873	1060	1933
<i>N. cunninghamii</i> & <i>N. gunnii</i>	Mtx Richness	107	150	188
	Mtx Abundance	2133	2564	4697

Table 5.42. Between-year comparison (Sampling Set 5): morphotaxon (Mtx) richness and abundance per *Nothofagus* species; and for both *Nothofagus* combined, per year and 2-year totals.

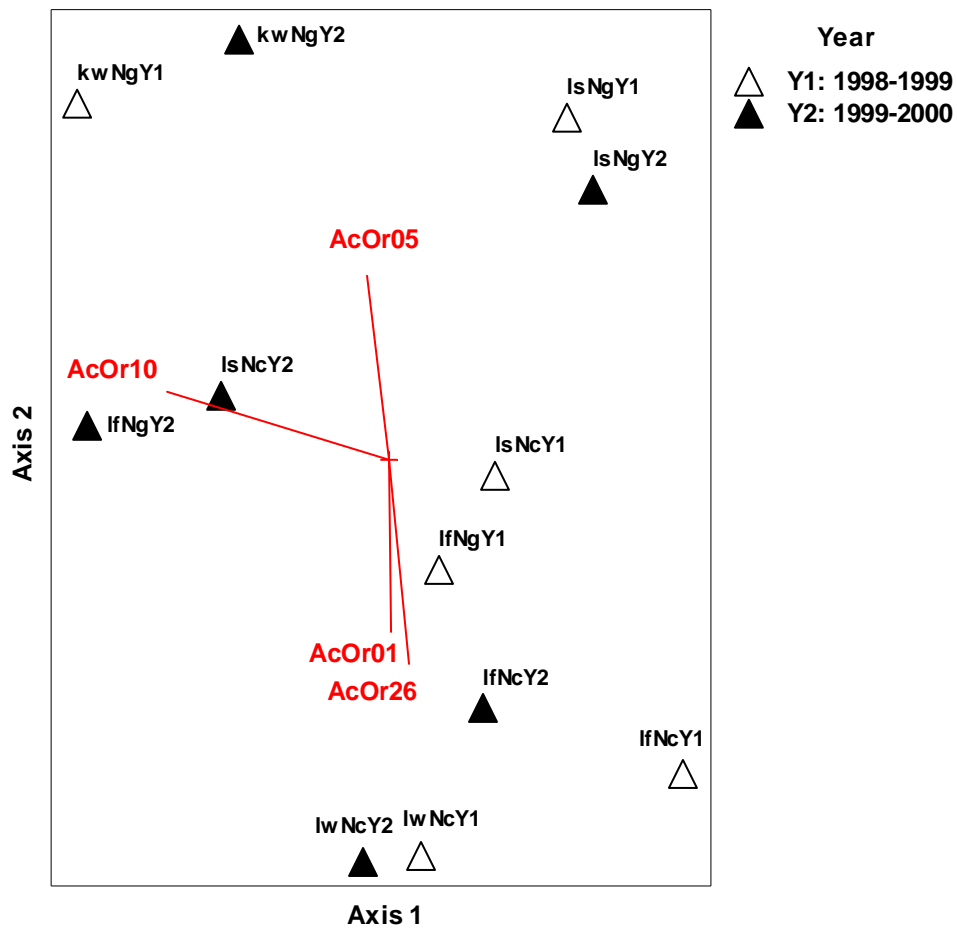
5.5.1 Between Year Variation: Morphotaxa

Prior to multivariate analysis of between-year morphotaxa variation, the data were corrected for sampling effort (to the equivalent of 9 x 10 beats per site per host) and non-morphotaxa and singletons removed. Within year difference was found to be greater than that between years on MRPP analysis grouped by year (table 5.43), while Indicator Species Analysis revealed a single morphotaxon with an indicator value significant at $p < 0.1$: thrip ThTh3, in Year 2 ($p = 0.06$, IV = 66.7).

A	p	Average Euclidean Distance (Group size)	
		Year 1	Year 2
-0.031	0.807	76.693 (6)	102.906 (6)

Table 5.43 Morphotaxon MRPP grouped by year. Yr1: 1998-1999; Yr2: 1999-2000.

The MRPP results were reflected on ordination grouped by year (figure 5.24), with no separation of sampling years on axes 1 and 2; however the sites separated on axis 2, and for Lake Skinner and Lake Fenton the *Nothofagus* species separated on axis 1. The morphotaxa joint plot (cutoff $r^2 = 0.4$) and main matrix correlation showed strong axis correlations for four oribatid mites: negative correlation on axis 1 for AcOr10, corresponding with heavy bias towards *N. gunnii* at Lake Fenton in Year 2 and at King William in both years; positive correlation with axis 2 for AcOr05 (heavy bias to *N. gunnii* at King William Year 2); negative correlation on axis 2 for AcOr01 (heavy bias to *N. cunninghamii* at Lyrebird Walk in both years) and AcOr26 (bias to *N. cunninghamii*, at Lyrebird Walk and Lake Skinner in both years, and at Lake Fenton in Year 2).



Morphotaxon	Axis 1			Axis 2		
	r	r-sq	τ	r	r-sq	τ
AcOr01	0.09	0.008	0.159	-0.704	0.496	-0.795
AcOr05	-0.265	0.07	0	0.73	0.532	0.636
AcOr10	-0.8	0.64	-0.604	0.444	0.197	0.064
AcOr26	0.239	0.057	0.137	-0.764	0.584	-0.687

Figure 5.24. Ordination by Year with morphotaxa biplot and main matrix correlations, morphotaxa trimmed of singletons (N = 96). Minimum stress 3 axes = 5.031, $p = 0.0323$, cutoff $r^2 = 0.4$. If: Lake Fenton, Is: Lake Skinner, lw Lyrebird Walk, kw, King William. Nc: *N. cunninghamii*; Ng: *N. gunnii*. Year 1: 1998-1999; Year 2: 1999-2000. Ac, Acarina: AcOr, Oribatida.

5.6 ARTHROPOD FEEDING GUILDS

Individuals were assigned to one of six feeding guilds according to that most likely for their order, suborder or family, and life stage (Appendix A7. Tasmanian *Nothofagus* Arthropod Fauna: Morphotaxa, *Nothofagus* Host Plant, Feeding Guilds). Herbivores accounted for four feeding guilds: nectivores; and three folivore guilds – leaf chewers, leaf miners and sap-suckers. Predators and fungivore/detritivores comprised the remaining guilds.

After a general overview of structure and taxon abundance of the feeding guilds on *N. cunninghamii* and *N. gunnii*, and removal of the preliminary visit information, the data were corrected for sampling effort (to the equivalent of 1 x 10 beats per site). The feeding guild data were then compared between the two hosts (Sampling Set 2), and variations with season (Sampling Set 3) and between sampling years (Sampling Set 6) were explored, using the multivariate analysis software package PC_ORD for Windows Version 4.7 (McCune & Mefford, 1999).

5.6.1 Feeding Guilds: Overview

The fungivore/detritivores had the greatest taxon abundance, overall and for both *Nothofagus* species, followed by the predators, then the herbivores (table 5.44). On *N. cunninghamii* there were twice as many fungivore/detritivores (6707 individuals) as predators (3025 individuals); and nearly three times as many predators as herbivores (1060 individuals) (table 5.44). While on *N. gunnii*, there were three times as many fungivore/detritivores (3178 individuals) as predators (934 individuals); the there were more than five times as many predators as herbivores (169 individuals) (table 5.44).

Feeding Guild	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Overall
Leaf Chewers	538	100	638
Leaf Miners	48	0	48
Sap-suckers	422	63	485
Folivores total	1008	163	1171
Nectivores	52	6	58
Herbivores Total	1060	169	1229
Fungivores/Detritivores	6707	3178	9885
Predators	3025	934	3959

Table 5.44. *Nothofagus* arthropod fauna feeding guilds, taxa abundance. All fieldtrips, all taxa (adults, larvae and miscellaneous immatures): total specimen counts by feeding guild and host plant, and overall. Herbivores subdivided into: Leaf Chewers, Leaf Miners and Sap-suckers (Folivores) and Nectivores.

Six orders contributed to the fungivore/detritivores (Coleoptera, Lepidoptera, Plecoptera, Psocoptera, Collembola, Acarina), three orders contributed to the predators (Coleoptera, Acarina, Araneae), and the herbivores came from four orders (Coleoptera, Lepidoptera, Hemiptera, Thysanoptera). The leaf miners were the only feeding guild not found on both *Nothofagus* species, being restricted to *N. cunninghamii*.

While the fungivore/detritivores and predators were not all identified below the level of order, the herbivores were identified to morphotaxon (adult or immature) and were further subdivided into folivores (leaf chewers, leaf miners, sap-suckers) and nectivores. Of the folivores, the leaf chewers had the highest taxon richness overall (60 morphotaxa from 9 families and 2 orders); the sap-suckers came from the largest number of families (48 morphotaxa from 14 families and 2 orders); while the leaf miners had only two morphotaxa (from 2 families and 1 order) and occurred only on *N. cunninghamii* (table 5.45).

While the same four orders (Coleoptera, Lepidoptera, Hemiptera, Thysanoptera) contributed to the herbivores on both *Nothofagus* species, *N. cunninghamii* had a higher diversity within the orders than *N. gunnii* (in families and morphotaxa) for each of the herbivore guilds; and also a higher taxon abundance than *N. gunnii* for each of the herbivore guilds (table 5.45).

On *N. cunninghamii*, leaf chewers (folivore morphotaxon richness 54.7%; abundance 53.4%) had proportionally the highest, and leaf miners (folivore morphotaxon richness 2.1%; abundance 4.8%) proportionally the lowest,

morphotaxon richness and abundance of the folivore guilds. Nectivores made up over a quarter of all herbivore morphotaxon richness, but less than 5% of the herbivore abundance on *N. cunninghamii*. In contrast, on *N. gunnii* there were no leaf miners; and sap-suckers (folivore morphotaxon richness 55%) were proportionally the most diverse of the folivores; but the leaf chewers (folivore morphotaxon abundance 61.3%) were proportionally the most abundant.

Feeding Guild/ Nothofagus sp.	Orders	Families	Morphotaxa			Abundance		
			S	% Fol.	% Herb.	Ind.	% Fol.	% Herb.
N. cunninghamii								
Leaf Chewers	2	9	52	54.7	40.3	538	53.4	50.8
Leaf Miners	1	2	2	2.1	1.6	48	4.8	4.5
Sap-suckers	2	14	41	43.2	31.8	422	41.9	39.8
All Folivores	4	25	95		73.6	1008		95.1
Nectivores	2	9	34		26.4	52		4.9
All Herbivores	4	31	129			1060		
N. gunnii								
Leaf Chewers	2	4	18	45	39.1	100	61.3	59.2
Leaf Miners	0	0	0	0	0	0	0	0
Sap-suckers	2	10	22	55	47.8	63	38.7	37.3
All Folivores	4	14	40		87.0	163		96.4
Nectivores	2	4	6		13.0	6		3.6
All Herbivores	4	18	46			169		
Tasmanian Nothofagus (N. cunninghamii and N. gunnii combined)								
Leaf Chewers	2	9	60	54.5	40.3	638	54.5	51.9
Leaf Miners	1	2	2	1.8	1.3	48	4.1	3.9
Sap-suckers	2	14	48	43.6	32.2	485	41.4	39.5
All Folivores	4	25	110		73.8	1171		95.3
Nectivores	2	10	39		26.2	58		4.7
All Herbivores	4	32	149			1229		

Table 5.45. Tasmanian *Nothofagus* arthropod fauna, all fieldtrips. Herbivore feeding guilds taxon composition: number of orders and families per feeding guild; morphotaxon richness (S), abundance (Ind.) and proportions per guild: folivore (% Fol.) and herbivore (% Herb.).

Six morphotaxa on *N. cunninghamii* accounted for more than half of the total folivore abundance, four of which were also among the most widespread on this host tree, occurring at more than one third of sites (table 5.46). For *N. gunnii*, four morphotaxa comprised more than half of the folivore abundance, two of which occurred at more than one third of sites (table 5.46).

Feeding Guild/ <i>Nothofagus</i> sp.	Mtx	Abundance per <i>Nothofagus</i> sp.		Occurrence per <i>Nothofagus</i> sp.	
		Individuals	% of all Phytophages	Sites per Mtx	% of all Sites
<i>N. cunninghamii</i>					
Leaf Chewers	CpCh01	35	4	6	35
	CpCh03	103	11	5	29
	CpCh08	54	6	6	35
	CpChL1	103	11	4	24
Sap-suckers	HeAp1	85	9	14	82
	ThTh2	81	9	13	76
<i>N. cunninghamii</i> Total		461	51		
<i>N. gunnii</i>					
Leaf Chewers	CpCh01	34	21	3	25
	CpCh10	17	11	4	33
	CpCu02	15	9	2	17
Sap-suckers	ThTh2	19	12	7	58
<i>N. gunnii</i> Total		85	53		

Table 5.46. Tasmanian *Nothofagus* arthropod fauna feeding guilds, all fieldtrips. The most abundant (accounting for 9% or more of folivores) and/or widespread (occurring at more than one third of sites) of the phytophagous morphotaxa (Mtx) on each *Nothofagus* species. Leaf Chewers: CpCh01, *Platycolaspis mcquillani*; CpCh03 (adult) and CpChL1 (larva), *Ewanius nothofagi*; CpCh08, *Microdonacia octodentata*; CpCh10, *Microdonacia truganina*; CpCu02, *Merimnetes* spp. Sap-suckers: HeAp1, *Taiwanaphis tasmaniae*; ThTh2, *Pseudanaphothrips pallidus*.

Seven further folivores occurred on *N. cunninghamii* at more than one third of its sites, although numbers of these morphotaxa were sparse (table 5.47).

Feeding Guild/ <i>Nothofagus</i> sp.	Mtx	Occurrence per <i>Nothofagus</i> sp.		Abundance per <i>Nothofagus</i> sp.	
		Sites per Mtx	% of all Sites	Individuals	% of all Phytophages
<i>N. cunninghamii</i>					
Leaf Chewers	LeGeL1	8	47	18	2
	LeGeL4	6	35	11	1
	LeToL5	8	47	16	2
Leaf Miners	LeGrL1	9	53	41	5
Sap-suckers	HeMeJ3	7	41	19	2
	ThPhL1	8	47	25	3

Table 5.47. Tasmanian *Nothofagus* arthropod fauna feeding guilds, all fieldtrips. Folivorous morphotaxa (Mtx) on *N. cunninghamii* which occurred at more than one third of sites, but in small numbers of individuals. Leaf Chewers: LeGeL1, *Nacophorini* sp. novum; LeGeL4, *Euloxia leucochorda*; LeToL5, Tortricidae sp.1. Leaf Miners: LeGrL1, *Caloptilia ostracodes*. Sap-Suckers: HeMeJ3, *Acanthuchus* spp.; ThPhL1, *Haplothrips ?victoriensis*.

5.6.2 Feeding Guilds: Between Host Variation

With the all-site (Sampling Set 2) data corrected for sampling effort, the fungivores/detritivores remained the most abundant overall, accounting for nearly two thirds of specimens (62%), followed by the predators (28%), while all herbivores (leaf chewers, sap-suckers, leaf miners and nectivores) amounted to just 10% of the total abundance (figure 5.25.a). The guild proportions differed between the two *Nothofagus* species: *N. gunnii* having a higher proportion of fungivores/detritivores (79%) than *N. cunninghamii* (57%); and lower proportions of the other guilds (leaf miners absent altogether) compared with *N. cunninghamii* (figures 5.25.c & d). However, on comparison of the relative abundances of predators and folivores (leaf chewers, sap-suckers and leaf miners), *N. gunnii* was found to have a higher ratio of predators to folivores than *N. cunninghamii* (figures 5.25.e - g).

Multivariate analysis of the guilds grouped by host showed between host difference to be greater than that within host on MRPP (table 5.48) and on Indicator Species analysis (table 5.49) all guilds on *N. cunninghamii*, except the fungivores/detritivores, had indicator values significant at $p < 0.05$, with leaf chewers (IV = 70.8) significant at $p < 0.005$.

A	p	Average Euclidean Distance (Group size)	
		<i>N. cunninghamii</i>	<i>N. gunnii</i>
0.078	0.009	25.026 (17)	12.071 (12)

Table 5.48. MRPP results: guilds grouped by host (Sampling Set 2).

Guild	Host	IV	mean	SD	p
P	Nc	79.4	55.7	4.52	0.001
Hss	Nc	83	53.9	6.08	0.001
Hne	Nc	73.9	35.4	8.05	0.001
Hmn	Nc	58.8	27.5	8.35	0.003
Hch	Nc	70.8	51.3	6.87	0.012
FD	Nc	60.8	56.2	4.84	0.177

Table 5.49. Indicator Values (IV): guilds grouped by host (Sampling Set 2). Significance at: $p < 0.005$ in red, $p < 0.05$ in blue. Nc: *N. cunninghamii*. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. P: Predators. F/D: Fungivores/Detritivores.

On ordination, the *Nothofagus* species separated on axes 1 and 2 (figure 5.25.b); and guild joint plot (cutoff $r^2 = 0.3$) and main matrix correlation revealed fungivores/detritivores ($r = 0.875$, $\tau = 0.941$) to have strong positive correlation with axis 2, while predators ($r = 0.882$, $\tau = 0.849$), sap-suckers ($r = 0.06$, $\tau = 0.573$) and

nectivores ($r = 0.588$, $\tau = 0.495$) were positively correlated with axis 1, all four guilds being biased towards *N. cunninghamii*.

5.6.3 Feeding Guilds: Host & Season Variation

In order to investigate seasonal variation in guild structure and abundance in the *Nothofagus* arthropod fauna, the Sampling Set 3 beat-corrected data was used. Morphotaxa were again allocated to feeding guilds using the most likely guild according to suborder and/or family. Before the data were sorted by season, the total abundances of guilds on the two *Nothofagus* species were compared.

5.6.3.1 Feeding Guilds: Host Variation

As with Sampling Set 2 the fungivores/detritivores were the most abundant overall (59%), although in this data set the herbivores are relatively more abundant (13%), while the proportion of predators (28%) remained the same as the previous guild data set (figure 5.26.a). *N. gunnii* again had a higher proportion of fungivores/detritivores (75%) than *N. cunninghamii* (55%); and lower proportions of the other guilds (leaf miners absent altogether) compared with *N. cunninghamii* (figures 5.26.c, d); and on comparison of the relative abundances of predators and folivores (leaf chewers, sap-suckers and leaf miners), *N. gunnii* was again found to have a higher ratio of predators to folivores than *N. cunninghamii* (figures 5.26.e - g).

Between host difference was found to be greater than that within host on MRPP (table 5.50) and Indicator Species analysis showed all guilds on *N. cunninghamii*, except the fungivores/detritivores, to have indicator values significant at $p < 0.05$; leaf chewers (IV = 86.4), sap-suckers (IV = 86) and predators (IV = 71.2) being significant at $p < 0.005$ (table 5.51).

A	p	Average Euclidean Distance (Group size)	
		<i>N. cunninghamii</i>	<i>N. gunnii</i>
0.081	0.025	207.296 (12)	102.766 (7)

Table 5.50 MRPP results: guilds grouped by host (Sampling Set 3).

Guild	Host	IV	Mean	SD	p
Hch	Nc	86.4	61.3	8.18	0.002
Hss	Nc	86	58	6.4	0.002
P	Nc	71.2	56.2	5.1	0.009
Hne	Nc	69.2	43.3	9.73	0.02
Hmn	Nc	58.3	32.5	11.42	0.048
F/D	Nc	57.1	55.3	4.22	0.305

Table 5.51 Indicator Values (IV): Guilds grouped by host (Sampling Set 3). Significance at: **p < 0.005** in red, **p < 0.05** in blue. Nc: *N. cunninghamii*. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. P: Predators. F/D: Fungivores/Detritivores.

On ordination (figure 5.26.b), the *Nothofagus* species separated on axes 3 except for *N. gunnii* at Lake Fenton (IfNg). Guild joint plot (cutoff $r^2 = 0.3$) and main matrix correlation revealed fungivores/detritivores ($r = 0.589$, $\tau = 0.418$) to be positively correlated with axis 2, while predators ($r = 0.923$, $\tau = 0.789$) and nectivores ($r = 0.701$, $\tau = 0.556$) had strong positive correlations with axis 2, all three guilds being biased towards *N. cunninghamii*, but the predators were also strongly influenced by *N. gunnii* at Lake Fenton.

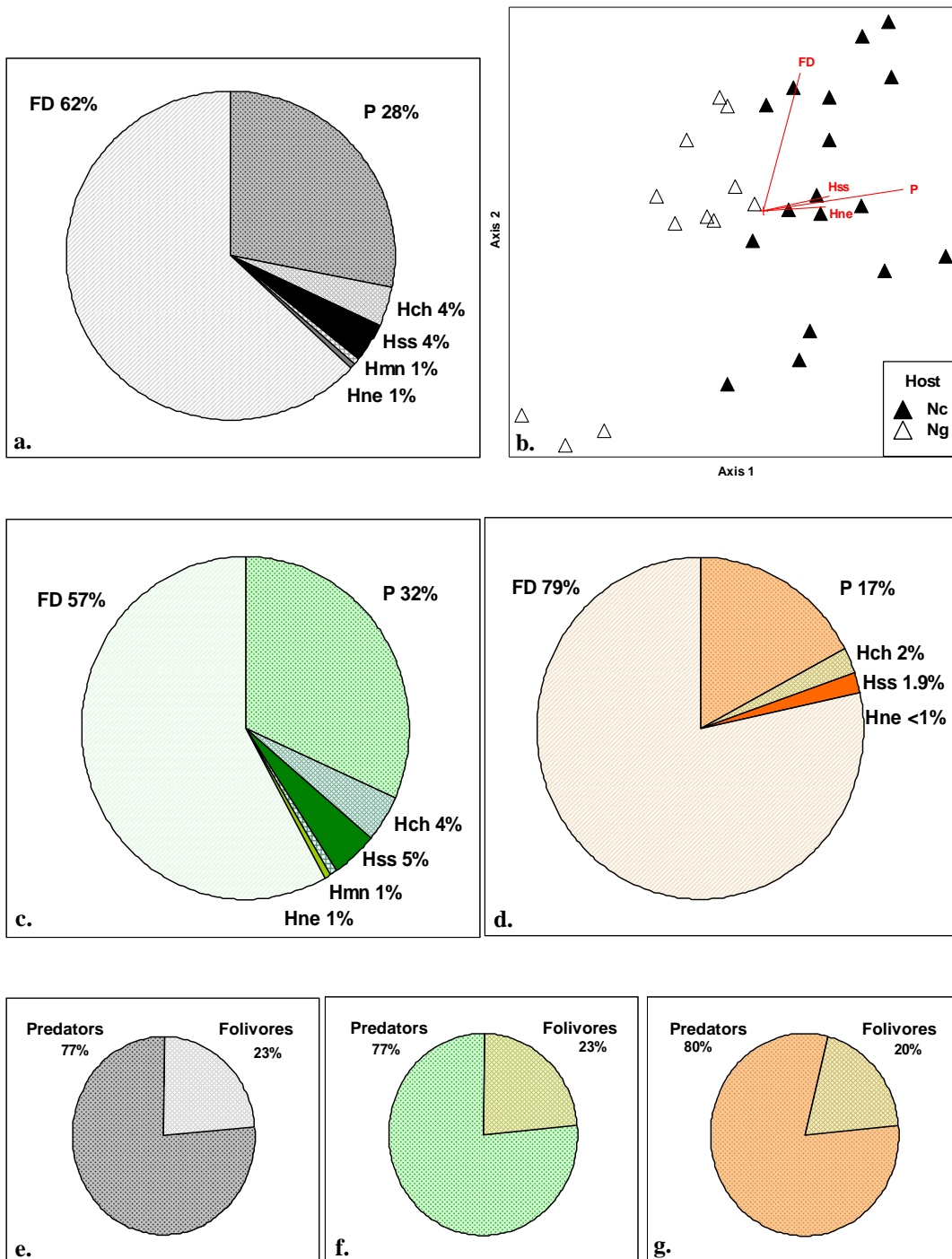


Figure 5.25 a - g. Arthropod guilds on *N. cunninghamii* and *N. gunnii* (all sites).

a. Overall guild composition: % total abundance per guild, *Nothofagus* species combined.

b. Ordination of guilds by host (sampling set 3) with morphotaxa biplot and main matrix correlations (guild totals). Minimum stress 3 axes = 4.648, $p = 0.0323$, cutoff $r^2 = 0.3$.

Nc: *N. cunninghamii*; Ng: *N. gunnii*.

c, d. Guild composition per host, % total abundance per guild: c. *N. cunninghamii*, d. *N. gunnii*. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores.

P: Predators. F/D: Fungivores/Detritivores.

e, f, g. Predator/Folivore comparison, % total abundance per guild: e. *N. cunninghamii* and *N. gunnii* combined; f. *N. cunninghamii* only; g. *N. gunnii* only.

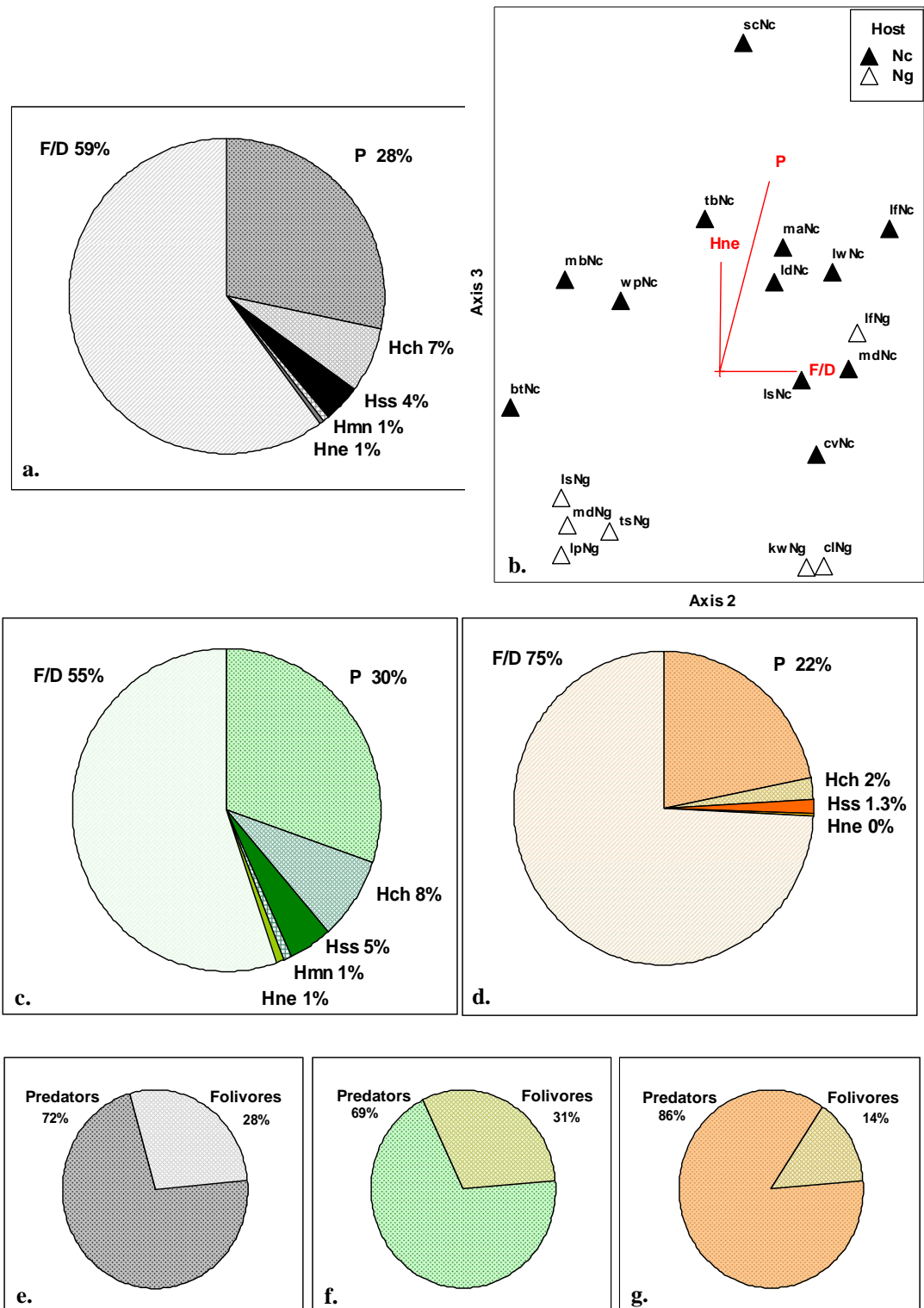


Figure 5.26. a - g. Arthropod guilds on *N. cunninghamii* and *N. gunnii* (sampling set 3).

a. Overall guild composition: % total abundance per guild, *Nothofagus* species combined.

b. Ordination of guilds by host (sampling set 3) with morphotaxa biplot and main matrix correlations (guild totals). Minimum stress 3 axes = 4.035, $p = 0.0645$, cutoff $r^2 = 0.3$.

Nc: *N. cunninghamii*; Ng: *N. gunnii*. Hne, Nectivores. P: Predators.

F/D: Fungivores/Detritivores. c, d. Guild composition per host, % total abundance per guild: c. *N. cunninghamii*, d. *N. gunnii*. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. P: Predators. F/D: Fungivores/Detritivores.

e, f, g. Predator/Folivore comparison, % total abundance per guild: e. *N. cunninghamii* and *N. gunnii* combined; f. *N. cunninghamii* only; g. *N. gunnii* only.

5.6.3.2 *Feeding Guilds: Season Variation*

Overall, the proportions of fungivores/detritivores increased, and those of herbivores decreased, from spring to autumn, while the predators reached a modest peak in summer (figure 5.27). However, the trends differed between the two *Nothofagus* species: proportions of herbivores decreased from spring to autumn on both species, but more markedly on *N. cunninghamii*; and proportions of fungivores/detritivores and predators increased gradually from spring to autumn on *N. cunninghamii*, but on *N. gunnii* the proportions of fungivores/detritivores increased markedly while those of predators fell by half from Spring to autumn (figure 5.28). On *N. cunninghamii* and *N. gunnii* the relative proportions of leaf chewers to sap-suckers altered between the seasons, the leaf chewers having their highest proportion in spring and the sap-suckers in summer.

When guild abundances are compared, fungivores/detritivores and folivores (leaf chewers, sap-suckers and leaf miners) increased in abundance from spring to autumn, while predator abundance peaked in summer (figure 5.29).

MRPP and Indicator Species Analysis could not be applied to the guild data grouped by season, or host and season, because none of the groups had more than two members. Ordination, guild joint plot and main matrix correlation grouped by season showed summer to separate from spring and autumn on axis 2, while spring and summer separated from autumn on axis 3 (figure 5.30). Fungivores/detritivores were strongly negatively correlated with axis 3, corresponding with a bias to autumn; leaf chewers had a strongly positive correlation with axis 3, corresponding with a bias to spring; the remaining guilds had strong positive correlations with axis 2 corresponding with a bias towards summer, this being most marked for nectivores, with strong correlations on both axes (figure 5.30).

On ordination of guilds grouped by season and host, the *Nothofagus* species separated on axis 1, as did the seasons for each, although with summer and autumn in opposite order for the two host species (figure 5.32); and all guilds had negative correlations with both axes 1 and 3 on guild joint plot and main matrix correlation grouped by host and season, corresponding with a bias to *N. cunninghamii*.

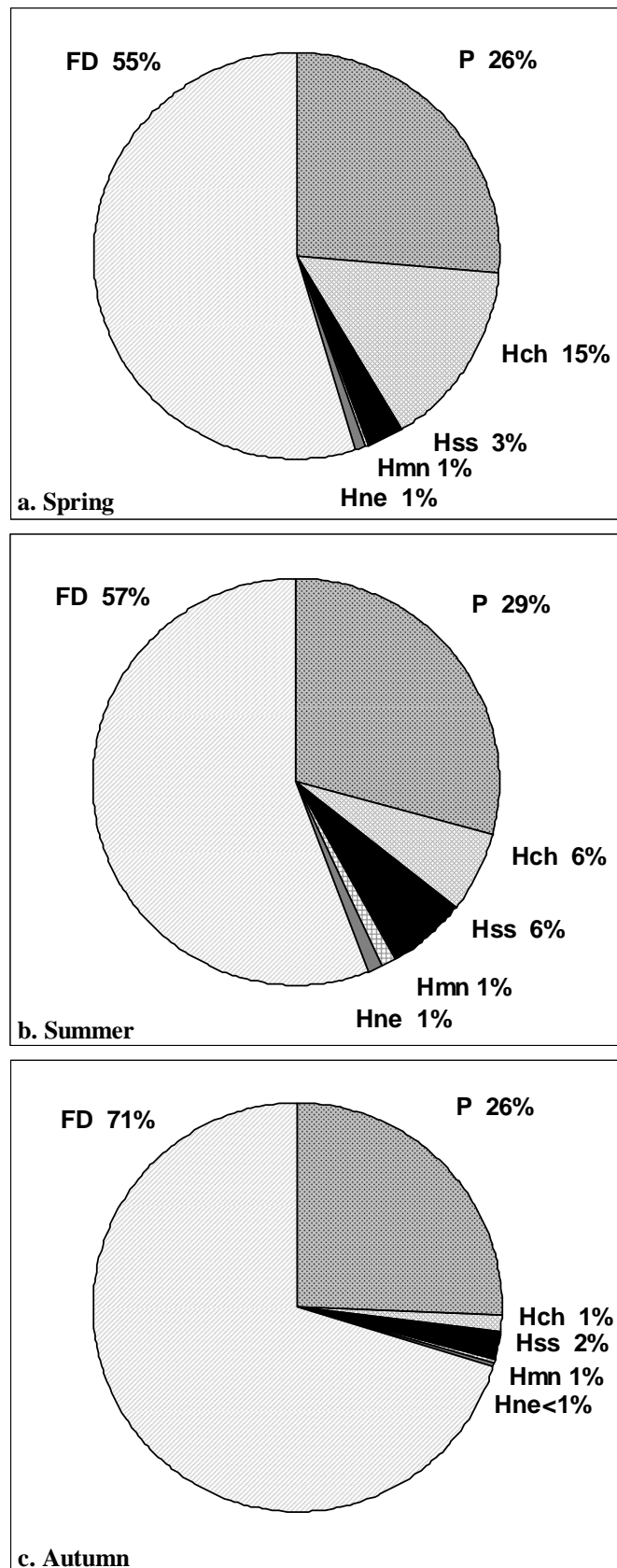


Figure 5.27. a - c. Seasonal variation in arthropod guilds on *N. cunninghamii* and *N. gunnii* (sampling set 3): Guild composition per host and season, % total abundance per guild. *N. cunninghamii* and *N. gunnii* combined: a. Spring, b. Summer, c. Autumn. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. P: Predators. F/D: Fungivores/Detritivores.

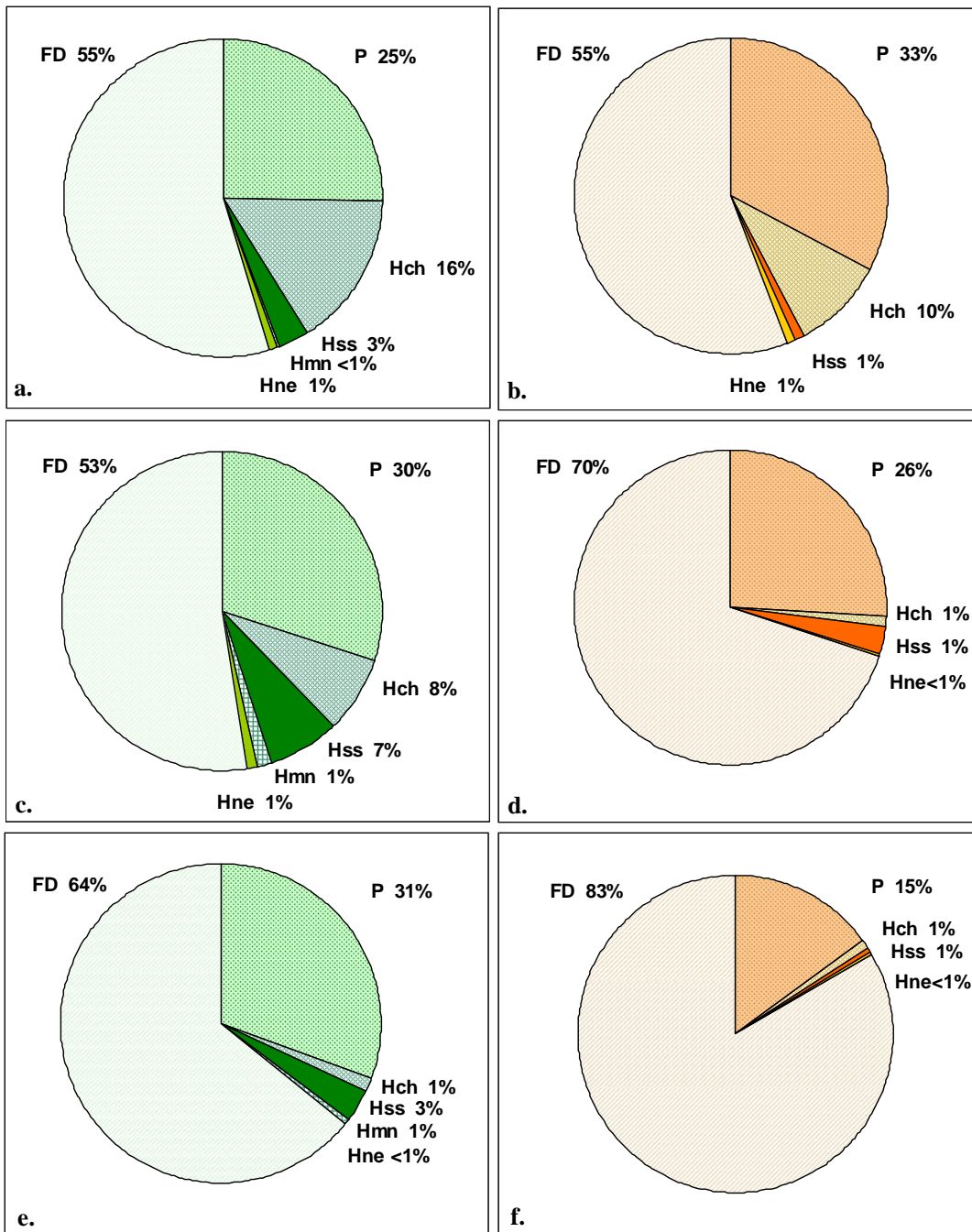


Figure 5.28. a - e. Seasonal variation in arthropod guilds on *N. cunninghamii* and *N. gunnii* (sampling set 3): Guild composition per host and season, % total abundance per guild. a, c, e, *N. cunninghamii*; b, d, f, *N. gunnii*. a, b, Spring; c, d, Summer; e, f, Autumn. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. P: Predators. F/D: Fungivores/Detritivores.

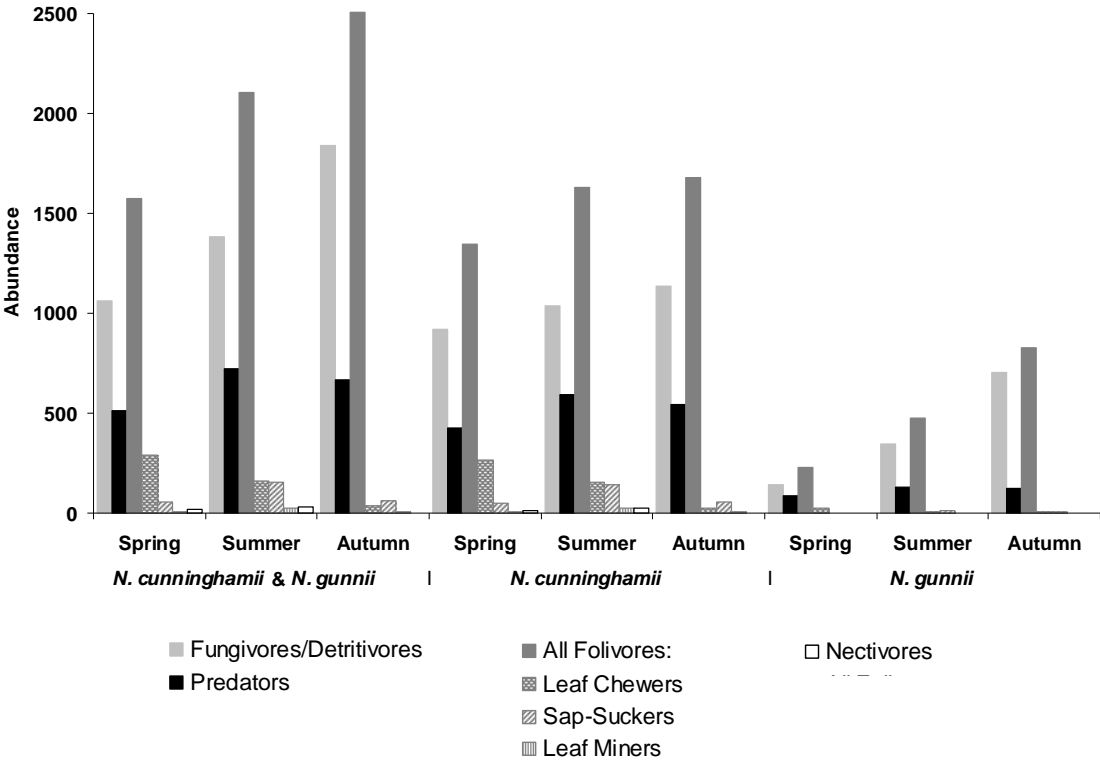
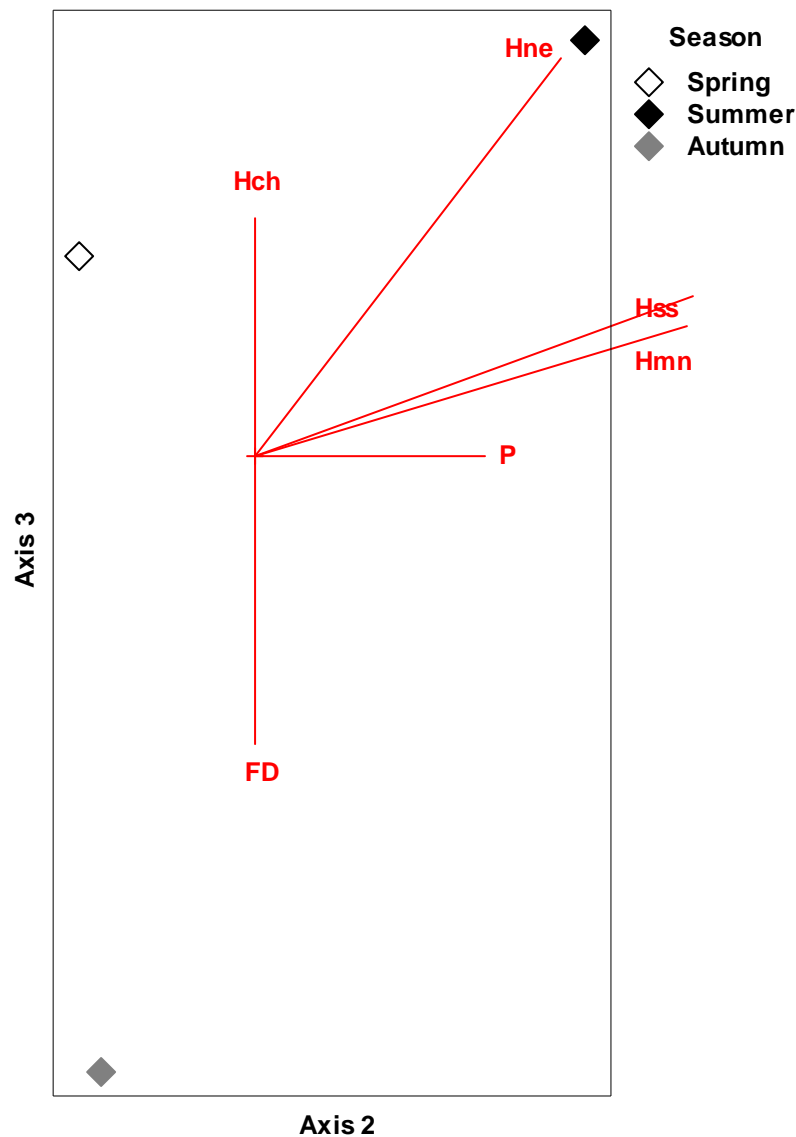


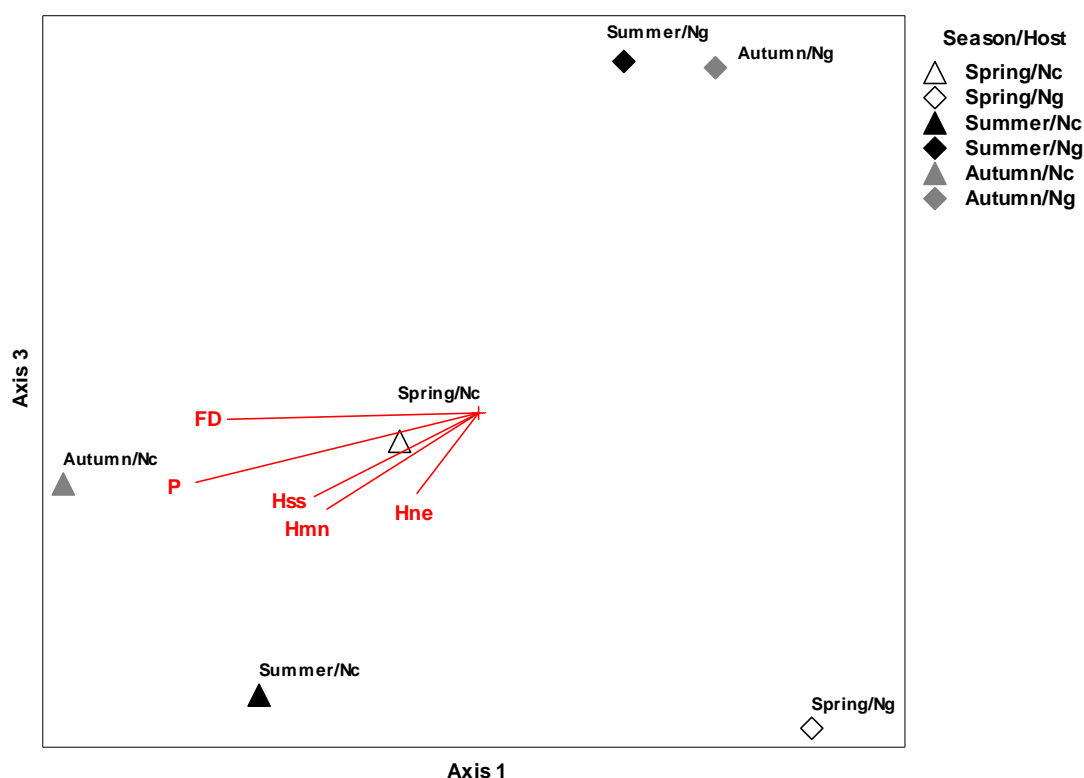
Figure 5.29. Seasonal variation in arthropod guilds on *N. cunninghamii* and *N. gunnii*.



Guild	Axis 2			Axis 3		
	r	r-sq	τ	r	r-sq	τ
FD	-0.063	0.004	0.333	-0.811	0.658	-0.333
Hch	-0.051	0.003	-0.333	0.739	0.547	0.333
Hmn	0.994	0.988	1	0.545	0.297	0.333
Hne	0.835	0.698	0.333	0.955	0.912	1
Hss	0.999	0.999	1	0.607	0.369	0.333
P	0.725	0.526	1	-0.072	0.005	0.333

Figure 5.30. Ordination of guilds by season (sampling set 3) with guild joint plot and main matrix correlations. Minimum stress 3 axes = 0.000, $p = 1.000$, cutoff $r^2 = 0.3$.

Nc: *N. cunninghamii*; Ng: *N. gunnii*. Herbivores: Hch, Leaf choppers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. P: Predators. F/D: Fungivores/Detritivores.



Guild	Axis 1			Axis 3		
	r	r-sq	τ	r	r-sq	τ
FD	-0.891	0.793	-0.867	-0.141	0.02	-0.2
P	-0.943	0.89	-0.867	-0.466	0.218	-0.2
Hss	-0.721	0.521	-0.867	-0.517	0.268	-0.2
Hmn	-0.692	0.479	-0.745	-0.552	0.305	-0.447
Hne	-0.442	0.195	-0.447	-0.502	0.252	-0.298
Hch	-0.358	0.128	-0.2	-0.362	0.131	-0.333

Figure 5.32. Ordination of guilds by season and host (sampling set 3) with guild joint plot and main matrix correlations. Minimum stress 3 axes = 0.000, $p = 0.7097$, cutoff $r^2 = 0.3$. Nc: *N. cunninghamii*; Ng: *N. gunnii*. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. P: Predators. F/D: Fungivores/Detritivores.

With the guild data sorted by site/host and season, and grouped by host and season, MRPP revealed between group difference to be greater than that within groups (table 5.52).

A	p	Average Euclidean Distance (Group size)					
		Spring/ Nc	Spring/ Ng	Summer/ Nc	Summer/ Ng	Autumn/ Nc	Autumn/ Ng
0.124	0.0005	71.253 (12)	17.421 (6)	82.525 (12)	21.623 (6)	95.313 (12)	60.214 (7)

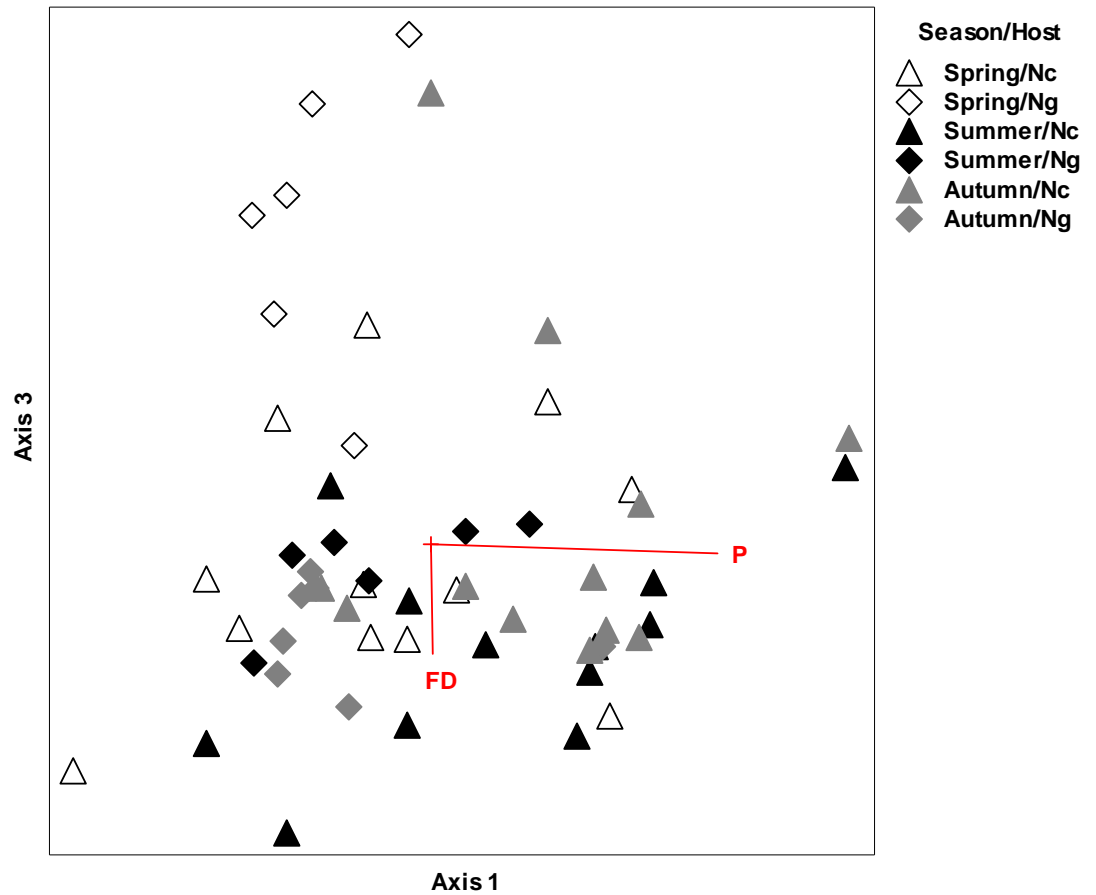
Table 5.52. MRPP results: guilds grouped by season host (site/host and season data, Sampling Set 3).

Indicator Species Analysis of these groups revealed four guilds to have indicator values significant at $p < 0.05$: leaf chewers on *N. cunninghamii* in spring, and sap-suckers, nectivores and predators on *N. cunninghamii* in summer; while leaf miners on *N. cunninghamii* and fungivores/detritivores on *N. gunnii* in autumn had indicator values significant at $p < 0.5$ (table 5.53).

Guild	Season/Host	IV	Mean	SD	p
Hch	Spring/Nc	46.9	26.7	6.84	0.014
Hss	Summer/Nc	48.5	22.9	4.51	0.001
Hne	Summer/Nc	37.7	16.4	5.53	0.007
P	Summer/Nc	27	21.9	2.33	0.029
Hmn	Summer/Nc	26	16.4	7.29	0.109
FD	Autumn/Ng	22.8	22.1	2.4	0.331

Table 5.53. Indicator Values (IV): guilds grouped by season and host (site/host and season data, Sampling Set 3). Significance at: $p < 0.05$ in red, $p < 0.5$ in blue. Nc: *N. cunninghamii*. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. P: Predators. F/D: Fungivores/detritivores.

Ordination of guilds by season, site and host, with guild joint plot and main matrix correlation (cutoff $r^2 = 0.3$) showed the *N. gunnii* sites to separate by season along axis 3, spring having the highest values, autumn the lowest, and summer overlapping both; the seasons were less clearly defined for the *N. cunninghamii* sites (figure 5.33). Predators were strongly correlated with axis 1, corresponding with a bias to *N. cunninghamii* in summer and autumn; while fungivores/detritivores had a strong negative correlation with axis 3, with an autumnal bias on both *Nothofagus* species.



Guild	Axis 1			Axis 3		
	r	r-sq	τ	r	r-sq	τ
FD	0.085	0.007	0.005	-0.57	0.325	-0.643
P	0.919	0.844	0.697	-0.18	0.033	-0.071

Figure 5.33. Ordination of guilds by season, site and host (sampling set 3) with guild joint plot and main matrix correlations. Minimum stress 3 axes = 7.706, $p = 0.0323$, cutoff $r^2 = 0.3$. Nc: *N. cunninghamii*; Ng: *N. gunnii*. P: Predators. F/D: Fungivores/ Detritivores.

5.6.3.3 *Feeding Guilds in More Detail: Seasonality of Leaf Chewers; and Spiders and their Prey*

The most frequently visited sites between Spring 1999 and Autumn 2000 were those in the South. Subsets of data from these sites enabled more detailed examination of relationship between leaf chewer abundance and the emergence of new leaves on *N. cunninghamii*; and also the variation over time in the abundances of spiders and their potential prey on both *N. cunninghamii* and on *N. gunnii*.

5.6.3.3.1 *Leaf Chewers and Leaf Flush on N. cunninghamii*

Between Spring 1999 and Autumn 2000, the most abundant leaf chewers on *N. cunninghamii* at the Southern sites were: the adult Chrysomelidae beetles *Platycolaspis macquillani* Reid (CpCh1) and *Ewanius nothofagi* Reid (CpCh3); together with the larva of *Ewanius nothofagi* Reid (CpChL1); and the Geometrid moth caterpillar Nacophorini *sp.novum* (LeGeL1). A graph of consecutive site visit abundances of these morphotaxa from Lake Dobson, Lake Fenton, Lake Skinner, Lyrebird Walk and Mt. Arthur was superimposed over a block representing the period of leaf flush, during which new foliage was first appearing at those sites (figure 5.34). This revealed that a rise in the abundances of all four leaf chewers coincided with the time over which leaf flush was occurring: between late spring 1999 and early summer 2000. The adult Chrysomelidae beetles (CpCh1, CpCh3) and the Geometrid moth larva (LeGeL1) reached peak abundance during leaf flush and declined in numbers thereafter. During this time, *Ewanius nothofagi* Reid (CpCh3) adult beetles showed the sharpest rise in abundance of the four morphotaxa, reaching a peak of 53 individuals in December 1999; although its larvae (CpChL1) reached an even higher abundance (73 individuals), before declining in numbers, a month later (figure 5.34). By mid-March 2000, of the four morphotaxa, just a single *Platycolaspis macquillani* Reid (CpCh1) adult beetle was found, at Lake Fenton.

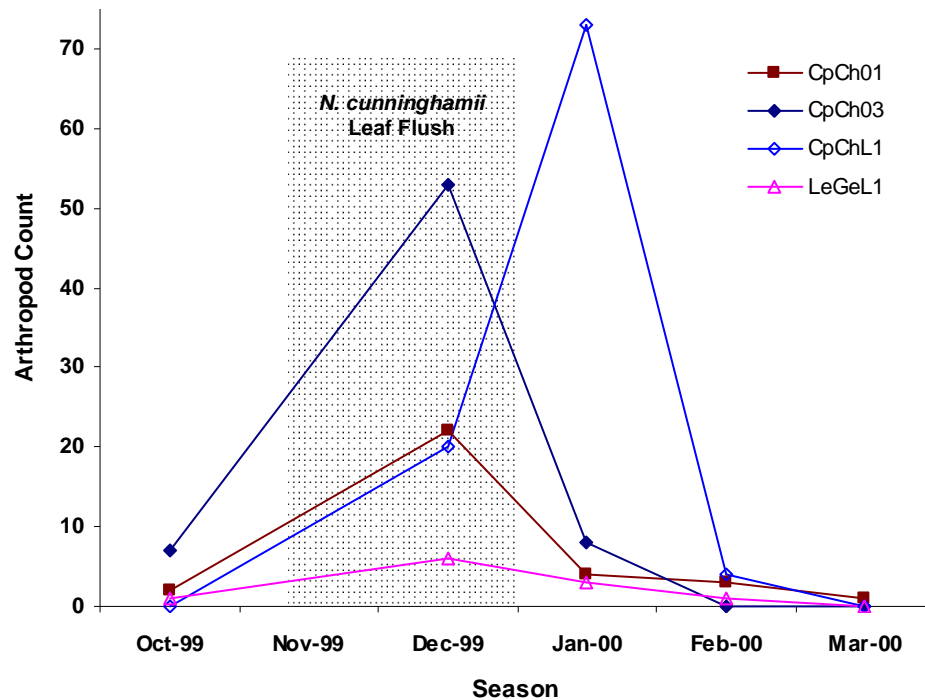


Figure 5.34. Leaf flush and the most abundant leaf chewers on *N. cunninghamii*, from Spring to Autumn 1999/2000. Combined data from five sites: Lake Dobson, Lake Fenton, Lake Skinner, Lyrebird Walk and Mt. Arthur. Coleoptera Chrysomelidae Cryptocephalinae incertae sedis *Platycolaspis macquillani* Reid (CpCh1). Coleoptera Chrysomelidae Chrysomelinae Goniocetenini *Ewanius nothofagi* Reid, adult (CpCh03) and larva (CpChL1). Lepidoptera Geometridae Ennominae Nacophorini sp. novum, larva (LeGeL1).

5.6.3.3.2. Spiders and their Prey: Season Variation

In order to compare the variation over time between abundances of spider members of the predator feeding guild with abundances of their potential arthropod prey, the Araneae data subset described in sub-chapter 5.1.9 was used, with the accompanying data of the other arthropod families collected in those samples. These data comprised specimens collected from both *N. cunninghamii* and *N. gunnii*, at Lake Fenton and Lake Skinner between 16/10/1999 and 25/09/2000.

Spider abundances peaked in summer, but there was no clear relationship between total spider abundances, or between abundances of the spider suborders, with those of the other arthropod families for either *Nothofagus* species at the two sites. (figures 5.35 and 5.36).

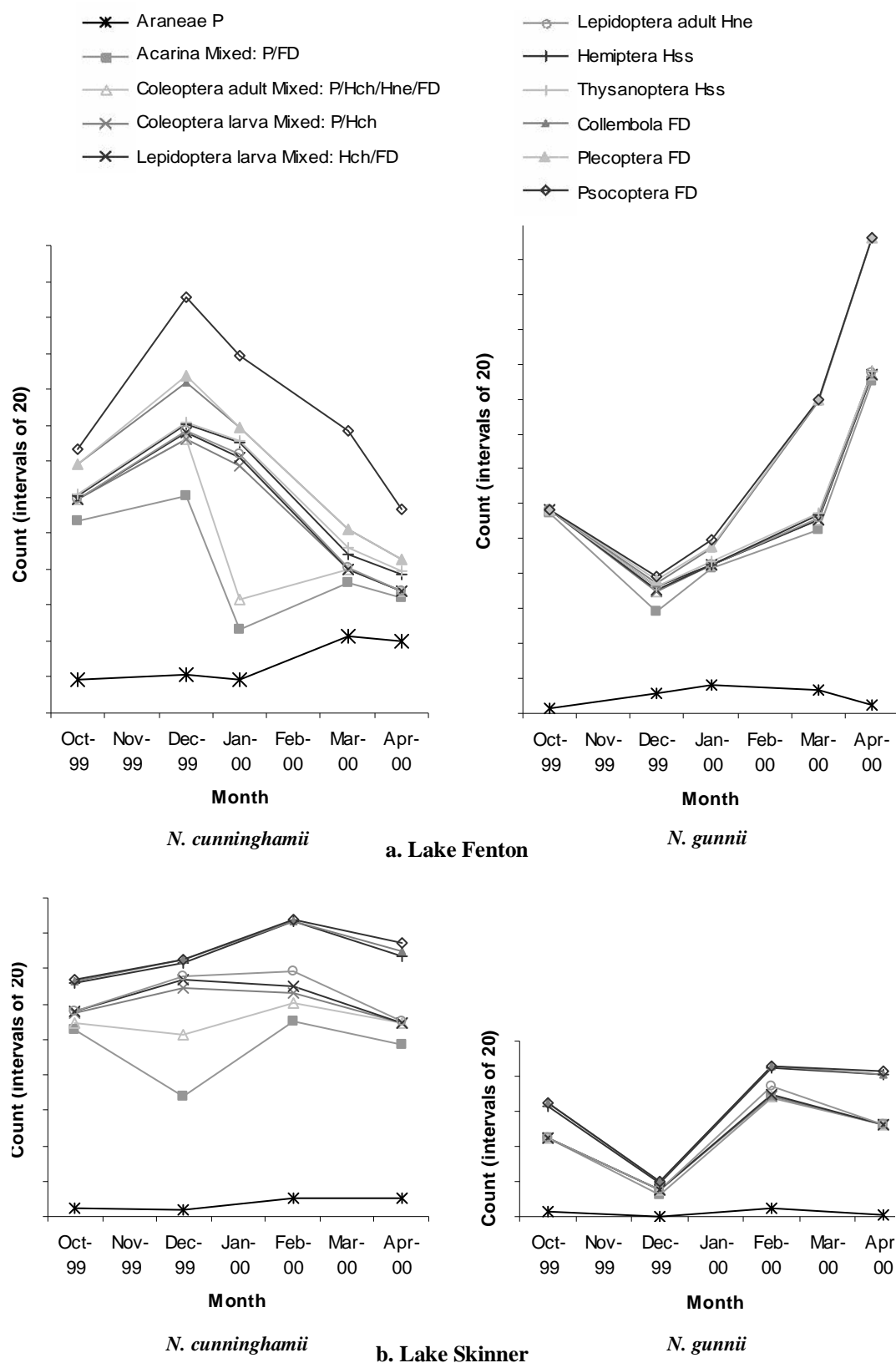


Figure 5.35. Seasonal variation in Araneae and other arthropod families/feeding guilds on *N. cunninghamii* and *N. gunnii*, at Lake Fenton (a) and Lake Skinner (b), between October 1999 and April 2000.

P: Predators. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. F/D: Fungivores/Detritivores.

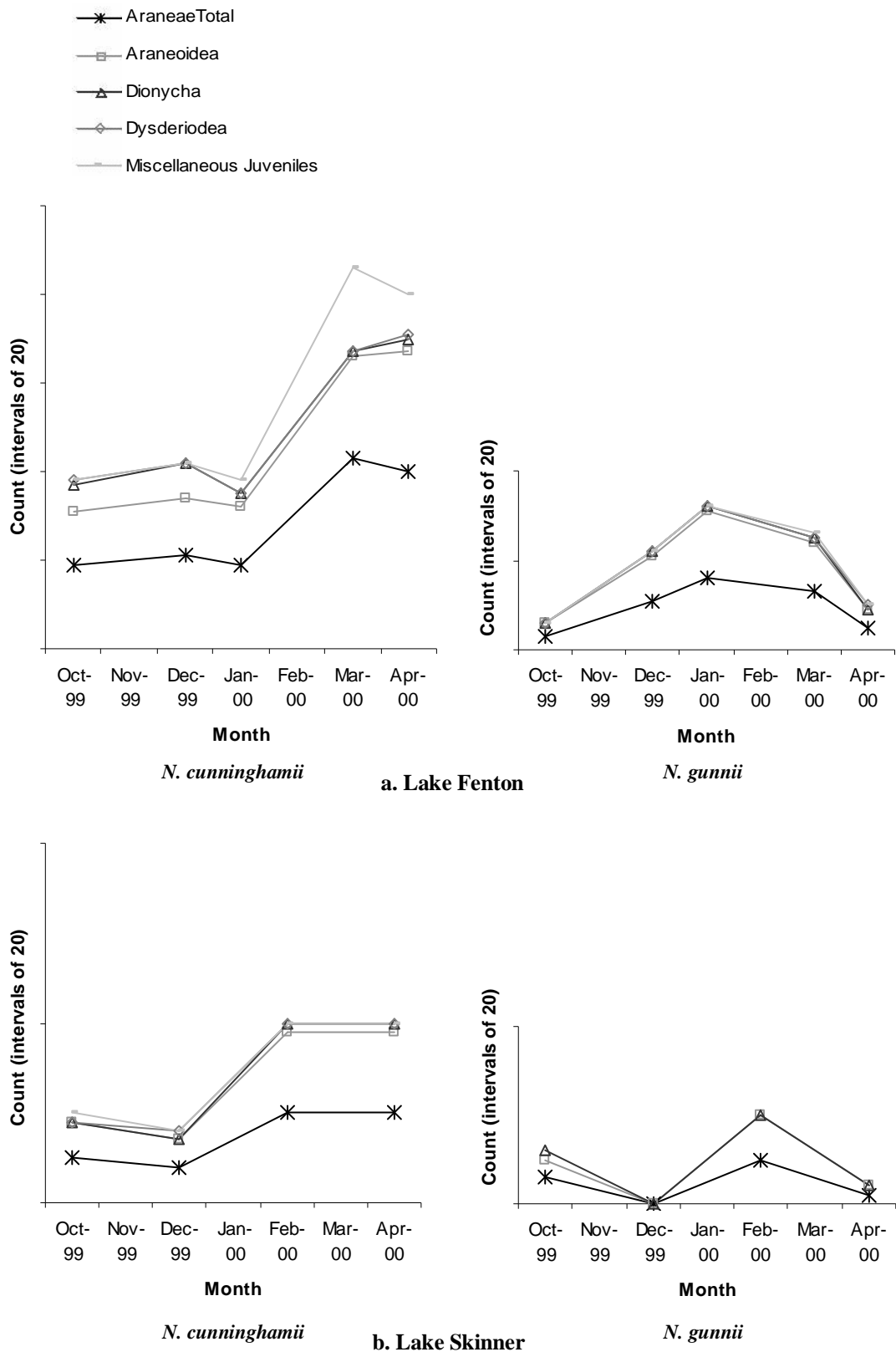


Figure 5.36. Seasonal variation in Araneae, overall and by family, on *N. cunninghamii* and *N. gunnii*, at Lake Fenton (a) and Lake Skinner (b), between October 1999 and April 2000.

5.6.3.3.3 Spiders and their Prey: Proximity to a Body of Water

Among the fungivore/detritivore prey of spiders are those which inhabit the canopy of riparian vegetation, including the Stoneflies (Plecoptera) and scirtid beetles. As *N. cunninghamii*, and especially *N. gunnii*, are frequently found in close proximity to water, the effect of proximity of a water body on spider abundance was explored using the Araneae totals from all sites.

Overall, spiders were more than 5 times more abundant per sample on *N. cunninghamii* than on *N. gunnii* (table 5.54, ANOVA, $F_{1,27} = 21.35$, $P < 0.0001$).

Host species	n	Mean \pm SE
<i>N. cunninghamii</i>	17	8.00 \pm 0.92
<i>N. gunnii</i>	12	1.41 \pm 1.09

Table 5.54. Effect of host on mean spider abundance per sample, all sites and seasons combined.

For *N. cunninghamii* there was no significant difference in the mean number of spiders per sample (ANOVA, $F_{2,14} = 0.7051$, $p = 0.5108$) however, the highest number of spiders recorded was at a lakeside site (Lake St. Clair). Similarly, for *N. gunnii*, proximity to water was not a significant factor in spider abundance (table 5.55, ANOVA, $F_{2,9} = 0.92$, $P = 0.4331$) although the highest mean value occurred closest to water (Lake Eros).

Host species	Proximity to waterbody	n	Mean \pm SE
<i>N. cunninghamii</i>	<2m	6	9.09 \pm 1.96
	>2m<20m	2	10.38 \pm 3.40
	>20m	9	6.74 \pm 1.60
<i>N. gunnii</i>	<2m	7	1.93 \pm 0.63
	>2m<20m	3	0.44 \pm 0.96
	>20m	2	1.00 \pm 1.17

Table 5.55. Mean spider abundance per sample in relation to proximity of host tree to water body.

5.6.4 Feeding Guilds: Between Year Variation

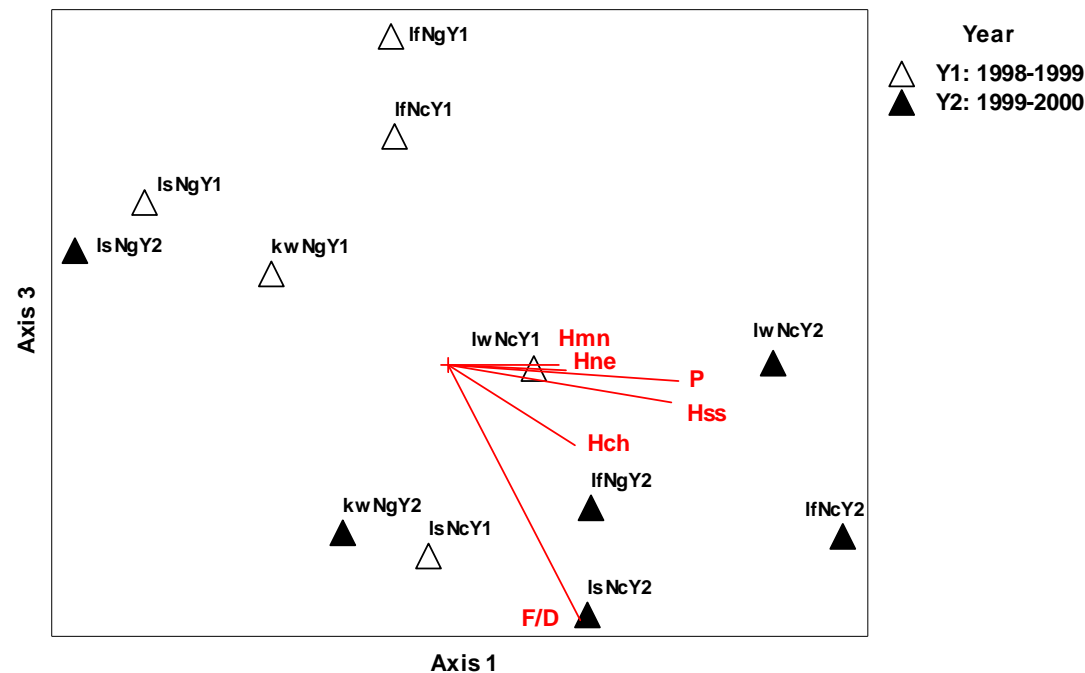
Differences in feeding guild structure and taxon abundance between the two sampling years, 1998-1999 (Year 1) and 1999-2000 (Year 2), were investigated using beat-corrected data, from three sites each *Nothofagus* species: Lake Fenton, (lfNc), Lake Skinner (lsNc) and Lyrebird Walk (lwNc) for *N. cunninghamii*; and Lake Fenton, (lfNg), Lake Skinner (lsNg), and King William (kwNg) for *N. gunnii*. Between year difference was found greater than within year difference on MRPP analysis grouped by year (table 5.56), but on Indicator Species Analysis only fungivores/detritivores in Year 2 had an indicator value significant at $p < 0.1$ ($p = 0.057$, $IV = 61.4$).

A	p	Average Euclidean Distance (Group size)	
		Year 1	Year 2
0.094	0.081	99.54 (6)	130.737 (6)

Table 5.56. Guild MRPP grouped by year. Yr1: 1998-1999; Yr2: 1999-2000.

Ordination (figure 5.37) showed no separation by year on either axis, although guild joint plot (cutoff $r^2 = 0.3$) and main matrix correlation showed a heavy bias of all guilds towards Year 2 (positive correlations with axis 1, negative correlations with axis 3), except on *N. gunnii* at Lake Skinner and King William.

Bar chart plots of site and host guild abundance show more clearly the year to year differences (figure 5.38), with predators and folivores being markedly more abundant in year 2 on both *Nothofagus* species and at all sites. Fungivore/detritivore abundance remains stable on both species at Lake Skinner but increases in year 2 on both species at the other sites, particularly at Lake Fenton.



Guild	Axis 1			Axis 2		
	r	r-sq	τ	r	r-sq	τ
F/D	0.638	0.407	0.424	-0.887	0.786	-0.636
P	0.84	0.706	0.697	-0.225	0.051	-0.121
Hch	0.627	0.393	0.606	-0.501	0.251	-0.273
Hss	0.831	0.691	0.636	-0.34	0.116	-0.242
Hmn	0.588	0.345	0.51	-0.079	0.006	-0.134
Hne	0.601	0.362	0.453	-0.139	0.019	-0.035

Figure 5.37. Ordination by Year with guild joint plot and main matrix correlations. Minimum stress 3 axes = 1.675, $p = 0.2581$, cutoff $r^2 = 0.3$. If: Lake Fenton, Is: Lake Skinner, lw Lyrebird Walk, kw, King William. Nc: *N. cunninghamii*; Ng: *N. gunnii*. Year 1: 1998-1999; Year 2: 1999-2000. Herbivores: Hch, Leaf chewers; Hss, Sap-suckers; Hmn, Leaf miners; Hne, Nectivores. P: Predators. F/D: Fungivores/detritivores.

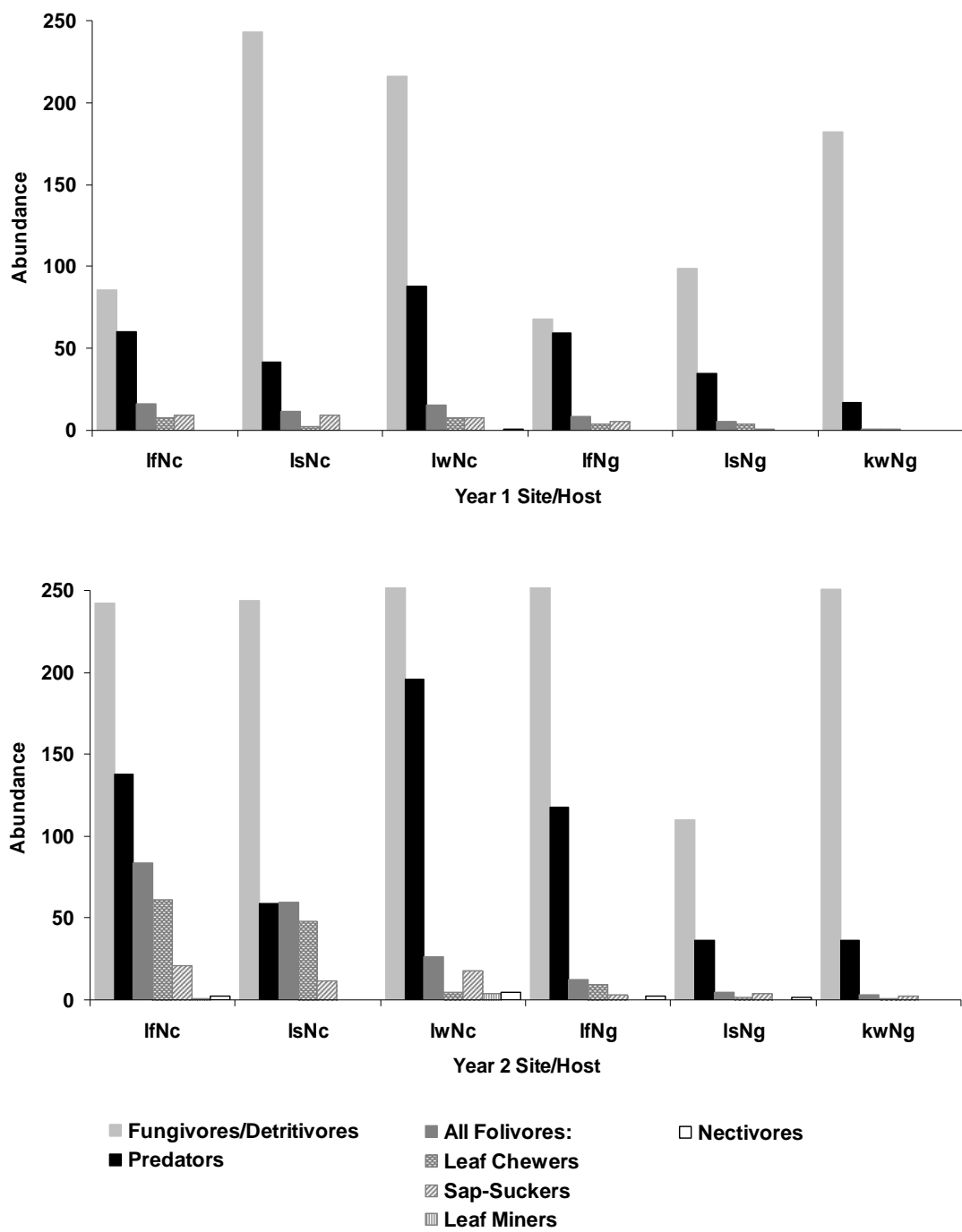


Table 5. 38. Year to year variation in guild abundance. If: Lake Fenton, Is: Lake Skinner, Iw Lyrebird Walk, kw, King William. Nc: *N. cunninghamii*; Ng: *N. gunnii*. Year 1: 1998-1999; Year 2: 1999-2000. All Folivores = Leaf Chewers, Sap-suckers and Leaf Miners combined.

5.7 ARTHROPOD FAUNA: SUMMARY OF RESULTS

Overall, a total of 15,155 individuals were collected between March 1998 and March 2002, from 17 sites for *N. cunninghamii* and 12 sites for *N. gunnii*. Two thirds of this arthropod total came from *N. cunninghamii* samples; and all of the main orders, except Plecoptera, were more abundant on *N. cunninghamii*. Acarina was the most abundant order overall, and the most abundant order on each *Nothofagus* host.

N. cunninghamii had a greater morphotaxon richness and abundance than *N. gunnii* in all families except Plecoptera. Of the 310 morphotaxa identified: 83 occurred on both *Nothofagus* species; 193 only on *N. cunninghamii*; and 34 only on *N. gunnii*. Coleoptera was the most morphotaxon rich order overall and on each of the *Nothofagus* species. Almost 42% of all morphotaxa occurred as singletons, this proportion being similar for both *Nothofagus* species.

Acarina accounted for the top ten morphotaxon abundances overall and on each *Nothofagus* species: oribatids AcOr26 and AcOr05 being most abundant on *N. cunninghamii* and *N. gunnii* respectively. No morphotaxon was found at all sites: mesostigmatid mite AcMe01 was the most widespread, occurring on *N. cunninghamii* at 15 sites and on *N. gunnii* at 10 sites.

Notable differences in the arthropod fauna of the two *Nothofagus* species include the low morphotaxon richness and abundance of Coleoptera, and particularly of Psocoptera, on *N. gunnii* compared with *N. cunninghamii*. Only Plecoptera had the higher morphotaxon richness and abundance on *N. gunnii*.

5.7.1 Multivariate Analysis

All morphotaxa analyses revealed a separation of the two *Nothofagus* species. On regional analysis, host and region groups were distinct on MRPP and ordination. For *N. cunninghamii*, the regional groups were distinct on MRPP, and on ordination the North East separates from the other regions, although there was some overlap between South and West/Central. For *N. gunnii* the regions overlap, with southern sites appearing as a subset of the West/Central sites on ordination. Host/season groups were distinct on MRPP, but on ordination summer was seen to overlap spring and autumn. Ordination by region/season showed seasonal separation within each region.

No variation was found between north-facing or south-facing aspect, or with close proximity between the two *Nothofagus* species. When consecutive sampling years were compared, although the morphotaxon richness and abundance varied, there was no significant difference between the years on MRPP and ordination.

5.7.2 *Feeding Guilds*

Fungivores/detritivores had the highest abundance of the feeding guilds, especially on *N. gunnii*. The predators and folivores had a higher relative abundance on *N. cunninghamii* than on *N. gunnii*, although the ratio between the predators and folivores on each *Nothofagus* species was comparable.

Seasonal comparison revealed an overall increased proportion of fungivores/detritivores from spring to autumn, and this occurred on both *Nothofagus* species. On *N. cunninghamii*, the proportion of predators increased and leaf chewers decreased from spring to autumn, while the sap-suckers peaked in summer. On *N. gunnii* the proportions of both predators and leaf chewers decreased from spring to autumn, while the sap-suckers again peaked in summer.

Comparison of the consecutive sampling years revealed markedly increased abundance in Year 2, especially in predators and folivores, and of fungivores/detritivores at Lake Fenton.

Chapter 6 RESULTS II: HERBIVORY LEVELS

Whereas Chapter 5 documented the ordinal communities of arthropod fauna collected from *N. cunninghamii* and *N. gunnii* between March 1998 and March 2002, this chapter describes the levels and patterns of herbivory sustained by the two *Nothofagus* species, revealed by leaves sampled over the same time interval. The initial sub-chapters deal with leaf-chewing herbivory, firstly (6.1) the comparison of numbers and of intact and chewed leaves in the samples, and secondly (6.2) the examination of the proportion of the leaf area lost from the chewed leaves. Sub-chapter 6.3 documents the variation in areas of unchewed leaves and, at the most visited sites, the attempt to assess the growth of a hole in the leaf lamina compared with the overall growth of its parent leaf; while sub-chapter 6.4 gives a brief overview of aspects of leaf damage, or of infestation, by non-chewers. The final sub-chapter (6.5) provides a summary of the herbivory results. The relevant graphs are clustered at the end of each sub-section.

6.1 LEAF-CHEWING HERBIVORY: LEAVES INTACT OR CHEWED

A combined total of more than 57,000 leaves were examined for evidence of leaf-chewing herbivory, nearly 46,600 from *N. cunninghamii* and just over 10,700 from *N. gunnii* between March 1998 and March 2002. The data were accessed (Sampling Sets 1-5, Table 4.2) to provide comparisons between the *Nothofagus* species; and for each species, to explore variation between regions, seasons, sampling aspect, and cumulative herbivory in consecutive sampling years. The numbers of intact and chewed leaves were summarised and compared using bar graphs of the raw counts of each, and also of their relative proportions. However, it must be noted that only at the southern sites and the 1998-1999 visits to King William were the branchlets tagged for cumulative data gathering; for the remainder, the total numbers of leaves differed between the branchlets removed for examination in the lab. Consequently, the percentages of chewed leaves were used for comparisons between sites, regions, and seasons and aspects.

6.1.1 Between *Nothofagus* species and Regional Variation, All Sites

The leaf-chewing data from all sites (Sampling Set 1, Table 4.2) revealed general trends in the variation between the two *Nothofagus* species and between regions in Tasmania. *N. cunninghamii* had the higher proportion of chewed to intact leaves compared with *N. gunnii*, both overall, and in the regions where they co-occur.

Of the overall total of 57,305 leaves sampled from both *Nothofagus* species, 26.52% (15,199 leaves) displayed some evidence of chewing damage (figure 6.1). However, more than twice the proportion of *N. cunninghamii* leaves were chewed (29.75%: 13, 857 of 46,574 leaves), compared with for *N. gunnii* (12.51%: 1342 of 10,731 leaves).

Regional comparison (figures 6.2) revealed considerable variability for *N. cunninghamii*, the proportions of chewed leaves ranging more than twofold, from 15.04% in West Central, to 37.34% in the South; with the North West at 18.66% and the North East at 22.2%. In contrast, *N. gunnii* showed much less regional variability in proportions of chewed leaves (South: 13.45%, West/Central: 11.88%).

However, for both *Nothofagus* species, variation within the regions is evident when the individual sites were compared (figures 6.3 and 6.4). This within-region variation, in proportions of chewed leaves, is most marked for *N. cunninghamii* in the South (figure 6.3.b).

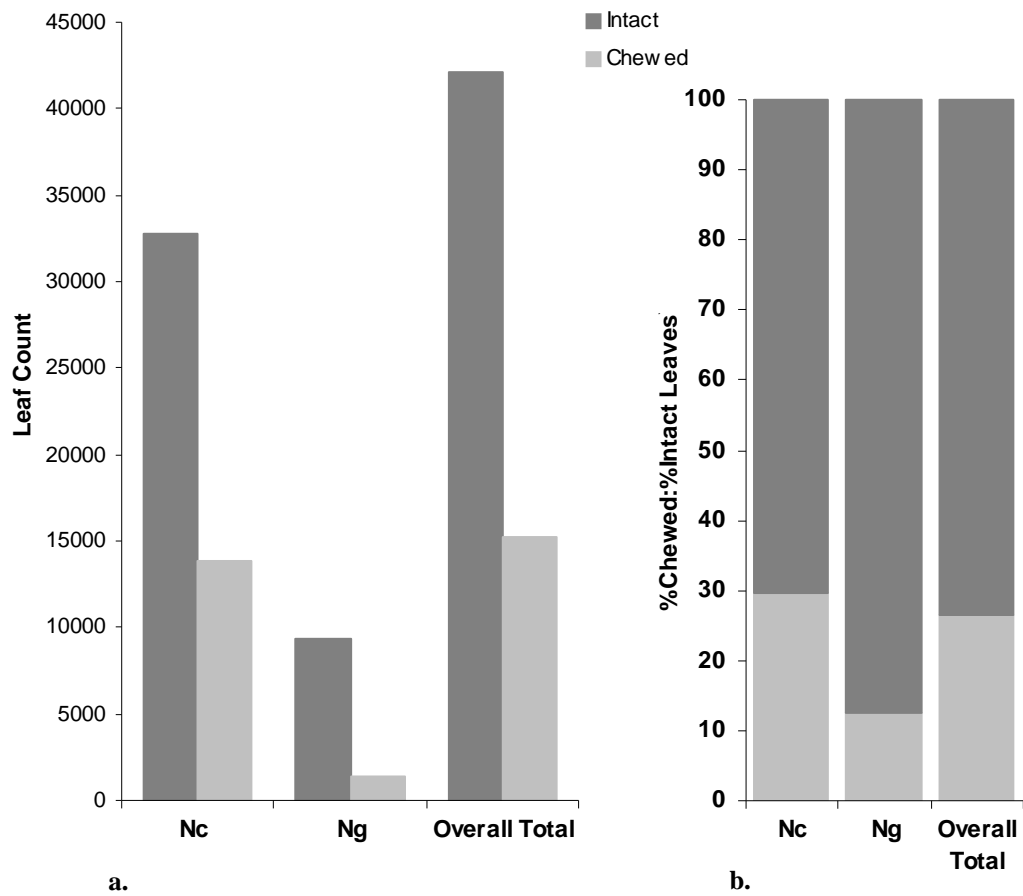


Figure 6.1. a & b. Totals (a) and proportions (b) of intact and chewed leaves, all sites, 1998-2002: *N. cunninghamii* (Nc), *N. gunnii* (Ng) and overall.

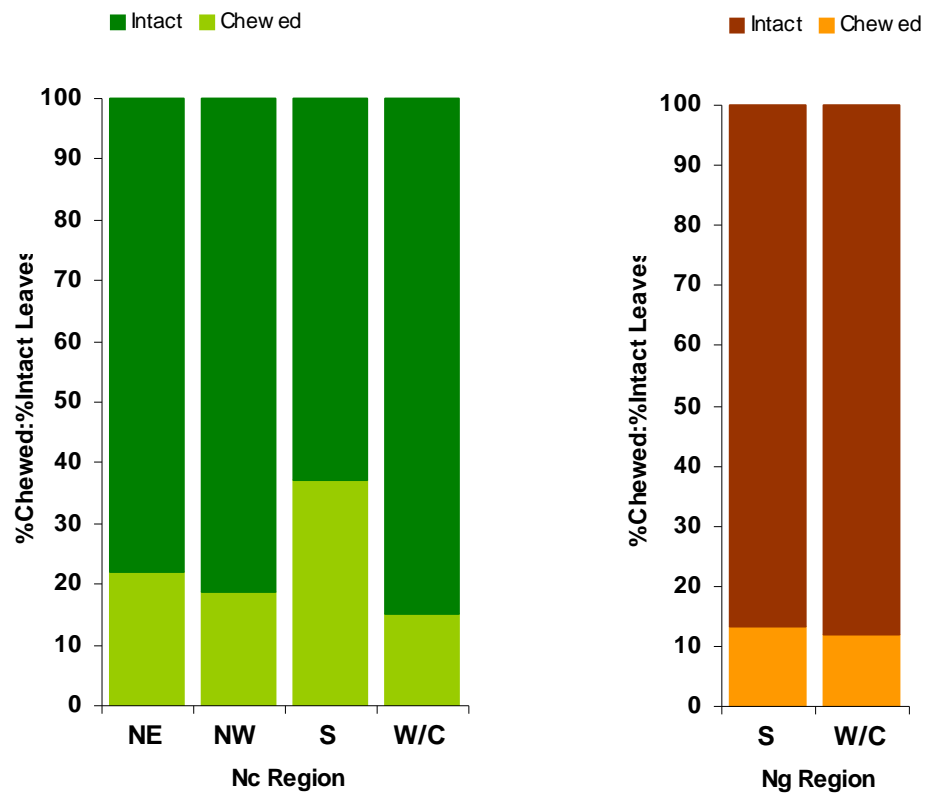
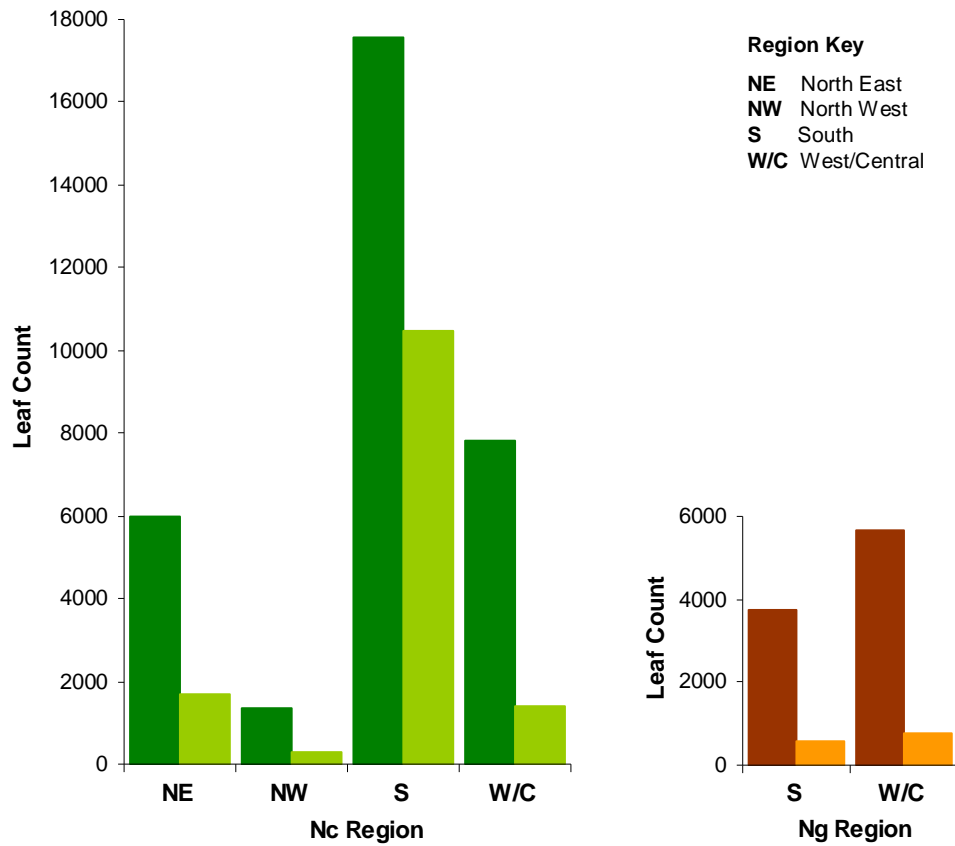
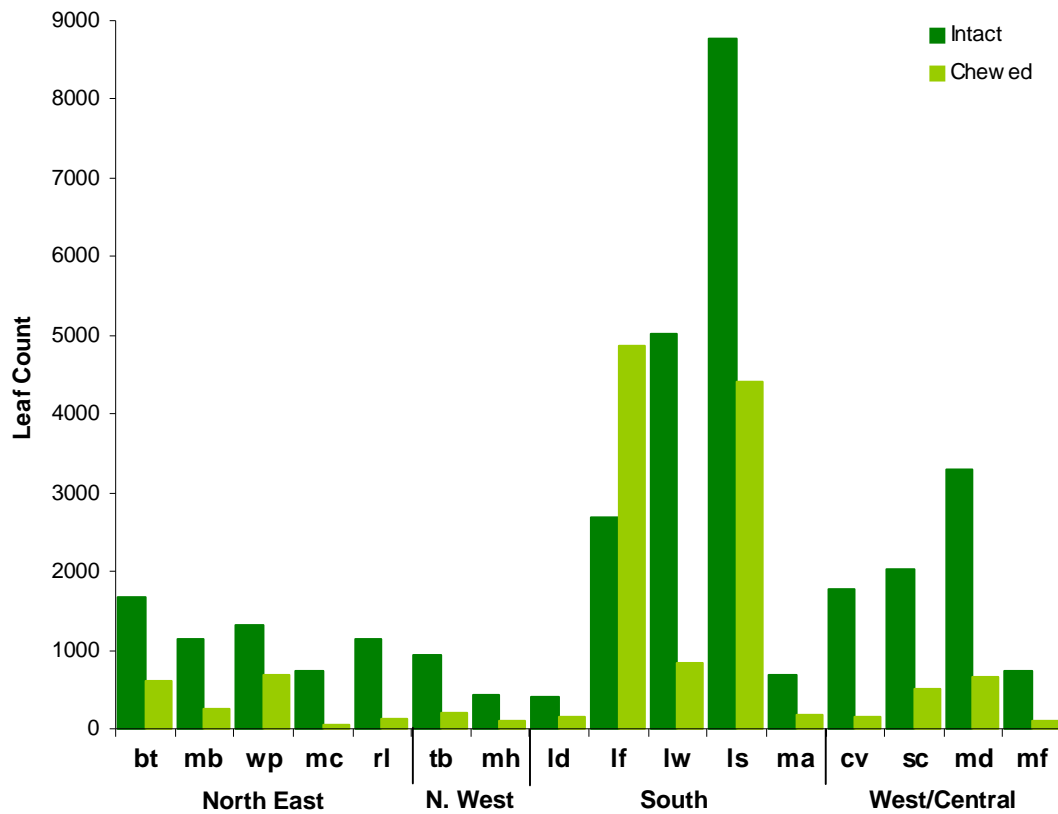
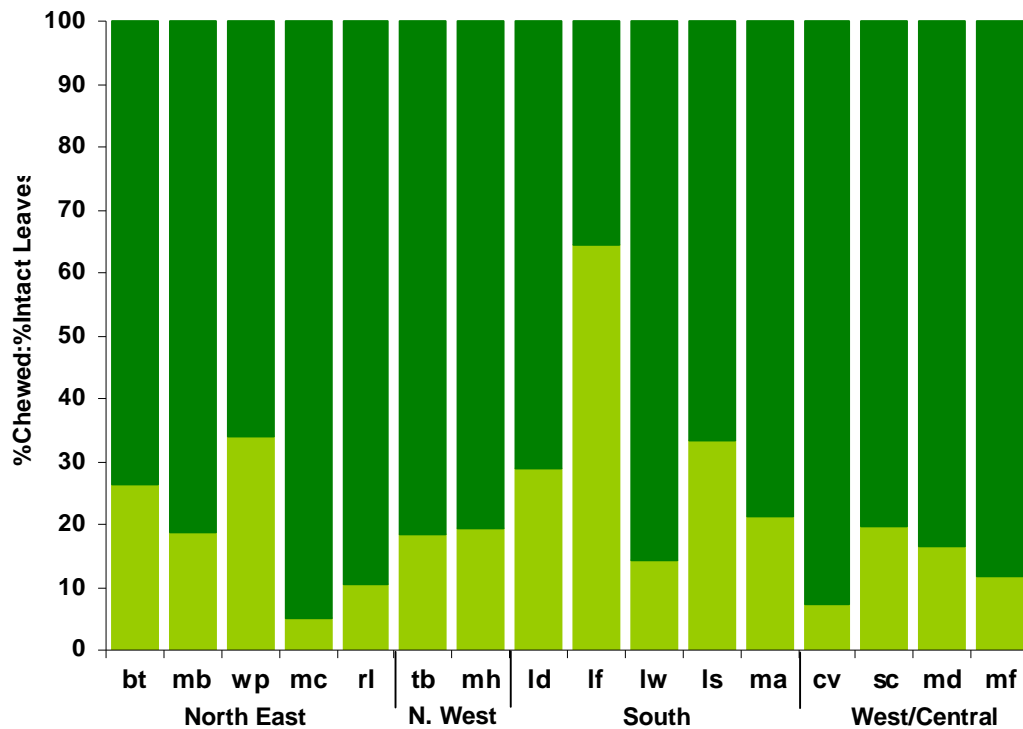


Figure 6.2. a & b. Totals (a) and proportions (b) of intact and chewed leaves, *N. cunninghamii* (Nc) and *N. gunnii* (Ng), all sites by region 1998-2002.



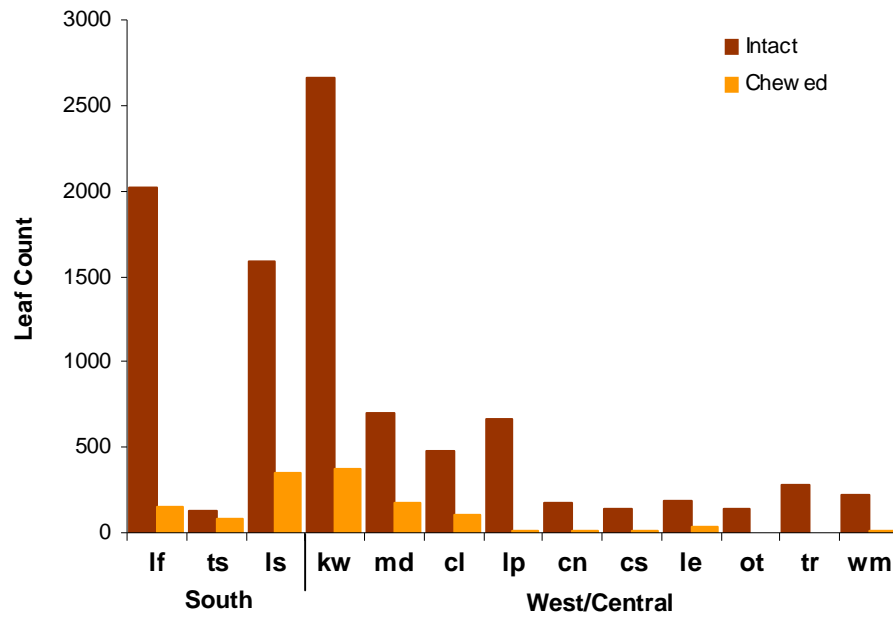
a. *N. cunninghamii*: Region/Site Counts of Intact and Chewed Leaves



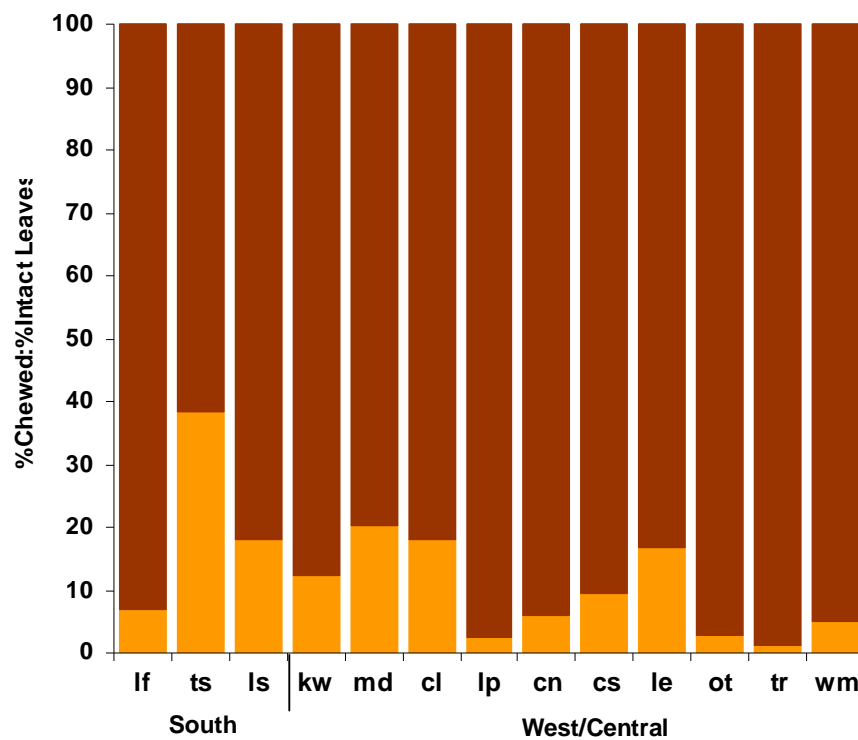
b. *N. cunninghamii*: Region/Site Proportions of Intact and Chewed Leaves

Figure 6.3. a & b. Totals (a) and proportions (b) intact and chewed leaves, *N. cunninghamii*, all sites by region 1998-2002.

North East: bt: Blue Tier, mb: Mt. Barrow, wp: Weldborough Pass, mc: Myrtle Creek, rl: Rainforest Ledge. **North West:** tb: Tayatea Bridge, mh: Milkshake Hills. **South:** ld: Lake Dobson, lf: Lake Fenton, lw: Lyrebird Walk, ls: Lake Skinner, ma: Mt. Arthur. **West/Central:** cv: Cradle Valley, sc: Lake St Clair, md: Mt. Dundas, mf: Meander Forest.



a. *N. gunnii*: Region/Site Counts of Intact and Chewed Leaves



b. *N. gunnii*: Region/Site Proportions of Intact and Chewed Leaves

Figure 6.4. Totals (a) and proportions (b) intact and chewed leaves, *N. gunnii*, all sites by region 1998-2002.

South: lf: Lake Fenton, ts: Tarn Shelf, ls: Lake Skinner. **West/Central:** kw: King William, md: Mt. Dundas, cl: Crater Lake, lp: Little Plateau, cn & cs: Cradle Cirque, North and South, le: Lake Eros, ot: Ossa Track, tr: Traveller Range, wm: Lake Windermere.

Regional and Seasonal Variation, Region/Season Sites

The Region/Season data subset (Sampling Set 2, table 4.2) comprised an overall total of 15,657 leaves examined for evidence of leaf chewing (*N. cunninghamii*: 10,753 leaves; *N. gunnii*: 4,904 leaves) from spring, summer and autumn visits to 12 sites for *N. cunninghamii* and 7 sites for *N. gunnii*, between November 1999 and May 2000. Of the combined total, 17.47% (2,735 leaves) were chewed and although *N. cunninghamii* had a higher proportion (18.85%: 2027 leaves) of chewed leaves than *N. gunnii* (14.44%: 708 leaves), the difference was less marked than for the results for all sites and years above (figure 6.5).

Regional comparison (all seasons combined) for *N. cunninghamii* showed the North East and South to each have more than 20% of leaves chewed, West/Central had 12.48%, while Tayatea Bridge, the single North West site, had 7.25% (figure 6.6). The proportions of chewed leaves on *N. gunnii* in the South and West/Central were between 14-15% (figure 6.6). Site comparisons again revealed within-region variation for both *Nothofagus* species (figures 6.7, 6.8).

Both *Nothofagus* species demonstrated seasonal trends, the overall proportions of chewed leaves being lowest in the spring, increasing into the summer, and then on into the autumn for *N. cunninghamii*, but with a slight autumnal decrease for *N. gunnii* (figure 6.9). There were however, regional differences for each species: *N. cunninghamii* in the North East and South had increasing proportions of chewed leaves from spring to autumn, in West/Central there was a gradual decrease over the same seasons, while at Tayatea Bridge in the North West there was a sharp rise between spring and summer then a decline in autumn (figure 6.10); *N. gunnii* in the South had an autumn peak, and in West/Central a summer peak, in proportions of chewed leaves (figure 6.11).

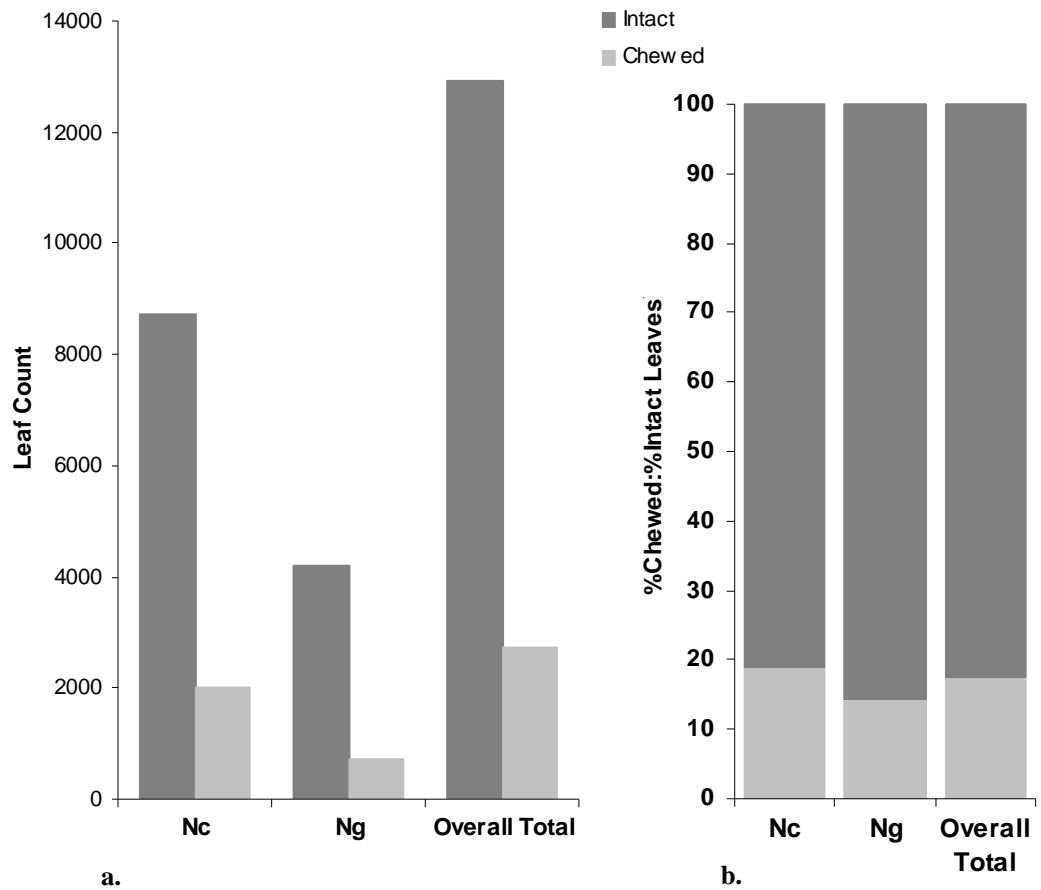


Figure 6.5. a & b. Totals (a) and proportions (b) of intact and chewed leaves, 1999-2000: *N. cunninghamii* (Nc) 12 sites, *N. gunnii* (Ng) 7 sites.

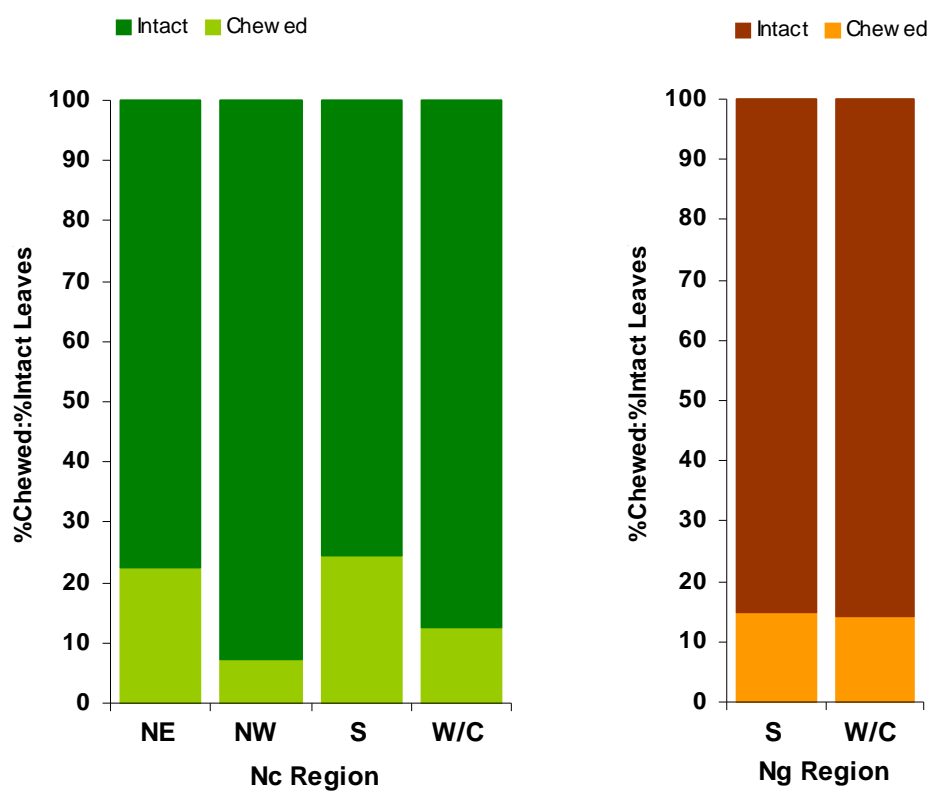
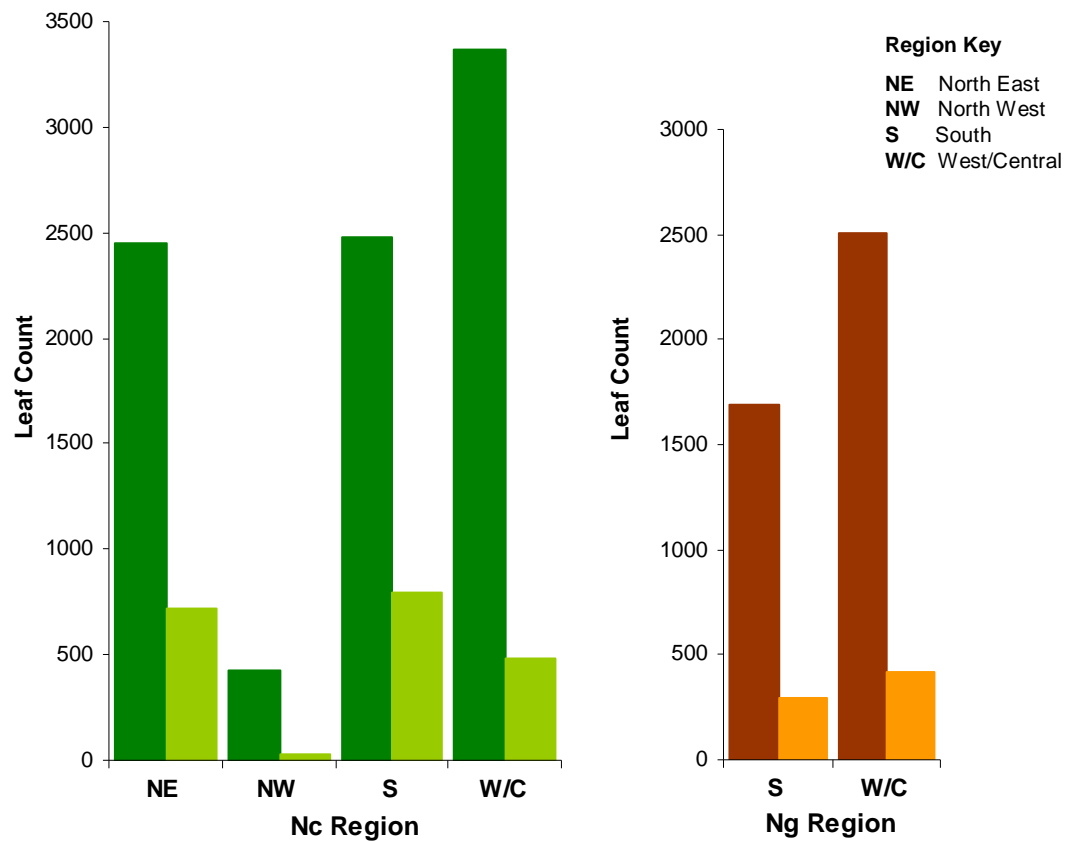
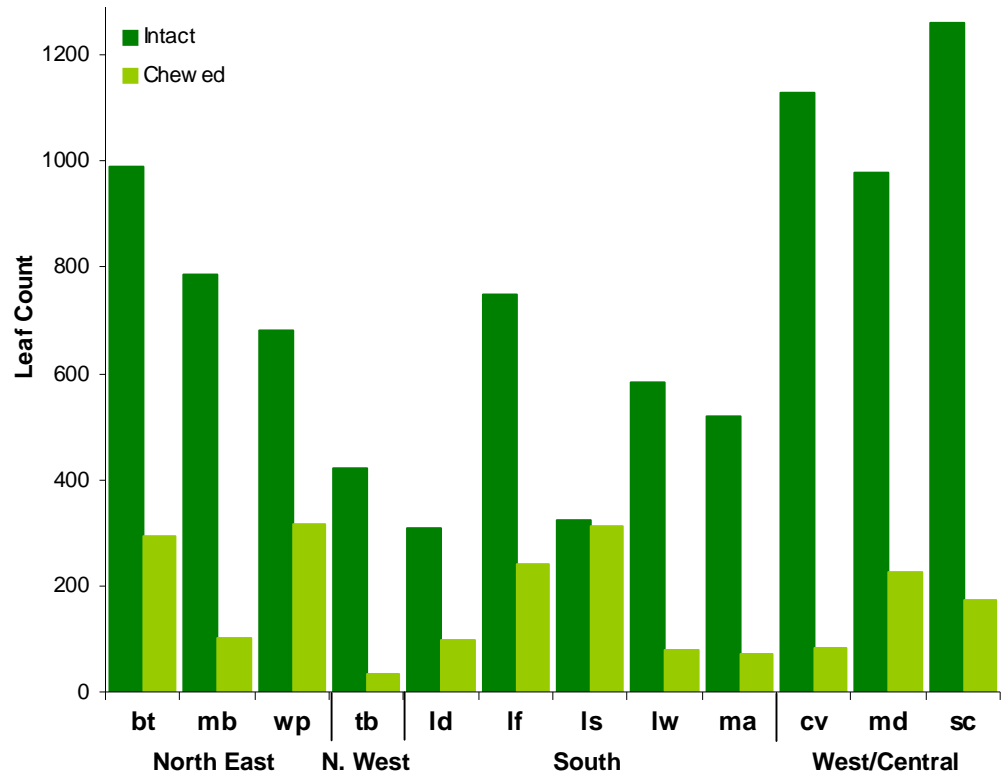
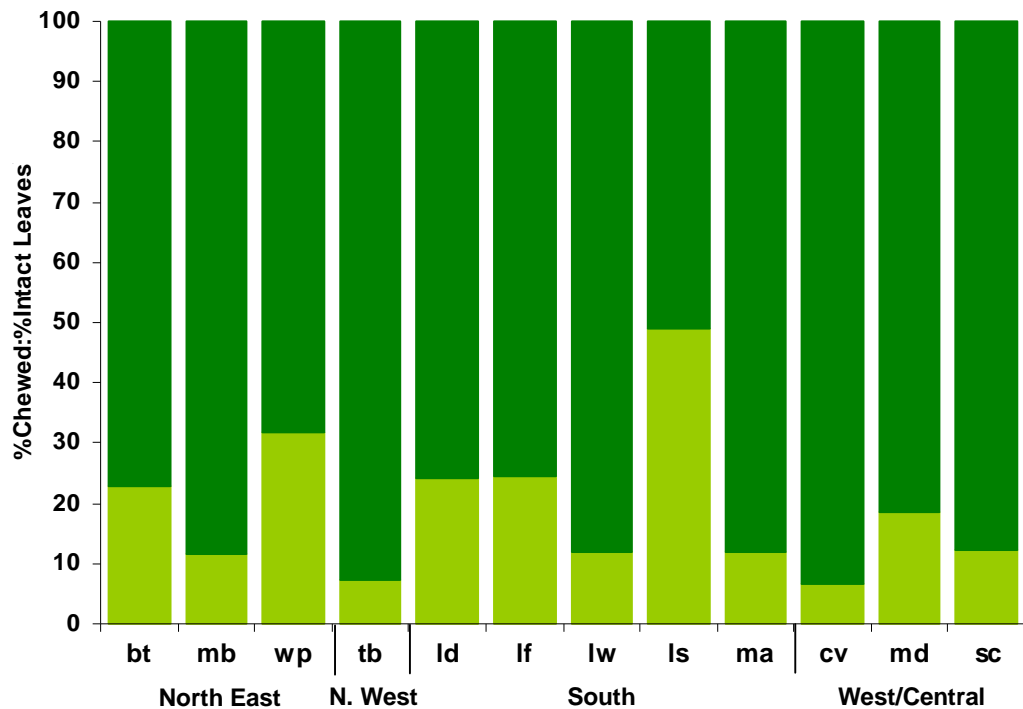


Figure 6.6. a & b. Totals (a) and proportions (b) of intact and chewed leaves, 1999-2000 by *Nothofagus* species and region. *N. cunninghamii* (Nc) 12 sites, *N. gunnii* (Ng) 7 sites.

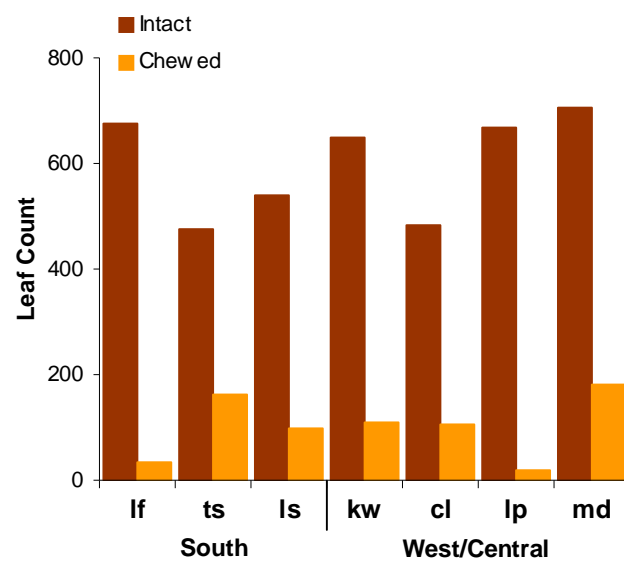


a. *N. cunninghamii*: Region/Site Counts of Intact and Chewed Leaves

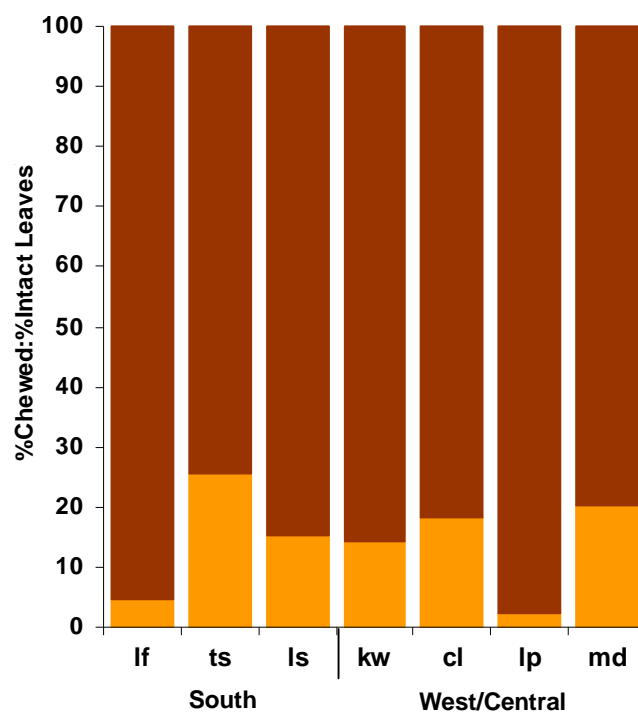


b. *N. cunninghamii*: Region/Site Proportions of Intact and Chewed Leaves

Figure 6.7. a & b. Totals (a) and proportions (b) intact and chewed leaves, *N. cunninghamii*, 12 sites by region 1999-2000. North East: bt: Blue Tier, mb: Mt. Barrow, wp: Weldborough Pass. North West: tb: Tayatea Bridge. South: ld: Lake Dobson, lf: Lake Fenton, lw: Lyrebird Walk, ls: Lake Skinner, ma: Mt. Arthur. West/Central: cv: Cradle Valley, sc: Lake St Clair, md: Mt. Dundas.

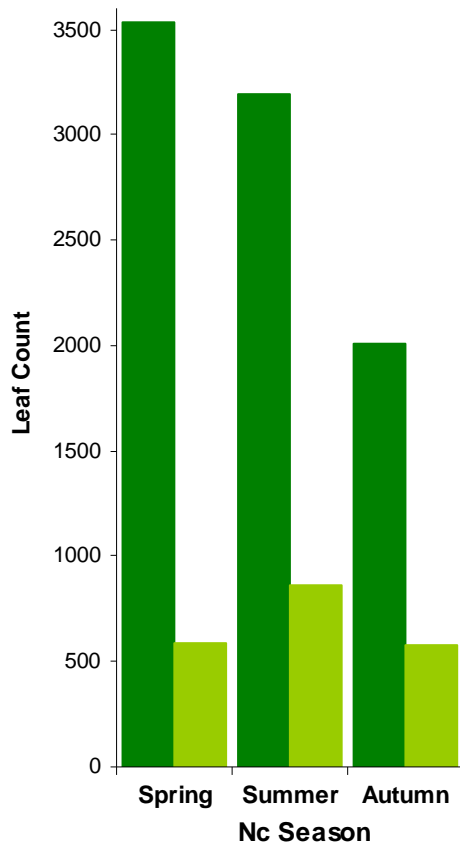


a. *N. gunnii*: Region/Site Counts of Intact and Chewed Leaves

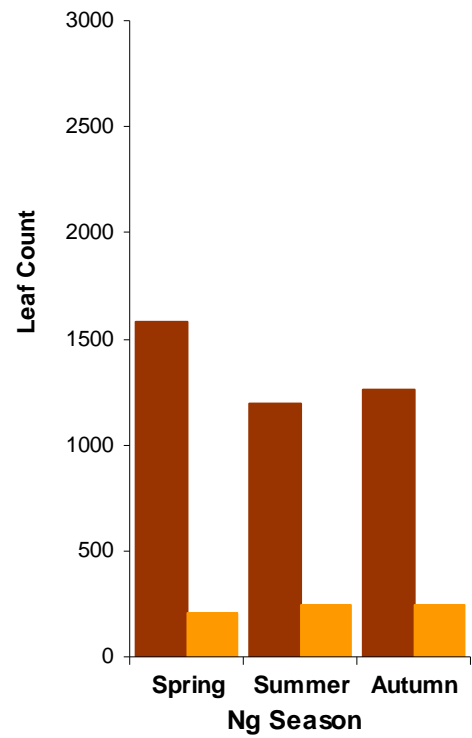


b. *N. gunnii*: Region/Site Proportions of Intact and Chewed Leaves

Figure 6.8. a & b. Totals (a) and proportions (b) intact and chewed leaves, *N. gunnii*, 7 sites by region 1999-2000. South: lf: Lake Fenton, ts: Tarn Shelf, ls: Lake Skinner. West/Central: kw: King William, cl: Crater Lake, lp: Little Plateau, md: Mt. Dundas.

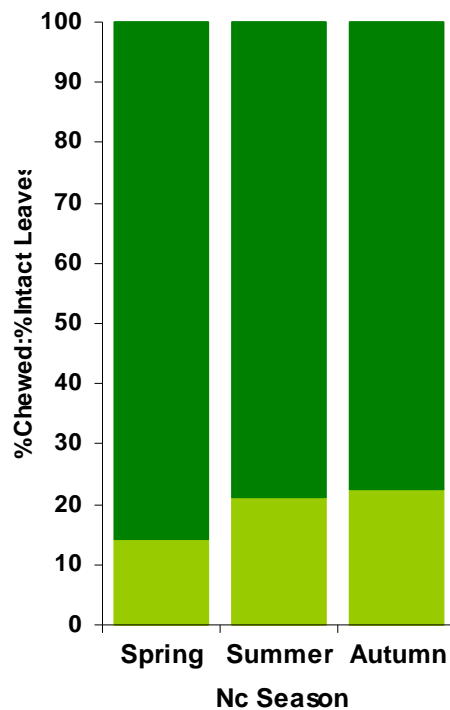


a. Counts of Intact and Chewed Leaves

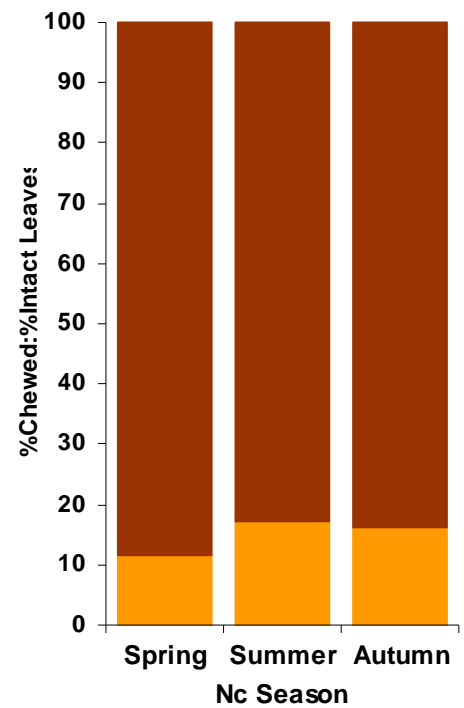


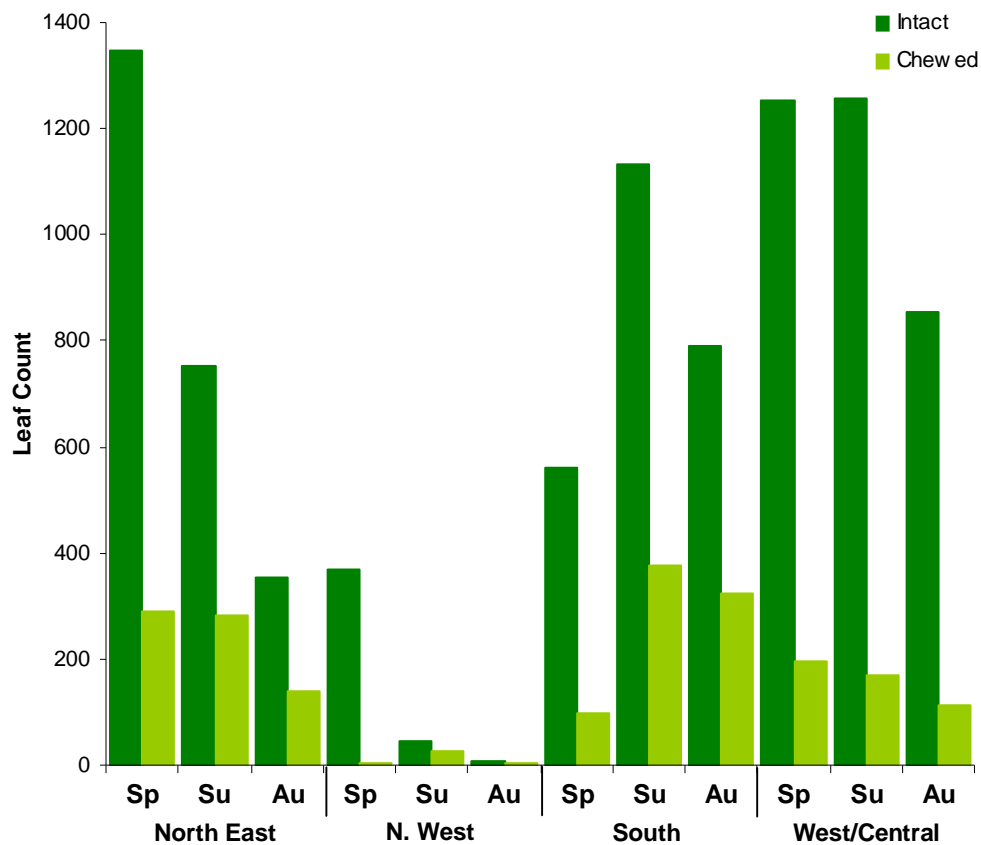
■ Intact ■ Chewed

■ Intact ■ Chewed

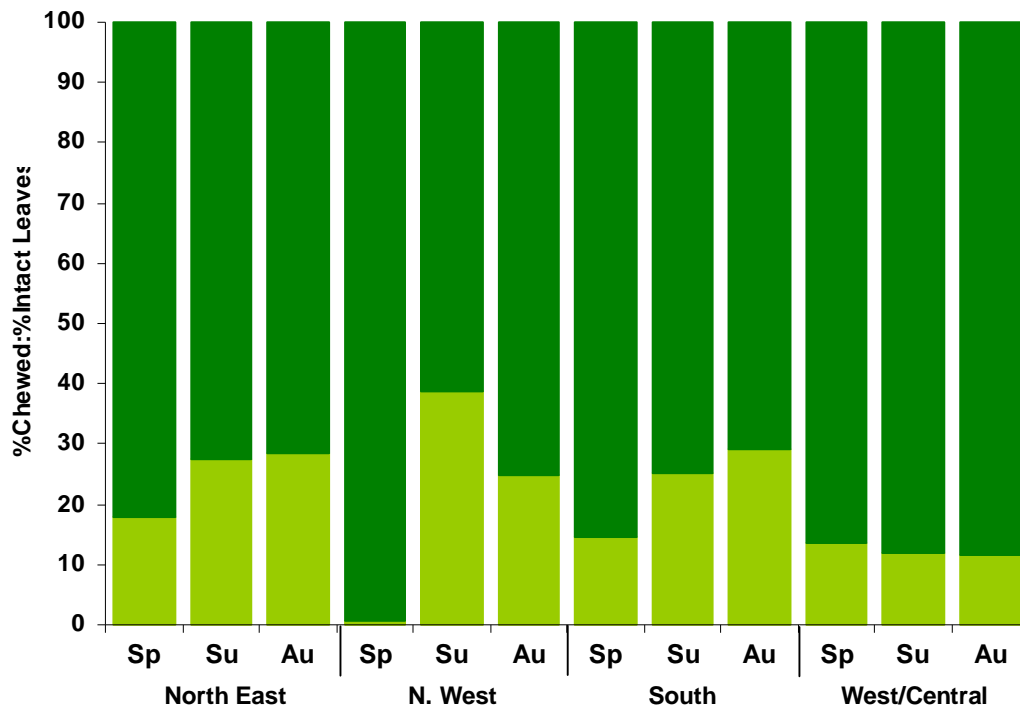


b. Proportions of Intact and Chewed Leaves

Figure 6.9. a & b. Totals (a) and proportions (b) of intact and chewed leaves, 1999-2000 by *Nothofagus* species and season. *N. cunninghamii* (Nc) 12 sites, *N. gunnii* (Ng) 7 sites.

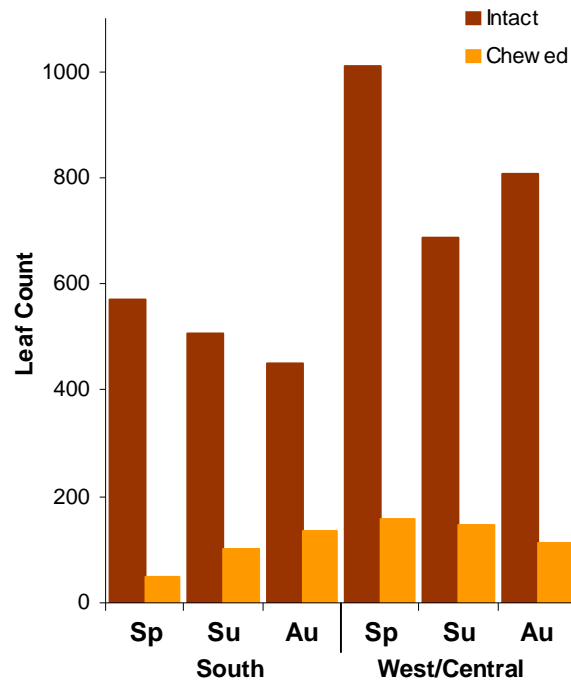


a. Counts of Intact and Chewed Leaves

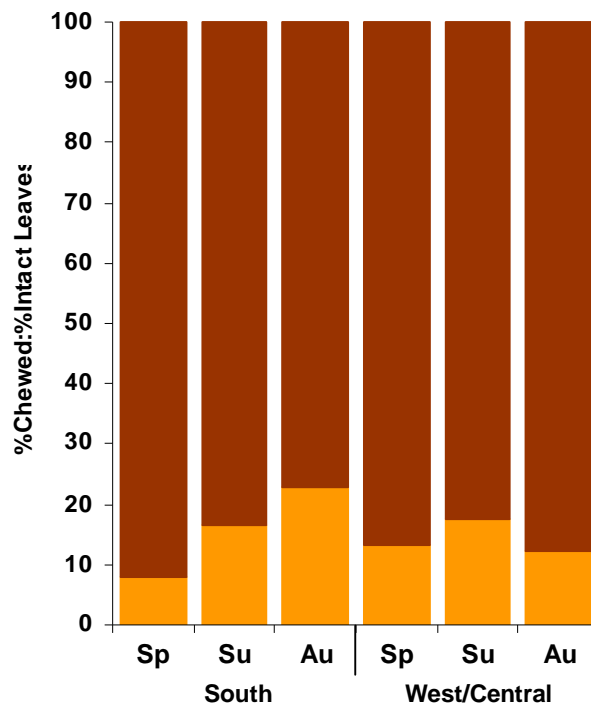


b. Proportions of Intact and Chewed Leaves

Figure 6.10. a & b. Totals (a) and proportions (b) intact and chewed leaves, *N. cunninghamii*, 12 sites, by region and season 1999-2000. Sp: Spring, Su: Summer, Au: Autumn.



a. Counts of Intact and Chewed Leaves



b. Proportions of Intact and Chewed Leaves

Figure 6.11. a & b. Totals (a) and proportions (b) intact and chewed leaves, *N. gunnii*, 7 sites, by region and season 1999-2000. Sp: Spring, Su: Summer, Au: Autumn.

6.1.2 Aspect Variation

When leaf aspect was taken into consideration (Sampling Set 3, table 4.2), *N. cunninghamii* (figures 6.12.a & 6.14.a) was found to have higher proportion of chewed leaves on the south-facing aspects (43.45% of a total 5784 leaves) compared with the north-facing aspects (33.69% of a total 6115 leaves), while for *N. gunnii* (figures 6.12.b & 6.14.b), the reverse was true (north-facing 13.93% chewed of a total 2499 leaves; south-facing 7.46% of a total 2412 leaves). For each *Nothofagus* species the adjacent aspects, at 63.37% for *N. cunninghamii* and 27.9% for *N. gunnii*, had higher proportions of chewed leaves than either the north-facing or south-facing aspects, although fewer leaves in total (*N. cunninghamii*: 4783; *N. gunnii*: 656) were examined (figures 6.13 & 6.15).

Site comparison revealed a markedly higher proportion of chewed leaves on *N. cunninghamii* at Lake Fenton than at Lake Skinner for all aspects, particularly north-facing (figures 6.15.a, 6.16.a, 6.17.a, 6.18.a, 6.19.a). For *N. gunnii*, Lake Skinner had the highest proportion of chewed leaves for each of the aspects, although King William also had a high proportion of north-facing chewed leaves (figures 6.15.b, 6.16.b, 6.17.b, 6.18.b, 6.19.b).

When the autumn 1998 data (i.e. end of the leaf growth year 1997-1998) were compared with the leaf growth year 1998-1999 data, for young and old leaves on *N. cunninghamii*, the north-facing leaves, both young and old, had higher proportions of chewed leaves in the 1998-1999 samples; while the south-facing aspect had the higher proportions of chewed leaves in the Autumn 1998 samples (figure 6.20). The *N. cunninghamii* adjacent leaves had higher proportions of chewed leaves than either the north-facing or south-facing aspects, with the exception of the 1998-1999 north-facing young leaves (figures 6.20, 6.22.a & c). The two consecutive *N. gunnii* leaf year cohorts had higher proportions of chewed leaves on the north-facing than on the south-facing aspects; however the proportions of chewed leaves on the adjacent trees at Lake Fenton and Lake Skinner differed markedly between the two samples (figure 6.21).

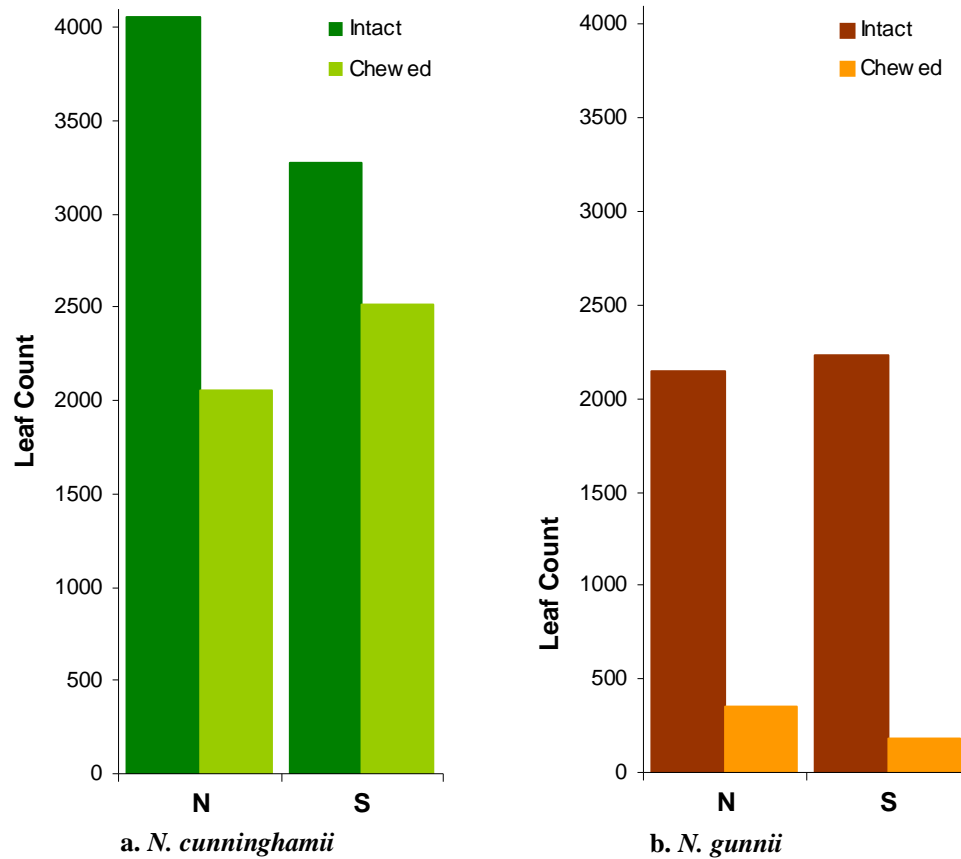


Figure 6.12. a & b. Totals of intact and chewed leaves, sampled in autumn 1998 and spring/summer 1999, from North-facing (N) and South-facing (S) aspects, at 2 sites for *N. cunninghamii*: Lake Fenton and Lake Skinner; and 3 sites for *N. gunnii*: Lake Fenton, Lake Skinner and King William.

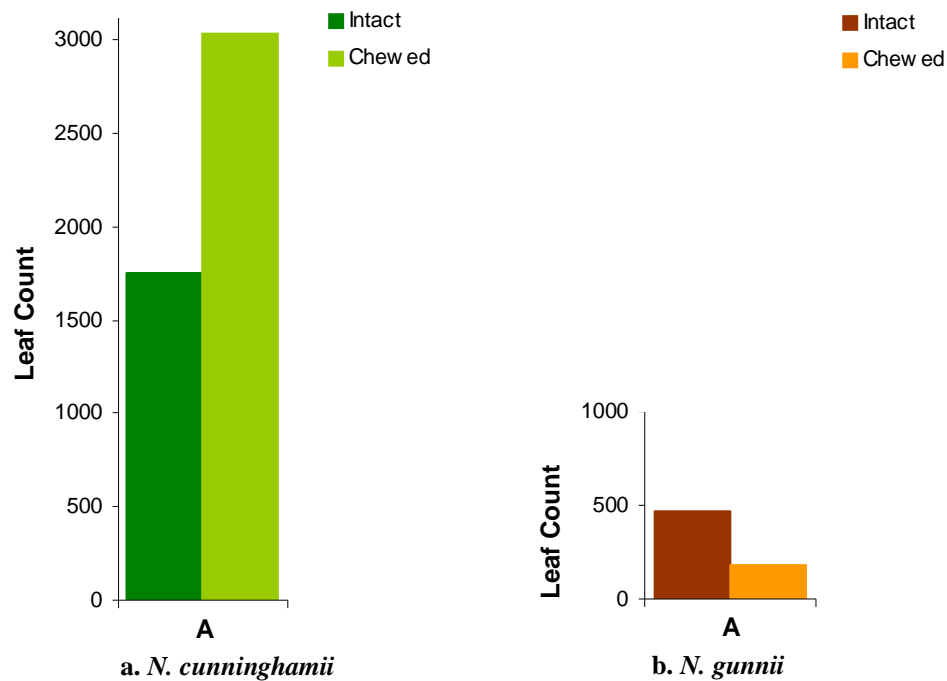


Figure 6.13. a & b. Totals of intact and chewed leaves, sampled in autumn 1998 and spring/summer 1999, from adjacent aspects (A) of trees of *N. cunninghamii* and *N. gunnii* at two sites: Lake Fenton and Lake Skinner.

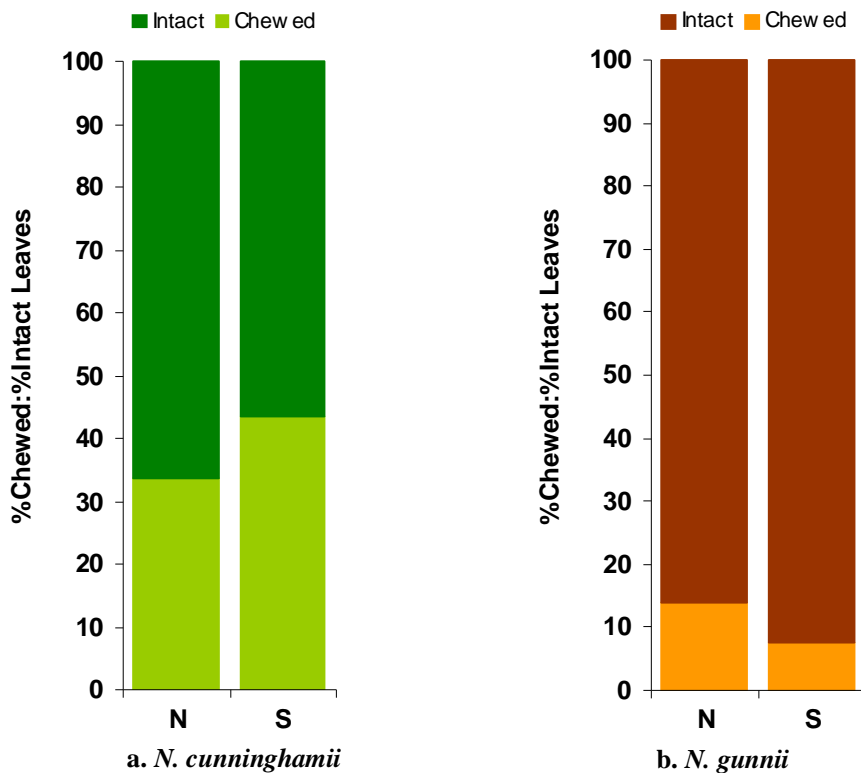


Figure 6.14. a & b. Proportions of intact and chewed leaves, sampled in autumn 1998 and spring/summer 1999, from North-facing (N) and South-facing (S) aspects, at 2 sites for *N. cunninghamii*: Lake Fenton and Lake Skinner; and 3 sites for *N. gunnii*: Lake Fenton, Lake Skinner and King William.

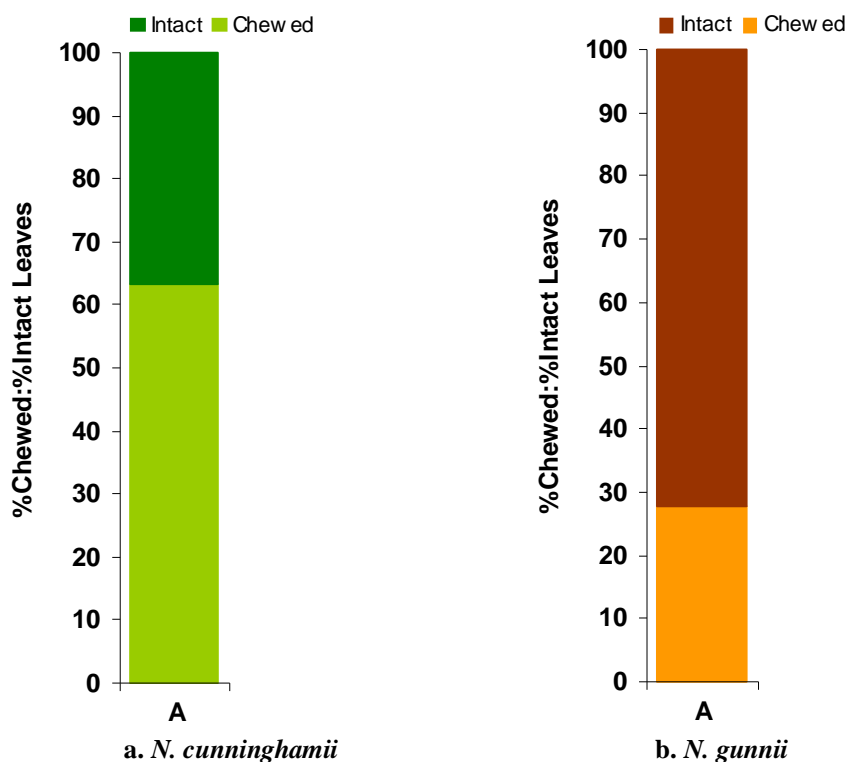


Figure 6.15. a & b. Proportions of intact and chewed leaves, sampled in autumn 1998 and spring/summer 1999, from adjacent aspects (A) of trees of *N. cunninghamii* and *N. gunnii* at two sites: Lake Fenton and Lake Skinner.

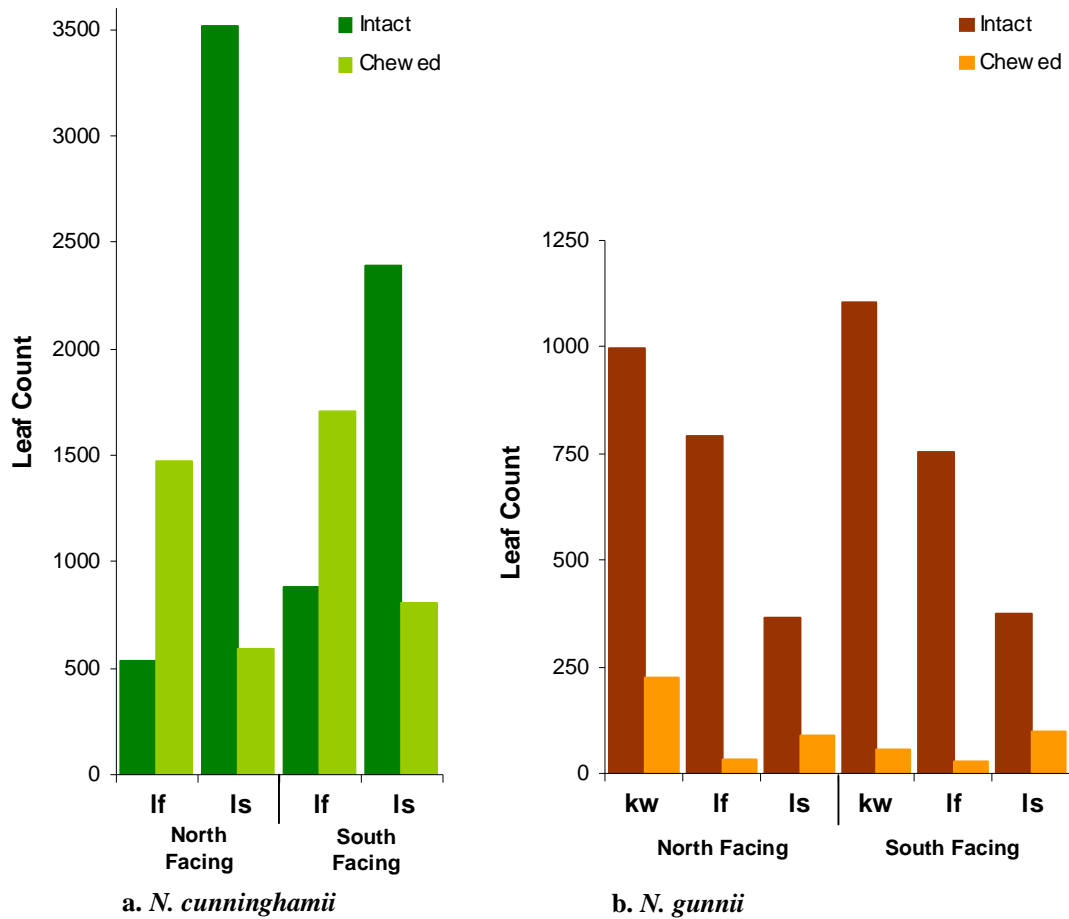


Figure 6.16. a & b. Site records of intact and chewed leaves, sampled in autumn 1998 and spring/summer 1999, from North-facing and South-facing aspects, at 2 sites for *N. cunninghamii*: Lake Fenton (lf) and Lake Skinner (ls); and 3 sites for *N. gunnii*: Lake Fenton (lf), Lake Skinner (ls) and King William (kw).

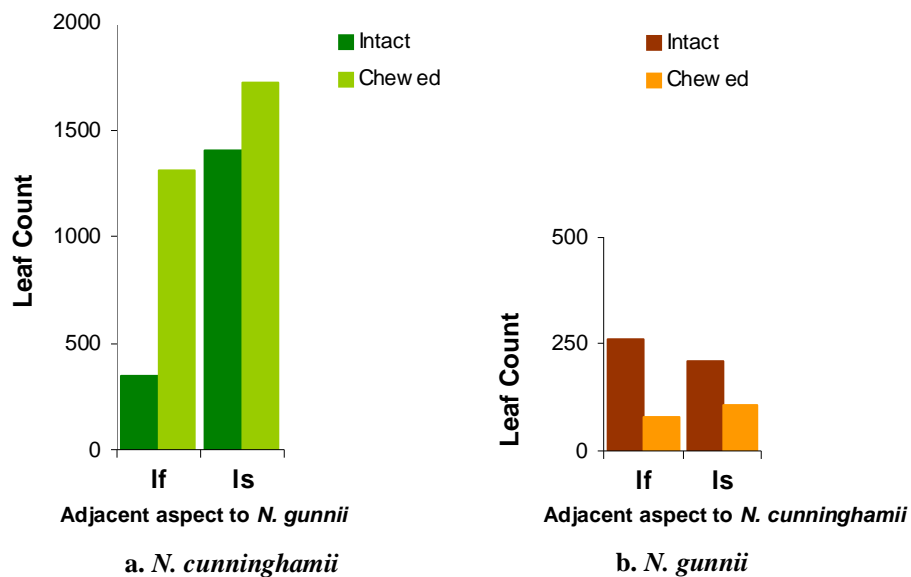


Figure 6.17. a & b. Site records of intact and chewed leaves, sampled in autumn 1998 and spring/summer 1999, from adjacent aspects of trees of *N. cunninghamii* and *N. gunnii* at two sites: Lake Fenton (lf) and Lake Skinner (ls).

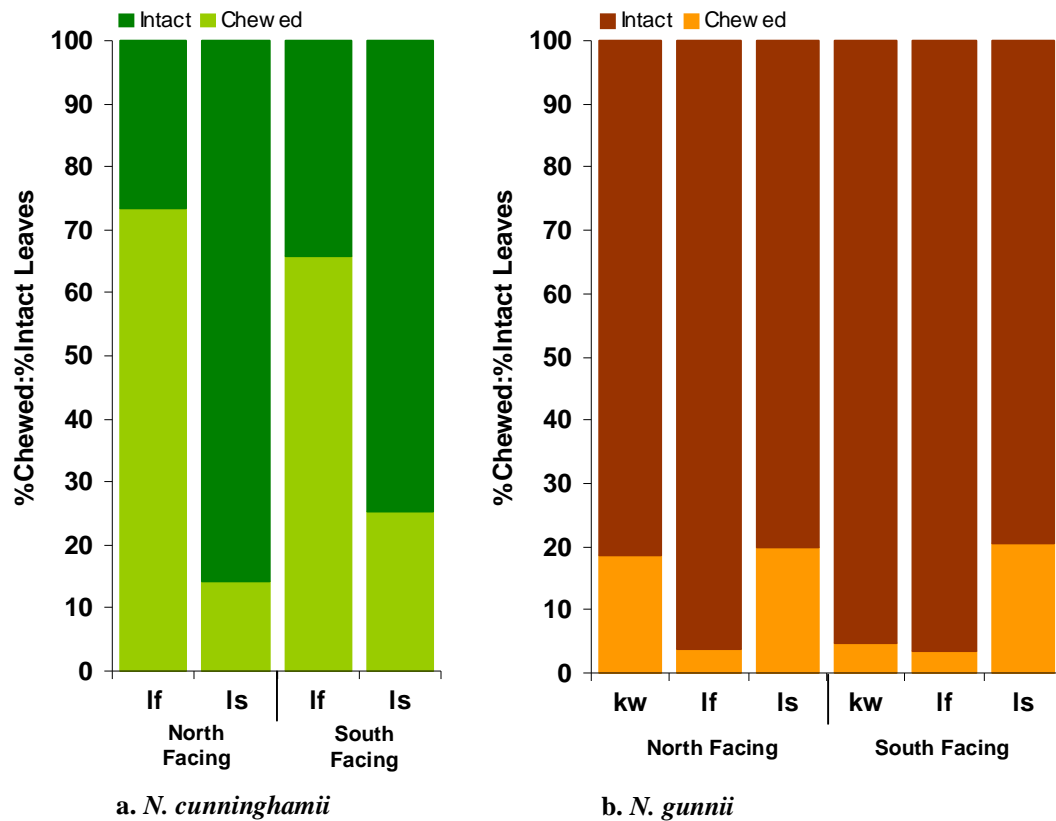


Figure 6.18. a & b. Proportions of intact and chewed leaves, sampled in autumn 1998 and spring/summer 1999, from North-facing and South-facing aspects, at 2 sites for *N. cunninghamii*: Lake Fenton (lf) and Lake Skinner (ls); and 3 sites for *N. gunnii*: Lake Fenton (lf), Lake Skinner (ls) and King William (kw).

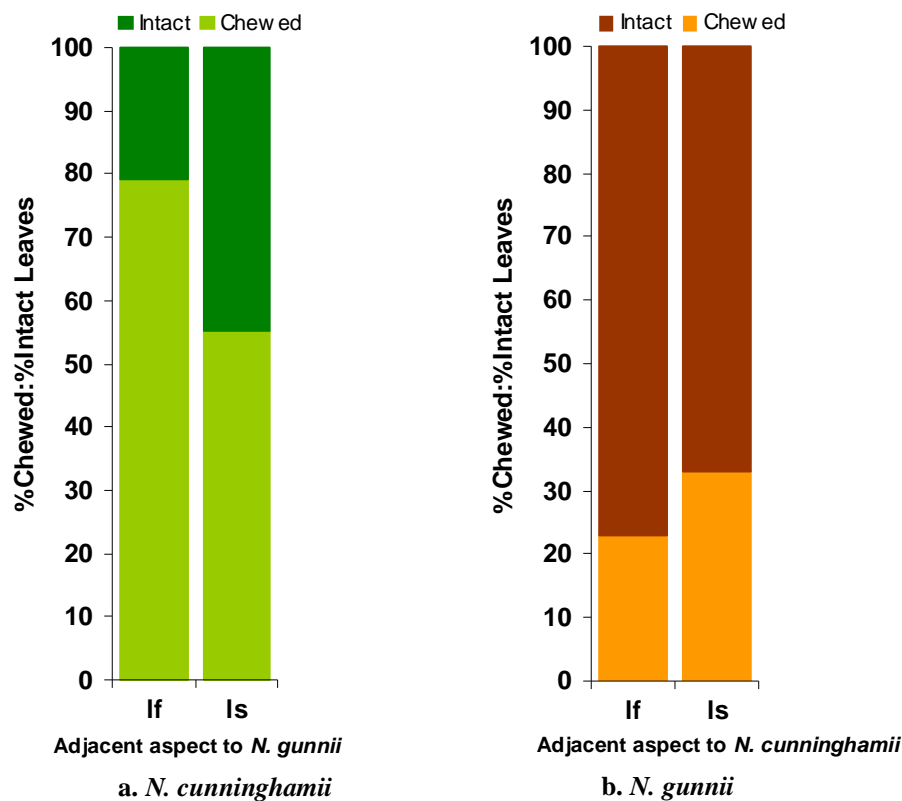


Figure 6.19. a & b. Proportions of intact and chewed leaves, sampled in autumn 1998 and spring/summer 1999, from adjacent aspects of trees of *N. cunninghamii* and *N. gunnii* at two sites: Lake Fenton (lf) and Lake Skinner (ls).

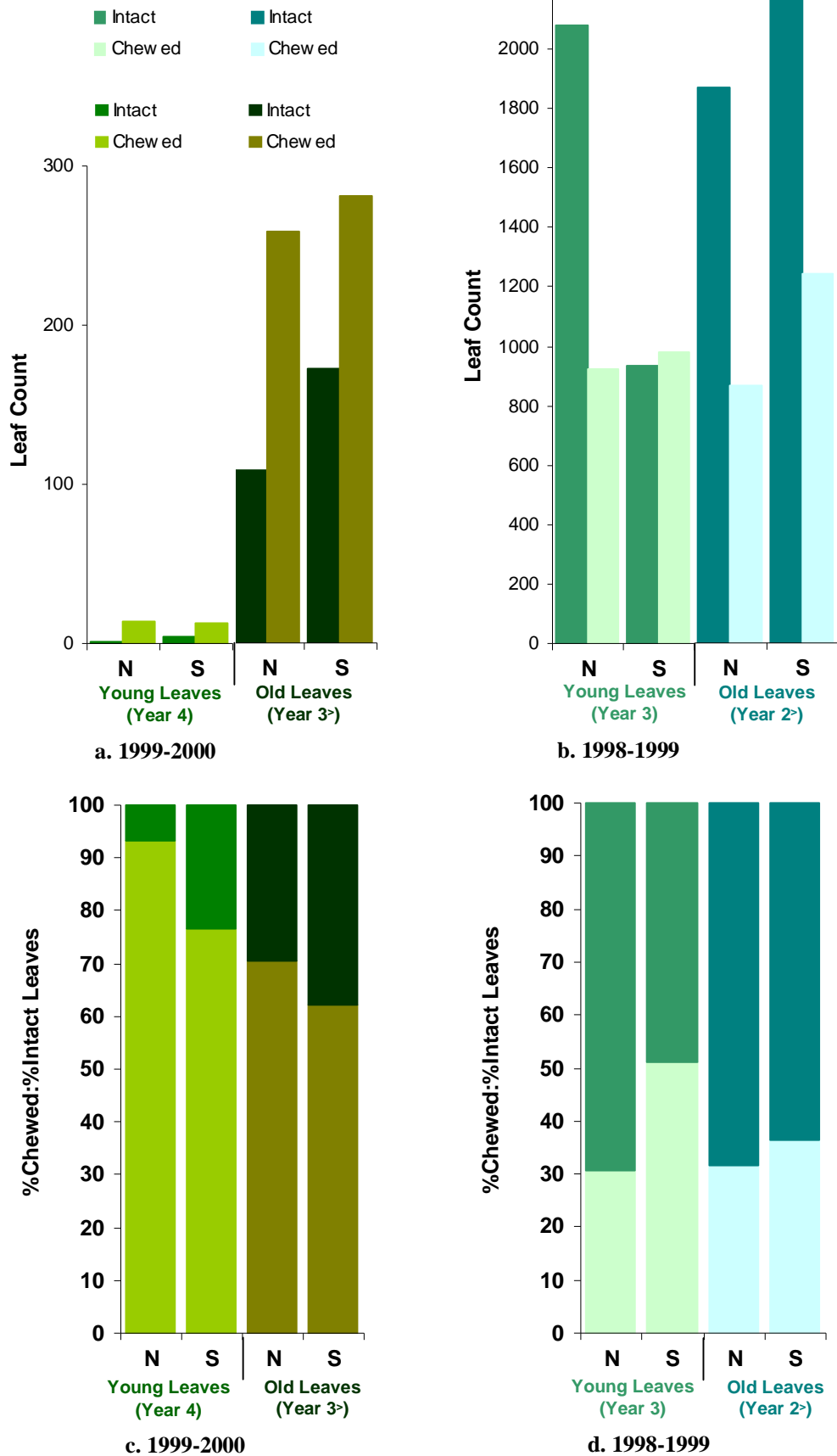


Figure 6.20. a - d. *N. cunninghamii*, totals (a, b) and proportions (c, d) of intact and chewed leaves, sampled from North-facing (N) and South-facing (S) aspects, at 2 sites: Lake Fenton and Lake Skinner. a, c. Spring/summer 1999: young leaves (Leaf Year 4) and old leaves (Leaf Year 3 and earlier). b, d. Autumn 1998 : young leaves (Leaf Year 3) and old leaves (Leaf Year 2 and earlier).

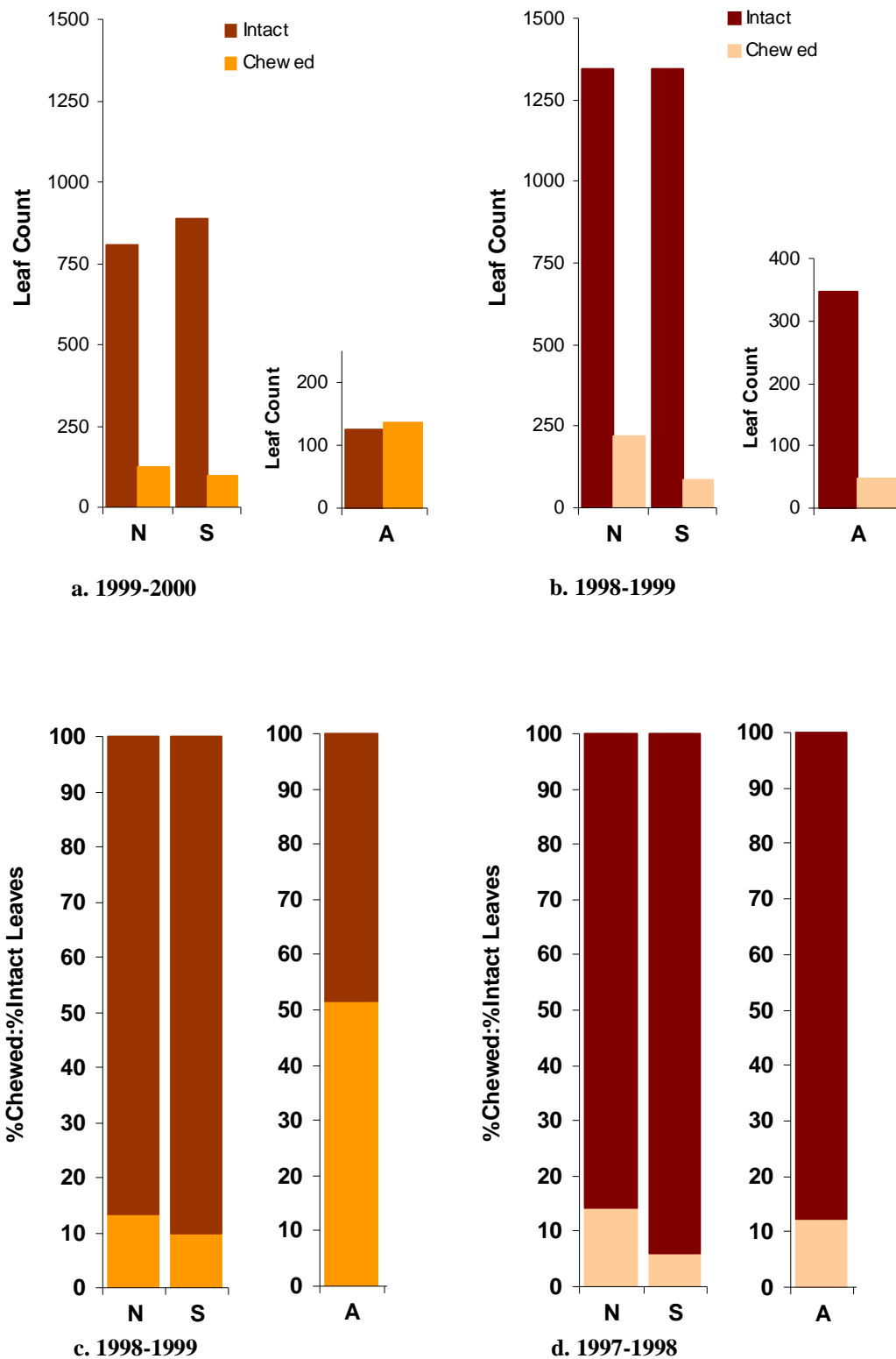


Figure 6.21 a - d. *N. gunnii*, totals (a,b) and proportions (c,d) of intact and chewed leaves, sampled from North-facing (N) and South-facing (S) aspects, at 3 sites: Lake Fenton, Lake Skinner and King William. a, c. Spring/summer 1999. b, d. Autumn 1998.

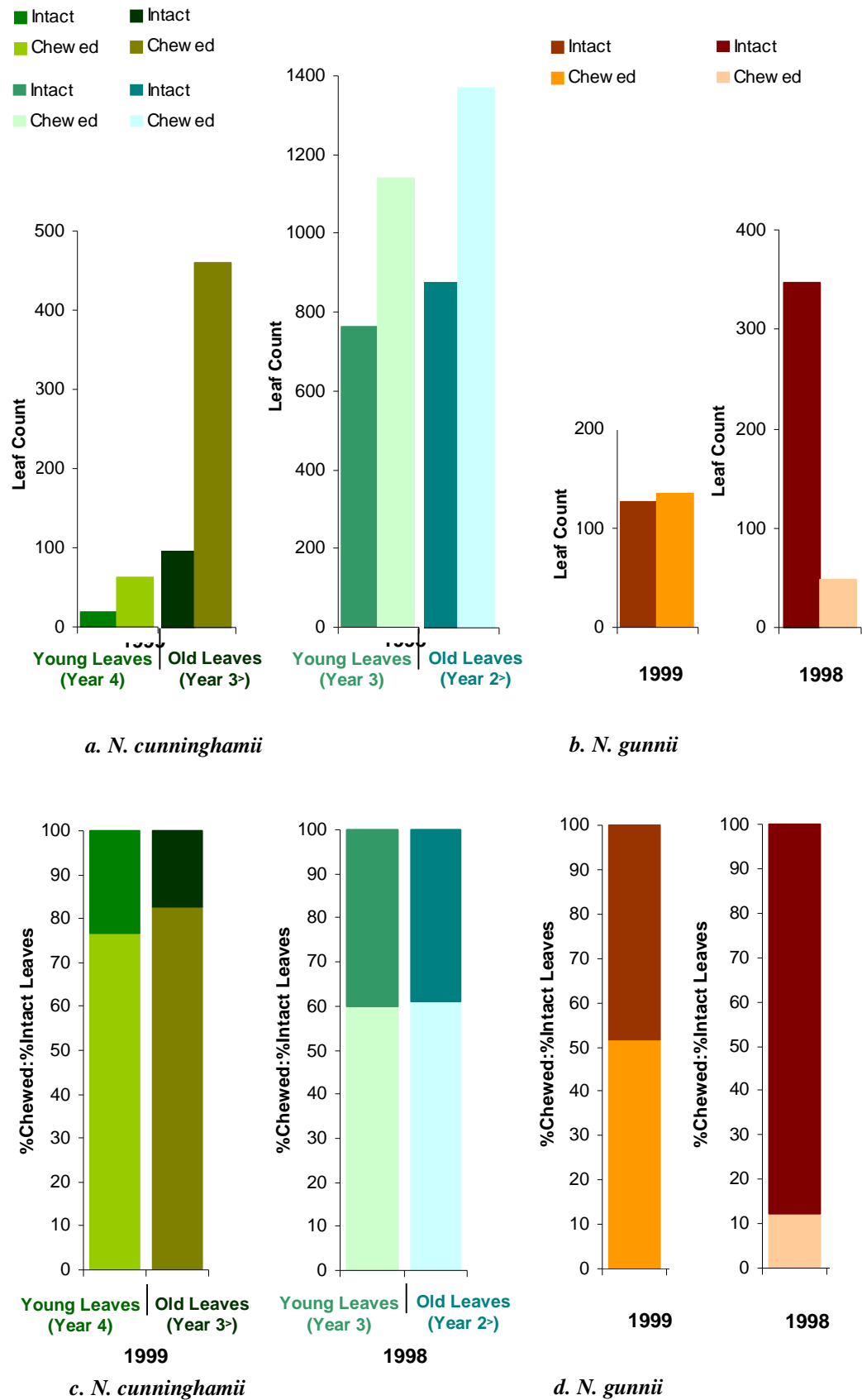


Figure 6.22. a - d. Totals (a,b) and proportions (c,d) of intact and chewed leaves, sampled from adjacent aspects of trees of *N. cunninghamii* and *N. gunnii*, in autumn 1998 and spring/summer 1999, at 2 sites: Lake Fenton and Lake Skinner. *N. cunninghamii* leaf ages: Spring/summer 1999: young leaves (Leaf Year 4) and old leaves (Leaf Year 3 and earlier). Autumn 1998 : young leaves (Leaf Year 3) and old leaves (Leaf Year 2 and earlier).

6.1.3 Cumulative Sampling and Yearly Variation

The cumulative sampling data (Sampling Set 3, table 4.2) provided an indication of the changes in levels of leaf chewing and overall numbers of leaves at the sites during the sampling periods and also a comparison between consecutive years for each *Nothofagus* species.

6.1.3.1 Cumulative Sampling Results: *N. cunninghamii*

For *N. cunninghamii*, the overall total numbers of leaves (intact plus chewed) varied over the sampling periods (figures 6.23 and 6.24), the old leaves declining in number in both years on the tagged and bagged branchlets. For the young leaves, in 1999-2000 the overall young tagged leaf total peaked in March/April 2000, the bagged young leaves peaking in September/November 2000 (figure 6.23); while in 1998-1999, the overall young tagged leaf total peaked in January 1999 and the bagged young leaves reached their highest number in February/March 1999 (figure 6.24).

However, there were differences over time in leaf totals between the sites and between sampling years at those sites (figures 6.25, 6.26). In 1999-2000, the time of peak numbers of young tagged leaves varied from October 1999 at Lyrebird Walk, through December 1999 at Lake Dobson to January 2000 for Lakes Fenton and Skinner and Mt. Arthur (figures 6.25, 6.26), while the bagged young leaves at Lake Dobson and Mt. Arthur peaked in September 2000 (the Lake Fenton cumulative young bagged leaves were discounted because of branchlet damage). In 1998-1999, the young leaf totals, tagged or bagged, peaked in February 1999 at Lake Fenton and April 1999 at Lyrebird Walk, while at Lake Skinner there were most tagged young leaves in January 1999 and most bagged young leaves in March 1999 (figures 6.25, 6.26). The numbers of old leaves, tagged or bagged, declined at each site over both sampling periods (figures 6.25, 6.26).

The bags failed to catch any leaf consumers concealed in the new leaf buds, but where the bags remained *in situ*, they did collect dehiscid leaves. At Lake Dobson and Mt. Arthur in 1999-2000, the leaves in the bags accounted for the decline in numbers of old leaves on the branches, suggesting a rate of old-leaf loss of 22.6% (38 of 168 leaves) at Lake Dobson and 38% (65 of 171 leaves) at Mt. Arthur in that year (table 6.1).

Site	Detached Leaves from Bagged Branchlets			All Bagged Old Leaves (attached +detached)			% of Leaves Detached
	Intact	Chewed	Total	Intact	Chewed	Total	
Lake Dobson	33	5	38	141	27	168	22.62
Mt Arthur	49	16	65	141	30	171	38.01
Total	82	21	103	282	57	339	30.38

Table 6.1. *N. cunninghamii* detached leaves collected from bagged branchlets at Lake Dobson and Mt. Arthur, at the end of the 1999-2000 sampling.

When the 1999-2000 cumulative record of *N. cunninghamii* intact and chewed leaves is viewed (figure 6.27), the March/April 2000 overall peak in young tagged leaves is seen to comprise a peak in numbers of both those intact and those chewed, while the old leaves, tagged or bagged, declined in numbers of both intact and chewed leaves over the sampling period. The peak in numbers of intact young tagged leaves depended on time of leaf flush and varied from October 1999 at Lyrebird walk, through December 1999 at Lake Skinner and Lake Dobson, to January 2000 at Lake Fenton and Mt. Arthur, while the intact bagged young leaves increased in number throughout the sampling period at both Lake Dobson and Mt. Arthur (figures 6.29, 6.30). The numbers of chewed young tagged leaves at each site showed an initial peak after leaf expansion, then levelled off, except at Lyrebird Walk where the increase in numbers of chewed young leaves was more gradual (figures 6.29, 6.30).

The 1998-1999 cumulative record of *N. cunninghamii* intact and chewed leaves showed that the overall number of intact young tagged leaves peaked in January 1999, while the intact young bagged leaves and chewed young tagged leaves peaked in February/March 1999 (figure 6.28). This data set however has fewer site visits, and the emergence of new leaves was later, than in 1999-2000. The old leaves intact or chewed, bagged or tagged, all declined in numbers over the 1998-1999 sampling period (figure 6.28).

The overall proportions of chewed to intact *N. cunninghamii* leaves varied over time in both sampling years. In 1999-2000 (figure 6.31), the young tagged leaves showed an initial sharp rise in the overall proportion of chewed leaves from 6% in October 1999, through 14.6% in December 1999 and up to 26.9% in January/February 2000, then levelled off between March/April 2000 (26.9%) and September-November 2000 (26.8%). This trend occurred at Lake Fenton, Lake Skinner and Lake Dobson, but was less marked at Lyrebird Walk, and at Mt. Arthur the proportion of chewed leaves remained fairly constant throughout the sampling period (figures 6.30, 6.33). The young bagged leaves show a small increase in the proportion of chewed leaves due to one of the bags at Lake Dobson having been punctured, and later repaired.

The 1999-2000 old tagged leaves show an overall decrease in proportion of chewed leaves from 32% in October 1999 to 27% in September-November 2000 (figure 6.31), and this trend was followed at Lake Fenton, Lake Dobson and Mt. Arthur, but was less marked at Lyrebird Walk, and reversed at Lake Skinner (figures 6.30, 6.33). The overall proportion of chewed old bagged leaves increased from 27.8% to 30.4%, possibly reflecting the lower incidence of chewed compared with intact amongst the dehiscid leaves collected in the bags at Lake Dobson and Mt. Arthur (table 6.1).

Overall, the young control branches had a similar proportion of chewed leaves as the young tagged branchlets at the September-November 2000 sampling, while the overall proportion of chewed leaves on the old control branchlets was closer to the October 1999 sampling (figure 6.31, 6.32). However, there is considerable variation between the sites in the relative proportions of chewed leaves, young and old, on the control branchlets compared with the corresponding tagged branchlets (figures 6.30, 6.33).

In 1998-1999, there had been an initial sharp rise, similar to that in 1999-2000, in the overall proportions of chewed young tagged leaves, although this pattern occurred only at Lyrebird Walk; at Lake Fenton 100% of the young tagged leaves were chewing-damaged in both February 1998 and in April 1998; and at Lake Skinner around 60% of young tagged leaves had been chewed in both January and March 1998 (figures 6.32, 6.33). Similarly, the overall increase in proportions of chewed

young bagged leaves was also strongly influenced by Lyrebird Walk (where bags became detached during the sampling period). The old tagged leaves in 1998-1999 showed an overall initial increase in the proportion of chewed leaves, followed by a decline, reflecting the patterns at Lyrebird Walk and Lake Skinner, while at Lake Fenton the proportion of chewed old tagged leaves remained constant at around 75% (figures 6.32, 6.33). Overall the old bagged leaves showed a peak in the proportion of chewed leaves in February/March due to damaged or detached bags at Lake Fenton and Lyrebird Walk.

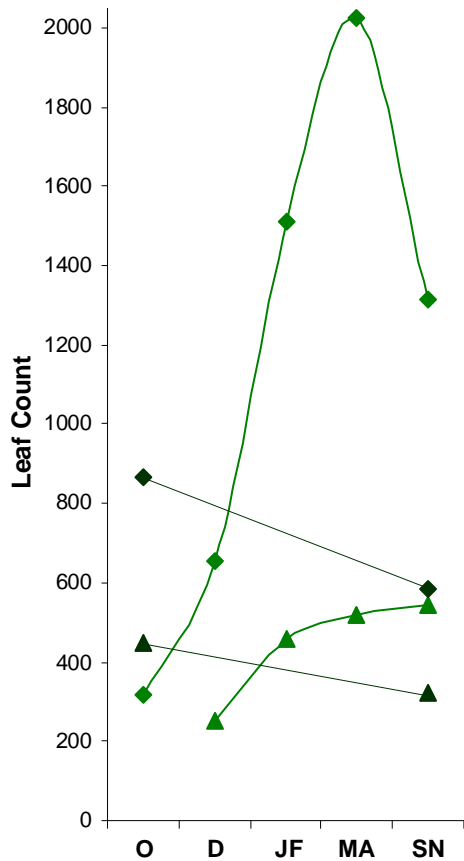


Figure 6.23. 1999-2000 cumulative record of *N. cunninghamii* combined leaf totals (intact + chewed leaves) on bagged branches and tagged (unbagged) branches at 5 sites: Lake Fenton, Lyrebird Walk, Lake Skinner, Lake Dobson and Mt. Arthur. Young leaves (Leaf Year 5) recorded at ~6 weekly intervals October – April and in the following Spring. Old leaves (Leaf Year 4 and earlier) recorded at beginning and end of sampling period. O: October 1999; D: December 1999; JF: late January/early February 2000; MA: early March/early April 2000; SN: September/November 2000.

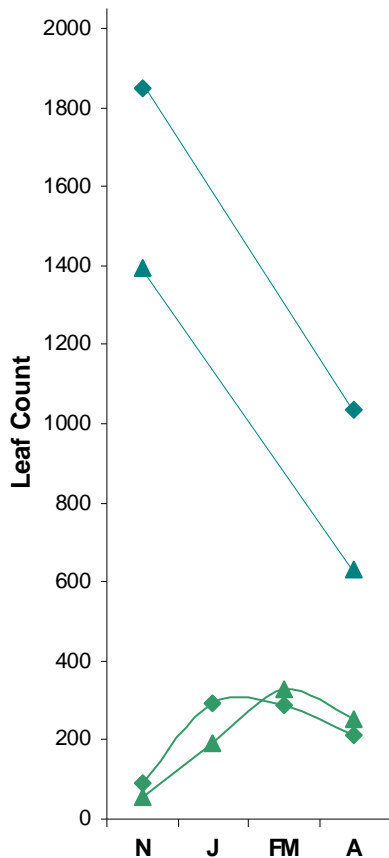


Figure 6.24. 1998-1999 cumulative record of *N. cunninghamii* combined leaf totals (intact + chewed leaves), young leaves (Leaf Year 4) and old leaves (Leaf Year 3 and earlier), on bagged branches and tagged (unbagged) branches at 3 sites: Lake Fenton, Lyrebird Walk, Lake Skinner. ND: late November /early December 1998; J: mid January 1999; FM: late February/mid March 1999; A: mid April 1999.

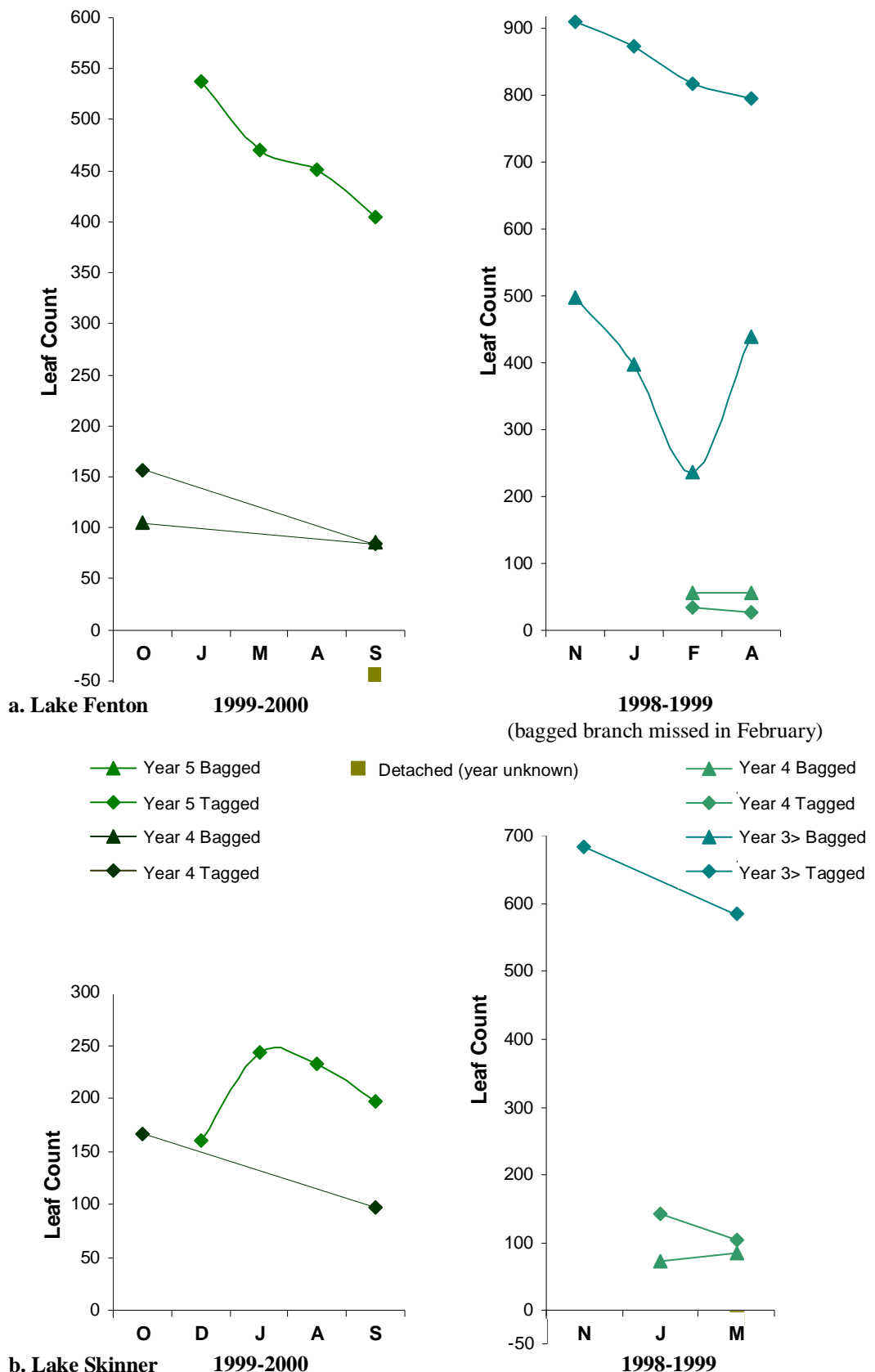


Figure 6.25. a - c. Cumulative records for consecutive sampling years of *N. cunninghamii*, combined leaf totals (intact + chewed leaves), on bagged branches and tagged (unbagged) branches) at 3 sites: Lake Fenton (a), Lake Skinner (b) and Lyrbird Walk (c, overleaf). 1999-2000: young leaves (Year 5); old leaves (Year 4 and earlier). O: Oct. 1999; D: Dec. 1999; JF: late Jan./early Feb. 2000; MA: early Mar./early Apr. 2000; SN: Sept./Nov. 2000. 1998-1999: young leaves (Year 4) and old leaves (Year 3 and earlier). ND: late Nov./early Dec. 1998; J: mid Jan. 1999; FM: late Feb./mid Mar. 1999; A: mid Apr. 1999.

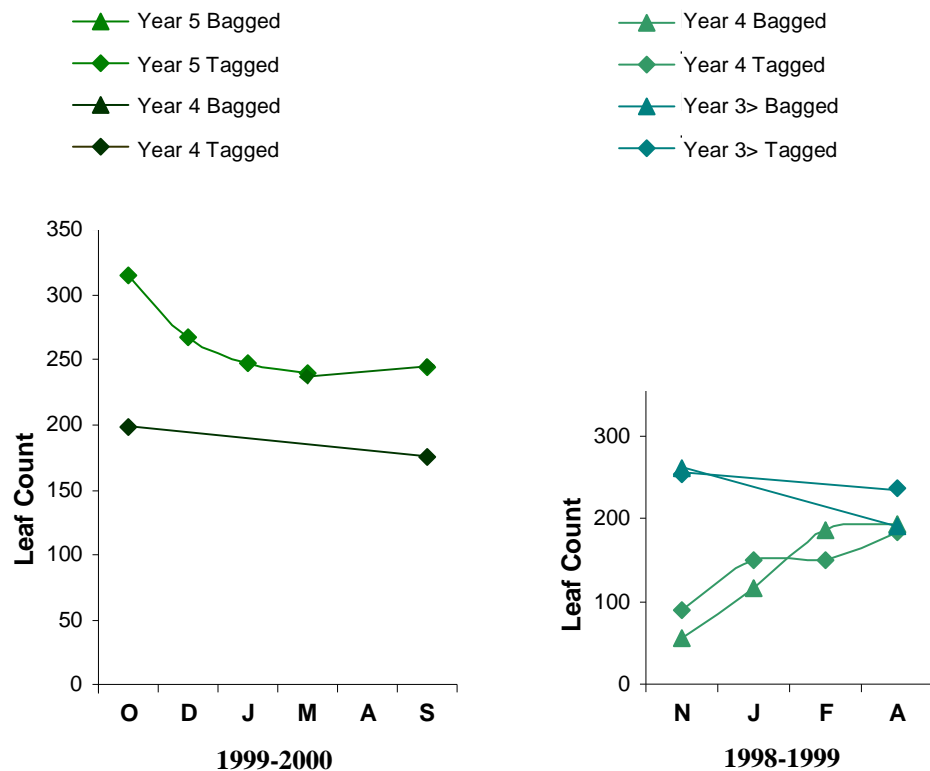


Figure 6.25. c. Lyrebird Walk (continued from previous page)

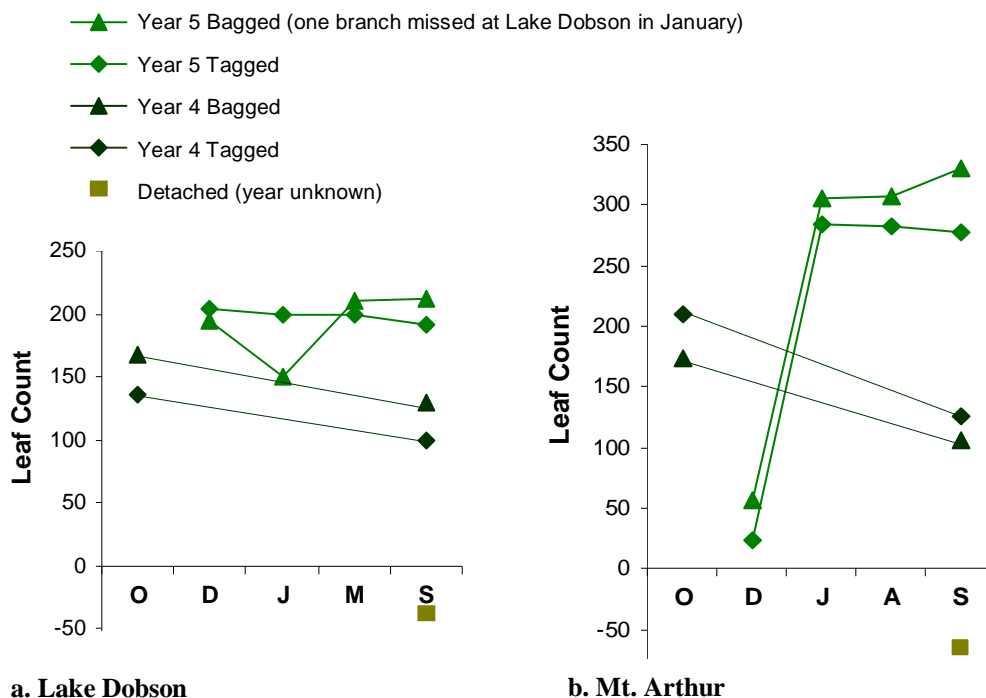


Figure 6.26. a & b. 1999-2000 cumulative records of *N. cunninghamii*, combined leaf totals (intact + chewed leaves), on bagged branches and tagged (unbagged) branches at Lake Dobson (a) and Mt. Arthur (b). Young leaves (Leaf Year 5) recorded at ~6 weekly intervals October – April and in the following Spring. Old leaves (Leaf Year 4 and earlier) recorded at beginning and end of sampling period. O: October 1999; D: December 1999; JF: late January/early February 2000; MA: early March/early April 2000; SN: September/November 2000.

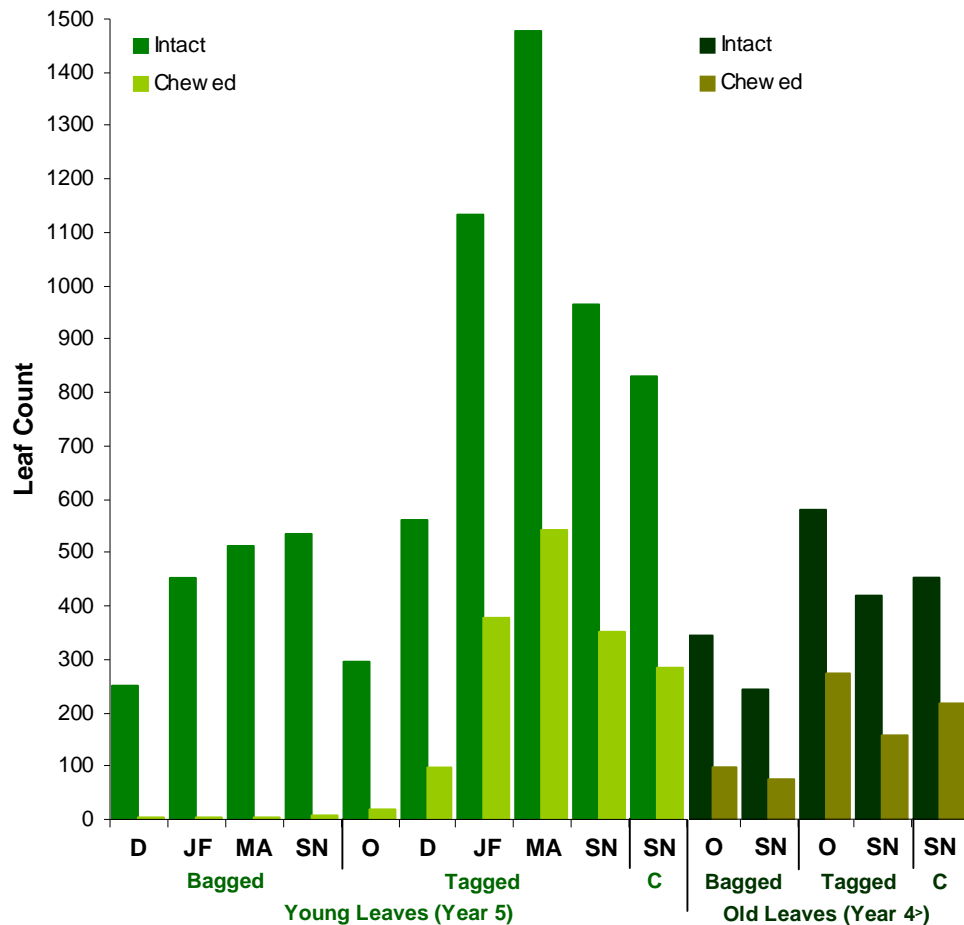


Figure 6.27. 1999-2000 cumulative record of *N. cunninghamii* intact and chewed leaves on bagged branches, tagged (unbagged) branches, and controls (C) at 5 sites: Lake Fenton, Lyrebird Walk, Lake Skinner, Lake Dobson and Mt. Arthur. Young leaves (Leaf Year 5) recorded at ~6 weekly intervals October – April and in the following Spring. Old leaves (Leaf Year 4 and earlier) recorded at beginning and end of sampling period. O: October 1999; D: December 1999; JF: late January/early February 2000; MA: early March/early April 2000; SN: September/November 2000.

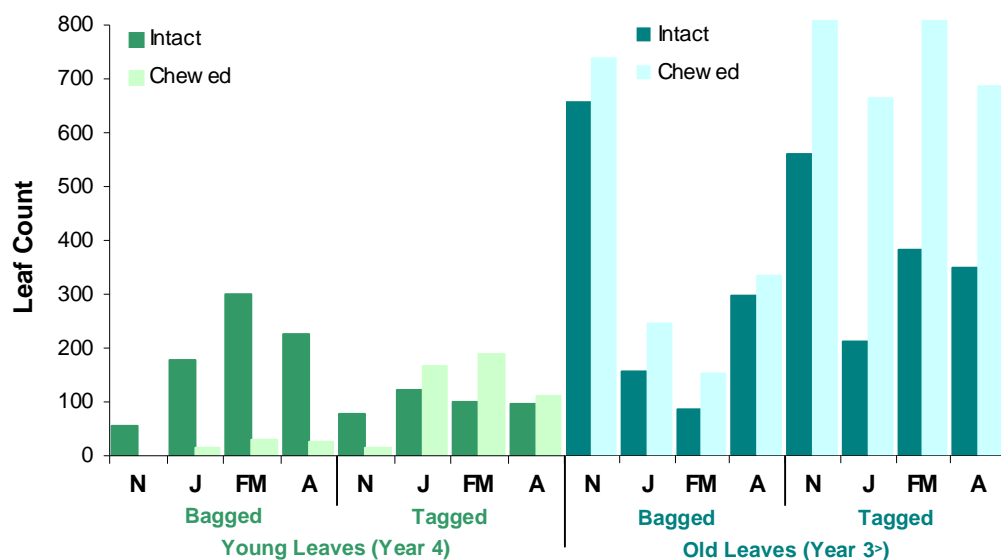


Figure 6.28. 1998-1999 cumulative record of *N. cunninghamii* young leaves (Leaf Year 4) and old leaves (Leaf Year 3 and earlier), intact and chewed, on bagged branches and tagged (unbagged) branches at 3 sites: Lake Fenton, Lyrebird Walk, Lake Skinner. ND: late November /early December 1998; J: mid January 1999; FM: late February/mid March 1999; A: mid April 1999.

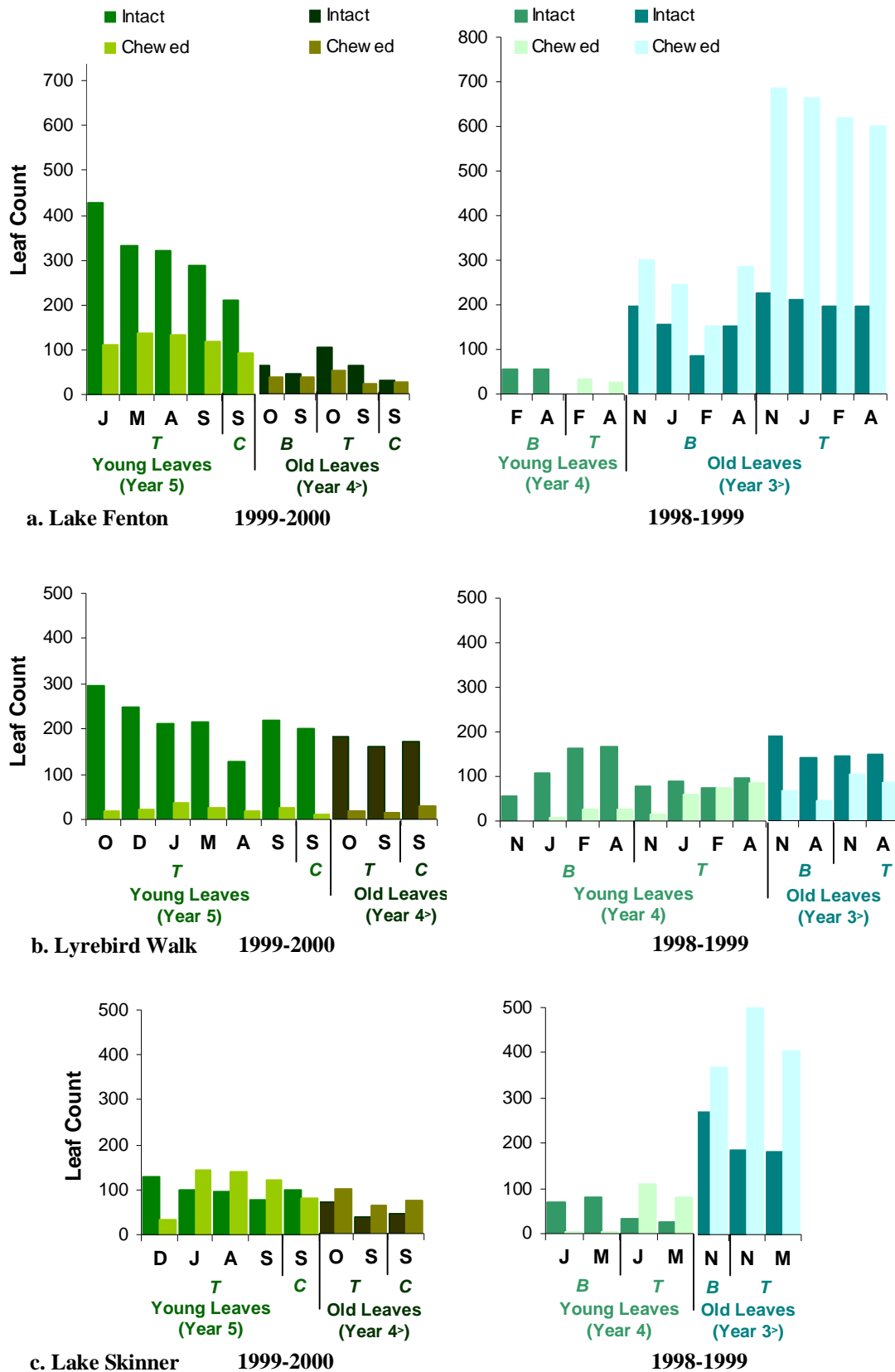


Figure 6.29. Cumulative records for consecutive sampling years of *N. cunninghamii* intact and chewed leaves on bagged branches (B), tagged (unbagged) branches (T) and controls (C) at 3 sites: Lake Fenton (a), Lyrebird Walk (b), Lake Skinner (c).

1999-2000: young leaves (Year 5); old leaves (Year 4 and earlier). O: Oct. 1999; D: Dec. 1999; JF: late Jan./early Feb. 2000; MA: early Mar./early Apr. 2000; SN: Sept./Nov. 2000.

1998-1999: young leaves (Year 4) and old leaves (Year 3 and earlier). ND: late Nov./early Dec. 1998; J: mid Jan. 1999; FM: late Feb./mid Mar. 1999; A: mid Apr. 1999.

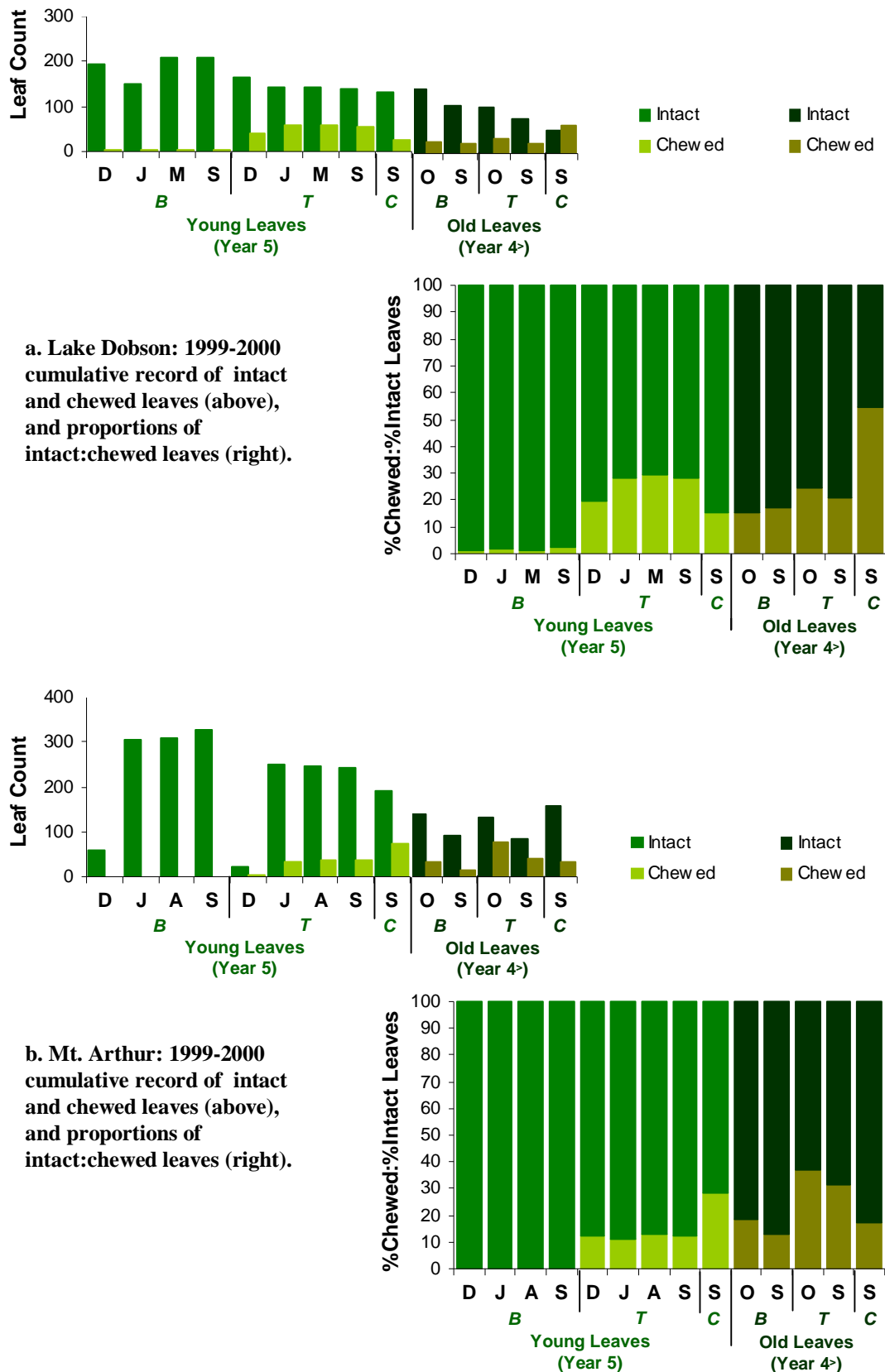


Figure 6.30. a & b. 1999-2000 cumulative record of *N. cunninghamii* intact and chewed leaves, and proportions thereof, on bagged branches (B), tagged (unbagged) branches (T), and controls (C) at Lake Dobson (a) and Mt. Arthur (b). Young leaves (Leaf Year 5) recorded at ~6 weekly intervals October – April and in the following Spring. Old leaves (Leaf Year 4 and earlier) recorded at beginning and end of sampling period. O: October 1999; D: December 1999; JF: late January/early February 2000; MA: early March/early April 2000; SN: September/November 2000.

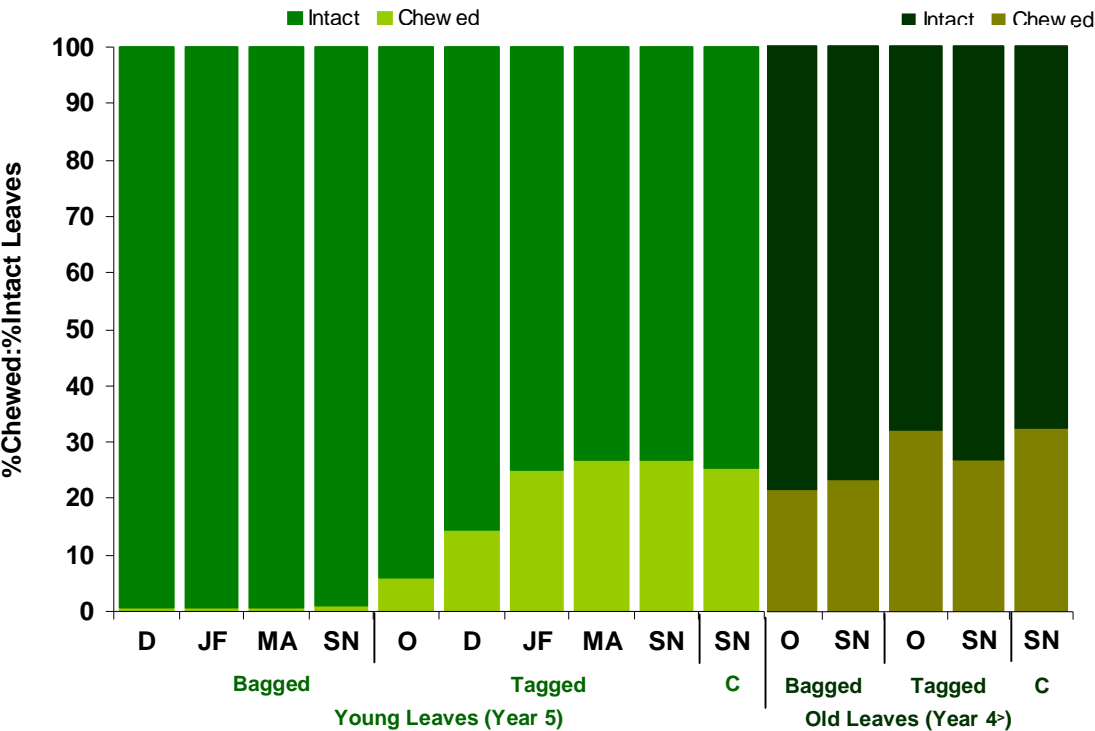


Figure 6.31. 1999-2000 cumulative record of *N. cunninghamii* proportions of intact and chewed leaves on bagged branches, tagged (unbagged) branches, and controls (C) at 5 sites: Lake Fenton, Lyrebird Walk, Lake Skinner, Lake Dobson and Mt. Arthur. Young leaves (Leaf Year 5) recorded at ~6 weekly intervals October – April and in the following Spring. Old leaves (Leaf Year 4 and earlier) recorded at beginning and end of sampling period. O: October 1999; D: December 1999; JF: late January/early February 2000; MA: early March/early April 2000; SN: September/November 2000.

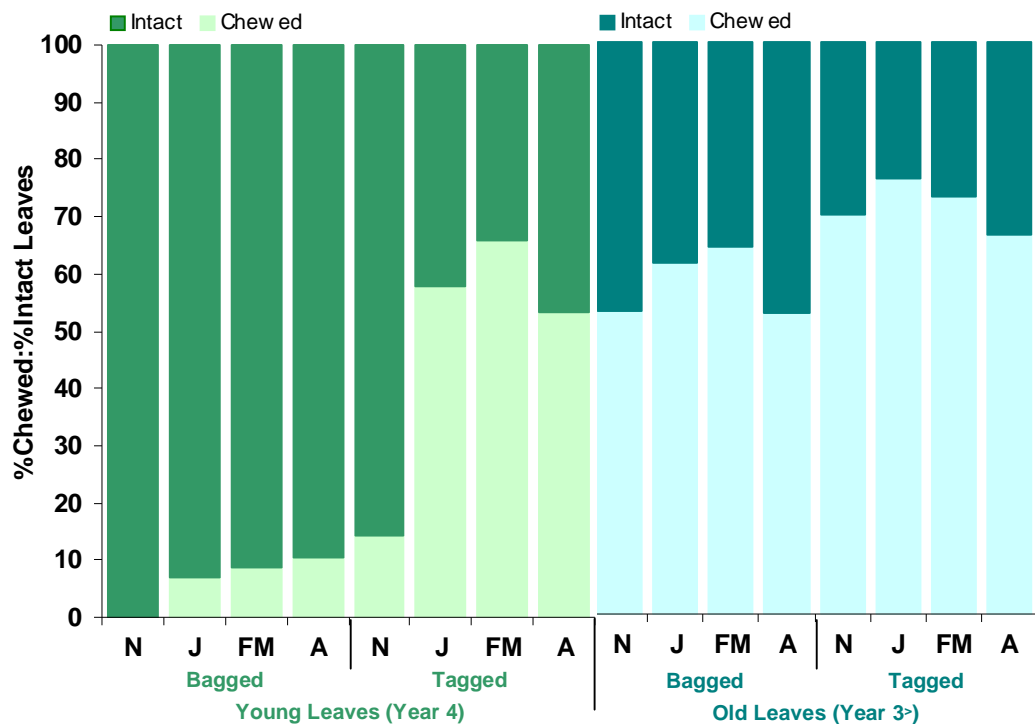


Figure 6.32. 1998-1999 cumulative record of *N. cunninghamii* young leaves (Leaf Year 4) and old leaves (Leaf Year 3 and earlier), proportions of intact and chewed, on bagged branches and tagged (unbagged) branches at 3 sites: Lake Fenton, Lyrebird Walk, Lake Skinner. ND: late November/early December 1998; J: mid January 1999; FM: late February/mid March 1999; A: mid April 1999.

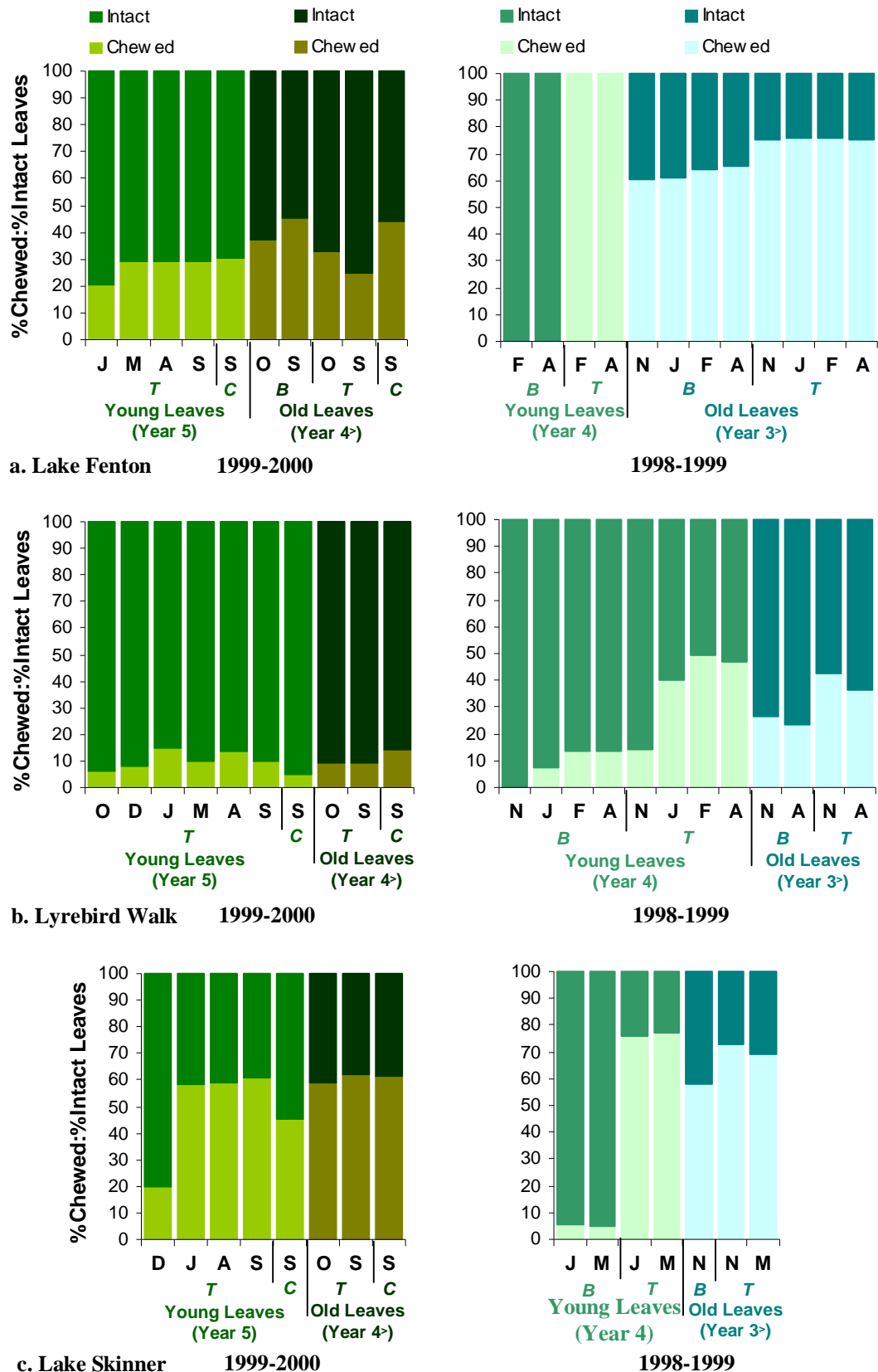


Figure 6.33. Cumulative records for consecutive sampling years of *N. cunninghamii*, proportions of intact and chewed leaves on bagged branches (B), tagged (unbagged) branches (T), and controls (C) at 3 sites: Lake Fenton (a), Lyrebird Walk (b), Lake Skinner (c). 1999-2000: young leaves (Year 5); old leaves (Year 4 and earlier). O: Oct. 1999; D: Dec. 1999; JF: late Jan./early Feb. 2000; MA: early Mar./early Apr. 2000; SN: Sept./Nov. 2000. 1998-1999: young leaves (Year 4) and old leaves (Year 3 and earlier). ND: late Nov./early Dec. 1998; J: mid Jan. 1999; FM: late Feb./mid Mar. 1999; A: mid Apr. 1999.

6.1.3.2 Cumulative Sampling Results: *N. gunnii*

For *N. gunnii* the overall, and individual site, total leaf counts (intact plus chewed leaves) differed between the two sampling years. In 1999-2000, the overall leaf total peaked at 603 leaves in December 1999 and fell by 3.3%, to 583 leaves in April 2000, reflecting a gradual fall in leaf numbers at each of the sites (figure 6.34). In comparison, the previous year the combined total leaf count at Lakes Fenton and Lake Skinner declined by 15.6% from 1800 leaves in November/December 1998 to 1519 leaves in February March 1999, although this was strongly influenced by Lake Skinner. The total leaf count at Lake Fenton decreased more gradually, as did that between the two visits to King William (figure 6.35).

The overall cumulative records, and graphs, of counts of intact and chewed leaves were influenced by the differing frequency of site visits (figures 6.36, 6.37). However when the sites were viewed individually, a common trend emerges of declining numbers of intact leaves and increasing numbers of chewed leaves throughout the sample periods (figures 6.38, 6.39), this being most marked at Lake Skinner in 1998-1999 (figure 6.39).

The overall proportions of intact and chewed leaves reported in 1999-2000 (figure 6.40) were again influenced by the differing frequency of site visits, while at each of the three sites there was an increase in the proportions of chewed leaves throughout the sampling period (figure 6.42). However in 1998-1999, the January and February/March 1999 peaks in the overall proportion of chewed leaves (figure 6.41) were heavily influenced by the high rates of chewed leaves at Lake Skinner: these were 2-site, instead of 3-site totals (Lake Fenton and Lake Skinner in January; King William and Lake Skinner in February/March). As in 1999-2000, at each of the sites in 1998-1999 the proportions of chewed leaves increased throughout the sampling period, but the rise is most marked at Lake Skinner, between November 1998 and January 1999 (figure 6.43).

Figure 6.34. (Top Right).
1999-2000 cumulative record of leaf totals
 (intact plus chewed leaves) on *N. gunnii*, at 3
 sites: Combined total; and site totals for
 Lake Fenton, Lake Skinner, Tarn Shelf.
 * Lake Skinner: no sampling in March 2000,
 and in April, intact leaf count not recorded
 for one branchlet. Lake Skinner 2-branch
 and 3-branch site totals as indicated in
 figure.
 The Combined Total uses the Lake Skinner
 2-branch data.
 O: mid/late October; D: early December;
 JF: late January/early February; M: early
 March; A: early April.

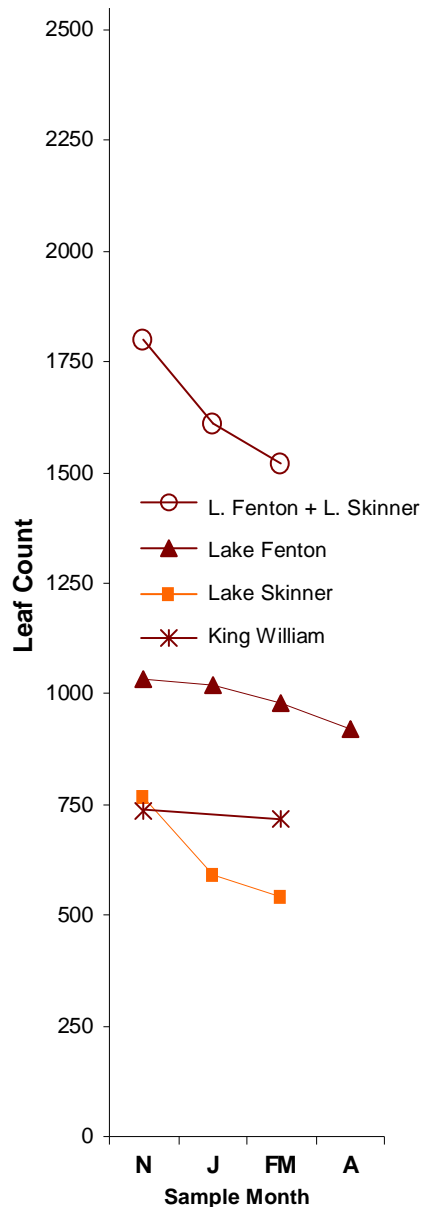
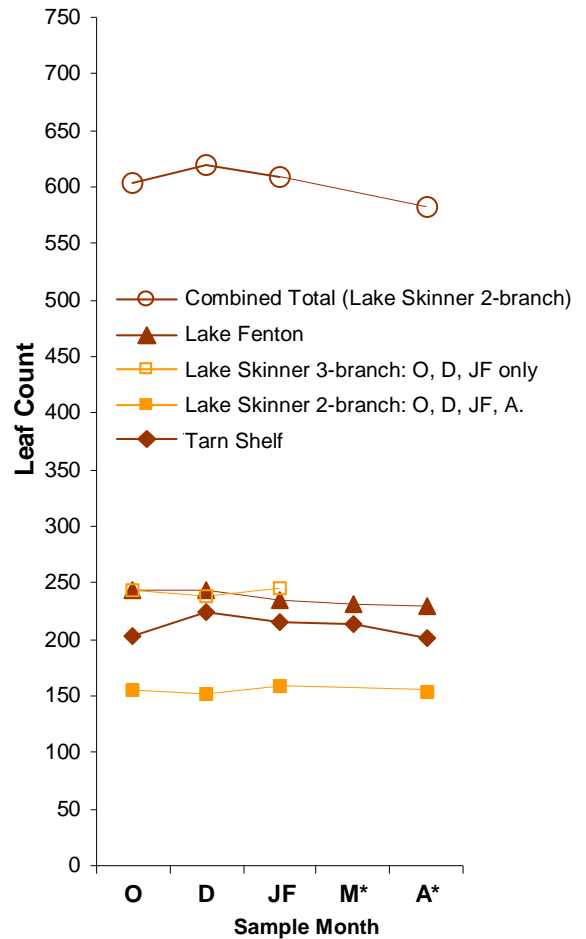


Figure 6.35. (Bottom Left).
1998-1999 cumulative record of leaf totals
 (intact + chewed leaves) on *N. gunnii*: Lake
 Fenton + Lake Skinner combined total; and site
 totals for Lake Fenton, Lake Skinner, King
 William. ND: late November/early December;
 J: mid January; FM: late February/mid March;
 A: mid April.

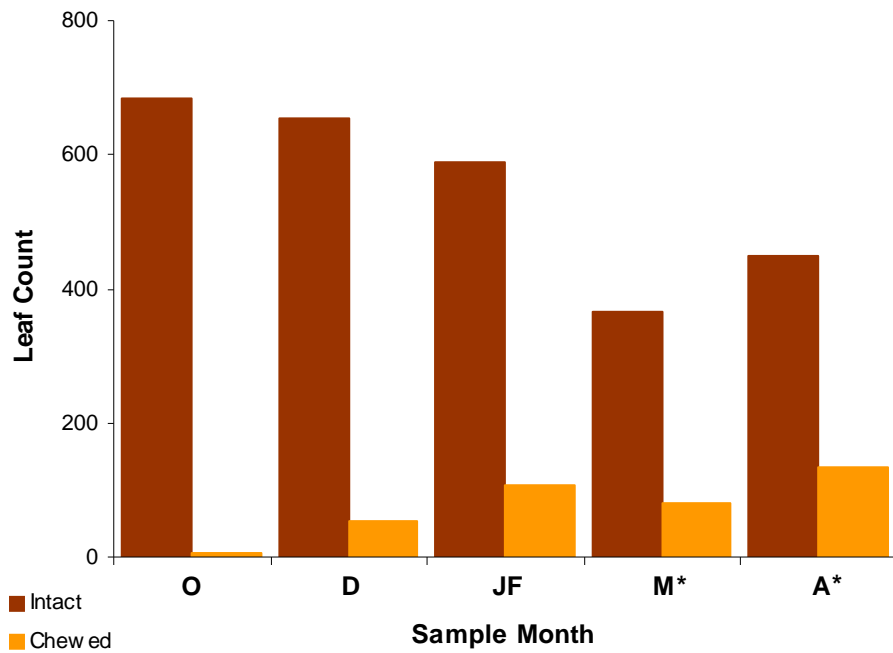


Figure 6.36. 1999-2000 cumulative record of *N. gunnii* intact and chewed leaves at 3 sites: Lake Fenton, Lake Skinner, Tarn Shelf. O: mid/late October 1999; D: early December 1999; JF: late January/early February 2000; M: early March 2000; A: early April 2000. *Lake Skinner data missing from totals for March (less 3 branches) and April (less 1 branch) – see text.

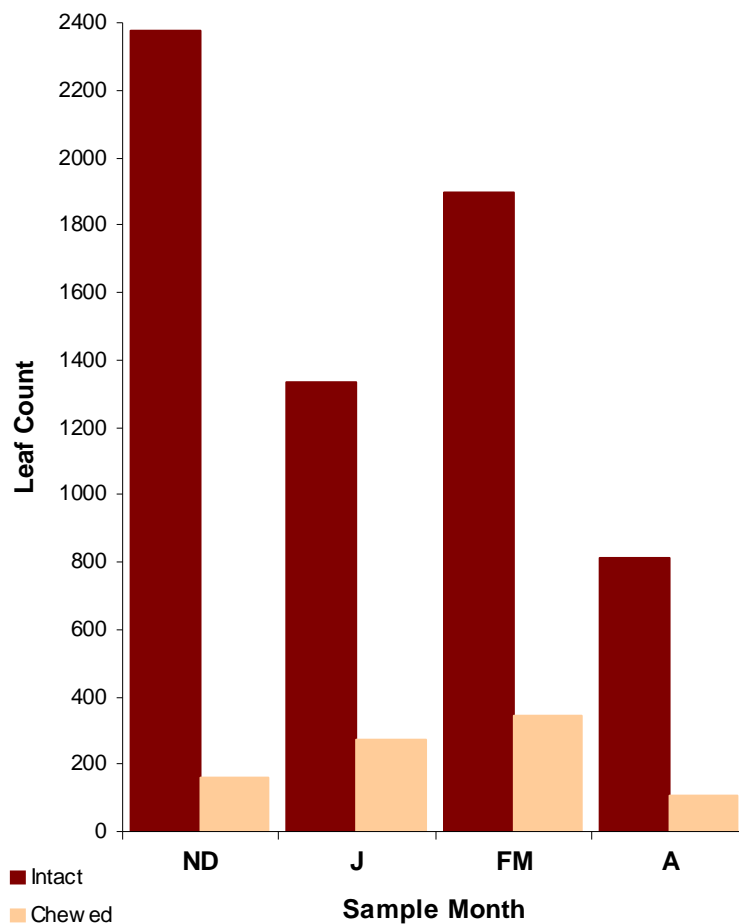


Figure 6.37. 1998-1999 cumulative record of *N. gunnii* intact and chewed leaves at 3 sites: Lake Fenton, Lake Skinner, King William. ND: late November/early December 1998; J: mid January 1999; FM: late February/mid March 1999; A: mid April 1999.

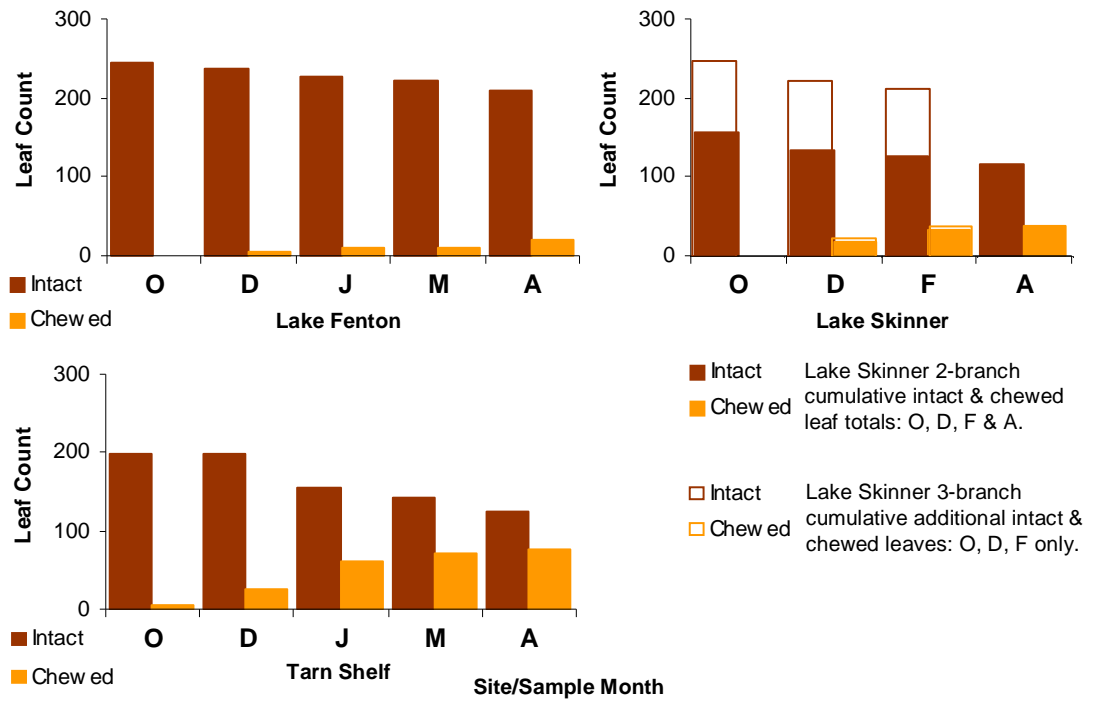


Figure 6.38. 1999-2000 cumulative site record of *N. gunnii* intact and chewed leaves: Lake Fenton and Tarn Shelf. Lake Skinner 2-branch and 3-branch totals as indicated in figure. O: mid/late October 1999; D: early December 1999; J: late January 2000; F: early February 2000; M: early March 2000; A: early April 2000.

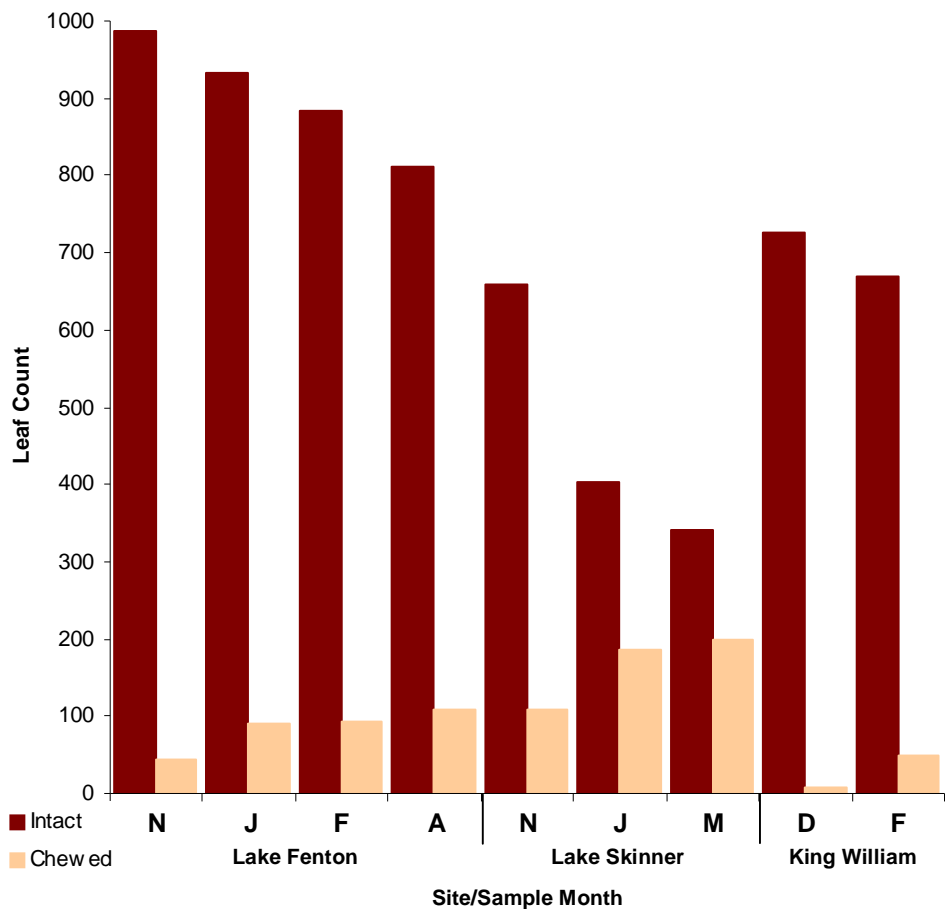


Figure 6.39. 1998-1999 cumulative site record of *N. gunnii* intact and chewed leaves: Lake Fenton, Lake Skinner, King William. N: late November 1998; D: early December 1998; J: mid January 1999; F: February 1999; M: mid March 1999; A: mid April 1999.

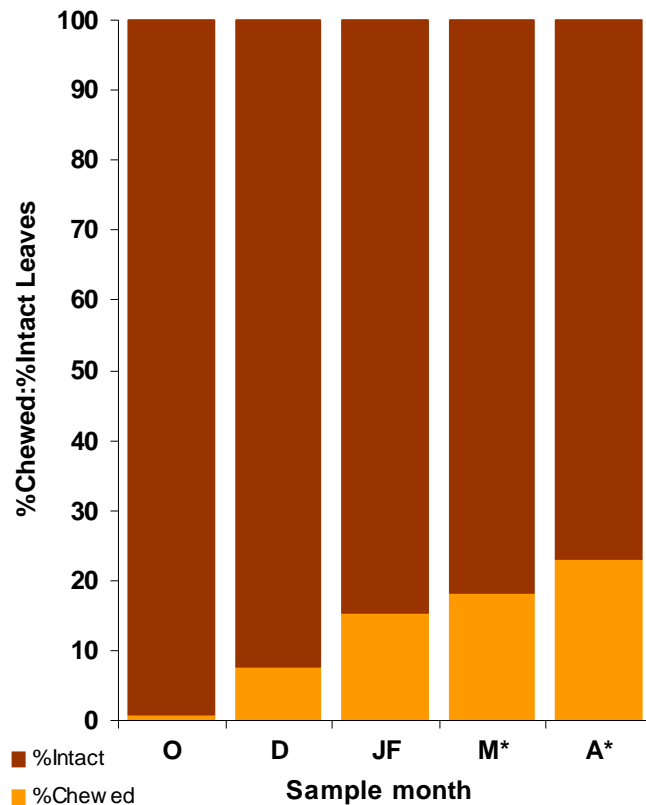


Figure 6.40. 1999-2000 cumulative record of proportions of *N. gunnii* intact and chewed leaves at 3 sites: Lake Fenton, Lake Skinner, Tarn Shelf. O: mid/late October 1999; D: early December 1999; JF: late January/early February 2000; M: early March 2000; A: early April 2000. *Lake Skinner data missing from totals for March (less 3 branches) and April (less 1 branch) – see text.

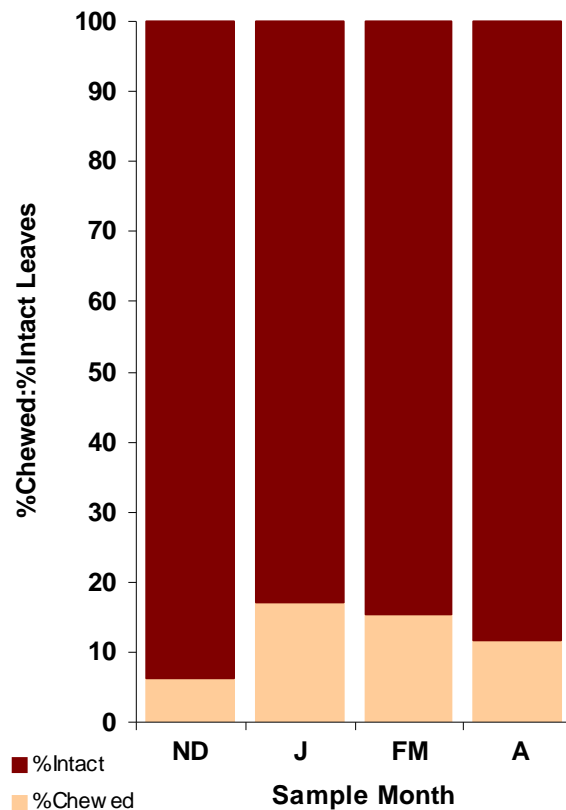


Figure 6.41. 1998-1999 cumulative record of proportions of *N. gunnii* intact and chewed leaves at 3 sites: Lake Fenton, Lake Skinner, King William. ND: late November/early December 1998; J: mid January 1999; FM: late February/mid March 1999; A: mid April 1999.

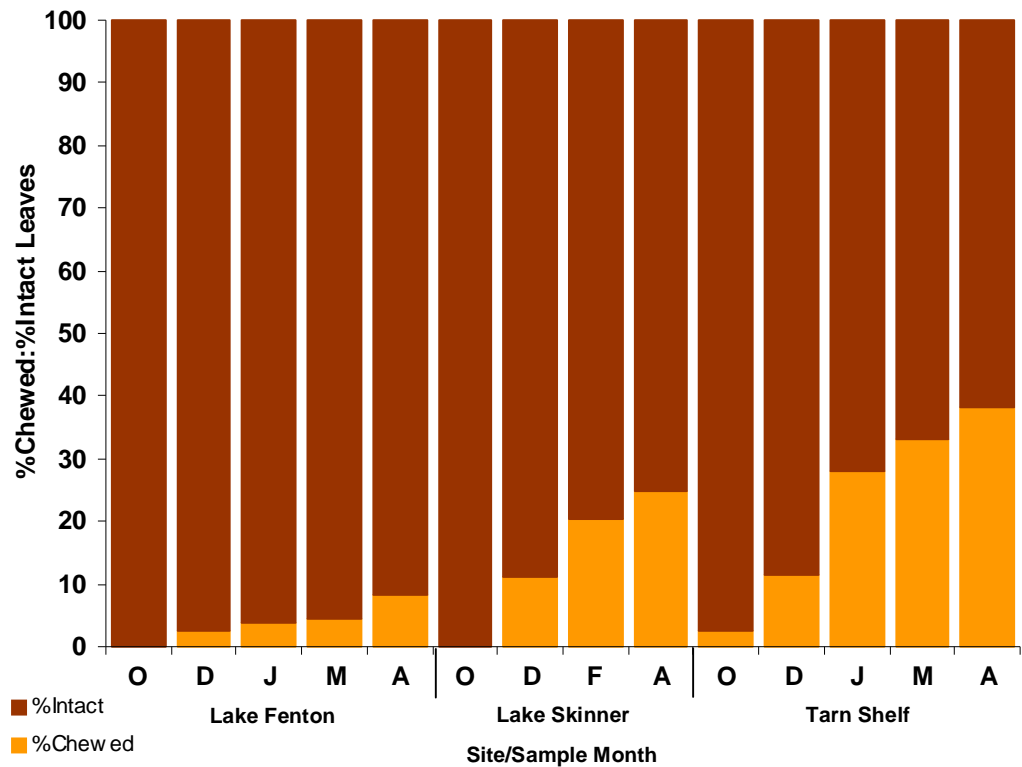


Figure 6.42. 1999-2000 cumulative site record of proportions of *N. gunnii* intact and chewed leaves: Lake Fenton, Lake Skinner (2-branch data – see text), Tarn Shelf. O: mid/late October 1999; D: early December 1999; J: late January 2000; F: early February 2000; M: early March 2000; A: early April 2000.

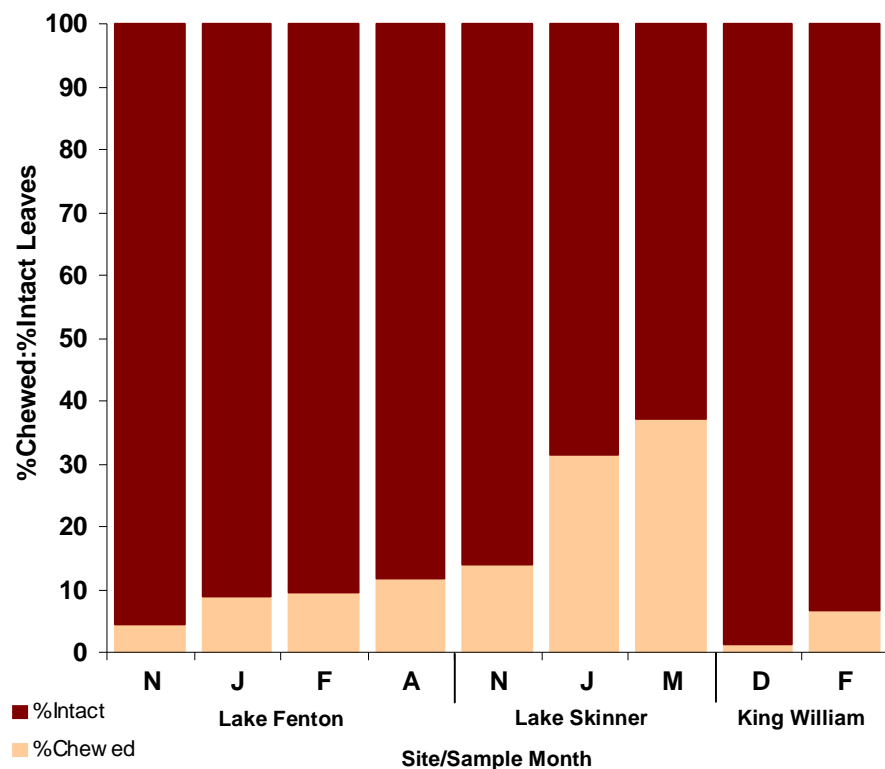


Figure 6.43. 1998-1999 cumulative site record of proportions of intact and chewed *N. gunnii* leaves: Lake Fenton, Lake Skinner, King William. N: late November 1998; D: early December 1998; J: mid January 1999; F: February; M: mid March 1999; A: mid April 1999.

6.1.3.3 *Autumn 1998 and the Three Year Autumn Comparison*

During the preliminary sampling of autumn 1998 an overall total of 24,603 leaves were examined. Of these, 37.6% of the *N. cunninghamii* leaves showed chewing damage (7,780 chewed from a total of 20,677) compared with 9.5% chewed for *N. gunnii* (371 chewed from a total of 3,555) (figure 6.44).

The autumn 1998 site comparison for *N. cunninghamii* revealed a considerably higher proportion of chewed leaves at Lake Fenton at 71.2% (3881 chewed from a total of 5,452), compared with 29.6% (3,448 chewed from a total of 11,664) at Lake Skinner, and 12.7% at Lyrebird Walk (451 chewed from a total of 3,561) (figure 6.45). The high proportion of chewed leaves at Lake Fenton, compared with the other sites, occurred in each leaf age (figures 6.46, 6.47).

Site comparison for *N. gunnii* in autumn 1998 showed King William to have the highest proportion of chewed leaves at 14% (234 chewed from a total of 1,662), followed by 8.8% at Lake Skinner (109 chewed from a total of 1,240), while *N. gunnii* at Lake Fenton had the lowest proportion of chewed leaves at 2.7% (28 chewed from a total of 1,024) (figure 6.45) and although this sample was taken a month or so earlier than those at the other sites, the proportions of *N. gunnii* chewed leaves at Lake Fenton were consistently lower than those at Lake Skinner from autumn 1998 to autumn 2000, as documented below.

The overall rates of leaf chewing herbivory varied between successive years as shown by the three-year comparison of autumn samples from 1998, 1999 and 2000 (Sampling Set 5, table 4.2). Both *Nothofagus* species had the highest proportion of chewed leaves in autumn 1999 (*N. cunninghamii* young leaves: 61.3% chewed; *N. gunnii*: 19.6% chewed); and the lowest proportion of *N. cunninghamii* chewed leaves (34.7%) occurred in autumn 2000, while the lowest proportion for *N. gunnii* (10.4%) occurred in autumn 1998 (figure 6.48).

The three-year site comparison for *N. cunninghamii* young leaves showed all sites to have the highest proportions of chewed leaves in 1999, ranging from 100% chewed at Lake Fenton, to 77% at Lake Skinner and 46.7% at Lyrebird Walk (figure 6.49), although the year of lowest proportion of chewed leaves varied between sites: Lake Fenton 2000 (29% chewed), Lake Skinner 1998 (22% chewed), Lyrebird Walk

2000 (13.5% chewed). For *N. gunnii*, Lake Skinner had the highest proportion of chewed leaves in 2000 (24.8%) and 1999 (37%), but King William had the highest proportion in 1998 (14%); Lake Fenton had the lowest proportion of chewed leaves in 2000 (8.3%) and 1998 (2.7%), while King William had the lowest (6.8%) in 1999 (figure 6.50).

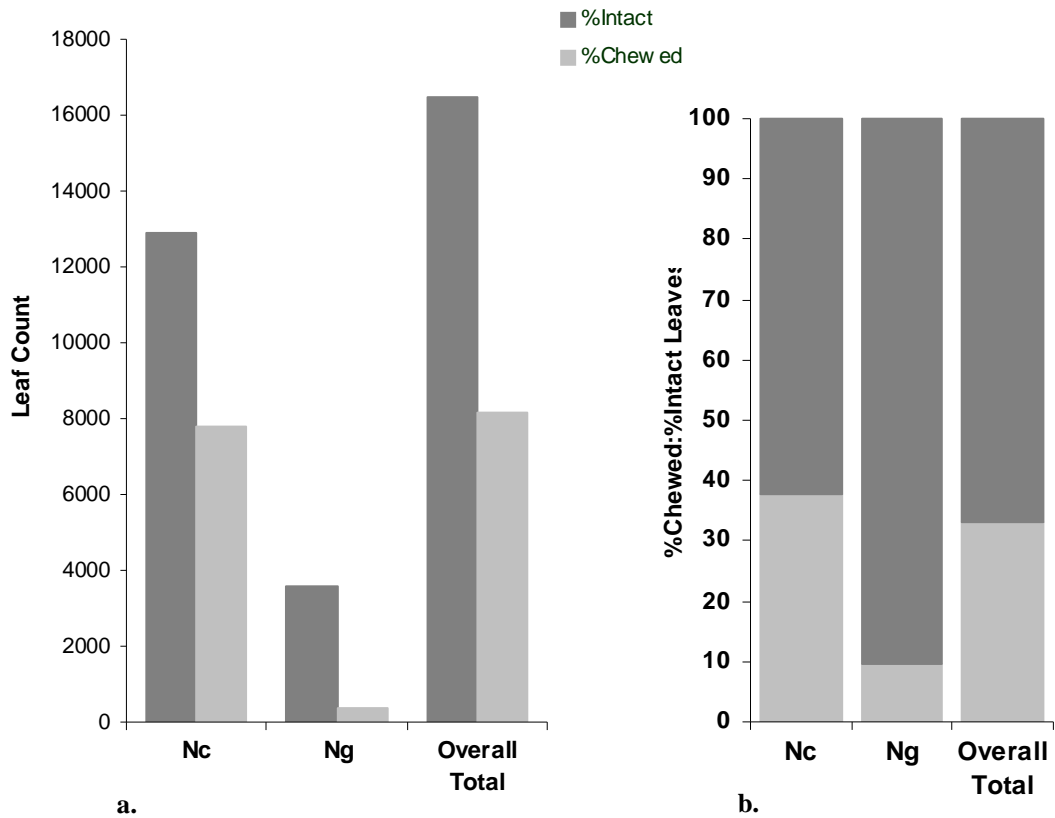
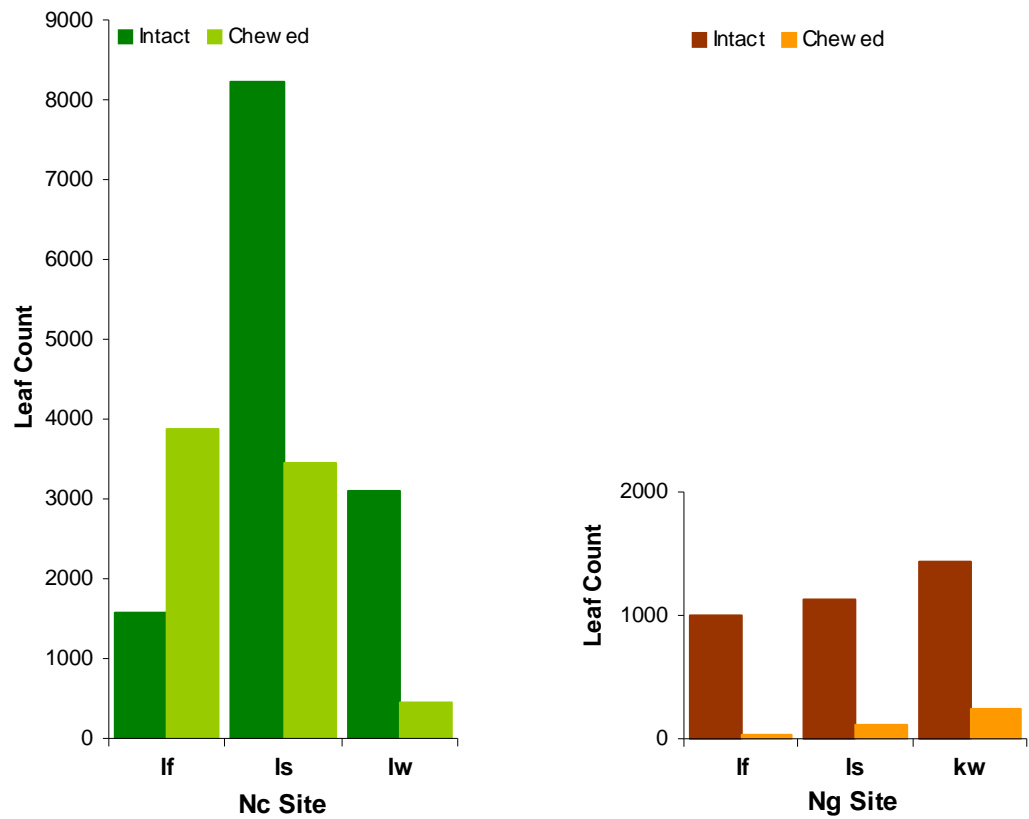
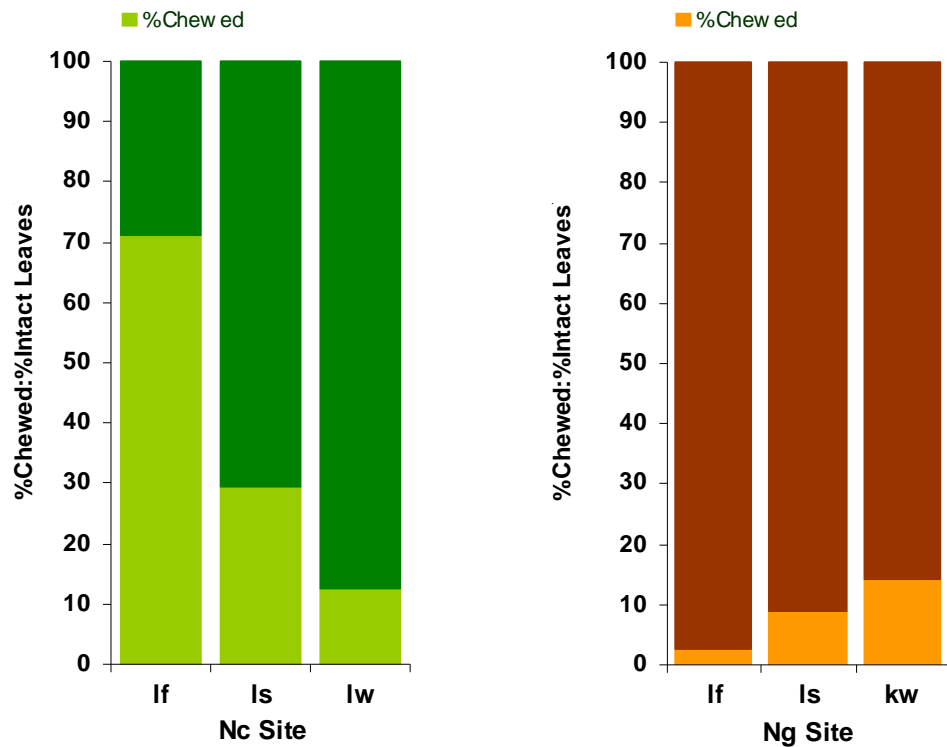


Figure 6.44. Totals (a) and proportions (b) of intact and chewed leaves, Autumn 1998: *N. cunninghamii* (Nc), *N. gunnii* (Ng) and overall.



a. Counts of Intact and Chewed Leaves



b. Proportions of Intact and Chewed Leaves

Figure 6.45. Totals (a) and proportions (b) of intact and chewed leaves, Autumn 1998, *Nothofagus* species and site. *N. cunninghamii* (Nc) and *N. gunnii* (Ng). If: Lake Fenton, lw: Lyrebird Walk, Is: Lake Skinner, kw: King William.

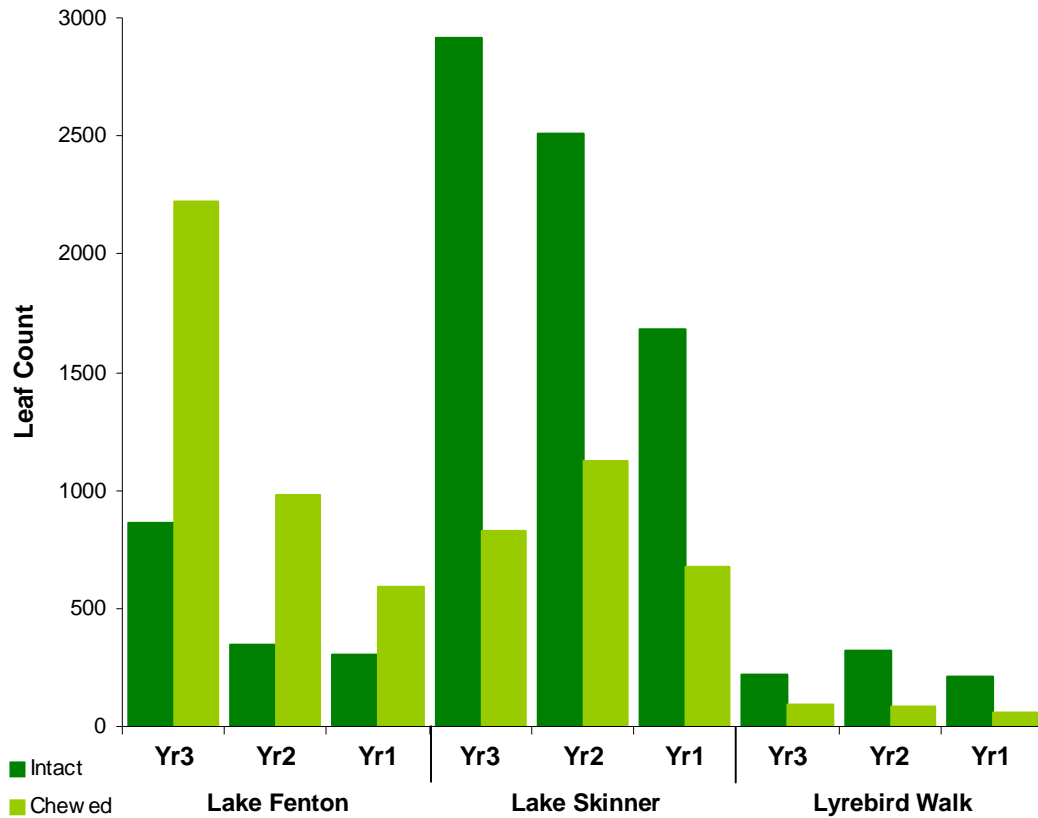


Figure 6.46. Intact and chewed leaves, Autumn 1998: *N. cunninghamii*, site and leaf age. lf: Lake Fenton, lw: Lyrebird Walk, ls: Lake Skinner. Youngest leaves: Yr3 (1997-1998). Old leaves: Yr2 (1996-1997), Yr1 (1996 and earlier).

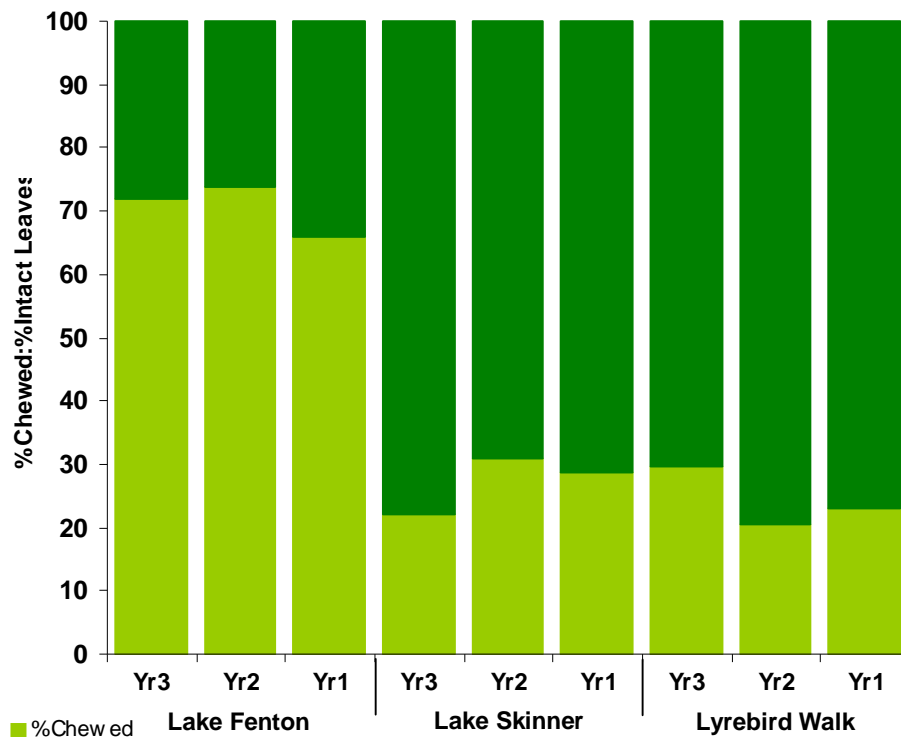
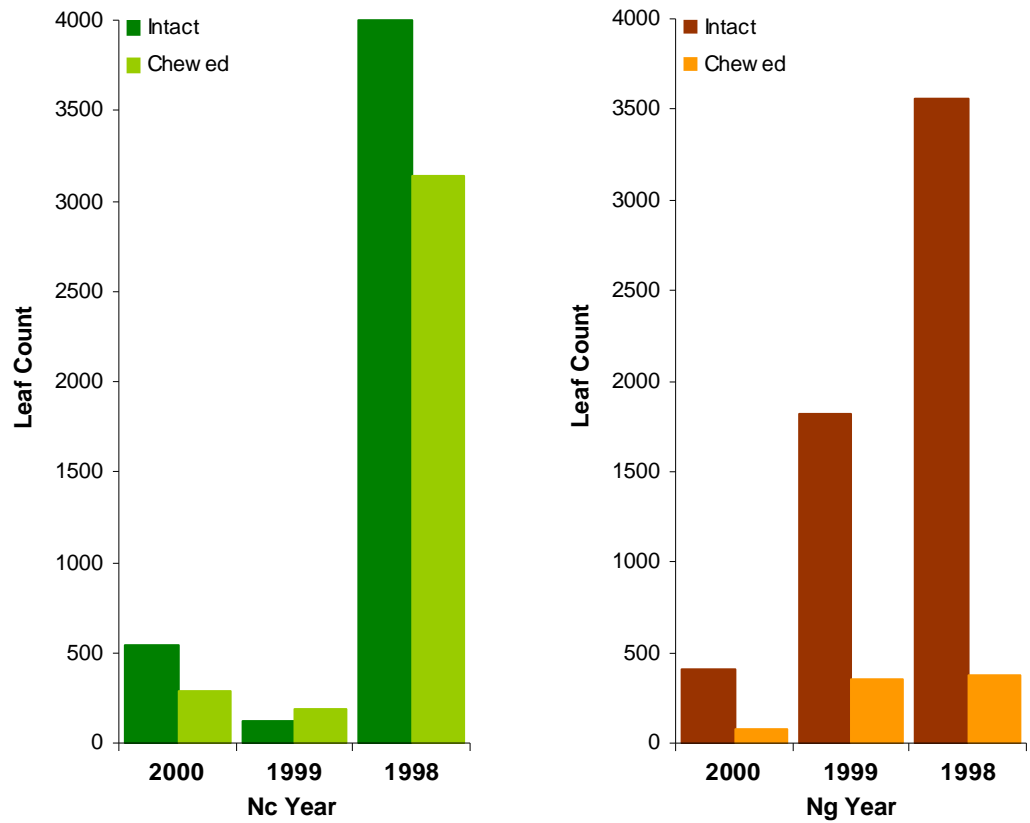
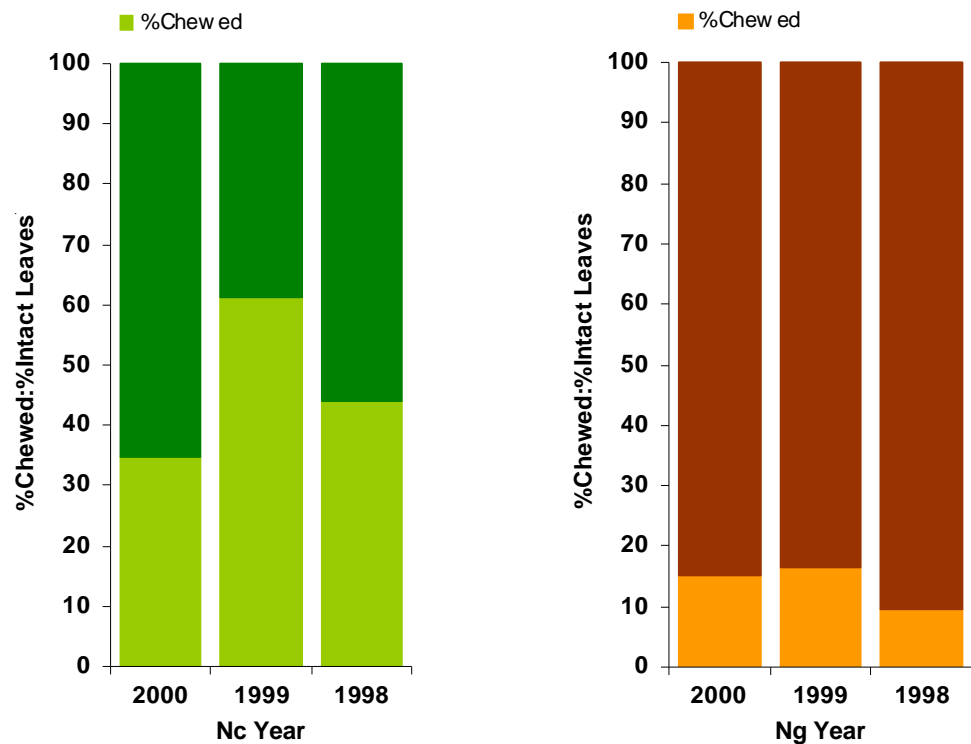


Figure 6.47. Proportions of intact and chewed leaves, Autumn 1998: *N. cunninghamii*, site and leaf age. lf: Lake Fenton, lw: Lyrebird Walk, ls: Lake Skinner. Youngest leaves: Yr3 (1997-1998). Old leaves: Yr2 (1996-1997), Yr1 (1996 and earlier).

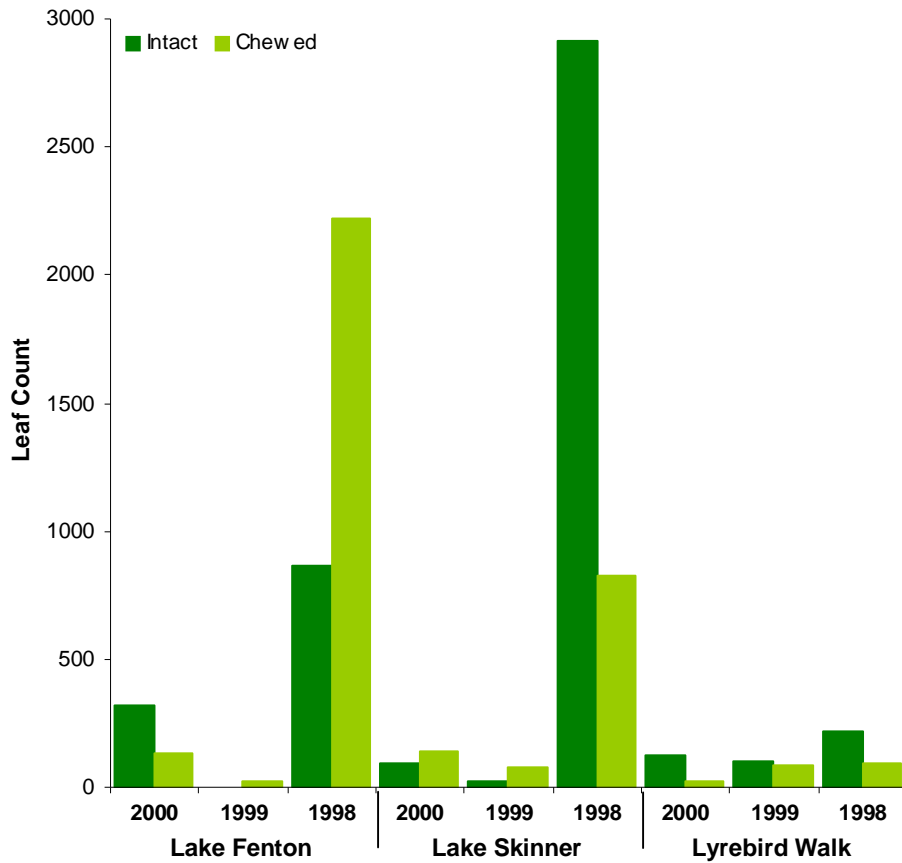


a. Counts of Intact and Chewed Leaves

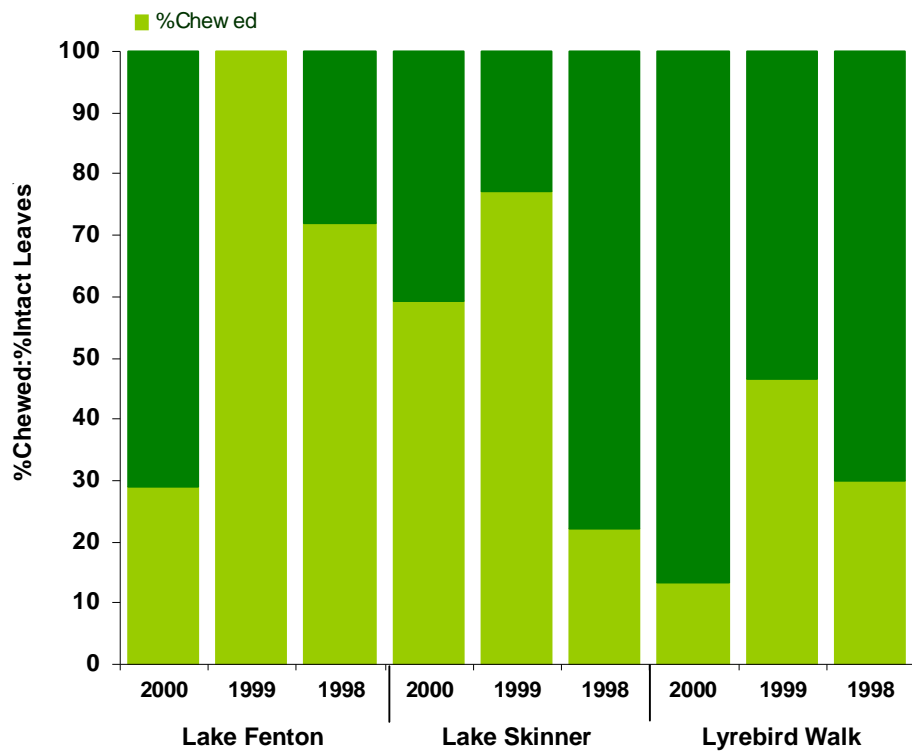


b. Proportions of Intact and Chewed Leaves

Figure 6.48. Totals (a) and proportions (b) of intact and chewed leaves, comparison between autumn 2000, autumn 1999 and autumn 1998 at 3 sites for each *Nothofagus* species. *N. cunninghamii* (Nc), young leaves only: Lake Fenton, Lake Skinner, Lyrebird Walk. *N. gunnii* (Ng): Lake Fenton, Lake Skinner, King William.

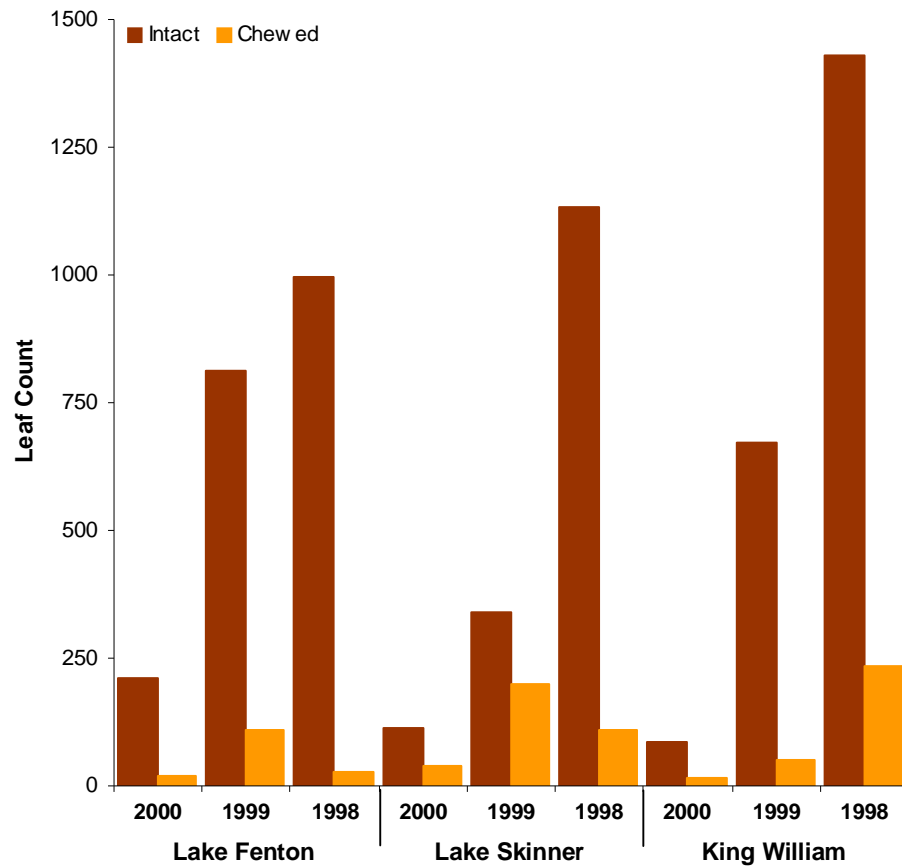


a. Counts of Intact and Chewed Leaves: Site and Sampling Year

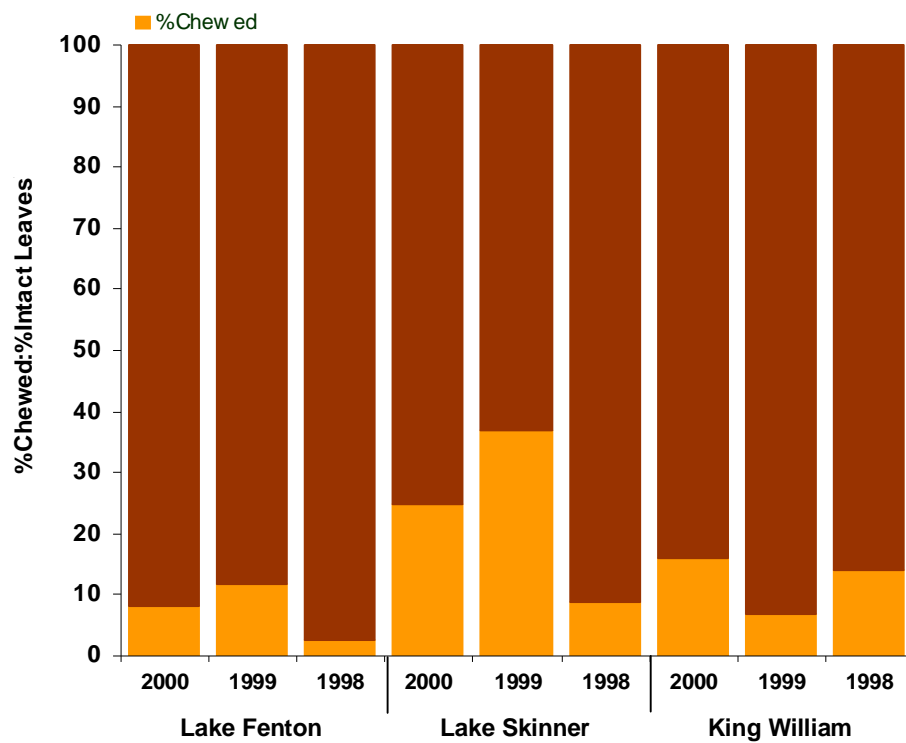


b. Proportions of Intact and Chewed Leaves: Site and Sampling Year

Figure 6.49. *N. cunninghamii* site totals (a) and proportions (b) of young intact and chewed leaves, comparison between Autumn 2000, (leaf year 5), Autumn 1999 (leaf year 4) and Autumn 1998 (leaf year 3): Lake Fenton, Lake Skinner, Lyrebird Walk.



a. Counts of Intact and Chewed Leaves: Site and Sampling Year



b. Proportions of Intact and Chewed Leaves: Site and Sampling Year

Figure 6.50. *N. gunnii* site totals (a) and proportions (b) of intact and chewed leaves, comparison between Autumn 2000, Autumn 1999 and Autumn 1998: Lake Fenton, Lake Skinner, King William.

6.2 LEAF-CHEWING HERBIVORY: % LEAF AREA LOSS

Having documented the counts and ratios of intact and chewed leaves for the Sampling Sets, the amount of leaf tissue lost from the chewed leaves, the percentage leaf area loss (%LAL), was then estimated as described in sub-chapter 4.3.

6.2.1 Between *Nothofagus* species, and Regional Variation, All Sites

Overall, the chewed leaves from all sites (Sampling Set 2, table 4.1), and both *Nothofagus* species, sustained a percentage leaf area loss (% LAL) of 12.56%. However, the overall leaf area loss on *N. cunninghamii* at 16.19% is five times that on *N. gunnii* at 3.23% (figure 6.51).

Regional comparison of all *N. cunninghamii* sites revealed the South (%LAL = 18.71) to have the highest percentage leaf area loss, and the North West (%LAL = 4.14) to have the lowest, while the North East (%LAL = 14.01) and West/Central (%LAL = 14.39) have similar levels of leaf area loss (figure 6.52.a). *N. gunnii* sustained similar levels of percentage leaf area loss in the South and West/Central, at 3.36% and 3.10% respectively (figure 6.52).

In addition to variation in percentage leaf area loss between regions, *N. cunninghamii* shows variation between sites within those regions (figure 6.53.a). *N. gunnii* shows little difference between sites in the South, although those in West/Central were more variable, with up to 13.54% LAL at Little Plateau (figure 6.53.b).

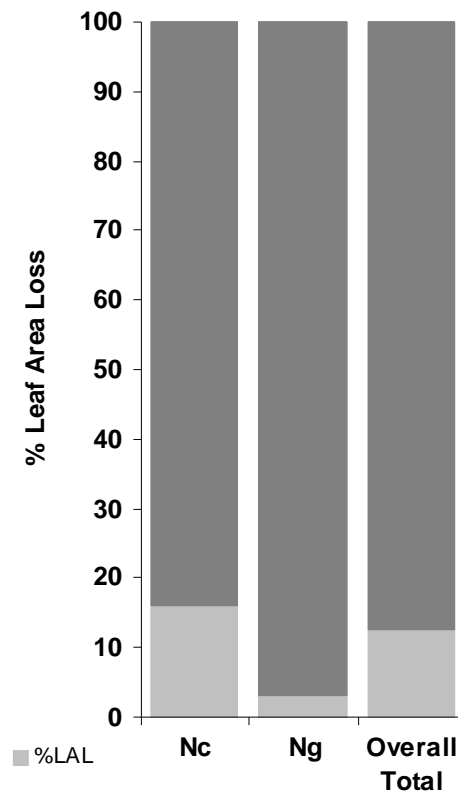


Figure 6.51. % Leaf Area Loss (%LAL), all sites, 1998-2002: *N. cunninghamii* (Nc), *N. gunnii* (Ng) and overall.

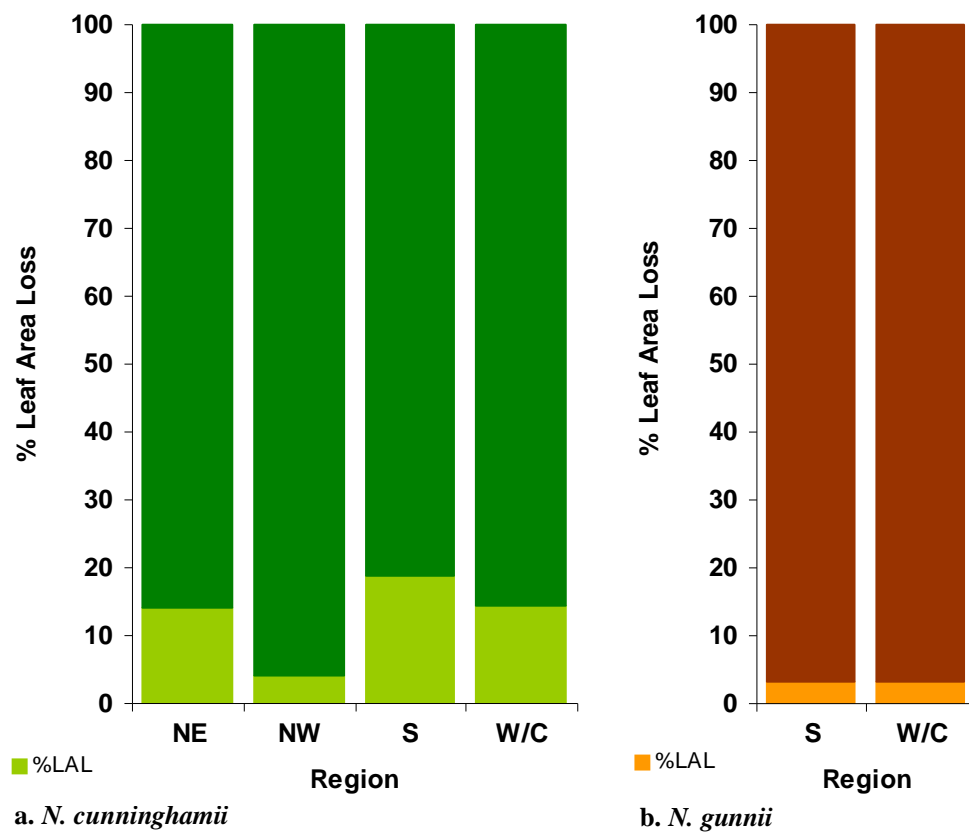


Figure 6.52. a & b. % Leaf Area Loss (%LAL), all sites, 1998-2002: *Nothofagus* species and region.

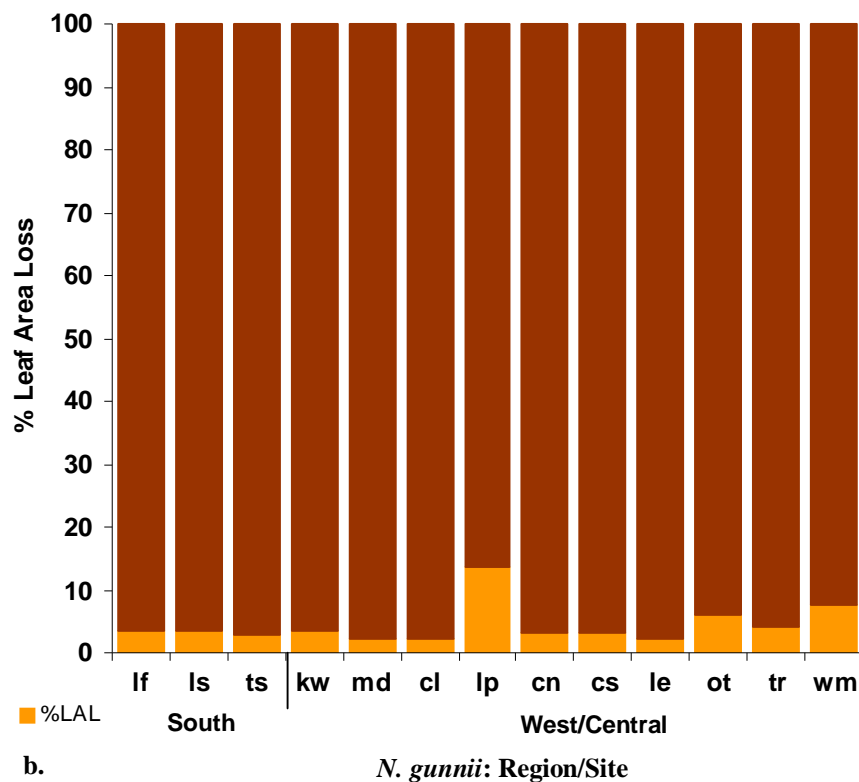
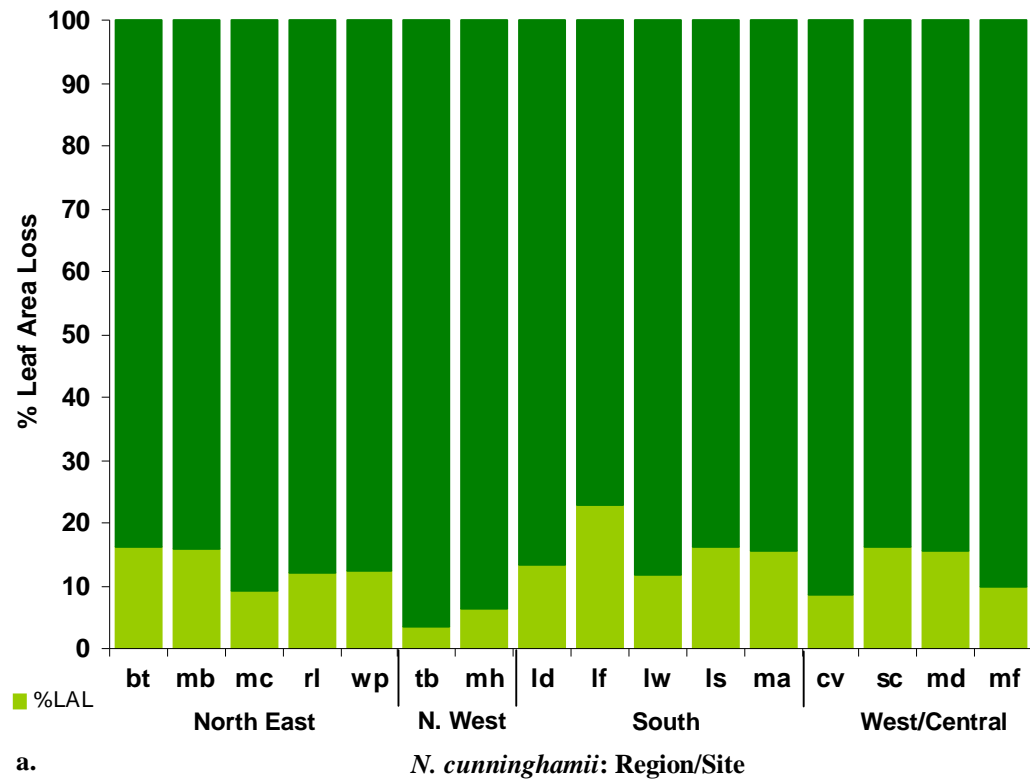


Figure 6.53. a & b. % Leaf Area Loss (%LAL), all sites, 1998-2002: *Nothofagus* species, region and site. a. *N. cunninghamii*, b. *N. gunnii*. North East: bt: Blue Tier, mb: Mt. Barrow, wp: Weldborough Pass, mc: Myrtle Creek, rl: Rainforest Ledge. North West: tb: Tayatea Bridge, mh: Milkshake Hills. South: ld: Lake Dobson, lf: Lake Fenton, lw: Lyrebird Walk, ts: Tarn Shelf, ls: Lake Skinner, ma: Mt. Arthur. West/Central: cv: Cradle Valley, sc: Lake St Clair, md: Mt. Dundas, mf: Meander Forest, kw: King William, cl: Crater Lake, lp: Little Plateau, cn & cs: Cradle Cirque, North and South, le: Lake Eros, ot: Ossa Track, tr: Traveller Range, wm: Lake Windermere.

6.2.2 Regional and Seasonal Variation, Region/Season Sites

The Region/Season sites (Sampling Set 3, table 4.1) showed an overall total percentage leaf area loss, for both *Nothofagus* species, of 8.43%; that of *N. cunninghamii* (15.56%) being over five times that of *N. gunnii* (2.76%) (figure 6.54).

The *N. cunninghamii* regional comparison revealed a markedly lower percentage leaf area loss in the North West (3.65%) compared with the other regions. The North East had the highest percentage leaf area loss at 17.31%, while the South and West/Central had levels of 15.5% and 14.23% respectively (figure 6.55.a). *N. gunnii* showed little regional variation between the South (2.92%) and West/Central (2.64%) (figure 6.55.b).

Examination of the percentage leaf area loss by region and site for *N. cunninghamii*, reveals considerable variation between the twelve sites, ranging from 3.65% at Tayatea Bridge (North West), to 27.55% at Mt. Arthur (South); and also site variation within the regions (figure 6.56.a). In contrast, *N. gunnii* shows little between-site or within-region variation in percentage leaf area loss, with the exceptions of Lake Fenton (South) at 1.63%, and Little Plateau (West/Central) at 13.54% (figure 6.56.b).

Overall comparison by season revealed a very small decrease in percentage leaf area loss between spring and autumn for both *Nothofagus* species: from 16.22% to 14.1% for *N. cunninghamii*; and from 3.11% to 2.4% for *N. gunnii* (figure 6.57). However, for *N. cunninghamii* there was considerable regional variation between seasons, the South having a spring peak in percentage leaf area loss, the North East and West/Central having summer peaks, and the North West peaking in autumn (figure 6.58.a). There was little regional variation for *N. gunnii*, with both the South and West/Central showing a small decline in percentage leaf area loss from spring to summer to autumn (figure 6.58.b).

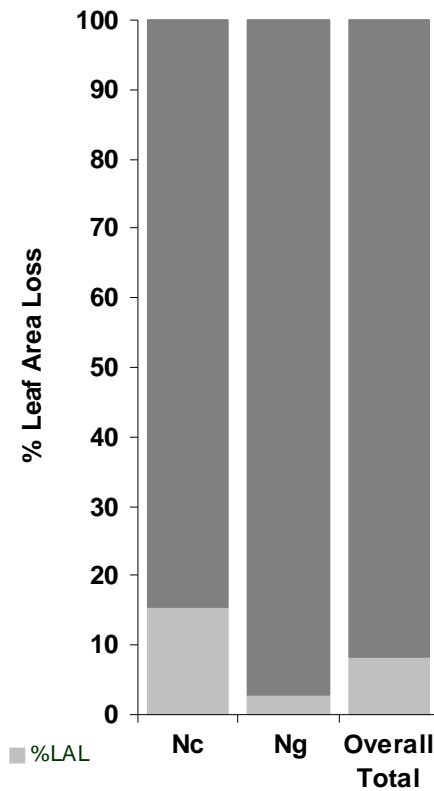


Figure 6.54. % Leaf Area Loss (%LAL), 1999-2000: *N. cunninghamii* (Nc), *N. gunnii* (Ng) and overall.

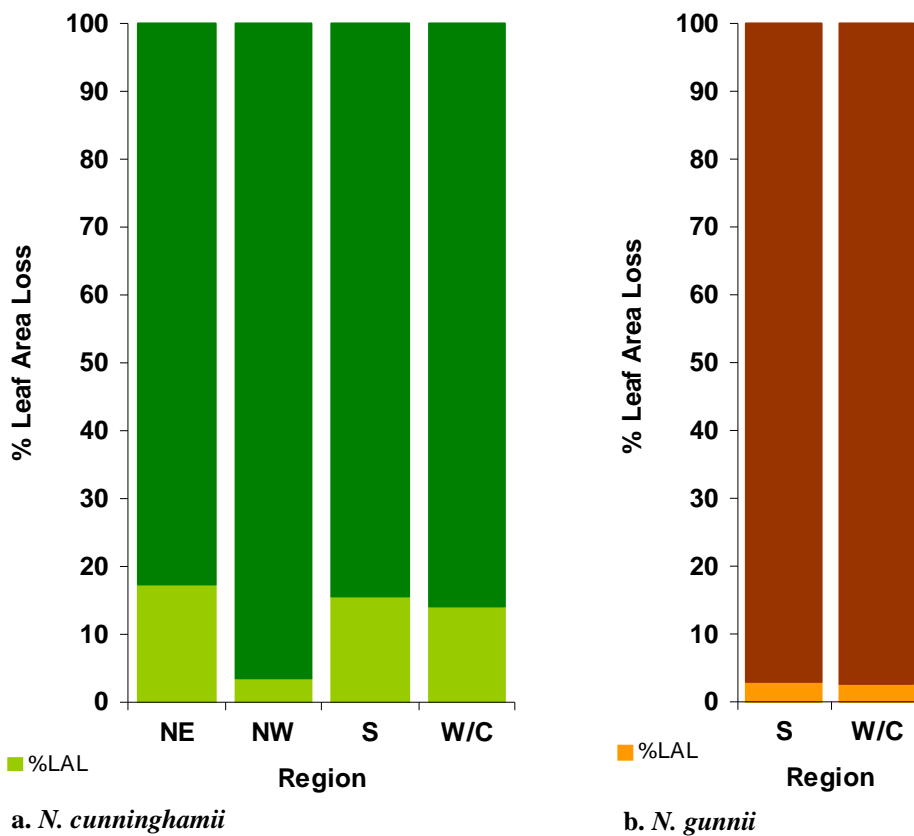
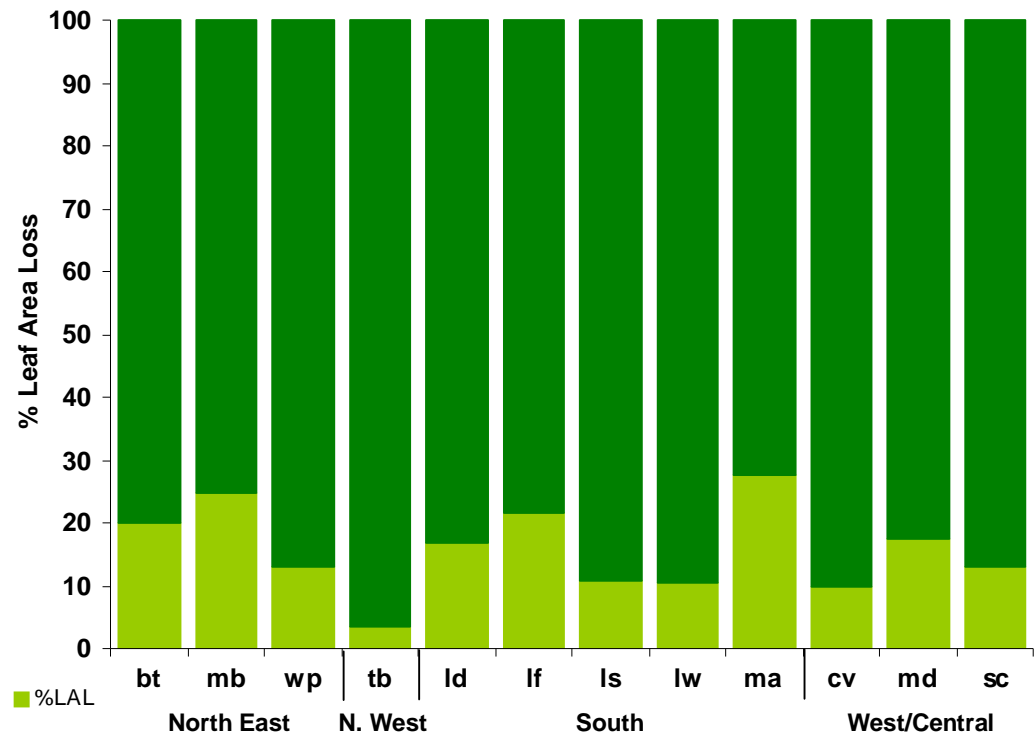
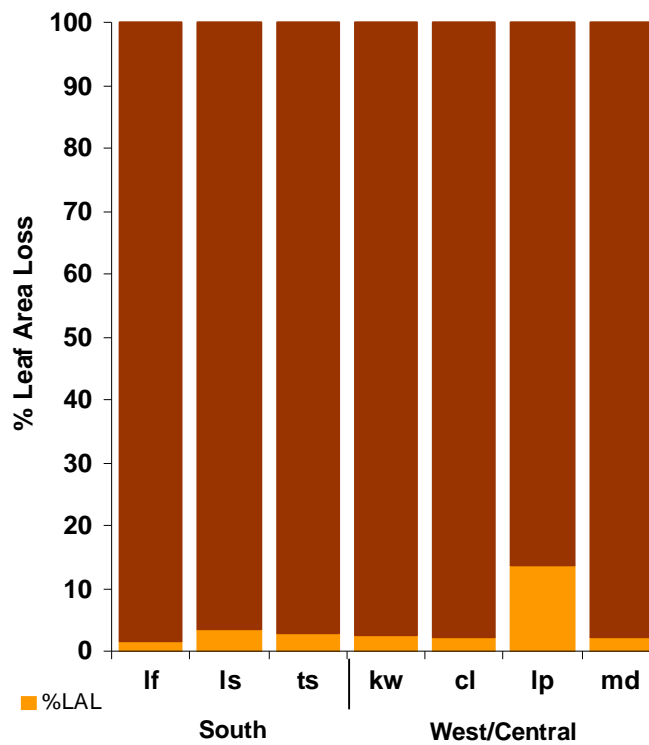


Figure 6.55. a & b. % Leaf Area Loss (%LAL), 1999-2000: *Nothofagus* species and region.



a. *N. cunninghamii*: Region/Site



b. *N. gunnii*: Region/Site

Figure 6.56. a & b. % Leaf Area Loss (%LAL), 1999-2000: *Nothofagus* species, region and site. a. *N. cunninghamii*, b. *N. gunnii*. North East: bt: Blue Tier, mb: Mt. Barrow, wp: Weldborough Pass. North West: tb: Tayatea Bridge. South: ld: Lake Dobson, lf: Lake Fenton, lw: Lyrebird Walk, ts: Tarn Shelf, ls: Lake Skinner, ma: Mt. Arthur. West/Central: cv: Cradle Valley, sc: Lake St Clair, md: Mt. Dundas, kw: King William, cl: Crater Lake, lp: Little Plateau.

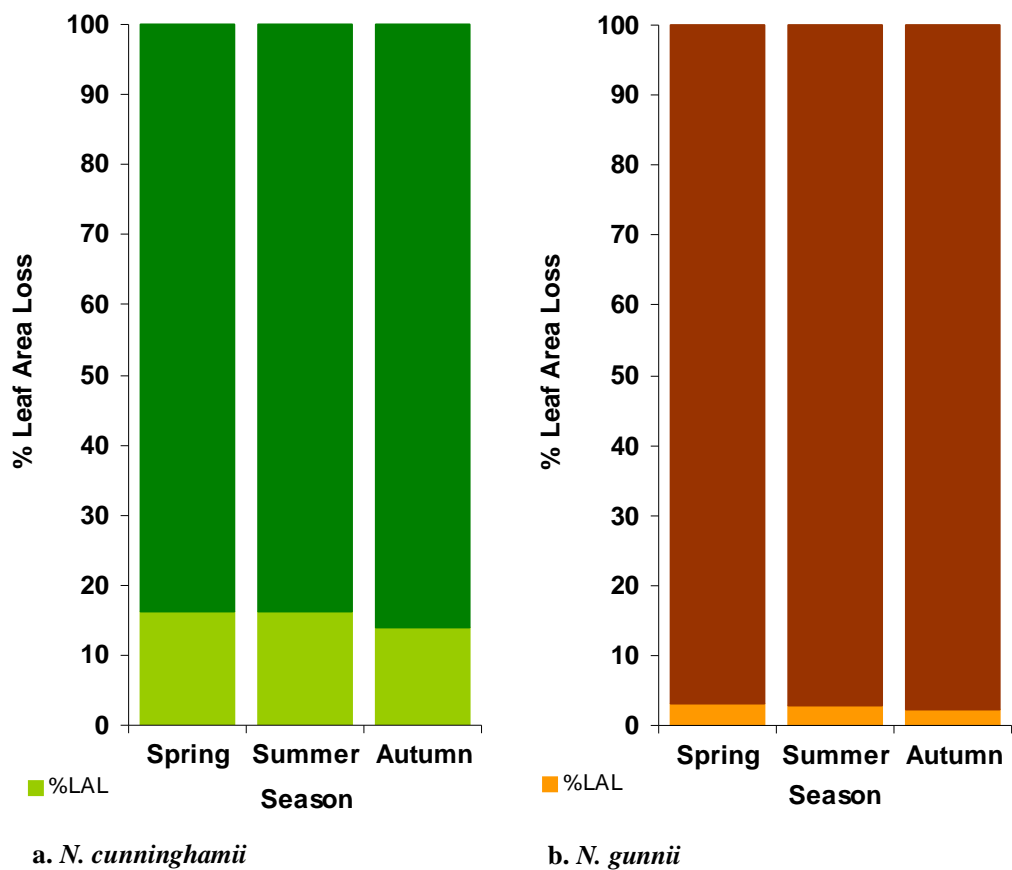


Figure 6.57. a & b. % Leaf Area Loss (%LAL), 1999-2000: *Nothofagus* species and season.

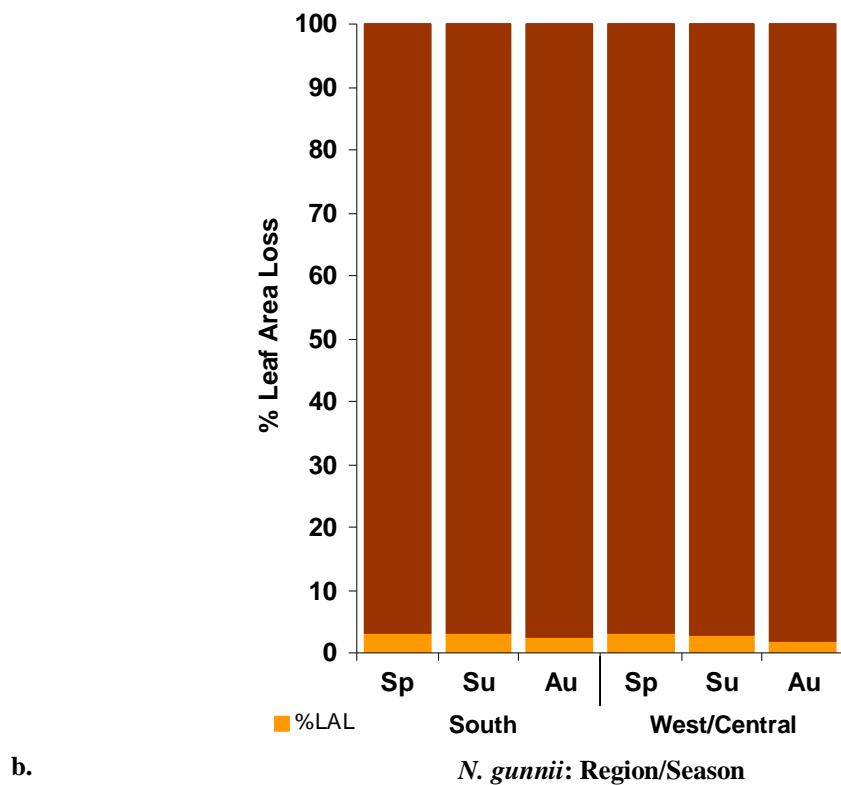
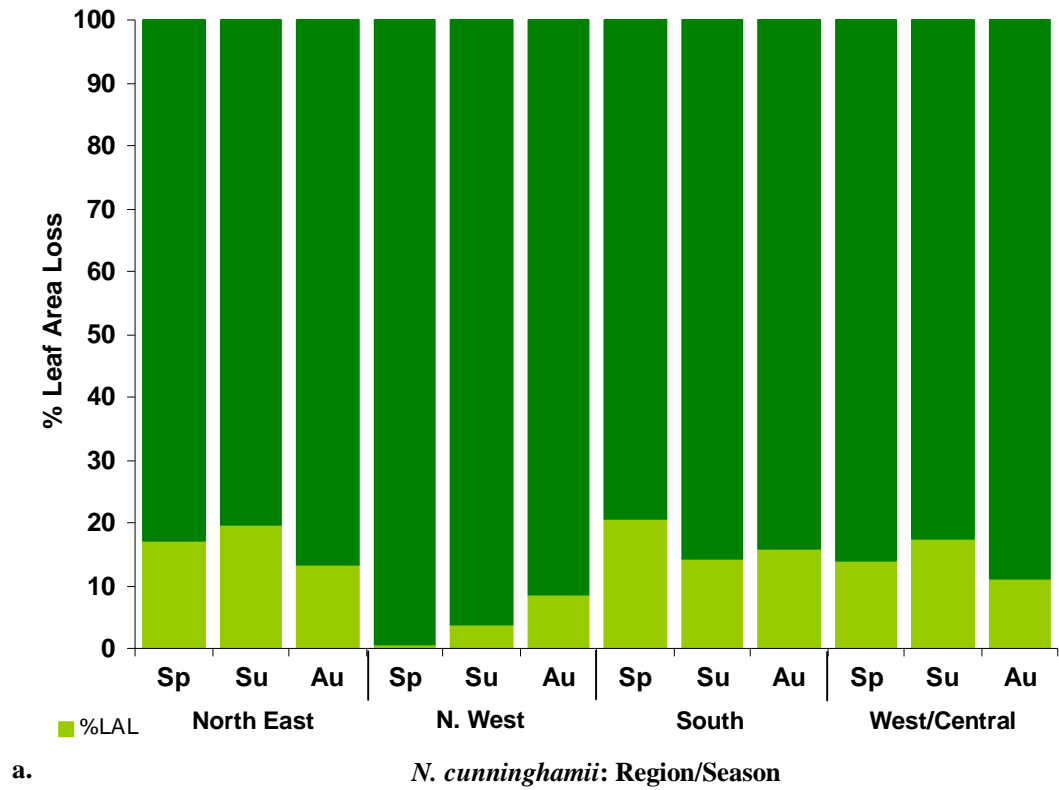


Figure 6.58. a & b. % Leaf Area Loss (%LAL), 1999-2000: *Nothofagus* species, region and season. a. *N. cunninghamii*, b. *N. gunnii*. Sp: Spring, Su: Summer, Au: Autumn.

6.2.3 Aspect Variation

The aspect sampling (Sampling Set 5, table 4.1) for *N. cunninghamii* revealed little difference between north-facing (21.24%) and south-facing (21.87%) aspects in overall percentage leaf area loss, although these were a little higher than the leaves adjacent to *N. gunnii* (20.46%) (figures 6.59.a, 6.60.a). For *N. gunnii*, the overall percentage leaf area loss varied little between the three aspects (figures 6.59.b, 6.60.b).

Site comparison between Lake Fenton and Lake Skinner for *N. cunninghamii* revealed higher percentage leaf area loss at Lake Fenton for both north-facing and south-facing aspects (figures 6.61.a). The *N. gunnii* site comparison showed King William to have higher percentage leaf area loss on the south facing than the north facing leaves, whereas the two aspects were similar at Lake Fenton and Lake Skinner, the latter having the lowest levels of percentage leaf area loss of the three sites for either aspect (figure 6.61.b). The adjacent aspects at Lake Fenton and Lake Skinner had similar levels of percentage leaf area loss for each *Nothofagus* species (figure 6.62); but for *N. cunninghamii* at Lake Fenton this was lower than the north and south facing aspects, whereas at Lake Skinner the reverse occurred, with the adjacent aspect leaves having the highest percentage leaf area loss (figures 6.61.a, 6.62.a); while for *N. gunnii*, at Lake Fenton the levels of percentage leaf area loss on both north and south facing aspects were higher than the adjacent aspect, but at Lake Skinner all aspects had comparable levels of percentage leaf area loss (figures 6.61.b, 6.62.b).

When the two sampling years were compared, *N. cunninghamii* had a higher percentage leaf area loss, at all aspects, in spring/summer 1999 young leaves compared with autumn 1998; and in spring/summer 1999, the north facing leaves had the highest percentage leaf area loss, whereas in autumn 1998 the north and south facing young leaves had similar percentage leaf area loss (figure 6.63). The adjacent *N. cunninghamii* leaves had lower percentage leaf area loss than the other aspects in both years (figure 6.65). *N. gunnii* had similar levels of percentage leaf area loss across all aspects in both years (figures 6.64, 6.66).

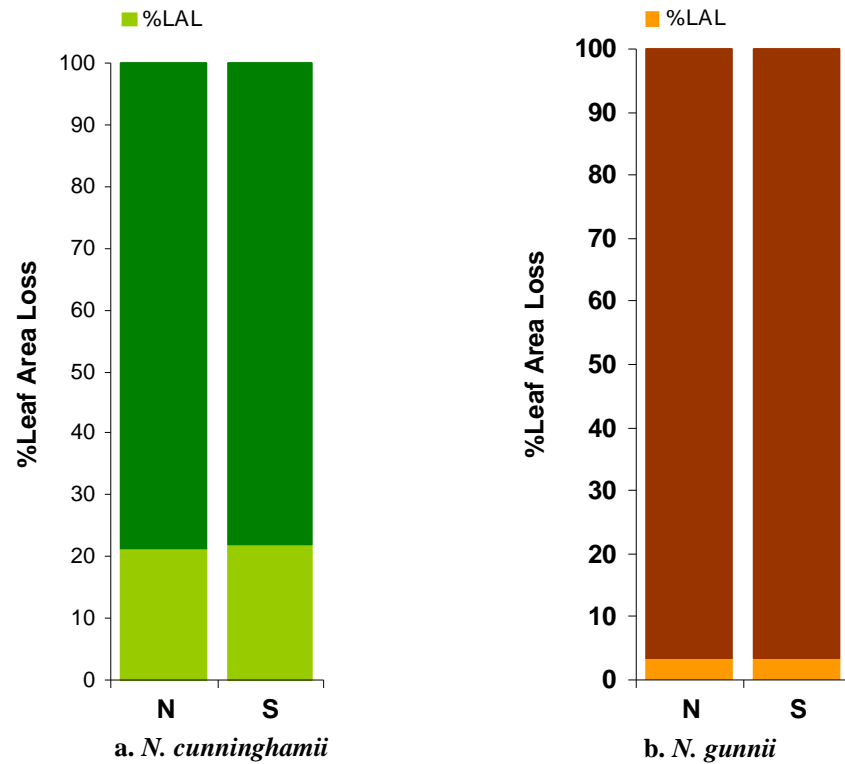


Figure 6.59. a & b. % Leaf Area Loss (%LAL): autumn 1998 and spring/summer 1999, North-facing (N) and South-facing (S) aspects, at 2 sites for *N. cunninghamii*: Lake Fenton and Lake Skinner; and 3 sites for *N. gunnii*: Lake Fenton, Lake Skinner and King William.

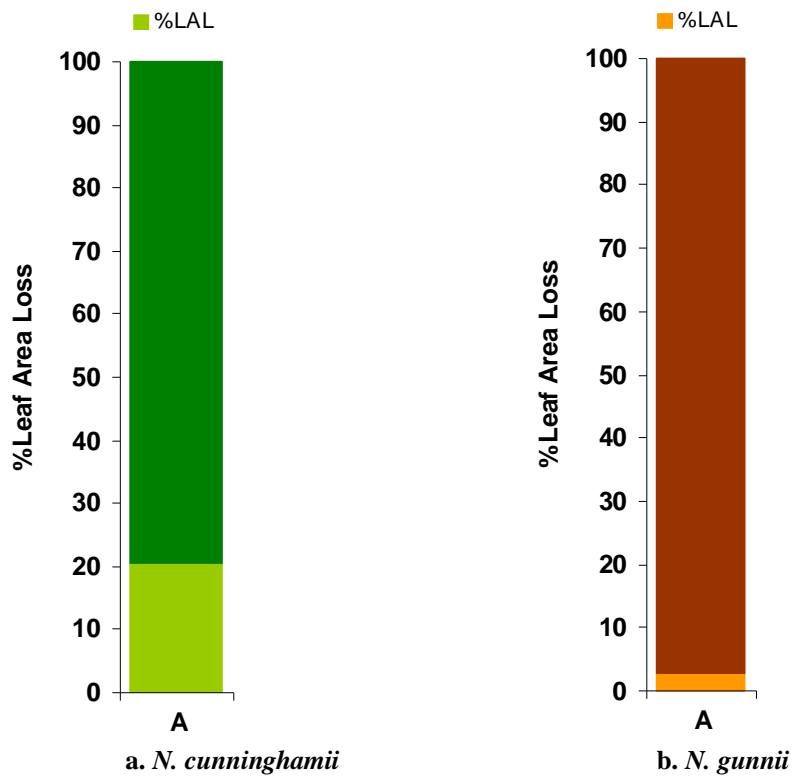


Figure 6.60. a & b. % Leaf Area Loss (%LAL): autumn 1998 and spring/summer 1999, adjacent (A) aspects of trees of *N. cunninghamii* and *N. gunnii* at two sites: Lake Fenton and Lake Skinner.

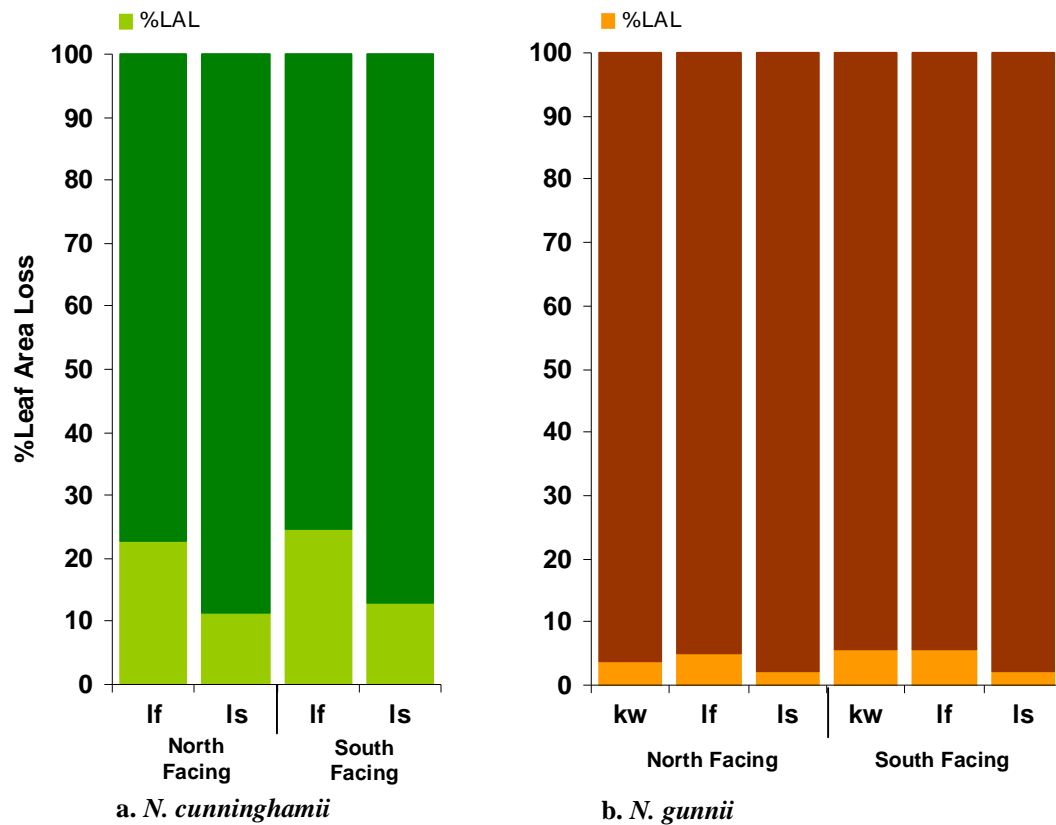


Figure 6.61. a & b. % Leaf Area Loss (%LAL): autumn 1998 and spring/summer 1999, North-facing and South-facing aspects, at 2 sites for *N. cunninghamii*: Lake Fenton (lf) and Lake Skinner (ls); and 3 sites for *N. gunnii*: Lake Fenton (lf), Lake Skinner (ls) and King William (kw).

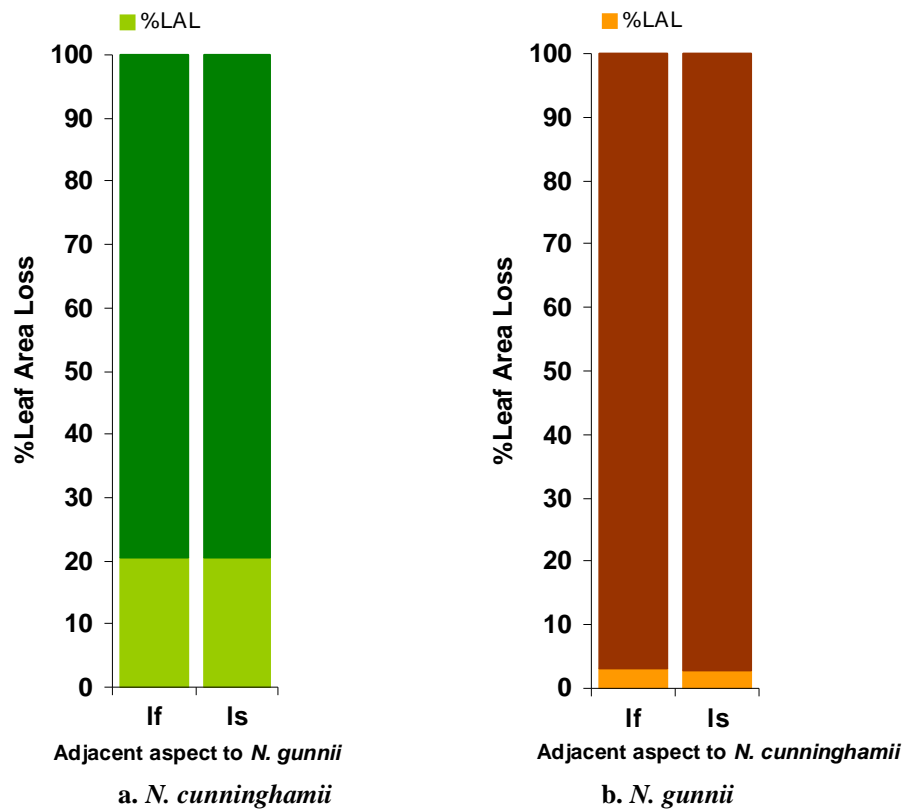


Figure 6.62. a & b. % Leaf Area Loss (%LAL): autumn 1998 and spring/summer 1999, adjacent aspects of trees of *N. cunninghamii* and *N. gunnii* at two sites: Lake Fenton (lf) and Lake Skinner (ls).

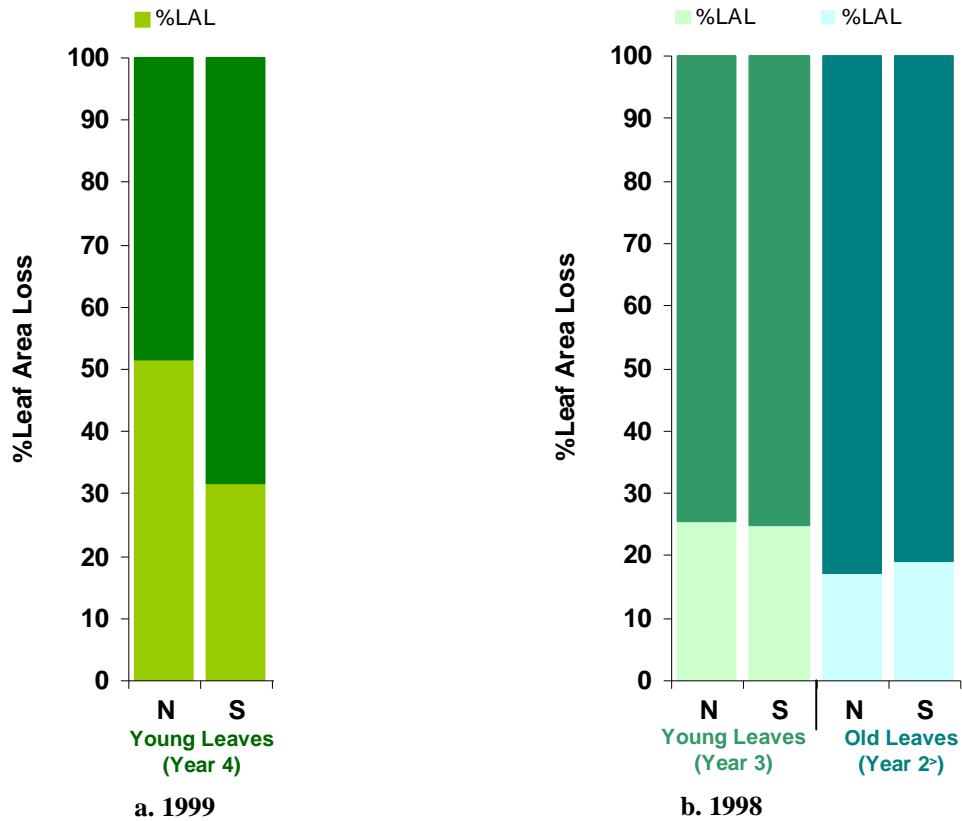


Figure 6.63. a & b. *N. cunninghamii*, % Leaf Area Loss (%LAL): North-facing (N) and South-facing (S) aspects, at 2 sites: Lake Fenton and Lake Skinner.
a. Spring/summer 1999: young leaves (Leaf Year 4) only. b. Autumn 1998 : young leaves (Leaf Year 3) and old leaves (Leaf Year 2 and earlier).

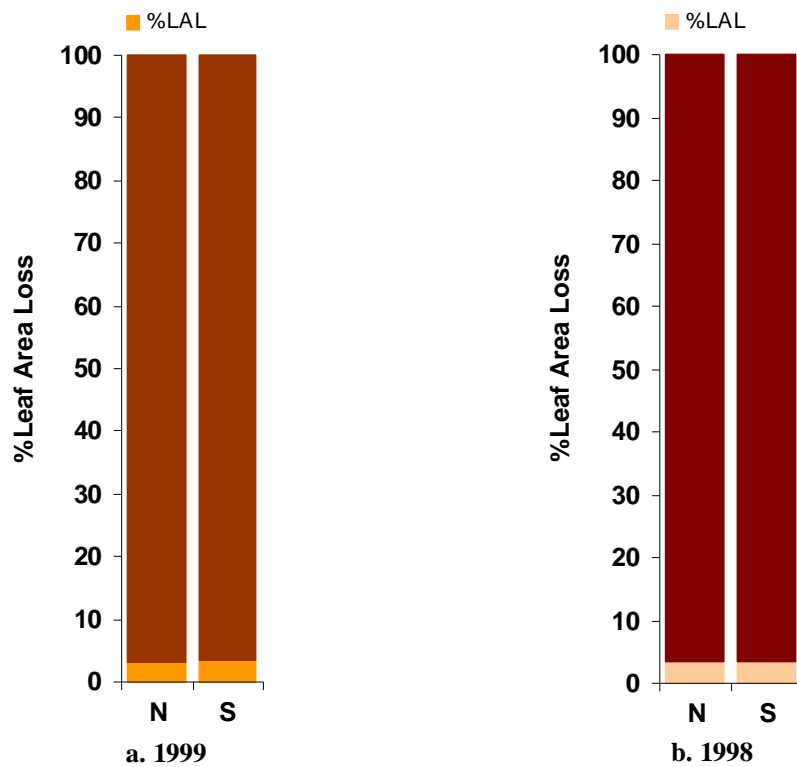


Figure 6.64. a & b. *N. gunnii*, % Leaf Area Loss (%LAL): North-facing (N) and South-facing (S) aspects, at 3 sites: Lake Fenton, Lake Skinner and King William.
a. Spring/summer 1999. b. Autumn 1998.

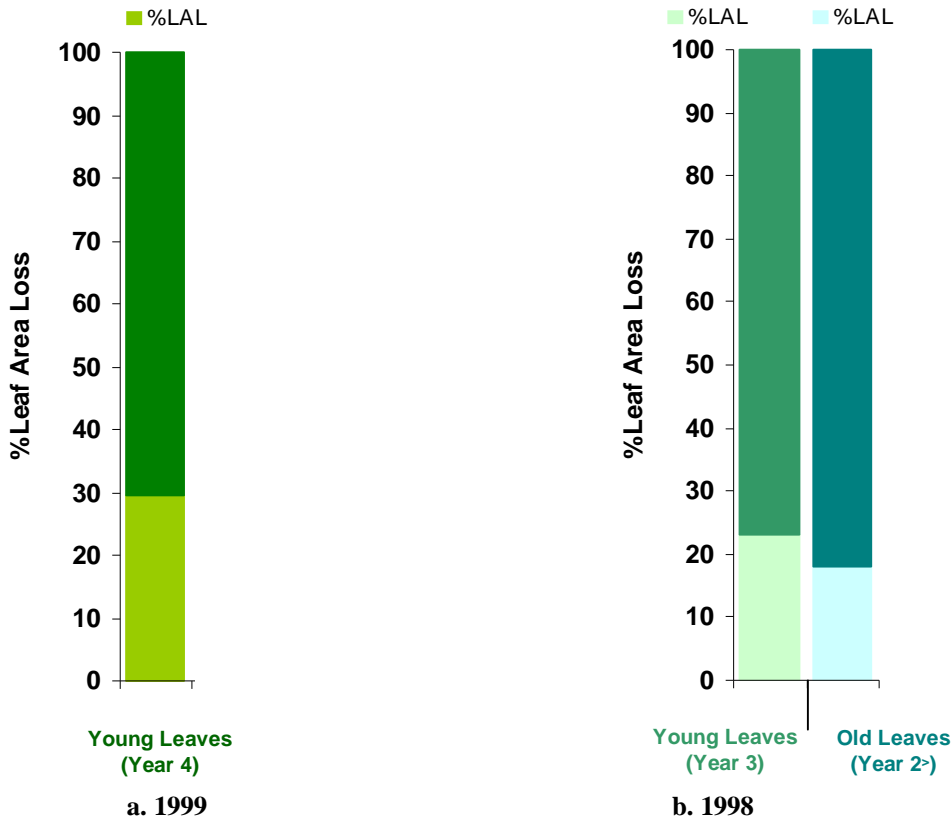


Figure 6.65. a & b. *N. cunninghamii*, % Leaf Area Loss (%LAL): aspect adjacent to *N. gunnii*, at 2 sites: Lake Fenton and Lake Skinner.
a. Spring/summer 1999: young leaves (Leaf Year 4) and old leaves (Leaf Year 3 and earlier).
b. Autumn 1998 : young leaves (Leaf Year 3) and old leaves (Leaf Year 2 and earlier).

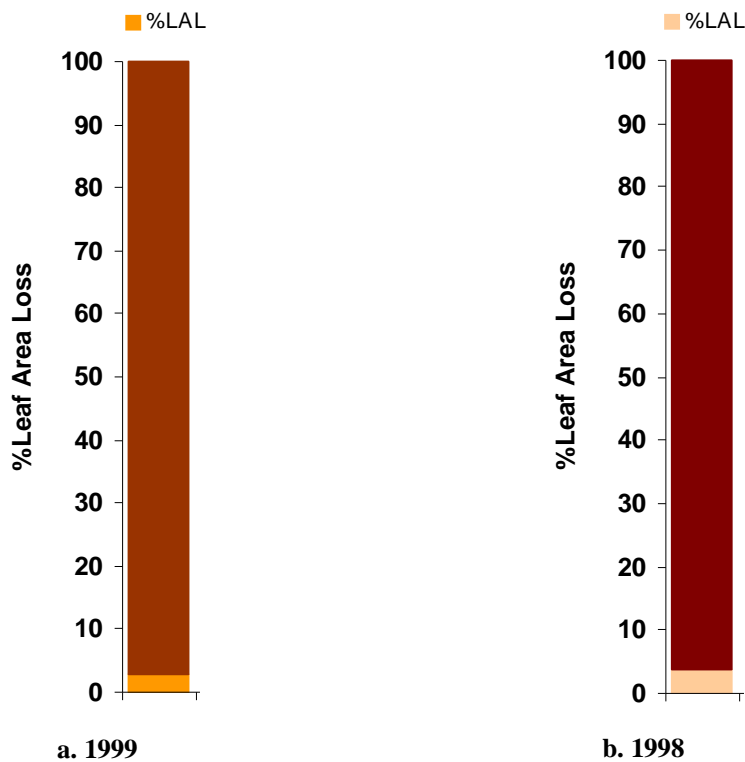


Figure 6.66. a & b. *N. gunnii*, % Leaf Area Loss (%LAL): aspect adjacent to *N. cunninghamii*, at 3 sites: Lake Fenton, Lake Skinner and King William.
a. Spring/summer 1999. b. Autumn 1998.

6.2.4 Cumulative Sampling and Yearly Variation

The chewed leaves in the consecutive year cumulative sampling, from spring 1998 to autumn 1999 and from spring 1999 to spring 2000 (Sampling Set 6, table 4.1), were assessed at each site visit for percentage leaf area loss. The preliminary sampling in autumn 1998 again provided a third year for an autumn comparison.

6.2.4.1 Cumulative Sampling Results: *N. cunninghamii*

Percentage leaf area loss was measured for young and old leaves on the *N. cunninghamii* tagged and control branches and, at the appropriate sites, on the bagged branches from spring 1999 to autumn 2000. The previous year, spring 1998 to autumn 1999, the young leaves only were assessed.

Overall, from spring 1999 to autumn 2000 (figure 6.67), the general trend was for a decrease in percentage leaf area loss over the sampling period, in both young and old, bagged and tagged branches (the young bagged branches have an apparent increase in September/November 2000 because percentage leaf area loss was recorded only at the final site visit to Mt Arthur). However the year before, from spring 1998 to autumn 1999, there had been a greater variability in the young leaves percentage leaf area loss (figure 6.68). There was also variation in percentage leaf area loss between the sites in each year, and between years at Lake Fenton, Lyrebird Walk and Lake Skinner (figure 6.69).

In 1999-2000, the level of young leaf percentage leaf area loss on the tagged branches varied greatly between sites: three sites had an early peak (Mt. Arthur, 59.77% in December 1999; Lyrebird Walk, 23.1% in October 1999; Lake Dobson, 17.91% in December 1999) after which the level of young leaf percentage leaf area loss declined over the sampling period; while the levels at Lake Fenton and Lake Skinner remained relatively steady at around 23% and 10.93% respectively (figures 6.69, 6.70). The percentage leaf area loss of the bagged young leaves fell between December 1999 and September 2000 at Lake Dobson, and at all the sites the old leaves, bagged or tagged, showed a decline in levels of percentage leaf area loss between the beginning and end of the sampling period (figures 6.69, 6.70).

In 1998-1999, the tagged young leaves percentage leaf area loss remained relatively steady at Lake Fenton and Lyrebird Walk, but the levels differed greatly from around 48% to around 6% respectively, while at Lake Skinner there was an increase from 24.83% in January 1999 to 31.09% in March 1999 (figure 6.69). Percentage leaf area loss of young bagged leaves at Lyrebird Walk fluctuated between 11.12% and 16.45%, and at Lake Skinner remained steady at around 22% (figure 6.69).

6.2.4.2 Cumulative Sampling Results: *N. gunnii*

Overall percentage leaf area loss on *N. gunnii* was consistently low in both sampling years, varying between 2.44% and 3.19% in 1999-2000; and between 2.06% and 3.36% between 1998-1999 (figures 6.71, 6.72). In 1999-2000, Lake Fenton had the lowest levels of percentage leaf area loss and Lake Skinner the highest; and the general trend was a decrease in percentage leaf area loss over the sampling period (figure 6.73). In 1998-1999, the general trend was an increase in percentage leaf area loss over the sampling period, particularly at Lake Fenton (figure 6.74).

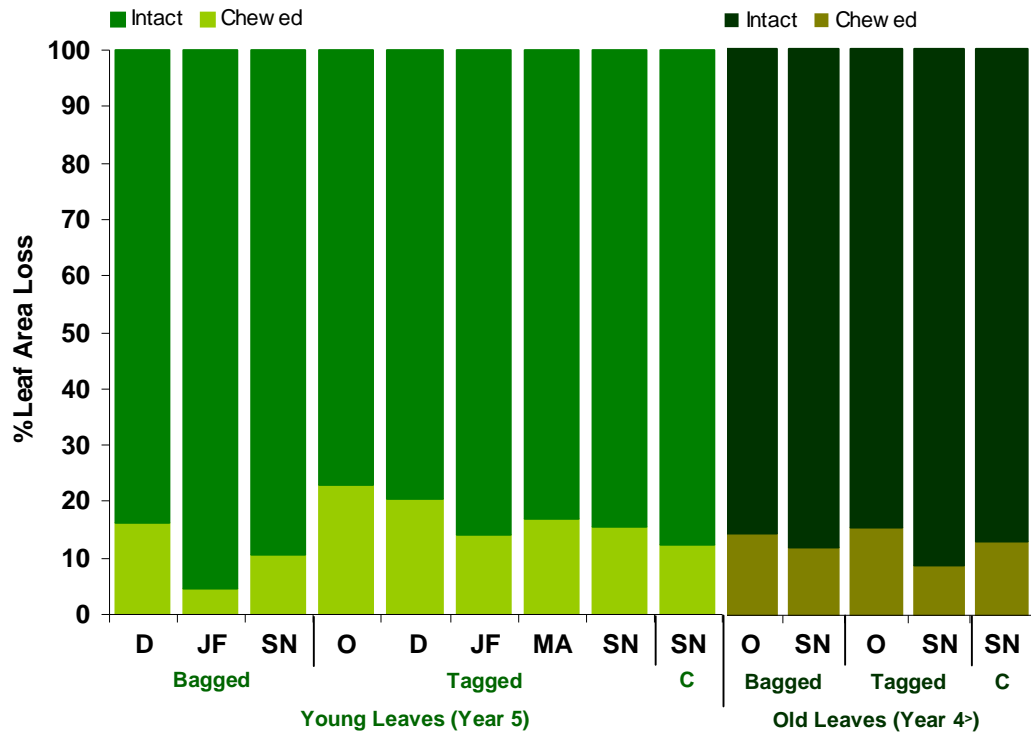


Figure 6.67. 1999-2000 cumulative record of *N. cunninghamii* % Leaf Area Loss (%LAL) on bagged branches, tagged (unbagged) branches, and controls (C), 5 sites combined: Lake Fenton, Lyrebird Walk, Lake Skinner, Lake Dobson and Mt. Arthur. Young leaves (Leaf Year 5) recorded at ~6 weekly intervals October – April and in the following Spring. Old leaves (Leaf Year 4 and earlier) recorded at beginning and end of sampling period. O: October 1999; D: December 1999; JF: late January/early February 2000; MA: early March /early April 2000; SN: September/November 2000.

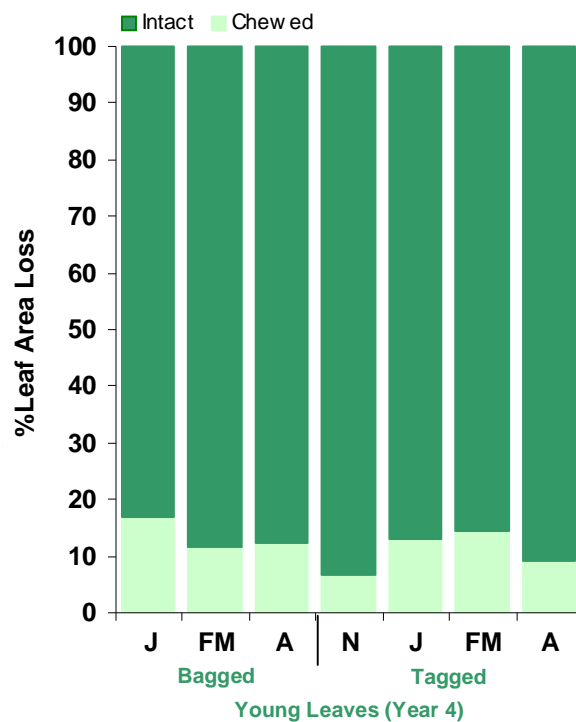


Figure 6.68. 1998-1999 cumulative record of *N. cunninghamii* % Leaf Area Loss (%LAL), young leaves (Leaf Year 4) only, on bagged branches and tagged (unbagged) branches, 3 sites combined: Lake Fenton, Lyrebird Walk, Lake Skinner. ND: late November/early December 1998; J: mid January 1999; FM: late February/mid March 1999; A: mid April 1999.

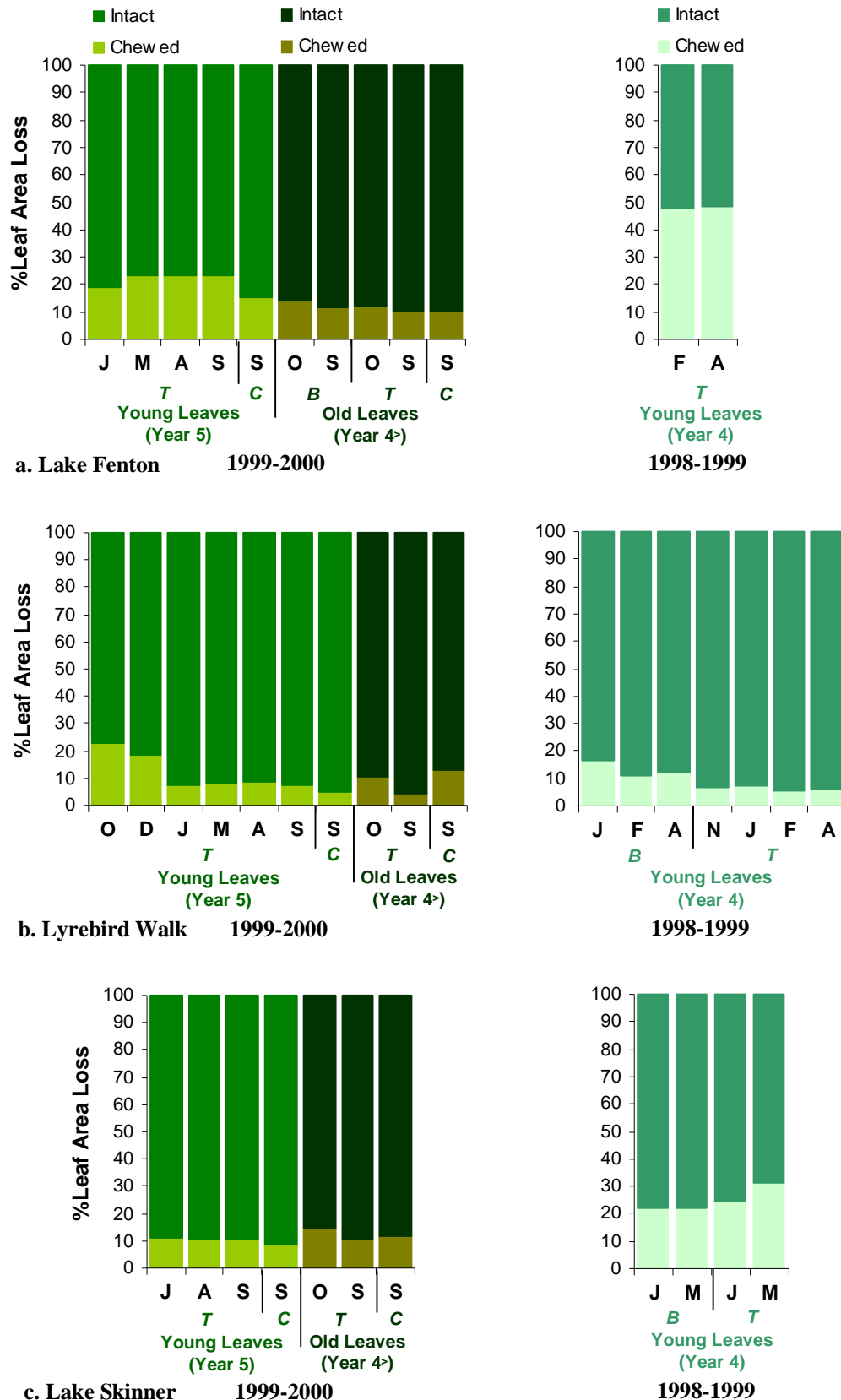


Figure 6.69. Cumulative records for consecutive sampling years of *N. cunninghamii*, % Leaf Area Loss (%LAL) on bagged branches (B), tagged (unbagged) branches (T), and controls (C) at 3 sites: Lake Fenton (a), Lyrebird Walk (b), Lake Skinner (c).

1999-2000: young leaves (Year 5); old leaves (Year 4 and earlier). O: Oct. 1999; D: Dec. 1999; JF: late Jan./early Feb. 2000; MA: early Mar./early Apr. 2000; SN: Sept./Nov. 2000.

1998-1999: young leaves (Year 4) only. ND: late Nov./early Dec. 1998; J: mid Jan. 1999; FM: late Feb./mid Mar. 1999; A: mid Apr. 1999.

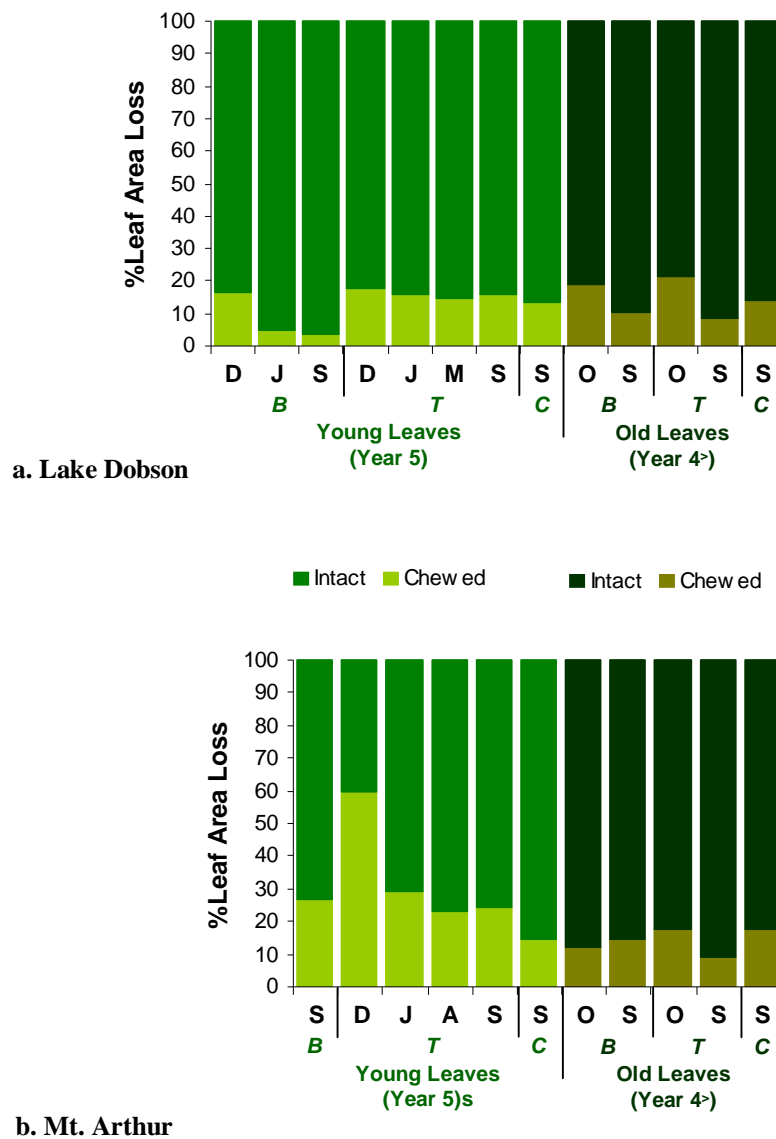


Figure 6.70. Cumulative records for consecutive sampling years of *N. cunninghamii*, % Leaf Area Loss (%LAL) on bagged branches (B), tagged (unbagged) branches (T), and controls (C) at Lake Dobson (a) and Mt. Arthur (b). 1999-2000: young leaves (Year 5); old leaves (Year 4 and earlier). O: Oct. 1999; D: Dec. 1999; JF: late Jan./early Feb. 2000; MA: early Mar./early Apr. 2000; SN: Sept./Nov. 2000.

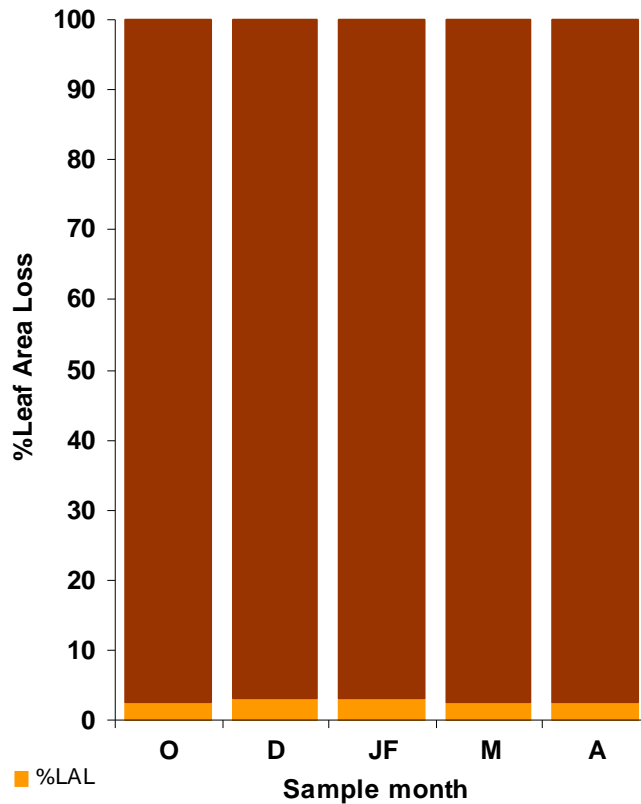


Figure 6.71. 1999-2000 cumulative record of *N. gunnii* % Leaf Area Loss (%LAL), 3 sites combined: Lake Fenton, Lake Skinner, Tarn Shelf. O: mid/late October 1999; D: early December 1999; JF: late January/early February 2000; M: early March 2000; A: early April 2000.

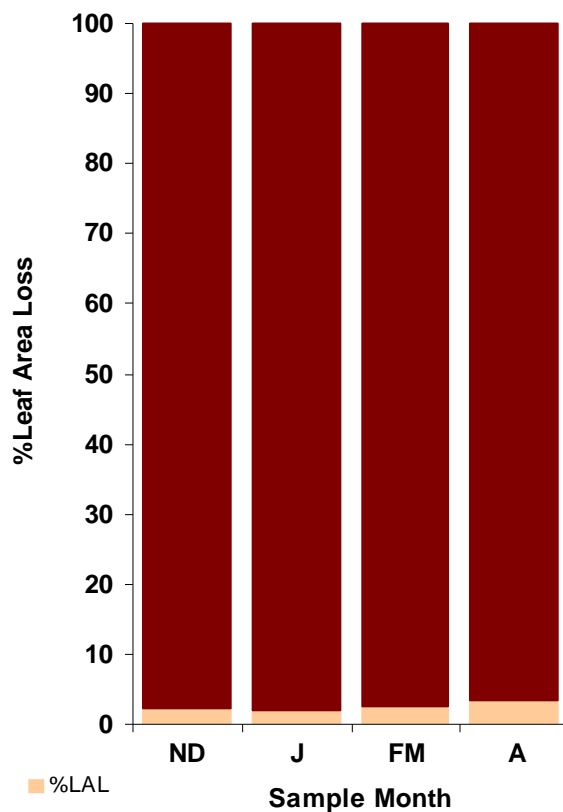


Figure 6.72. 1998-1999 cumulative record of *N. gunnii* % Leaf Area Loss (%LAL), 3 sites combined: Lake Fenton, Lake Skinner, King William. ND: late November/early December 1998; J: mid January 1999; FM: late February/mid March 1999; A: mid April 1999.

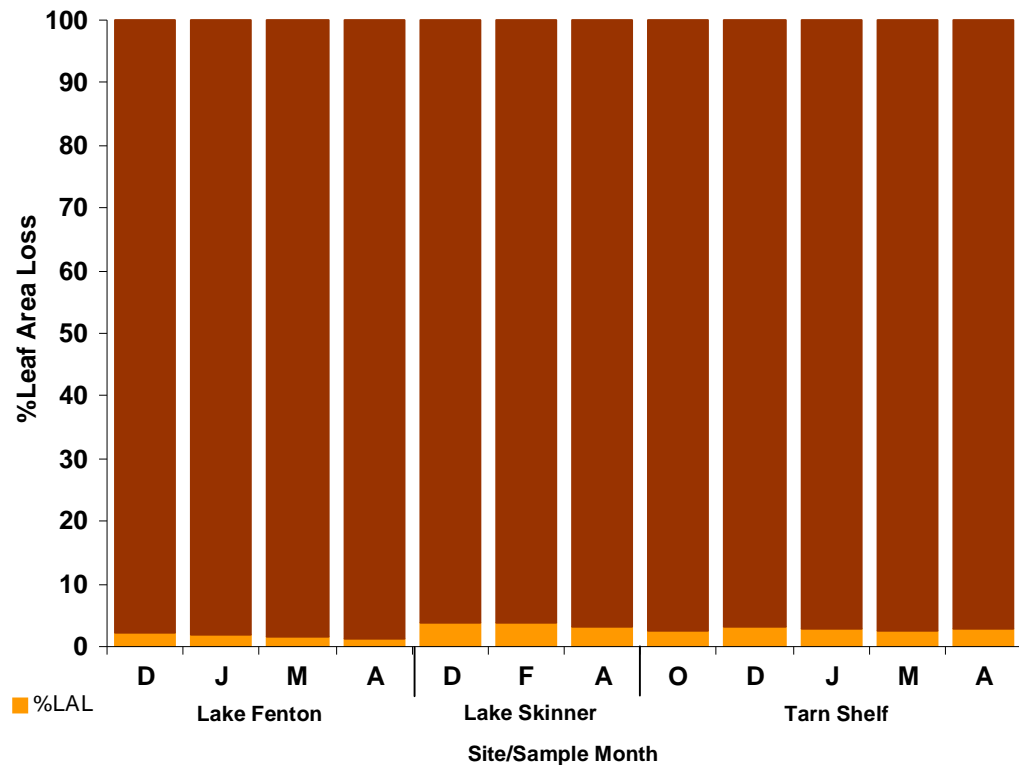


Figure 6.73. 1999-2000 cumulative site record of *N. gunnii* % Leaf Area Loss (%LAL): Lake Fenton, Lake Skinner, Tarn Shelf. O: mid/late October 1999; D: early December 1999; J: late January 2000; F: early February 2000; M: early March 2000; A: early April 2000.

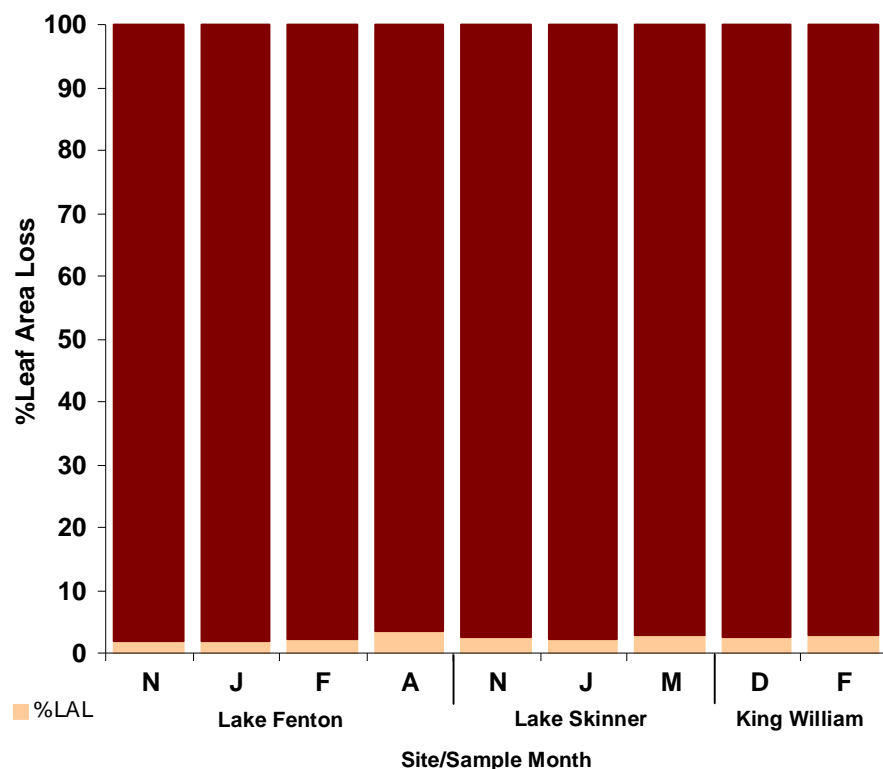


Figure 6.74. Figure 6.Y. 1998-1999 cumulative site record of *N. gunnii* % Leaf Area Loss (%LAL): Lake Fenton, Lake Skinner, King William. N: late November 1998; D: early December 1998; J: mid January 1999; F: February 1999; M: mid March 1999; A: mid April 1999.

6.2.4.3 *Three Year Autumn Comparison*

Of the chewed leaves from the initial sampling in autumn 1998, *N. cunninghamii* had an overall percentage leaf area loss of 19.87% and *N. gunnii* an overall percentage leaf area loss of 4.68% (figure 6.75). Site comparison revealed that for *N. cunninghamii*, the highest percentage leaf area loss was at Lake Fenton (22.96%), followed by Lake Skinner (17.07%) and Lyrebird Walk (13.3%); and for *N. gunnii* the highest percentage leaf area loss was also at Lake Fenton (5.7%), followed by Lake Skinner (4.53%) and King William (4.48%) (figure 6.76).

When the three year autumn samples were compared, the *N. cunninghamii* young chewed leaves can be seen to have had a markedly higher level of percentage leaf area loss than the *N. gunnii* chewed leaves in each year; and both *Nothofagus* species had the highest percentage leaf area loss in autumn 1998 (figure 6.77). However, there was considerable variation in percentage leaf area loss between the sites and years, particularly for *N. cunninghamii* (figure 6.78 & 6.79). For *N. cunninghamii*, percentage leaf area loss was highest in at Lake Fenton (48.53%) in 1999 and lowest at Lyrebird Walk (6.3%) in the same year; and although the percentage leaf area loss varied between years at the three sites, Lake Fenton had the highest level, and Lyrebird Walk the lowest level, in each year (figure 6.78). For *N. gunnii*, percentage leaf area loss was spread more evenly between sites and years, although the highest levels occurred at each site in 1998; and Lake Fenton had both the highest (5.7% in 1998) and lowest (1.37% in 2000) percentage leaf area loss of the three *N. gunnii* sites (figure 6.79).

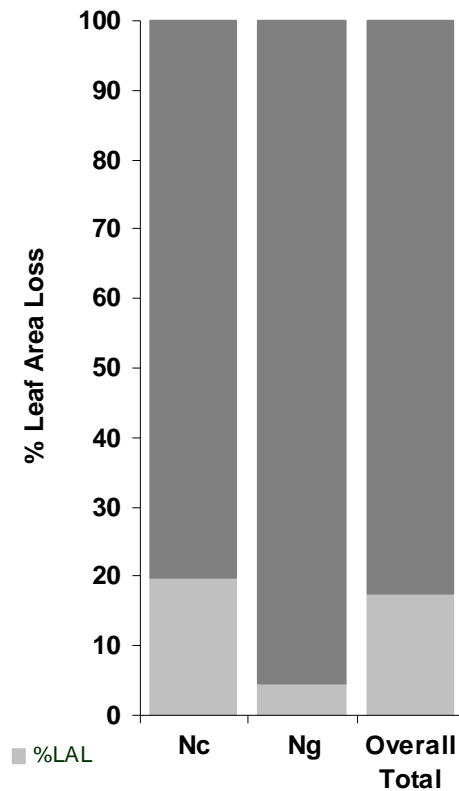


Figure 6.75. % Leaf Area Loss (%LAL), Autumn 1998: *N. cunninghamii* (Nc), *N. gunnii* (Ng) and overall.

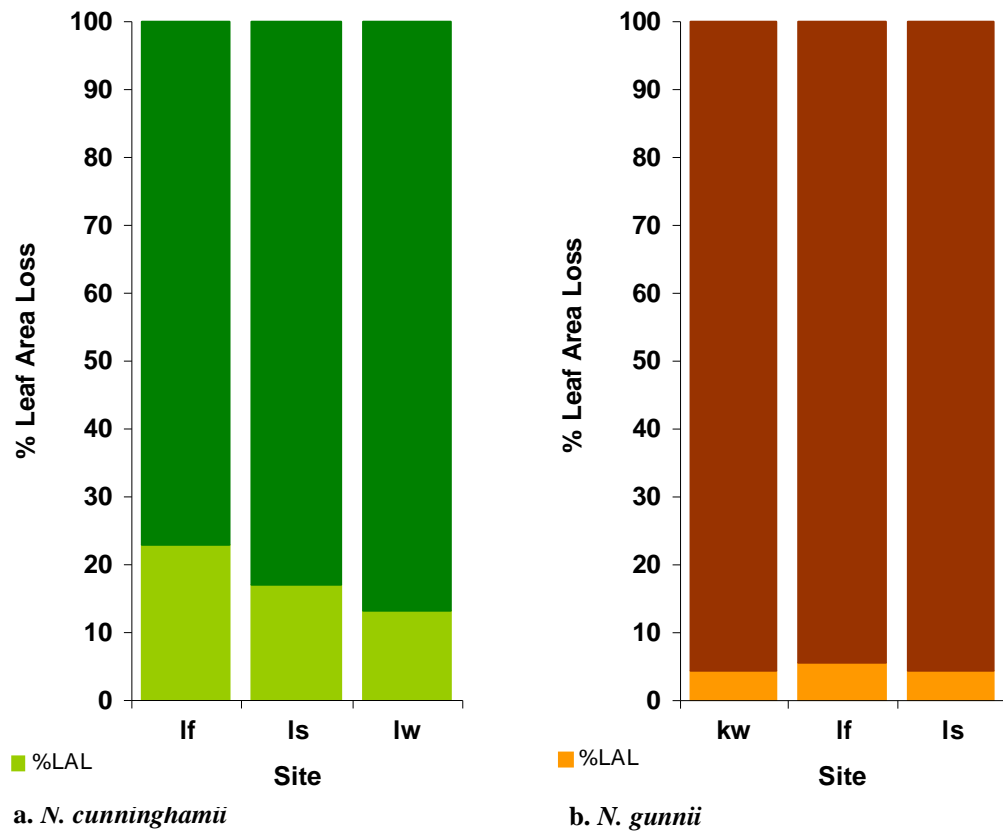


Figure 6.76. a & b. % Leaf Area Loss (%LAL) Autumn 1998: *Nothofagus* species and site. If: Lake Fenton, lw: Lyrebird Walk, Is: Lake Skinner, kw: King William.

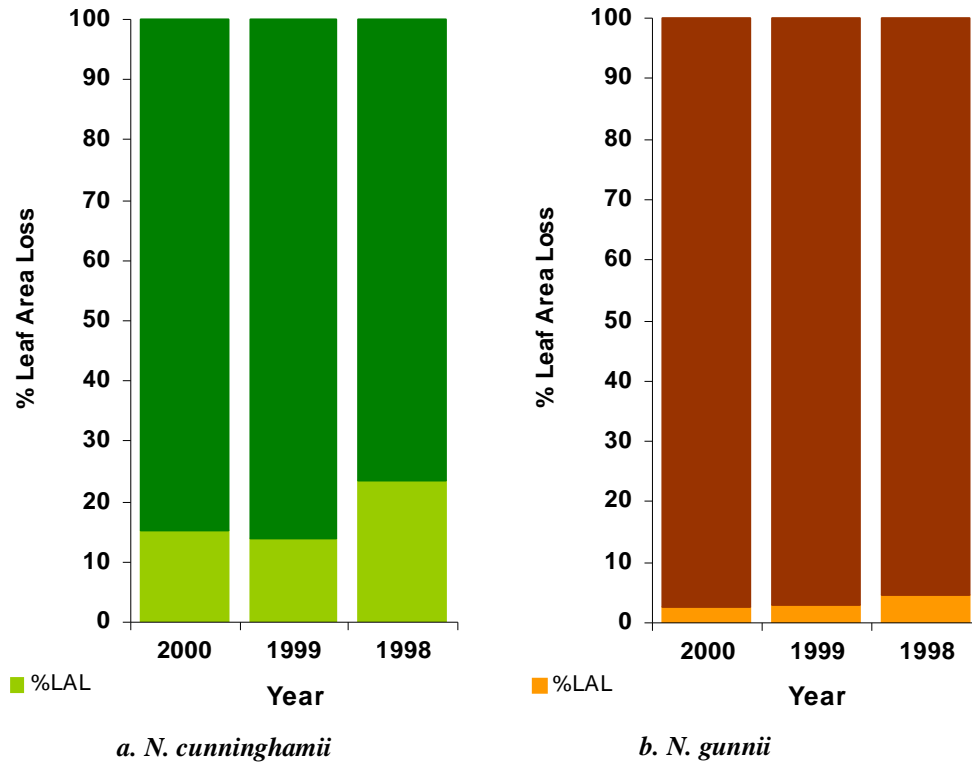


Figure 6.77. a & b. % Leaf Area Loss (%LAL), comparison between autumn 2000, autumn 1999 and autumn 1998 at 3 sites for each *Nothofagus* species.

a. *N. cunninghamii*, young leaves only: Lake Fenton, Lake Skinner, Lyrebird Walk.

b. *N. gunnii*: Lake Fenton, Lake Skinner, King William.

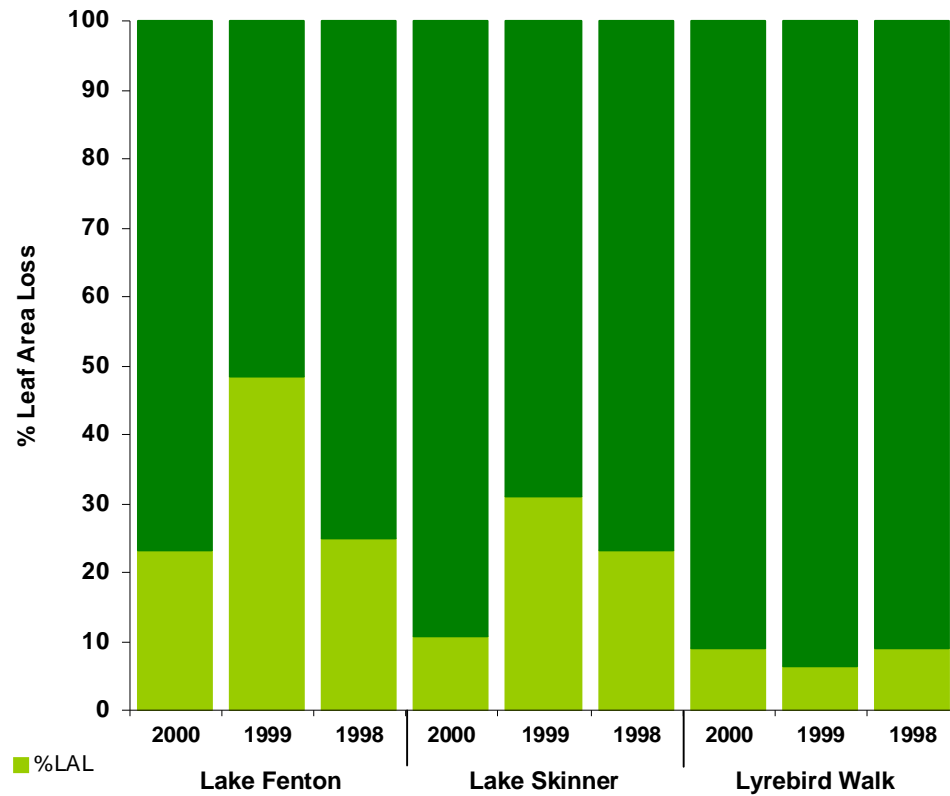


Figure 6.78. *N. cunninghamii* % Leaf Area Loss (%LAL), young leaves, site comparison between Autumn 2000, (leaf year 5), Autumn 1999 (leaf year 4) and Autumn 1998 (leaf year 3): Lake Fenton, Lake Skinner, Lyrebird Walk.

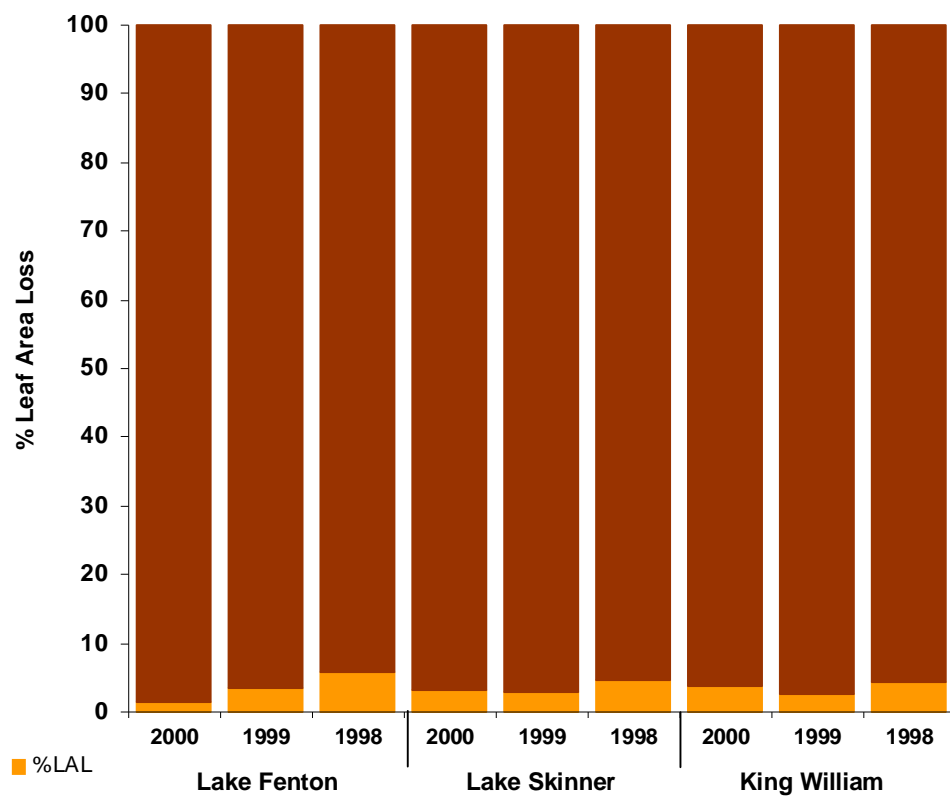


Figure 6.79. *N. gunnii* % Leaf Area Loss (%LAL), site comparison between Autumn 2000, Autumn 1999 and Autumn 1998: Lake Fenton, Lake Skinner King William.

6.3 LEAF AREAS AND HOLE GROWTH

6.3.1 Leaf Areas

In total, the areas of 2,700 *N. cunninghamii* leaves and 1400 *N. gunnii* leaves were measured in order to explore the variation in leaf area across the sampling sites.

6.3.1.1 *N. cunninghamii* Leaf Areas

N. cunninghamii mean leaf area differed between regions and was largest in the North East (ANOVA, $F_{2, 2697} = 593.48$, $P < 0.0001$). The North East leaves were also the most variable in size (figure 6.80). When the altitude of the sites was considered, the GLM showed that altitude did not influence leaf area independent of region.

The influence of sampling aspect on leaf area was compared at two sites, Lake Fenton and Lake Skinner. At Lake Fenton, sampling aspect showed no significant influence of on leaf area (ANOVA, $F_{1, 198} = 0.87$, $P = 0.3516$), however, at Lake Skinner leaves were larger on the southern aspect of the trees (ANOVA, $F_{1, 198} = 50.58$, $P < 0.001$) (figure 6.81).

The effect of leaf age on leaf area was explored at 8 sites, 100 young and 100 old *N. cunninghamii* leaves being measured from each site. Mean leaf area differed between old and young leaves (ANOVA, $F_{1, 1598} = 18.56$, $P < 0.0001$), the old leaves (NcO) having the larger mean area, however the two sets of leaves had a similar range of leaf areas (figure 6.82). Leaf areas differed significantly between sites for both the old leaves (ANOVA, $F_{7, 792} = 56.08$, $P < 0.0001$), and the young leaves (ANOVA, $F_{7, 792} = 40.78$, $P < 0.0001$), leaves from the eastern sites (Blue Tier, Mt. Barrow, Myrtle Creek, Rainforest Ledge, Weldborough Pass) having the largest mean area and the most variability in size for both leaf ages (figure 6.83).

Whether or not leaves had chewing damage had no effect on mean leaf area at Meander Forest, although the chewed leaves were less variable in leaf area than intact leaves (figure 6.84). Mean leaf area differed between sampling years at Lake Skinner (ANOVA, $F_{1, 298} = 247.22$, $P < 0.0001$), being larger in 2000 than in 1998, and the variability in leaf size was also greater in 2000 (figure 6.85). At Mt Dundas,

leaf area was affected by altitude, with smaller leaves at higher elevations (ANOVA, $F_{2, 297} = 31.00$, $P < 0.0001$) (figure 6.86). The post hoc Tukey test showed that mean leaf area differed between all three altitudes.

6.3.1.2 *N. gunnii* Leaf Areas

For *N. gunnii* there was only a weak influence of region on mean leaf area (ANOVA, $F_{1, 1298} = 4.28$, $P = 0.0387$), the southern leaves having the larger mean leaf area, but there was a similar variation in leaf size in the two regions (figure 6.87).

There was significant difference in mean leaf area between the three sites sampled in autumn 1998 (ANOVA, $F_{2, 597} = 97.52$, $P < 0.0001$), Lake Skinner having the largest; while King William had the smallest mean leaf area and the smallest variation in leaf size (figure 6.88). A linear regression suggests that site altitude has a weak but significant negative effect on leaf area for *N. gunnii* (cutoff $r^2 = 0.245$, $p < 0.0001$) (figure 6.89). At the same three sites in autumn 1998, sampling aspect (north- or south- facing) was found to have differing influence on mean leaf area. The most marked effect occurred at Lake Skinner (ANOVA, $F_{1, 198} = 13.08$, $P = 0.0004$), where the north-facing leaves had the larger mean leaf area, but the variation in leaf size was similar for both aspects (figure 6.90). At King William the north-facing leaves also had the larger mean leaf area, but the effect was weaker (ANOVA, $F_{1, 198} = 7.10$, $P = 0.0084$) than at Lake Skinner, and the variation in leaf size was greater in the north-facing leaves than in the south-facing leaves (figure 6.91). The reverse occurred at Lake Fenton, the effect was weak (ANOVA, $F_{1, 198} = 7.41$, $P = 0.0071$), but the south-facing leaves had the larger mean area and the greater variation in leaf size (figure 6.92).

An additional sample was collected from the King William leaf litter in late autumn 2000. Comparison with the autumn 1998 sample revealed a significant difference between the mean leaf areas (ANOVA, $F_{1, 298} = 88.58$, $p < 0.0001$), the 2000 litter sample (kw6) having the larger mean leaf area and greater variation in leaf size than the earlier sample (kw1) (figure 6.93).

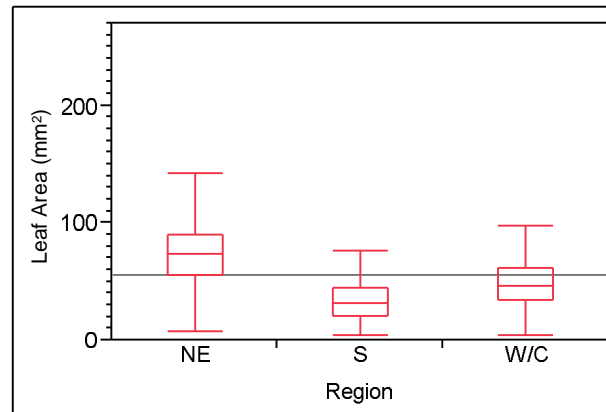


Figure 6.80. Boxplot of *N. cunninghamii* leaf area (mm²) by region: 13 sites, 1998-2001. NE; North East; S: South; W/C: West/Central.

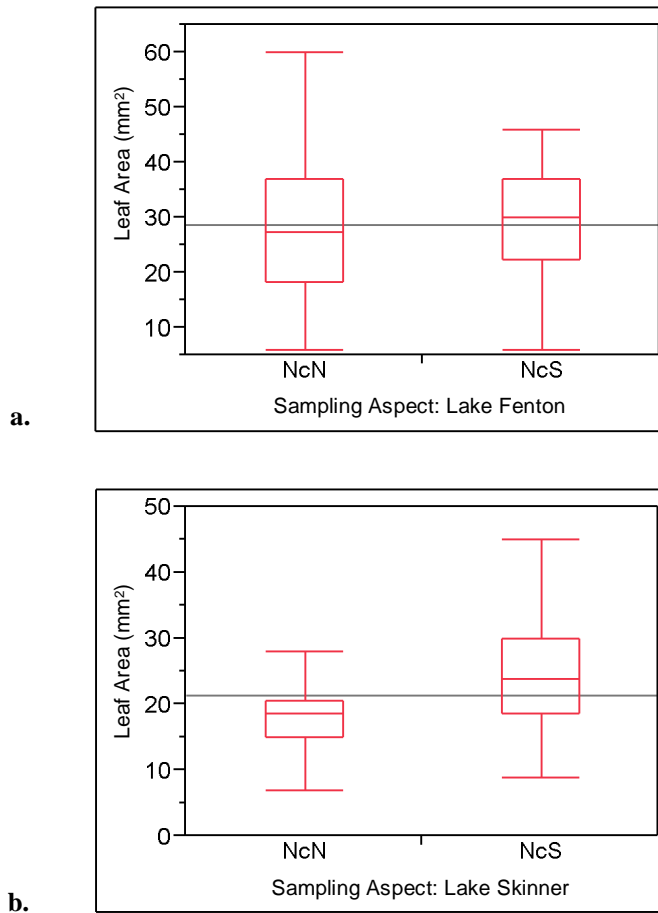


Figure 6.81. Boxplots of *N. cunninghamii* leaf area (mm²) by sampling aspect and site, autumn 1998. a. Lake Fenton, b. Lake Skinner. NcN: north-facing leaves; NcS: south-facing leaves.

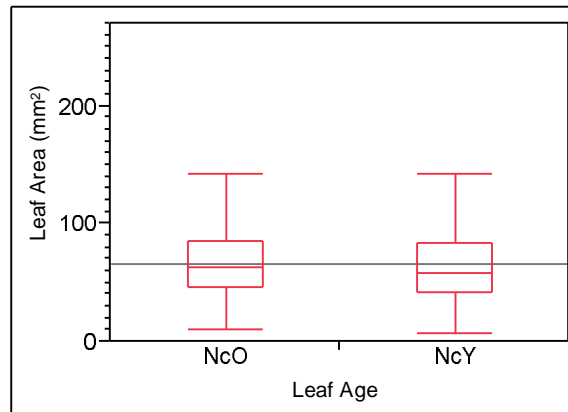


Figure 6.82. Boxplot of *N. cunninghamii* leaf area (mm²) by leaf age: 8 sites, 1999-2001. NcO: old leaves; NcY: young leaves.

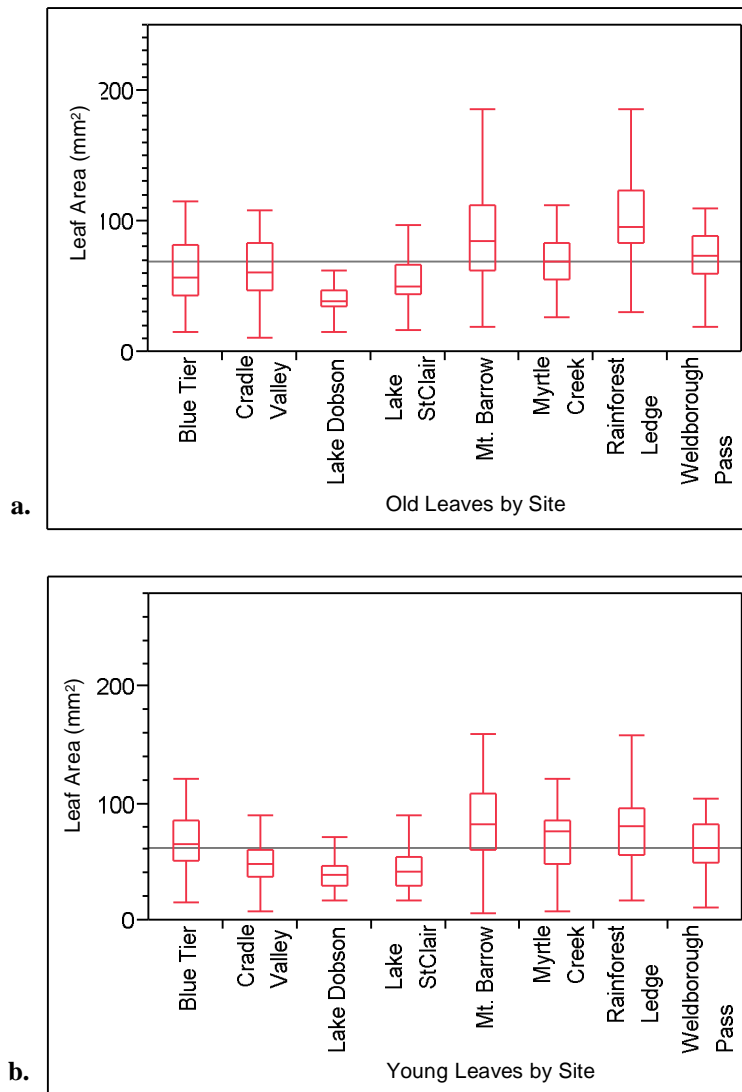


Figure 6.83. Boxplots of *N. cunninghamii* leaf area (mm²) by leaf age and site, 1999-2001. a. old leaves, b. young leaves

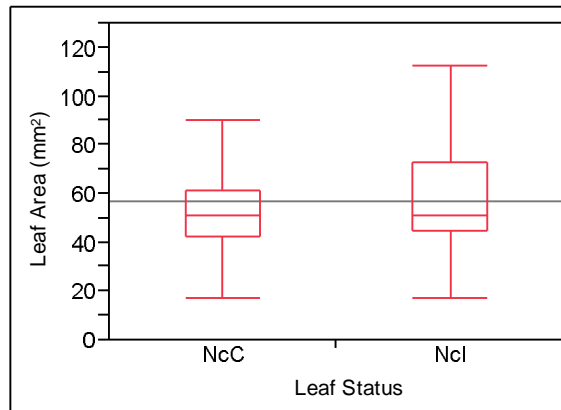


Figure 6.84. Boxplot of *N. cunninghamii* leaf area (mm²) by leaf status at Meander Forest, 2001. NcC: chewed leaves; NcI: intact leaves.

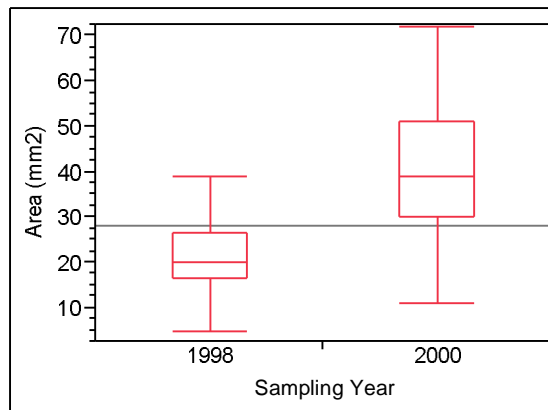


Figure 6.85. Boxplot of *N. cunninghamii* leaf area (mm²) by sampling year at Lake Skinner.

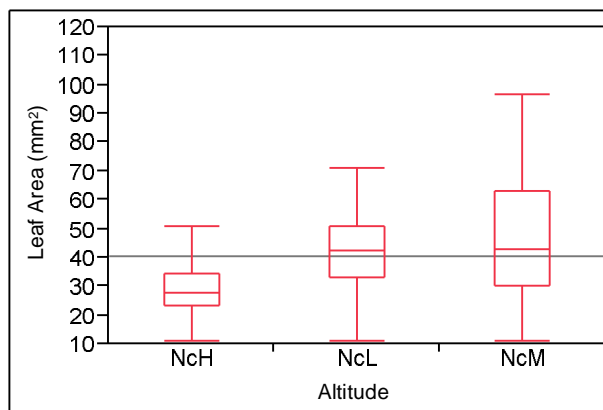


Figure 6.86. Boxplot of *N. cunninghamii* leaf area (mm²) by altitude at Mt. Dundas, 2000. NcH: high (900m); NcL: low (260m); NcM: mid (615m).

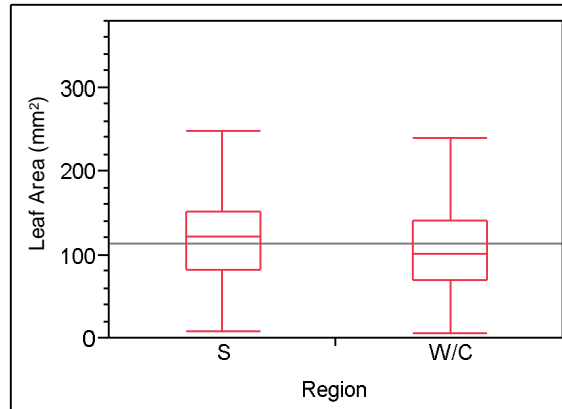


Figure 6.87. Boxplot of *N. gunnii* leaf area (mm²) by region: 10 sites, 1998-2002. S: South; W/C: West/Central.

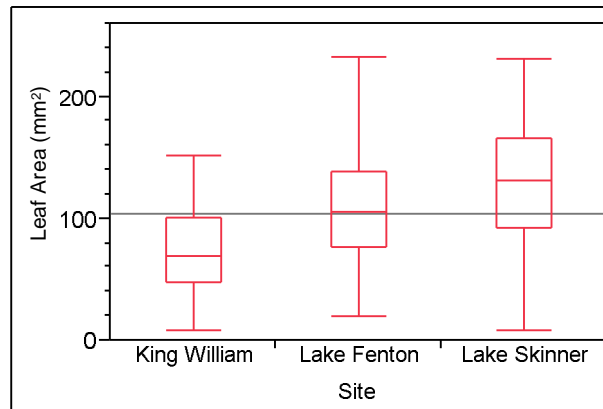


Figure 6.88. Boxplot of *N. gunnii* leaf area (mm²) by site, autumn 1998.

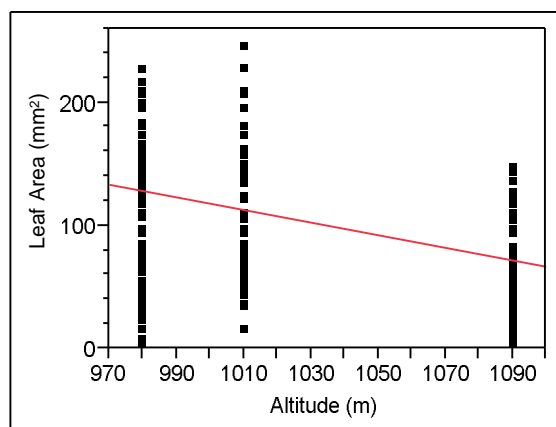


Figure 6.89. Bivariate fit of *N. gunnii* leaf area (mm²) by site altitude, 1998: Lake Skinner (980m), Lake Fenton (1010m) and King William (1090m) .

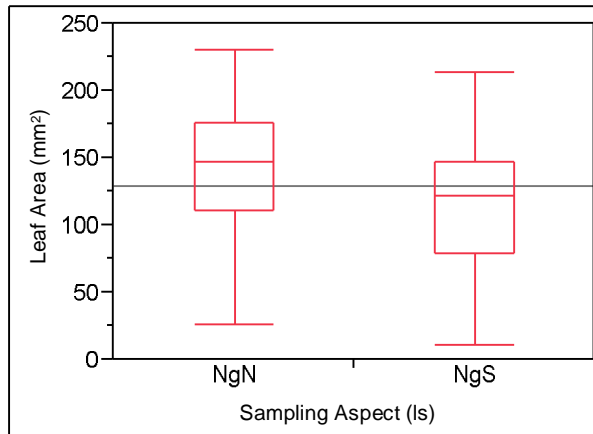


Figure 6.90. Boxplot of *N. gunnii* leaf area (mm²) by sampling aspect at Lake Skinner (ls), autumn 1998. NgN: north-facing leaves; NgS: south-facing leaves.

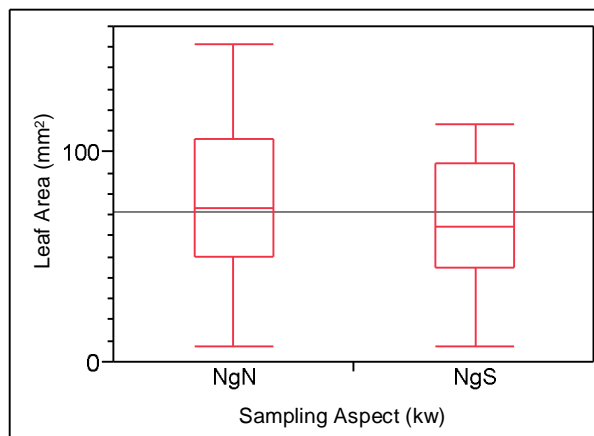


Figure 6.91. Boxplot of *N. gunnii* leaf area (mm²) by sampling aspect at King William (kw), autumn 1998. NgN: north-facing leaves; NgS: south-facing leaves.

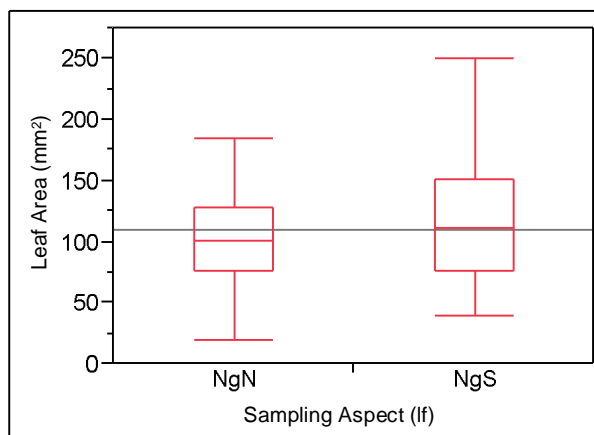


Figure 6.92. Boxplot of *N. gunnii* leaf area (mm²) by sampling aspect at Lake Fenton (lf), autumn 1998. NgN: north-facing leaves; NgS: south-facing leaves.

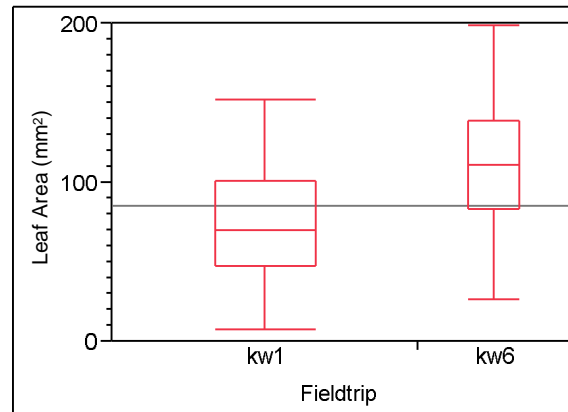


Figure 6.93. Boxplot of *N. gunnii* leaf area (mm²) by fieldtrip/sampling year at King William. kw1: autumn 1998; kw6: autumn 2000 litter sample.

6.3.2 *Hole growth*

For both *Nothofagus* species, there was considerable variation between sites in the patterns and rates of hole and leaf growth. This occurred in both the 1999-2000 and the 1998-1999 sampling periods.

In the first month at all the *N. cunninghamii* sites, the mean hole diameter showed an increase of up to 17% (maximum 0.26 mm at Lyrebird Walk, December 1999) from the initial hole puncture of 1.5 mm (figures 6.94.a, 6.96a). Thereafter, the patterns of the *N. cunninghamii* mean hole diameters, and hole areas, varied considerably, plateauing at Lyrebird Walk, tailing off at Lake Fenton and Mt Arthur, or increasing at Lake Skinner and Lake Dobson (figure 6.94.a, b). The *N. cunninghamii* mean leaf lengths also showed the greatest increase in the first month of sampling (by up to 25% at Lyrebird Walk, December 1999), then levelled off at each site except at Lake Fenton and Lake Skinner in 1999-2000 (figure 6.94.c, 6.96.c). The increases in mean leaf areas in 1999-2000 matched the increases in mean leaf lengths at Lyrebird Walk and Lake Skinner, but not at Lake Fenton, Lake Dobson and Mt Arthur (figure 6.94.c, d). The control and hole-punched leaves at Lyrebird Walk showed a similar pattern of growth in both mean lengths and areas (figure 6.94.a, b). Finally, comparison of the rates of hole growth to leaf growth at each *N. cunninghamii* site, when plotted as the ratio of mean hole diameter to mean leaf length, and the ratio of mean hole area to mean leaf area, revealed variation over time at each site and between the sites (figure 94.e, f; 6.96.e).

For *N. gunnii* in both sampling years, the increases in mean hole diameters and mean hole areas, had the greatest increase in the first month and were variable thereafter at each site except Lake Skinner (figure 6.95.a, b; 6.96.b). Unlike *N. cunninghamii*, the rates of increase in *N. gunnii* mean leaf lengths and mean leaf areas were similar at all sites, for hole-punched and control leaves (figure 6.95.c, d; 6.96.d). The rates of hole growth to leaf growth for *N. gunnii* revealed less marked variation over time compared with *N. cunninghamii* in both sampling years, especially at Lake Fenton (figure 6.96.e, f).

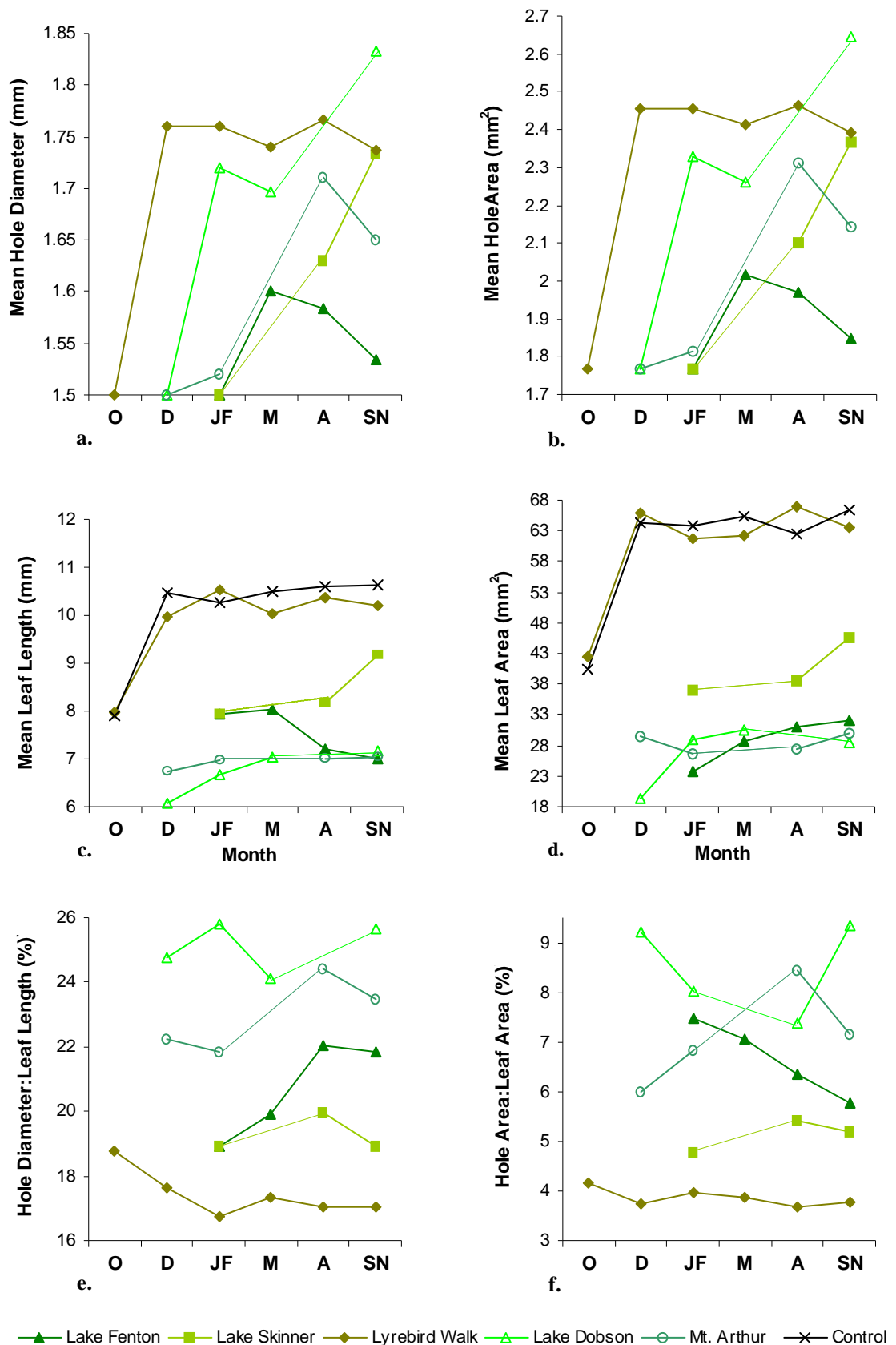


Figure 6.94. *N. cunninghamii* 1999-2000 cumulative hole growth record. Means of up to 5 leaves, with a 1.5mm diameter hole punched in the lamina, from 5 sites, plus control tagged but unpunched leaves: a. Hole diameter (mm), b. Hole area (mm²), c. Leaf length (mm), d. Leaf area (mm²); and ratios of : e. Hole diameter to leaf length (%), f. Hole area to leaf area (%). Recording month on x-axes: O: October 1999; D: December 1999; JF: late January/early February 2000; MA: early March/early April 2000; SN: September/November 2000.

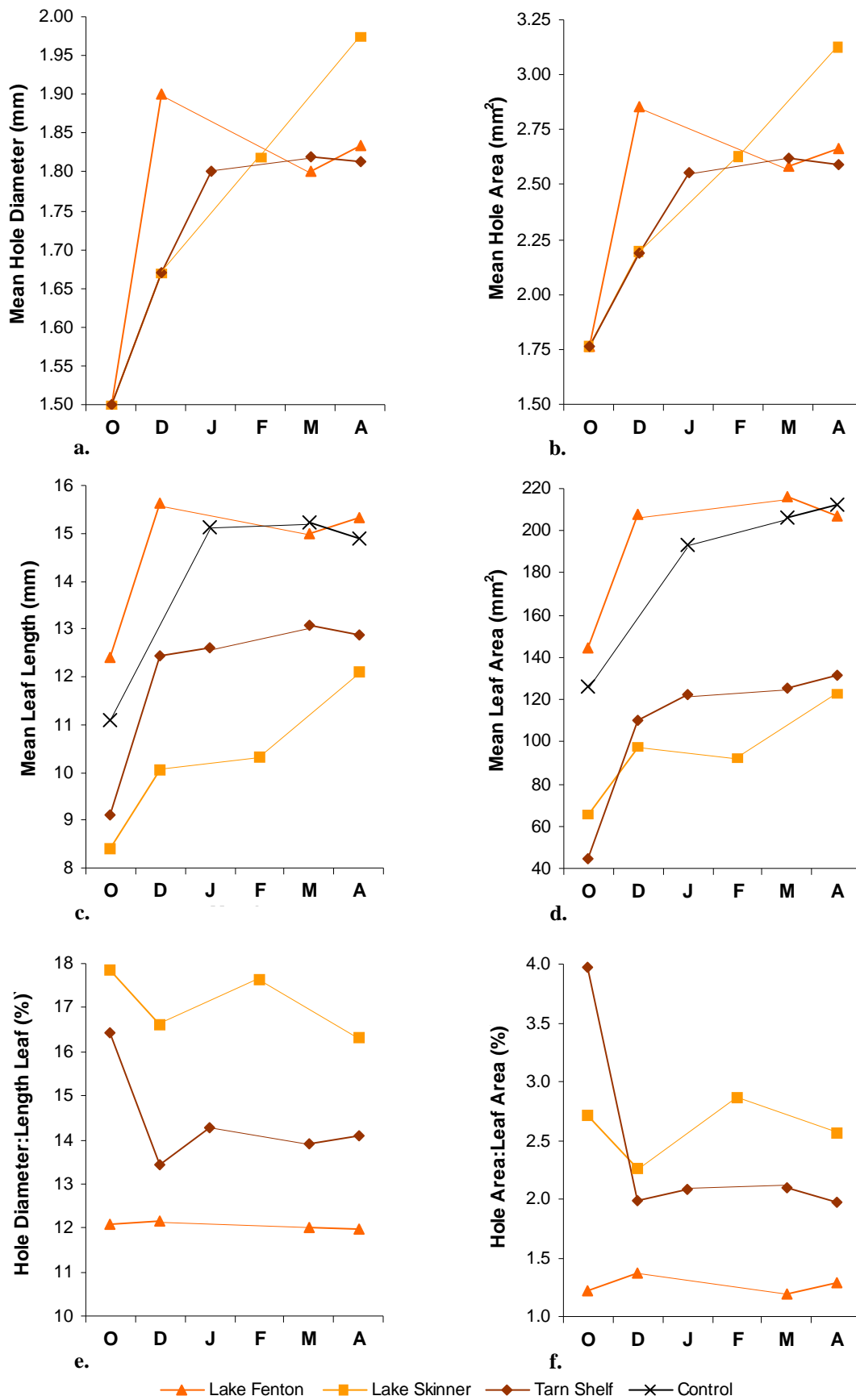


Figure 6.95. *N. gunnii* 1999-2000 cumulative hole growth record. Means of up to 5 leaves, with a 1.5mm diameter hole punched in the lamina, from 3 sites, plus control tagged but unpunched leaves: a. Hole diameter (mm), b. Hole area (mm²), c. Leaf length (mm), d. Leaf area (mm²); and ratios of : e. Hole diameter to leaf length (%), f. Hole area to leaf area (%). Recording month on x-axes: O: October 1999; D: December 1999; J: January 2000; F: February 2000; M: March 2000; A: April 2000.

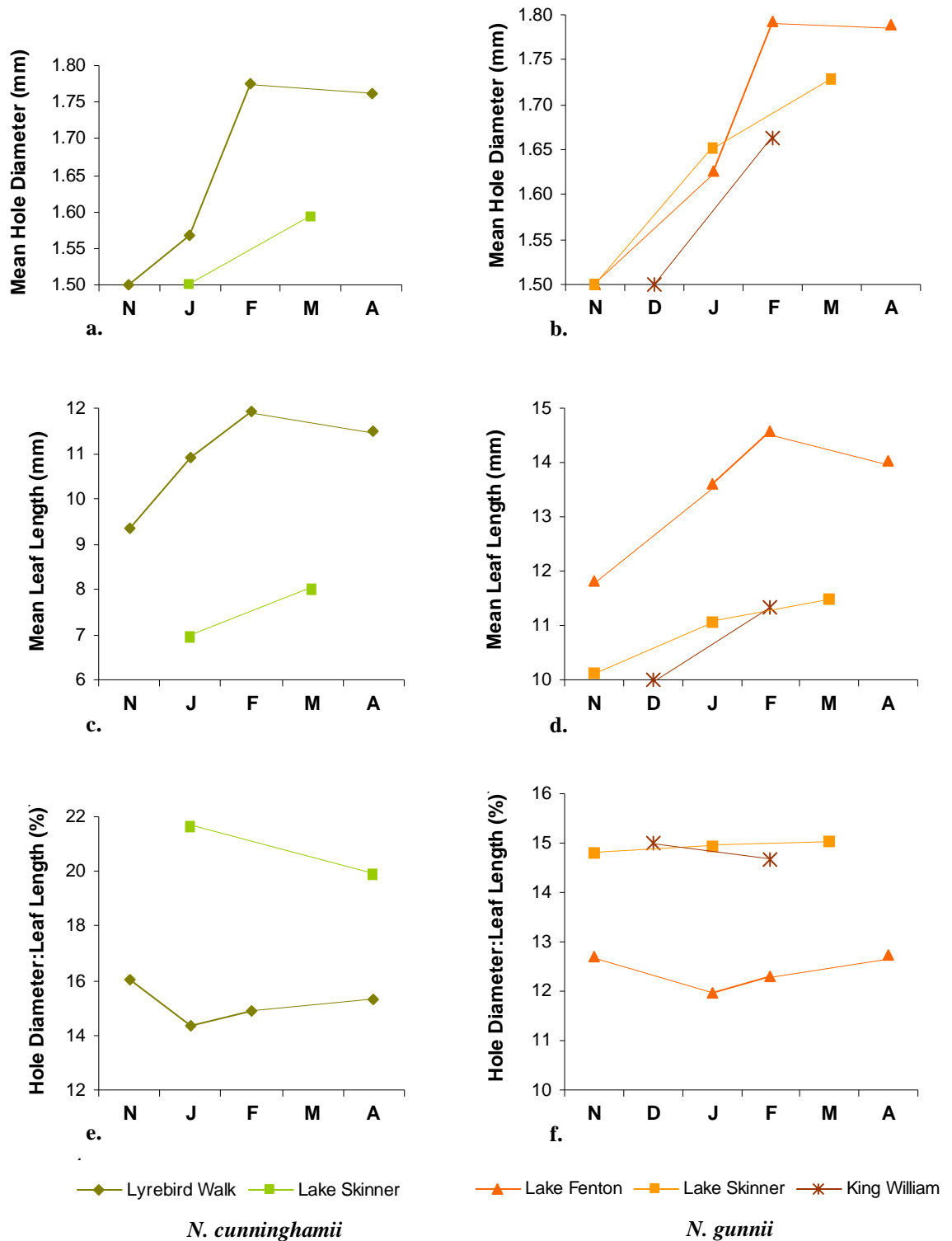


Figure 6.96. *N. cunninghamii* and *N. gunnii* 1998-1999 cumulative hole growth record. Means of up to 5 leaves, with a 1.5mm diameter hole punched in the lamina, from 2 sites for *N. cunninghamii* (left) and 3 sites for *N. gunnii* (right): a, b. Hole diameter (mm); c,d. Hole area (mm²); and e, f. Ratio of hole diameter to leaf length (%). Recording month on x-axes: N: November 1998; D: December 1998; J: January 1999; F: February 1999; M: March 1999; A: April 1999.

6.4 NON-CHEWING LEAF FEATURES

Erineum - the leaf feature caused by eriophyid mites (Acarina, Prostigmata, Eriophyoidea) - was found on both *N. cunninghamii* (figure 6.97.a, b) and *N. gunnii* (figure 6.97.c, d) -and the incidence on each is documented in section 6.4.1. The other leaf features, documented in section 6.4.2, were found only on *N. cunninghamii*: single eggs laid by flies; leaf galls (figure 6.97.e, f) due to mites; leaf mines (figure 6.97.g) caused by early instar moth larvae of the genus *Cyphosticha* (Gracillariidae); leaf ties (figure 6.97.h) created by moth larvae of Gracillariidae or Tortricidae; scale insects (Hemiptera, Eriococcidae and Pseudococcidae), both the numerous small male lerps and the large solitary females (figure 6.97.i); and sooty mould, which develops on the secretions of the scale insects.

6.4.1 Erineum: *N. cunninghamii* and *N. gunnii*

6.4.1.1 Erineum: *N. cunninghamii*

Of the 1999-2001 total of 22,275 *N. cunninghamii* leaves examined for erineum, nearly 500 (2.23%) showed evidence of the feature, the incidence on the young leaves being 2.37% (284 of 11,973 leaves), while the incidence on the old leaves was 2.07% (213 of 10,302 leaves) (figure 6.98).

The *N. cunninghamii* Region/Season data subset (Sampling Set 2, table 4.2) yielded an overall incidence of erineum of less than 1% on the young leaves (97 of 10,952 leaves). This incidence differed between regions, being highest at the West/Central sites (1.59%: 61 of 3,847 leaves) and lowest in the North East (0.13%: 4 of 3,168 leaves) (figure 6.99.a). The overall seasonal incidence for the young leaves increased from less than 0.5% (17 of 4,114 leaves) in spring 1999, to just over 0.5% (21 of 4050 leaves) in summer 1999-2000 to a little over 2% (59 of 2788 leaves) in autumn 2000 (figure 6.99.b). The seasonal incidence varied between the regions: the lowest incidence occurring in spring for the South and West/Central, and in the summer for the North West; while the highest incidence occurred in the autumn for the North West, South and West/Central (figure 6.99.c). The incidence for the North East was very low throughout.

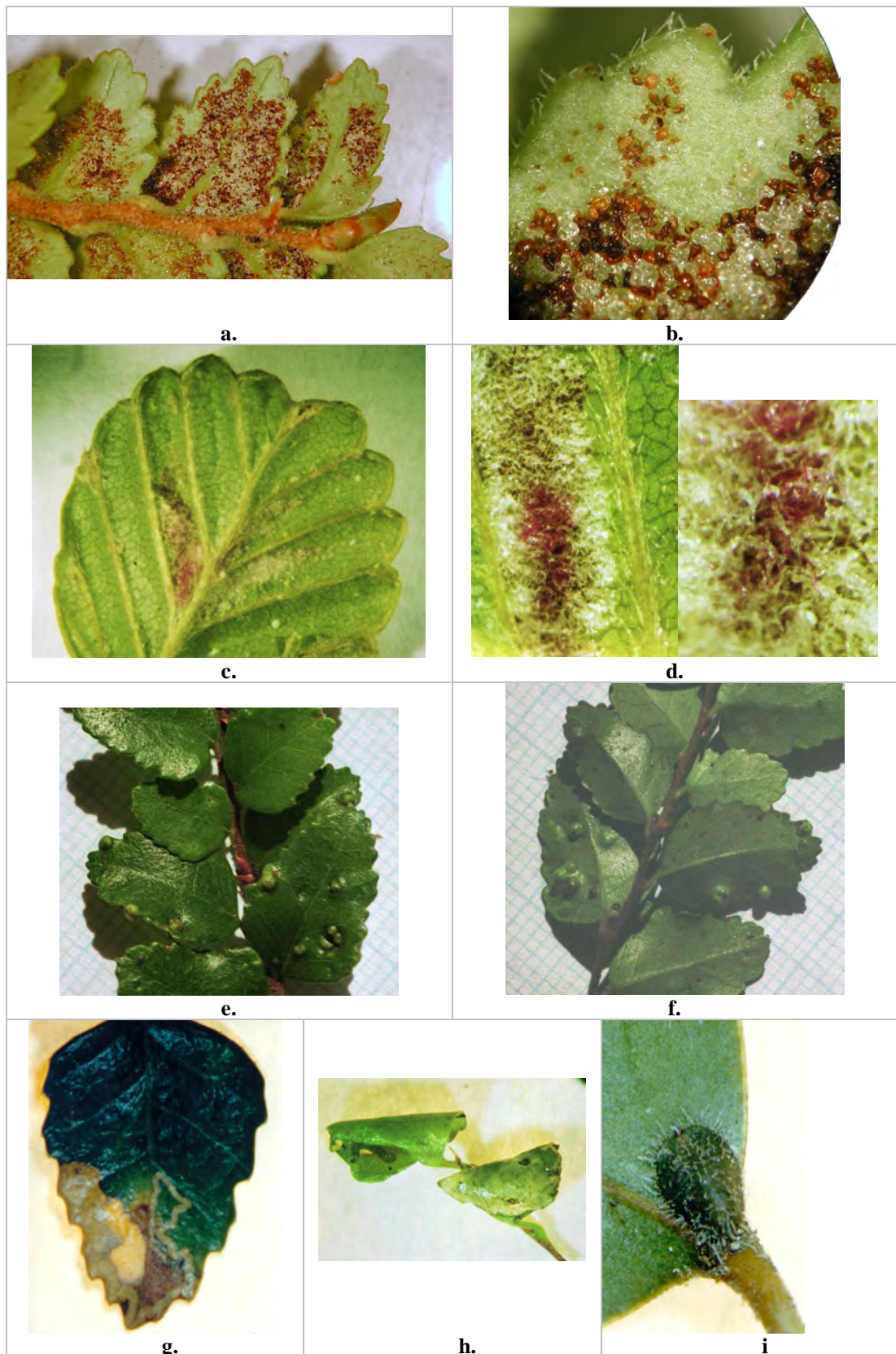


Figure 6.97. a - i . Non-Chewing Leaf Features.

Erineum on the underside of *N. cunninghamii* leaf (a) and detail (b). Erineum on the underside of *N. gunnii* leaf (c) and details (d).

Other *N. cunninghamii* leaf features: galls on upper leaf surfaces (e) and underside of same leaves (f); leaf mine of moth larva, *Stigmella* spp. (g); tied leaves of torricid moth larva (h); female scale insect (Eriococcidae) at base of leaf (i).

At the seven sites (from North East, North West and West/Central) where seasonal sampling was applied to both young and old leaves, overall the highest incidence of erineum was found to be in the spring on the old leaves as compared with the autumn for the young leaves (figure 6.100). However, when the incidence of erineum on the young and old leaves was compared by site, the results can be seen to be skewed by considerably higher incidences on the young leaves in the autumn at Tayatea Bridge (8.33%) and Lake St Clair (4.59%); and on the old leaves in the spring at Weldborough Pass (14.5%) and Cradle Valley (7.87%) (figure 6.101.a, b).

At the five Southern sites there was considerable variation in the incidence of erineum on the young leaves, varying from no erineum throughout the sampling at Mt Arthur, to 22% in September 2000 at Lake Dobson (figure 6.102). For the old leaves in Spring 2000, the incidence of erineum ranged from less than 0.5% at Mt Arthur to over 14% at Lake Skinner (figure 6.103).

Comparison of the *N. cunninghamii* all leaf age samples from autumn 1998 and autumn 2000, at Lake Fenton, Lake Skinner and Lyrebird Walk, revealed wide variation in the incidence of erineum, between years and between sites. An overall total of 22,949 leaves were examined, revealing an overall incidence of erineum of 1.17%, however the incidence in autumn 2000 was 5.55% (126 of 2,272 leaves) compared with 0.69% (268 of 20,677 leaves) in autumn 1998 (figure 6.104.a). The incidence of erineum in autumn 2000 varied from 0.12% (1 of 848 leaves) at Lake Fenton, to 11.64% (69 of 593 leaves) at Lake Skinner; but in autumn 1998 the incidence varied from 0.02% (2 of 11,664 leaves) at Lake Skinner, to 3.48% (124 of 3,561 leaves) at Lyrebird Walk (figure 6.104.b). Leaf age was not documented at Lake Fenton in autumn 1998, and so the leaf age sampling year comparison is for two sites: Lake Skinner and Lyrebird Walk. The combined incidence of erineum is at similar levels for both old and young leaves in each sampling year, but for both leaf ages the incidence is considerably higher in autumn 2000 (young 9.23%, 77 of 834 leaves; old 8.14%, 48 of 590 leaves) compared with autumn 1998 (young 0.57%, 23 of 4,050 leaves; old 0.4%, 27 of 6,671 leaves) (figure 6.105). In autumn 2000, Lake Skinner had a higher incidence of erineum in both young and old leaves compared with Lyrebird Walk, however in autumn 1998 the reverse had occurred (figure 6.105).

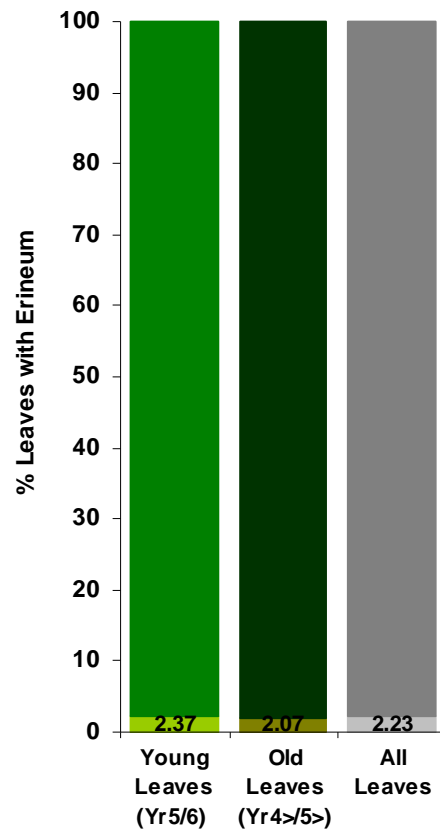


Figure 6.98. 1999-2001 percentages of *N. cunninghamii* young, old and total leaves with erineum, from 16 sites. Yr6: 2000-2001 young leaves; Yr5: 1999-2000 young leaves. Yr5>: 1999 leaves and older; Yr4>: 1998 leaves and older.

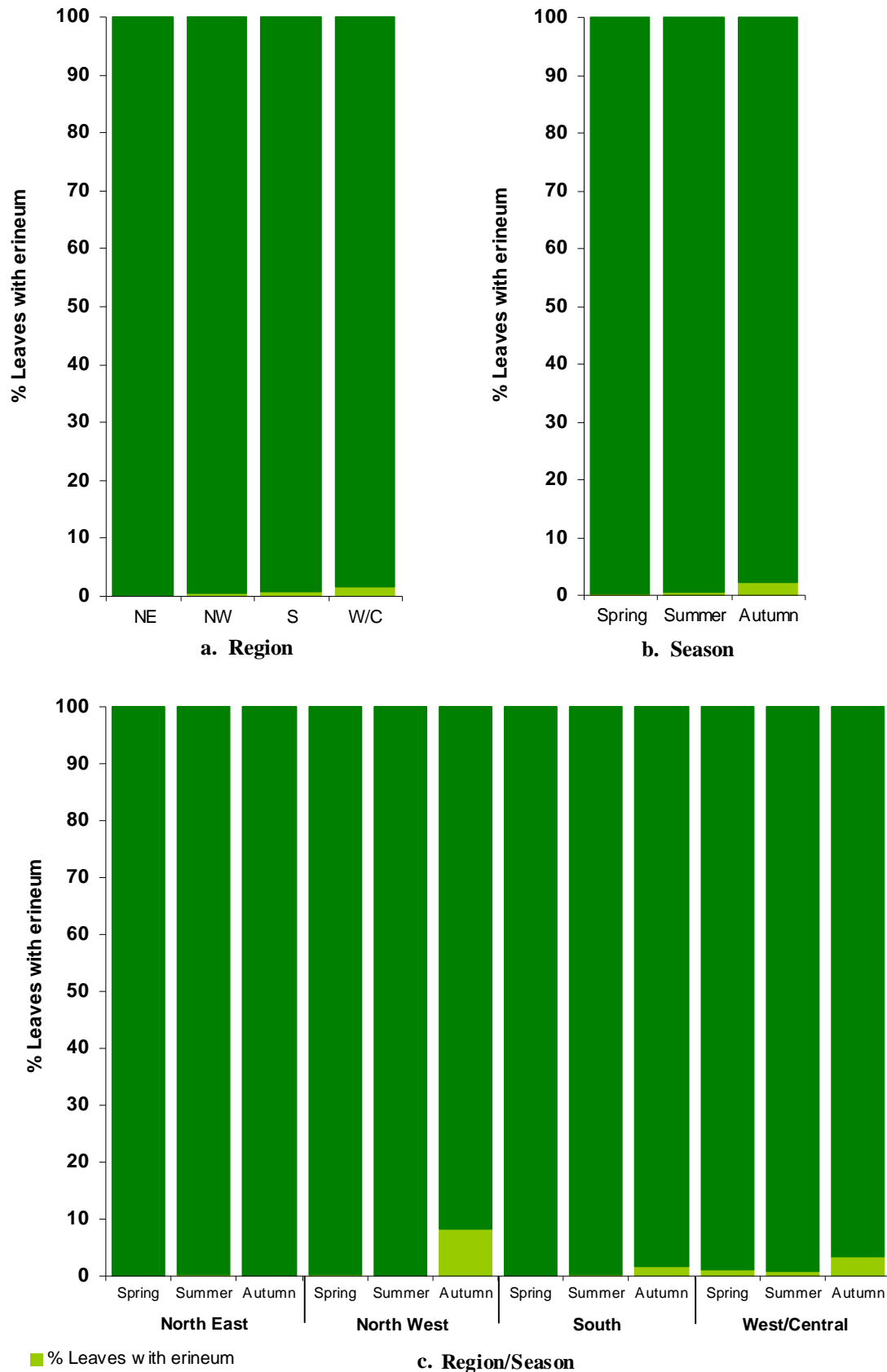


Figure 6.99. a – c. 1999-2000 Percentages of *N. cunninghamii* young leaves with erineum by region (a), season (b), region and season (c), from 12 sites: Blue Tier, Mt Barrow, Weldborough Pass (North East); Tayatea Bridge (North West); Lake Dobson, Lyrebird Walk, Lake Fenton, Mt Arthur (South); Cradle Valley, Mt Dundas, Lake St Clair (West/Central).

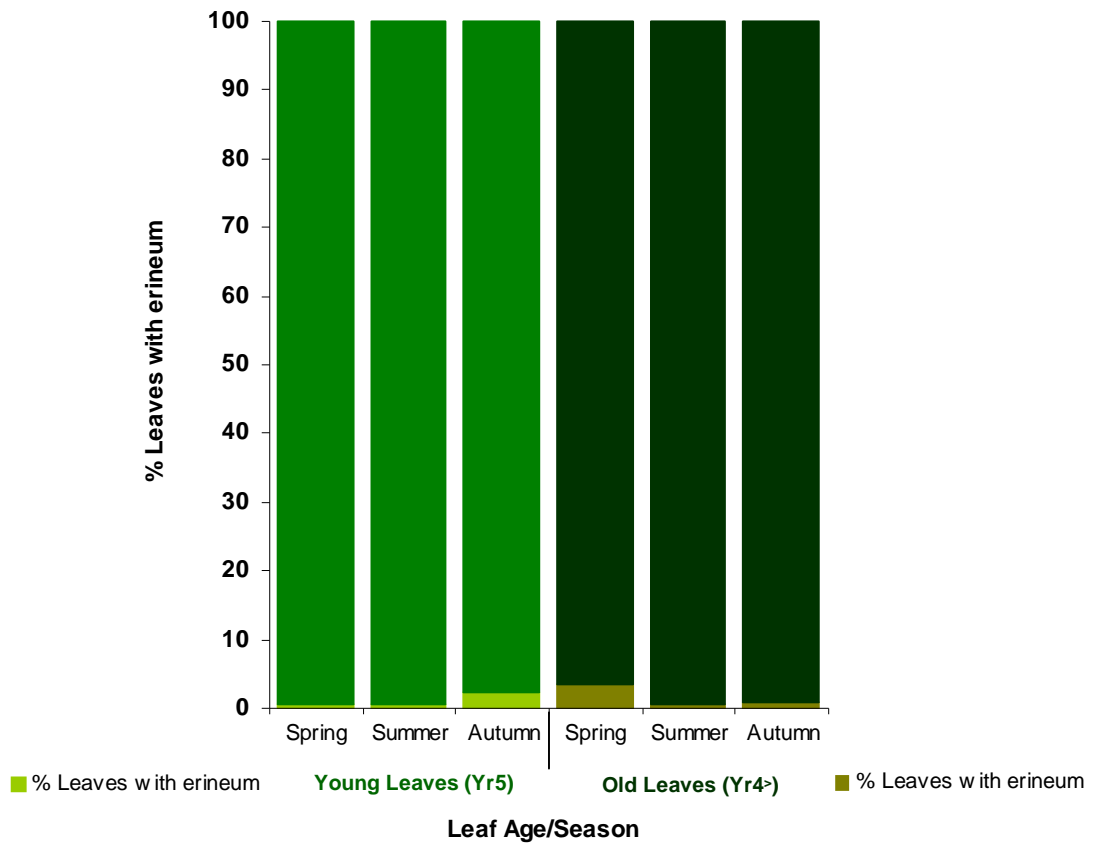


Figure 6.100. 1999-2000 Percentages of *N. cunninghamii* young and old leaves with erineum by season, from 7 sites: Blue Tier, Mt Barrow, Weldborough Pass, Tayatea Bridge, Cradle Valley, Mt Dundas, Lake St Clair.

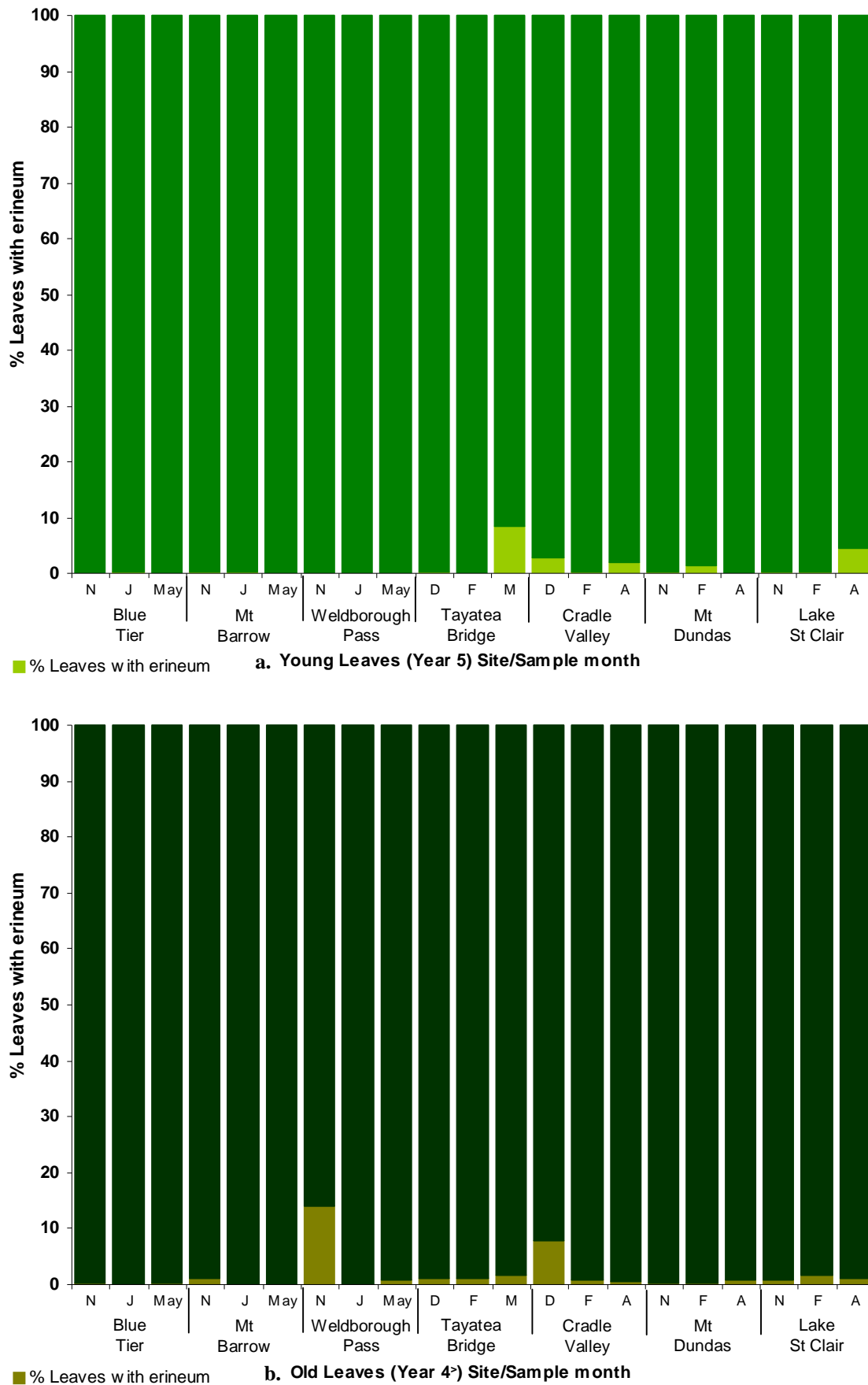


Figure 6.101. a & b. 1999-2000 Percentages of *N. cunninghamii* young leaves (a) and old leaves (b) with erineum by site and sampling month, from 7 sites visited in spring, summer and autumn 1999-2000. Spring: November (N) and December (D) 1999; Summer: January (J) and February (F) 2000; Autumn: late March (M), April (A) and May 2000.

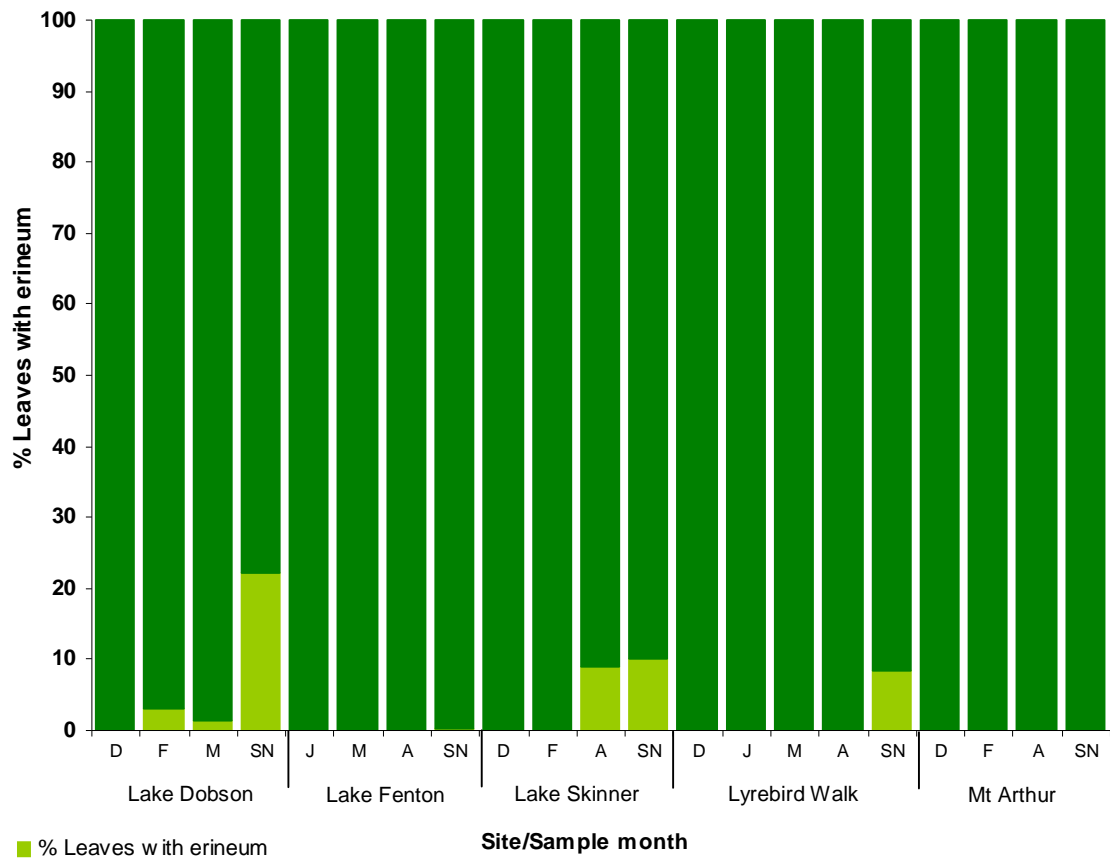


Figure 6.102. 1999-2000 Percentages of *N. cunninghamii* young leaves with erineum by site and cumulative sampling month, from 5 sites 1999-2000. November (N) or December (D) 1999; January (J) or February (F) 2000; early March (M) 2000; April (A) 2000; and September-November 2000.

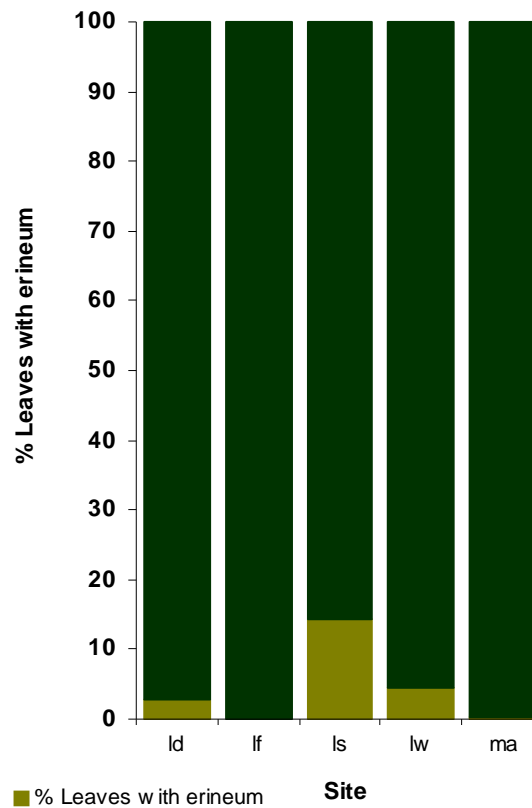


Figure 6.103. 1999-2000 Percentages of *N. cunninghamii* old leaves with erineum from the same five sites as figure 6.102, September-November 2000 sample only. ld: Lake Dobson; lf: Lake Fenton; ls: Lake Skinner; lw: Lyrebird Walk; ma: Mt Arthur

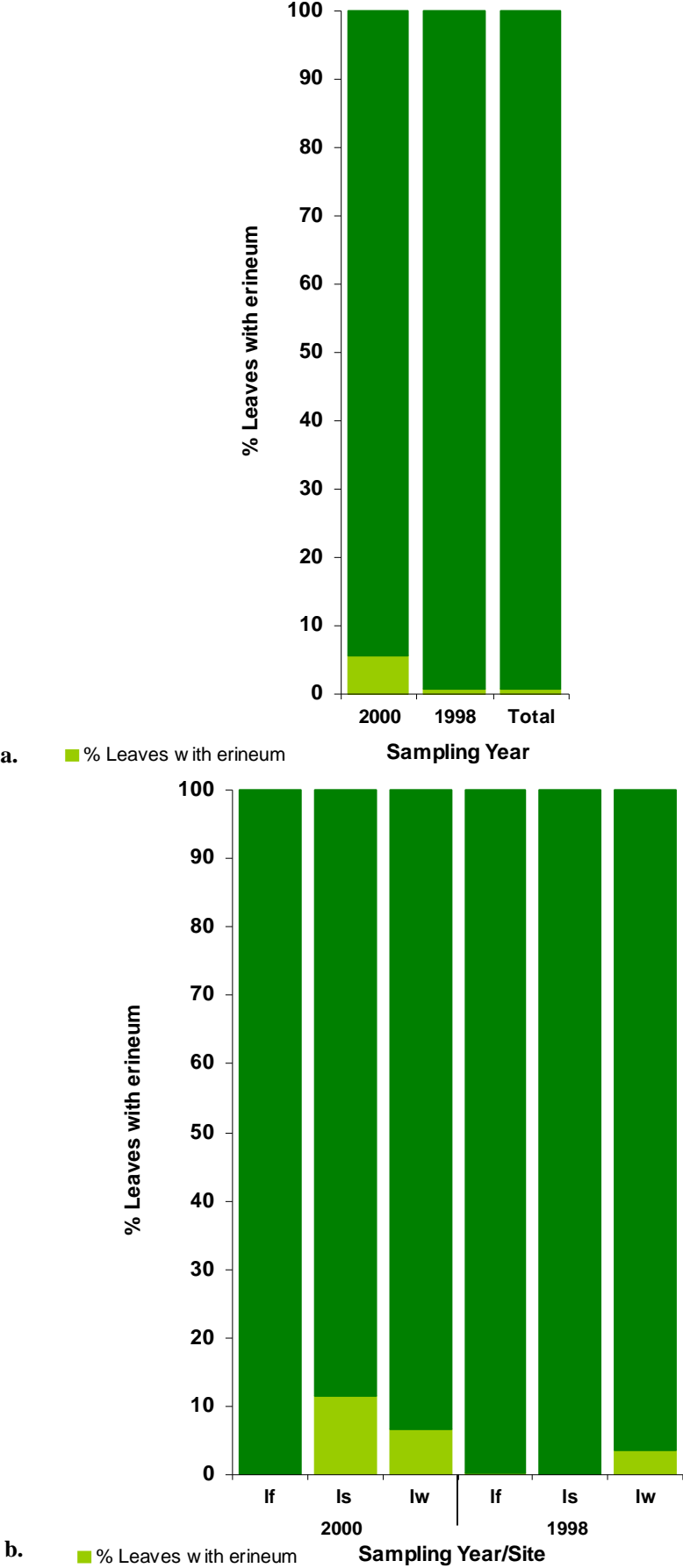


Figure 6.104. a & b. Percentages of *N. cunninghamii* leaves with erineum, 2-year comparison: all leaves for Autumn 2000 and Autumn 1998. a. year totals and combined total, and b. site comparison from Lake Fenton (lf), Lake Skinner (ls) and Lyrebird Walk (lw).

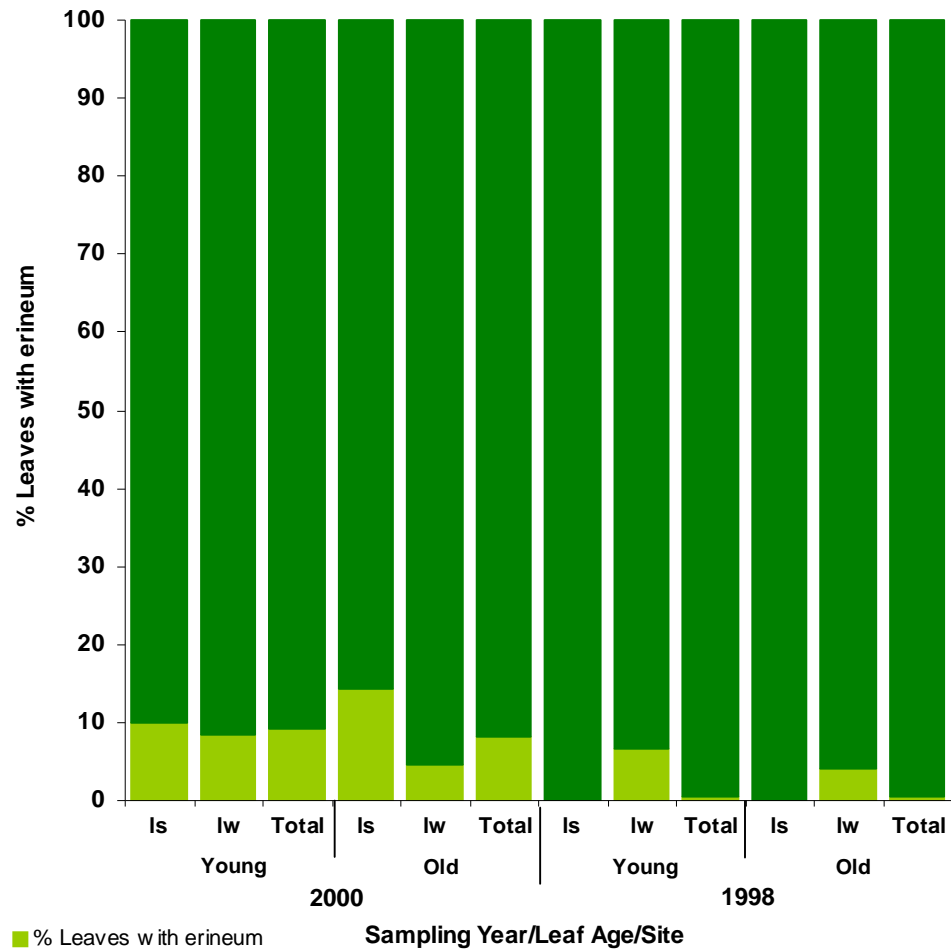


Figure 6.105. Percentages of *N. cunninghamii* leaves with erineum, 2-year leaf age comparison for 2 sites: young leaves, old leaves and combined total for Autumn 2000 and Autumn 1998 at Lake Skinner (Is) and Lyrebird Walk (Lw) .

6.4.1.2 Erineum: *N. gunnii*

During the sampling from 1998 to 2000, a total of 13,265 *N. gunnii* leaves examined for erineum, of which 1,872 (14.11%) displayed the feature. Although the incidence of erineum on *N. gunnii* was consistently higher than on *N. cunninghamii*, there was considerable variation in the *N. gunnii* levels of erineum between regions, seasons, sites, sampling aspects and sampling years.

The 1999-2000 Region/Season subset comprised a total of 4,918 leaves from *N. gunnii* branchlets, with an overall incidence of erineum of 14.78% (727 leaves); and the additional leaf litter samples had an incidence of erineum of 14% (42 of 300 leaves). The regional data revealed the South (22% with erineum, 440 of 2000 leaves) to have more than twice the incidence than West/Central (9.84% with erineum, 287 of 2918 leaves) (figure 6.106.a). The seasonal trend overall was for the spring incidence of erineum (5.29%), to have more than doubled by the summer (13.33%), and then to have doubled again by the autumn (27.99%) (figure 6.106.b). The incidence of erineum increased more steeply in the South (spring, 6.22%; summer, 17.10%; autumn, 46.4%) compared with West/Central (spring, 4.72%; summer, 10.19%; autumn, 16.1%) (figure 6.107). However, although almost half of the Southern leaves sampled in the autumn had evidence of erineum, by the following spring, just 14% of the leaves in the litter samples had erineum (figure 6.107).

The 1999-2000 erineum site data revealed an increase in levels of erineum, from the spring visits through to the autumn visits, at all sites except Mt Dundas and Little Plateau where the levels were steady through the sampling period, the autumn incidence of erineum ranging from 4% (9 of 231 leaves) at Little Plateau, to 60% (138 of 229 leaves) at Lake Fenton (figure 6.108.a, b). At each of the Southern sites, the incidence of erineum in the early spring leaf litter samples was considerably lower than those of the previous autumn (figure 6.108.a).

The overall incidence of erineum in 1998-1999 had also increased from spring through summer and into autumn, but there was wide variation between the sites (figure 6.109). As in 1999-2000, Lake Fenton had the highest incidence of erineum, although it rose abruptly from 5% in November 1998 to 33% in January 1999, then

remained at over 33% in February 1999 and April 1999; at Lake Skinner the increase was more modest (0, November 1998; 10% January 1999; 13%, March 1999); while at King William the incidence was less than 0.5% in February 1999 (in contrast to 12% in February 2000) (figure 6.110).

When the 1998-1999 sampling aspects were compared, the south-facing aspect (17.87%, 431 of 2,412 leaves) had a higher level of erineum than the north-facing (11.99%, 299 of 2494 leaves), however the highest incidence of erineum occurred on the adjacent aspect (33%, 217 of 656 leaves), this data being from two sites (Lake Fenton and Lake Skinner) rather than three (Lake Fenton, Lake Skinner and King William) (figure 6.111). Site comparison revealed a higher incidence of erineum on the south-facing than the north-facing leaves at Lake Fenton and Lake Skinner, but the reverse occurred at King William; and Lake Fenton (54%, 186 of 399 leaves) had a much higher incidence of erineum than Lake Skinner (9.78%, 31 of 317 leaves) on the adjacent leaves (figure 6.112).

The three-year (2000, 1999, 1998) autumn samples revealed a marked difference between the years in the levels of erineum, the highest being nearly 52% (205 of 396 leaves) in 2000; with 27% (395 of 1459 leaves) in 1999; and 14.5% (251 of 1727 leaves) (figure 6.113). This trend occurred at Lake Fenton, although at Lake Skinner 2000 (40%) had the highest incidence of erineum but 1998 (13.94%) was slightly higher than 1999 (12.96%) (figure 6.114).

6.4.1.3 *Erineum: N. cunninghamii and N. gunnii*

N. cunninghamii and *N. gunnii* co-occurred at three of the sites (Lake Fenton, Lake Skinner, Mt Dundas) sampled in 1999-2000, and the levels of erineum differed markedly between the two *Nothofagus* species. Overall, *N. cunninghamii* had an incidence of 1.62% (71 of 4385 leaves) compared with an incidence of 18.24% (577 of 3164 leaves) on *N. gunnii* (appendix). *N. cunninghamii* at Lake Fenton had fewer than 0.5% of leaves with erineum, Lake Skinner had a maximum of 10% in November 2000, and Mt Dundas had a maximum of less than 1.5% in February 2000; in comparison, *N. gunnii* reached a maximum of 60% in April 2000 at Lake Fenton, 40% in April 2000 at Lake Skinner, and nearly 11% in November 1999 at Mt Dundas (figure 6.115.a, b).

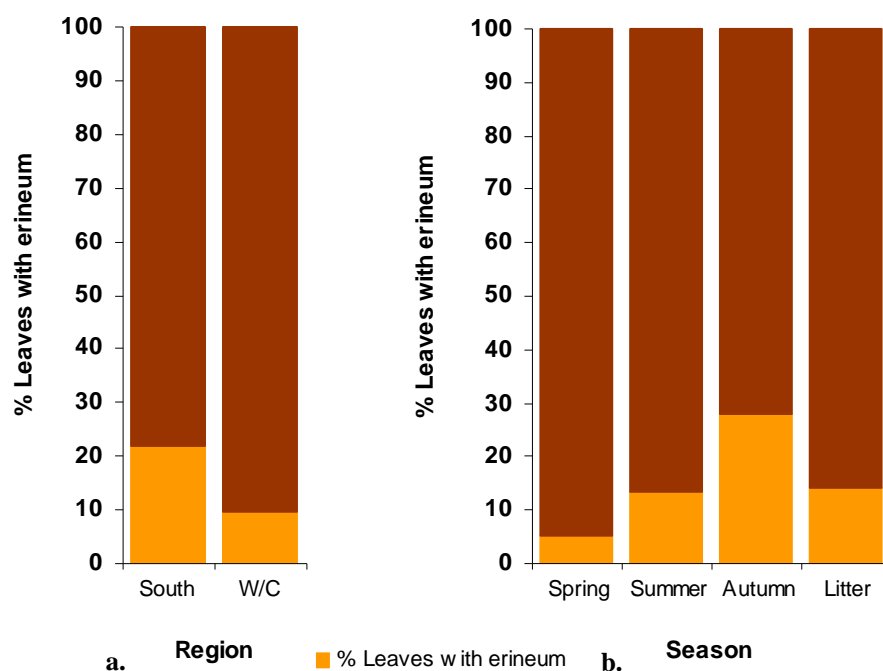


Figure 6.106. a & b. 1999-2000 percentages of *N. gunnii* leaves with erineum, from 7 sites.
a. Region: South: Lake Fenton, Lake Skinner, Tarn Shelf; and West/Central (W/C): King William, Mt. Dundas, Little Plateau, Crater Lake.
b. Season: Spring 1999, Summer 2000, Autumn 2000 and litter samples collected in spring 2000, from 3 sites (Lake Fenton, Lake Skinner, Tarn Shelf).

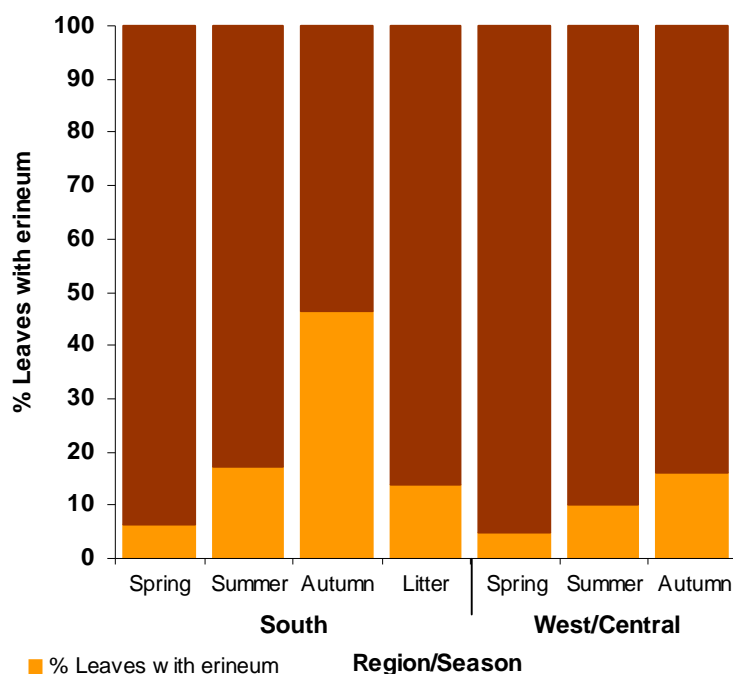
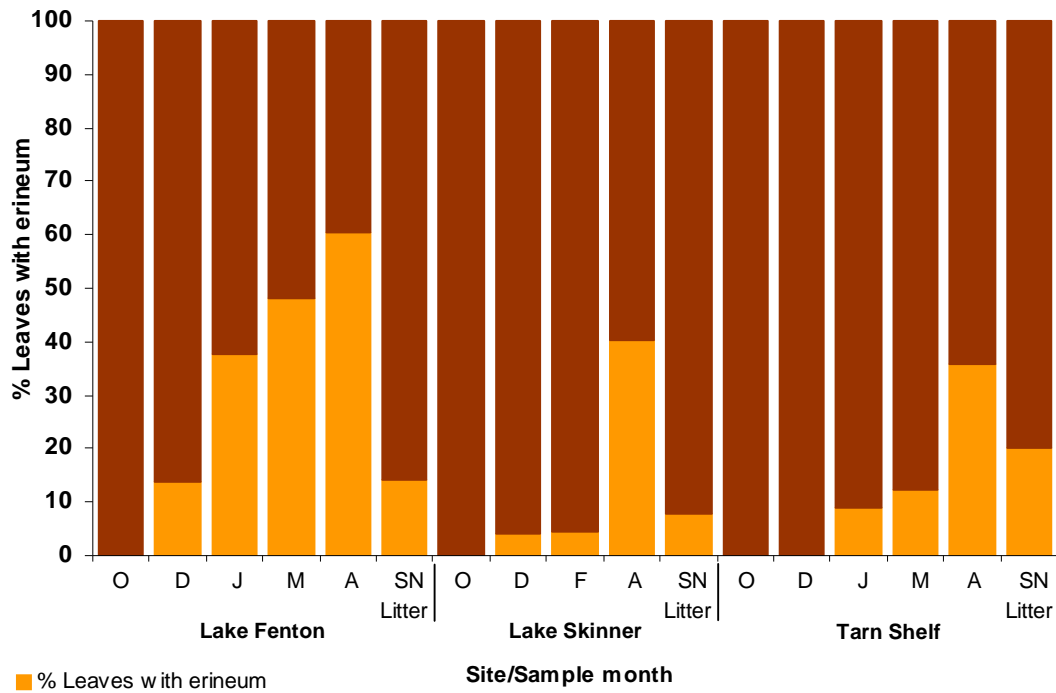
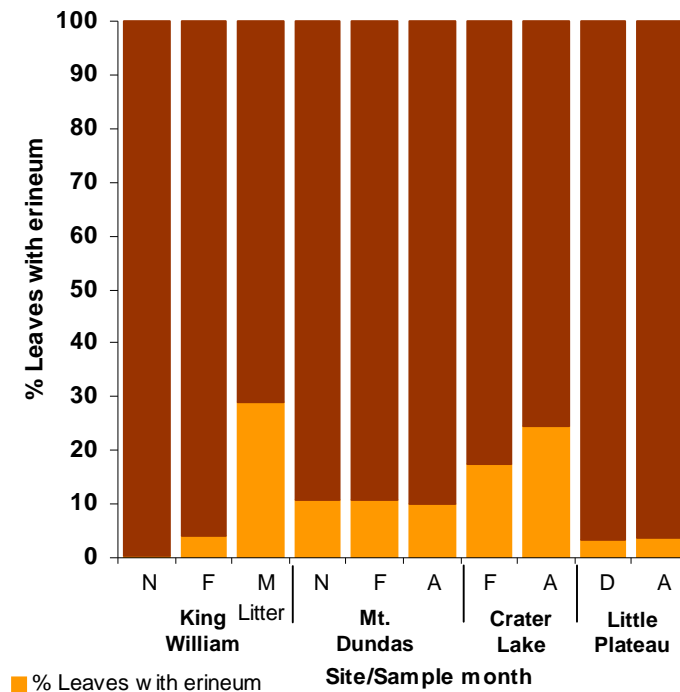


Figure 6.107. 1999-2000 Percentages of *N. gunnii* leaves with erineum, by region and season. South, 3 sites: Lake Fenton, Lake Skinner, Tarn Shelf: Spring 1999, Summer 2000, Autumn 2000 and Litter samples collected in spring 2000. West/Central, 4 sites: King William, Mt. Dundas, Little Plateau, Crater Lake: Spring 1999, Summer 2000, Autumn 2000.



a. Southern Sites



b. West/Central Sites

Figure 6.108. a & b. 1999-2000 Percentages of *N. gunnii* leaves with erineum over the sampling period November 1999 – November 2000, by site.

a. Southern sites, cumulative sampling: Lake Fenton, Lake Skinner, Tarn Shelf.

b. West/Central sites, discrete sampling: King William, Mt. Dundas, Little Plateau, Crater Lake.

N: Late November 1999; D: early December 1999; J: late January 2000; F: early February 2000; M: early March 2000; A: early April 2000; M Litter: May 2000 litter sample (King William only); SN Litter: September-November litter samples (Lake Fenton, Lake Skinner, Tarn Shelf).

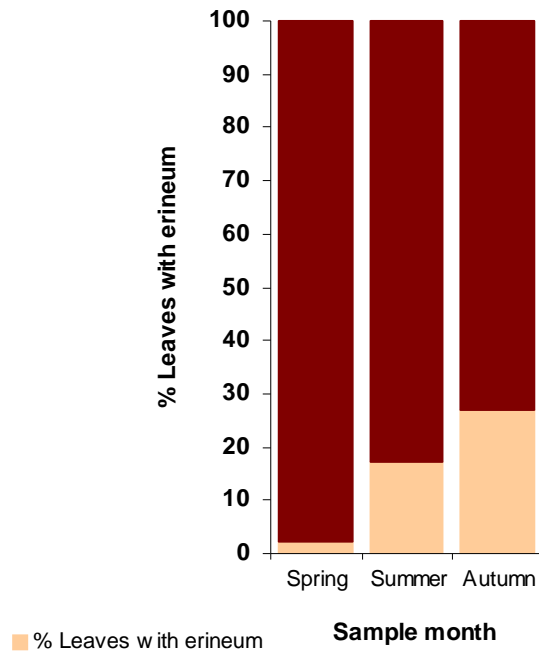


Figure 6.109. 1998-1999 Percentages of *N. gunnii* leaves with erineum by season: Spring 1998, Summer 1999, Autumn 1999, from 3 sites: Lake Fenton, Lake Skinner, King William.

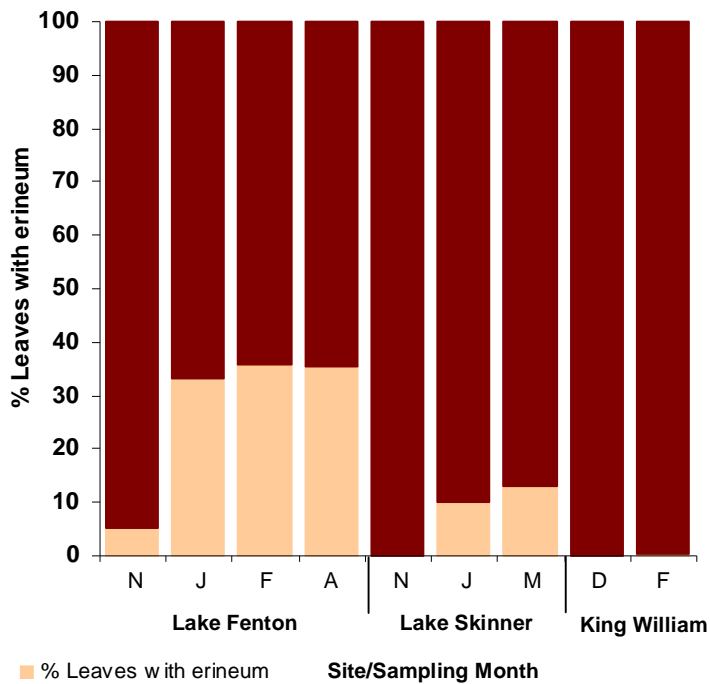


Figure 6.110. 1998-1999 Percentages of *N. gunnii* leaves with erineum over the sampling period November 1998 – April 1999, by site: Lake Fenton, Lake Skinner, King William. N: Late November 1998; D: early December 1998; J: January 1999; F: late February 1999; M: early March 1999; A: April 1999.

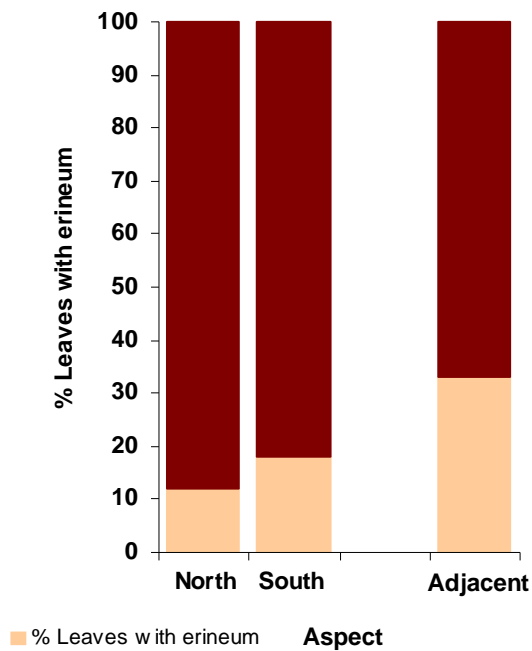


Figure 6.111. 1998-1999 Percentages of *N. gunnii* leaves with erineum): autumn 1998 and summer 1999, by sampling aspect. North-facing and South-facing aspects, at 3 sites: Lake Fenton, Lake Skinner and King William. Adjacent aspects of *N. gunnii* (next to *N. cunninghamii*) at two sites: Lake Fenton and Lake Skinner.

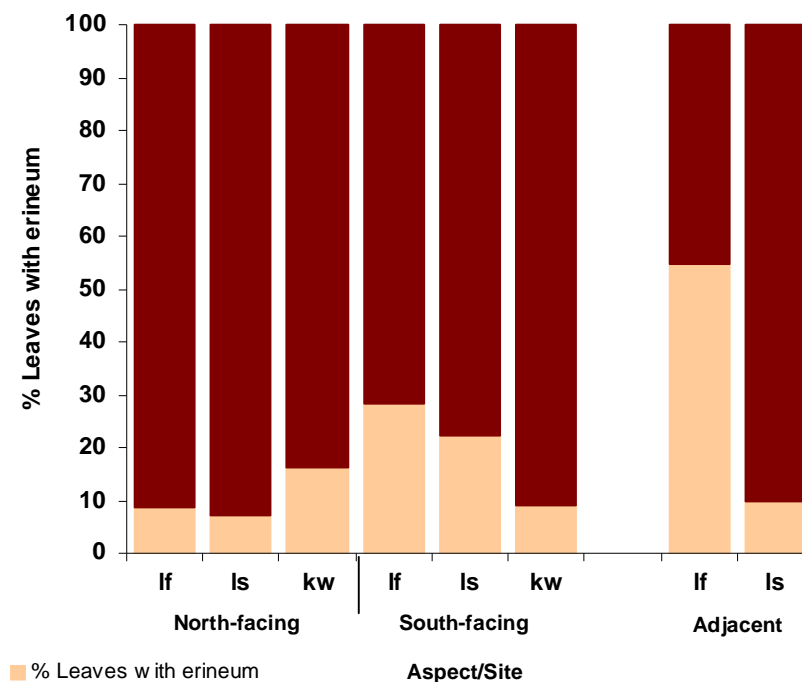


Figure 6.112. 1998-1999 Percentages of *N. gunnii* leaves with erineum: autumn 1998 and summer 1999, by sampling aspect and site. North-facing and South-facing aspects, at 3 sites: Lake Fenton, Lake Skinner and King William. Adjacent aspects of *N. gunnii* (next to *N. cunninghamii*) at two sites: Lake Fenton and Lake Skinner.

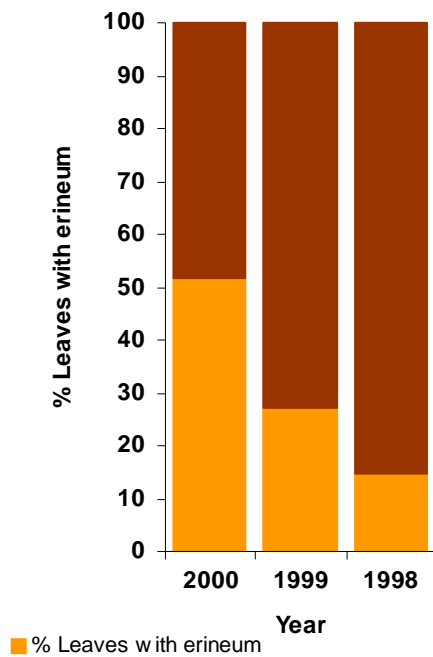


Figure 6.113. Percentages of *N. gunnii* leaves with erineum, 3-year comparison: Autumn 2000, Autumn 1999 and Autumn 1998, combined total from Lake Fenton and Lake Skinner.

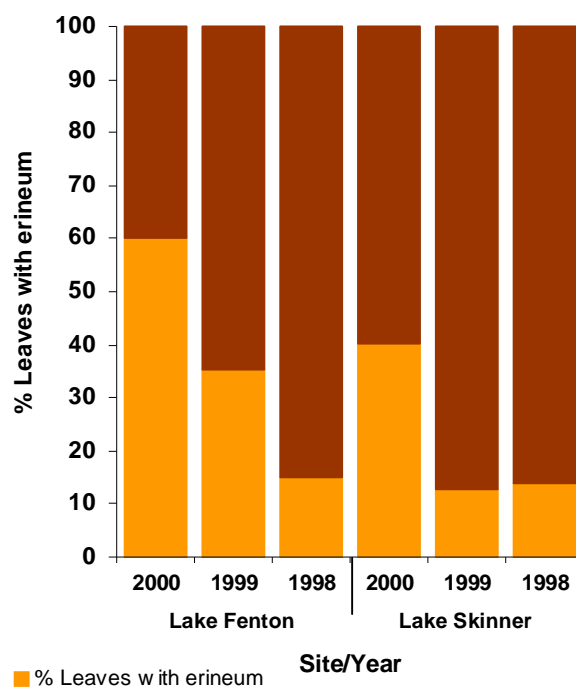


Figure 6.114. Percentages of *N. gunnii* leaves with erineum, 3-year site comparison: Autumn 2000, Autumn 1999 and Autumn 1998, for Lake Fenton and Lake Skinner.

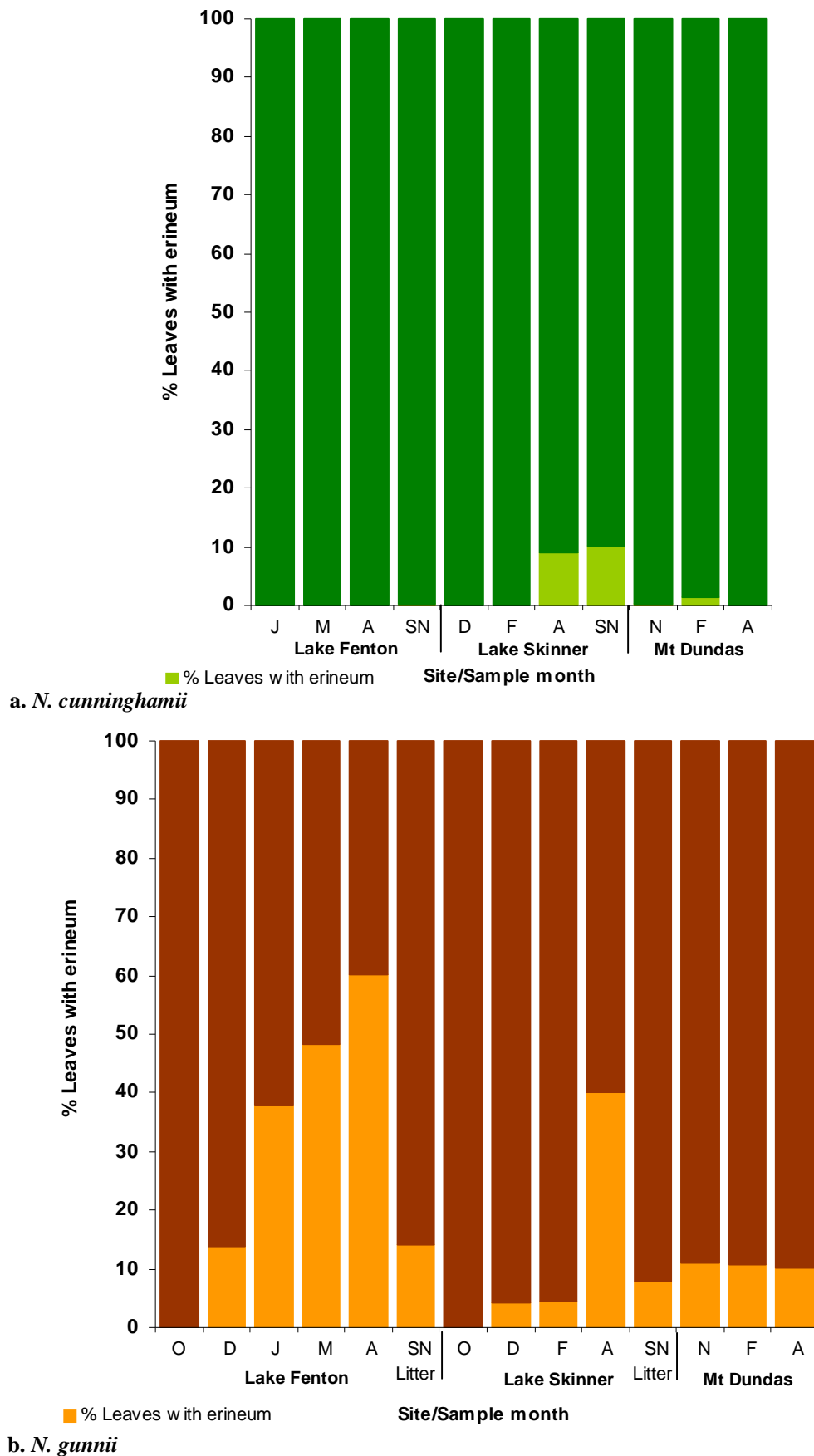


Figure 6.115. a & b. Percentages of leaves with erineum: comparison between a. *N. cunninghamii* (young leaves only) and b. *N. gunnii* at the sites where they co-occurred. Cumulative sampling 1999-2000 from 3 sites: Lake Fenton, Lake Skinner and Mt Dundas. O: October; N: November; D: December 1999; J: January, F: February, M: March, A: April 2000; and SN: September-November 2000 at Lake Fenton and Lake Skinner (*N. gunnii* litter samples).

6.4.2 Other Non-Chewing Leaf Features: *N. cunninghamii* only

Overall, 42,952 *N. cunninghamii* leaves were examined for evidence of non-chewing leaf features, the types including erineum, eggs, leaf galls, leaf mines, leaf ties, scale insects or sooty mould. Of these leaves, over 10% (4817 leaves) had evidence of such non-chewing features (NCF). In the 1999-2001 samples the incidence of NCF was just over 7% (1637 of 22,275 leaves); and in the 1998 samples the incidence was just over 15% (3180 of 20,677 leaves).

The 1999-2001 data revealed a difference in overall levels of NCF, and in the relative proportions of the NCF types between young and old leaves (figure 6.116). The overall incidence of NCF on the young leaves was less than half that on the old leaves (4.669% and 10.464% respectively) (figure 6.116.a). Erineum accounted for over half and leaf galls for over one third of young leaves with NCF, and the proportions of these, together with leaf mines and leaf ties, were more than twice that on the old leaves, whereas the reverse occurred for eggs and scale insect lerps; and female scale insects and sooty mould were absent from the young leaves but occurred on over one third of the old leaves (figure 6.116).

The 1999-2000 young leaves Region/Season data subset revealed lowest incidence of NCF occurred in the North East (1.74%, 55 of 3,168 leaves), two thirds of the incidence in the South (3.189%, 111 of 3481 leaves) and less than half that of West/Central (4.055%, 156 of 3,847 leaves) and the North West (5.263%, 24 of 456 leaves) (figure 6.117.a).

There was a marked difference in the proportions of NCF types between the regions. Leaf galls had the highest incidence in each region, but their proportions of ranged from under a third of NCF leaves in the North East, to half in the South, and two thirds of NCF leaves in West/Central and the North West (figure 6.117.b - e). Only in West/Central did all six of the young-leaf NCF types occur; scale insect lerps were absent from the North East; and only three NCF types occurred in the South (erineum, leaf galls and leaf mines) and in the North West (erineum, leaf galls and scale insect lerps) (figure 6.117.b-e).

When the seasons were compared, the incidence of non-chewing features rose from 2% in spring 1999 (83 of 4,114 leaves), to nearly 4% in the summer 1999-2000

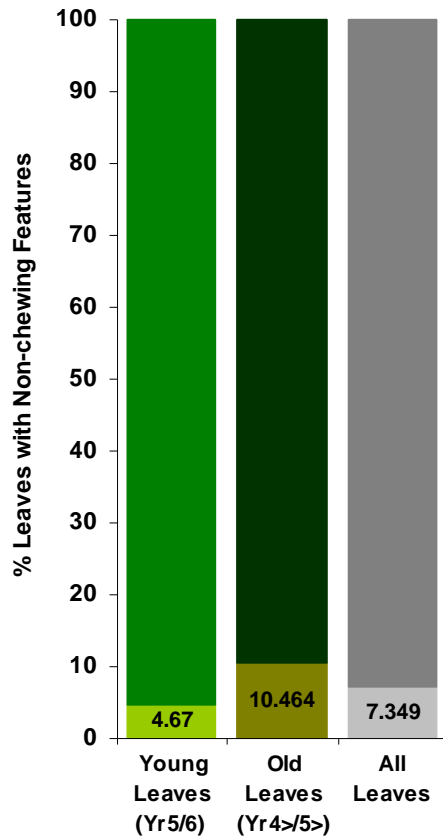
(153 of 4050 leaves) and dropped to less than 0.5% in the autumn 2000 (110 of 2,788 leaves) (figure 6.118.a). Neither leaf mines or scale insect lerps were found on the spring leaves, nearly three quarters of the spring NCF leaves having leaf galls, a fifth had erineum, the remainder having eggs or leaf ties; in the summer, the proportion of leaves with leaf galls rose to nearly two thirds and leaf mines and scale insect lerps were found in addition to the other NCF types; by the autumn, the proportion of leaf galls had fallen to just over one third, while erineum occurred on more than half of the NCF leaves and the proportion of scale insect lerps had doubled, to nearly 6.5% (figure 6.118.b - d).

At the seven sites (from North East, North West and West/Central) where seasonal sampling was applied to both young and old leaves, the incidence of non-chewing features was considerably lower on the young leaves compared with the old leaves in the spring and summer (six-fold and two-fold respectively); but in the autumn, the NCF incidence on the young leaves was twice that on the old leaves (figure 6.119). At these sites the proportions of the NCF types varied with the seasons between and within the leaf ages. On the young leaves, leaf galls predominated in spring (65%) and summer (51%), while nearly two thirds of the NCF leaves had erineum (58%) in the autumn (figure 6.120. left column). Sooty mould predominated on the old leaves in spring and summer but levels fell in the autumn (36%, 58%, and 22% respectively); while the incidence of scale insect lerps increased through the seasons (spring 3%, summer 13%, autumn 38%) (figure 6.120. right column).

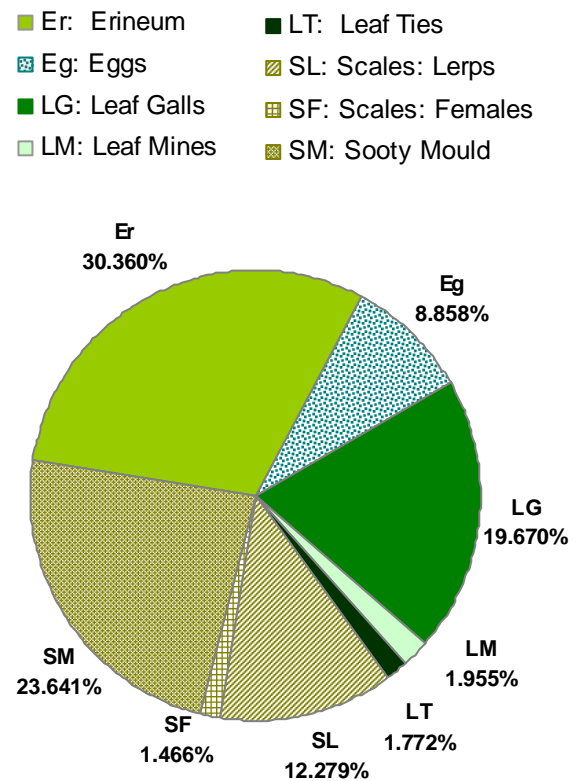
There was a marked difference in the incidence of non-chewing features between the three-site (Lake Fenton, Lake Skinner, Lyrebird Walk) autumn samples of 2000 and 1998. The incidence of NCF in autumn 2000 (4.6%, 105 of 2,272 leaves) was a third of that in autumn 1998 (15.4%, 3,180 of 20,677 leaves) (figure 121.a). The main differences in proportions of NCF type were: a six-fold greater incidence of leaf galls in 2000 compared with 1998; while there was nearly half the incidence of scale insect lerps, and a third of the incidence of sooty mould on the autumn 2000 compared with autumn 1998; whereas the incidence of erineum, and leaf galls, was a third, and a sixth, less in 1998 than 2000, and no leaf mines were recorded in 1998 (figure 6.121.b, c). When the leaf ages at Lake Skinner and Lyrebird Walk were

compared, the young leaves were seen to have a higher incidence of NCF in 2000 (young leaves: 13.55%; old leaves: 10.77%), compared with the old leaves having a higher incidence of NCF in 1998 (young leaves: 25.16%; old leaves: 27.91%) (figure 6.122.a). Of the 2000 NCF leaves, young and old, the highest proportion had evidence of erineum (68% and 80% respectively), followed by leaf galls (27% and 13% respectively) and no scale insects (lerps or females) or sooty mould were found (figure 6.122. b, c). In contrast in 1998, on both young and old leaves scale insect lerps and sooty mould predominated; and scale insect females were found on the old leaves (figure 6.122. d, e).

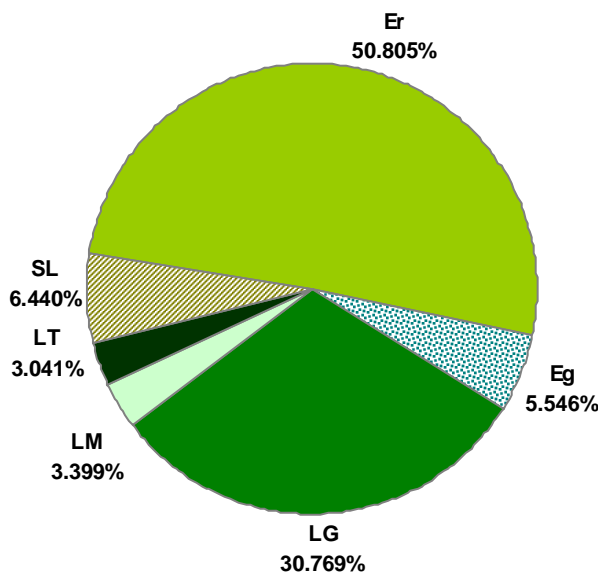
The autumn 1998 aspect sampling at Lake Fenton and Lake Skinner revealed a more than ten-fold difference in the incidence of non-chewing features between the north-facing (44%) and the south-facing (2.9%) leaves and the leaves adjacent to *N. gunnii* (4.3%) (figure 6.124.a). Scale insect lerps occurred on over half (53%), and sooty mould occurred on more than a third, of the north-facing NCF leaves (figure 6.124.c). The south-facing leaves had the highest proportion of erineum (5.8%) and eggs (59.3%) of the three sampling aspects, while sooty mould was found on more than a third (34.8%) of the south-facing leaves (figure 6.124.d). The adjacent leaves had the highest proportion of sooty mould (63.1%) of the three sampling aspects (figure 6.124.a). Leaf galls and scale insect lerps and females were found only on the north-facing leaves (figure 6.124.b, c, d). There was a marked difference between the two sites. At Lake Fenton, erineum was found on each of the sampling aspects and was the only NCF type on the north-facing and south-facing leaves, while on adjacent NCF leaves sooty mould (97.4%) was found on the majority and erineum on just 2.6% (figure 6.125.a, b, c, left column). The leaf galls, scale insect lerps and females occurred only on the Lake Skinner north-facing leaves, the lerps being found on more than half (53%) of those leaves (figure 6.125.a. right column). Also at Lake Skinner, eggs occurred on over 60% and sooty mould on over a third of both the south-facing and adjacent leaves and a small proportion of erineum (1.9%) was found on the adjacent leaves (figure 6.125.b, c, right column).



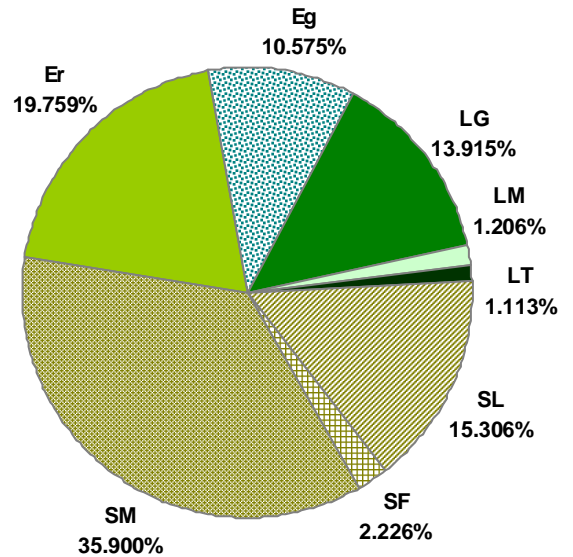
a. Percentages of Leaves with Non-chewing Features



b. All Leaves with Non-chewing Features



c. Young Leaves with Non-chewing Features

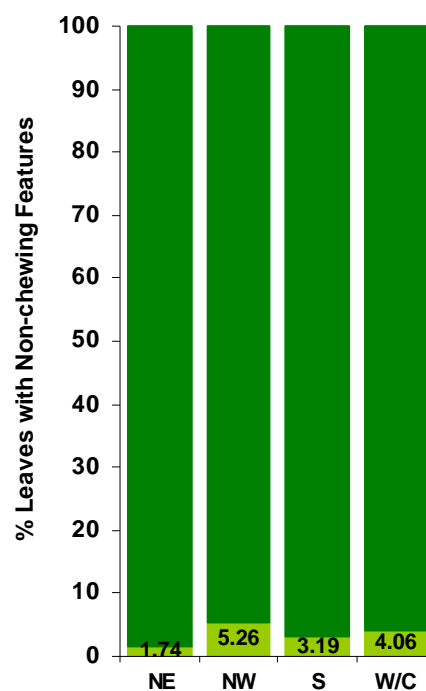


d. Old Leaves with Non-chewing Features

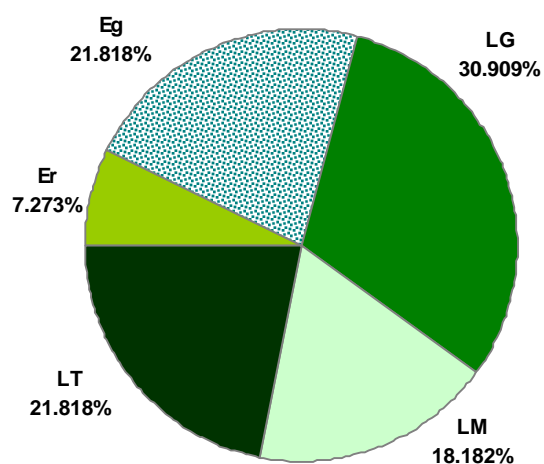
Figure 6.116. a - d. 1999-2001 Percentages of *N. cunninghamii* young, old and all leaves with non-chewing features, from 16 sites (a); non-chewing types as percentages of the non-chewing features by leaf age: young (b), old (c) and all leaves (d). Yr6: 2000-2001 young leaves; Yr5: 1999-2000 young leaves. Yr5[>]: 1999 leaves and older; Yr4[>]: 1998 leaves and older.

Figure 6.117. a. 1999-2000
Percentages of *N. cunninghamii*
young leaves with non-chewing
features by region, from 12 sites:
Blue Tier, Mt Barrow, Weldborough
Pass (North East); Tayatea Bridge
(North West);
Lake Dobson, Lyrebird Walk,
Lake Fenton, Mt Arthur (South);
Cradle Valley, Mt Dundas,
Lake St Clair (West/Central).

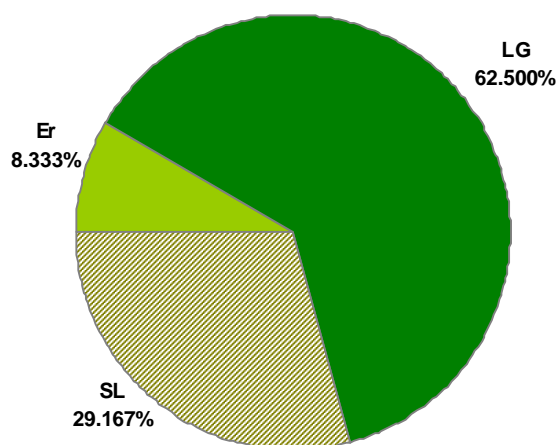
Er: Erineum LT: Leaf Ties
 Eg: Eggs SL: Scales: Lerps
 LG: Leaf Galls SF: Scales: Females
 LM: Leaf Mines SM: Sooty Mould



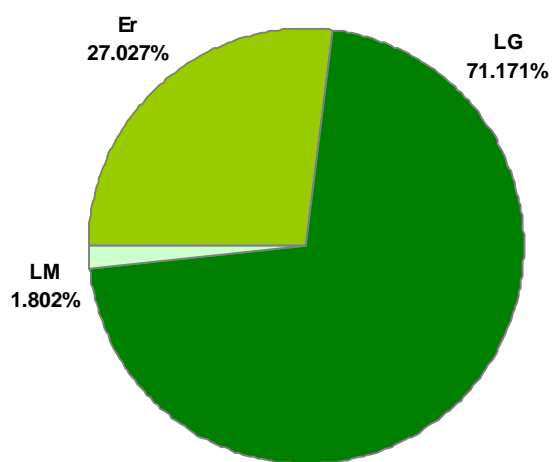
a. % Leaves with Non-chewing Features by Region



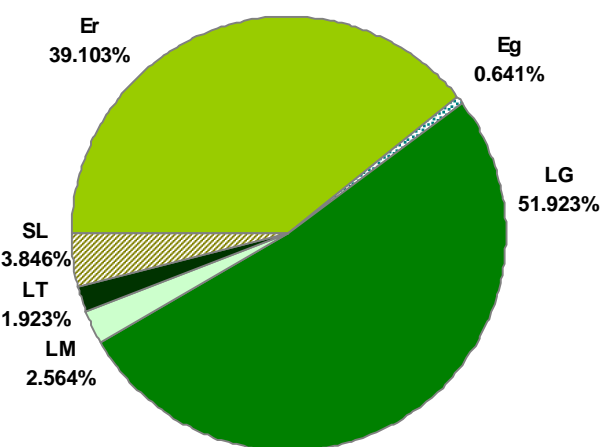
b. North East



c. North West



d. South



e. West/Central

Figure 6.117. b, c, d, e, 1999-2000 *N. cunninghamii* young leaves: non-chewing types as percentages of the non-chewing features, by region: North East (a), North West (b) South (c) and West/Central (d).

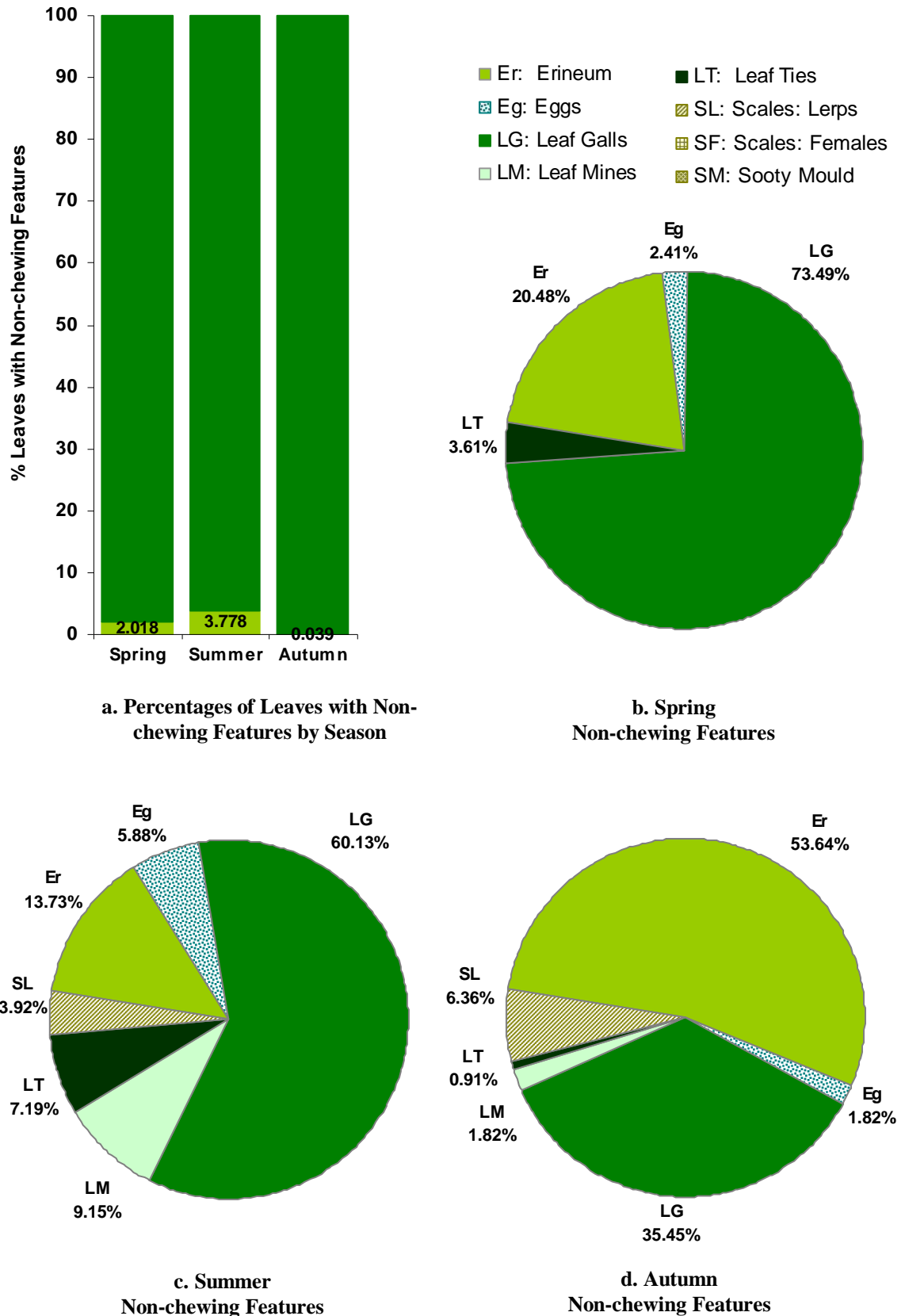


Figure 6.118. a - d. 1999-2000 Percentages of *N. cunninghamii* young leaves with non-chewing features by season, from 12 sites (a): Blue Tier, Mt Barrow, Weldborough Pass, Tayatea Bridge, Lake Dobson, Lyrebird Walk, Lake Fenton, Mt Arthur, Cradle Valley, Mt Dundas, Lake St Clair; non-chewing types as percentages of the non-chewing features by season: spring (b), summer (c) and autumn (d).

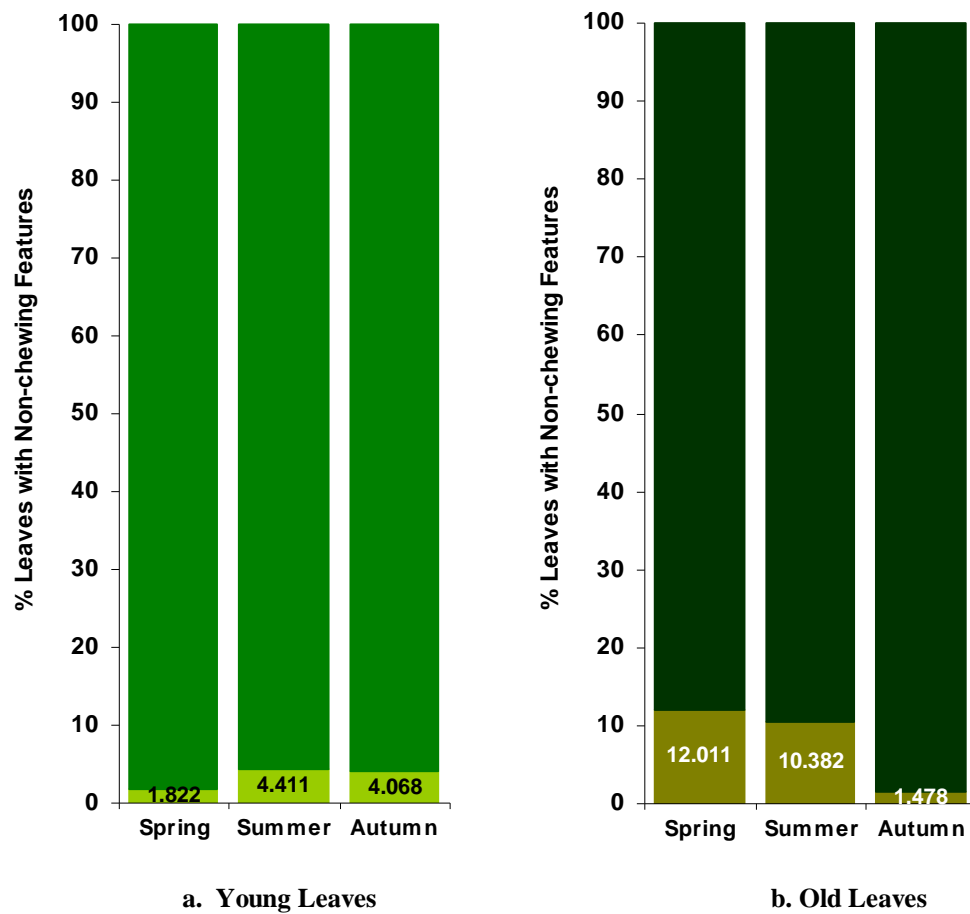


Figure 6.119. 1999-2000 Percentages of *N. cunninghamii* young (a) and old (b) leaves with non-chewing features by season, from 7 sites: Blue Tier, Mt Barrow, Weldborough Pass, Tayatea Bridge, Cradle Valley, Mt Dundas, Lake St Clair.

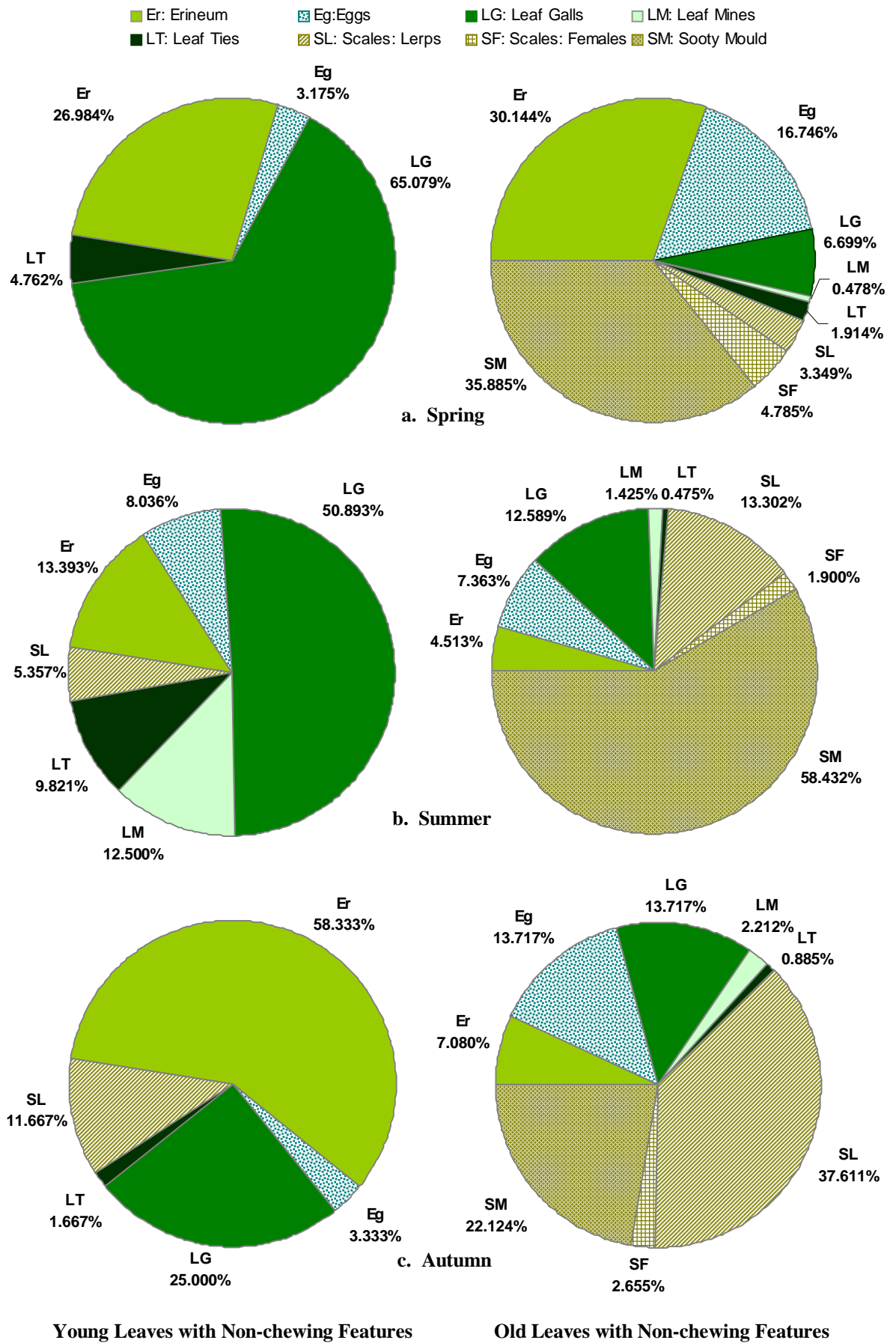
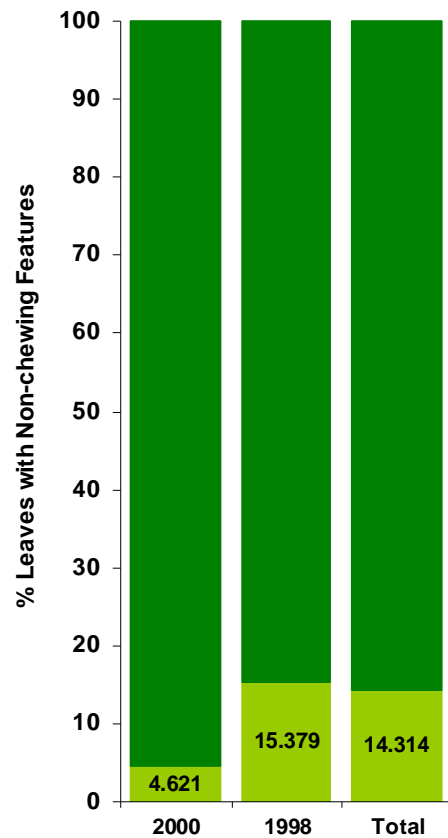


Figure 6.120. a – c. 1999-2000 *N. cunninghamii* young (left column) and old (right column) leaves: non-chewing types as percentages of the non-chewing features by season: spring (a), summer (b) and autumn (c). Leaves from the seven sites in figure 6.119.



a. 2-Year Comparison of Percentages of Leaves with Non-chewing Features

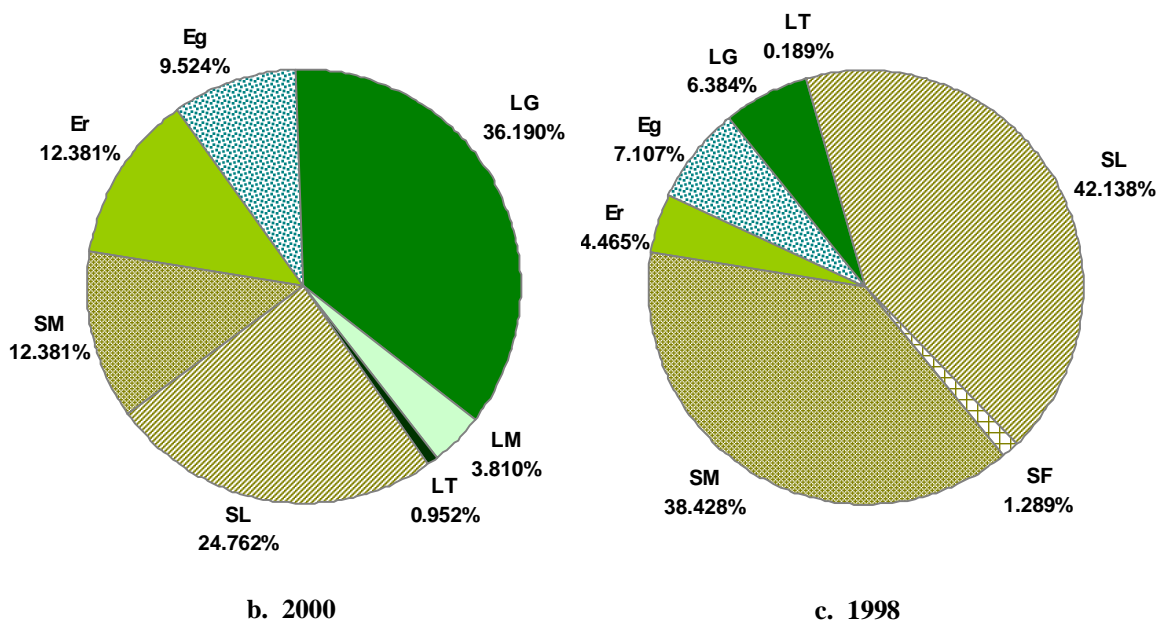
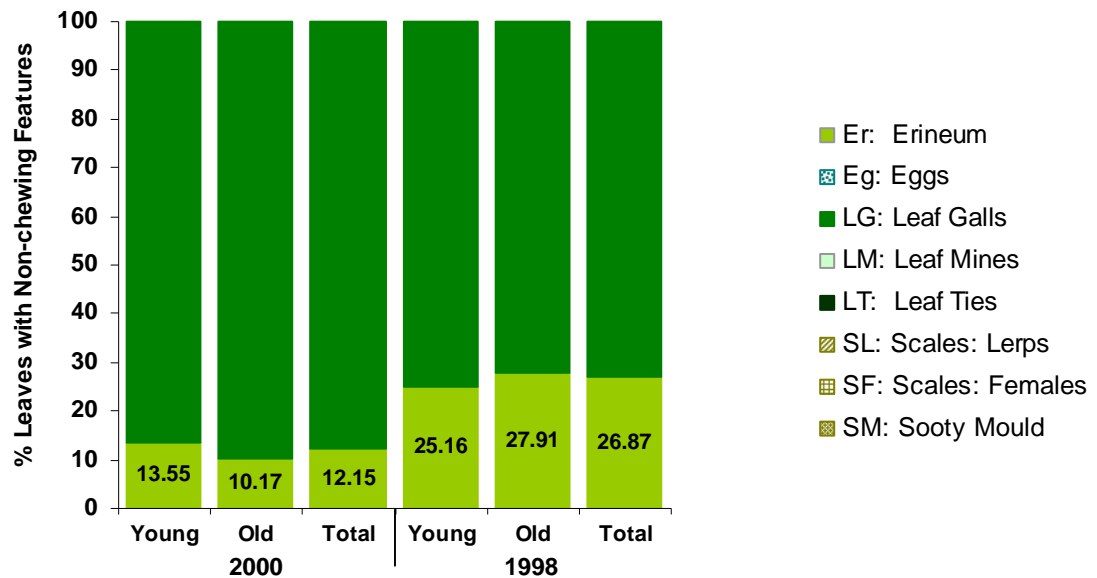
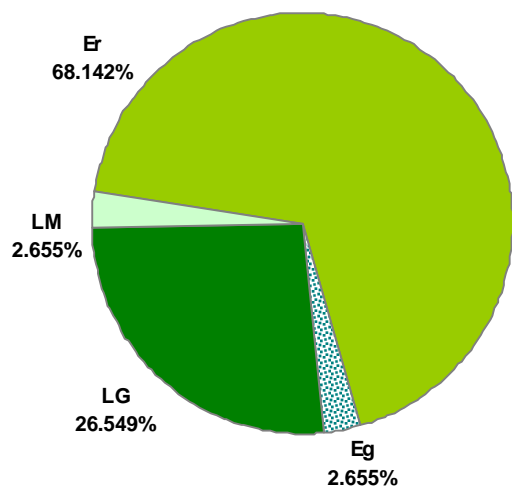


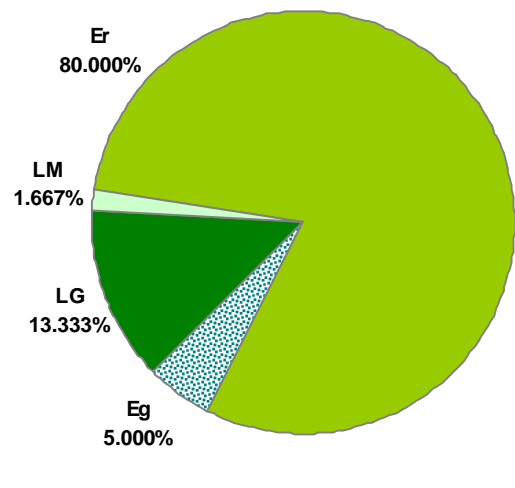
Figure 6.121. a - c. Percentages of *N. cunninghamii* leaves with non-chewing features, 2-year comparison: all leaves for Autumn 2000 and Autumn 1998, from 3 sites (a): Lake Fenton, Lake Skinner and Lyrebird Walk; non-chewing types as percentages of the non-chewing features by year: 2000 (b) and 1998 (c).



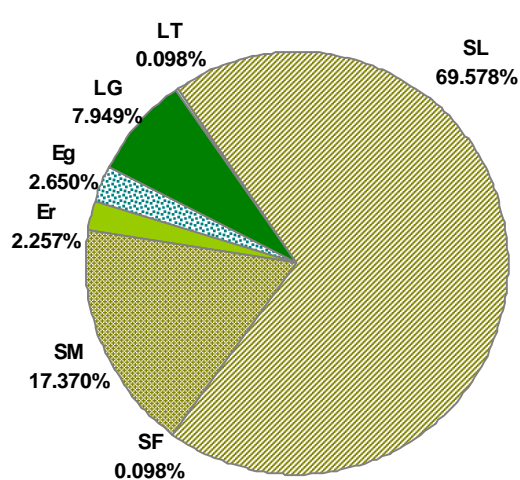
a. Percentages of Leaves with Non-chewing Features by Year and Leaf Age



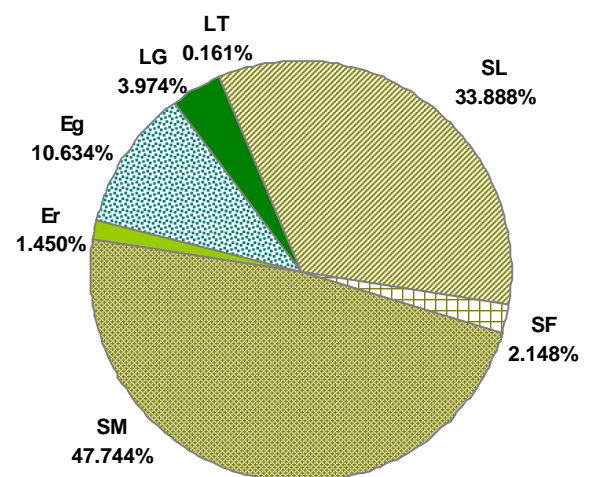
b. 2000 Young Leaves



c. 2000 Old Leaves

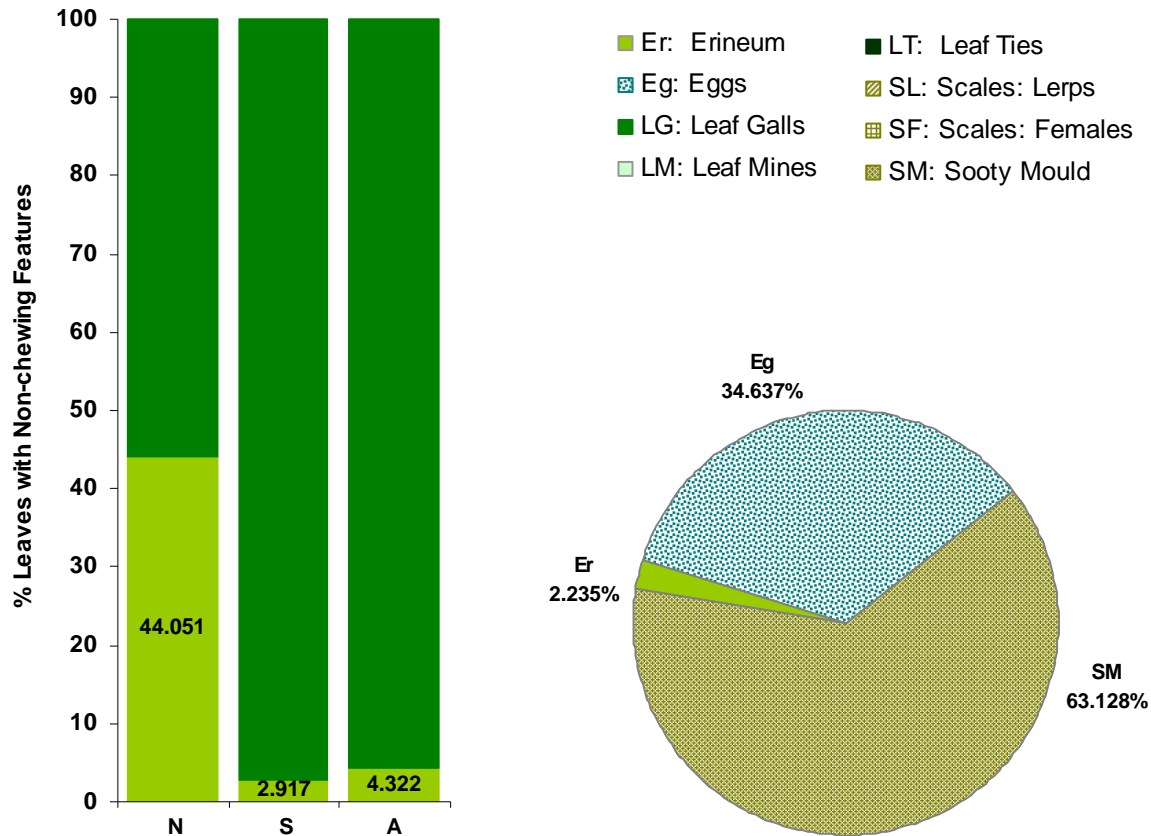


d. 1998 Young Leaves

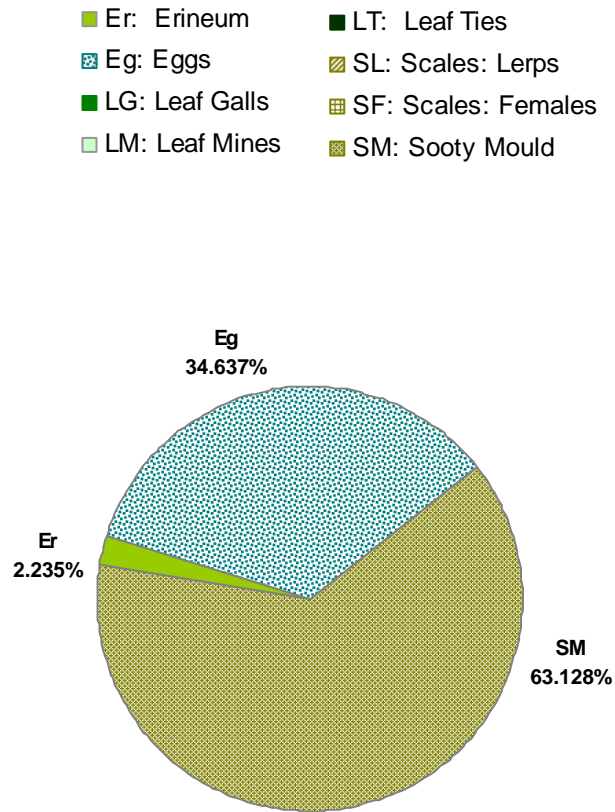


e. 1998 Old Leaves

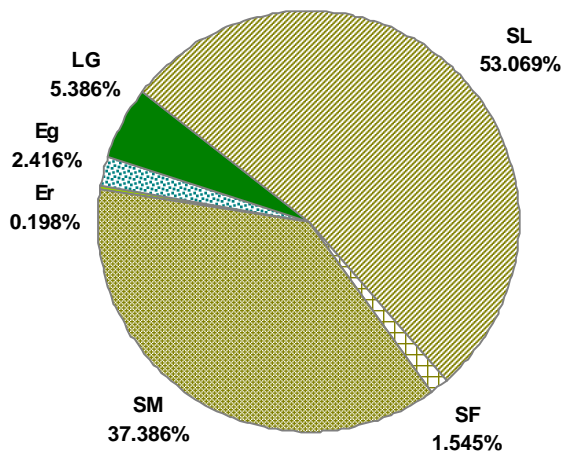
Figure 6.122. a - e. 1999-2001 Percentages of *N. cunninghamii* leaves with non-chewing features, 2-year comparison (a): all leaves for Autumn 2000 and Autumn 1998, from 2 sites: Lake Skinner and Lyrebird Walk; non-chewing types as percentages of the non-chewing features by year: 2000 (b) and 1998 (c).



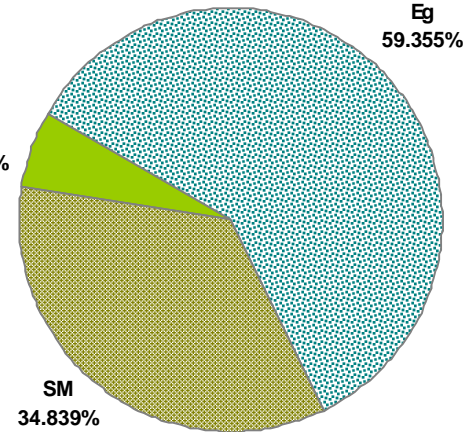
a. Percentages of Leaves with Non-chewing Features by Aspect



b. Adjacent Leaves



c. North-facing Leaves



d. South-facing Leaves

Figure 6.123. a - d. Percentages of *N. cunninghamii* leaves with non-chewing features (a), on north-facing (N) and south facing (S) aspects and leaves adjacent to *N. gunnii* (A): all leaf ages for Autumn 1998, from 2 sites: Lake Fenton and Lake Skinner; non-chewing types as percentages of the non-chewing features by aspect: adjacent (b), north-facing (c) and south-facing (d).

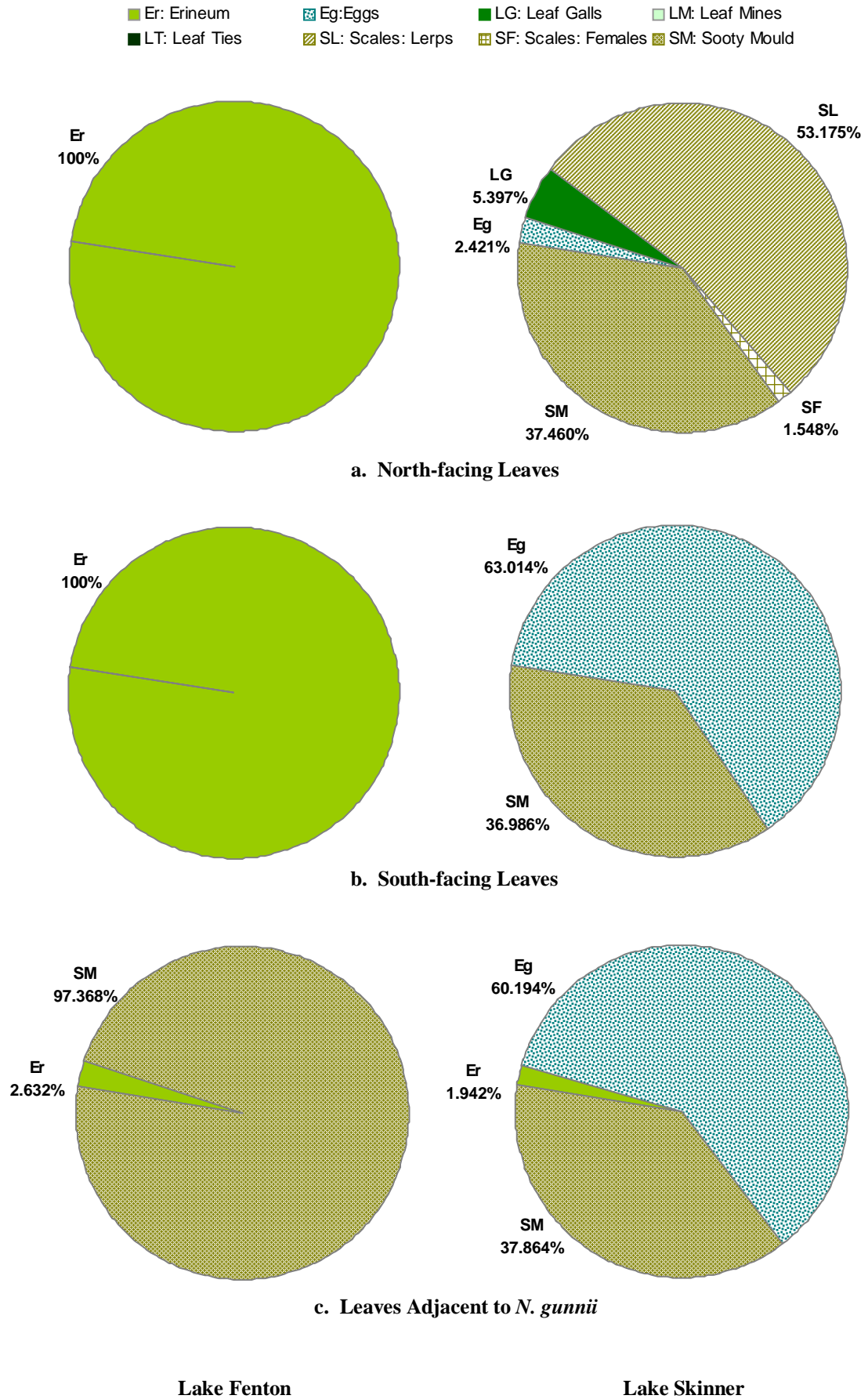


Figure 6. 125. a - c. Autumn 1998 *N. cunninghamii*, all leaf ages, non-chewing types as percentages of the non-chewing features by site and aspect: Lake Fenton (left column) and Lake Skinner (right column); North-facing leaves (a), south-facing leaves (b) and leaves adjacent to *N. gunnii* (c).

6.5 HERBIVORY LEVELS: SUMMARY OF RESULTS

6.5.1 Leaf-Chewing Herbivory

N. cunninghamii typically had a higher level of herbivory than *N. gunnii*, both in terms of numbers of individual leaves chewed compared with those remaining intact, and in the percentage leaf area loss from the chewed leaves. These overall differences were consistent across regions, sites, seasons, sampling years and sampling aspect.

For *N. cunninghamii* the ratio of chewed to intact leaves showed more regional variation than that of *N. gunnii*, but for both *Nothofagus* species there is between-site variation within the regions. In addition for both *Nothofagus* species, within sites there is year to year variation.

The Region/Season data indicated a spring or summer peak in chewed-leaf counts for *N. cunninghamii*, depending upon the region; and a summer or autumn peak for *N. gunnii*, again differing between regions. The Cumulative Site data revealed that for *N. cunninghamii* young leaves, the peak in chewed-leaf counts coincided with the peak in the combined total of chewed plus intact leaves.

The percentage leaf area loss from chewed leaves of *N. cunninghamii* ranged from low to high values, varying widely between regions, sites, seasons, sampling years and sampling aspect; while that for *N. gunnii* was consistently very low.

6.5.2 Leaf Areas

N. cunninghamii had a lower mean leaf area and less variation in leaf size than *N. gunnii*. There was variation in leaf areas between sites for both species but regional influence was strongest for *N. cunninghamii*. For both *Nothofagus* species, leaf areas (means and variation in size) differed between sampling years; and leaves from the highest sampling altitudes had the smallest areas. The effect of sampling aspect on leaf area differed between sites.

N. cunninghamii intact old leaves had a higher mean area and more size variability than the intact young leaves. Chewing damage to *N. cunninghamii* leaves had no effect on mean leaf area but the chewed leaves were less variable in size than intact leaves.

6.5.3 Hole Growth

For both *Nothofagus* species, after an initial marked increase in size of the punched 1.5mm holes and their parent leaves in spring, the subsequent patterns and rates of growth varied considerably between sites, particularly for *N. cunninghamii*.

At the sites with control (unpunched) leaves, these showed a similar pattern of growth, in both mean lengths and areas, to their corresponding hole-punched leaves. However in the hole-punched leaves, while the rates of increase in mean leaf length and mean leaf area were similar at each site for *N. gunnii*, these rates differed for *N. cunninghamii*.

6.5.4 Non-Chewing Leaf Features: Erineum

N. gunnii had a far greater incidence of leaves with erineum than *N. cunninghamii*, although the incidence of leaves with erineum varied with region, season, sampling aspect, site and sampling year for both *Nothofagus* species.

In both species there was an autumn peak in erineum incidence. For *N. gunnii*, litter leaves examined in spring had a lower incidence of erineum than the *in situ* leaf sample from the previous autumn.

6.5.5 Non-Chewing Leaf Features on *N. cunninghamii*

On *N. cunninghamii*, the old leaves had twice the overall incidence of non-chewing leaf features (NCF's) than the young leaves, however the proportions of the NCF types differed between the leaf ages.

Besides varying with leaf age, the overall incidence of non-chewing leaf features, and the relative proportions of the NCF types, showed considerable variation with region, season, sampling aspect, site and sampling year.

Chapter 7 RESULTS III: TASMANIAN *NOTHOFAGUS* CANOPY ARTHROPOD FAUNA AND HERBIVORY LEVELS: COMPARISONS WITH OTHER TREE TAXA

In this chapter the results of the Tasmanian *Nothofagus* canopy arthropod fauna, and herbivory levels as indicators of arthropod herbivore activity, were compared with tree taxa from other regions to provide an indication of whether, as has been suggested, the Tasmanian *Nothofagus* arthropod fauna is impoverished, or ‘depauperate’.

But this concept needs defining: the literal meaning of the word ‘depauperate’, given by the Shorter Oxford English Dictionary is ‘(of a flora or fauna) lacking in numbers or variety of species’ (OED1, 1993: 648). However this implies a comparison – ‘lacking’ compared with what? Raising the question of what the typical arthropod fauna of a tree taxon might be, and the taxonomic level at which to measure it: all morphotaxa, selected arthropod orders, feeding guilds, or specialist herbivores? Data available for comparison is presented at each of these levels (table 3.3) and they have been collected by a variety of sampling methods (table 3.2) or by reference to fauna lists. Accordingly, the Tasmanian *Nothofagus* arthropod data below have been tabulated to most closely resemble the presentation of the different studies with which they were being compared, and the data collection methods of those studies have been indicated.

The Tasmanian *Nothofagus* data were compared with: closely related tree species (*Nothofagus* elsewhere, northern temperate Fagales); other Australian tree taxa, now widespread (*Acacia* and *Eucalyptus*); with tree taxa from the Tropics. The results of these comparisons are considered further in the Discussion (Chapter 8) below.

7.1 ARTHROPOD FAUNA DIVERSITY: OVERALL SPECIES RICHNESS

Reviewing the Tasmanian *Nothofagus* arthropod data from Chapter 5, a combined total of 311 adult and immature morphotaxa were found on the two *Nothofagus* species, of which 83 morphotaxa were shared by both species, 193 occurred only on *N. cunninghamii* and 34 occurred only on *N. gunnii* (table 5.2). Thus, a total of 276 morphotaxa were found on *N. cunninghamii*, while 117 were found on *N. gunnii*. However among these morphotaxa, in each order except Acarina and Plecoptera, were adults and immatures identified as being the same species (e.g. Geometrid moth *Euloxia leucochorda*: adult morphotaxon LeGe4, larval morphotaxon LeGeL4; and Leaf Beetle *Ewanius nothofagi* Reid: adult morphotaxon CpCh3, larval morphotaxon CpChL1), or possibly the same species - where the adults and immatures were of the same family, subfamily or genus but identified no further (e.g. Treehoppers *Acanthuchus* spp.: adult morphotaxa *Acanthuchus trispinifer* Fairmaire, HeMe2 and *Acanthuchus* sp.2, HeMe3; and immature morphotaxon *Acanthuchus* spp., HeMeJ3). Accordingly, for the species richness comparisons, the possible adult-immature overlaps were corrected so that the putative species counts for *N. cunninghamii* and *N. gunnii* became 251 and 114 respectively, with corresponding reductions in the orders concerned (table 7.1). After correction, Coleoptera, with 90 species, remained the most taxon rich order for *N. cunninghamii*, but Lepidoptera, with 51 species, became less speciose than Acarina (57 species); for *N. gunnii* Acarina, with 39 species, remained the most taxon rich order followed by Coleoptera with 32 species, and Lepidoptera, with 10 species, became less speciose than Hemiptera (12 species).

Even taking account of possible overlap between adults and immatures, at first glance both *N. cunninghamii* and *N. gunnii* appear well endowed with arthropod taxa compared with a study of *Nothofagus* in New Zealand and Chile (table 7.2, data from Russell *et al.*, 2000). This study used branchlet shaking, a sampling method similar to branch beating, however the sample size per *Nothofagus* species was relatively small and was acknowledged as such, it being part of a investigation into chemical defence in the *Nothofagus* species sampled (Russell *et al.*, 2000). The difference between overall taxon richness in these records as opposed to those of *N. cunninghamii* and *N. gunnii* above is likely to be due to the sample sizes (considerably higher Coleoptera species richness was found on *N. dombeyi* and *N.*

obliqua by Arias *et al.*, 2008 – see below) and also to the absence of Acarina from the New Zealand and Chile data.

Host Order	All Morphotaxa ^a			Additional Mtx ^b			'Species' Count ^c		
	Nc	Ng	NcNg	Nc	Ng	NcNg	Nc	Ng	NcNg
Acarina	57	39	60	0	0	0	57	39	60
Coleoptera	98	32	109	8	0	8	90	32	101
Hemiptera	26	14	31	5	2	5	21	12	26
Lepidoptera	59	10	65	8	0	8	51	10	57
Plecoptera	6	9	13	0	0	0	6	9	13
Psocoptera	16	6	16	2	1	2	14	5	14
Thysanoptera	15	8	17	3	1	3	12	7	14
Total	277	118	311	26	4	26	251	114	285

Table 7.1. Arthropod diversity on Tasmanian *Nothofagus*: morphotaxon richness for *N. cunninghamii* (Nc) and *N. gunnii* (Ng) and overall morphotaxon richness for the genus (NcNg) in Tasmania (all fieldtrips). ^a overall morphotaxa count (all adults and immatures); ^b additional morphotaxa which are possible adult/immature overlaps with group (^a); ^c count of putative species.

However, with similar sampling conditions per *Nothofagus* species, the Russell *et al.* (2000) data revealed that overall taxon richness varied between New Zealand and Chile, and among *Nothofagus* subgenera and species within the two countries (table 7.2). In order to discover if these differences in taxon richness varied with latitudinal range of the host plant, regression analysis was carried out for the *Nothofagus* species for which latitudinal ranges were available (all except *N. glauca* and *N. leoni*). This revealed that taxon richness was not influenced by latitudinal range overall, within countries or subgenera; Chile subgenus *Nothofagus* being closest to significance at $p = 0.66$ (Figure 7.1). *Nothofagus obliqua* (Chile, subgenus *Lophozonia*), with an arthropod taxon richness of 103 and latitudinal range of 8.2°, was an outlier on both the overall plot (figure 7.1.a) and on the Chile plot (figure 7.1.b)

As on *N. cunninghamii*, Coleoptera was the most taxon rich order on the New Zealand *Nothofagus* species, except for *N. fusca* (Lepidoptera most speciose); while in Chile either Coleoptera or Araneae were the most taxon rich orders (table 7.2). The feeding guild composition of these arthropod fauna is considered in section 7.2 below.

Location	New Zealand							Chile													Overall Mean
Subgenus	Fuscospora					L	F	Lophozonia					Nothofagus							Chile Mean	
Nothofagus Species	N. fusca	N. solandri	N. solandri var. cliff	N. truncata	NZ Fuscospora Mean	N. menziesii		N. alessandri*	N. alpina*	N. glauca*	N. leoni	N. obliqua*	Chile Lophozonia Mean	N. antarctica*	N. betuloides	N. dombeyi	N. nitida	N. pumilio*	Chile Nothofagus Mean		
Coleoptera	8	15	9	10	10.5	13	11	4	9	2	5	29	11.3	18	7	15	9	16	13	11	11.3
Hemiptera	2	3	3	1	2.3	1	2	5	9	5	6	11	7.8	8	9	12	6	9	8.8	8	6
Lepidoptera	15	13	8	7	10.8	7	10	0	5	0	3	13	5.3	18	10	6	5	4	8.6	6.4	7.6
Diptera	4	11	11	1	6.8	7	6.8	2	3	0	0	5	2	1	6	3	1	5	3.2	2.6	4
Hymenoptera	1	5	6	1	3.3	2	3	0	4	3	4	17	7	4	5	2	1	4	3.2	4.4	3.9
Spiders	3	12	9	3	6.8	6	6.6	17	18	7	22	19	16.5	9	12	7	10	10	9.6	13	10.9
Other	2	5	5	5	4.3	0	3.4	3	3	5	5	9	5.5	6	4	3	4	3	4	4.5	4.1
Total	34	64	51	28	44.3	38	43	31	56	22	45	103	56.5	64	53	48	36	51	50.4	51	48.3

Table 7.2. Arthropod diversity (morphotaxa per order) on *Nothofagus* in New Zealand and Chile by species and subgenus. F: *Fuscospora*; L: *Lophozonia*. * Denotes deciduous species. Data from Russell *et al.*, 2000, table 1, p 47; two samples by branchlet shaking, from 5 trees per species, December 1995 and February 1996.

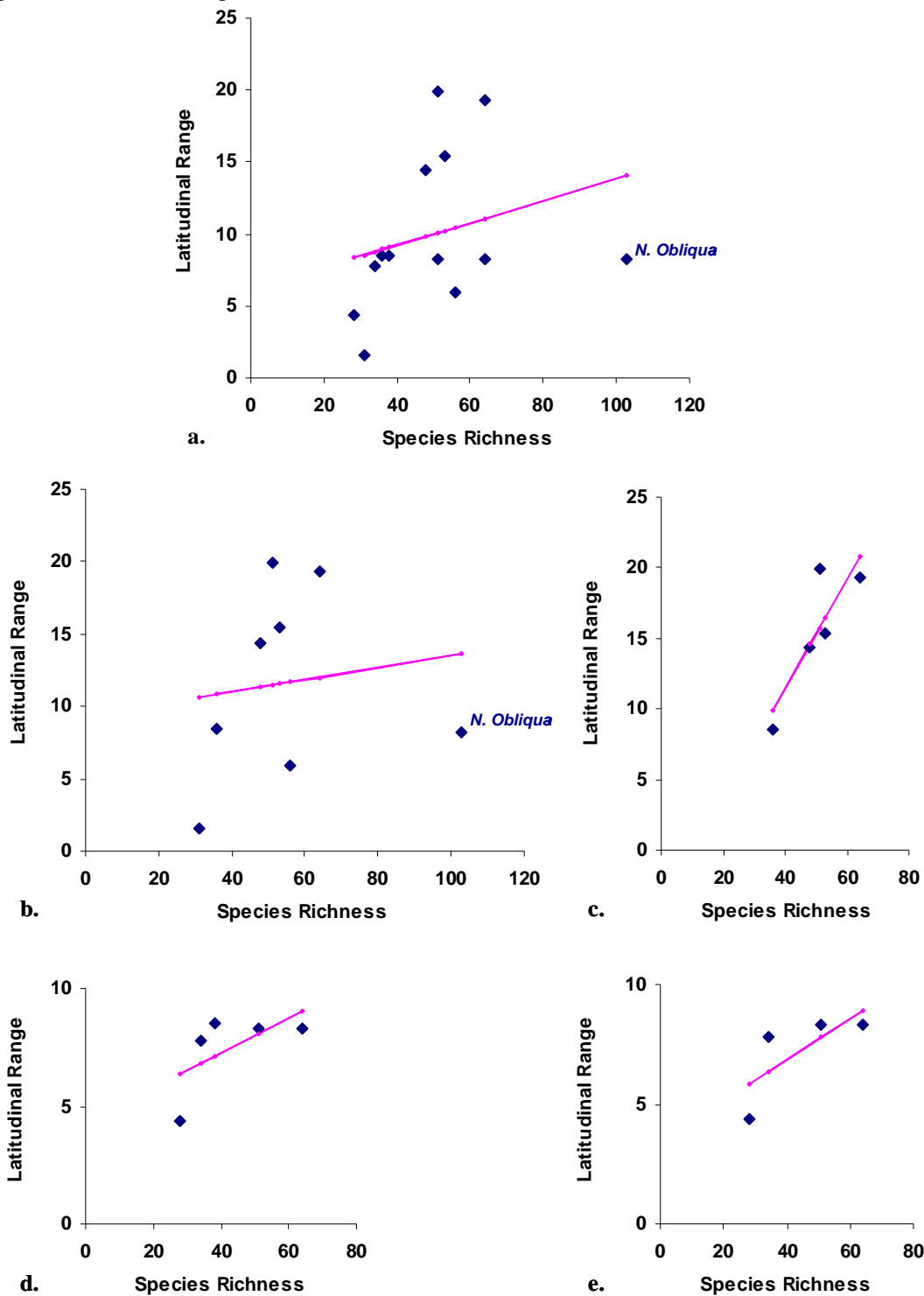


Figure	Location	Subgenus	R Square	P-value
a	NZ & Chile	All	0.07	0.37
b	Chile	All	0.02	0.75
c	Chile	<i>Nothofagus</i>	0.73	0.07
d	NZ	All	0.38	0.26
e	NZ	<i>Fuscospora</i>	0.55	0.26

Figure 7.1. a - e. Coefficients of determination (correlation-squared) between arthropod species richness and latitudinal range for *Nothofagus* in Chile and New Zealand (NZ). Note: *N. obliqua* is an outlier (a, b). Species richness data from Russell *et al.*, 2000. Latitudinal ranges estimated from Ogden *et al.*, 1996 (NZ); Veblen *et al.*, 1996 and Donoso, 1996 (Chile).

In contrast to the above New Zealand and Chilean *Nothofagus* sampled by branchlet shaking, Majer, Recher and Ganesh (2000) used chemical knockdown in their comparison of Eucalypts from Eastern (New South Wales i.e. NSW) and Western Australia (WA). While the overall taxon richness of selected orders on the Western *Eucalyptus* species fell between that on *N. cunninghamii* (251) and *N. gunnii* (114), the Eastern *Eucalyptus* species had a considerably more speciose arthropod fauna (table 7.3). Coleoptera had the highest taxon richness for each *Eucalyptus* species, in all cases having roughly twice the number of species as the next most taxon rich order, Hemiptera (table 7.3). Notably, on both Eastern and Western Eucalypts the taxon richness of Acarina and Lepidoptera was lower than that on either of the two Tasmanian *Nothofagus* species (table 7.3).

Location	NSW			WA			Overall Mean
Tree species	<i>E. moluccana</i>	<i>E. crebra</i>	NSW Mean	<i>E. marginata</i>	<i>E. (Corymbia) calophylla</i>	WA Mean	
Acarina	24	24	24	17	20	18.5	21.3
Coleoptera	168	157	162.5	99	90	94.5	128.5
Hemiptera	82	80	81	44	52	48	64.5
Lepidoptera	0	2	1	1	0	0.5	0.75
Plecoptera	0	0	0	1	1	1	0.5
Psocoptera	28	21	24.5	17	17	17	20.8
Thysanoptera	14	14	14	12	10	11	12.5
Total	316	298	307	191	190	190.5	248.8

Table 7.3. Species diversity, of selected arthropod orders, found on *Eucalyptus* in Eastern (NSW) and Western (WA) Australia: morphotaxa per order per tree species. Data modified from Majer, Recher & Ganesh, 2000, Table 1, pp298-300; sampling by chemical knockdown, 10 trees per host species, 4 seasons over 1 year.

7.2 ARTHROPOD FAUNA, DIVERSITY IN MORE DETAIL: COLEOPTERA SPECIES RICHNESS AND FEEDING GUILDS

Coleoptera is the largest order of insects (Gullan & Cranston, 2000; Lawrence & Britton, 1991), and has long been regarded so, as epitomised by J.B.S. Haldane's oft quoted remark in response to questioning by an eminent cleric, that the Almighty must have 'an inordinate fondness for beetles' (as in Fortey, 2008: 33). On the Tasmanian *Nothofagus*, Coleoptera had the highest taxon richness of the orders on *N. cunninghamii*, although on *N. gunnii* Coleoptera came second to Acarina in taxon richness.

When compared with studies of *Nothofagus* elsewhere, more species of Coleoptera were found on both *N. cunninghamii* and *N. gunnii* than on the New Zealand and Chile *Nothofagus* sampled by Russell *et al.* (2000). However, the more extensive chemical fogging samples of Arias *et al.* (2008) for *N. dombeyi* and *N. obliqua* in Chile yielded considerably higher Coleoptera species richness than that on either *N. cunninghamii* or *N. gunnii* (table 7.4, sources ^{1, 2}).

N. gunnii in particular had a low Coleoptera species richness (32 spp.) compared with other temperate tree taxa in Australia and the UK, most of these having nearly three-times (*Acacia baileyana*: 88 species) up to nearly seven times (*Nothofagus dombeyi*: 289 spp.) the number of Coleoptera species found on *N. gunnii*, with *Acacia pravissima* (46 species) being a notable exception to the other temperate tree taxa (table 7.4, sources ^{1, 3-6}). *N. cunninghamii*, with 82 Coleoptera species, had a greater species richness than was found on *Acacia pravissima* and approached the species counts for *A. baileyana* and the Western Australia Eucalypts (*E. marginata*: 99 spp.; *E. (Corymbia) calophylla*: 90 spp.), but had half to less than a third of the number of Coleoptera species on the remaining temperate tree taxa (table 7.4, sources ^{1, 3-6}). All the temperate tree taxa had a considerably lower species richness than those in tropical (Brunei, mixed canopy: 875 spp.; Panama, *L. seemannii*: 1255 spp.) or subtropical regions (Queensland mixed canopy: 454 spp.) (table 7.4, sources ^{1, 3-9}).

Region	Location	Host Tree Species	Coleoptera Species
Temperate	¹ Tasmania, Australia	<i>N. cunninghamii</i>	82
		<i>N. gunnii</i>	32
	² New Zealand	<i>N. fusca</i>	8
		<i>N. menziesii</i>	13
		<i>N. solandri</i>	15
		<i>N. solandri</i> var. <i>cliff</i>	9
		<i>N. truncata</i>	10
		<i>N. alessandri</i>	4
	² Chile	<i>N. alpina</i>	9
		<i>N. antarctica</i>	18
		<i>N. betuloides</i>	7
		<i>N. dombeyi</i>	15
		<i>N. glauca</i>	2
		<i>N. leoni</i>	5
		<i>N. nitida</i>	9
		<i>N. obliqua</i>	29
		<i>N. pumilio</i>	16
	³ Chile	<i>N. dombeyi</i>	289
		<i>N. obliqua</i>	176
		<i>A. araucana</i>	167
	⁴ Victoria, Australia	<i>A. dealbata</i>	115
		<i>A. decurrens</i>	127
		<i>A. baileyana</i> [#]	88
		<i>A. pravissima</i>	46
	⁵ Eastern Australia	<i>E. moluccana</i>	168
		<i>E. crebra</i>	157
	⁵ Western Australia	<i>E. marginata</i>	99
		<i>E. (Corymbia) calophylla</i>	90
	⁶ UK	Mixed Deciduous	200
Subtropical	⁷ Queensland, Australia	Mixed Canopy	454
Tropical	⁸ Brunei	Mixed Canopy	875
Tropical	⁹ Panama	<i>L. seemannii</i>	1255
Sources and Sampling Methods: ¹ This Study: Branch beating, <i>N. cunninghamii</i> 70, & <i>N. gunnii</i> 46, site visits over 3 years. ² Russell <i>et al.</i> , 2000: Branchlet shaking, 5 trees per <i>Nothofagus</i> species, 2 site visits. ³ Arias <i>et al.</i> , 2008: Chemical knockdown, 4 sites, 2 or 3 samples per site (9 visits total), single summer (2001 or 2003), <i>Nothofagus</i> and <i>Araucaria</i> . ⁴ New, 1979: branch beating, weekly, up to 2 years, <i>Acacia</i> . <i>A. baileyana</i> [#] is not native to Victoria. ⁵ Majer, Recher & Ganesh, 2000: Chemical knockdown, 10 trees per host species, 4 seasons, 1 year, <i>Eucalyptus</i> . ⁶ Hammond & Owen, 1996 (in Hammond, Kitching & Stork, 1996): Chemical fogging, 818m ² mixed deciduous canopy, mostly English Oak (<i>Quercus robur</i>). ⁷ Hammond, Kitching & Stork, 1996: Chemical fogging, 110m ² mixed canopy "Argyrodendron actinophyllum alliance, Suballiance 11 (<i>Caldelyvia-Cryptocarya erythroxylon-Orites-Melicope octandra-Acmene ingens</i>)". ⁸ Stork, 1991 (in Hammond, Kitching & Stork, 1996): Chemical fogging, 200m ² canopy from 10 trees of 5 species. ⁹ Erwin & Scott, 1980 (in Hammond, Kitching & Stork, 1996): Chemical fogging, canopies of 19 trees of <i>Luehea seemannii</i> .			

Table 7.4. Coleoptera species richness: this study compared with eight others, from Southern Temperate, Subtropical, Tropical and Northern Temperate Regions.

Where the data were available, the Coleoptera species were subdivided into feeding guilds (table 7.5). This revealed that the proportions of herbivorous Coleoptera species found on *N. cunninghamii* and on *N. gunnii* were greater than that found in the UK mixed deciduous forest and also in both the tropical and subtropical mixed canopies; but were less than the temperate *Eucalyptus* species, and the tropical *Luehea seemannii*, particularly for *N. cunninghamii*. Conversely, the proportions of fungivores/detritivores on Tasmanian *Nothofagus* were slightly less than on the UK mixed deciduous forest; comparable with the tropical and subtropical mixed canopies; and greater than that on the Australian temperate Eucalypts and the tropical *Luehea seemannii*. The proportion of Coleoptera predators on *N. cunninghamii* fell within the limits of the tree taxa in the other studies, whereas the proportion of Coleoptera predators on *N. gunnii* was considerably less than on the other tree taxa.

Overall, *N. gunnii* had the lowest Coleoptera diversity of any of the tree taxa: in terms of species richness, and of numbers of families and superfamilies represented (table 7.5). The numbers of Coleoptera species, families and superfamilies found on *N. cunninghamii* approached that of the Western Australia Eucalypts, but fell short of the remaining temperate tree taxa and those of the tropical and subtropical regions (table 7.5).

Region	Location	Coleoptera Tree Species	Herbivores		Fungivores/ Detritivores		Predators		Taxa Structure		
			spp.	%	spp.	%	spp.	%	spp.*	F	Sf
Temperate	¹ Tasmania	<i>N. cunninghamii</i>	34	42	25	31	22	27	81	25	11
		<i>N. gunnii</i>	15	47	12	38	5	16	32	14	6
	Tas.: <i>Nothofagus</i> Mean		24.5	44.4	18.5	34.2	13.5	21.4	56.5	19.5	8.5
	² Eastern Australia	<i>E. moluccana</i>	93	55	35	21	40	24	168	40	12
		<i>E. crebra</i>	76	48	43	27	38	24	157	40	12
	² Western Australia	<i>E. marginata</i>	50	52	24	25	23	24	97	29	13
		<i>E. (Corymbia) calophylla</i>	46	52	21	24	22	25	89	31	13
	Aus.: <i>Eucalypt</i> Mean		66.3	51.7	30.8	24.1	30.8	24.1	127.8	35	12.5
	³ UK	Mixed Deciduous	55	28	81	41	64	32	200	41	14
All Temperate Mean			52.7	46.2	34.4	29.3	30.6	24.5	117.7	31.4	11.6
Subtropical	⁴ Queensland, Australia	Mixed Canopy	148	33	171	38	135	30	454	51	13
Tropical	⁵ Brunei	Mixed Canopy	326	37	309	35	240	27	875	56	14
	⁶ Panama	<i>L. seemannii</i>	609	49	330	26	314	25	1253	55	16
Tropical/Subtropical Regions Mean			361	39.5	270	33.1	229.7	27.4	860.7	54	14.3
Overall Mean			145.2	44.2	105.1	30.5	90.3	25.3	340.6	38.2	12.4
Sources and Sampling Methods: ¹ This Study: Branch beating, <i>N. cunninghamii</i> 70, & <i>N. gunnii</i> 46, site visits over 3 years. ² Majer, Recher & Ganesh, 2000: Chemical knockdown, 10 trees per host species, 4 seasons, 1 year, <i>Eucalyptus</i> . ³ Hammond & Owen, 1996 (in Hammond, Kitching & Stork, 1996): Chemical fogging, 818m ² mixed deciduous canopy, mostly English Oak (<i>Quercus robur</i>). ⁴ Hammond, Kitching & Stork, 1996: Chemical fogging, 110m ² mixed canopy "Argyrodendron actinophyllum alliance, Suballiance 11 (<i>Caldelyvia-Cryptocarya erythroxylon-Orites-Melicope octandra-Acmena ingens</i>)". ⁵ Stork, 1991 (in Hammond, Kitching & Stork, 1996): Chemical fogging, 200m ² canopy from 10 trees of 5 species. ⁶ Erwin & Scott, 1980 (in Hammond, Kitching & Stork, 1996): Chemical fogging, canopies of 19 trees of <i>Luehea seemannii</i> .											

Table 7.5. Feeding guild and taxa structure of Coleoptera in this study and five others from table 7. 4.: Coleoptera species count per tree species per feeding guild (spp.); feeding guilds as a proportion of all species (%); all Coleoptera species, less unknown morphotaxa (spp.*), families (F) and superfamilies (Sf) per tree species.

Finally, using the data from the studies referred to in table 7.5, the species richness of the families were ranked per tree taxon and the most common Coleoptera families among all the tree taxa were identified. A summary of these results was tabulated to show the twelve most common Coleoptera families and the six most speciose families per tree taxon by rank (table 7.6). Five families were found on all tree taxa (Coccinellidae, Chrysomelidae, Curculionidae, Lathridiidae, Nitidulidae), while seven families were absent from one tree taxon (Tenebrionidae from *N. cunninghamii*; Carabidae, Corylophidae, Cleridae, Scarabaeidae, Staphylinidae from *N. gunnii*; Melandryidae from Brunei tropical mixed canopy).

Curculionidae contributed the highest number of species on all tree taxa except for the UK mixed deciduous forest and the Brunei tropical mixed canopy on both of which Staphylinidae was the most speciose family with Curculionidae ranked second. Chrysomelidae was ranked joint first on *N. gunnii*, and also on the tropical *Luehea seemannii* in Panama although this latter tree species had considerably higher species richness. Chrysomelidae was ranked second on *N. cunninghamii* and on the Australian temperate Eucalypts; with Coccinellidae ranked third on these tree taxa and on *N. gunnii*. Curculionidae, Chrysomelidae and Coccinellidae were also the three families with the highest numbers of species on the tree taxa in tropical and subtropical. However, the UK mixed deciduous canopy stood alone in having Lathridiidae ranked third after Staphylinidae and Curculionidae, with Chrysomelidae ranked fifth, behind Cryptophagidae – a family that ranked 15 or more, if it occurred at all, on the other tree taxa.

			Family	Curculionidae*	Staphylinidae*	Chrysomelidae*	Coccinellidae*	Lathridiidae*	Carabidae*	Tenebrionidae*	Scarabaeidae*	Corylophidae*	Cleridae*	Melandryidae*	Nitidulidae*	Anobiidae	Aderidae	Attelabidae	Cerambycidae	Cryptophagidae	Elateridae	Mordellidae	Pselaphidae	Ptilidae	Scirtidae	Anthribidae
Region	Location	Tree Taxon																								
Temperate	1 Tasmania	<i>N. cunninghamii</i>	Rank spp.	1 17	6 4	2 13	3 9	5 5	9 1		9 1	7 3	9 1	9 1	9 1	• •	9 1	• •	• •	• •	6 4	• •	9 1	• •	4 8	9 1
		<i>N. gunnii</i>	Rank spp.	1 6	• •	1 6	3 4	5 2	• •	7 1	• •	• •	• •	5 2	7 1	• •	• •	• •	• •	• •	• •	7 1	• •	• •	3 4	• •
	2 Eastern Australia	<i>E. moluccana</i>	Rank spp.	1 38	8 4	2 26	3 16	17 2	5 6	5 6	8 4	14 3	14 3	24 1	24 1	4 7	• •	8 4	8 4	24 1	8 4	17 2	• •	24 1	• •	• •
		<i>E. crebra</i>	Rank spp.	1 27	4 9	2 21	3 10	23 1	7 6	4 9	8 5	15 3	15 3	23 1	23 1	8 5	23 1	6 7	11 4	18 2	11 4	23 1	• •	18 2	• •	23 1
	2 Western Australia	<i>E. marginata</i>	Rank spp.	1 31	5 4	2 8	3 7	6 3	5 4	6 3	4 5	18 1	6 3	18 1	11 2	6 3	• •	11 2	• •	18 1	• •	11 2	18 1	• •	• •	• •
		<i>E. (Corymbia) calophylla</i>	Rank spp.	1 24	7 2	2 10	3 8	6 3	6 3	6 3	4 4	15 1	4 1	4 1	15 1	15 1	6 3	7 2	15 1	15 1	15 1	• •	7 2	15 1	• •	• •
	3 UK	Mixed Deciduous	Rank spp.	2 19	1 22	5 10	8 9	3 13	10 7	26 2	30 1	19 3	30 1	11 5	16 4	11 5	30 1	19 3	19 3	4 12	10 7	19 3	19 3	5 10	16 4	• •
Subtropical	4 Queensland, Australia	Mixed Canopy	Rank spp.	1 76	2 55	3 30	8 13	14 10	11 11	9 12	33 3	4 27	24 4	9 12	33 3	33 9	16 4	24 10	14 4	24 11	11 6	21 6	6 15	7 14	41 1	5 22
Tropical	5 Brunei	Mixed Canopy	Rank spp.	2 115	1 116	3 97	11 20	49 1	25 9	6 33	38 4	7 31	22 10	• •	15 15	20 11	4 45	16 14	13 18	• •	9 27	10 23	8 29	38 4	29 7	5 39
	6 Panama	<i>L. seemannii</i>	Rank spp.	1 250	3 164	1 ~205	7 36	41 3	6 41	9 33	41 3	27 10	19 12	14 14	11 22	14 14	23 11	57 ?	4 62	29 9	19 12	5 43	34 7	• •	19 12	23 11

Table 7.6. Coleoptera in Temperate, Subtropical and Tropical regions (details ¹⁻⁶ as Table 7.5.): the twelve most common Coleoptera families among the tree taxa (*); and the six most speciose families per tree taxon by rank. Ranks 1-6 in bold, the family with greatest species richness per tree taxon is highlighted in red; 'spp.' denotes the number of species per Coleoptera family per tree taxon.

7.3 ARTHROPOD FAUNA, FEEDING GUILDS: PROPORTIONS BY ABUNDANCE AND SPECIES RICHNESS

Whereas for the species richness data the Tasmanian *Nothofagus* morphotaxa were corrected for overlaps between adults and immatures of the same species, in the feeding guild data adults and immatures of the same species are included where they belong to different guilds. Examining the proportions of Tasmanian *Nothofagus* arthropod feeding guilds by abundance, fungivores/detritivores accounted for nearly two thirds (62.2%) of the arthropod count on *N. cunninghamii* and nearly three quarters (74.2%) of that on *N. gunnii*; predators accounted for over a quarter (28%) of the arthropod count on *N. cunninghamii* and just over a fifth (21.8%) on *N. gunnii*; and herbivores made up the remainder on each *Nothofagus* species (table 7.7).

Feeding Guild	<i>N. cunninghamii</i>		<i>N. gunnii</i>		Total	
	Count	%	Count	%	Count	%
Herbivores Total	1060	9.8	169	4	1229	8.2
Fungivores/Detritivores	6707	62.2	3178	74.2	9885	65.6
Predators	3025	28	934	21.8	3959	26.3
Total	10792	100	4281	100	15073	100

Table 7.7. *Nothofagus* arthropod fauna feeding guilds, taxa abundance. All fieldtrips, all taxa (adults, larvae and miscellaneous immatures): total specimen counts by feeding guild and host plant, and overall.

This contrasts with the New Zealand and Chile *Nothofagus* data of Russell *et al.* (2000) in which herbivores account for 15-68% of arthropods in New Zealand species and 24-82% in Chile; and predators account for 15-49% and 12-59% respectively; fungivores/detritivores are not documented (table 7.8).

Similarly on native Oaks in the UK, phytophages (*Q. petraea* 31.5%; *Q. robur* 27.3%) have been found to be proportionally more numerous, and predators (*Q. petraea* 12.4%; *Q. robur* 10.1%) less so, than herbivores and predators on Tasmanian *Nothofagus*; while epiphyte fauna and scavengers were proportionally more numerous on the introduced oaks (*Q. cerris* 60.3%; *Q. Ilex* 65.5%) than on the UK natives, these levels approaching the Tasmanian *Nothofagus* fungivore/detritivore proportions (table 7.9).

Location	New Zealand					Chile									
Subgenus	<i>Fuscospora</i>					<i>L</i>	<i>F</i>	<i>Lophozonia</i>				<i>Nothofagus</i>			
<div><div><i>Nothofagus</i> Species</div><div>Feeding Guild</div></div>	<i>N. fusca</i>	<i>N. solandri</i>	<i>N. solandri</i> var. <i>cliff</i>	<i>N. truncata</i>	<i>N. menziesii</i>	<i>N. alessandri</i> *	<i>N. alpina</i> *	<i>N. glauca</i> *	<i>N. leoni</i> *	<i>N. obliqua</i> *	<i>N. antarctica</i> *	<i>N. betuloides</i>	<i>N. dombeyi</i>	<i>N. nitida</i>	<i>N. pumilio</i> *
Total Abundance	112	205	230	75	124	64	182	54	238	512	553	217	158	101	490
Leaf Chewers (%)	67	34	11	36	60	17	25	13	19	15	68	11	17	19	11
Sap-suckers (%)	1	3	4	2	2	19	11	11	17	35	14	41	23	17	63
Predators (%)	23	49	30	39	15	58	51	52	59	33	12	36	46	43	17
Others (%)	9	14	55	23	23	6	13	24	5	17	6	12	14	21	9

Table 7.8. Feeding guilds on New Zealand and Chilean *Nothofagus*: proportion of total abundance per guild per tree species. * Denotes deciduous species. Data from Russell *et al.*, 2000, table 2, p 48; two samples by branchlet shaking, from 5 trees per species, December 1995 and February 1996.

Feeding Guild	<i>Q. petraea</i>	<i>Q. robur</i>	<i>Q. cerris</i> [#]	<i>Q. ilex</i> [#]
Phytophages	31.5	27.3	16.9	14.1
Predators	12.4	10.1	9.1	8.9
Parasitoids	13.7	12.4	6.8	2.5
Scavengers	3.2	3.5	4	4
Epiphyte Fauna	34.3	43.9	60.3	65.5
Tourists	4.9	2.8	2.9	5
Total number (%)	100	100	100	100

Table 7.9. Feeding guild proportions by abundance, (count per guild per tree species) found on four species of oak in the UK. Source: Southwood *et al.*, 2005, table 7, p.70; sampling by chemical knockdown, spring-autumn over 5 years, 1980 – 1984 (details in Southwood *et al.*, 2004). [#] Denotes introduced tree species.

However, the proportions by abundance of leaf chewers on *N. cunninghamii* (4.99%) and *N. gunnii* (2.34%) fall within the proportions of leaf chewers on subtropical tree taxa in Papua New Guinea (table 7.10). In particular, the proportion of leaf chewers on *N. cunninghamii* closely matches that on *Castanopsis acuminatissima*, a member of the Fagaceae.

Host Tree	Tree Family	Leaf Chewers			Insects Total
		Species	Ind.	% of Total	
<i>N. cunninghamii</i>	Nothofagaceae	52	538	4.99	10792
<i>N. gunnii</i>	Nothofagaceae	18	100	2.34	4281
<i>Elmerrilla tsiampacca</i>	Magnoliaceae	20	75	1.08	6920
<i>Cinnamomum</i> cf. <i>culilaban</i>	Lauraceae	37	212	3.04	6974
<i>Piper plagiophyllum</i>	Piperaceae	18	339	3.62	9361
<i>Ficus nodosa</i>	Moraceae	61	517	6.80	7606
<i>Pipturus argenteus</i>	Urticaceae	52	629	8.05	7816
<i>Castanopsis acuminatissima</i>	Fagaceae	94	408	4.57	8936
<i>Caldcluvia brassii</i>	Cunoniaceae	39	454	9.66	4699
<i>Aleurites moluccana</i>	Euphorbiaceae	25	111	1.26	8839
<i>Melicope denhamii</i>	Rutaceae	36	335	4.50	7449
<i>Cordia dichotoma</i>	Boraginaceae	45	262	3.67	7136

Table 7.10. Leaf chewers on Tasmanian *Nothofagus* compared with those collected in tropical submontane forest in Papua New Guinea: counts of species and individuals (Ind.) per host tree and their proportion of all insects collected.

Source for Papua New Guinea data: Basset, Samuelson & Miller, 1996, table 1, p. 162; sampling by hand collecting, beating, branch clipping, flight intercept traps, chemical knockdown, varying sampling frequencies between January 1992 and April 1993.

Herbivore Guild	<i>N. cunninghamii</i>	<i>N. gunnii</i>	Total
Leaf Chewers:			
Coleoptera (adults)	33	14	39
Coleoptera (immatures)	4	0	4
Lepidoptera (immatures)	15	4	17
Leaf Chewers Total	52	18	60
Leaf Miners:			
Lepidoptera (immatures)	2	0	2
Leaf Miners Total	2	0	2
Sap-suckers:			
Hemiptera (adults)	21	12	26
Hemiptera (immatures)	5	2	5
Thysanoptera (adults)	12	7	14
Thysanoptera (immatures)	3	1	3
Sap-suckers Total	41	22	48
All Folivores	95	40	110
Nectivores:			
Coleoptera (adults)	1	1	2
Lepidoptera (adults)	33	5	37
Nectivores Total	34	6	39
All Herbivores	129	46	149

Table 7.11. Tasmanian *Nothofagus* arthropod fauna, herbivore feeding guild diversity: morphotaxa per order (adults or immatures) and per feeding guild, with totals for all folivores and all herbivores; per *Nothofagus* species and overall.

The Tasmanian *Nothofagus* herbivores were then subdivided into folivores – leaf chewers, leaf miners, sap-suckers – and nectivores, by species richness and by family (table 7.11) for comparison with data from the Phytophagous Insect Data Bank, which documents (from literature searches) phytophagous arthropods that have been associated with plant taxa, native and introduced, in the UK (table 7.12). This revealed that on UK native tree taxa within the Fagales, and introduced species including *Nothofagus* and *Eucalyptus*, Lepidoptera accounted for the majority of phytophagous/folivorous species; as opposed to Coleoptera being the most speciose family on *N. cunninghamii* and *N. gunnii*, unless nectivores are included in ‘phytophages’ (tables 7.11 and 7.12). Of the sap-suckers, more Hemiptera have been found on UK Fagales compared with *N. cunninghamii* and fewer Thysanoptera species than on either Tasmanian *Nothofagus* species (tables 7.11 and 7.12).

Tree species Order	UK Native								Introduced							
	<i>Betula pendula</i>	<i>Betula pubescens</i>	<i>Betula</i> Mean	<i>Fagus sylvatica</i>	<i>Quercus petraea</i>	<i>Quercus robur</i>	<i>Quercus</i> Mean	UK Natives Mean	<i>Castanea sativa</i>	<i>Eucalyptus</i> spp.	<i>Nothofagus</i> spp.	<i>Nothofagus obliqua</i>	<i>Nothofagus procera</i>	<i>Nothofagus</i> Mean	<i>Quercus ilex</i>	Introduced spp. Mean
Acari	6	4	5	5	0	5	2.5	4	0	0	0	0	0	0	1	0.2
Coleoptera	29	15	22	81	23	29	26	35.4	11	0	3	3	3	3	11	5.2
Diptera	8	9	8.5	7	9	11	10	8.8	0	0	0	0	0	0	2	0.3
Hemiptera	35	30	32.5	22	26	36	31	29.8	25	5	2	6	6	4.7	2	7.7
Hymenoptera	8	4	6	1	45	43	44	20.2	0	0	0	0	0	0	3	0.5
Lepidoptera	131	74	102.5	81	49	124	86.5	91.8	37	1	3	22	13	12.7	24	16.7
Thysanoptera	0	0	0	0	0	3	1.5	0.6	0	0	0	0	0	0	0	0.0
Total	217	136	176.5	197	152	251	201.5	190.6	73	6	8	31	22	20.3	43	30.5
<i>Total less Diptera & Hymenoptera</i>	<i>201</i>	<i>123</i>	<i>162</i>	<i>189</i>	<i>98</i>	<i>197</i>	<i>147.5</i>	<i>161.6</i>	<i>73</i>	<i>6</i>	<i>8</i>	<i>31</i>	<i>22</i>	<i>20.3</i>	<i>38</i>	<i>29.7</i>

Table 7.12. Arthropods associated with trees in the UK, five native and six introduced tree taxa: number of arthropod species per tree taxon. Source: PIDB: Phytophagous Insect Data bank. www.brc.ac.uk/dbif. Accessed 2.iv.2011.

7.4 HERBIVORY LEVELS

The overall herbivory levels on Tasmanian *Nothofagus* were compared with those found by Lowman (1984, 1985b) on tree species in cool temperate, warm temperate and subtropical rainforest in mainland Australia (table 7.13). The herbivory levels on *N. gunnii*, at 3.2%, were closest to the subtropical deciduous *Toona australis* (4.5%), both having considerably lower herbivory levels than the other species (table 7.13). Herbivory levels on *N. cunninghamii* (16.2%) were comparable with *Doryphora sassafras* in each region (13.6 - 22.7%) and with the warm temperate *Ceratopetalum apetalum* (22%), but about one third that of the subtropical *Dendrocnide excelsa* (42%) and half that of sister species in the subgenus *Lophozonia*, *Nothofagus moorei* (31%) (table 7.13).

Climatic Region	Tree Order	Tree Family	Tree Species	%LAL
Cool temperate	Fagales	Nothofagaceae	<i>Nothofagus cunninghamii</i>	16.2
	Fagales	Nothofagaceae	<i>N. gunnii</i> *	3.2
Cool temperate	Fagales	Nothofagaceae	<i>N. moorei</i>	31
	Laurales	Atherospermataceae	<i>Doryphora sassafras</i>	13.6
Warm temperate	Laurales	Atherospermataceae	<i>D. sassafras</i>	22.7
	Oxidales	Cunoniaceae	<i>Ceratopetalum apetalum</i>	22
Subtropical	Rosales	Urticaceae	<i>Dendrocnide excelsa</i>	42
	Laurales	Atherospermataceae	<i>D. sassafras</i>	15
	Salpindales	Meliaceae	<i>Toona australis</i> *	4.5

Table 7.13. Levels of herbivory, measured as % Leaf Area Loss (%LAL), in Australian rainforest trees (source Lowman, 1984, 1985b) compared with Tasmanian *Nothofagus*.

* Denotes deciduous species.

Rinker and Lowman (2004) summarised herbivory results from several forest types. Compared with these levels, *N. gunnii* remained at the lower end of the scale of herbivory sustained, but *N. cunninghamii* sat within the range of herbivory levels on temperate deciduous forest and subtropical forest, and approached that of warm temperate forest (table 7.14).

Forest Type	% Herbivory	Source
Australian Dry Forest	13 – 300% ⁺	(Lowman & Heatwole, 1992)
Australian Wet Forest	8.60%	(Shaw, Ernest, Rinker & Lowman, pers. comm.)
Temperate Deciduous Forest	15%	(Lowman 1999)
Pacific Northwest	1.6%	(Shaw, Ernest, Rinker & Lowman, pers. comm.)
Cloud Forest	26%	(Lowman, 1992)
Subtropical Forest	16%	(Lowman, 1985a)
Warm Temperate Forest	21%	(Lowman, 1985a)
Tropical Forest	12 - 300% ⁺	(Lowman, 1995b)

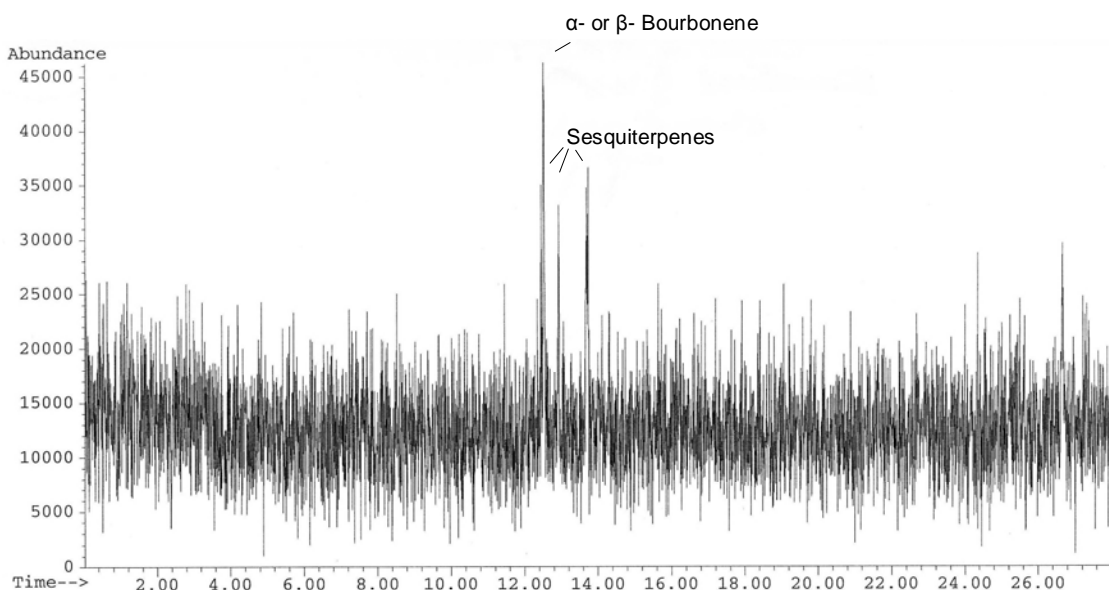
Table 7.14. Herbivory in different forest types (after Rinker & Lowman, 2004, Table 18.1, p 368). ⁺ Australian Eucalypts can re-foliate successively after leaf loss, hence such high herbivory levels.

7.5 DEFENSIVE PHYTOCHEMISTRY

A full investigation of phytochemical defences in Tasmanian *Nothofagus* was not within the remit of this research project. However in December 2000, a single sample set was analysed for volatile compounds and waxes from leaves of *N. cunninghamii* (collected from Lake Fenton and Lyrebird walk) and *N. gunnii* (collected from Lake Fenton), as described in Appendix 8 Analysis of *N. cunninghamii* and *N. gunnii* Leaf Volatiles & Waxes.

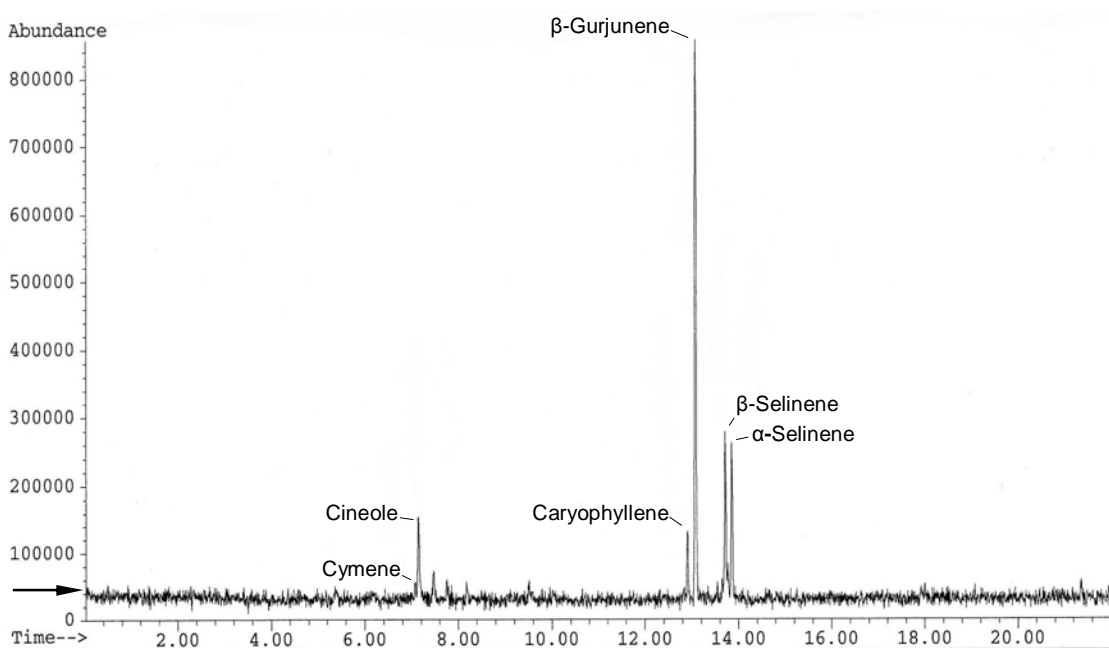
These analyses revealed that the two species differed strongly in their young leaf chemistry (figure 7.2, table 7.15). The aromatic leaves of *N. gunnii* were found to have a characteristic profile and strong concentrations of volatiles, particularly the cyclopropane β -Gurjunene; also the sesquiterpenes Caryophyllene, α -Selinene and β -Selinene; and to a lesser extent, the monoterpenes Cineole and Cymene. In contrast, *N. cunninghamii* had a smaller range of volatiles: sesquiterpenes in low concentration, with α - or β - Bourbonene the most abundant.

The species also differed strongly in the higher molecular weight sesquiterpene oils and cuticular leaf waxes (figure. 7.3, table 7.16). *N. gunnii* was characterised by a blend sesquiterpenes, which were minimal in the *N. cunninghamii* leaves. Both species shared a similar profile of mid-molecular weight waxes although concentrations were again considerably lower for *N. cunninghamii*, especially for its young leaves.



a.

N. cunninghamii young leaves



b.

N. gunnii early summer leaves

Figure 7.2. a & b. *Nothofagus* leaf volatiles. Leaves collected in early summer 2000: *N. cunninghamii* (a) and *N. gunnii* (b).

Of note is the difference in the abundance scales on the y-axes: the arrow (→) in (b) marks the approximate peak of the *N. cunninghamii* volatiles compared with those of *N. gunnii*.

Chemical analysis c/o Associate Professor Noel Davies, Central Science Laboratory, University of Tasmania, see Appendix 7.

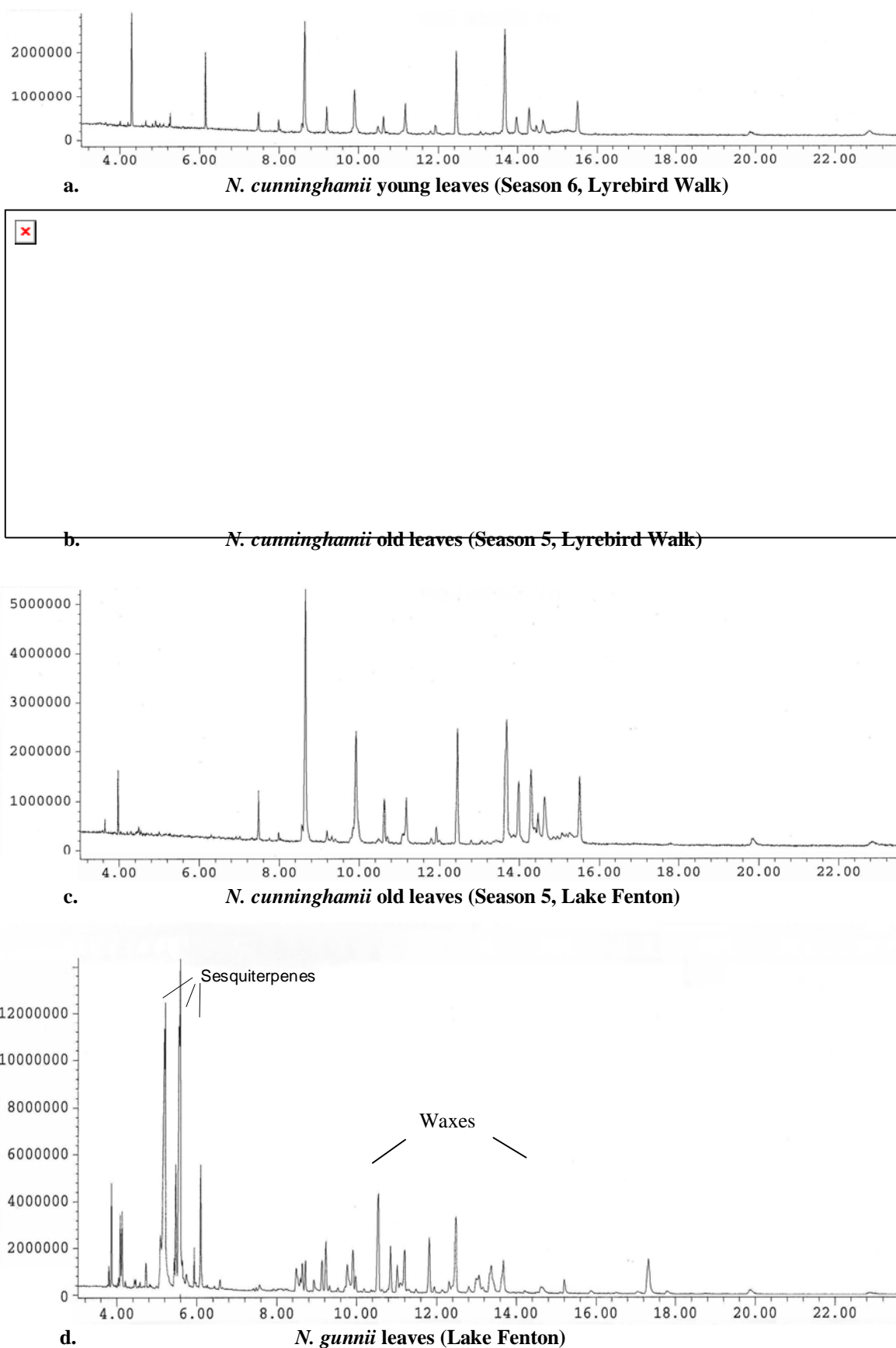


Figure 7.3. a – d. *Nothofagus* leaf waxes. Leaves collected in early summer 2000: *N. cunninghamii* from Lyrebird Walk (a, b) and Lake Fenton (c); *N. gunnii* from Lake Fenton (d). x-axes: elapsed time; y-axes: compound abundance. The arrow (→) in (d) marks the approximate peak of the *N. cunninghamii* waxes (b, c) compared with those of *N. gunnii*. Chemical analysis c/o Associate Professor Noel Davies, Central Science Laboratory, University of Tasmania, see Appendix 7.

7.5.1 Comparison with Other Tree Species: Leaf Volatiles

The terpenoids found in the *N. gunnii* leaves occur in several Australian tree genera (table 7.15); while β -gurjunene is found in addition to α - and β - Selinene, Cineole and Cymene, in the Tasmanian Blue Gum, *Eucalyptus globulus*.

Order	Family	Chemical Class	Cyclo- propane	Mono- terpenes		Sesquiterpenes						
		Chemical Species	β -gurjunene	Cineole	Cymene	Caryophyllene	α - Bourbonene /	β -Bourbonene	α -Selinene	β -Selinene	Unknown 1	Unknown 2
Fagales	Nothofagaceae	<i>N. gunnii</i>	+++++	+	+	+			+++	+++		
		<i>N. cunninghamii</i>					+				+	+
Myrtales	Myrtaceae	<i>E. globulus</i>	•	•	•			•	•	•		
		<i>Eucalyptus</i> spp		•	•	•						
		<i>Leptospermum</i> spp			•	•				•		
		<i>Melaleuca</i> spp		•	•							
Pinales	Cupressaceae	<i>Callitris</i> spp							•	•		
	Podocarpaceae	<i>Microstrobos</i> spp			•							

Table 7.15. Leaf volatiles extracted by SPME from *N. cunninghamii* and *N. gunnii*. + denotes relative amounts of the chemicals (see also figure 7.2; Appendix 8).

• denotes the presence of these chemicals in other tree species occurring in Australia (sources: The Good Scents Company. <http://www.thegoodscentscompany.com>. Accessed 4.iv.2011. The PubChem Project. <http://pubchem.ncbi.nlm.nih.gov/>. Accessed 4.iv.2011).

Analysis of leaf volatiles associated with South American *Nothofagus* species (Quiroz *et al.*, 1999) has shown that the leaves of *N. glauca* and *N. obliqua* (both subgenus *Lophozonia* and deciduous) are very well endowed with sesquiterpenes, having considerably more sesquiterpenoid compounds than either *N. cunninghamii* or *N. gunnii*, or the remaining South American species (table 7.16). Few monoterpenes were found, the highest number being four compounds in *N. dombeyi* leaves.

7.5.2 Comparison with Other Tree Species: Leaf Phenolics

Nothofagus leaf exudates, including waxes, have been found to contain flavonoids and other feeding-deterrent phenolic compounds (Russel *et al.*, 2000; Wollenweber *et al.*, 1997; Wollenweber *et al.*, 2003).

Wollenweber *et al.* (2003) found that the flavonol Galangin and its derivatives occurred most widely in their study of eleven species of *Nothofagus*; followed by the

flavonone Pinocebrin (table 7.17). The flavonoid profile of *N. cunninghamii* most closely resembled those of its sister species within the subgenus *Lophozonia*; while that of *N. gunnii* strongly resembled the profiles of three sister species in the subgenus *Fuscospora*: *N. alessandri*, *N. fusca* and *N. solandri*.

Region	Nothofagus species	Monoterpenes	Sesquiterpenes
Tasmania	<i>N. gunnii</i> *	••	•••
	<i>N. cunninghamii</i>		•••
South America	<i>N. alessandri</i> *	•	
	<i>N. glauca</i> *	••	••••••••
	<i>N. obliqua</i> *	••	••••••••
	<i>N. antarctica</i> *	••	•••
	<i>N. dombeyi</i>	••••	•
	<i>N. pumilio</i> *	•••	••••

Table 7.16. Occurrence of leaf volatiles associated with eight species of *Nothofagus* (* deciduous species. Subgenera: blue - *Nothofagus*; orange - *Fuscospora*; green - *Lophozonia*). • denotes a single compound within the chemical class. Sources: Tasmanian species: this study; South American *Nothofagus* species: Quiroz *et al.* 1999, table 2, pages 1049-1051.

Chemical Class	Flavonols						Flavones		Flavanones	Flavandols	Chalcones	Stilbenes
Chemical <i>Nothofagus</i> species	Galangin	Kaempferol	Herbacetin	Quercetin	Myricetin	Other flavonols	Apeigenin	Other flavones	Pinocebrin	Pinobanksin	Chalcone spp	Pinosylvin
<i>N. antarctica</i> *	Xxx			x	Xx				X			
<i>N. alessandri</i> *	Xxxxx(x)								(X)		(x)	X
<i>N. fusca</i>	Xxxxx(x)								X		x	X
<i>N. gunnii</i> *	Xxx								X		(x)	X
<i>N. solandri</i>	Xxxxxxxxx							x	Xx	X		(X)
<i>N. truncata</i>	xxx	x										
<i>N. cunninghamii</i>		xxx		xxx			Xx	xx				
<i>N. menziesii</i>	x	xxx	xx	x		xx	Xxx					
<i>N. moorei</i>			X	(X)x		x						
<i>N. nervosa</i>	x	xxx	Xx	x		xx	Xxx		X			
<i>N. obliqua</i> *		X		Xx(x)(x)					X			

Table 7.17. Occurrence of flavonoid compounds associated with eleven species of *Nothofagus* (* deciduous species. Subgenera: blue - *Nothofagus*; orange - *Fuscospora*; green - *Lophozonia*). 'X' denotes the presence of the named chemical; and 'x' where appropriate, denotes the presence of derivatives of that chemical. X/x - major constituents; (X)/(x) - minor constituents. Source: Wollenweber *et al.* 2003, table 1, page 1127.

7.6 SUMMARY OF COMPARISONS WITH OTHER TAXA

Direct comparisons between studies of canopy arthropod fauna are difficult because of the differences in sampling methods and their duration. However, given these constraints, and compared with the vast samples obtained with chemical fogging, the species richness on *N. cunninghamii* was comparable with that found on some *Eucalyptus* (Majer, Recher & Ganesh, 2000) and *Acacia* (New, 1979) species in temperate Australia, although it was far less than the species richness on tropical and subtropical tree taxa. The canopy arthropod fauna on *N. gunnii* was considerably less diverse than the other tree taxa.

Comparisons of feeding guild structure revealed that Tasmanian *Nothofagus* species had higher proportions of Fungivores/Detritivores than New Zealand or Chilean *Nothofagus* (Russell *et al.*, 2000), or British Oaks (Southwood *et al.*, 2005). The most diverse of the folivore orders on Tasmanian *Nothofagus* was Coleoptera, compared with Lepidoptera on UK Fagales (PIDB).

Herbivory levels on *N. cunninghamii* were within the range of those on temperate deciduous forest and subtropical forest, and approached that of warm temperate forest (Rinker & Lowman, 2004). Herbivory levels on *N. gunnii* however, were considerably lower than those on most other tree taxa.

In keeping with several *Nothofagus* species, a range of leaf volatiles occurred in *N. gunnii* leaves and the profile is similar to other Australian tree genera. Compared with *N. gunnii*, the leaves of *N. cunninghamii* had a narrower range, and considerably lower concentrations, of both leaf volatiles and cuticular waxes. The profiles of leaf phenolic compounds for each of the Tasmanian *Nothofagus* species has been found to most closely resemble sister species of their respective subgenera (Wollenweber *et al.*, 2003).

Chapter 8 DISCUSSION AND CONCLUSIONS

This study has documented in detail the diversity and structure of the invertebrate communities associated with two species *Nothofagus* over their Tasmanian range. By selecting a cross section of survey sites, including some where the hostplants are sympatric, the confounding influence of spatial effects has been minimised. This has allowed a comprehensive test of the four key research questions posed at the beginning of this thesis.

The first of the research questions - whether either or both of the Tasmanian *Nothofagus* species are indeed depauperate in their arthropod fauna compared with tree taxa elsewhere - was initially addressed with a general overview of the data. Then, in order to engage the subsequent research questions - which compared the arthropod fauna, herbivory levels and regionality of the two *Nothofagus* species - the data were explored in greater depth with more detailed analyses. This led to deeper insights into the structure of canopy arthropod communities of *N. cunninghamii* and *N. gunnii*.

8.1 RESEARCH QUESTION 1.

Is the Tasmanian *Nothofagus* Arthropod Fauna Truly Depauperate?

There was a strong contrast in the diversity and taxonomic profile of the arthropod fauna between the two *Nothofagus* species. For *N. cunninghamii*, the associated fauna was relatively rich in taxa and comparable with other temperate zone trees in both its diversity and guild structure (sub-chapters 7.1, 7.2, 7.3). Similarly estimates of the *N. cunninghamii* herbivory levels, a measure of the influence of the associated phytophagous taxa, were within the range of those reported from temperate and subtropical tree taxa elsewhere (sub-chapter 7.4). However, *N. gunnii* was clearly depauperate in comparison, particularly lacking many important folivorous groups such as chrysomelid beetles, leafminers and aphids.

There are a number of possible reasons why the Tasmanian *Nothofagus* species would be more, or less, well endowed with an associated arthropod fauna. At this stage a general overview is worthwhile, as an outline of the main issues, taking

account of the taxonomy and palaeohistory of the genus *Nothofagus* as set out in Chapter 2 and the synopsis of arthropod-plant interactions presented in Chapter 3.

The fossil record in Australia reveals *Nothofagus* to have shown long persistence, high diversity and widespread distribution since the Cretaceous (Hill, 2001). With such a history, this southern Fagalean tree genus could be expected to have accreted a large and diverse arthropod fauna. Indeed, extant members of Fagales in the northern hemisphere support many of the most basal arthropod families (Imada *et al.*, 2011). Consequently the opportunity exists for Fagales, including *Nothofagus*, to have accumulated herbivores and an associated arthropod fauna over a very long period of time. Additionally, while *Nothofagus* was undergoing contraction in diversity and area of occupation during the warming and drying climates of the Tertiary (conditions associated with loss of arthropod fauna) its southern sister family in the Fagales, Casuarinaceae, was concurrently expanding in Australia (Hill, 2004). *Nothofagus* has readily recruited herbivores when planted extra-limitally (Welch & Greated-Davies, 1993) and so Casuarinaceae, being a related family and of similar life form, could potentially have supported a residual species pool, helping to maintain the diversity of arthropods on *Nothofagus*.

Conversely, there are arguments favouring a depletion of the arthropod fauna on *Nothofagus*, particularly in Tasmania. Casuarinaceae notwithstanding, *Nothofagus* is taxonomically isolated within the extant Australian flora. With the exception of *Lithocarpus* and *Castanopsis* which enter the New Guinea highlands from SE Asia (Allison *et al.*, 1997), its other sister genera including the broadleaved Fagales are confined to the northern hemisphere. In addition, Australia underwent a diminution in *Nothofagus* species diversity and area of occupation during Tertiary, at a time when the continent became cut off from other sites of *Nothofagus* (Veblen *et al.*, 1996a). Within Tasmania, further contraction to isolated refugia during the glacial cycles of the Pleistocene (Kirkpatrick & Fowler, 1998), has been compounded by its insularity, with isolation from mainland Australia since that time (Lambeck & Chappell, 2001). In this regard, the longevity of the genus would have acted against maintaining a diverse arthropod fauna, as island populations tend to lose species over time due to the island area effect and stochastic losses due to smaller population sizes (Whittaker, 1998; Gurd, 2006).

Thus, circumstances favouring a potentially diverse arthropod fauna on Tasmanian *Nothofagus* include: the longevity of the genus; its former history of wide diversity and distribution; and associated tree genera providing a potential pool from which to recruit canopy arthropod taxa. In contrast, factors promoting a depauperate arthropod fauna on Tasmanian *Nothofagus* include: the relative taxonomic isolation of the genus; the reduction in its species diversity and distribution over time; and its modern insularity.

Both sets of factors are likely to have acted upon both *N. cunninghamii* and *N. gunnii*. Clearly, for there to be such a contrast in the arthropod fauna between the two, local factors including attributes of each species, have had a major influence in addition to the issues above. Subsequent research questions explored these differences between *N. cunninghamii* and *N. gunnii* in greater detail.

8.2 RESEARCH QUESTION 2.

Within That Fauna, Do *N. cunninghamii* and *N. gunnii* Have Characteristic but Different Core Species Organised in a Similar Way?

As members of the same ancient and once widespread tree genus, *N. cunninghamii* and *N. gunnii* might be expected to have similar canopy arthropod faunas and indeed, the two *Nothofagus* species shared nearly a quarter of the of all the morphotaxa found in this study. However, while there was greater morphotaxon richness and morphotaxon abundance on *N. cunninghamii* than on *N. gunnii* in all orders except Plecoptera, the *N. gunnii* arthropod fauna was not a subset of that on *N. cunninghamii*, i.e. they were quite distinct (see ordination figures 5.2.1 & 2). For example, Acarina was the most abundant order found on both *N. cunninghamii* and *N. gunnii*, but different mite morphotaxa predominated on each *Nothofagus* species.

Within the context of this research question, core species were regarded as those known to be monophagous on one or other *Nothofagus* species as well as other morphotaxa which were abundant and/or widespread on either of the tree species, whether herbivores, fungivores/detritivores or predators. Although the monophages are most clearly associated with a tree species, the fungivores/detritivores of the

tree's epiphytic flora and the predators upon those taxa form an important and distinctive part of the community.

The above definition of the term 'core', which includes host specificity, abundance and occurrence, differs from that coined in the original core-satellite hypothesis of Hanski (1982a). Used in analyses of patterns of a species' regional distribution, or occupancy (e.g. Hanski, 1982a, 1982b; Hanski & Gyllenberg, 1993; Ulrich & Zalewski, 2006), the terms 'core' and 'satellite', as originally defined, refer to classes of species' occupancy distribution: core species having the highest percentage occupancy, satellite species the lowest. This study of *Nothofagus* canopy arthropod fauna did not specifically set out to test a species' occupancy distribution or the validity of the core-satellite hypothesis, however the concept of 'satellite' species is perhaps of relevance if taken to its extreme – the singleton specimen of a morphotaxon.

Two fifths of the morphotaxa collected from *N. cunninghamii* and *N. gunnii* were represented by singletons. This could have been an artefact of the sampling protocol: large numbers of small sample units spread over a large area may bias towards satellite species, as can a high proportion of tourist species in the sample (McGeoch & Gaston, 2002). Alternatively, biological factors might be implicated, including differences in local habitat and climate at the sampling sites, a wide distribution of the sites within the geographic range of a species, or a high proportion of sampling at the edge of a species' range: any of which may result in a bias towards satellite species (McGeoch & Gaston, 2002). In their study of insect herbivores on thirty species of tropical trees and shrubs, Novotný and Basset (2000) found that the average proportion of rare (singleton) herbivore species was 45%, and that these comprised both monophages and generalist feeders on a given plant species. They also found that while a herbivore species might be rare on one plant host, it could be common on another, frequently related, host (Novotný & Basset, 2000). In addition, mobile species which occur in the general habitat can exploit the host trees as resting sites and hence be represented as haphazard occurrences in samples. Examples in this study would be stoneflies at locations close to water and moths with ground dwelling litter-feeding larvae.

In addition to the herbivores reliant on *Nothofagus* foliage there is a diverse fauna of additional species, sometimes overlooked, which depend upon other resources supported by the host tree. Notable among these are the fungivore/detrivore taxa associated with epiphytic plants, tourist taxa which enter the tree-based foodweb indirectly, and the predatory taxa, especially the spiders.

Most sampling methods of the arboreal fauna in trees will yield numerous invertebrates associated with foodwebs dependent upon the epiphytic flora (Coy *et al.*, 1993). The epiphytic micro-flora of *Nothofagus*, over most of its range, comprises a rich diversity of lichens, algae, epiphyllous fungi and bryophytes (Galloway, 1988; Marshall & Beehler, 2007; Morley & Gibson, 2010) and is responsible for hosting numerous arboreal arthropods (Coy *et al.*, 1993). The cool humid microclimate maintained by these forests favours abundant epiphytes which may achieve a considerable biomass and be important in nutrient capture and recycling (Cornelissen *et al.*, 2007; Michel *et al.*, 2011). Macrolichens on South American *Nothofagus*, at similar latitudes to Tasmania, grow year round but fastest in winter (Caldiz, 2004) when foliage growth is dormant or at a minimum.

The corticolous lichen flora on *Nothofagus* is relatively well documented in Tasmania (Kantvilas, 1990; Kantvilas & Jarman, 1993) and Victoria (Milne & Louwhoff, 1999; Morley & Gibson, 2010) where it is known to differ strongly from that of other tall trees in wet forests with persistent bark such as *Eucalyptus obliqua*, on which the lichen flora is depauperate (Kantvilas & Jarman, 2004); however, the epiphytic flora of *Nothofagus cunninghamii* is somewhat similar to *Atherosperma moschatum* which can be a canopy co-dominant (Morley & Gibson, 2010) and the rainforest podocarp *Lagarostrobos franklinii* (Jarman & Kantvilas, 1995), suggesting relatively low host specificity.

As trees age, the epiphytic flora becomes more diverse and usually increases in biomass, generating a greater variety of microhabitats and food diversity for invertebrates. The bark texture of *N. cunninghamii* changes with tree size and age, becoming more complex and offering a greater range of microhabitats over time. In addition to the water content of the substrate, these changes are important for epiphytic lichen communities in Tasmanian rainforest (Kantvilas & Minchin, 1989) and a single *N. cunninghamii* tree can support 50 species of lichens (Kantvilas,

1990). Small to medium sized trees have mostly smooth textured bark, but in larger trees deeper fissures begin to form in the bark along with bryophyte mats. In very large trees, deeply dissected ‘plates’ of bark that are easily dislodged from the tree begin to form. This diversity is reflected in the lichen flora which grows on the bark (Morley & Gibson, 2010). Smooth barked outer branches and leaf-bearing twigs were the most commonly sampled item in this study and these are characterised by a community of pioneer crustose lichens such as *Opegrapha stellata* and *Coccotrema cucurbitula* sometimes supplemented by foliose *Usnea* spp. (Kantvilas & Minchin, 1989; Kantvilas, 1990).

The black, felt-like sooty moulds, saprophytic ascomycete fungi largely dependent upon honeydew, are ecologically important in many *Nothofagus* forests, especially in New Zealand (Morales *et al.*, 1988) where they form an important resource for many insects (Didham, 1993) and yeasts (Serjeant *et al.*, 2008). In Tasmania, only *N. cunninghamii* supports sooty moulds as a result of hosting sap-sucking hemipterans such as eriococcid scale insects and aphids. However, the biomass of sooty moulds in Tasmania never approaches that seen in parts of New Zealand where dense aggregations of the sooty beech scale insect (*Ultracoelostoma* spp.: Margarodidae) infest the trunks and branches of *Nothofagus* trees (Morales *et al.*, 1988). The very low numbers of arboreal ants taken in Tasmanian canopy samples is consistent with findings in other *Nothofagus* biomes (Moeed & Meads, 1983; Majer *et al.*, 2001, Ward, 2009) and contrasts strongly with the large numbers of ants associated with honeydew in eucalypt forests (Buckley, 1987). In effect, it may be an under-exploited resource for social insects. The attendance of the ant *Camponotus chilensis* at a pseudococcid (*Eurycoccus chubutensis*) on the roots of *N. dombeyi* is one of the few observations of such an interaction in austral beech forests (Granara de Willink & Miller, 2004). The comprehensive sequestering of the honeydew resource by introduced social wasps (*Vespula* spp.) in New Zealand forests has had serious knock-on effects resulting in recalibration of the foodweb in these forests.

The most abundant free-living invertebrates on Tasmanian *Nothofagus* trees were mites (Acarina), notably members of the suborder Oribatida, and were generally associated with epiphytic plants. Oribatid mites similarly dominate comparable

communities on tall trees in the wet forests of cool temperate North America (Winchester, 1997, 2006) and this may be a feature of temperate forests more broadly (Behan-Pelletier *et al.*, 2008). The 29 morphotaxa of *Nothofagus* oribatids reported here is double the diversity reported for arboreal oribatids recorded from epiphytic lichens in old-growth wet forest canopy trees in British Columbia (Lindo & Stevenson, 2007). Little overlap between the ground litter oribatid fauna and that in the canopy was noted in the Canadian forest. The food preferences of litter oribatids can be related to their body size, with the largest species directly consuming detritus and dead organic matter, mid-sized species consuming fungal hyphae and the smallest species feeding upon fungal spores; facultative predation on small collembolans and other tiny organisms is also reported (Walter & Proctor, 1999). Many oribatids also specialise on lichens (Seyd & Seaward, 1984). The asexual diaspores (soredia) of some corticolous lichens are spread by oribatid mites (Stubbs, 1995) and soredia have been observed attached to the exterior of other invertebrates including psocids (Gerson & Seaward, 1977) while some oribatids are implicated in dispersing both partners of lichen symbiosis via their faecal pellets (Meier *et al.*, 2002). Spore feeding mites are associated with sooty moulds in New Zealand (Clark, 2009, 2010) but no information is available for Australia.

The largest invertebrate members of these epiphyte-based foodwebs are the lichenivorous larvae of several species of moths, notably Arctiidae-Lithosiinae and Psychidae-Taleporinae (Common, 1990). At least four species of lithosiine arctiid moths are known to inhabit Tasmanian rainforests (Marriott, 2009). Lithosiine larvae elsewhere are known to make choices among lichens as food sources (Pöykkö & Hyvärinen, 2003) but no information is available on host specificity in the Australian fauna. However, it is clear that the high diversity of lichens in Tasmanian rainforests is not reflected in a corresponding increase in lithosiine diversity. Taleporiine psychid moth (*Narycia* spp.) larvae live within portable silken fusiform sheaths decorated with fragments of lichen or detritus. [Naryciinae are paraphyletic with respect to Taleporiinae (Mutanen *et al.*, 2010)]. Little can be said about the diversity of this group within Tasmanian at this time.

Non-phytophagous beetles on the trees include mite predators such as pselaphids and scydmaenids. A suite of small beetles (3-4 mm in length) are associated with

sooty moulds on *Nothofagus* in New Zealand and elsewhere including Derodontidae, Phloeostichidae, Nitidulidae, Phalacridae and Colydiidae (Lawrence, 1985) as well as various Staphylinidae, Salpingidae, Silvanidae, Cryptophagidae, Latridiidae and others (Crowson, 1984). Nitidulid sap beetles (genus *Soronia* and allies) are associated with sooty mould on *Nothofagus* in New Zealand (Carlton & Leschen, 2007) and Tasmania.

Psocid booklice (Psocoptera) are also known to eat sooty moulds (Thornton, 1985) and the ready availability of this resource on *N. cunninghamii* could explain why psocids are most diverse and abundant on this host. Although psocids also consume lichens (Laundon, 1971), they were notably scarce on *N. gunnii*. Conversely, the absence of aphids and paucity of scale insects on *N. gunnii* explains the virtual absence of sooty moulds from this tree and a consequently limited variety of small fungivorous beetles.

Springtails (Collembola) are diverse in Tasmanian rainforests (Coy *et al.*, 1993) and were abundant on both trees but the proportions of suborders differed strongly between them. The Symphypleona (cf *Katianna* and other globular forms) were best represented on *N. gunnii* but for reasons that are unclear. Some members of this group can erode the epidermis of living leaves (Ireson, 1993) but others are thought to be fungivorous or detritivorous (Greenslade & Ireson, 1986). The low stature of *N. gunnii* may also assist its colonisation by particular terrestrial or litter dependent groups since vertical stratification between the ground litter and canopy fauna is previously documented in Australian rainforest Collembola (Rodgers & Kitching, 1998). For example, poduromorph springtails are common in litter and include fungivores associated with fungal fruiting bodies. Entomobryomorpha include paronellid springtails which are largely arboreal in Australian rainforests (Coy *et al.*, 1993) and contributed to the domination of this suborder on *N. cunninghamii*. Little comparative work is published for *Nothofagus* in other biomes but Collembola are reported to be associated with lichens on *Nothofagus dombeyi* in Argentina (Messuti & Kun, 2007). A small range of arboreal gastropods also rasp epiphytes from stems and foliage, but are generally rare in Tasmania.

Arboreal spiders were conspicuous members of the predator guild on both host plants but tended to be small-bodied species. Highest diversity was observed among

theridiids and small araneids, but salticids were widespread. In contrast to the deciduous bark of many *Eucalyptus* species, the persistent bark of *Nothofagus* does not provide a diversity of living space. *Nothofagus* is often abundant in habitats adjacent to watercourses and this proximity may explain the occurrence of a number of aquatic taxa collected in beat samples. Stoneflies (Plecoptera), caddisflies (Trichoptera), scirtid beetles, chironomid midges (Chironomidae) are among the invertebrates which take refuge in the canopy of riparian vegetation. These insects represent a potentially important nutrient subsidy to arboreal spiders embedded in the *Nothofagus* foodweb. Similarly, the most diverse moth family present in the beat samples, Oecophoridae, are ground litter feeders in the larval stage (Common, 1990) but the adult moths commonly ascend the trees to roost. Although, scaly winged moths are thought to be relatively resistant to ensnarement in orb-webs (Uetz, 1990), they are readily captured and eaten by salticid jumping spiders (Jackson & Pollard, 1990). Various small flies such as Sciaridae, Keroplatidae and Lauxaniidae with larvae reliant on fungal or bacteria-enriched terrestrial substrates are also regularly beaten from *Nothofagus* foliage (P.B. McQuillan, personal communication).

Prior to this study, the living foliage of *N. cunninghamii* was known to support a modest variety of herbivores including monophagous taxa among the Coleoptera, Lepidoptera and Hemiptera (sub-chapter 3.2.4, tables 3.4 & 3.5), many of which are taxonomically isolated or phylogenetically basal taxa (e.g. the leafminer *Stigmella*), and probably a legacy of the Tertiary rainforests once widespread across the Australian landmass (McQuillan, 1993). In contrast, the most conspicuous monophage known on *N. gunnii* was an undescribed species of eriophyid mite, recognised by its distinctive erineum on the underside of the leaves. Otherwise, the *N. gunnii* herbivore community had been found to consist of polyphages such as the leaf-tier *Epiphyas xyloides* and the *Merimnetes* weevils (sub-chapter 3.2.4, table 3.4). The leaf beetles *Ewanius nothofagi* and *Platycolaspis mcquillani*, had been documented on both *N. cunninghamii* and *N. gunnii* (Reid, 1994, 2002) and could perhaps be considered monophagous at the generic level on Tasmanian *Nothofagus*.

The taxa recorded in this study have confirmed and significantly augmented the lists of herbivores previously associated with either *Nothofagus* species (Appendix 7: Tasmanian *Nothofagus* Arthropod Fauna), especially so for *N. cunninghamii*. Two

species of scale insect (Hemiptera, Coccoidea, Eriococcidae) have been newly described (Hardy *et al.*, 2008): *Madarococcus cunninghamii* Hardy & Gullan, found on *N. cunninghamii* at Lyrebird Walk; and *M. osculus* Hardy & Gullan, found on *N. cunninghamii* at Lyrebird Walk, and also on *N. gunnii* at Tarn Shelf. The thrip *Pseudanaphothrips pallidus* (Thysanoptera), not previously listed on *Nothofagus* but thought to be associated with *N. cunninghamii* (L. Mound, CSIRO, personal communication), was one of the most widespread and abundant of the herbivorous taxa found on both *N. cunninghamii*, and the most widespread herbivore on *N. gunnii*.

Returning to the concept of a core suite of taxa on each of the two *Nothofagus* species (i.e. those taxa which are most abundant, most widespread, and/or monophagous), in addition to the ubiquitous Oribatid mite taxa on each *Nothofagus* species, certain Psocids on *N. cunninghamii*, and Plecoptera on *N. gunnii*, the herbivorous morphotaxa dependant on living foliage have several candidates which could be considered core species on Tasmanian *Nothofagus* (subchapter 5.6, tables 5.46 & 5.47).

The obviously more speciose and complex invertebrate foodweb supported by *N. cunninghamii* begs the question whether this might be reflected in higher levels of herbivory on this host relative to *N. gunnii*, as discussed in relation to Research Question 3.

8.3 RESEARCH QUESTION 3.

Do the Herbivorous Taxa Attack the Two *Nothofagus* Species to the Same Degree?

In keeping with the diversity and taxonomic profile of its arthropod fauna, particularly the folivores, the herbivory levels found on *N. cunninghamii* were within the range of those found on temperate and subtropical tree taxa (subchapter 7.4, tables 7.13 & 7.14). In contrast *N. gunnii*, with its paucity of folivores, was distinctive for the consistently low rates of herbivory evident across sites and seasons. This may result from several factors acting alone or in concert, making its

foliage less conducive to leaf chewing arthropod taxa: its small area of distributional extent; subalpine environment; deciduousness; and phytochemistry.

N. gunnii is restricted to subalpine regions in the south and west of Tasmania, a distribution which is considerably smaller and more fragmented than that of *N. cunninghamii* in the same regions (Chapter 2, figure 2.9 Extant distribution of Tasmanian *Nothofagus*). This harsh environment favoured by *N. gunnii* may be tolerated by fewer herbivorous species, since weather conditions suitable for foraging by insects may be confined to shorter periods of time, resulting in less opportunity for feeding. In addition, being confined within the subalpine flora may mean that *N. gunnii* is taxonomically isolated, and therefore less likely to recruit folivores from other tree taxa; whereas *N. cunninghamii* in rainforest is in close proximity to the potential pool of folivorous taxa associated with wet sclerophyll forest.

Deciduousness could be another isolating factor for *N. gunnii*. The extensive northern temperate deciduous forests support a diverse arthropod fauna, and many of the canopy invertebrates have life stages which can overwinter in the ground (Dajoz, 2000), resulting in a large emerging species pool the following spring. Whereas *N. gunnii*, the only winter deciduous tree species in Australia, has a restricted and fragmented distribution as discussed above, and its associated overwintering arthropod fauna would be small, and vulnerable to climatic extremes.

Evergreen leaves, as in *N. cunninghamii*, might be expected to accumulate herbivore damage over an extended period relative to deciduous species, and this alone may have accounted for the lower value seen in *N. gunnii*. However, for *N. cunninghamii*, while the folivore damage to the soft, nutritious expanding young leaves increased from spring through to autumn, that of the mature leaves remained fairly constant; and the level of herbivory on the old leaves reflected the attack on them the previous year, when they had been ‘young leaves’ (subchapter 6.1.4.1). Or, the higher levels of herbivory on *N. cunninghamii* compared with *N. gunnii* may be the result of *N. cunninghamii* young leaves having relatively poor foliar chemical defences against herbivores adapted to the highly defended Eucalypts and *Acacias* to which *N. cunninghamii* is in closer proximity than *N. gunnii*.

That young leaves are preferred over the tougher, less nutritious, mature leaves has been well documented (e.g. Coley & Aide, 1991; Feeny, 1970; Read *et al.*, 2003; Selman & Loman, 1983;) and that young leaves have better chemical defence than mature leaves (Brunt *et al.*, 2006). This raises the question of whether *N. gunnii* being deciduous, and therefore having only ‘young’ leaves, might have a high level of foliar chemical defence in a situation where neighbouring plant taxa, including *N. cunninghamii*, are evergreen and so have a reserve of less vulnerable photosynthetic tissue. In addition, although the modest numbers of chewed leaves on *N. gunnii* increased through the growing season, the percentage leaf area loss showed no such increase, suggesting that *N. gunnii* may mobilise induced defences against herbivory.

The limited investigation of *N. cunninghamii* and *N. gunnii* leaf chemicals undertaken in this study was insufficient to provide answers for the above speculations, but these provide some directions for further research. However, the leaves of *N. cunninghamii* were found to have a narrower range, and considerably lower concentrations, of both leaf volatiles and cuticular waxes, than the leaves of *N. gunnii*. The profile of leaf volatiles found in *N. gunnii* leaves from Lake Fenton (Appendix 8 Analysis of *N. cunninghamii* and *N. gunnii* for Leaf Volatiles and Waxes) was similar to that of other Australian tree genera (subchapter 7.5, table 7.15); while a comparison of the profiles of leaf phenolic compounds of eleven species of *Nothofagus* (Wollenweber *et al.*, 2003), revealed each of the Tasmanian *Nothofagus* species to be most closely resemble sister species in their respective subgenera (subchapter 7.5, table 7.17).

These contrasting chemical profiles could account for the differences in herbivorous invertebrate communities and levels of herbivory between *N. cunninghamii* and *N. gunnii*. The phytochemical profile of *Nothofagus* host plants has been argued to be important factor to account for insect species richness (Lavandero *et al.*, 2009). Deciduous *Nothofagus alessandrii*, the South American species with the most unique chemistry, had very few and mostly specialised herbivores, whereas the evergreen *Nothofagus dombeyi*, with the least unique chemistry, had the highest number of related insect species (Lavandero *et al.*, 2009). Thus account needs to be taken of plant phytochemistry in addition to other

explanatory factors such as phylogenetic relatedness and geographic range when exploring invertebrate folivore communities and the causes of herbivory.

So far, the broad patterns of invertebrates associations revealed in this study have been interpreted in terms of food resources, local habitats provided by the host trees, and their foliar defences. However, geographical differences in host range, both historic and contemporary, are known to influence insect associations with plants and the potential importance of this is considered below.

8.4 RESEARCH QUESTION 4.

Are There Regional Characteristics to the Fauna and Levels of Herbivory ?

The results from this study showed convincingly that regional differences were apparent at order level within the arthropod communities on *N. cunninghamii* in Tasmania; and at the north eastern sites in particular taxa occurred, such as species of Curculionidae beetle, which were not found elsewhere despite considerably higher sampling effort at other sites. *N. gunnii*, restricted as it is to the alpine areas of the south and west, displayed far less regional variation in its attendant arthropod fauna.

There are a number of possible explanations for the regional variation seen in *N. cunninghamii* arthropod populations: changing landscapes under Pleistocene climate cycles and associated changes in the range and community structure of vegetation (Sniderman, 2011); effects due to habitat loss and fragmentation; and island area effects (Whittaker, 1998). The present north eastern populations of *N. cunninghamii* show evidence of having passed through a distributional bottleneck in the last iceage when rainforest retreated to multiple refugia in protected slopes and valleys below 440m (Kirkpatrick & Fowler, 1998; Worth *et al.*, 2009). A recent study reveals that haplotype diversity in the North east is less than half that in western Tasmania, but the presence of a unique haplotype in northeast Tasmanian populations suggests longterm occupation of the NE highlands, plausibly through multiple climate cycles during the Pleistocene (Worth *et al.*, 2009).

Perhaps as a result of this history, the invertebrate fauna of north eastern Tasmanian rainforests includes both local endemics and unexpected absences. Among the well documented endemics are ground dwelling taxa such as stag beetles

(Munks *et al.*, 2004), velvetworms and millipedes (Mesibov, 1994, 1997). Regional absences include the butterfly *Nesoxenica leprea* despite an abundance of its foodplant (McQuillan, 1994) suggesting that some species have yet to recolonise. Alternatively, for *N. cunninghamii* to recolonise the north east from the nearest documented refugia in western Tasmania, dispersal must have occurred across more than 150km, which is thought to be unlikely given the species low dispersal capacity (Dodson & Ono, 1997; Kirkpatrick & Fowler, 1998).

The absence of *N. gunnii* from the north east remains something of an enigma because suitable habitat exists at higher elevations on the Ben Lomond plateau above 1000m. It may have been locally eliminated by stochastic events in the Pleistocene acting upon small populations. *N. gunnii* is known to be very sensitive to fire and extensive bush fires are common in Tasmania which occasionally penetrate the highlands.

The greater regional diversity on *N. cunninghamii* would be expected to reinforce the diversity in its associated insect communities as whole, and so contribute to the higher overall faunal diversity found on *N. cunninghamii* than on *N. gunnii*. However for both *N. cunninghamii* and *N. gunnii*, there was considerable variation in the arthropod communities and levels of herbivory between sites within a region; and at a single site, there were differences between consecutive sampling years. This suggests that within the same region, site factors such as vegetation structure and local climatic events, play an important part in determining the arthropod communities on *N. cunninghamii* and *N. gunnii*.

8.5 CONCLUSIONS

In conclusion, this study has revealed that although sister species in the ancient, once widespread and diverse tree genus *Nothofagus*, the Tasmanian endemics *N. cunninghamii* and *N. gunnii* have strongly contrasting canopy arthropod faunas, both in terms of diversity and taxonomic profile. Far from being depauperate, the associated fauna on *N. cunninghamii* was found to be relatively rich in taxa and comparable with other temperate zone trees in both its diversity and guild structure. Similarly the *N. cunninghamii* herbivory levels were within the range of those found

on temperate and subtropical tree taxa. By contrast, *N. gunnii* was clearly depauperate, having a sparse fauna which was nevertheless, distinct from that on *N. cunninghamii*.

Possible reasons for these differences have been proposed including the restricted distribution, harsh habitat, taxonomic isolation, deciduousness and phytochemistry of *N. gunnii* compared with *N. cunninghamii*. Fully exploring these factors was beyond the scope of this study, but future research might use a similarly structured survey to directly compare: Tasmanian *Nothofagus* with that in South America and New Zealand; other Tasmanian tree taxa, such as *Eucalyptus* and *Acacia*; the effect of habitat types e.g. the transition of wet sclerophyll to rainforest; a long-term study at one or more sites; or a revisit, a decade on, to sites used in this study. One issue only touched upon was leaf chemistry, a speciality in itself, which is open to extensive investigation, such as: comparing the Tasmanian *Nothofagus* species and exploring the variations with time and location within a species; and comparisons with *Nothofagus* elsewhere and with other Australia tree taxa.

The strong regional signal in the arthropod fauna associated with *N. cunninghamii*, in particular the invertebrate communities on *N. cunninghamii* in northeastern Tasmania, would bear closer scrutiny, both of *N. cunninghamii* and the neighbouring flora.

Finally, account should be taken of the considerable local variation, that was found for the two *Nothofagus* species, in the arthropod communities and levels of herbivory between regions, between sites within a region, and within a site, seasonal variation, and also differences between consecutive sampling years. These insights have significance for the design of effective biodiversity surveys and conservation strategies.

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Appendix A1. Site Details: tables A.1.a-e.

N.B. The site name is a label only, denoting the grid referenced location where sampling was carried out, it does not refer to the whole geographical area of that name.

Sources: ^a Tasmaps (table A.1.c), Geodata Services Branch; Department of Primary Industries, Water and Environment (DPIWE); © Tasmanian Government

^b Google Earth data: Latitude/Longitude: downloaded 21/04/2010

^c Land Systems of Tasmania: Regions 3, 4, 5, 6 (Davies, 1988; Pemberton, 1986; Pinkard, 1980; Richley, 1978)

^d data from Australian Government Bureau of Meteorology, Rainfall Contour Map based on a standard 30-year climatology, 1961-1990, © Commonwealth of Australia 2005; and Weather Station data for Mt. Wellington, Maydena P.O., Cradle Valley, Lake St. Clair, Queenstown, Preolenna

^e Harris and Kitchener (2005) and TASVEG Version 1.0 Data collection: 1998-2003, Projection: Grid of Australia 1994 (MGA94); MGA zone 55 (GDA94), Original data scale: 1:25,000 across the whole State; ©Tasmanian Vegetation Mapping Program, DPIWE.

Table A.1.a. Multiple Visit Sites.

Site	Site Code	Region	Location	Universal Grid Reference ^a	Latitude ^b (°decimal N)	Longitude ^b (°decimal E)	Altitude ^a (m)	Substrate ^c	Ave. Ann. Ppt. ^d (mm)	<i>Nothofagus</i> sp.	TASVEG code ^e
Blue Tier	bt	NE	North East	55GEQ820391	-41.19531	147.97790	725	Devonian Granite	1200	<i>N. cunninghamii</i>	RMT
Cradle Valley	cv	W/C	Cradle Mt-Lake St Clair N.P.	55GDP122898	-41.63726	145.94636	890	Quaternary PD	2700	<i>N. cunninghamii</i>	RML?
Crater Lake	cl	W/C	Cradle Mt-Lake St Clair N.P.	55GDP121878	-41.65491	145.94535	1040	PreCambrian1	2700	<i>N. gunnii</i>	RKF
King William	kw	W/C	Mt King William I	55GDP283226	-42.24351	146.13287	1090	Jurassic Dolerite3	1900	<i>N. gunnii</i>	RPF
Lake Dobson	ld	S	Mt Field N.P.	55GDN662743	-42.68097	146.58901	1080	Jurassic Dolerite1	1200	<i>N. cunninghamii</i>	DCO
Lake Fenton	lf	S	Mt Field N.P.	55GDN692748	-42.67633	146.62559	1010	Jurassic Dolerite1	1200	both spp.	WSU/RKF
Lake Skinner	ls	S	Snowy Range	55GDN737456	-42.93977	146.67945	980	Jurassic Dolerite1	1100	both spp.	RPF
Lake St Clair	sc	W/C	Cradle Mt-Lake St Clair N.P.	55GDP312385	-42.10030	146.16896	800	Jurassic Dolerite2	1900	<i>N. cunninghamii</i>	RMT
Little Plateau	lp	W/C	Cradle Mt-Lake St Clair N.P.	55GDP122847	-41.68408	145.94653	1230	Parmeneer1	2700	<i>N. gunnii</i>	RPF
Lyrebird Walk	lw	S	Mt Field N.P.	55GDN728746	-42.67906	146.67041	680	Jurassic Dolerite1	1200	<i>N. cunninghamii</i>	WDR
Mt Arthur	ma	S	Wellington Range	55GEN182520	-42.88388	147.22342	1080	Jurassic Dolerite1	1000	<i>N. cunninghamii</i>	DCO
Mt Barrow	mb	NE	North East	55GEQ359202	-41.36834	147.43065	895	Jurassic Dolerite1	1200	<i>N. cunninghamii</i>	RMT
Mt Dundas (high)	mdH	W/C	West Coast	55GCP734593	-41.90634	145.47591	900	Cambrian1	2400	both spp.	RKF
Mt Dundas (low)	mdL	W/C	West Coast	55GCP728560	-41.93596	145.46720	260	Cambrian2	2400	<i>N. cunninghamii</i>	RMS
Mt Dundas (mid)	mdM	W/C	West Coast	55GCP730579	-41.91807	145.47009	615	Cambrian3	2400	<i>N. cunninghamii</i>	RMS/RKP
Tarn Shelf	ts	S	Mt Field N.P.	55GDN639758	-42.66739	146.56096	1160	Jurassic Dolerite1	1200	<i>N. gunnii</i>	RPF
Tayatea Bridge	tb	NW	North West	55GCQ484526	-41.06256	145.19667	80	PreCambrian2	1600	<i>N. cunninghamii</i>	WOU
Weldborough Pass	wp	NE	North East	55GEQ799360	-41.22171	147.95500	560	Tertiary Basalt	1200	<i>N. cunninghamii</i>	RMT

Table A.1.b. Single visit Sites.

Site	Site Code	Region	Location	Universal Grid Reference ^a	Latitude ^b (°decimal N)	Longitude ^b (°decimal E)	Altitude ^a (m)	Substrate ^c	Ave. Ann. Ppt. ^d (mm)	<i>Nothofagus</i> sp.	TASVEG code ^e
Cradle Cirque North	cn	W/C	Cradle Mt-Lake St Clair N.P.	55GDP123825	-41.70451	145.94655	1210	Parmeneer1	2400	<i>N. gunnii</i>	RFS
Cradle Cirque South	cs	W//C	Cradle Mt-Lake St Clair N.P.	55GDP122820	-41.70803	145.94742	1210	Parmeneer1	2400	<i>N. gunnii</i>	RFS
Lake Eros	le	W/C	Walls of Jerusalem N.P.	55GDP310558	-41.94466	146.16916	1125	Jurassic Dolerite3	2000	<i>N. gunnii</i>	RPF
Lake Windermere	wm	W/C	Cradle Mt-Lake St Clair N.P.	55GDP125765	-41.75729	145.94923	1040	Quaternary PD	2000	<i>N. gunnii</i>	RFS
Meander Forest	mf	W/C	Great Western Tiers	55GDP603797	-41.73278	146.52407	880	Parmeneer2	2000	<i>N. cunninghamii</i>	RSH
Milkshake Hills	mh	NW	North West	55GCQ459480	-41.10173	145.17062	190	PreCambrian2	1600	<i>N. cunninghamii</i>	WOU
Myrtle Creek	mc	NE	Douglas-Apsley N.P.	55GEP939717	-41.79801	148.13328	400	Jurassic Dolerite1	1200	<i>N. cunninghamii</i>	RLS
Ossa Track	ot	W/C	Cradle Mt-Lake St Clair N.P.	55GDP213646	-41.86467	146.05365	1200	Parmeneer1	2000	<i>N. gunnii</i>	RPF
Pelion Plains	pp	W/C	Cradle Mt-Lake St Clair N.P.	55GDP200684	-41.82997	146.03869	870	Parmeneer1	2000	<i>N. cunninghamii</i>	RKP
Rainforest Ledge	rl	NE	Douglas-Apsley N.P.	55GFP016781	-41.74177	148.22389	450	Jurassic Dolerite1	1200	<i>N. cunninghamii</i>	RLS
Traveller Range	tr	W/C	Walls of Jerusalem N.P.	55GDP274505	-41.99215	146.12513	1190	Jurassic Dolerite3	2000	<i>N. gunnii</i>	RPW

Table A.1.c. Tasmaps^a.

Site	TASMAP	
	1:25,000	1:100,000
Blue Tier	Blue Tier 5843	Forester
Cradle Cirque North	Cradle 4038	Sophia
Cradle Cirque South	Cradle 4038	Sophia
Cradle Valley	Cradle 4038	Sophia
Crater Lake	Cradle 4038	Sophia
King William	Arrowsmith 4232	Nive
Lake Dobson	Dobson 4627	Tyenna
Lake Eros	Du Cane 4235	Mersey
Lake Fenton	Dobson 4627	Tyenna

Site	TASMAP	
	1:25,000	1:100,000
Lake Skinner	Nevada 4624	Tyenna
Lake St Clair	Rufus 4233	Nive
Lake Windermere	Will 4037	Sophia
Little Plateau	Cradle 4038	Sophia
Lyrebird Walk	Dobson 4627	Tyenna
Meander Forest	Breona 4638	Meander
Milkshake Hills	Holder 3444	Arthur River
Mt Arthur	Mt. Wellington Walk Map: 1:15,000	Derwent
Mt Barrow	Nunamara 5241	Pipers

Site	TASMAP	
	1:25,000	1:100,000
Mt Dundas, all sites	Oceana 3635	Pieman
Myrtle Creek	St John 5837	Break O'Day
Ossa Track	Cathedral 4236	Mersey
Pelion Plains	Cathedral 4236	Mersey
Rainforest Ledge	Piccaninny 6038	Break O'Day
Tarn Shelf	Dobson 4627	Tyenna
Tayatea Bridge	Holder 3444	Arthur River
Traveller Range	Du Cane 4235	Mersey
Weldborough Pass	Ringarooma 5643	Forester

Table A.1.d. Substrate Abbreviations^b (Davies, 1988; Pemberton, 1986; Pinkard, 1980; Richley, 1978).

Substrate	Land Systems of Tasmania Geological Description
PreCambrian1	Precambrian metaquartzite and pelitic sequences
PreCambrian2	Precambrian slaty mudstone, with extensive areas of dolomite
Cambrian1	Cambrian acid & intermediate volcanic rocks:
Cambrian2	Cambrian rocks, soils shallow and gravelly
Cambrian3	Cambrian greywacke turbidite sequences, with some basic-intermediate volcanic rocks
Devonian Granite	Devonian granite and graniorite
Parmeneer1	Upper Carboniferous to Triassic (Lower and Upper) Parmeneer supergroup sediments
Parmeneer2	Triassic (Upper) Parmeneer, Jurassic dolerite scree

Substrate	Land Systems of Tasmania Geological Description
Jurassic Dolerite1	Jurassic dolerite
Jurassic Dolerite2	Extensive Pleistocene glacial deposits with Jurassic dolerite outcrop.
Jurassic Dolerite3	Jurassic dolerite and Pleistocene glacial deposits.
Tertiary Basalt	Tertiary basalt
Quaternary PD	Quaternary periglacial deposits

Table A.1.e. Vegetation Key^d (Harris & Kitchener, 2005).

Vegetation Group		Code	Vegetation Community	Canopy Dominant: and Associations
Rainforest and Related Scrub		RFS	<i>Nothofagus gunnii</i> rainforest and scrub	<i>N.gunnii</i> : over short, closed canopy rainforest, with emergent <i>Athrotaxis cupressoides</i> and/or <i>A. selaginoides</i>
		RKF	<i>Athrotaxis selaginoides</i> – <i>Nothofagus gunnii</i> short rainforest	<i>N. gunnii</i> , <i>Athrotaxis selaginoides</i> : over short rainforest spp.
		RKP	<i>Athrotaxis selaginoides</i> rainforest	<i>N. cunninghamii</i> , <i>Athrotaxis selaginoides</i> : over rainforest spp.
		RLS	<i>Leptospermum</i> with rainforest scrub	<i>Leptospermum</i> spp., <i>L. lanigerum</i> : Subdominants include sparse <i>N. cunninghamii</i> , <i>Eucalyptus</i> spp.
		RML	<i>Nothofagus</i> – <i>Leptospermum</i> short rainforest	<i>Leptospermum</i> spp., <i>N. cunninghamii</i> : often merges with RKP
		RMS	<i>Nothofagus</i> – <i>Phyllocladus</i> short rainforest	<i>Nothofagus cunninghamii</i> , <i>Phyllocladus aspleniifolius</i> , <i>Eucryphia lucida</i>
		RMT	<i>Nothofagus</i> – <i>Atherosperma</i> rainforest	<i>N. cunninghamii</i> : <i>Atherosperma moschatum</i> may co-dominate
		RPF	<i>Athrotaxis cupressoides</i> – <i>Nothofagus gunnii</i> short rainforest	<i>A. cupressoides</i> : <i>N.gunnii</i> , and possibly <i>N. cunninghamii</i> , in dense understorey
		RPW	<i>Athrotaxis cupressoides</i> open woodland	Scattered <i>A. cupressoides</i> : over a coniferous heath understorey containing <i>N. gunnii</i>
		RSH	Highland low rainforest and scrub	Dwarf <i>Nothofagus cunninghamii</i> : over mixed rainforest and subalpine species
Eucalypt Forest and Woodland	Wet	WOU	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)	<i>E. obliqua</i> and possibly other Eucalypt spp.: <i>N. cunninghamii</i> subdominant
		WSU	<i>Eucalyptus subcrenulata</i> forest and woodland	<i>E. subcrenulata</i> , <i>E. coccifera</i> : <i>N. cunninghamii</i> in understorey
		WDR	<i>Eucalyptus delegatensis</i> forest over rainforest	<i>E. delegatensis</i> : Subdominants: <i>N. cunninghamii</i> , <i>Atherosperma moschatum</i>
	Dry	DCO	<i>Eucalyptus coccifera</i> forest and woodland	<i>E. coccifera</i> : Subalpine community with <i>N. cunninghamii</i> and/or <i>N.gunnii</i>

Appendix A2. Site Images: Plates A.1-4.









	
a. Lake Fenton: <i>N. cunninghamii</i> in understory beneath <i>E. coccifera</i> <i>E. subcrenulata</i> .	b. Lake Fenton: <i>N. cunninghamii</i> , bagged branch (arrow).
	
c. Lake Fenton: <i>N. gunnii</i> in summer (beneath <i>E. coccifera</i> / <i>E. subcrenulata</i>).	d. Lake Fenton: <i>N. gunnii</i> in autumn colours.
	
e. Lake Fenton: Adjacent trees of <i>N. gunnii</i> (left) and <i>N. cunninghamii</i> (right).	f. Lake Skinner: field site in lower right portion of the image, above the boulders.
	
g. Lake Skinner: <i>N. cunninghamii</i> and <i>N. gunnii</i> in summer.	h. Lake Skinner: Autumn.

Plate A.1. Multiple visit sites. Southern: Lake Fenton (a - e); Lake Skinner (f - h).



a. Tarn Shelf in summer.



b. Tarn Shelf in autumn.



c. Lyrebird Walk: *N. cunninghamii* subdominant to *E. deligatensis*.



d. Lake Dobson: *N. cunninghamii* beneath *E.coccifera*.



e. Mt. Arthur: *N. cunninghamii* with *E. coccifera*.

Plate A.2. Multiple visit sites. Southern continued: Tarn Shelf, Lyrebird Walk, Lake Dobson, Mt Arthur (a - e).



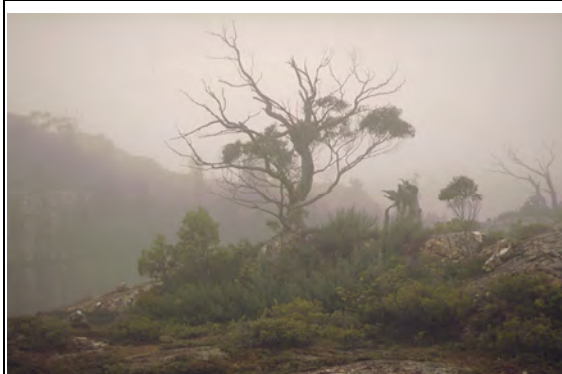
Plate A.3. Multiple visit sites. West/Central: King William, Crater Lake, Little Plateau (a - d); North East (images c/o Gwilym Keble-Williams): Mt Barrow, Weldborough Pass (e - g).



a. *N. gunnii* beside Lake Eros.



b. *N. gunnii* leaves among leaf litter in Lake Eros.



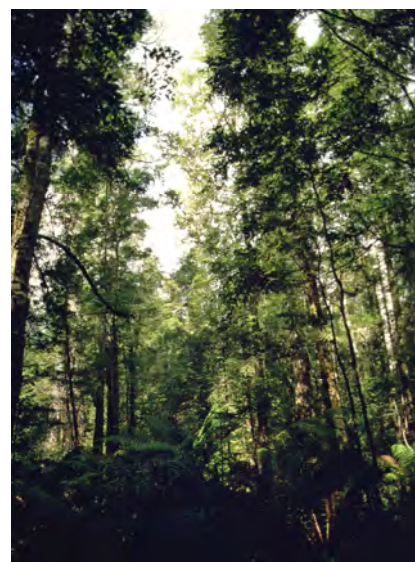
c. Traveller Range: shrubby *N. gunnii* with *A. cupressoides*, beneath *E. coccifera*.



d. Cradle Cirque: *N. gunnii* in foreground.



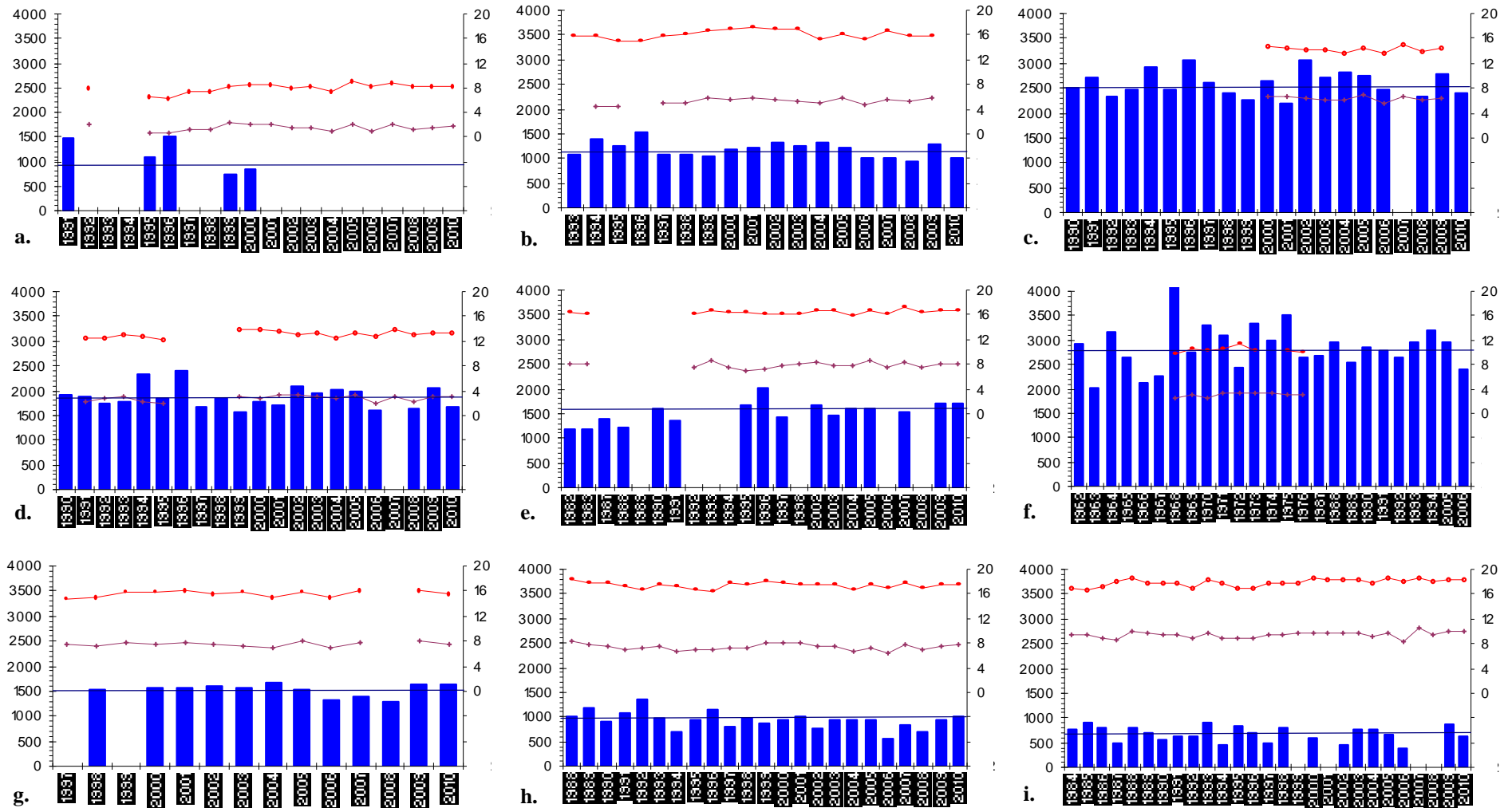
e. Lake Windermere: *N. gunnii* in foreground.



f. Milkshake Hills: *N. cunninghamii*.

Plate A.4. Single visit sites. West/Central: Lake Eros, Traveller Range, Cradle Cirque, Lake Windermere (a - e) within in Cradle Mountain - Lake St Clair National Park. North West: Milkshake Hills (f).

Appendix A3. Climate Data.



Annual rainfall ■ ; long-term mean rainfall — ; mean minimum annual temperature ◆ ; mean maximum annual Temperature ◆ .

Weather Stations: South: a. Mt Wellington, b. Maydena, c. Strathgordon. West/Central: d. Lake St Clair, e. Strahan, f. Cradle Valley. North West: g. Luncheon Hill. North East: h. Scottsdale, i. Bicheno. Data from Australian Bureau of Meteorology website: <http://www.bom.gov.au>.

Appendix A4. Fieldtrip Schedule, tables A.4.a-e.

Table A.4.a. *N. cunninghamii* Multiple Visit Sites.

Site	Date	Fieldtrip/Host	Branch Beats	Sampling Details
Blue Tier	02 Nov. 1999	bt1Nc	3x10	Herbivory & Beats
	19 Jan. 2000	bt2Nc	3x10	Herbivory & Beats
	23 May 2000	bt3Nc	3x10	Herbivory & Beats
Cradle Valley	13 Dec. 1999	cv1Nc	3x10	Herbivory & Beats
	6 Feb. 2000	cv2Nc	3x10	Herbivory & Beats
	26 Apr. 2000	cv3Nc	3x10	Herbivory & Beats
Lake Dobson	25 Oct. 1999	ld1Nc	3x10	Herbivory & Beats
	6 Dec. 1999	ld2Nc	3x10	Herbivory & Beats
	25 Jan. 2000	ld3Nc	3x10	Herbivory & Beats
	6 Mar. 2000	ld4Nc	3x10	Herbivory & Beats
	11 Apr. 2000	ld5Nc	3x10	Herbivory & Beats
	25 Sep. 2000	ld6Nc	3x10	Herbivory & Beats
	13 Jan. 2001	ld7Nc	0	Leaf areas only
Lake Fenton	3 Mar. 1998	lf1Nc	0	Preliminary Fieldtrip, Herbivory only
	27 Mar. 1998	lf2Nc	6x10	Herbivory & Beats:N, S, A, 2x10 each
	17 Jun. 1998	lf3Nc	8x10	Herbivory & Beats:N, S, 3x10; A, 2x10
	24 Nov. 1998	lf4Nc	10x10	Herbivory & Beats:N, S, 4x10; A, 2x10
	15 Jan. 1999	lf5Nc	6x10	Herbivory & Beats:N, S, A, 2x10 each
	28 Feb. 1999	lf6Nc	6x10	Herbivory & Beats:N, S, A, 2x10 each
	17 Apr. 1999	lf7Nc	0	Herbivory only
	16 Oct. 1999	lf8Nc	3x10	Herbivory & Beats
	6 Dec. 1999	lf9Nc	3x10	Herbivory & Beats
	25 Jan. 2000	lf10Nc	3x10	Herbivory & Beats
	6 Mar. 2000	lf11Nc	3x10	Herbivory & Beats
	10 Apr. 2000	lf12Nc	3x10	Herbivory & Beats
	25 Sep. 2000	lf13Nc	3x10	Herbivory & Beats
Lake Skinner	11 Mar. 1998	ls1Nc	1x10?	Preliminary Fieldtrip, Herbivory & Beats
	2 May 1998	ls2Nc	6x10	Herbivory & Beats:N, S, A, 2x10 each
	25 Nov. 1998	ls3Nc	6x10	Nc:N, S, A, 2x10 each
	17 Jan. 1999	ls4Nc	6x10	Nc:N, S, A, 2x10 each
	18 Mar. 1999	ls5Nc	6x10	Nc:N, S, A, 2x10 each
	24 Oct. 1999	ls6Nc	3x10	Herbivory & Beats
	5 Dec. 1999	ls7Nc	3x10	Herbivory & Beats (affected by rain)
	1 Feb. 2000	ls8Nc	3x10	Herbivory & Beats
	7 Apr. 2000	ls9Nc	3x10	Herbivory & Beats
	1 Nov. 2000	ls10Nc	3x10	Herbivory & Beats
Lyrebird Walk	3 Mar. 1998	lw1Nc	1x10?	Preliminary Fieldtrip, Herbivory & Beats
	17 Jun. 1998	lw2Nc	3x10	Herbivory & Beats
	24 Nov. 1998	lw3Nc	4x10	Herbivory & Beats
	15 Jan. 1999	lw4Nc	4x10	Herbivory & Beats
	28 Feb. 1999	lw5Nc	4x10	Herbivory & Beats
	17 Apr. 1999	lw6Nc	0	Herbivory only
	16 Oct. 1999	lw7Nc	3x10	Herbivory & Beats
	7 Dec. 1999	lw8Nc	3x10	Herbivory & Beats
	24 Jan. 2000	lw9Nc	3x10	Herbivory & Beats
	6 Mar. 2000	lw10Nc	3x10	Herbivory & Beats
	10 Apr. 2000	lw11Nc	3x10	Herbivory & Beats
	25 Sep. 2000	lw12Nc	3x10	Herbivory & Beats

Table A.4.b. *N. cunninghamii* Multiple Visit Sites contd.

Site	Date	Fieldtrip/Host	Branch Beats	Sampling Details
Mt Arthur	17 Oct. 1999	ma1Nc	3x10	Herbivory & Beats
	22 Dec. 1999	ma2Nc	3x10	Herbivory & Beats
	10 Feb. 2000	ma3Nc	3x10	Herbivory & Beats
	6 Apr. 2000	ma4Nc	3x10	Herbivory & Beats
	9 Oct. 2000	ma5Nc	3x10	Herbivory & Beats
Mt Barrow	3 Nov. 1999	mb1Nc	3x10	Herbivory & Beats
	18 Jan. 2000	mb2Nc	3x10	Herbivory & Beats
	22 May 2000	mb3Nc	3x10	Herbivory & Beats
Mt Dundas	29 Nov. 1999	md1Nc	3x10	Herbivory & Beats
	14 Feb. 2000	md2Nc	8x10	Herbivory & Beats: H, M, L, 2x10 each
	25 Apr. 2000	md3Nc	3x10	Herbivory & Beats
Lake St Clair	30 Nov. 1999	sc1Nc	3x10	Herbivory & Beats
	12 Feb. 2000	sc2Nc	3x10	Herbivory & Beats
	24 Apr. 2000	sc3Nc	3x10	Herbivory & Beats
Tayatea Bridge	15 Dec. 1999	tb1Nc	3x10	Herbivory & Beats
	15 Feb. 2000	tb2Nc	3x10	Herbivory & Beats
	25 Mar. 2000	tb3Nc	3x10	Herbivory & Beats
Weldborough Pass	2 Nov. 1999	wp1Nc	3x10	Herbivory & Beats
	18 Jan. 2000	wp2Nc	3x10	Herbivory & Beats
	23 May 2000	wp3Nc	3x10	Herbivory & Beats (affected by rain)

Table A.4. c. *N. cunninghamii* Single Visit Sites.

Site	Date	Fieldtrip/Host	Branch Beats	Sampling Details
Meander Falls	2 Feb. 2001	mf1Nc	3x10	Herbivory & Beats
Milkshake Hills	25 Mar. 2000	mh1Nc	3x10	Herbivory & Beats
Myrtle Creek	21 Jan. 2001	mc1Nc	3x10	Herbivory & Beats
Pelion Plains	23 Mar. 2002	pp1Nc	3x10	Beats Only
Rainforest Ledge	23 Dec. 2000	rl1Nc	3x10	Herbivory & Beats

Table A.4.d. *N. gunnii* Multiple Visit Sites.

Site	Date	Fieldtrip/Host	Branch Beats	Sampling Details	
Crater Lake	06 Feb. 2000	cl1Ng	3x10	Herbivory & Beats	6 Feb. 2000: sampled instead of Little Plateau
	26 Apr. 2000	cl2Ng	3x10	Herbivory & Beats	
King William	10 Apr. 1998	kw1Ng	8x10	Herbivory & Beats:N & S4x10 each	
	2 Dec. 1998	kw2Ng	4x10	Herbivory & Beats:N & S2x10 each	
	20 Feb. 1999	kw3Ng	4x10	Herbivory & Beats:N & S2x10 each	
	28 Nov. 1999	kw4Ng	3x10	Herbivory & Beats	
	13 Feb. 2000	kw5Ng	3x10	Herbivory & Beats	
	10 May 2000	kw6Ng	3x10	Herbivory & Beats	
Lake Fenton	3 Mar. 1998	lf1Ng	1x10?	Preliminary Fieldtrip, Herbivory & Beats	
	27 Mar. 1998	lf2Ng	6x10	Herbivory & Beats:N, S, A, 2x10 each	
	17 Jun. 1998	lf3Ng	8x10	Herbivory & Beats:N, S, 3x10:A,2x10	
	24 Nov. 1998	lf4Ng	2x10	Herbivory & Beats:N, S, 4x10:A,2x10	
	15 Jan. 1999	lf5Ng	6x10	Herbivory & Beats:N, S, A, 2x10 each	
	28 Feb. 1999	lf6Ng	6x10	Herbivory & Beats:N, S, A, 2x10 each	
	17 Apr. 1999	lf7Ng	0	Herbivory only	
	16 Oct. 1999	lf8Ng	3x10	Herbivory & Beats	
	6 Dec. 1999	lf9Ng	3x10	Herbivory & Beats	
	25 Jan. 2000	lf10Ng	3x10	Herbivory & Beats	
	6 Mar. 2000	lf11Ng	3x10	Herbivory & Beats	
	10 Apr. 2000	lf12Ng	3x10	Herbivory & Beats	
	25 Sep. 2000	lf13Ng	3x10	Herbivory & Beats	
Lake Skinner	11 Mar. 1998	ls1Ng	1x10?	Preliminary Fieldtrip, Herbivory & Beats	
	2 May 1998	ls2Ng	6x10	Herbivory & Beats:N, S, A, 2x10 each	
	25 Nov. 1998	ls3Ng	6x10	Herbivory & Beats:N, S, A, 2x10 each	
	17 Jan. 1999	ls4Ng	6x10	Herbivory & Beats:N, S, A, 2x10 each	
	18 Mar. 1999	ls5Ng	6x10	Herbivory & Beats:N, S, A, 2x10 each	
	24 Oct. 1999	ls6Ng	3x10	Herbivory & Beats	
	5 Dec. 1999	ls7Ng	3x10	Herbivory & Beats (affected by rain)	
	1 Feb. 2000	ls8Ng	3x10	Herbivory & Beats	
	7 Apr. 2000	ls9Ng	3x10	Herbivory & Beats	
	1 Nov. 2000	ls10Ng	3x10	Herbivory & Beats	
Little Plateau	14 Dec. 1999	lp1Ng	3x10	Herbivory & Beats	6 Feb. 2000: bad weather prevented access, Crater Lake sampled instead
	26 Apr. 2000	lp2Ng	3x10	Herbivory & Beats	
Mt Dundas	29 Nov. 1999	md1Ng	3x10	Herbivory & Beats	
	14 Feb. 2000	md2Ng	3x10	Herbivory & Beats	
	25 Apr. 2000	md3Ng	3x10	Herbivory & Beats	
Tarn Shelf	25 Oct. 1999	ts1Ng	3x10	Herbivory & Beats	
	6 Dec. 1999	ts2Ng	3x10	Herbivory & Beats	
	24 Jan. 2000	ts3Ng	3x10	Herbivory & Beats	
	6 Mar. 2000	ts4Ng	3x10	Herbivory & Beats	
	11 Apr. 2000	ts5Ng	3x10	Herbivory & Beats	
	7 Nov. 2000	ts6Ng	3x10	Herbivory & Beats	

Table A.4.e. *N. gunnii* Single Visit Sites.

Single Visit Sites	Fieldtrip/Host	Fieldtrip/Host	Branch Beats	Sampling Details
Cradle Cirque North	22 Mar. 2002	cn1Ng	3x10	Herbivory & Beats
Cradle Cirque South	22 Mar. 2002	cs1Ng	3x10	Herbivory & Beats
Lake Eros	5 Jan. 2000	le1Ng	3x10	Herbivory & Beats
Lake Windermere	22 Mar. 2002	wm1Ng	3x10	Herbivory & Beats
Ossa Track	24 Mar. 2002	ot1Ng	0	Herbivory only
Traveller Range	3 Jan. 2000	tr1Ng	3x10	Herbivory & Beats

Appendix A5. Arthropod Archiving.

The arthropod orders Acarina, Coleoptera, Hemiptera, Lepidoptera, Plecoptera, Psocoptera, Thysanoptera, and a small sample of Araneae, were sorted to family, then genus and species where possible, otherwise to morphospecies. As few relevant identification keys or other descriptions of the individual families or species were available, a reference collection was assembled with a type specimen for each morphotaxon. Specimens were pinned where appropriate, or stored in glass vials containing 70% ethanol, then labelled and archived to museum standard (figure A.5.1).

The type specimens were photographed, initially using a 35mm SLR camera (Olympus OM1) for larger specimens; or for the majority of specimens, using a Leica 35mm camera attached to a Leica Wild M8 microscope (figure A.5.2.a, b). The slides or negatives were then scanned onto a computer. Later in the project, a digital camera (Nikon Coolpix 990) was acquired and attached to a Zeiss Stemi 2000C microscope. The specimens were photographed beside a microscale (figure A.5.2.c, d.) and views of the specimens included dorsal, lateral and /or ventral aspects, and more detailed images where appropriate.

A photolog of the type specimens was produced, with notes about key characters for ease of recognition of subsequent samples (figure A.5.3). Finally, copies of the images were formatted and a scale bar added to each image in order to create a visual reference of Tasmanian *Nothofagus* Arthropods (figure A.5.3). These images were stored both digitally, and in hard copy as presented in Appendix B: Photorecord of Tasmanian *Nothofagus* Arthropods Collected in this Study.

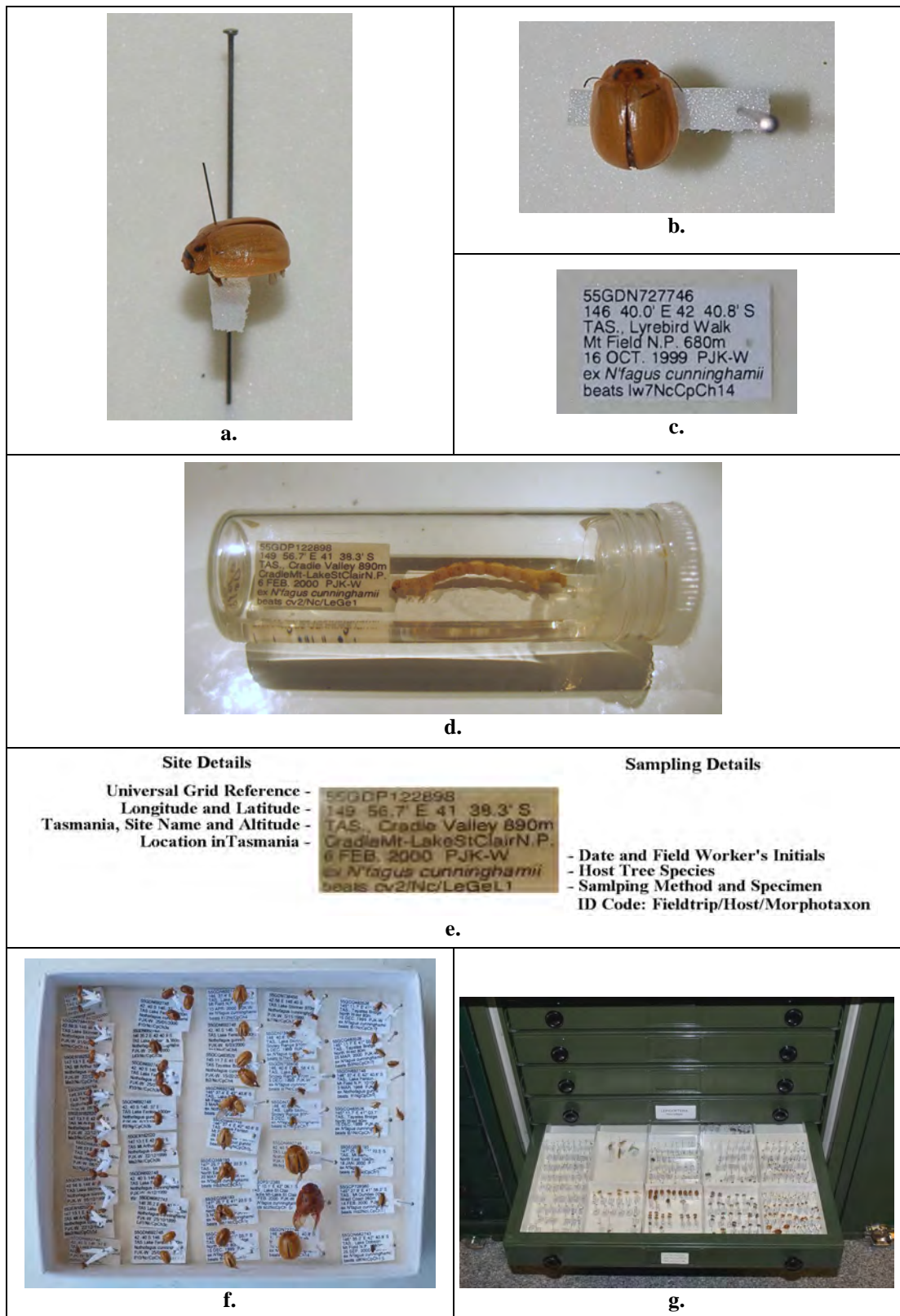


Figure A.5.1. Arthropod Archiving. Pinned specimen of *Chrysophtharta bimaculata*, CpCh14 (Coleoptera, Chrysomelidae) with its label (a, b, c). Soft-bodied specimen, *Nacophorini* sp. novum immature, LeGeL1 (Lepidoptera, Geometridae) with label in a vial containing 70% ethanol (d). Details noted on the specimen labels (e), label from image 'd' above. Pinned specimens mounted by family (f), here Chrysomelidae beetles. Trays of pinned specimens in the drawer of a storage cabinet (g), Biodiversity Laboratory, School of Geography and Environmental Studies, Hobart Campus, University of Tasmania.

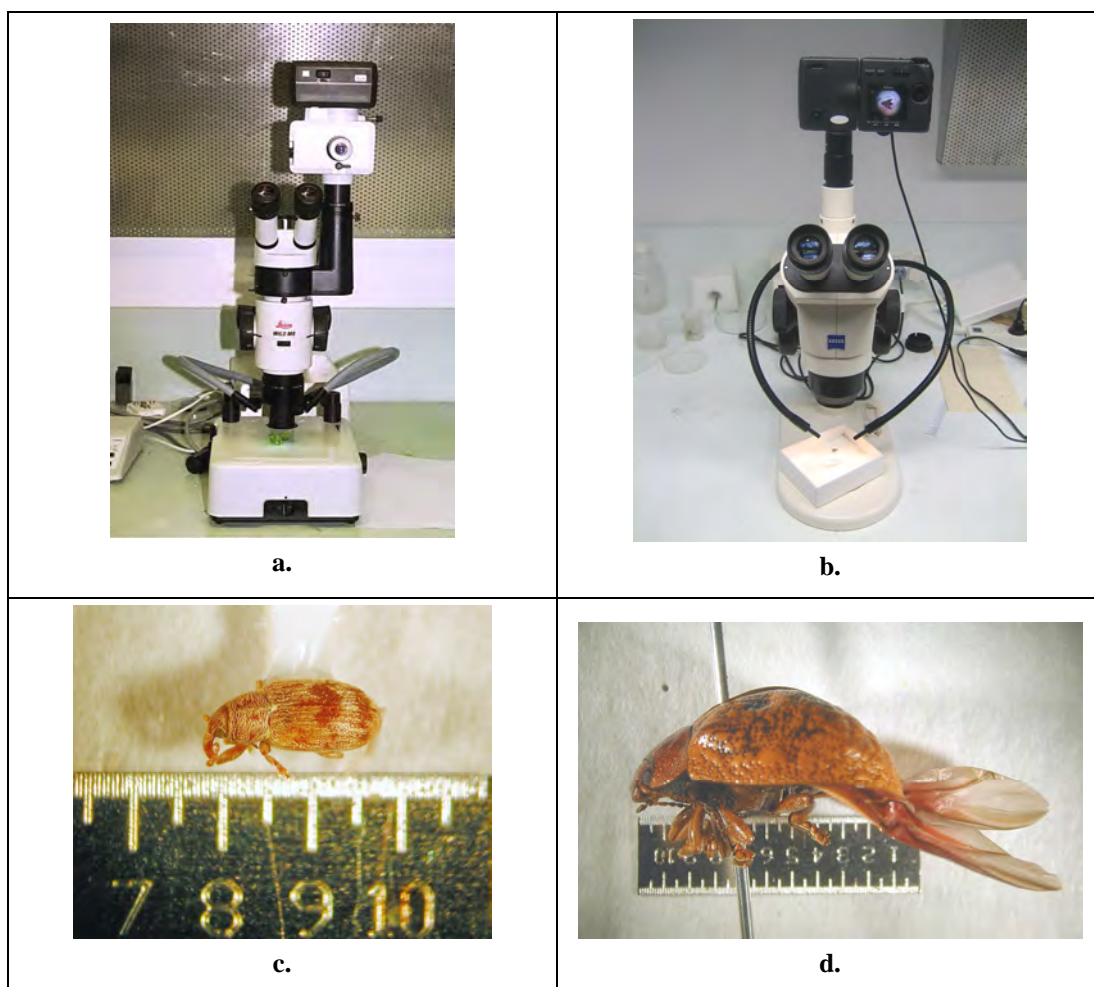


Figure A.5.2. Microphotography. The original setup (a): Leica Wild M8 microscope with attached 35mm Leica camera. The later digital system (b): Nikon Coolpix 990 camera atop Zeiss Stemi 2000C microscope; an image of the specimen is seen on the camera screen. Digital images of specimens beside a 10mm microscale: dorsal view (c) of CpCu21, Tychiini sp.5 (Coleoptera, Curculionidae); left lateral view (d) of CpCh6, *Paropsis* sp.1 (Coleoptera, Chrysomelidae).

Nothofagus Arthropods – Coleoptera:

Family **Chrysomelidae**

Subfamily **Chrysomelinae**

Tribe **Goniocentini** (subtribe **Goniocentina**)

Genus/species ***Ewanius nothofagi* Reid**

Code **CpCh3**

4.5-5 mm. Elongate/oval.

Colour variation amongst individuals: from entirely sandy-brown to deep orange brown, with distinct black patterning over elytra and pronotum.

Elytra simple (no overhang), sculpted linearly, with pale slightly elevated interspace at periphery. Shoulder prominences. Scutellum: equilateral triangle with rounded edges.

Hairless, except single seta at each angle of pronotum.

Pronotum and frons sparsely and irregularly punctured.

Antennae filiform, darker distally.

Apical maxillary palpi *not* expanded.

Third tarsal segment large, pad-like and setose. Tarsal claws appendiculate. ♀ tibia and tarsal segments slender. ♂ tibia and tarsal segments more robust.



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Coleoptera: Chrysomeloidea: Chrysomelidae

(1101Ne) Cp Ch3

a.



b.



c.



d.

Figure A.5.3. Examples from the Tasmanian *Nothofagus* Coleoptera Photolog and the Tasmanian *Nothofagus* Arthropod Type Specimen Image Archive. Photolog entry: *Ewanius nothofagi*. Reid (Coleoptera, Chrysomelidae) CpCh3, the adult beetle (a). Image Archive entries, with 1mm scale bar: *Ewanius nothofagi*. Reid (Coleoptera, Chrysomelidae): the adult beetle CpCh3, (b. dorsal view; c. left lateral view) and the larval stage CpChL1 (d). See also Appendix B. Plate B.2. a -c.

Appendix A6. Manual versus digitally scanned measurement of leaf area and proportion of leaf area to chewing damage (% Leaf Area Loss).

Thirty *N. gunnii* leaves were sorted into classes according to their size and shape and the area traced for each class onto 1mm² graph paper. The number of millimetre squares contained within each outline was counted, rounding up or down for incomplete squares. This gave an area template for all the leaves. Leaf area lost was estimated by placing chewed leaves on the appropriate area template and counting the number of squares left uncovered by the hole.

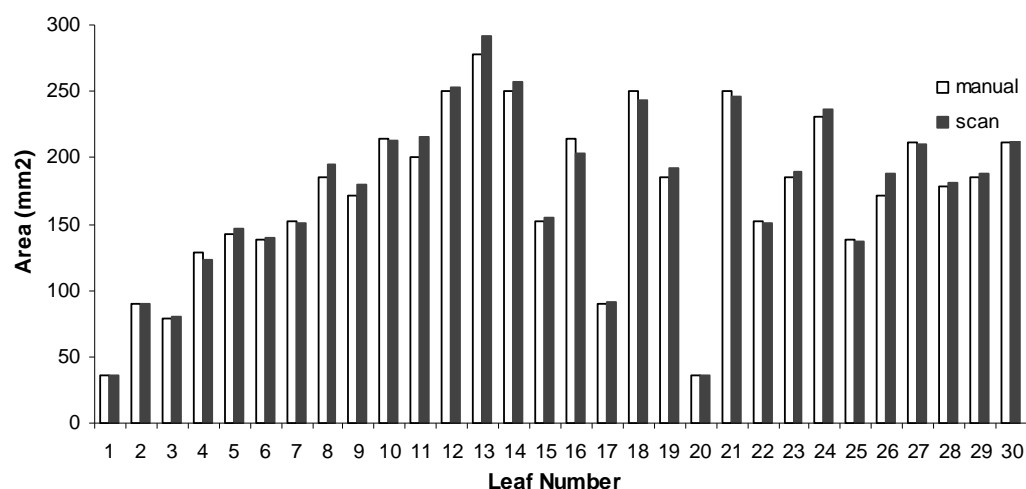
The same thirty leaves were then attached to plain paper with clear tape and the sheet photocopied. The photocopy was scanned using a Hewlett Packard ScanJet 4c scanner; the image saved with Corel Draw. Using the Jandel software package Sigma Scan, the perimeters of total area, and missing area of the damaged leaves, were traced and the areas calculated for those perimeters.

For each set of data the percentage leaf area loss (%LAL) from the chewed leaves was calculated (as described in Chapter 4) using the formula

$$\%LAL = (LAL / TPA) \times 100$$

where LAL is the leaf area lost from the leaf and TPA the total potential area had the leaf remained intact.

The leaf areas and percentage leaf area loss calculated for the two measurement methods were then compared graphically and statistically as below (figures A.6.1 & 2, respectively). There was no significant difference between the manual or digital measurement of either the leaf areas (ANOVA, $F_{1,58} = 0.021$, $P = 0.8843$) or percentage leaf area loss and measurement by digital scanning of the leaves (ANOVA, $F_{1,38} = 0.0005$, $P = 0.9830$).



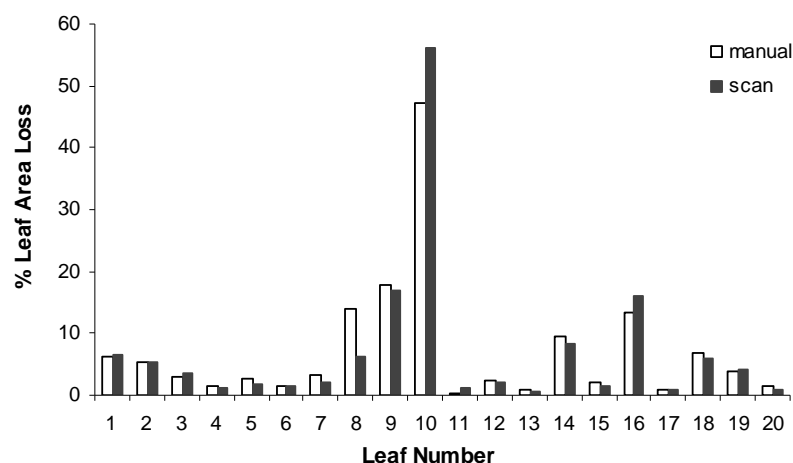
Leaf Areas (mm²) Summary

Groups	Count	Sum	Average	Variance
Manual	30	5158.5	171.95	3893.299
Scan	30	5229.81	174.327	4043.353

Leaf Areas Analysis of Variance

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	84.75194	1	84.75194	0.021357	0.884317	4.006873
Within Groups	230162.9	58	3968.326			
Total	230247.7	59				

Figure A.6.1. Manual versus digitally scanned measurement of leaf areas: summary of results for 30 *N. gunnii* leaves.



% Leaf Area Loss (%LAL) Summary

Groups	Count	Sum	Average	Variance
Manual	20	144.11023	7.205512	113.0416
scan	20	142.54004	7.127002	155.335

% Leaf Area Loss (%LAL) Analysis of Variance

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	0.061637	1	0.061637	0.000459	0.983013	4.098172
Within Groups	5099.157	38	134.1883			
Total	5099.218	39				

Figure A.6.2. Manual versus digitally scanned measurement of proportion of leaf damage, % Leaf Area Loss (%LAL): for 20 *N. gunnii* leaves.

**Appendix A7. Tasmanian *Nothofagus* Arthropod Fauna, collected between March 1998 and March 2002:
Morphotaxa, *Nothofagus* Host Plant, Feeding Guilds (tables A.7.a - h.).**

Taxonomy Tabulated by Order and Morphotaxon Code (Mtx Code)

Table A.7.a. Coleoptera

Table A.7.e. Thysanoptera

Table A.7.b. Hemiptera

Table A.7.f. Plecoptera

Table A.7.c. Lepidoptera

Table A.7.g. Acarina

Table A.7.d. Psocoptera

Table A.7.h. Araneae

Host Plant

Nc: Morphotaxon was found only on *N. cunninghamii*

Ng: Morphotaxon was found only on *N. gunnii*

Nc&Ng: Morphotaxon was found on both *N. cunninghamii* and *N. gunnii*

Feeding Guilds

Herbivores

Hch: Leaf chewers

Hss: Sap-suckers

Hmn: Leaf miners

Hne: Nectivores

Non-herbivores

P: Predators

F/D: Fungivores/Detritivores

Table A.7.a. Coleoptera: Adult Morphotaxa.

Mtx Code	Superfamily	Family	Subfamily	Tribe	Genus	Species	Host Plant	Feeding Guild
CpAd1	Tenebrionoidea	Aderidae			<i>Aderus</i>	sp.1	Nc	FD
CpAd2	Tenebrionoidea	Aderidae			<i>Aderus</i>	sp.2	Nc	FD
CpAp1	Curculinoidea	Apionidae	Apioninae		<i>Apion</i>	<i>microscopicum</i> Lea	Nc&Ng	Hch
CpAr1	Curculinoidea	Anthribidae			<i>Xynotropis</i>	<i>micans</i> Blackburn	Nc	FD
CpBu1	Buprestoidea	Buprestidae	Buprestinae	Buprestini	<i>Nascioides</i>	<i>quadrinotata</i> Van de Poll	Nc	Hne
CpCa1	Caraboidea	Carabidae	Carabinae	Ctenodactylini	<i>Plagiotelus</i>	sp.1	Nc	P
CpCh1	Chrysomeloidea	Chrysomelidae	Cryptocephalinae	incertae sedis	<i>Platycolaspis</i>	<i>mcquillani</i> Reid	Nc&Ng	Hch
CpCh2	Chrysomeloidea	Chrysomelidae	Eumolpinae		<i>Eboo</i>	sp.1	Nc	Hch
CpCh3	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Goniocetenini	<i>Ewanius</i>	<i>nothofagi</i> Reid	Nc&Ng	Hch
CpCh4	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Goniocetenini	<i>?Paropsina</i>	sp.1	Nc&Ng	Hch
CpCh5	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Goniocetenini	<i>Chrysophtharta</i>	sp.1	Ng	Hch
CpCh6	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Goniocetenini	<i>Paropsis</i>	sp.1	Nc	Hch
CpCh7	Chrysomeloidea	Chrysomelidae	Cryptocephalinae	incertae sedis	<i>Semelvillea</i>	<i>tasmaniae</i> Reid	Nc	Hch
CpCh8	Chrysomeloidea	Chrysomelidae	Galerucinae	incertae sedis	<i>Microdonacia</i>	<i>octodentata</i> Reid	Nc	Hch
CpCh9	Chrysomeloidea	Chrysomelidae	Galerucinae	Galerucini	<i>Monolepta</i>	sp.1	Nc&Ng	Hch
CpCh10	Chrysomeloidea	Chrysomelidae	Galerucinae	incertae sedis	<i>Microdonacia</i>	<i>truganina</i> Monros	Nc&Ng	Hch
CpCh11	Chrysomeloidea	Chrysomelidae	Galerucinae	Galerucini	<i>Monolepta</i>	sp.2	Nc	Hch
CpCh12	Chrysomeloidea	Chrysomelidae	Galerucinae	incertae sedis	<i>Microdonatia</i>	<i>incurva</i> Reid	Nc	Hch
CpCh13	Chrysomeloidea	Chrysomelidae	Galerucinae	Alticini	<i>?Aphthona</i>	sp.1	Nc	Hch
CpCh14	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Goniocetenini	<i>Chrysophtharta</i>	<i>bimaculata</i>	Nc	Hch
CpCm1	Eucinetoidae	Clambidae	Clambinae		<i>Clambus</i>	sp.1	Nc	FD
CpCo1	Cucujoidea	Coccinellidae	Scymninae	Coccidulini	<i>Rhyzobius</i>	sp.1	Nc&Ng	P
CpCo2	Cucujoidea	Coccinellidae	Scymninae	Coccidulini	<i>Rhyzobius</i>	sp.2	Nc	P
CpCo3	Cucujoidea	Coccinellidae	Scymninae	Coccidulini	<i>Rhyzobius</i>	sp.3	Nc&Ng	P
CpCo4	Cucujoidea	Coccinellidae	Scymninae	Coccidulini	<i>Rhyzobius</i>	sp.4	Nc&Ng	P
CpCo6	Cucujoidea	Coccinellidae	Scymninae	Coccidulini	<i>Rhyzobius</i>	sp.5	Nc&Ng	P
CpCo7	Cucujoidea	Coccinellidae	Scymninae	Coccidulini	<i>Rhyzobius</i>	<i>Alphabeticus</i> Lea	Nc	P
CpCo8	Cucujoidea	Coccinellidae	Scymninae	Scymnini	<i>Stethorus</i>	sp.1	Nc	P

Table A.7.a. continued. Coleoptera: Adult Morphotaxa.

Mtx Code	Superfamily	Family	Subfamily	Tribe	Genus	Species	Host Plant	Feeding Guild
CpCo9	Cucujoidea	Coccinellidae	Scymninae	Coccidulini	<i>?Rhyzobius</i>	sp.1	Nc	P
CpCo10	Cucujoidea	Coccinellidae	Scymninae	Coccidulini	<i>Rhyzobius</i>	sp.6	Nc	P
CpCr1	Cleroidea	Cleridae			<i>Lemidia</i>	sp.1	Nc	P
CpCu1	Curculinoidea	Curculionidae	Cryptorhynchinae	Cryptorhynchini	<i>Decilaus</i>	sp.1	Nc	Hch
CpCu2	Curculinoidea	Curculionidae	Entiminae	Entimini	<i>Merimnetes</i>	spp.	Nc&Ng	Hch
CpCu3	Curculinoidea	Curculionidae	Curculioninae	Tychiini		sp.1	Nc	Hch
CpCu4	Curculinoidea	Curculionidae	Cryptorhynchinae		<i>near Exithius</i>	sp.1	Nc	Hch
CpCu5	Curculinoidea	Curculionidae	Curculioninae	Tychiini		sp.2	Nc	Hch
CpCu6	Curculinoidea	Curculionidae	Curculioninae	Storeini		sp.1	Ng	Hch
CpCu7	Curculinoidea	Curculionidae	Curculioninae	Tychiini		sp.3	Ng	Hch
CpCu8	Curculinoidea	Curculionidae	Cryptorhynchinae	Cryptorhynchini	<i>Microcryptorhynchus/Miocalles</i>	<i>pygmaeus</i> Lea	Nc	Hch
CpCu9	Curculinoidea	Curculionidae	Cryptorhynchinae	Cryptorhynchini	<i>Decilaus</i>	sp.2	Nc	Hch
CpCu10	Curculinoidea	Curculionidae	Entiminae	Entimini	<i>Merimnetes</i>	sp.1	Ng	Hch
CpCu11	Curculinoidea	Curculionidae	Eugnominae		<i>near Elleschodes</i>	sp.1	Ng	Hch
CpCu12	Curculinoidea	Curculionidae	Baridinae		<i>Baris</i>	<i>vagans</i>	Nc	Hch
CpCu13	Curculinoidea	Curculionidae	Molytinae		<i>Orthorhinus</i>	<i>cylindrirostris</i>	Nc	Hch
CpCu14	Curculinoidea	Curculionidae	Cryptorhynchinae		<i>Decilaus</i>	sp.3	Nc	Hch
CpCu15	Curculinoidea	Curculionidae	"Adelognatha"			sp.1	Ng	Hch
CpCu16	Curculinoidea	Curculionidae	Cryptorhynchinae		<i>"Decilaus"</i>	sp.1	Nc	Hch
CpCu17	Curculinoidea	Curculionidae	"Adelognatha"		<i>near Enchymus</i>	sp.1	Nc	Hch
CpCu18	Curculinoidea	Curculionidae	"Adelognatha"		<i>near Enchymus</i>	sp.2	Nc	Hch
CpCu19	Curculinoidea	Curculionidae	"Adelognatha"		<i>near Enchymus</i>	sp.3	Nc	Hch
CpCu20	Curculinoidea	Curculionidae	Curculioninae	Tychiini		sp.4	Nc	Hch
CpCu21	Curculinoidea	Curculionidae	Curculioninae	Tychiini		sp.5	Nc	Hch
CpCu22	Curculinoidea	Curculionidae	Cryptorhynchinae		<i>Exithius</i>	<i>caryosus</i>	Nc	Hch
CpCy1	Cucujoidea	Corylophidae	Sericoderinae		<i>Sericoderus</i>	sp.1	Nc	FD
CpCy2	Cucujoidea	Corylophidae	Sericoderinae		<i>?Sericoderus/?Anisomeristes</i>	sp.1	Nc	FD
CpCy3	Cucujoidea	Corylophidae	Sericoderinae		<i>?Anisomeristes</i>	sp.1	Nc	FD

Table A.7.a. continued. Coleoptera: Adult Morphotaxa.

Mtx Code	Superfamily	Family	Subfamily	Tribe	Genus	Species	Host Plant	Feeding Guild
CpEt1	Elateroidea	Elateridae				sp.1	Nc	P
CpEt2	Elateroidea	Elateridae	Athionae		<i>near Crepidomenus</i>	sp.1	Nc	P
CpEt3	Elateroidea	Elateridae	Athionae		<i>Crepidomenus</i>	sp.1	Nc	P
CpEt4	Elateroidea	Elateridae			<i>near Crepidomenus</i>	sp.2	Nc	P
CpLa1	Cucujoidea	Lathridiidae	Corticariinae		<i>Corticicara</i>	spp.	Nc&Ng	FD
CpLa2	Cucujoidea	Lathridiidae	Corticariinae		<i>Corticaria</i>	sp.1	Nc&Ng	FD
CpLa3	Cucujoidea	Lathridiidae	Lathridiinae		<i>?Enicmus</i>	sp.1	Nc	FD
CpLa4	Cucujoidea	Lathridiidae	Lathridiinae		<i>?Aridius</i>	sp.1	Nc	FD
CpLe1	Staphylinoidea	Leiodidae	Cholevinae	Nemadini	<i>?Nargomorphus</i>	sp.1	Nc	FD
CpMe1	Tenebrionoidea	Melandryidae	Melandryinae		<i>Orchesia</i>	sp.1	Nc&Ng	FD
CpMe2	Tenebrionoidea	Melandryidae	Melandryinae		<i>Orchesia</i>	sp.2	Nc&Ng	FD
CpMe3	Tenebrionoidea	Melandryidae	Melandryinae		<i>Orchesia</i>	sp.3	Nc	FD
CpMe4	Tenebrionoidea	Melandryidae	Melandryinae		<i>Orchesia</i>	sp.4	Nc	FD
CpMe5	Tenebrionoidea	Melandryidae	Melandryinae		<i>Orchesia</i>	sp.5	Nc	FD
CpMe6	Tenebrionoidea	Melandryidae	Melandryinae		<i>Orchesia</i>	sp.6	Nc	FD
CpMr1	Tenebrionoidea	Mordellidae	Mordellinae	Mordellini	<i>?Mordella</i>	sp.1	Ng	Hne
CpMy1	Cleroidea	Melyridae	Malachiinae		<i>Hypattalus</i>	sp.1	Nc	FD
CpMy2	Cleroidea	Melyridae	Malachiinae		<i>Hypattalus</i>	sp.2	Nc	FD
CpMy3	Cleroidea	Melyridae	Malachiinae		<i>?Hypattalus</i>	sp.1	Nc	FD
CpNt1	Cucujoidea	Nitidulidae	Carpophylinae		<i>?Carpophilus</i>	sp.1	Ng	FD
CpNt2	Cucujoidea	Nitidulidae	Cillaeninae		<i>Brachypeplus</i>	sp.1	Nc	FD
CpNt3	Cucujoidea	Nitidulidae	Cybocephalinae		<i>?Cybocephalus</i>	sp.1	Nc	FD
CpPh1	Cucujoidea	Phalacridae			<i>?Phalacrus</i>	sp.1	Ng	FD
CpPs1	Staphylinoidea	Pselaphidae	Pselaphinae			sp.1	Nc	P
CpRh1	Curculinoidea	Rhynchitidae	Rhynchitinae		<i>Auletobrius</i>	sp.1	Nc&Ng	Hch
CpSa1	Tenebrionoidea	Salpingidae			<i>Notosalpingus</i>	sp.1	Nc&Ng	FD
CpSb1	Scarabaeoidea	Scarabaeidae	Melolonthinae	Sericini	<i>Adossa</i>	sp.1	Nc	Hch
CpSd1	Staphylinoidea	Scydmaenidae	Scydmaeninae		<i>Euconnus</i>	sp.1	Nc&Ng	P

Table A.7.a. continued. Coleoptera: Adult Morphotaxa.

Mtx Code	Superfamily	Family	Subfamily	Tribe	Genus	Species	Host Plant	Feeding Guild
CpSd2	Staphylinoidea	Scydmaenidae	Scydmaeninae		<i>Euconnus</i>	sp.2	Nc	P
CpSr1	Eucinetoidae	Scirtidae			<i>Pseudomicrocara</i>	sp.1	Nc&Ng	FD
CpSr02	Eucinetoidae	Scirtidae			<i>Pseudomicrocara</i>	sp.2	Nc&Ng	FD
CpSr03	Eucinetoidae	Scirtidae			<i>Pseudomicrocara</i>	sp.3	Nc&Ng	FD
CpSr04	Eucinetoidae	Scirtidae			? <i>Pseudomicrocara</i>	sp.1	Nc	FD
CpSr05	Eucinetoidae	Scirtidae			<i>Macrohelodes</i>	<i>montanus</i>	Ng	FD
CpSr06	Eucinetoidae	Scirtidae			? <i>Genus</i>	sp.1	Nc	FD
CpSr07	Eucinetoidae	Scirtidae			? <i>Genus</i>	sp.2	Nc	FD
CpSr08	Eucinetoidae	Scirtidae			<i>Pseudomicrocara</i>	sp.4	Nc	FD
CpSt1	Staphylinoidea	Staphylinidae	Aleocharinae		<i>Atheta</i>	sp.1	Nc	P
CpSt02	Staphylinoidea	Staphylinidae	Aleocharinae		<i>near Atheta</i>	sp.1	Nc	P
CpSt03	Staphylinoidea	Staphylinidae	Tachyporinae		? <i>Sepedophilus</i>	sp.1	Nc	P
CpSt04	Staphylinoidea	Staphylinidae	Tachyporinae		? <i>Tachinus</i>	sp.1	Nc	P
CpSv1	Cucujoidea	Silvanidae	Silvaninae		? <i>Ahasversus</i>	sp.1	Nc	FD
CpTe1	Tenebrionoidea	Tenebrionidae	Tenebrioninae	Titaenini	<i>Leaus</i>	<i>tasmanicus</i> Matthews & Lawrence	Ng	FD

Table A.7.a. continued. Coleoptera: Immature Morphotaxa.

Mtx Code	Superfamily	Family	Subfamily	Tribe	Genus	Species	Host Plant	Feeding Guild
CpChL1	Chrysomeloidea	Chrysomelidae	Chrysomelinae	Goniocetenini	<i>Ewanius</i>	<i>nothofagi</i> Reid	Nc	Hch
CpChL2	Chrysomeloidea	Chrysomelidae				sp.2	Nc	Hch
CpChL3	Chrysomeloidea	Chrysomelidae				sp.3	Nc	Hch
CpChL4	Chrysomeloidea	Chrysomelidae				sp.4	Nc	Hch
CpCoL1	Cucujoidea	Coccinellidae				sp.1	Nc	P
CpCoL2	Cucujoidea	Coccinellidae				sp.2	Nc	P
CpCoL3	Cucujoidea	Coccinellidae				sp.3	Nc	P
CpCoL4	Cucujoidea	Coccinellidae			? <i>Rhyzobius</i>	sp.1	Nc	P

Table A.7.b. Hemiptera: Adult Morphotaxa.

Mtx Code	Suborder	Superfamily	Family	Subfamily	Genus	Species	Host	Feeding Guild
HeAc1	Heteroptera	Pentatomoidea	Acanthosomatidae			sp.1	Nc	Hss
HeAp1	Sternorrhyncha	Aphidiodea	Aphididae		Taiwanaphis	<i>Tasmaniae</i> Carver & Martyn	Nc&Ng	Hss
HeAp2	Sternorrhyncha	Aphidiodea	Aphididae			sp.2	Ng	Hss
HeAp3	Sternorrhyncha	Aphidiodea	Aphididae			sp.3	Ng	Hss
HeAr1	Auchenorrhyncha	Cercopoidea	Aphrophoridae		Anyllis	<i>leiala</i> Kirkaldy	Nc	Hss
HeAr2	Auchenorrhyncha	Cercopoidea	Aphrophoridae		Anyllis	<i>sp. nov.</i>	Nc	Hss
HeAr3	Auchenorrhyncha	Cercopoidea	Aphrophoridae		Anyllis	<i>spinostylus</i> Liang	Nc	Hss
HeCi1	Auchenorrhyncha	Membracoidea	Cicadellidae	Deltocephalinae	Diemoides	<i>?smithtoniensis</i> Evans	Nc	Hss
HeCi2	Auchenorrhyncha	Membracoidea	Cicadellidae	Deltocephalinae	?Diemoides	sp.1	Nc&Ng	Hss
HeCi3	Auchenorrhyncha	Membracoidea	Cicadellidae	Macropsinae		sp.1	Ng	Hss
HeCx1	Auchenorrhyncha	Fulgoroidea	Cixiidae	Cixiinae	Aka	sp.2	Nc&Ng	Hss
HeCx2	Auchenorrhyncha	Fulgoroidea	Cixiidae	Cixiinae	Aka	<i>hardyi</i> Muir	Nc&Ng	Hss
HeEr1	Sternorrhyncha	Coccoidea	Eriococcidae		Madarococcus	<i>cunninghamii</i> Hardy & Gullan.	Nc	Hss
HeEr2	Sternorrhyncha	Coccoidea	Eriococcidae		Madarococcus	near <i>osculus</i> Hardy & Gullan.	Nc&Ng	Hss
HeLy1	Heteroptera	Lygaeoidea	Lygaeidae		Trichobothria	sp.1	Nc	Hss
HeLy2	Heteroptera	Lygaeoidea	Lygaeidae		Nysius	sp.1	Nc&Ng	Hss
HeMe1	Auchenorrhyncha	Membracoidea	Membracidae		Pogonella	<i>bispinus</i> Stål	Nc	Hss
HeMe2	Auchenorrhyncha	Membracoidea	Membracidae	Centrotinae	Acanthuchus	<i>trispinifer</i> Fairmaire	Nc	Hss
HeMe3	Auchenorrhyncha	Membracoidea	Membracidae	Centrotinae	Acanthuchus	sp.2	Nc	Hss
HeMi1	Heteroptera	Miroidea	Miridae			sp.1	Ng	Hss
HeMi2	Heteroptera	Miroidea	Miridae			sp.2	Nc	Hss
HePc1	Sternorrhyncha	Coccoidea	Pseudococcidae			sp.1	Nc&Ng	Hss
HePe1	Heteroptera	Pentatomoidea	Pentatomidae			sp.1	Nc	Hss
HeTi1	Heteroptera	Tingoidea	Tingidae			sp.1	Nc	Hss
HeTi2	Heteroptera	Tingoidea	Tingidae			sp.2	Ng	Hss
HeTi31	Heteroptera	Tingoidea	Tingidae			sp.3	Nc	Hss

Table A.7.b. continued. Hemiptera: Immature Morphotaxa.

Mtx Code	Suborder	Superfamily	Family	Subfamily	Genus	Species	Host	Feeding Guild
HeAcJ1	Heteroptera	Pentatomoidea	Acanthosomatidae			? sp.1	Nc&Ng	Hss
HeCiJ1	Auchenorrhyncha	Membracoidea	Cicadellidae	Deltocephalinae		spp.	Nc	Hss
HeCiJ2	Auchenorrhyncha	Membracoidea	Cicadellidae	Ledrinae		spp.	Nc	Hss
HeMeJ1	Auchenorrhyncha	Membracoidea	Membracidae		Pogonella	spp.	Nc	Hss
HeMeJ3	Auchenorrhyncha	Membracoidea	Membracidae	Centrotinae	Acanthuchus	spp.	Nc&Ng	Hss

Table A.7.c. Lepidoptera: Adult Morphotaxa.

Mtx Code	Superfamily	Family	Subfamily	Tribe	Genus	Species	Host	Feeding Guild
LeAL		?Anthelidae / ?Lasiocampidae				sp.1	Nc	Hne
LeGT		?Gracillariidae / ?Tortricidae				sp.1	Nc	Hne
LeGc1	Gelechioidea	Gelechiidae				sp.1	Nc	Hne
LeGe4	Geometroidea	Geometridae	Geometrinae		<i>Euloxia</i>	<i>leucochorda</i>	Nc	Hne
LeGr1	Tineoidea	Gracillariidae	Gracillarinae		<i>Caloptilia</i>	<i>ostracodes</i>	Nc	Hne
LeHe1	Incurvaroidea	Heliozelidae				sp.1	Nc	Hne
LeHe2	Incurvaroidea	Heliozelidae				sp.2	Ng	Hne
LeHe3	Incurvaroidea	Heliozelidae				sp.3	Nc	Hne
LeHe 4	Incurvaroidea	Heliozelidae				sp.4	Nc	Hne

Table A.7.c. continued. Lepidoptera: Adult Morphotaxa.

Mtx Code	Superfamily	Family	Subfamily	Tribe	Genus	Species	Host	Feeding Guild
LeOe1	Gelechioidea	Oecophoridae	Oecophorinae	Wingia group	<i>Paneutricha</i>	<i>hypertricha</i> Turner	Ng	Hne
LeOe2	Gelechioidea	Oecophoridae	Oecophorinae	Chezala group	<i>Chezala</i>	sp.1	Nc&Ng	Hne
LeOe3	Gelechioidea	Oecophoridae	Oecophorinae	Barea group	<i>Barea</i> Walker, 1864	sp.1	Nc	Hne
LeOe4	Gelechioidea	Oecophoridae	Oecophorinae	Barea group	<i>Barea</i> Walker, 1865	sp.2	Nc	Hne
LeOe5	Gelechioidea	Oecophoridae	Oecophorinae	Eulechria group	<i>Eulechria</i>	sp.1	Nc	Hne
LeOe6	Gelechioidea	Oecophoridae	Oecophorinae	Barea group	<i>Locheutis</i> Meyrick, 1883	sp.1	Nc	Hne
LeOe7	Gelechioidea	Oecophoridae	Oecophorinae	Eulechria group	near <i>Eulechria</i>	sp.1	Nc	Hne
LeOe8	Gelechioidea	Oecophoridae	Oecophorinae	Wingia group	near <i>Tortricopsis</i>	sp.1	Nc	Hne
LeOe9	Gelechioidea	Oecophoridae	Oecophorinae	Wingia group	" <i>Ocystola</i> "	sp.1	Nc	Hne
LeOe11	Gelechioidea	Oecophoridae	Oecophorinae	Philobota group	<i>Philobota</i>	sp.1	Nc	Hne
LeOe12	Gelechioidea	Oecophoridae	Stathmopodinae		<i>Philobota</i> / <i>Eulechria</i>	sp.1	Nc	Hne
LeOe13	Gelechioidea	Oecophoridae	Oecophorinae		<i>Stathmopoda</i> Herrich-Schäffer, 1853	sp.1	Nc	Hne
LeOe14	Gelechioidea	Oecophoridae	Oecophorinae	Chezala group	<i>Tachystola</i> Meyrick, 1914	sp.1	Ng	Hne
LeOe15	Gelechioidea	Oecophoridae	Oecophorinae	Chezala group	<i>Telanepsia</i>	sp.1	Nc	Hne
LeOe16	Gelechioidea	Oecophoridae	Oecophorinae	Chezala group	<i>Telanepsia</i>	<i>stictocrossa</i>	Nc	Hne
LeOe17	Gelechioidea	Oecophoridae				sp.1	Nc	Hne
LeOe18	Gelechioidea	Oecophoridae				sp.2	Nc	Hne
LeOe19	Gelechioidea	Oecophoridae				sp.3	Nc	Hne
LeOe20	Gelechioidea	Oecophoridae				sp.4	Nc	Hne
LeOe21	Gelechioidea	Oecophoridae				sp.5	Nc	Hne
LeOp1	Nepticuloidea	Opostegidae			<i>Opostega</i>	sp.1	Nc	Hne
LeTo1	Tortricoidea	Tortricidae	Tortricinae		<i>Tortrix</i>	<i>asemantica</i>	Nc	Hne
LeTo2	Tortricoidea	Tortricidae	Tortricinae		<i>Tortrix</i>	? <i>asemantica</i>	Ng	Hne
LeTo4	Tortricoidea	Tortricidae	Tortricinae		<i>Tortrix</i>	<i>incompta</i>	Nc	Hne
LeTo7	Tortricoidea	Tortricidae	Tortricinae		<i>Tortrix</i>	<i>adoxophanes</i> '	Nc	Hne
LeTo8	Tortricoidea	Tortricidae	Tortricinae		<i>Capua</i>	sp.1	Nc	Hne
LeTo9	Tortricoidea	Tortricidae	Tortricinae		<i>Isochorista</i>	sp.1	Nc	Hne
LeYp1	Yponomeutoidea	Yponomeutidae			<i>Zelleria</i>	sp.1	Nc	Hne

Table A.7.c. continued. Lepidoptera: Immature Morphotaxa.

Mtx Code	Superfamily	Family	Subfamily	Tribe	Genus	Species	Host	Feeding Guild
LeAnL1	Bombycoidea	Anthelidae	Anthelinae		<i>Anthela</i>	sp.1	Nc	Hch
LeArL1	Noctuoidea	Arctiidae	Lithosiinae		<i>Caprimima</i>	sp.1	Nc	FD
LeArL2	Noctuoidea	Arctiidae	Lithosiinae			sp.2	Nc	FD
LeArL3	Noctuoidea	Arctiidae	Lithosiinae			sp.3	Nc	FD
LeArL4	Noctuoidea	Arctiidae	Lithosiinae			sp.4	Nc	FD
LeArL5	Noctuoidea	Arctiidae	Lithosiinae			sp.5	Nc	FD
LeArL6	Noctuoidea	Arctiidae	Lithosiinae		<i>Palaeosia</i>	<i>bicosta</i>	Nc	FD
LeArL7	Noctuoidea	Arctiidae	Lithosiinae			sp.7	Nc	FD
LeArL8	Noctuoidea	Arctiidae	Lithosiinae			sp.6	Nc	FD
LeGeL1	Geometroidea	Geometridae	Ennominae	Nacophorini		<i>sp. novum</i>	Nc&Ng	Hch
LeGeL2	Geometroidea	Geometridae	Ennominae	Nacophorini	<i>Chlenias</i>	<i>?aucteria</i>	Ng	Hch
LeGeL3	Geometroidea	Geometridae	Geometrinae		<i>not Euloxia</i>	sp.1	Nc	Hch
LeGeL4	Geometroidea	Geometridae	Geometrinae		<i>Euloxia</i>	<i>leucochorda</i>	Nc	Hch
LeGeL5	Geometroidea	Geometridae	Ennominae	Nacophorini	<i>?Nisista</i>	sp.1	Nc&Ng	Hch
LeGeL6	Geometroidea	Geometridae		?Boarmiini		sp.1	Nc	Hch
LeGrL1	Tineoidea	Gracillariidae	Gracillarinae		<i>Caloptilia</i>	<i>ostracodes</i>	Nc	Hmn
LeNoL1	Noctuoidea	Noctuidae	Catocalinae		<i>?Pantydia</i>	sp.1	Nc	Hch
LePsL1	Tineoidea	Psychidae	Taleporiinae		<i>Narycia</i>	spp.	Nc&Ng	FD
LeRoL1	Tineoidea	Roeslerstammiidae			<i>Chalcoteuches</i>	<i>phlogera</i>	Nc	Hmn
LeToL1	Tortricoidea	Tortricidae	Tortricinae		<i>Tortrix</i>	<i>asemantica</i>	Nc	Hch
LeToL3	Tortricoidea	Tortricidae	Tortricinae		<i>Tortrix</i>	<i>?incompta</i>	Nc	Hch
LeToL4	Tortricoidea	Tortricidae	Tortricinae		<i>Tortrix</i>	<i>incompta</i>	Nc	Hch
LeToL5	Tortricoidea	Tortricidae				sp.1	Nc	Hch
LeToL7	Tortricoidea	Tortricidae	Tortricinae		<i>Tortrix</i>	<i>adoxophanes'</i>	Nc	Hch
LeToL9	Tortricoidea	Tortricidae				sp.4	Nc	Hch
LeToL10	Tortricoidea	Tortricidae	Tortricinae		<i>Epiphyas</i>	<i>xylodes</i>	Nc	Hch
LeToL11	Tortricoidea	Tortricidae	Tortricinae		<i>Epiphyas/Tortrix</i>	<i>xylodes/asemantica</i>	Nc	Hch

Table A.7.d. Psocoptera: Fully winged Morphotaxa.

Mtx Code	Superfamily	Family	Species	Host	Feeding Guild
PsCc1	Caecilioidea	Caeciliusidae	sp.1	Nc&Ng	FD
PsCc2	Caecilioidea	Caeciliusidae	sp.2	Nc&Ng	FD
PsEt1	Homilopsocidea	Ectopsocidae	sp.1	Nc	FD
PsPd1	Homilopsocidea	Pseudocaeciliidae	sp.1	Nc	FD
PsPp1	Homilopsocidea	Peripsocidae	sp.1	Nc	FD
PsPp2	Homilopsocidea	Peripsocidae	sp.2	Nc	FD
PsPp3	Homilopsocidea	Peripsocidae	sp.3	Nc	FD
PsPp4	Homilopsocidea	Peripsocidae	sp.4	Nc	FD

Table A.7.d. continued. Psocoptera: Brachypterous Morphotaxa.

Mtx Code	Superfamily	Family	Species	Host	Feeding Guild
PsBr1	Homilopsocidea	Elipsocidae	sp.1	Nc	FD
PsBr2	Homilopsocidea	Elipsocidae	sp.2	Nc&Ng	FD
PsBr3	Homilopsocidea	Elipsocidae/Peripsocidae	sp.3	Nc&Ng	FD
PsBr4	Homilopsocidea	Ectopsocidae	sp.1	Nc	FD
PsBr5	Homilopsocidea	Ectopsocidae	sp.2	Nc&Ng	FD
PsBr6	Homilopsocidea	Ectopsocidae	sp.3	Nc	FD
PsBr7	Homilopsocidea	Ectopsocidae	sp.4	Nc	FD
PsBr8	Homilopsocidea	Ectopsocidae	sp.5	Nc&Ng	FD

Table A.7.e. Thysanoptera: Adult Morphotaxa.

Mtx Code	Suborder	Superfamily	Family	Subfamily	Genus	Species	Host	Feeding Guild
ThPh1	Tubulifera		Phlaeothripidae	Phlaeothripinae	<i>?Haplothrips</i>	sp.2	Nc	Hss
ThPh2	Tubulifera		Phlaeothripidae	Phlaeothripinae	<i>?Haplothrips</i>	sp.3	Nc	Hss
ThPh3	Tubulifera		Phlaeothripidae	Phlaeothripinae	<i>Haplothrips</i>	<i>victoriensis</i>	Nc	Hss
ThPh4	Tubulifera		Phlaeothripidae	Phlaeothripinae	<i>?Holothrips</i>	sp.1	Ng	Hss
ThPh5	Tubulifera		Phlaeothripidae	Idolothripinae	<i>Carientothrips</i>	sp.1	Nc	Hss
ThPh6	Tubulifera		Phlaeothripidae			sp.1	Nc	Hss
ThTh1	Terebrantia	Thripodea	Thripidae	Thripinae	<i>Pseudanaphothrips</i>	<i>achaetus</i>	Nc	Hss
ThTh2	Terebrantia	Thripodea	Thripidae	Thripinae	<i>Pseudanaphothrips</i>	<i>pallidus</i>	Nc&Ng	Hss
ThTh3	Terebrantia	Thripodea	Thripidae	Thripinae	<i>Thrips</i>	<i>australis</i>	Nc&Ng	Hss
ThTh4	Terebrantia	Thripodea	Thripidae	Thripinae	<i>Thrips</i>	<i>imuginis</i>	Nc&Ng	Hss
ThTh5	Terebrantia	Thripodea	Thripidae	Thripinae	<i>Thrips</i>	<i>seticollis</i>	Ng	Hss
ThTh6	Terebrantia	Thripodea	Thripidae	Thripinae	<i>Thrips</i>	<i>tabaci</i>	Nc	Hss
ThTh7	Terebrantia	Thripodea	Thripidae	Thripinae	<i>Thrips</i>	<i>?wellsae</i>	Nc&Ng	Hss
ThTh8	Terebrantia	Thripodea	Thripidae	Thripinae	<i>Chirothrips</i>	<i>manicatus</i>	Nc&Ng	Hss

Table A.7.e. continued. Thysanoptera: Immature Morphotaxa.

Mtx Code	Suborder	Superfamily	Family	Subfamily	Genus	Species	Host	Feeding Guild
ThPhL1	Tubulifera		Phlaeothripidae	Phlaeothripinae	<i>Haplothrips</i>	<i>?victoriensis</i>	Nc	Hss
ThPhL2	Tubulifera		Phlaeothripidae	Idolothripinae	<i>?Idolothrips</i>	sp.1	Nc	Hss
ThThL1	Terebrantia	Thripodea	Thripidae		<i>Pseudanaphothrips</i>	<i>pallidus</i>	Nc&Ng	Hss

Table A.7.f. Plecoptera: Adult Morphotaxa.

Mtx Code	Suborder	Superfamily	Family	Subfamily	Genus	Species	Host	Feeding Guild
PcGr1	Antarctoperlaria	Gripopterygoidea	Gripopterygidae	Leptoperlinae	<i>Leptoperla</i>	varia	Ng	FD
PcGr2	Antarctoperlaria	Gripopterygoidea	Gripopterygidae	Leptoperlinae	<i>Riekoperla</i>	<i>pulchra</i>	Nc&Ng	FD
PcGr3	Antarctoperlaria	Gripopterygoidea	Gripopterygidae	Leptoperlinae	<i>Cardioperla</i>	<i>edita</i>	Ng	FD
PcGr4	Antarctoperlaria	Gripopterygoidea	Gripopterygidae	Leptoperlinae	<i>Cardioperla</i>	<i>nigrifrons?</i>	Ng	FD
PcGr5	Antarctoperlaria	Gripopterygoidea	Gripopterygidae	Dinotoperlinae	<i>Dinotoperla</i>	<i>marmorata</i>	Ng	FD
PcGr6	Antarctoperlaria	Gripopterygoidea	Gripopterygidae	Leptoperlinae	<i>Cardioperla</i>	spp. (<i>lobata</i> , <i>falsa</i> or <i>media</i>)	Ng	FD
PcGr7	Antarctoperlaria	Gripopterygoidea	Gripopterygidae	Gripopteryginae	<i>Trinotoperla</i>	spp. (<i>zwicki</i> or <i>comprimata</i>)	Ng	FD
PcGr8	Antarctoperlaria	Gripopterygoidea	Gripopterygidae	Dinotoperlinae	<i>Dinotoperla</i>	<i>opposita</i>	Nc	FD
PcGr9	Antarctoperlaria	Gripopterygoidea	Gripopterygidae	Dinotoperlinae	<i>Dinotoperla</i>	sp.1	Nc	FD
PcNo1	Arctoperlaria	Nemouroidea	Notonemouridae		<i>Austrocercoides</i>	<i>zwicki</i>	Nc&Ng	FD
PcNo2	Arctoperlaria	Nemouroidea	Notonemouridae		<i>Austocerca</i>	<i>tasmanica</i>	Ng	FD
PcNo3	Arctoperlaria	Nemouroidea	Notonemouridae		<i>Kimminsoperla</i>	<i>albomacula</i>	Nc	FD
PcNo4	Arctoperlaria	Nemouroidea	Notonemouridae		<i>Austrocercoides</i>	<i>bullata</i>	Nc	FD

Table A.7.g Acarina: Adult Morphotaxa.

Mtx Code	Suborder	Cohort	Superfamily	Family	Genus	Species	Host	Feeding Guild
AcMe1	Mesostigmata	Dermanyssina	Monogynaspida			sp.1	Nc&Ng	P
AcMe2	Mesostigmata	Uropodina				sp.1	Nc	P
AcMe3	Mesostigmata	Dermanyssina	Monogynaspida			sp.2	Nc&Ng	P
AcMe4	Mesostigmata	Dermanyssina	Monogynaspida			sp.3	Nc&Ng	P
AcMe5	Mesostigmata					sp.1	Nc&Ng	P

Table A.7.g. continued. Acarina: Adult Morphotaxa.

Mtx Code	Suborder	Cohort	Superfamily	Family	Genus	Species	Host	Feeding Guild
AcMe6	Mesostigmata	Dermanyssina	Rhodacaroidea	Ologamasidae Ryke, 1962		sp.1	Nc	P
AcMe9	Mesostigmata	Dermanyssina	Rhodacaroidea	Ologamasidae Ryke, 1962		sp.2	Nc&Ng	P
AcMe10	Mesostigmata	Dermanyssina	Rhodacaroidea	Ologamasidae Ryke, 1962		sp.3	Nc	P
AcMe11	Mesostigmata					sp.2	Ng	P
AcOr1	Oribatida	Brachypilina	Ceratozetoidea			sp.1	Nc&Ng	FD
AcOr2	Oribatida	Brachypilina	Oribatelloidea			sp.1	Nc&Ng	FD
AcOr3	Oribatida	Brachypilina	Ameronthroidea	Ameronthridae		sp.1	Nc&Ng	FD
AcOr4	Oribatida	Brachypilina	Oripodoidea	Neotrichozetidae		sp.1	Nc	FD
AcOr5	Oribatida	Brachypilina	Tectocephoidea			sp.1	Nc&Ng	FD
AcOr6	Oribatida	Brachypilina	Plateremaeoidea	Pedrocortesellidae		sp.1	Nc&Ng	FD
AcOr7	Oribatida	Nothrina	Crotonioidea	Nothridae		sp.1	Nc&Ng	FD
AcOr9	Oribatida	Brachypilina	Oribatelloidea			sp.2	Nc&Ng	FD
AcOr10	Oribatida	Brachypilina	Ameronthroidea			sp.1	Nc&Ng	FD
AcOr11	Oribatida	Brachypilina	Gustavioidea			sp.1	Nc&Ng	FD
AcOr12	Oribatida	Brachypilina	Oppioidea			sp.1	Nc&Ng	FD
AcOr13	Oribatida	Brachypilina	Oripodoidea			sp.2	Nc&Ng	FD
AcOr14	Oribatida	Nothrina	Crotonioidea			sp.1	Nc	FD
AcOr15	Oribatida	Nothrina	Crotonioidea	Camisiidae		sp.1	Nc	FD
AcOr16	Oribatida	Brachypilina	Plateremaeoidea	Pedrocortesellidae	nr <i>Hexachaetoniella contigua/diversa</i>		Nc	FD
AcOr17	Oribatida	Euptyctima	Phthiracaridea	Phthiracaridae		sp.1	Nc&Ng	FD
AcOr20	Oribatida	Brachypilina	Oripodoidea	Oribatulidae		sp.1	Nc&Ng	FD
AcOr21	Oribatida	Brachypilina	Oripodoidea	Oribatulidae		sp.2	Nc	FD
AcOr22	Oribatida	Brachypilina	Ceratozetoidea	Ceratozetidae		sp.1	Nc	FD
AcOr23	Oribatida	Nothrina	Nanhermannioidea	Nanhermanniidae		sp.1	Nc&Ng	FD
AcOr24	Oribatida	Brachypilina	Oripodoidea	Oribatulidae	nr <i>Paraphanloppia novaezealandica</i>		Nc&Ng	FD
AcOr26	Oribatida	Brachypilina	Galumnoidea	Parakalummatidae		sp.1	Nc&Ng	FD
AcOr27	Oribatida	Brachypilina	Oripodoidea	Leibstadiidae		sp.1	Nc	FD

Table A.7.g. continued. Acarina: Adult Morphotaxa.

Mtx Code	Suborder	Cohort	Superfamily	Family	Genus	Species	Host	Feeding Guild
AcOr30	Oribatida					sp.1	Nc	FD
AcOr31	Oribatida	Brachypilina	Oripodoidea	near Oripodidae		sp.1	Nc	FD
AcOr32	Oribatida	Brachypilina	Oripodoidea	Mochlozetidae		sp.1	Nc	FD
AcOr33	Oribatida	Brachypilina	Oripodoidea	Haplozetidae		sp.1	Nc	FD
AcOr35	Oribatida	Brachypilina	Plateremaeoidea	near Pedrocortesellidae		sp.1	Ng	FD
AcOr36	Oribatida		Neoliodoidea	Neoliodidae		sp.1	Nc	FD
AcPr1	Prostigmata	Eupodina	Bdelloidea	Bdellidae		sp.1	Nc&Ng	P
AcPr2	Prostigmata	Parasitengona				sp.1	Nc&Ng	P
AcPr4	Prostigmata	Anystina	Anystoidea	Anystidae		sp.1	Nc&Ng	P
AcPr5	Prostigmata	Parasitengona				sp.2	Nc&Ng	P
AcPr7	Prostigmata	Anystina	Anystoidea	Anystidae		sp.2	Nc&Ng	P
AcPr8	Prostigmata	Anystina	Anystoidea	Anystidae		sp.3	Nc&Ng	P
AcPr11	Prostigmata	Parasitengona				sp.3	Nc&Ng	P
AcPr12	Prostigmata	Eupodina	Bdelloidea	Cunaxidae		sp.1	Nc&Ng	P
AcPr13	Prostigmata	Parasitengona	Trombiculoidea	Trombellidae		sp.1	Nc	P
AcPr14	Prostigmata	Parasitengona				sp.4	Nc&Ng	P
AcPr15	Prostigmata	Parasitengona				sp.5	Nc&Ng	P
AcPr16	Prostigmata	Eleuthrengona	Raphignathoidea	Stigmaeidae		sp.1	Nc	P
AcPr17	Prostigmata	Parasitengona				sp.6	Nc&Ng	P
AcPr18	Prostigmata	Parasitengona	Trombiculoidea	Trombellidae		sp.2	Nc	P
AcPr19	Prostigmata	Eleuthrengona	Raphignathoidea	Eupalopsellidae		sp.1	Ng	P
AcPr20	Prostigmata	Parasitengona				sp.7	Nc&Ng	P
AcPr21	Prostigmata	Eupodina	Bdelloidea	Cunaxidae		sp.2	Nc	P
AcPr22	Prostigmata	Eupodina	Eupodoidea	Eupodidae		sp.1	Nc	P
AcPr23	Prostigmata	Parasitengona				sp.8	Nc	P
AcPr24	Prostigmata	Eupodina	Eupodoidea	Penthaleidae		sp.1	Nc&Ng	P
AcPr25	Prostigmata	Eleuthrengona	Raphignathoidea	Mecognathidae		Mecognatha Wood 1967	Nc&Ng	P

Table A.7.h. Araneae: Adult Morphotaxa.

Mtx Code	Cohort	Superfamily	Family	Subfamily	Genus	Species	Host	Feeding Guild
ArAr1	Entelegynae	Araneoidea	Araneidae		<i>Eriophora</i>	sp.1	Nc&Ng	P
ArAr2	Entelegynae	Araneoidea	Araneidae		<i>Eriophora</i>	sp.2	Nc	P
ArAr3	Entelegynae	Araneoidea	Araneidae			sp.3	Ng	P
ArAr4	Entelegynae	Araneoidea	Araneidae			sp.4	Ng	P
ArAr6	Entelegynae	Araneoidea	Araneidae			sp.6	Nc	P
ArAr7	Entelegynae	Araneoidea	Araneidae			sp.7	Ng	P
ArCb1	Entelegynae	Dionycha	Clubionidae			sp.1	Nc	P
ArCb2	Entelegynae	Dionycha	Clubionidae	Clubioninae		sp.2	Nc	P
ArLn1	Entelegynae	Araneoidea	Linyphiidae			sp.1	Nc&Ng	P
ArLn2	Entelegynae	Araneoidea	Linyphiidae			sp.2	Nc	P
ArLn3	Entelegynae	Araneoidea	Linyphiidae	Erigoninae/Mynoglennae		sp.3	Nc&Ng	P
ArLn4	Entelegynae	Araneoidea	Linyphiidae	Erigoninae		sp.4	Nc	P
ArLn6	Entelegynae	Araneoidea	Linyphiidae			sp.6	Nc	P
ArLn7	Entelegynae	Araneoidea	Linyphiidae			sp.7	Nc	P
ArLn8	Entelegynae	Araneoidea	Linyphiidae			sp.8	Nc	P
ArLn10	Entelegynae	Araneoidea	Linyphiidae			sp.10	Ng	P
ArOr2	Haplogynae	Dysderoidea	Orsolobidae			sp.2	Nc	P
ArSa4	Entelegynae	Dionycha	Salticidae			Sp.4	Nc	P
ArTh3	Entelegynae	Araneoidea	Theridiidae		<i>Achaeearanea</i>	Sp.3	Nc	P
ArTh4	Entelegynae	Araneoidea	Theridiidae			Sp.4	Nc	P
ArTh5	Entelegynae	Araneoidea	Theridiidae		<i>Phoroncidia</i>	Sp.5	Nc	P
ArTh6	Entelegynae	Araneoidea	Theridiidae			Sp.6	Nc	P
ArTh7	Entelegynae	Araneoidea	Theridiidae			Sp.7	Ng	P
ArTo1	Entelegynae	Dionycha	Thomisidae		<i>Diaea</i>	sp.1	Nc	P
ArTs1	Entelegynae	Araneoidea	Theridosomatidae	Theridosomatinae		sp.1	Nc	P
ArTs2	Entelegynae	Araneoidea	Theridosomatidae	Theridosomatinae		sp.2	Nc	P

Table A.7.h. continued. Araneae: Immature Morphotaxa.

Mtx Code	Cohort	Superfamily	Family	Subfamily	Genus	Species	Host	Feeding Guild
ArArJ1	Entelegynae	Araneoidea	Araneidae		<i>Eriophora</i>	sp.1	Nc&Ng	P
ArArJ2	Entelegynae	Araneoidea	Araneidae		<i>Eriophora</i>	sp.2	Ng	P
ArArJ5	Entelegynae	Araneoidea	Araneidae			sp.5	Ng	P
ArArJ6	Entelegynae	Araneoidea	Araneidae			sp.6	Nc&Ng	P
ArCbJ1	Entelegynae	Dionycha	Clubionidae			sp.1	Nc	P
ArCbJ2	Entelegynae	Dionycha	Clubionidae	Clubioninae		sp.2	Nc&Ng	P
ArLnJ1	Entelegynae	Araneoidea	Linyphiidae			sp.1	Nc&Ng	P
ArLnJ2	Entelegynae	Araneoidea	Linyphiidae			sp.2	Nc&Ng	P
ArLnJ3	Entelegynae	Araneoidea	Linyphiidae	Erigoninae/Mynogleninae		sp.3	Nc	P
ArLnJ4	Entelegynae	Araneoidea	Linyphiidae	Erigoninae		sp.4	Nc	P
ArLnJ5	Entelegynae	Araneoidea	Linyphiidae	Erigoninae		sp.5	Nc&Ng	P
ArLnJ8	Entelegynae	Araneoidea	Linyphiidae			sp.8	Nc	P
ArLnJ9	Entelegynae	Araneoidea	Linyphiidae			sp.9	Nc	P
ArLnJ10	Entelegynae	Araneoidea	Linyphiidae			sp.10	Nc&Ng	P
ArLnJ11	Entelegynae	Araneoidea	Linyphiidae			sp.11	Nc	P
ArLnJ12	Entelegynae	Araneoidea	Linyphiidae			sp.12	Nc&Ng	P
ArLnJ14	Entelegynae	Araneoidea	Linyphiidae			sp.14	Ng	P
ArOrJ1	Haplogynae	Dysderoidea	Orsolobidae			sp.1	Nc	P
ArSaJ1	Entelegynae	Dionycha	Salticidae		<i>Lycedis</i>	Sp.1	Nc	P
ArSaJ2	Entelegynae	Dionycha	Salticidae			Sp.2	Nc	P
ArSaJ3	Entelegynae	Dionycha	Salticidae			Sp.3	Nc&Ng	P
ArThJ1	Entelegynae	Araneoidea	Theridiidae			Sp.1	Nc	P
ArThJ2	Entelegynae	Araneoidea	Theridiidae			Sp.2	Nc	P
ArThJ3	Entelegynae	Araneoidea	Theridiidae		<i>Achaearana</i>	Sp.3	Nc	P
ArThJ4	Entelegynae	Araneoidea	Theridiidae			Sp.4	Nc	P
ArThJ6	Entelegynae	Araneoidea	Theridiidae			Sp.6	Nc	P
ArThJ7	Entelegynae	Araneoidea	Theridiidae			Sp.7	Nc	P
ArToJ1	Entelegynae	Dionycha	Thomisidae		<i>Diaea</i>	sp.1	Nc	P
ArTsJ1	Entelegynae	Araneoidea	Theridosomatidae	Theridosomatinae		sp.1	Nc	P

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Dr Laurence Mound, CSIRO Entomology, Canberra: Thysanoptera.

Dr Cathy Young, Tasmanian Museum and Art Gallery, Hobart: Lepidoptera, Geometridae.

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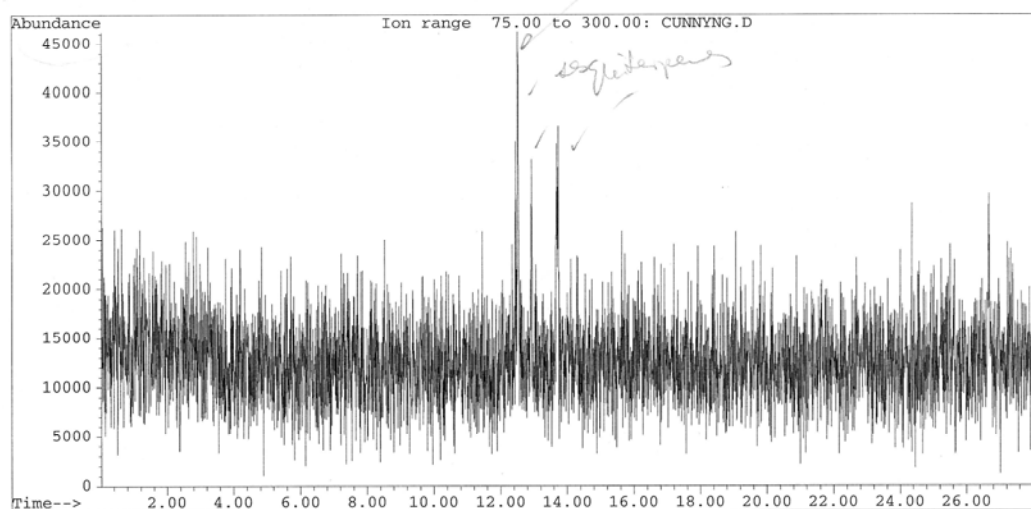
Appendix 8. Analysis of *N. cunninghamii* and *N. gunnii* Leaf Volatiles & Waxes.

Instruments and Methods (Associate Professor Noel Davies, Central Science Laboratory, University of Tasmania: personal communication):

- A HP5890 gas chromatograph was coupled to a HP5970B Mass Selective Detector. The gas chromatograph column was 25m x 0.32mm x 0.17µm HPL.
- Headspace volatiles were supplied by Solid Pulse Micro Extraction (SPME) using a 100 µm PDMS fibre, sampling for 10 minutes. The fibre was desorbed for 3 minutes at 280°C. Mass spectra were acquired from m/z 40 to 520 every 0.4 seconds.
- Waxes were analysed by injection of 1 µl of solution at 280 °C and running the gas chromatograph column from 100 °C to 300 °C.
- Peaks were identified by comparison of the mass spectra with the National Institute of Standards and Technology (USA), 'in-house' libraries, and first principle interpretation.

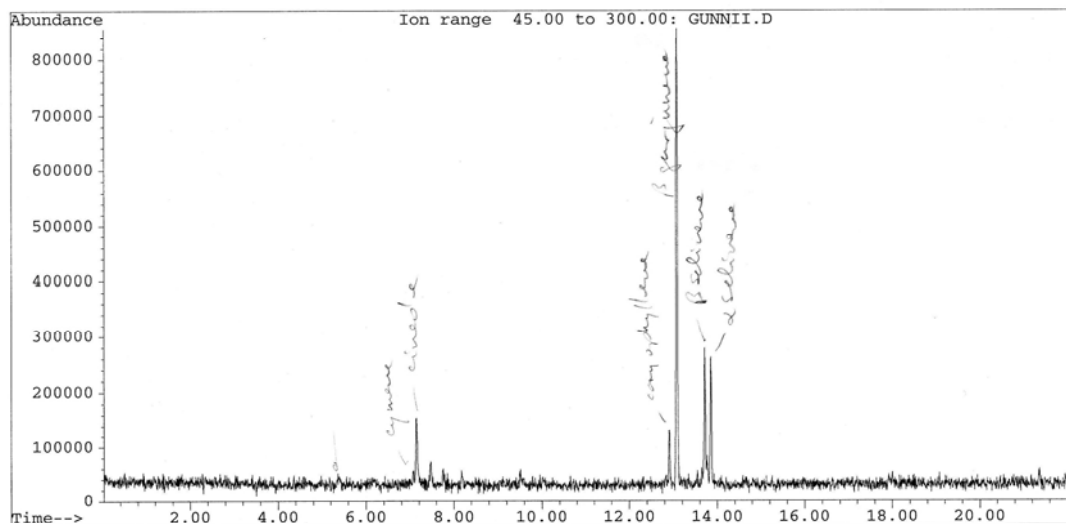
Copies of the original mass spectra are below:

File : G:\JANE\DEC-00\CUNNYNG.D
 Operator : ND
 Acquired : 12 Dec 100 4:26 am using AcqMethod SPMENOTH.M
 Instrument : 5970 - In
 Sample Name: Noth cunninghamii SPME injection 0.17u HP1
 Misc Info : 10 min sample, 3min desorb 15psi young leaf
 Vial Number: 1



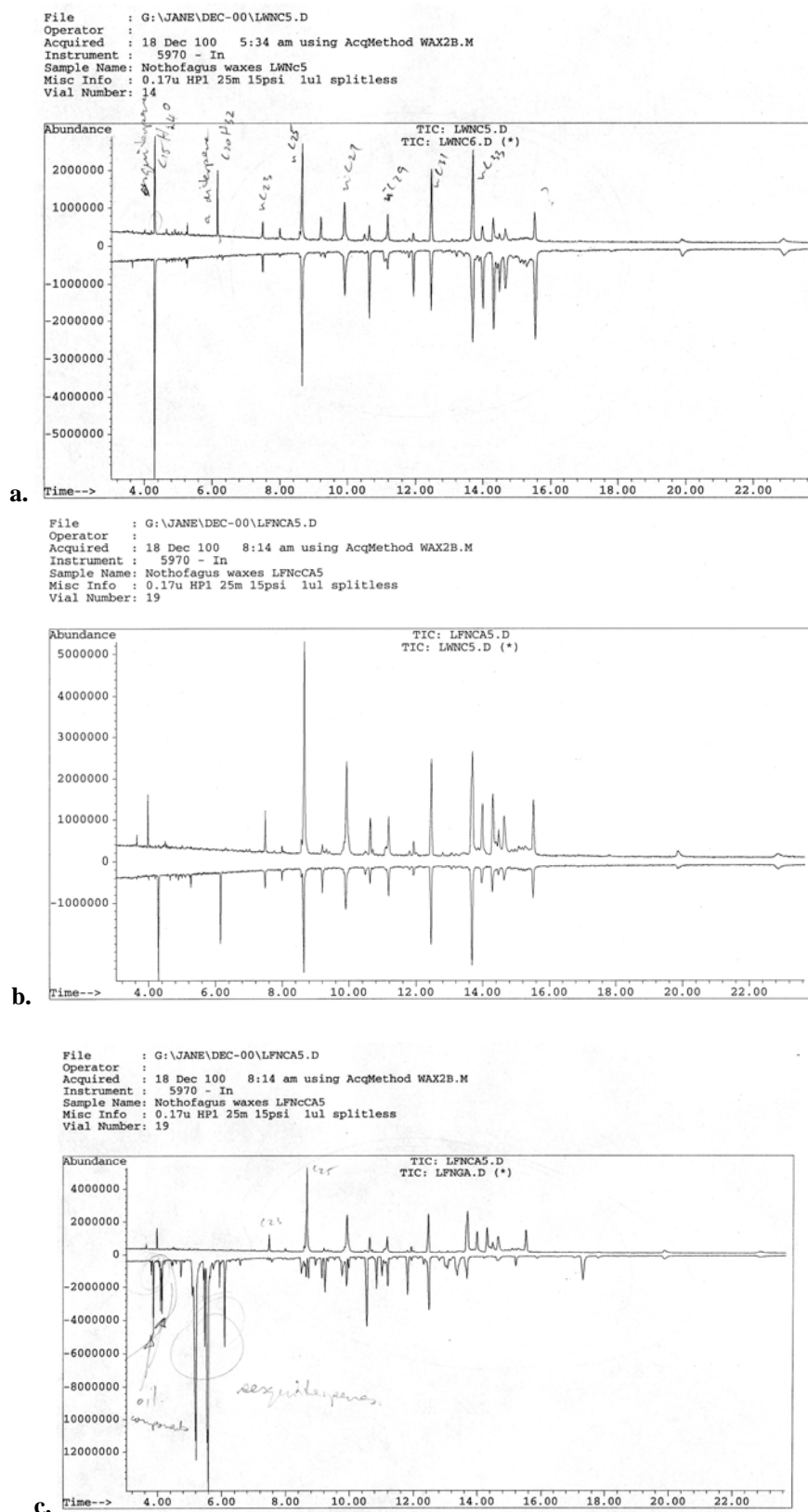
a.

File : G:\JANE\DEC-00\GUNNII.D
 Operator : ND
 Acquired : 12 Dec 100 2:37 am using AcqMethod SPMENOTH.M
 Instrument : 5970 - In
 Sample Name: Nothofagus gunnii SPME injection 0.17u HP1
 Misc Info : 10 min sample, 3min desorb 15psi
 Vial Number: 1



b.

Appendix 8 Figure A.8.1. Analysis of leaf volatiles, copy of original results: a, *N. cunninghamii*, young leaf, Lyrebird Walk; b, *N. gunnii*, Lake Fenton. Chemical analysis (and interpretive annotations) c/o Associate Professor Noel Davies, Central Science Laboratory, University of Tasmania.



For **Appendix B, Plates B.1 – B.120. Photo-record of Tasmanian *Nothofagus* Arthropods Collected in this study**, please see Volume 2:

‘Canopy Arthropods and Herbivory on the Tasmanian Southern Beeches,
Nothofagus cunninghamii and *Nothofagus gunnii*. Volume 2. Appendix B, Plates B.1
– B.120. Photo-record of Tasmanian *Nothofagus* Arthropods Collected in this study’