Examining the effects of distance from mature forest and successional stage on beetle community recolonisation and assembly

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Declaration

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Chapter 2 is in press:

Fountain-Jones, N.M., Baker, S.C. and Jordan, G. (in press). 'Moving beyond the guild concept: developing a consistent functional trait framework for terrestrial beetles' *Ecological Entomology.*

The candidate was the primary author. The Candidate as well as authors 2 and 3 contributed to developing the idea.

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The candidate was the primary author, undertook most of the field and laboratory work and conducted the data analysis. Authors 2, 3 and 5 assisted with data analysis and authors 7 and 8 assisted with field work, obtaining, and preparing data. The candidate as well as authors 2 and 3 contributed to developing the main idea, and approach. Authors 2, 3, 7 and 8 assisted with refining the text.

Chapter 4 is in preparation:

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The candidate was the primary author and was involved in all field and laboratory work. Measurments of beetle functional traits was done in collaboration with author 9. The candidate conducted all of the data analysis. The candidate as well as authors 2, 3 and 4 developed the main ideas, and approach. Authors 2, 3, 4, 5 and 7 assisted with refining the text.

Chapter 5 is submitted:

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beetle responses to habitat manipulation using a combined functional and phylogenetic approach. *Animal Ecology*.

Candidate was the primary author and conducted most of the field and laboratory work with assistance from author 8. The candidate conducted all of the data analysis. The candidate as well as authors 2 and 3 developed the main ideas and approach. Authors 2, 3, 4 and 8 assisted with refining the text.

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Abstract

How mature forest impacts adjacent disturbed forest, or "forest influence", is a poorly understood ecological concept that is important for sustainable forest management worldwide. Specifically, this thesis investigated whether beetles can recolonise disturbed areas from adjacent mature forests, and how this changed with forest succession. Furthermore, I applied a combined functional trait and phylogenetic approach to better understand what processes were important for succession and recolonisation. This involved a review and three studies based on two large-scale experiments.

Functional trait approaches for beetles lack consistent methodology and conceptual basis. Chapter 2 reviews previous beetle functional trait studies and outlines a broadly applicable trait framework, including a potentially useful list of traits, analysis approaches and future challenges for this discipline. This manuscript is accepted for publication in *Ecological Entomology*.

Chapter 3 illustrates that forest influence operates for beetle communities, and that these effects changed greatly over time. This was based on analysing beetle community composition from pitfall traps at fifteen sites, using replicated transects across mature forest boundaries into adjacent harvested stands, over a chronosequence of three secondary forest stages (~7, ~27 and ~45 years old). Environmental characteristics were measured at each plot and used to model how beetle communities were responding across the forest boundaries, and to assess if successional beetle communities were responding to the same environmental forces. Within 200 m from mature forest, the beetle community in ~45 year old secondary forest had largely recovered. The important environmental factors differed in each forest age, yet leaf litter variables and microclimate were consistently correlated with species distribution. This manuscript is accepted in *Ecological Applications*.

Chapter 4 uses functional trait and phylogenetic approaches on data collected from the experiment described in Chapter 3 to gain deeper insights into community assembly processes underlying beetle succession. I also test whether different beetle

trophic groups (decomposers/primary consumers versus predators) assembled the same way. A molecular phylogeny constructed from two DNA barcoding regions and 14 functional traits were calculated for 133 common species. Successional patterns in the phylogenetic and trait datasets were modelled using 16 environmental variables. Environmental filtering was the dominant process shaping beetle community succession for both trophic groups, yet the traits driving this pattern, and evolutionary forces underpinning them, were strongly divergent. Microclimate and leaf litter were key trait filters, particularly for decomposers/primary consumers. This manuscript is in pre–review with Axios.

Microclimate and leaf litter inputs were manipulated in an experimental trial (Chapter 5) to understand the role of dispersal limitation and habitat on beetle recolonisation. The trial was established within a recently harvested site with a mature forest boundary nearby, and beetle communities were sampled using pitfall traps under sterilized leaf litter, artificial shade plots and control (no litter or shade) in a randomized block design. Litter addition and shading significantly altered beetle abundance and community composition and allowed some species adapted to older forest to successfully recolonise. Species functional traits and phylogenetic relationships were also used to explore how environment affects community assembly. Environmental filtering was also the dominant process overall, yet biotic interactions were important for community assembly in open control plots. This manuscript is submitted to Animal Ecology.

My results demonstrate that forest influence is important for beetles in production forests and that forest influence may alter the successional trajectory of beetle communities. Microclimate and leaf litter were both important in facilitating recolonisation, yet dispersal limitation still plays a role. Furthermore, this thesis has helped elucidate what forces shape beetle community assembly over succession, and demonstrates that litter addition and shade not only alters species composition it also changes how beetle communities assemble.

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First and foremost, I am enormously thankful for my three supervisors Greg Jordan, Sue Baker and Chris Burridge, for without them this thesis would not be possible. Their dedication to my project was beyond belief and their guidance, editing efforts and overall support was extraordinary. Even when I chose to explore entirely unfamiliar techniques, they believed in my capabilities and each effectively learnt a new ecological sub-dicipline to assist. Their editing efforts were superhuman, as I would often get manuscripts fully editied back by all three of them in the space of a week. 'Thankyou very much' does not seem to capture how grateful I am.

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Finally I dedicate this thesis to my late father Michael Jones who passed away during the course of my PhD. He imparted his love of the natural world and the discipline to achieve my dreams.

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Chapter 1
General introduction

1.1 Background

Being able to predict and understand how communities respond to human disturbance has been a longstanding goal of community ecologists across the world. Disturbance alters habitats, which in turn leads to species turnover. The extent of species recovery and recolonisation has been the focus of much work, particularly for ground-dwelling beetle communities (Didham et al., 1998; Driscoll, 2005; Baker et al., 2009a; Hopp et al., 2010).

The abundance, diversity and sensitivity to environmental change of ground-dwelling beetles make them an ideal group to understand and predict how communities respond to disturbance and to forest management in particular. Beetles make up a major component of terrestrial biodiversity across the globe with a predicted 1.1 million species (Ødegaard, 2000). In Tasmanian forests alone, approximately 2 000 species have been collected, with 60% of these being undescribed morphospecies (Grove, 2010). The leaf litter layer provides habitat for a highly diverse variety of invertebrate taxa (Olson, 1994; Vandewalle et al., 2010) with ground-dwelling beetles making up a substantial portion of this diversity (Baker et al., 2004; Hopp et al., 2010). Ground-dwelling beetles are also functionally diverse (Woodcock et al., 2014) and have representatives across a broad range of trophic groups (Davies et al., 2000). Furthermore, this group is known to be sensitive to forest management in many ecosystems, including Tasmanian wet forest (Michaels & McQuillan, 1995; Koivula et al., 2002; Buddle et al., 2006; Baker et al., 2007).

This introduction will outline the concept of ‘forest influence’ or the effect that mature forest has on adjacent secondary forests, and place this concept in a forest management context. I will then discuss what the possible drivers of forest influence

on beetles could be and how forest succession may alter these processes. Succession is also likely to alter beetle community assembly, and this introduction will summarise how functional trait and phylogenetic tools can be used to disentangle what forces structure beetle communities.

1.2 Forest influence and forest management

Anthropogenic landscape modification has resulted in boundaries between forest types becoming increasingly common in forest landscapes across the world (Didham, Hammond et al. 1998; Driscoll and Weir 2005; Harper, Macdonald et al. 2005; Ewers and Didham 2008). There has been particular focus on the spatial scale of edge effects and a large literature has developed looking at how open areas affect the character of adjacent mature forest (Didham, 1998; Ewers, 2008; Magura, 2001; Baker, 2007). There have been, however, relatively few studies that have looked at the mirror of these classic edge effects: 'forest influence'. Forest influence is defined as the biophysical effects of mature forest on the environment of nearby disturbed forests (Beese et al. 2003). Forest influence is particularly important in mature forest adapted species in fragmented landscapes. For such species, proximity to mature forest may facilitate recolonisation of disturbed adjacent forest by providing increased habitat, or by providing a source population for dispersal. Depending on the species, these effects may be positive, negative or neutral (Bradshaw, 1992), and are likely to change over time (Figure 1.1).

Forest influence has been found in Tasmania for microclimatic gradients (Baker et al., in press) vascular plant communities (Tabor et al. 2007) and bryophytes (Baker, 2010). Tabor et al. (2007) found that, up to 15 years post disturbance, vascular plants adapted to mature habitats were more abundant in the disturbed forest the closer you got to the mature edge. Baker (2010) found similar effects with bryophytes 48 years post-disturbance. The forest influence effect on beetles, and invertebrates in general, is even less well understood (Rosenvald & Lohmus, 2008; Baker et al., 2013a). Some studies have assessed clearfelled beetle assemblages compared to mature forest in the period <5 years post-disturbance (Heliölä, 2001; Hyvarinen, 2005; Baker, 2006). The

presence of large differences in beetle community composition between mature forest and disturbed forest makes it plausible that forest influence occurs. These studies have found very different beetle assemblages in the clear-cut compared to the mature forest, with mature-adapted species not dispersing into the clearfelled area. However, as the forest ages and structural heterogeneity returns, we hypothesize that mature forests can act as dispersal sources for old-growth beetle species. There has been a significant amount of the research on beetle species composition changes with forest successional stage (Pohl et al., 2007; Hopp et al., 2010). For example, Pohl et al. (2007) and Hopp et al. (2010) examined beetle assemblages from 1 to 50 years post-logging. Hopp et al. (2010) found that old secondary forests in Brazil (50 years post logging) had a beetle assemblage similar to old-growth stands, whereas younger forests (5-15 years post disturbance) were significantly different. Pohl et al. (2007) found that Canadian beetle communities in regenerating stands became similar to mature forest assemblages over time, but were still different 27 years post logging. Both of these studies tried to minimise the edge effect by sampling at least 50m from the nearest forest edge. However, little is known about how this edge influences the regowing forest over time.

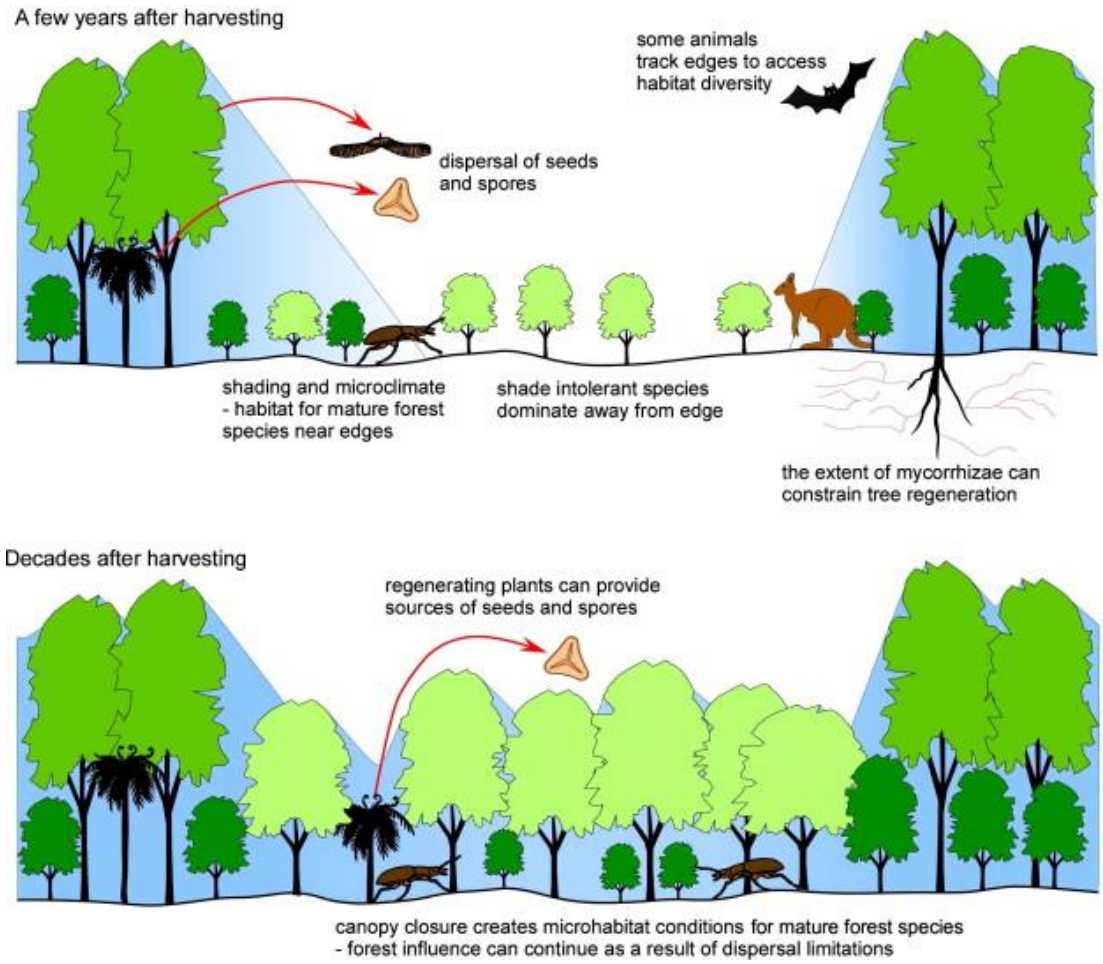

Figure 1.1. A conceptual diagram of forest influence and how it changes as a forest ages for both animal and plant taxa. Reproduced from Baker et al. (2013a).

1.2.1 Variable retention forestry

The forest influence concept is fundamental to the justification for variable retention (VR) or retention forestry silvicultural systems (Franklin et al., 1997; Gustafsson et al., 2012) (Fig. 1.2). Clearcutting has long been favoured by the industry as an efficient, safe and effective way to regenerate forests after logging in temperate areas (Lindenmayer and Franklin 1997), and has been used extensively in temperate regions including Tasmania. The need for VR forestry came out of the social and ecological shortcomings associated with clearfelling, particularly in old-growth forests (Lindenmayer & Franklin, 1997; Beese et al., 2003). There are many who consider clearfelling as a less than acceptable forestry technique, for reasons such as

its perceived impacts on biodiversity conservation, including in Tasmania (Tasmanian Public Land Use Commission, 1996; Ford et al., 2009). Retention forestry techniques aim to preserve biodiversity by retaining some of the original forest structures and habitat within harvested areas. These forest structures act as 'life boats' for species that rely on mature forest attributes (Rosenvald & Lohmus, 2008). There are three common variable retention strategies: 1. Retain trees scattered throughout a stand (dispersed retention); 2. Preserve trees in patches (aggregated retention (ARN)); or 3. Using a combination of both these approaches at one site (mixed retention) (Franklin et al., 1997). There has been significant research suggesting that the retained patches do have positive impacts on beetle biodiversity over the short to medium term (Lemieux & Lindgren, 2004; Müller et al., 2008; Baker et al., 2009; Hyvarinen, et al., 2009). For example, Baker et al. (2009) found that even after only 3 years, small numbers of mature-specialist beetles were recolonising the surrounding logged forest. The success of VR patches at preserving mature-dependent species over the long term, and allowing re-colonisation into adjacent logged areas, is largely unknown.

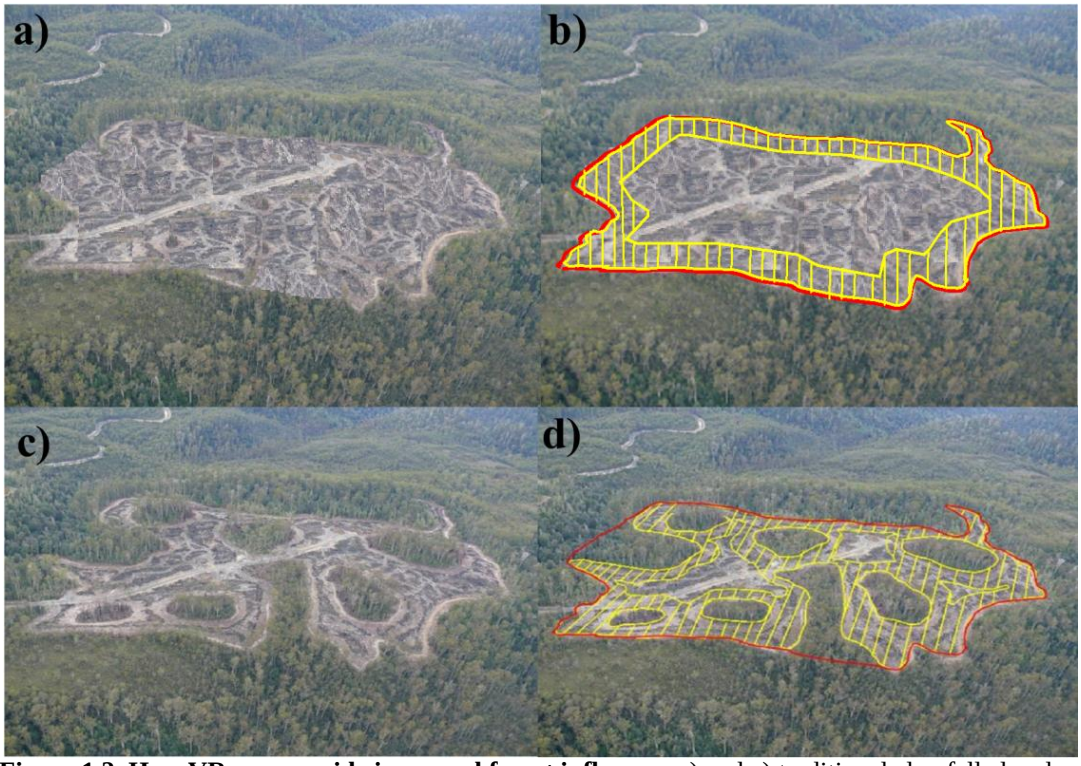

Figure 1.2. How VR can provide increased forest influence. a) and c):traditional clearfelled and ARN coupes from above. b) and d): how much forest of the logged habitat maybe under forest influence (yellow shading indicates areas approximately one-tree-height from edge). This example shows the large increase in expected forest influence using ARN silviculture (Baker et al., 2013b), with 23% of the harvested area lost to production.

Aggregated retention methods are commonly employed VR technique across the world (Nelson & Halpern, 2005; Martínez-Pastur et al., 2011; Gustafsson et al., 2012). In Tasmania, ARN has been adopted and used operationally since the late 2000s, mostly in areas of tall, wet oldgrowth forest. In lowland wet eucalypt forests, variable retention is the most commonly applied alternative to clearfelling. As in British Columbia (Mitchell & Beese, 2002), forest influence targets are factored into the design of ARN harvest layout in Tasmania (Baker & Read, 2011). Current management protocol in Tasmania and British Columbia stipulates that at least 50% of the harvested area must be within one canopy tree height from mature forest (Mitchell & Beese, 2002; Baker & Read, 2011), with the implication that this is the extent of forest influence (Baker et al., 2013a). Whether or not this is a realistic estimate for beetle communities and how this changes as forest succession proceeds is unknown, but is critical to assessing the conservation value of this silvicultural

system. Better understanding of the magnitude and depth of forest influence on biodiversity could encourage greater explicit consideration of this process by forest managers globally.

1.2.2 Dispersal mechanisms or habitat?

It is reasonable to assume that forest influence reflects the combined effects of dispersal limitation and impacts of proximity to older forest on habitat conditions. However, beyond this generalisation, the mechanisms behind forest influence are also poorly understood. There have been significant amounts of research into the environmental gradients that affect forest edges and beetle communities (e.g. Didham et al., 1998; Magura et al., 2001; Koivula et al., 2002; Hopp et al., 2010). These studies found that ground temperature, moisture, soil richness and percentage vegetation cover are all important in determining beetle assemblages within mature forest near edges, and led to distinctive edge communities. These studies, however, have either been conducted immediately post disturbance or along natural vegetation boundaries (e.g. forest/grassland) and do not directly appraise beetle dispersal into disturbed habitat.

There are many possible factors that could impact mechanisms for beetle dispersal from unlogged edges into the interior of harvested sites. In the limited forest influence literature, it has been suggested that areas of disturbed forest close to the edge are shaded (Baker et al., in press) and therefore tree species adapted to light-restricted mature forest are favoured (Nelson & Halpern, 2005; Tabor et al., 2007). As succession proceeds, the greater number of mature-forest tree species at the edge provide more shade for example, that may extend forest influence further into the harvested area over time (Fig. 1.3(b)). Increased leaf litter input from mature forest is also likely to be important for beetle recolonisation (Koivula et al., 1999; Nakamura et al., 2009). The environmental characteristics in secondary forest also start returning to pre-harvest values with increasing time since disturbance independently of forest influence (Guariguata & Ostertag, 2001). The forest influence mechanism in this case may be just due to retained mature forest ‘life boating’ species until suitable

habitat conditions allow recolonisation (Figure 1.3(b)) (Brouat, 2004). Furthermore, mature forest adapted species are often dispersal limited (Desender et al., 1994; Michaels & McQuillan, 1995), and whilst there is no evidence that dispersal-limitation alone drives beetle recolonisation patterns (Fig. 1.3(c)), it is also likely to be important for understanding forest influence. Trait based approaches, measuring dispersal and other traits, can provide further insight into the role of dispersal in recolonisation and help identify what underlying forces structure beetle communities.

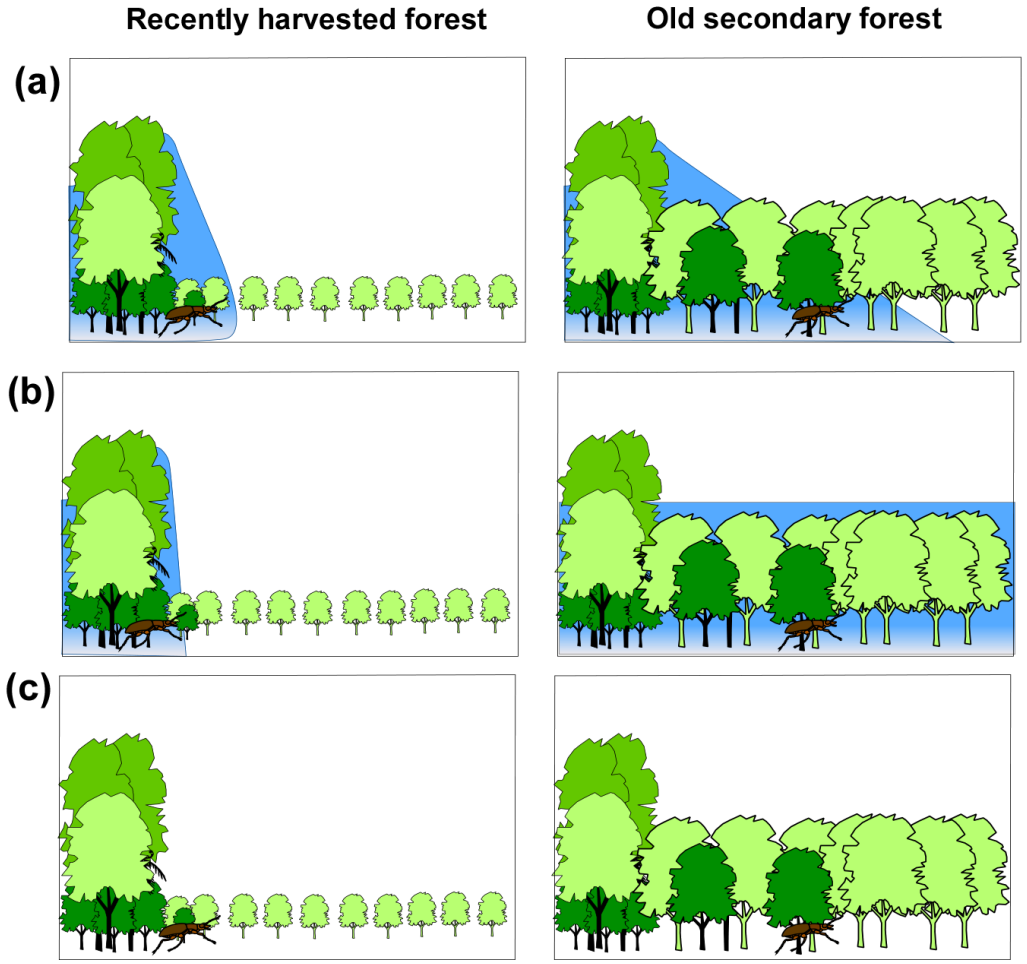

Figure 1.3. Three possible mechanisms driving forest influence. (a): Forest influence alters habitat in secondary forest allowing species to recolonise and this effect extends to older secondary forest. (b): Species only recolonise when secondary forest conditions are favourable, independent of the edge. (c) Species dispersal is the only limiting factor for recolonisation.

1.3 Community assembly processes

Community assembly processes, or the factors that either structure or constrain species assemblages (Weiher & Keddy, 1999), have been the focus of much research and debate over the last 40 years (e.g. Diamond, 1975; Pillar et al., 2009; Ernst et al., 2012). Community assembly theories can be categorised as either niche-based or neutral (Kraft et al., 2008). Niche-based approaches assess meaningful differences in ecological strategy between coexisting species (e.g. greater fecundity in unstable habitat), whilst neutral processes assumes that ecological drift (e.g. dispersal and stochastic processes) determine assembly (Hubbell, 2001).

Use of trait-environment models is one approach to understanding the importance of community assembly theories. The process for generating these models is as follows; (a) measure the important traits that the organism possesses, (b) model these traits against an environmental gradient, (c) illustrate how the environmental gradient alters trait composition, and (d) relate this to the organisms possessing these traits (Weiher & Keddy, 1999). Community trait values provide evidence about what forces are acting on it, either neutral or niche based (Fig.1.4). If trait values within a community are more convergent than a null model, environmental adversity may filter out species without these adapted trait values (niche based environmental filtering). If community trait values are divergent compared to a null model, competitive or facilitative forces are excluding species with similar traits (niche-based biotic interactions). If the null model cannot be excluded, i.e. there is no evidence that traits offer a competitive advantage, then stochastic forces, such as dispersal for example, are invoked to explain community assembly (neutral theory) (Hubbell, 2001).

Stephen Hubbell's unified neutral theory of biodiversity (Hubbell, 2001) has provoked extensive debate amongst ecologists (e.g. Wootton, 2005; McGill et al., 2006; Kraft et al., 2008). Communities, according to neutral theory, consist of functionally equivalent individuals derived from a regional species pool. Differences between communities come about via extinction and replacements over time or

'ecological drift' (Hubbell, 2001). The importance of neutral assembly processes have rarely been explicitly assessed for terrestrial beetles communities, although there has been some work on how these processes operate on aquatic invertebrate assembly (Thompson & Townsend, 2006).

Niche-based models have been central in ecology for a long time (Elton, 1927), and have generally been used to explain community assembly patterns (McGill et al., 2006b). Environmental filtering has long been considered an important assembly process for animal traits post-disturbance, with predominantly mobile species considered able to exploit highly disturbed and temporally restricted habitats (habitat template theory) (Southwood, 1977; Greenslade, 1983). Trait-environment models have demonstrated that environmental filtering is important in assembly of plant communities across tropical forest succession gradients (Lebrija-Trejos et al., 2010; Lohbeck et al., 2013). bit is not known if this is also true for terrestrial invertebrate communities Analysis approaches to identify biotic interactions and environmental filtering assembly patterns using traits have only relatively recently been developed (Pillar et al., 2009b; Pausas & Verdú, 2010), and are thus rare particularly for invertebrate communities.

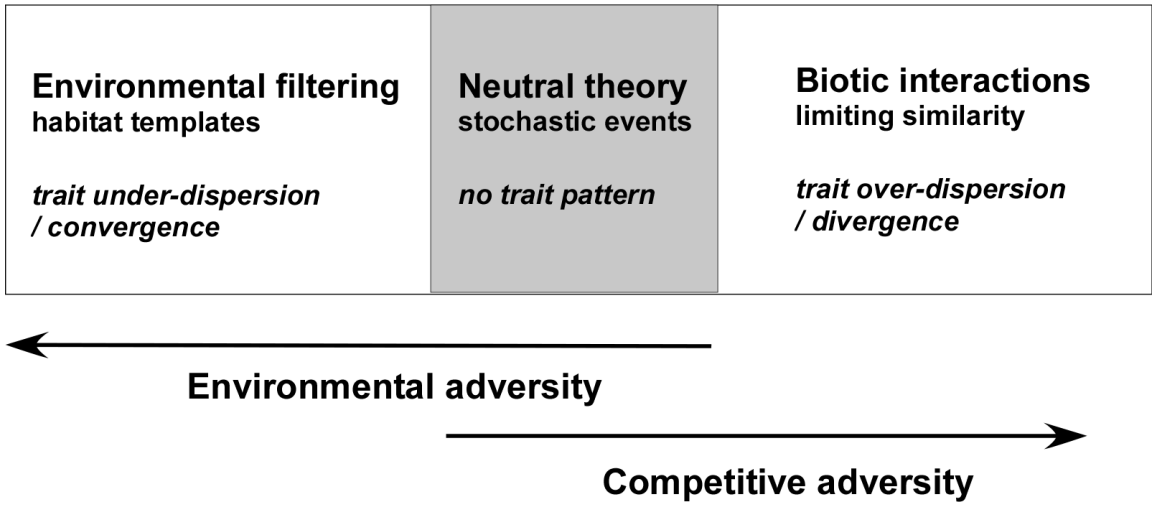

Figure 1.4. How environmental and competitive forces drive community assembly patterns (adapted fromWeiher and Keddy, 1999). How the assembly theories relate to trait-states is shown in italics.

1.3.1 Using phylogenetic techniques to understand beetle communities

The evolutionary structure of functional traits and the phylogenetic relationships between species are also important in understanding community assembly. Phylogenetic structure (the relationship between phylogenetic distance and environment) also provides complementary evidence for the importance of habitat filtering, biotic interactions and neutral processes on community assembly. For example, if co-existing individuals are more related to each other than expected by chance (phylogenetic convergence or clustering), environmental filtering is also likely, while if individuals are less related than expected (phylogenetic divergence or dispersion), biotic interactions are more important (e.g. Webb et al., 2002). Compared to traits, phylogenetic information can help gain insight into assembly patterns over an evolutionary time-scale, and help disentangle whether short- or long-term processes are driving community assembly. However, even with the increased availability of phylogenies and computing power, to my knowledge there has been only one study that has assessed beetle community phylogenetic structure. This Canadian study found that habitat filtering explained predaceous diving beetle (Dytiscidae) community structure (Vamosi & Vamosi, 2006). How phylogenetic structure varies across other beetle trophic groups is unknown.

1.3.2 DNA Barcoding

As ground-active beetle communities are hyper-diverse and species are often cryptic, accurate species identification is a challenge for ecologists. For example, species that look morphologically similar can have divergent life history strategies. Even in a geographically small and isolated location such as Tasmania, there is a ‘taxonomic impediment’ (Hoagland 1996) to understanding beetle communities. DNA-based methods have been increasingly used to overcome this problem. DNA barcoding using the cytochrome-c oxidase subunit 1 (COI) mitochondrial region is the most commonly applied approach to assess diversity and to delimit species, because this genetic marker varies consistently between species across a broad range of animals, including beetles (Hebert et al., 2003; Janzen et al., 2009; Thormann et al., 2011).

Nuclear markers have also been used in a similar way and, for example, the D3 expansion of nuclear 28S ribosomal gene has also been used successfully for species delimitation (Gillespie et al., 2004; Thormann et al., 2011). Generally, ribosomal genes are considered highly conserved, yet the expansion segments of 28S in particular, are fast-evolving and are thus also suitable barcode regions (Gillespie et al., 2004). The D3 expansion, however, is considered less variable than COI and may not contain species-level substitutions, but may provide better evidence than COI for higher taxonomic groupings (e.g. at a genus level) (Thormann et al., 2011). Combining both genes together as a 'super' barcode can be used both to detect cryptic species and to build molecular phylogenies (Erickson & Driskell, 2012). Molecular phylogenies are therefore valuable tools for understanding the evolutionary relationships between species, and also to help answer ecological questions.

1.4 Aims

In this thesis I:

1. provide a critical review of the beetle functional trait literature and outline a practical beetle functional trait framework and a list of potentially useful traits and analysis approaches.
2. test whether beetle communities respond to forest influence and whether responses vary across forest succession.
3. understand what environmental variables are important for facilitating beetle community recolonisation.
4. apply a combined functional trait and phylogenetic approach to disentangle the community assembly patterns that underlie beetle succession.
5. experimentally manipulate leaf litter and shade to assess the relative importance of these for beetle recolonisation and community assembly, and
6. synthesize trends in beetle community ecology to inform forest managers of the importance of forest influence and older secondary forest to help build habitat connectivity in fragmented landscapes.

1.5 Overview of chapters

My thesis consists of six chapters. Two of these chapters (Chapters 2 and 3) have been published as peer-reviewed articles (Fountain-Jones et al., in press (a), in press (b)) attached in Appendix E), Chapter 5 has been submitted and Chapter 4 is in pre-review with Axios. My contributions, and that of my co-authors, to each of the published or submitted articles are noted at the beginning of the relevant chapters. In all cases I was lead author, and developed and conducted the research under the guidance of my supervisors. All of these publications have been modified slightly for integration into this thesis.

In Chapter 2, I review previous terrestrial beetle functional approaches and outline a logical functional trait framework based on lessons learned by both plant and aquatic ecologists. Furthermore, based on the literature, I provide a general beetle trait list and discuss analysis approaches. This review provides the conceptual basis for the trait approaches used in Chapters 4 and 5.

Chapter 3 assesses whether beetle communities respond to forest influence, and how forest influence changes over forest succession. In particular, I analyse how known indicator species respond with distance from mature forest, and assess to what extent beetle communities have recovered ~45 years after logging. Furthermore, I model which particular environmental parameters drive these patterns.

Chapter 4 explores how beetle community assembly processes respond to succession. This chapter explores the role that environment, biotic interactions and neutral theory have on shaping beetle communities across successional stages using a trait-environment approach. The evolutionary mechanisms for these assembly patterns are also assessed using a study-specific molecular phylogeny that I developed.

In Chapter 5, I experimentally manipulated leaf litter and microclimate to test how these variables (both considered important in species distribution (Chapter 3) and for trait patterns (Chapter 4)) alter beetle community composition, abundance and assembly processes.

Finally, in Chapter 6, I synthesize my findings and discuss the relevance of forest influence to sustainable forest management. I also discuss my findings in relation to the broader community assembly debate, and suggest future research directions.

Chapter 2
Moving beyond the guild concept: developing a practical functional trait framework for terrestrial beetles.

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2.1 Summary

New logical and analytical frameworks for studying functional traits have led to major advances in plant and freshwater ecology at local and global scales. The ecological and taxonomic diversity of terrestrial adult beetles (Coleoptera) means that functional trait approaches should have considerable power to illuminate the function of not only these animals but also the ecosystems in which they occur.

This review outlines a logical framework for adult beetle functional trait studies using uniform terminology and methodology similar to those used by plant ecologists. We synthesize beetle life history and ecomorphological trait studies and show that a combination of both is analogous to the functional trait approach. A general functional trait list for beetles and potential functional links is outlined, as are potential analysis approaches. A consistent functional trait approach coupled with advances in molecular techniques has the capability to realize deeper insights into beetle community assembly, how beetles impact ecosystems and will help enable worldwide comparisons and predictions to be made.

2.2 Introduction

Linking the functional traits of organisms to environment has revolutionized our understanding of community structure and composition (e.g. Grime, 1974; Southwood, 1977; Greenslade, 1983). Habitat template theory (Southwood, 1977), for example, gave new insights into the ecological and evolutionary forces acting on many animal communities, including beetles (Greenslade, 1983). Nonetheless, most studies of arthropod communities are based on taxonomic approaches (including species composition and abundance). However, solely using such taxonomic data may restrict the predictive powers of community studies (McGill et al., 2006a; Menezes et al., 2010; Barton et al., 2011), especially when comparing regions with different species pools. Thus, functionally similar communities in different regions may be more different in both species and phylogenetic composition than functionally disparate communities within a region (McGill et al., 2006a). Functional traits (functionally significant characteristics of the morphology, ecology or life

history of organisms; Table 2.1) can provide a rich source of additional evidence that can supplement, test or even replace evidence from studies based on taxonomic composition. Whilst information on assumed feeding strategy or feeding guild does provide some insights in these areas, we argue that feeding guilds represent just a small proportion of the information that can be attained from functional traits. This new information can come in the form of not only individual traits, but also how these interact to create functional syndromes (see Table 2.1 for definitions of key terminology).

The aim of the functional trait approach is to find characteristics that are comparable across a range of organisms and environments, and to use these to investigate the function of ecosystems and groups of organisms. Functional trait approaches aim to predict , for example, community responses to disturbance (Poff et al., 2006; Gerisch et al., 2011) and consequent changes to ecosystem function (Díaz et al., 2013), extinction risk (Davies et al., 2000) and how community assembly processes change with environment (Pavoine & Bonsall, 2011; Podgaiski et al., 2013). In the last thirty years in particular, a diverse range of functional traits have been used to explore patterns from organism to ecosystem levels (Lavorel & Garnier, 2002a; Violle et al., 2007). Functional trait analysis has been applied broadly to plant communities (e.g. McIntyre et al., 1999), but less frequently to vertebrates (e.g. Porter & Kearney 2009), freshwater invertebrates and soft bodied soil organisms (Poff et al., 2006; Hedde et al., 2012), and rarely to terrestrial invertebrates (e.g. Bihn et al.., 2010; Vandewalle et al., 2010). There is also a recent trend towards using functional traits approaches across multiple trophic levels to elucidate broader trait and ecosystem relationships (Barbaro & van Halder, 2009; Moretti & Legg, 2009; de Bello et al., 2010; Rzanny & Voigt, 2012). However, comparison and synthesis of these studies has been hindered by the use of different methodologies and trait mixes (McIntyre et al., 1999; Mabry & Fraterrigo, 2009).

Table 2.1. Key terms used in this review.

Ecological performance trait: An ecological requirement of a species, such as habitats occupied or temperature or pollution tolerance. Ecological traits are usually a combination of morphological /physiological traits, e.g. large leaf surface area for shade tolerant plants (Violle et al., 2007).
Ecomorphological trait: A morphological trait that has a relationship with ecological variables (Menezes et al., 2010). For example, greater beetle abdomen length can correlate to open microhabitats (Barton et al., 2011). Unlike functional traits, there is no explicit link to individual performance.
Effect traits: Traits that impact ecosystem functioning. For example, larger decomposers break down leaf litter at a faster rate that leads to increased nutrient cycling (Díaz et al., 2013).
Functional diversity (FD): The diversity of functional traits observed or inferred within a system. A range of different calculation metrics can be used (Petchey & Gaston, 2006).
Functional syndrome: Mixtures of traits linked together by either environmental or evolutionary forces.
Functional trait: traits that indirectly impact individual fitness via their impacts on reproduction, growth and survival (adapted from Violle et al. 2007).
Guild: A group of species that have similar feeding strategies (not necessarily linked to trophic position), e.g. predator or detritivore.
Phenological trait Traits that correspond to the temporal aspects of the life cycle of the organism. For example, period of maximum abundance or overwintering period.
M-P-P-E traits: Morphological, physiological, phenological and ecological functional traits.
Response traits: Traits that impact an individual's capacity to colonize and persist in a habitat (Díaz et al., 2013). For example, beetles with increased leg length prefer structurally complex habitats (Barton et al., 2011).

In this review of beetle functional traits we will draw on the conceptual framework developed by Violle et al. (2007) for plants. These authors defined functional traits as the morphological-physiological-phenological (M-P-P) traits that affect individual fitness via their impacts on reproduction, growth and survival. However, we also

include ecological performance traits or traits quantifying how well an individual survives in an environment e.g. shade tolerance. Even though ecological traits are typically complex consequences of individual traits (Violle et al., 2007), our limited understanding of which traits are responsible for ecological performance in animals makes them a valuable addition. For animals, a morphological-physiological-phenological-ecological performance (M-P-P-E) trait approach is therefore more appropriate. Mlambo (2014) argues that this type of definition is problematic because nearly any trait may have a hypothesized link to performance, so therefore this definition is potentially lacks utility. However, some traits have more obvious links to function than others (e.g. body length compared to number of scales on the elytra), thus careful selection of traits with clear links to ecosystem function is critical to maximise the chances of detecting trait patterns. In addition, functional traits can be categorised according to whether they directly influence ecosystem function (effect traits, e.g. large decomposers increase the rate of nutrient cycling) or respond in such a way as to act as indicators of ecosystem processes (response traits, e.g. winged species are more likely to occur in disturbed habitats) (Lavorel & Garnier, 2002b; Díaz et al., 2013) (Table 2.1). Traits are often both response and effect traits, the choice of traits to measure for a given question is helped by considering this subjective classification (Laliberté & Legendre, 2010).

While patterns in individual functional traits can be informative, examination of the diversity of, and interactions between, traits expands the power of functional traits to help understand and predict ecosystem function and community assembly (Pavoine & Bonsall, 2011). Thus, it is increasingly accepted that functional diversity coupled with species richness provides a much more robust measure of ecosystem function and resilience than species richness alone & Cabido, 2001; Petchey & Gaston, 2006; Lavorel et al., 2013). Functional diversity can be defined as the values and range of biological traits that influence ecosystem function (Tilman et al., 2001; Petchey & Gaston, 2006) and can be partitioned into indices measuring functional richness, evenness, dispersion, and divergence (Mason et al., 2005; Laliberté & Legendre, 2010). All four of these components are increasingly being measured for many groups, including beetles (Vandewalle et al., 2010; Gerisch et al., 2011;

Schirmel et al., 2012). Comparison of these components can provide deeper insights into community composition (Petchey & Gaston, 2002; Petchey et al., 2007; Gerisch et al., 2011). For example, functional diversity that is not strictly proportional to species diversity can provide evidence that unexplained factors, such as historical processes, have operated on a system (Pavoine & Bonsall, 2011). Functional redundancy, or the number of species providing similar functions within ecosystems, is also a useful concept. Systems with high functional redundancy may be more resilient because species extirpation may not lead to loss of ecosystem function (Gerisch et al., 2011). Communities with lower than expected functional diversity tend to exhibit high levels of functional redundancy, which can be evidence for environmental filtering impacting community assembly (Petchey et al., 2007; Pavoine & Bonsall, 2011).

Functional trait frameworks are well established for aquatic arthropods, especially for use in predicting species composition along environmental gradients (Bournaud et al., 1992; Poff et al., 2006). This, in turn, has facilitated the use of functional trait values as bio-indicators of aquatic ecosystem degradation across the world (e.g. Doledec et al., 1999). Similarly, utilising functional trait approaches for terrestrial beetle groups should also enable predictive models, for example, of how well communities recover after disturbance. These models can be tested across the world and may expose general ecological patterns (McGill et al., 2006a). However, functional trait approaches are still rarely used to understand terrestrial arthropod ecology, are beset with inconsistent terminology and methodology, and to date has involved only a few taxonomic groups (Lambeets et al., 2008; Vandewalle et al., 2010; Barragán et al., 2011; Gerisch et al., 2011; Birkhofer et al., 2014). What constitutes a suitable set of functional traits for any group of terrestrial beetles, let alone a standardised way to measure them, is still open to debate.

Although beetles (Coleoptera) occupy almost every terrestrial niche and micro-habitat and are critical for ecosystem function (Erwin, 2004), almost two thirds of species await formal description, and even less is known about species' life histories. As a result, community ecologists often predict the ecology of poorly known species

from their family guild or by using patchy distribution data (e.g. Grimbacher & Stork 2007; Grove & Forster 2011). Given the difficulties imposed by this poor state of knowledge, a comprehensive functional trait approach has considerable scope to help us understand both the functional role of beetles in ecosystems and the effects of habitat modification on community assembly.

In this review we argue that functional trait approaches for beetles will improve how we understand and predict not only beetle ecology but also community effects on ecosystem processes. Even though entomological functional trait studies are becoming more common, to fully utilize and exploit trait approaches, robust methodological foundations are required. This review aims to help do this by synthesizing previous work on adult beetle life history, ecomorphological and functional traits and diversity. From this we will propose a general functional trait framework and methodology for adult beetles, including analytical approaches, and point to future research directions.

2.3 Beetle traits as tools for understanding community patterns

To understand the significance of the M-P-P-E approach, it is worthwhile to consider its alternatives and precursors. Trophic guild (Moran & Southwood, 1982; Novotny & Basset, 2000; Blaum et al., 2011), life history (Davies et al., 2000; Driscoll & Weir, 2005; Barbaro & van Halder, 2009; Inward et al., 2011; Schirmel et al., 2012) and ecomorphological approaches (Ribera et al., 2001; Barton et al., 2011) all contain elements of the functional trait approach, but fail to exploit the full potential of using a suite of diverse traits to explore organismal and ecosystem function.

2.3.1 Feeding guilds

In feeding guild analyses of beetles, species are usually assigned to guilds based on the feeding strategy typical of the family or subfamily to which they belong (Walter

& Ikonen, 1989). This approach has allowed for some rapid generalisations and comparisons of community structure, including comparisons between regions. Thus, studies from Sweden, Canada and Tasmania have shown that saproxylic beetle fauna were dominated by predators and fungivores (Johansson et al. 2007; Langor et al. 2008; Grove and Forster 2011). Similarly, feeding guilds have been used to show impacts of habitat fragmentation (e.g. Didham et al. 1996; Davies et al. 2000).

However, species within feeding guilds often vary markedly in function, so that the guild approach can fail to indentify finer community dynamics (Grimbacher & Stork, 2007; Blaum et al., 2011). For example, Barton et al. (2011) showed that whilst morphology of each guild related to family groups, forest microhabitat use varied considerably within families. Thus, expanding functional trait studies beyond guilds is likely to allow a greater understanding of beetle community patterns.

2.3.2 Life history and eco-morphological traits

Many studies have incorporated life history and ecomorphological traits of beetles to complement feeding guild as an indicator of community function. Such studies have often attempted to link life history traits to species decline (e.g. Davies et al., 2000; Fattorini et al., 2013). Most have found that interactions among multiple traits were most useful for predicting which species are more at risk of extinction (Davies et al., 2004; Henle et al., 2004; Driscoll & Weir, 2005; Fattorini et al., 2013). For example, species abundance combined with habitat selection (specialists/generalists) explains some species' sensitivity to decline (Davies et al., 2004). There have also been studies of successional processes (Ribera et al., 2001; Schirmel et al., 2012). However, these studies of succession and species decline have mostly used qualitative traits and excluded morphological measurements other than body size.

Conversely, studies incorporating morphological measurements and linking them to species ecology or 'ecomorphological' studies often exclude life history or physiological traits (i.e. just assessing M traits instead of M-P-P-E traits). Such studies typically choose ecological and morphological variables *a priori,* measure each variable for each species and then resolve inter-specific patterns of variation of

both sets of variables (e.g. Ribera et al., 2001; Menezes et al., 2010; Barton et al., 2011). For example, Vandewalle et al. (2010) found a correlation between increasing forest cover and larger body and leg lengths, greater eye diameter and darker colouration of carabid beetles (family Carabidae). The variables are then used to elucidate the relationship between form and function, but are not explicitly linked to performance (Irschick, 2002). Beetles are increasingly being studied using this strategy, with a range of different traits being assessed, with limited consistency across studies. Ecomorphological studies have investigated the relationships of morphological variables with habitat preference (Weiser & Kaspari, 2006; Talarico et al., 2007, 2011; Barton et al., 2011), diet and guild (Barton et al., 2011; Inward et al., 2011), invasive species (Laparie et al., 2010) and disturbance gradients (Ribera et al., 2001). Although these studies addressed different problems, some traits were identified as being important by multiple studies. These traits included antennae length, ommatidia number/density, head width, pronotum length and wing structure. As with studies using life history traits, inconsistent metrics and methodology makes direct comparison of studies difficult.

2.3.3 Functional traits and functional diversity

The generality of function of some traits and the importance of interactions between traits in predicting ecosystem function (as discussed above) together suggest that there will be substantial benefits in a functional trait approach that combines life history and ecomorphological traits in a systematic way. This unified approach may detect important impacts on ecosystem dynamics overlooked in non-combined studies. For example, Moretti & Legg, (2009) found that ground active saproxylic beetles were negatively correlated with loss of plant cover, whereas aerial species were not affected. Interesting links have been found between functional traits of plants and carabids, with autumn-germinating small-seeded weeds linked to smaller spring-feeding beetles (Brooks et al., 2012). In France, common carabid species were more likely to be active in summer and autumn and to occur in fragmented landscapes than rarer species (Barbaro & van Halder, 2009). In the terrestrial beetle functional trait literature, most studies have focussed on linking response traits to

environmental parameters, with few assessing the effect of beetle traits on ecosystem processes.

The overall associations of functional diversity to species richness, and the drivers of these patterns remain obscure, and are clearly ripe for deeper investigation. For example, the limited available literature often shows contrasting patterns in the relationship between species and functional diversity (Vandewalle et al., 2010; Woodcock et al., 2010, 2014; Gerisch et al., 2011; Pakeman, 2011; Schirmel et al., 2012). Relationships between disturbance and functional diversity also remain unclear, with some authors suggesting a positive relationship (Pakeman & Stockan, 2014) whilst others suggest the opposite is true (Gerisch et al., 2011; Schirmel et al., 2012). However these differences could be simply due to varying methodology, trait terminology and scale. Even a relatively simple character of wing type was calculated differently in these studies.

2.4 Towards a consistent functional trait framework

2.4.1 Selection of study groups

Due to the high morphological and trophic diversity of terrestrial beetles, sub-groups (e.g. beetle family, trapping method or trophic group) can have different functionally important features, and therefore trait lists may vary according to the study group and the questions being addressed (Fig. 2.1). Trophic level is likely to be a useful sub-grouping for beetles because the functionally significant traits of carnivores, for example, can be different from those of primary consumers or decomposers. When selecting groups, there is often a trade-off between the number of traits assessed and the phylogenetic or trophic diversity of the study group. Restricting studies to narrow taxonomic or trophic groups can enable effort to be invested in measuring more functional traits, but can come at the cost of reduced variation within these traits. For example, many beetle functional trait studies have focussed on carabids, thus missing much of the variation in traits such as feeding guild. Studies that measure traits from a wide phylogenetic range (e.g. across multiple families) may provide greater insight

into community assembly than more taxonomically restricted studies. However, because taxonomic groups tend to have specific traits, such studies should benefit from explicitly compensating for phylogenetic effects on traits (see *Incorporating phylogeny* section below).

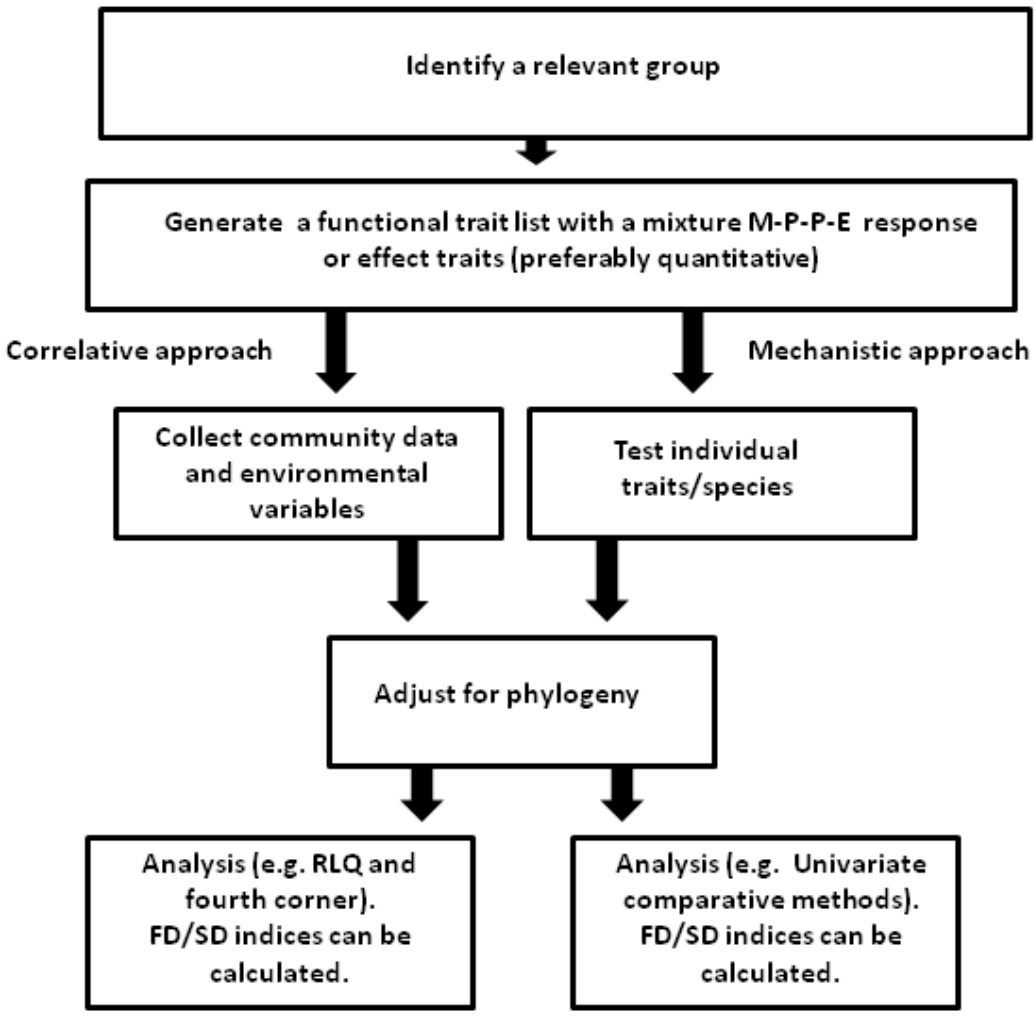

Figure 2.1. A systematic methodology for developing a taxon-specific trait list.

Ecological context and study objectives are also important to consider when choosing traits and groups to study (McIntyre et al., 1999; Cornelissen et al., 2003). Using plants as an example, the effects of herbivory and fire are best investigated using different plants groups and different traits (McIntyre et al., 1999). Leaf traits,

for example, are clearly important for understanding plant responses to herbivory whereas traits such as bark depth are less so, but are very relevant to fire sensitivity. We suggest that a similar principle applies in studies of beetles, with the general methodology we outline providing a useful starting point for trait selection.

2.4.2 Generating a functional trait list

To allow for regional and global comparisons using functional traits, a standardized but flexible trait list with a clear measurement methodology is useful, as has been demonstrated for plants (McIntyre et al., 1999; Cornelissen et al., 2003). Once the family/or trophic group is chosen, the taxon-specific literature can help generate a hypothetical M-P-P-E trait list (McIntyre et al., 1999), with taxonomic keys sometimes providing a starting point for described species or well known groups. Trait selection can be guided by some general considerations. If the intention is to assess impacts on ecosystem services ('effect traits'), traits such as colour may be less important as they mostly affect individual fitness, e.g. the cryptic ability of species. Dispersal traits, in contrast, are likely to have a greater impact on ecosystem services, as species with increased dispersal capabilities can enable broader redistribution of nutrients (see Díaz *et al.*., 2013 for more examples). Most traits considered in this review could be classified as response traits, so would be suitable for inclusion in any study looking at how species respond to environmental change, or colonize and thrive in habitats (Lavorel & Garnier, 2002b; Díaz et al., 2013). However, many of these traits are also likely to be important effect traits, even though the links to ecosystem services may not have been established.

The number of M-P-P-E traits used in any approach is also important to consider as in some cases using multiple traits can cloud predictions of ecosystem services (Butterfield & Suding, 2013) or alter functional redundancy patterns in the landscape (Petchey & Gaston, 2006). As long as the functional link of each trait is justified for the particular study, there still remains limited theoretical understanding of the optimum number of traits to use. However, if the aim is to understand and predict how trait variation changes, it may be beneficial to select the trait set that optimizes

this variation (Petchey & Gaston, 2006). See *Approaches to trait analysis* below for details.

Trait values for each species can be obtained directly or by using the literature or online databases (e.g. Carabids.org (Homburg et al., 2014)). Both sources have advantages and disadvantages. Attaining trait values from databases and the literature (i.e. taxonomic works) can allow for large scale trait patterns to be analysed quickly and cost effectively (Homburg et al., 2014) and some traits, such as feeding guild, are rarely measured directly. However, there is a paucity of functional information for most groups of beetles across the world. Direct measurement is labour intensive, particularly for beetle communities with high species diversity (e.g. in the tropics), but can help ensure that, for cryptic species particularly, averages are generated from individuals of the same species. With small sample sizes, trait values can be collected at the individual level rather than relying on trait averages (see below), thus minimising error from trait variability, and incorporating information from within species variation (Laforest-Lapointe et al., 2014). Finally, as noted above, the same trait can be measured in different ways, so a standardised protocol of trait measurement (like the protocol developed for plants (Cornelissen et al., 2003)) is helpful.

Quantitative measures of functional characteristics can be preferable to qualitative measures of the same characteristics, as they can have greater information content (McGill et al. 2006), although this is contingent on the practicalities of measurement. To allow for polymorphism and sexual dimorphism, most eco-morphological trait studies (see Appendix A) used at least six individuals to conduct analyses. We tested this on a variety of beetle families, and measurement of six individuals was sufficient to capture most within-species variation (Fountain-Jones, unpublished data). This benchmark level of minimum replication may need to be increased when the variation within species is large compared to that among species or if an objective was to assess intra-specific trait variation. Difficulties of measuring particular traits for certain beetle groups must also be considered. For example, measuring antennal length in subfamily Cryptorynchinae can be challenging because the antennae of

these weevils are concealed in most dead specimens. Similarly, accurately measuring mandible length or trochanter length on specimens <1mm in length is also prohibitively difficult without specialised microscopic techniques (such as scanning electron microscopy).

This review will only consider adult forms, as larvae are difficult to sample effectively, are rarely quantified in community studies and have very different morphology and possibly also functional roles than adult beetles.

Table 2.2 and the following text present a proposal for a potentially useful functional trait list for beetles, provide some examples of each trait's likely functional links and how that varies in some trophic groups, and suggests measurement methodology when required.

2.4.3 Body Size

Body size, measured as body length, mass or bio-volume (Braun et al., 2004) is functionally important and commonly measured for most groups of beetles. Size can be related to generation time, reproductive capacity, micro-habitat use and dispersal ability. Average body length in particular has been commonly employed as a response trait to understand community responses to disturbance (Ribera et al., 2001; Braun et al., 2004; Cunningham & Murray, 2007; Brooks et al., 2012; Gossner et al., 2013; Nichols et al., 2013), although the patterns vary considerably. For example, Cunningham and Murray (2007) found that arboreal beetles collected in young plantations (i.e. an early successional stage after intense disturbance) were larger than those collected in remnant vegetation. In contrast, body length of ground predators was greater in less disturbed, late-successional stages (Blake et al., 1994; Ribera et al., 2001; Gossner et al., 2013). Increased body length has also been shown to predict species decline, presumably due to potentially restricted dispersal capabilities for some larger species (Kotze & O'Hara, 2003).

Table 2.2. Summary of potentially useful functional traits for beetles and their likely links to function

Trait	*Trait type*	*Data type*	*Effect or response trait*	*Possible examples of functional links*	*Evidence*
Body length/size	M	Quan	ER	Fecundity	+++
Head width	M	Quan	R	Foraging capability Microhabitat use	++
Mandible length*	M	Quan	ER	Resource use	+
Eye length/width	M	Quan	ER	Predator avoidance	+++
Antennae length*	M	Quan	ER	Diurnal or nocturnal Habitat preference	+ ++
Maximum wing length/width* or wing	M	Quan/Qual	ER	Hunting capability Dispersal capabilities	+ ++
Abdomen length/width	M	Quan	R	Microhabitat use	+
Thorax length/width/depth	M	Quan	R	Microhabitat use	+
Leg length (rear and front)	M	Quan	R	Dispersal capability	++
Pronotum depth,	M	Quan	R	Microhabitat use	+
Elytra depth*	M	Quan	ER	Parasite resistance	+
Colour	M	Quan	R	Predator avoidance	+
Microclimate preference*	P	Qual	R	Thermal maintenance Thermal tolerance	+ +
Food as adult**	P	Qual	ER	Resource use	+
Season with adults**	Ph	Qual	R	Resource use	+
Overwintering strategy**	Ph	Qual	R	Thermal tolerance	+
Breeding season**	Ph	Qual	ER	Fecundity	++
Period of max. abundance	Ph	Qual	ER	Resource Use	+
Habitat occupation	E	Qual	R	Resource use	+
Habitat position/stratum preference	E	Qual	R	Resource use	+++
Guild	E	Qual	ER	Resource use	+++

** Possibly challenging to measure for some beetle groups. **Requires more research for some groups Trait types: E: Ecological performance, M: Morphological, P: Physiological, Ph: Phenological. Effect or response trait? E: Effect, R: Response, ER: Likely to be both. Data type: Qual: Qualitative, Quant: Quantitative. Evidence: +: some evidence, ++: reasonable evidence, +++: strong evidence (see Appendix A for data).*

Beetle body length has been proven to be a useful effect trait for dung beetles (e.g. Slade et al.., 2007; Nichols et al.., 2009). Larger dung beetles remove greater

amounts of dung, bury more seeds, bury larger seeds and bury seeds at a greater depth compared to smaller species (Slade et al., 2007). Loss of larger species is predicted to have a negative effect on ecosystem function (e.g. reduced seed dispersal) (Nichols et al., 2009). Similarly, larger beetle predators, like larger mammalian carnivores (Christiansen & Wroe, 2007), may regulate herbivores more efficiently than small beetles which may have a narrower size range of prey.

The scaling of other morphological traits relative to body length may reduce many trait inter-correlations (Barton et al., 2011). However, absolute size of some traits may be important, e.g. weevil rostrum size determines resource access (Toju & Sota, 2006).

2.6.4 Dispersal traits

Wings and flight capabilities are important and clearly linked to individual fitness (den Boer, 1970; Kotze et al., 2003; Driscoll & Weir, 2005; Pakeman & Stockan, 2014), yet the response pattern amongst beetle groups is not necessarily intuitive (e.g. As, 1984; Gibb et al., 2006). For example, Gibb et al. (2006) found that rare red-listed beetle species had larger wing areas compared to more common species, perhaps because increased dispersal ability may be necessary to access specialized patchily-distributed food resources (Gutiérrez & Menéndez, 1997). Yet the opposite has been shown for carabids (Kotze & O'Hara, 2003), and other arthropods such as grasshoppers (Reinhardt et al., 2005), with flightless species more likely to decline. Decreased relative elytra length is also linked to greater flying and dispersal efficiency (Forsythe, 1983; Ribera et al., 1999; Barton et al., 2011). Long elytra provide extra lift for flying and wing protection to allow access to rugose habitats without damaging wings but reduced overall flight efficiency (Johansson et al., 2012). Reduced elytra may allow for greater dispersal abilities through aerodynamic gains, though this is yet to be tested empirically.

Although wing function is often measured on a categorical scale (macropterous, brachypterous and apterous) (As, 1984), Gibb et al. (2006) made very accurate measurements of wing area using opto-electronics. Although such quantitative wing

measurements may provide useful additional information, in practice, such measurements are difficult and time consuming for small species.

Leg length also has clear functional links to dispersal, with increased relative leg length leading to greater walking speed that may facilitate hunting, predator escape and colonization for most beetle groups (Ribera & Nilsson, 1995; Krasnov et al., 1996; Laparie et al., 2010; Barton et al., 2011). Back leg to front leg ratio may be important for consumer groups, as a greater ratio may allow for increased jumping capability to avoid predators and possibly aid dispersal (Burrows & Sutton, 2008).

2.6.5 Sensory traits

Sensory traits may be important effect and response traits, but their functional significance can vary between trophic or taxonomic groups. Eye size and structure are significant in determining habitat use for predatory carabids (Bauer et al., 1998; Talarico et al., 2007, 2011). These studies found that visual hunters that operate diurnally in more open habitats have more ommatidia, and greater eye surface area and protrusion than nocturnal species, or species found in complex habitats. Larger relative eye size increased hunting success for one diurnal species (Bauer, 1981) and this could have ecosystem-wide effects. In contrast, some nocturnal species of dung beetle (decomposers) have relatively larger eyes than diurnal species to assist foraging (McIntyre & Caveney, 1998). However, other leaf litter decomposers have greatly reduced eyes compared to species living in more open conditions (Fountain-Jones unpublished data).

Eye size is sometimes measured by counting ommatidia using a compound microscope. However, to measure a large number of species this approach would be prohibitively slow, so we suggest that eye diameter and protrusion may be more practical traits.

Antennal length has also been found to be functionally important across trophic groups (Krasnov et al., 1996; Ribera et al., 1997; Bauer et al., 1998). Differences in antennae length are thought to be correlated with predator hunting ability and habitat

preference (Bauer et al., 1998; Talarico et al., 2007). Antennae length may diminish across beetle groups in open habitats compared to more rugose habitats (Barton et al., 2011), possibly because olfactory cues may be more important than tactile cues in open environments (Bauer et al., 1998).

2.4.6 Defensive traits

Colour and robustness are likely to be important response traits for defence for many taxonomic and trophic groups of beetles. Colour and reflectiveness provide visual (e.g. sexual attraction, avoidance of predation through crypsis in substrate or conspicuous colouration that signals non-palatability) and non-visual (e.g. thermoregulation) functions (Ribera et al., 2001; Seago et al., 2009). Spectral data from predatory tiger beetles (Carabidae: Cicindelinae) suggests coloration mimics substrate and small stones (Schultz & Bernard, 1989). Herbivorous beetles are also well known to use colour for camouflage in various systems (e.g. Price et al.., 1980). Diurnal beetles with lighter colouration may thermoregulate more effectively in hotter habitats (Seago et al., 2009). This may affect ecosystem processes by allowing prolonged activity time that could in turn impact such processes as pollination, although this has not been tested to our knowledge. Relative reflectiveness and colour coordinates (e.g. CIELAB (International Commission on Illumination, 2008), dominant wavelength) can be measured objectively and quantitatively using a spectrometer (see Harris & Weatherall, 1990).

Relative robustness, can be calculated from a combination of pronotum width, prothorax depth, abdomen width, head width and pronotum length can correlate to microhabitat choice in beetles (Barton et al., 2011). For example, Barton et al. (2011) observed more robust beetles in open habitats than in more complex habitats, possibly because improved defence provided by robust bodies may be beneficial in exposed habitats. However, for predator groups, increased robustness may be a functional disadvantage because of negative impact on locomotion and hunting abilities.

2.4.7 Ecological performance traits, phenology and physiology

Ecological performance, phenological and physiological traits are clearly important effect and response traits to consider for all groups. For, example, these types of traits are considered key predictors of extinction risk due to climate change (Pearson et al., 2014). However, outside of well-studied European beetle faunas, incorporating these trait groups into functional trait studies poses large challenges. Feeding guild is the main exception, since it can be readily determined from the literature, and should therefore be included in most trait studies. However, other traits may be inferred indirectly, for instance from patterns in abundance data derived from studies that sampled across environmental gradients and over different seasons. To assess ecological performance traits of beetles, simple ratios could be calculated. For example, the degree of habitat specificity might be measured as the ratio of the number of habitats occupied to the total number of habitats available along the particular gradient measured. This is similar to, but more general than, the method used by Davies et al. (2004) to determine degree of specialization in forest fragments. One weakness to this approach is that what constitutes a habitat is subjective and will vary with study design, thus making comparison between studies difficult. One possible way to circumvent this problem is to standardise for sampling method e.g. trap occupation for studies that use the commonly employed pitfall trap method.

Phenological data and physiological data can be derived if collecting is done throughout the year. For example, the period of seasonal activity of each species could be ascribed as a ratio of the numbers of seasons when a species is active to the number of seasons sampled. Species thermal tolerances could be calculated from abundance data coupled with fine scale microclimate data. However, advances in molecular methods may allow better characterization of beetle physiological and ecological performance traits. For example, two distinct Collembola transcriptome genotypes were found to have divergent fitness responses to Cadmium exposure (Nota et al., 2013). Genome wide analyses of enzymes in bees, mosquitoes and *Drosophila* have found certain genes that can characterize the metabolic strategy of

these groups (Kunieda et al., 2006). Increased research on the generality of these molecular patterns may allow traits to be characterized using molecular data alone.

2.5 Analysis approaches

2.5.1 Incorporating phylogeny

A significant amount of trait variation is constrained by evolutionary relationships (Felsenstein, 1985; Poff et al., 2006; Pausas & Verdú, 2010; Barton et al., 2011). For example, nearly all rove beetles (family Staphylinidae) have elongated bodies and truncated elytra regardless of habitat. As many statistical tests assume statistical independence amongst observations, it is clearly important to eliminate or minimise phylogenetic autocorrelation in trait data. Phylogenetic independent contrasts (Felsenstein, 1985; Garland et al., 1992; Barton et al., 2011) is one commonly employed method to phylogenetically transform trait data. However, this method only returns phylogenetically independent scores for nodes of the phylogenetic tree used and not for species themselves (Revell, 2009). As species identity is often important in ecological studies, this technique may not always be appropriate. Phylogenetic eigenvector regression (PVR) is a promising way to control for phylogenetic autocorrelation in quantitative (and qualitative) trait data whilst maintaining species identity (see Desdevises et al. (2003); Diniz-Filho et al. (2012) for method details).

However incorporating phylogeny into trait data can do more than simply control for autocorrelation. The phylogenetic structure of trait data also offers valuable insight into the evolution of the traits themselves and community composition (Jombart et al., 2010; Pavoine & Bonsall, 2011). For example, phylogenetic information coupled with trait data can help explore if communities are organised based on environmental filtering or competitive exclusion (Webb et al., 2002). For example, if closely related species have similar traits, ecological niche conservatism can be inferred (Webb et al., 2002; Pausas & Verdú, 2010). There are a large variety of methods to assess phylogenetic structure of traits, with Pausas & Verdú (2010) providing a useful overview.

Surprisingly, relatively few beetle trait studies have incorporated and controlled phylogeny in such a way. This is probably due to the fact that these approaches require a phylogeny for the target group, which for many beetle groups would be currently impossible at the species level. One possible solution is to use the level in each groups' specific phylogenetic tree with greatest resolution (e.g. for beetles at sub-family level (Hunt et al., 2007)) and treat species as soft polytomies (Barton et al., 2011). However, this solution is not optimal and with increasingly affordable molecular methods including whole genome analysis, incorporating and controlling for phylogeny will be much more viable. DNA can be easily extracted and sequenced from species collected for functional trait studies, and phylogenetic trees can be inferred using free software. For studies using trait data from online sources, incorporating phylogenetic data may be achieved by linking trait databases to Genbank for example.

Two general approaches can be applied to explore effect and response trait-environment relationships and test the efficacy of the phylogenetically corrected trait list (Fig. 2.1). The correlative approach generally attempts to analyse community patterns along an ecological gradient, and then relates the trait patterns to corresponding environmental variables (Dolédec et al., 1996; McGill et al., 2006a; Gerisch et al., 2011; Pakeman & Stockan, 2014). To help select type and number of traits to conduct this analysis on, iterative methods (e.g. Pillar & Sosinski, 2003) can be used to assess what trait best explain variability. The mechanistic approach selects individual species or traits with known or presumed functional significance and relates these traits more directly to ecosystem function and species fitness. The new information derived from these approaches can then be used to refine the trait list and help understand the trait-to-function relationships.

Analysing mechanistic traits is relatively straightforward with standard univariate techniques, however analysing multi-species correlative data requires the application of more complex multivariate methods.

2.5.2 Correlative approach

Many methodologies are used to analyse correlative trait data, and can be broadly categorized as direct and indirect. Indirect approaches, such as the commonly used 'emergent group analysis' (Aubin et al., 2009), rely on a two-step procedure which first links traits to species by allocating species to groups that have similar traits, and then relating these groups to environmental variables. This approach is relatively straightforward and useful in recognising coherent functional indicator groups, but may miss trait-level differences (see Aubin et al., 2009). Direct approaches employing multiple traits relate the traits to environmental variables by simultaneous analysis of a series of matrices (Aubin et al., 2009). The main method used to do this is a combination of RLQ ordination and 'fourth corner' permutation analysis (Dolédec et al., 1996; Legendre et al., 1997). This approach can test both quantitative and qualitative variables and allow for quantitative abundance data to be used (Dray & Legendre, 2008; Dray et al., 2014). RLQ analysis directly relates the matrices of **R** (environmental variables) against **Q** (species traits) through **L** (species abundance/presence) and the fourth corner analysis tests for trait environment relationships using permutation models chosen according to the study design (see Dray & Legendre (2008) and Dray et al.(2014) for analysis details).

2.5.3 Functional diversity indices

Functional diversity indices can be calculated in an increasingly large number of ways, using discontinuous (number of functional groups) or continuous (spread of species in a multidimensional trait space) measures (Petchey & Gaston, 2006; Schleuter et al.., 2010). In general, continuous measures are preferred because they do not rely on subjective decisions about which groups of species are functionally congruent (Mason et al., 2005; Petchey & Gaston, 2006; Laliberté & Legendre, 2010). There are a large number of possible indices choice of which will relate to data availability and study objectives, so we recommend Mouchet et al. (2010) Mason & Pavoine, (2013) and Chiu & Chao, (2014) for overviews. Community

weighted mean values for each plot and each trait can also be calculated to assess differences in functional composition (Shipley et al., 2006).

Synthesising information about species, phylogenetic and functional diversity has the potential to greatly enhance our knowledge of the mechanisms that drive community assembly over multiple temporal scales (Pavoine & Bonsall, 2011). For example, high trait diversity relative to species diversity can be evidence that competition is driving community assembly (Holdaway & Sparrow, 2006; Pavoine & Bonsall, 2011) To compare functional diversity indices with species or phylogenetic diversity, it is important for all components of functional diversity to be independent (Mason et al., 2013). However, this assumption may not be valid. For example, species diversity and functional richness may co-vary (Swenson, 2011; Mason et al., 2013). To remove this effect, many studies model functional richness and divergence against a matrix swap null model to calculate standardized effect size (Mason et al., 2013). The resultant data can then be used to examine relationships between metrics and to assess assembly processes.

2.6 Future research and conclusions

Whilst functional trait studies of beetles and other arthropods offer many advantages, there are also some conceptual and applied challenges (Table 2.3). As the functional traits listed in Table 2.2 are easily measured surrogates ("soft" traits) for the underlying characteristics driving the function of organisms (see Weiher et al., 1999), more mechanistic research relating these traits to function will increase the inferential power of these traits (Mlambo, 2014). Similarly, increasing our understanding of which traits are effect traits and/or response traits in various systems will also help optimise trait lists and may provide better predictions of ecosystem function and community assembly. Promisingly, applying this framework has already allowed us to attain novel insights into beetle community assembly and has allowed us to predict beetle responses to forest disturbance, even though for the

majority of species within these communities we had little biological knowledge (N.Fountain-Jones, unpublished data).

Understanding the optimal number of traits and how they interact with each other is also important as, for example, combining traits also may improve prediction of beetle extinction risk (Davies et al., 2004) or microhabitat use (Barton et al., 2011). Furthermore, using different trait sets may lead to different conclusions about community assembly (Pillar et al., 2009b) and different ecosystem service predictions (Butterfield & Suding, 2013).

Table 2.3. Practical and conceptual strengths and challenges of functional trait studies of beetles (adapted from Van den Brink et al. 2011)

Strengths	Challenges
• Can allow for worldwide comparisons across different species assemblages. • Community responses to environmental change can be predicted. • Allows for insights into community assembly patterns and the roles of forces such as environmental filtering and biotic interactions. • Provides a more informative approach to understanding community composition. • Data can be directly measured or generated from historical collections, literature and on online databases at minimal cost. • Functional diversity metrics coupled with species richness can help understanding ecosystem function and resilience.	• Paucity of knowledge about trait to function relationships. • Some traits may be inter-correlated with others. • Rare species (<6 specimens) are difficult to use yet may be functionally important. • Species misidentification can make comparisons difficult. • Difficulty in attaining physiological/ life history traits of beetle species. • How to integrate large evolutionary and spatial scales into trait approaches.

To fully utilise the utility of our framework, a standardised trait measurement approach across the world is also desirable. We therefore offer some protocol suggestions. However, developing a handbook similar to that developed for plants (Cornelissen et al., 2003) will greatly increase the utility of this approach. How to measure phenological and physiological traits in beetles for which there is limited information is also a challenge. Online databases have been developed for carabids (Homburg et al., 2014) and for some European saproxylic species (Stokland & Meyke, 2008) and these will allow for a rapid expansion of beetle trait analyses across the world. Further expanding these databases or establishing a more general a world-wide beetle and arthropod trait database would further synthesize and guide this research. Furthermore, attaching molecular data (such as DNA barcodes (Hebert & Gregory, 2005)) will help identify species and provide datasets to enable phylogenetic autocorrelation to be corrected in the trait data.

Molecular techniques will continue to revolutionize our understanding of these traits and functional traits in general. Meta-transcriptome studies similar to studies of soil microbial communities (e.g. Urich et al., 2008) , may be able to characterise beetle community functional and phylogenetic structure simultaneously.

Already, the studies that have moved beyond just using the guild concept and have used life history and morphological traits have gained valuable insights into community composition and links to environment. Speaking a similar language and using a similar framework should allow more global patterns and principles to be identified.

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Chapter 3
Living near the edge: Being close to mature forest increases the rate of succession in beetle communities

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This paper was conceived of by NF-J, SCB, GJJ and TJW. NF-J conducted the study, analysed the data and wrote the manuscript. JB and TPB helped collect environmental data and set up field sites. Guidance and corrections were provided by SCB and GJJ, and the manuscript was refined by TJW, TPB and JB.

3.1 Summary

In increasingly fragmented landscapes, it is important to understand how mature forest affects adjacent secondary forest (forest influence). Forest influence on ecological succession of beetle communities is largely unknown. We investigated succession and forest influence using 235 m long transects across boundaries between mature and secondary forest at 15 sites, sampling a chronosequence of three forest age classes (5–10, 23–29 and 42–46 years since clearcutting) in tall eucalypt forest in Tasmania. Our results showed that ground-dwelling beetle communities showed strong successional changes, and in the oldest secondary forests, species considered indicators of mature forest had re-colonised to abundance levels similar to those observed within adjacent mature forest stands. However, species composition also showed forest influence gradients in all age classes. Forest influence was estimated to extend 13 m and 20 m in the youngest and intermediate aged secondary forests, respectively. However, the estimated effect extended to at least 176 m in the oldest secondary forest. Our environmental modelling suggests that leaf litter, microclimate and soil variables were all important in explaining the spatial variation in beetle assemblages, and the relative importance of factors varied between secondary forest age classes.

Mature forest beetle communities can recolonise successfully from the edge and our results provide a basis for land managers to build mature habitat connectivity into forest mosaics typical of production forests. Our results also indicate the importance of forest influence in determining potential conservation value of older secondary forest for beetles.

3.2 Introduction

Natural and human induced disturbance have led to forest landscapes which are increasingly fragmented, especially in production forest. Species with a strong dependence on mature forest can be particularly vulnerable in such landscapes and biodiversity conservation strategies usually focus on protecting these species in large

reserves. However, these reserves are often disconnected and distant from production forest areas, and are unlikely to be large enough on their own to maintain viable populations of all these species. Complementary management of production forest landscapes may improve the long-term survival prospects of many such species (Spence et al., 1996). However, this management depends on understanding how mature forest species re-colonise secondary forest, and particularly the biotic effects of the forest edges found throughout fragmented landscapes (Hopp et al., 2010; Baker et al., 2013a).

The extensive literature describing edge effects largely focuses on the biotic impacts of disturbed forest on the interior of mature forest remnants (Harper et al. 2005). However, relatively few studies have assessed the opposite effect: how mature forest affects adjacent disturbed habitat (Baker et al., 2013a). This 'forest influence' (Keenan & Kimmins, 1993; Beese et al., 2003) involves a complex set of biotic and abiotic factors affecting the survival and establishment of many elements of the biota. In particular, proximity to mature forest may endow disturbed forest with mature-forest environmental attributes that can facilitate survival and/or re-establishment by species adapted to mature forest conditions (Tabor et al., 2007). Shading from the edge, for example, results in cooler and moister conditions that favour rainforest species (Tabor et al., 2007). Forest influence effects have been shown for vascular plants (e.g. Matlack, 1994; Tabor et al., 2007), non-vascular plants (Baker et al., 2013b) amphibians (Demaynadier & Hunter, 2008) and invertebrates (e.g. Koivula et al., 2002; Siira-Pietikäinen & Haimi, 2009). For invertebrates, several studies show declines in mature forest affiliated species with distance from old-growth forest (Spence et al., 1996; Buddle et al., 2006; Jonsson & Nordlander, 2006). Forest influence can facilitate re-colonisation for a variety of groups and in a variety of systems, though the underlying mechanisms are poorly understood.

Forest influence on regeneration operates through mature forest providing both a source of species for re-colonisation and by moderating the environment of the regenerating forest. Major disturbance will typically eliminate mature forest

microhabitat and the subset of species with strict dependence on such microhabitats (Spence et al., 1996), and species are typically presumed to re-colonise from adjacent mature forests (Lemieux & Lindgren, 2004; Chazdon et al., 2009; Hopp et al., 2010). Gradients of forest influence within regenerating forest may therefore involve dispersal limitation – species which are dispersal-limited are more likely to re-colonise areas closer to the source mature forest (Niemela et al., 1993; Michaels & McQuillan, 1995; Koivula et al., 2002). The successional processes of colonisation and stand development naturally lead to changes in the forest environment, particularly in the forest understorey, which in turn can facilitate the re-colonisation of mature forest species from other taxa. For example, plant detritus, forest canopy cover and microclimate all change with vegetation succession in ways that can be relevant to re-colonisation by invertebrates (Magura et al., 2002; Hopp et al., 2010; Roume et al., 2011). Leaf litter and course woody debris provide food resources, predator protection and increased insulation against microclimate extremes (Koivula et al., 1999; Jonsson & Nordlander, 2006; Entling et al., 2007; Nakamura et al., 2009; Grove & Forster, 2011). Other factors related to succession, e.g. soil chemistry, can affect invertebrates (Schwerk & Szyszko, 2007; Antvogel & Bonn, 2008; Cornellise & Hafernik, 2009; Walker et al., 2010). Shading provided by the mature forest causes microclimatic gradients that are important in determining beetle community composition (Spence et al., 1996; Nakamura et al., 2009), by affecting the beetles both directly and indirectly through impacts on vegetation and soil characteristics (Matlack, 1994). In particular, canopy closure is typically associated with large changes in microclimate that are pertinent to arthropod community succession (Niemelä et al., 1996; Nakamura et al., 2009).

Litter dwelling beetles (Coleoptera) are a particularly suitable group for investigating forest influence as they are both ecologically important and amenable to study. They are abundant, relatively easy to sample and identify, and many taxa are sensitive to forest disturbance, including disturbance created by forest harvesting (e.g. Rosenvald & Lohmus, 2008; Baker et al., 2009a; Hyvarinen et al., 2009). Determining the main factors driving forest influence on beetle communities is important for developing forest management practices that improve outcomes for biodiversity conservation

through the maintenance or restoration of landscape connectivity. How far the forest influence effect extends into secondary forest and how this pattern changes across successional time is largely unknown.

This study therefore aims to assess how ground-dwelling beetle communities respond to forest influence and community turnover from mature into secondary forest using a chronosequence approach. In particular, we focus on the spatial scale of forest influence (as measured using depth of forest influence, DFI). We hypothesize that dispersal is a critical factor that drives forest influence on successional change post harvest. Furthermore, we investigate and report on which environmental factors are driving edge gradients and beetle re-colonisation in three forest age classes (5–10, 23–29 and 42–46 years since clearcutting) in tall eucalypt forest in Tasmania.

3.3 Methods

3.3.1 Study sites

Fifteen sites were selected in Tasmania's Southern Forests region (see Fig. 3.1) within and adjacent to the Warra Long Term Ecological Research (LTER) area (see Brown et al., 2001). Each site was established to contain a boundary between mature unlogged forest and a harvested area in its first rotation after clearfell, burn and sow silviculture (see Hickey, 1994 for details). Mature forest was defined as forest possessing reproductively active eucalypt and rainforest species at the time of logging and had not been significantly disturbed by wildfire for at least 40 years before the site was harvested. The unlogged mature forest had at least one age cohort of eucalypts older than 110 years (Turner et al., 2009) that formed the upper canopy up to 50 m tall; had not been significantly disturbed by wildfires for at least 70 years; and had an understorey stratum comprising a heterogeneous mix of sclerophyllous and rainforest tree species: Sclerophyllous species dominate the understorey during

the initial period after the fire, with a progressive enrichment by rainforest elements as the interval since that last fire increases.

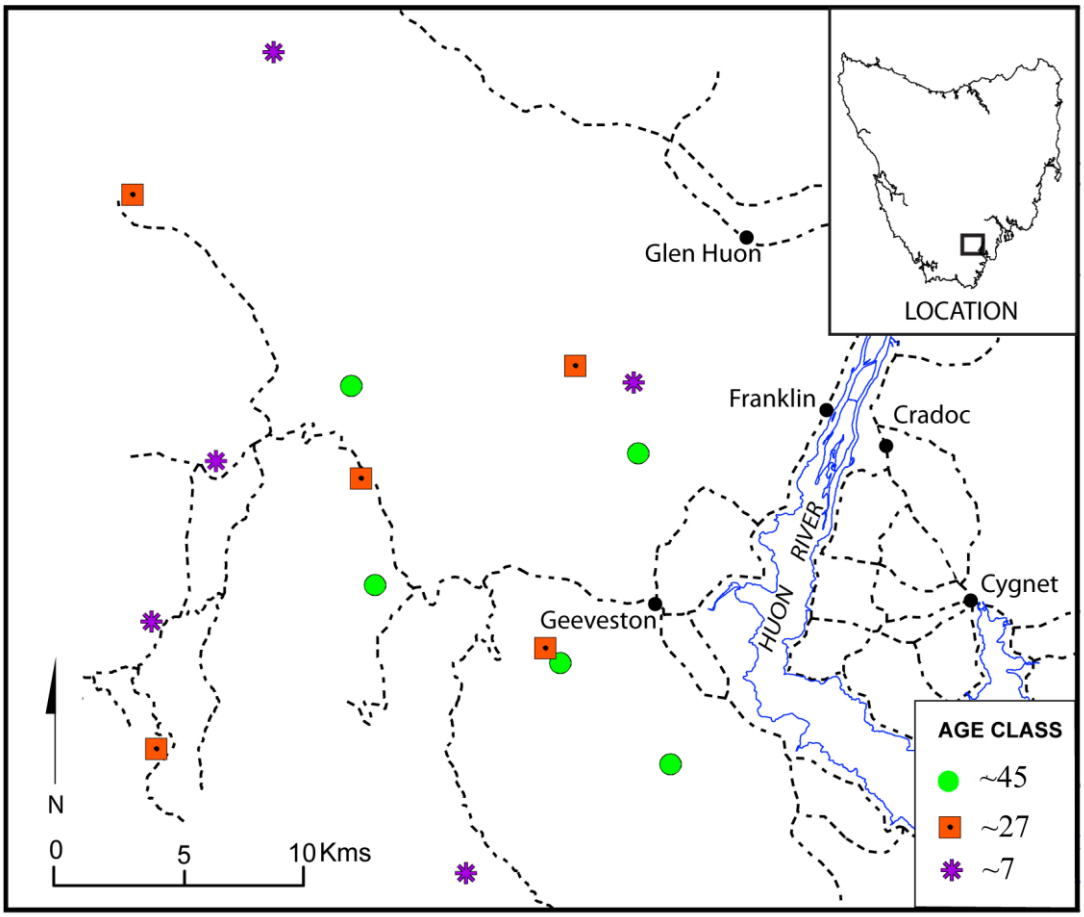

Figure 3.1. Map of the study region in Southern Tasmania, Australia.

The experiments employed a balanced design with five replicate sites for each of three age classes of silviculturally regenerated forest. The three age classes comprised sites averaging approximately 45 years (harvested between 1966 and 1970), 27 years (harvested between 1983 and 1989), and 7 years (harvested between 2002 and 2007) post disturbance (see Appendix B Table B.1). ~7 year old forests were dominated by emerging eucalypts and sclerophyllous species both up to 7 m in height, with the sedge *Gahnia grandis* forming a ground cover. After a further 20 years the eucalypts and sclerophyllous species have formed a dense canopy on average 22 m in height and the sedge is in decline. In ~45 year old forest, the canopy reached approximately 27 m.

At each site, three transects were established perpendicular to the boundary between mature and silvicultural forest, starting 35 m within mature forest and ending 200 m inside the harvested site. We used designs with unequal distances between plots to focus sampling where edge effects are more likely (Harper et al., 2005; Baker et al., 2007; Ewers & Didham, 2008). Plots were established in the mature forest at -35 and -15 metres from the edge and into the harvested areas at 15, 35, 70, 120 and 200 metres. Thus there were 315 plots (15 sites by 3 transects by 7 distances). The height of mature forest at our study sites was approximately 40–65 m, hence plot distances were located both within and beyond one mature-forest tree height into harvested areas. Spatial autocorrelation and depletion effects are not significant for pitfall trap sampling in this forest type (Baker & Barmuta, 2006).

Each site was controlled for slope (no greater than 10°), altitude (100-350 metres above sea level) and distance from the next site of the same age class (>5 kilometres). We excluded sites close to rivers and major creeks, but tolerated small creeks and streams as they are ubiquitous in the landscape. Sites bisected by roads were excluded and all plots were at least 40 metres from any road or track.

3.3.2 Beetle sampling

Pitfall trapping is a common method of collecting beetle community data in wet forests (Niemela et al., 1993; Baker et al., 2007, 2009a). We deployed a single pitfall trap in each of the 315 plots. To replace traps lost through flooding or disturbance, we placed an additional trap ~20 m from the main pitfall in the middle transect of each site. Only 33 of these additional pitfalls were required. Each trap was constructed from 150 mm lengths of 8.5 cm diameter PVC pipe buried into the soil, with plastic cups (diameter = 8.6 cm, height = 12.2 cm) inside the pipe, flush with the soil surface. Approximately 200 ml of 100% propylene glycol was added to each trap as preservative. A protective plastic plate (diameter 180 mm) was positioned 2 cm above the trap to prevent flooding and disturbance. Traps were operational for exactly 30 days for each of three sampling periods (spring, summer and autumn

2011/2012). Traps were then collected and the contents transferred immediately to 96% ethanol.

All beetles were then identified to morphospecies (sensu Oliver and Beattie, 1996). 27% of these morphospecies were assigned to species, another 58% to genus and the remainder (15%) to sub-family or family using keys (Lawrence et al., 1999), specimen matching to the Tasmanian Forest Insect Collection (TFIC) or by expert assistance. Seasonal effects were not central to our hypotheses, so data were pooled across seasons to maximise community signals.

3.2.3 Vegetation and environmental data

We measured 17 environmental and biotic variables from all plots and two microclimatic variables from the middle transect plots (Table 3.1). Vegetation cover, plant species diversity, average tree diameter and percentage litter, moss, and coarse woody debris (CWD) cover were measured in 10×10 m quadrats adjacent to the pitfall trap. Maximum diameter of woody material was also measured at each quadrat (minimum diameter 5 mm). At each quadrat, four 0-10 cm depth soil cores were taken and combined together. Within 48 hours of collection, each sample was stored in a paper bag in a cool dry area until ready for analysis. Soil was sieved using a 2mm sieve to remove leaf litter, roots and rocks and then ground in a mortar and pestle. The soil pH and conductivity were measured using a Palintest pH meter and an Elmetron CPC-411 conductivity meter, calibrated on each day of testing. We followed the Palintest Ltd procedure of shaking a 1:4 solution of soil to distilled water for one minute prior to taking the pH meter reading. For conductivity, we used a 1:5 solution of soil to distilled water shaken for 2 minutes and allowed this to settle before reading as per the manufacturer's instructions. Nitrogen and carbon were analysed using a Perkins Elmer Series II 2400 CHNS/O Elemental Analyser following the manufacturer's protocol.

Litter depth was also recorded, with four measurements taken to the nearest mm with vernier calipers within one metre of pitfall traps and averaged. Leaf area index (LAI) was measured directly over the trap using hemispherical photography and analysed

using Scion© Image (Bréda, 2003). Hobo© temperature and humidity loggers were placed within a two metre radius of each trap 20 cm above the ground on the middle transect at each site, and measured temperature and relative humidity every 15 minutes for the duration of the study.

Table 3.1. Environmental variables used in GFM for each age.

Variable	Unit	Sampling details
Carbon	% conc	4 soil sub-samples within 5 m of the trap
Nitrogen	% conc	4 soil sub-samples within 5 m of the trap
C:N ratio	C:N	4 soil sub-samples within 5 m of the trap
Soil pH	pH	4 soil sub-samples within 5 m of the trap
Conductivity	µS/cm	4 soil sub-samples within 5 m of the trap
Rock cover	% cover	10 ×10 m quadrat at the plot
Bare ground	% cover	10 ×10 m quadrat at the plot
Vegetation cover	% cover	10 ×10 m quadrat at the plot
Litter cover	% cover	10 ×10 m quadrat at the plot
Moss ground cover	% cover	10 ×10 m quadrat at the plot
CWD cover	% cover	10 ×10 m quadrat at the plot
Litter depth	mm	Average of 6 measurements around the pitfall trap
Tree diameter	mm	Average diameter breast height of stems (cm) within 10 ×10 m quadrat at the plot
Plant diversity	N1	Exponential Hill number (Chao et al., 2013) of plant species within the 10 x 10 m quadrat
Leaf Area Index	(LAI)	Directly above the pitfall trap
CWD diameter	mm	Largest CWD diameter within a 5 m radius of the trap
Distance	m	Plot distance from mature forest edge. Negative distances are in the mature forest

3.2.4 Statistical analysis

To test for distance and age effects on species abundance and richness, a two way factorial ANOVA was conducted with forest age and distance as factors. Indicator species analysis was performed for each age class on common species (>5 individuals). This analysis (presented in Appendix D, Table D1) was designed to provide information about likely habitat preferences of individual species. To enable this, plots were divided into mature (-15, -35), near edge (15, 35) and far from edge (120, 200) for each forest age, and 70 m plots were excluded to keep a balanced design. This analysis was performed using the package 'Indicspecies' in R (De

Cáceres et al., 2012). However, to ensure objectivity, unless otherwise stated, species categorized as mature forest indicators for further testing of the response of such species to distance or succession were based on a previous study (Baker, 2006), rather than the analysis of species from the present study.

For multivariate analyses, we used Bray-Curtis similarity matrices of square-root transformed abundance data. We predicted DFI using non-linear canonical analysis of principle coordinates (NCAP) to estimate the logistic gradient in the beetle community data (Millar et al., 2005). NCAP is an extension of canonical analysis of principle coordinates (CAP) (Anderson & Willis, 2003) with a link function to fit nonlinear models. Logistic curves were appropriate for our data as we assumed that the community gradient would be steepest at the edge (Millar et al., 2005) particularly for the ~7-year-old sites. To test if distance was linked to community change, permutation tests were performed on community data, and confidence limits of the logistic model were generated by bootstrapping (see Millar et al. 2005 for details). DFI was defined as the point at which the community composition was estimated to be 95% similar to interior disturbed forest along our 200 m long transects in harvested regeneration. Rare species were omitted from analyses if they occurred in <5 plots. NCAP was conducted in R version 3.02 (R Development Core Team, 2013) using 9,999 randomizations. The forest influence effect on the abundance of Tasmanian mature wet forest indicator species (see Baker et al. 2006) was analysed using quasi-Poisson regression as the variance was much greater than the mean.

The effects of site and distance from edge on beetle community composition were tested for each age using a mixed PERMANOVA model (Anderson, 2001) treating site as a random effect and distance as a fixed effect. The permutation tests of significance were based on 9999 unrestricted permutations of the raw data where the three transects were considered replicates. PERMANOVAs were also used to test for successional age differences. In this case, only data sampled from mature forest (-15 and -35 m) and from 120 and 200 m into secondary forest were analysed to avoid the edge transition zone. As mature plots were not independent of adjacent secondary

forest plots, one way fixed PERMANOVA was used to test for differences between mature forest and adjacent secondary forest for each age. Differences between secondary forest communities were separately tested using a two-way PERMANOVA with age fixed and site as a random factor. CAP analysis was also used to test and visualise the differences between mature forest and each of the age classes. The CAP ordination was constrained by distance. These tests were conducted using PRIMER 6 PERMANOVA+© (Anderson et al., 2008). Two way factorial ANOVA was also used to test the differences in abundance of mature forest indicator species (Baker, 2006) between each secondary forest stage and corresponding mature forest, with age and disturbance (i.e. mature or secondary forest) as factors.

Distance based linear models (DISTLM) (Anderson & Legendre, 1999; McArdle & Anderson, 2001) were used to model community response to the environmental predictors (Table 3.1). The complete environmental dataset was screened for multi-collinearity and, as DISTLM fits a linear model, leaf litter, rock and bare ground cover were log transformed to normalise variance. The procedure was performed using the BEST selection procedure in PRIMER 6 PERMANOVA +© (Anderson et al., 2008). Gradient Forest Modelling was not appropriate for use on the successional data set as, unlike DISTLM, this modelling procedure is not suitable when only a low number of plots are considered (<100) (Russell Thomson, pers. comm.).

To understand how vegetation and environmental covariates affected community turnover within age classes, we used Gradient Forest Modelling (GFM) (Ellis et al., 2012) on the beetle abundance dataset. GFM is an extension of the Random Forests machine learning tree ensemble model that analyses community-wide responses to environmental gradients (Ellis et al., 2012). Random Forest methods are useful for understanding community responses to gradients because they do not assume linearity of predictor or response variables and are not sensitive to highly correlated environmental variables (Strobl et al., 2008). GFM modelling assembles a large number of decision trees, and collates the distribution of splits in the tree (Thomson et al., 2014). Cumulative distribution of splits or cumulative importance curves, are

generated for each species and provide a measure of community change in *n* dimensional environmental space (Thomson et al., 2014). Each tree is generated using a random partitioning procedure based on a subset of plots and cross validated using the remaining plots. Each split is selected from ~27% of the predictor variables, in our case 5 out of 19 environmental variables. Covariate importance is calculated by randomly permuting each variable and estimating the degradation of explanatory performance (see Ellis et al. 2012 for more details). We modelled changes in community composition in each age class using 19 of the environmental variables measured (Table 3.1). Microclimatic variables were excluded because they were only available for one transect per site. All plots were included, and beetle abundance data was square root transformed and species were omitted from analysis if they occurred in <5 plots in each age. In total 1,000 trees were generated for each species. GFM analysis was conducted in R using the package 'gradientForest' (https://r-forge.r-project.org/projects/gradientforest).

Nonlinear regressions were conducted in R to further assess the relationships between distance and temperature, humidity and other important variables identified in the GFM for each age.

3.4 Results

3.4.1 Beetle forest influence gradient

In total 11,830 beetles from 271 species were collected. There was no overall significant relationship between distance from edge and total beetle abundance and species richness in any age class, although average beetle abundance was highest at 15 m plots in all ages. The NCAP results, however, showed that beetle assemblage composition was strongly correlated with distance from edge (Fig. 3.2). The DFI and community composition varied between secondary forest age classes. The NCAP model showed a sharp community composition gradient from mature forest at the edge of both the ~7 and ~27 year old classes of secondary forest with only a narrow predicted DFI (~13.2 and 20.4 m respectively, Fig. 3.2). In contrast, the gradient was gradual across the edge of the ~45 age class of secondary forest which had an

estimated DFI of 176 m (Fig. 3.2). The curve had not plateaued at 200m from the forest boundary and confidence intervals extended beyond 200 m, which suggests that the transects were not long enough to incorporate the entire edge gradient for this age class. The magnitude of community change was also much less for this age (~0.2 (i.e. 20%) over the transect compared to ~1 (i.e. 100%) for the younger stages). The confidence intervals were large for each forest age class (Fig. 3.2).

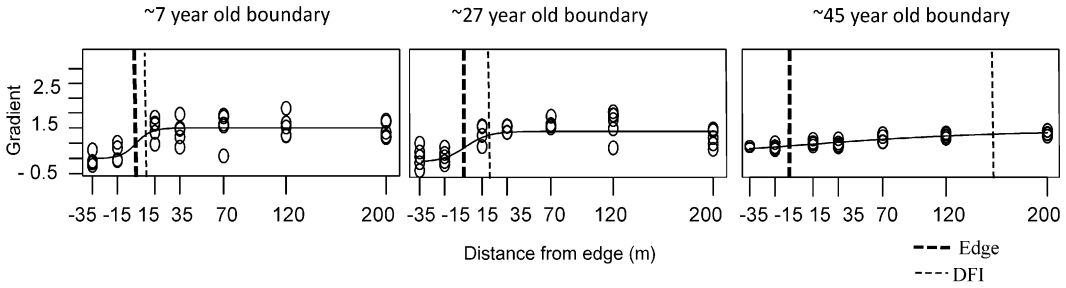

Figure 3.2. NCAP ordination of three forest ages fitted to beetle community data using the logistic model. 'Gradient' refers to the gradient of community change across the edge on the Bray-Curtis scale (i.e. 0-1). Estimated depth of forest influence for each age class are: ~7year old secondary forest: 13.23 m (total $R^2 = 0.6317$, CI: 2.2 - 161.3 m, $P < 0.001$); ~27 year old regrowth: 20.4 m (total $R^2 = 0.6264$ CI: 2.2 - 103.6 m, $P < 0.001$); ~45 year old regrowth: 175.8 m ($R^2 = 0.8148$, CI 127.7 - 254.6 m, $P < 0.001$).

The PERMANOVA results confirmed that distance from mature forest was an important factor for beetle communities in each age class (PERMANOVA pairwise tests:~7: pseudo $F_{(6)} = 1.366$, $P = 0.008$, ~27: pseudo $F_{(4,6)} = 1.47$, $P = 0.018$, ~45: pseudo $F_{(4,6)} = 1.31$, $P = 0.013$).

The relationship of pooled abundance of known mature forest indicator species with distance from edge also varied among successional stages (Fig. 3.3). There were significant distance gradients in mature forest indicator abundance across ~7 and ~27 year old edges (~7: $P < 0.001$, deviance: 166.71, ~27: 0.017, deviance: 265.62 Fig.3.3a, b) but not for ~45 year old edges ($P = 0.108$, deviance 197.68) Fig. 3.3c). All beetle species that were common in mature forest were also found in ~45 year old forest, and all but one of these (*Austronemadus* TFIC sp 03 (Leiodidae)) was relatively common (see Appendix B, Table B.4).

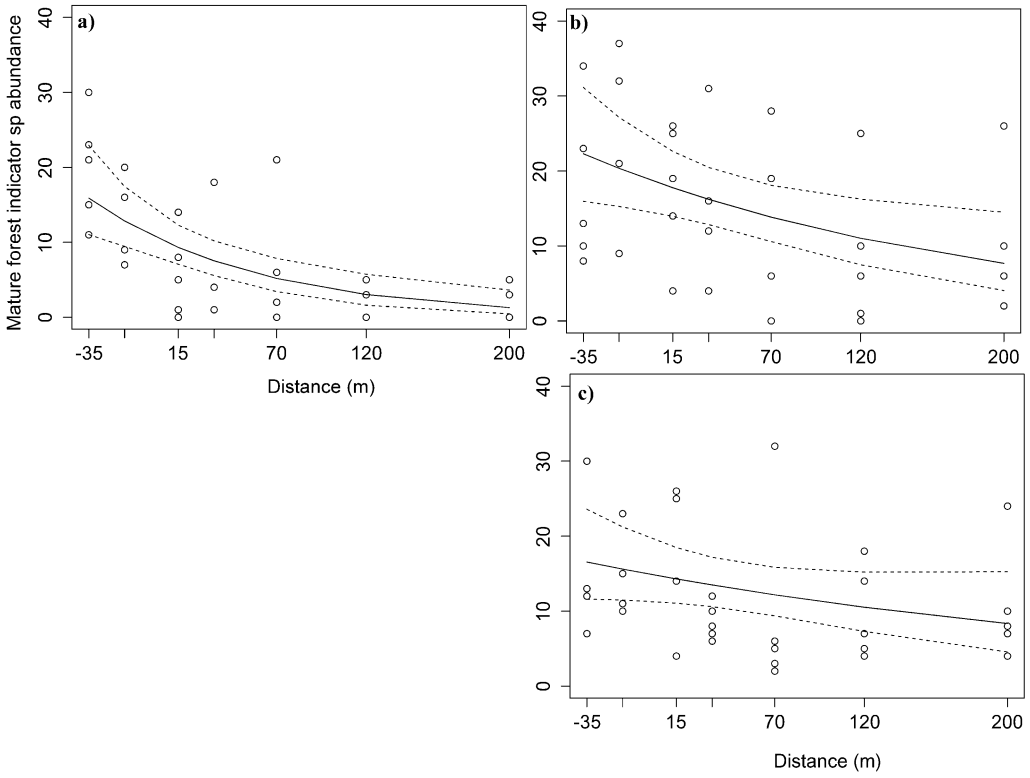

Figure 3.3. Quasi-Poisson regressions of pooled mature forest indicator species abundance vs. distance from mature into secondary forest of three ages: a) ~7 year old forest ($P < 0.001$); b) ~27 year old forest ($P = 0.017$); c) ~45 year old forest ($P = 0.112$).

3.4.2 Beetle succession

The CAP ordination examining differences in beetle community between forest age classes showed a clear separation (correlation² = 0.9285, $P < 0.001$) of both ~7 and ~27 year old secondary forest on the CAP 2 axis from the mature forest plots (Fig. 3.4). However, the beetle community in ~45 year old regrowth was only weakly differentiated from mature forest. The one way PERMANOVA confirmed that each age of regenerating forest was distinct from mature forest (~7: pseudo $F_{(1,18)} = 2.89$, $P < 0.001$; ~27: pseudo $F_{(1,18)} = 2.29$, $P = 0.009$; ~45: pseudo $F_{(1,18)} = 2.04$, $P = 0.002$).

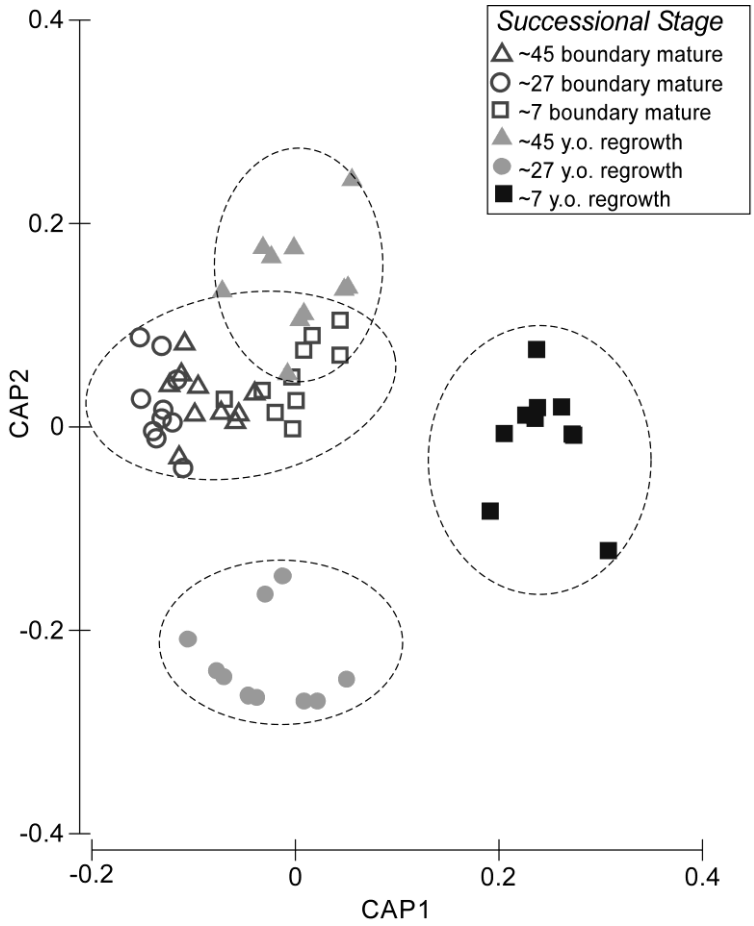

Figure 3.4. CAP constrained ordination of beetle succession data comparing the mature forest communities to the secondary forest (correlation² = 0.9285, P < 0.001). Dashed circles indicate groups distinguished by PERMANOVA pair-wise tests.

The pooled abundance of mature forest indicator species showed a similar pattern (Fig. 3.5). Factorial ANOVA was significant for age ($F_{(2,54)} = 4.78$, P = 0.012) and disturbance (mature forest or secondary forest) ($F_{(1,54)} = 36.120$, P < 0.001) effects, but not significant for the age x disturbance interaction ($F_{(2,54)} = 2.377$, P = 0.103). Holm-Sidak post hoc comparisons showed no significant difference in abundance of mature forest affiliated species in the mature forest associated with the different secondary forest age classes. The mature forest affiliated beetle abundance in ~45 year old secondary forest was statistically indistinguishable from mature forest, but in ~7 and ~27 year old forest, the pooled abundance of mature forest indicator beetles were both significantly lower than in mature forest communities.

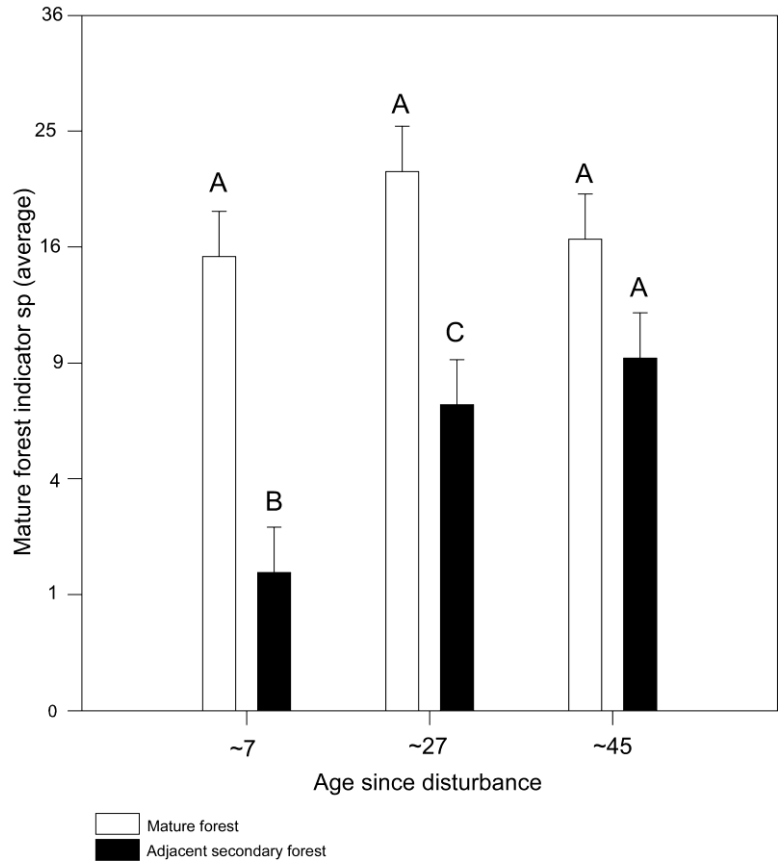

Figure 3.5. Average abundance of mature forest indicator species by age class. There were significant Age (ANOVA $F_{(2,54)} = 4.78$, $P = 0.012$) and Disturbance (mature or secondary forest) effects (ANOVA $F_{(1,54)} = 36.120$, $P < 0.001$). Classes sharing a common letter (A-C) were not significantly different from each other at the 0.05 level of confidence in the Holm-Sidak post hoc comparisons.

The DISTLM procedure showed that litter cover was the factor most strongly associated with differences in beetle assemblages among age class (16.72% of the model variance, $P < 0.001$). Other major factors were soil C:N (15.67% of model variance, $P < 0.001$) and LAI (7.9% of model variance, $P < 0.001$). Nitrogen and rock cover were excluded from the model as they were strongly collinear with other variables in the model. There was a significant age effect on litter cover (ANOVA $F_{(2,54)} = 13.502$, $P < 0.001$) and LAI ($F_{(2,54)} = 10.791$, $P < 0.001$) with average litter cover and LAI were greater in the ~45 and ~27 year old sites than the ~7 year old sites. There was also a significant age effect on C:N ratio ($F_{(2,54)}= 10.704$, $P < 0.001$), but conversely the C:N ratio was higher in the young forest than in the older

secondary forest. None of these factors showed a significant difference in the mature forest plots between age classes of the associated secondary forest (see Appendix B Fig. B.2).

3.4.3 Gradient Forest Modelling

The environmental variables selected by the GFM model and their relative importance in explaining the beetle community composition varied among age classes (Fig. 3.6). The most important factors in ~7 year-old sites were leaf litter depth and soil C:N ratio. The C:N ratio and plant diversity were also important in ~27 year-old sites, but less so in ~45 year-old regrowth. Litter cover was only of high importance in ~45 year old sites where it had by far the greatest cumulative importance, whereas litter depth was the factor explaining the most variation in young forest. LAI, pH and distance were relatively important in all three age classes. Running the GFM excluding mature forest plots provided congruent results, but we have presented the complete models because GFM is more reliable with a greater number of plots (preferably >100; Russell Thomson, pers. comm.).

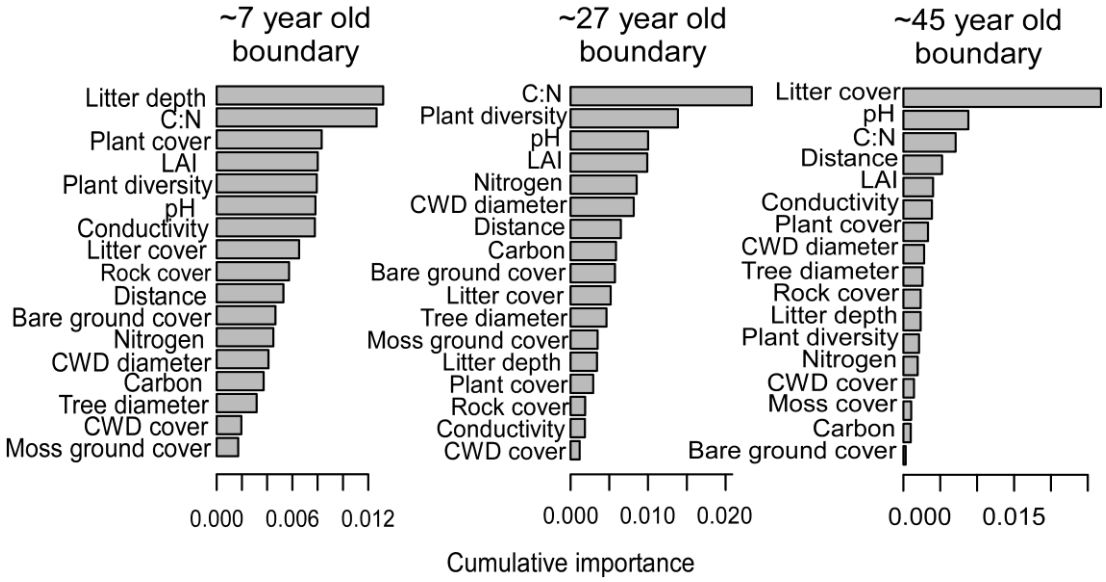

Figure 3.6. Gradient forests model ranking each environmental variable by their relative importance in predicting species assemblage within forest age class.

The three age classes showed different cumulative importance curves for environmental factors (see Appendix B.3). With increasing LAI, for example, the community turnover was quite steep in ~7 and ~27 year old forest, but much more gradual in older secondary forest. Similarly, as the C:N ratio increased, species turnover changed rapidly in the early and intermediate stages, but in the ~45 year old beetle community the turnover was more gradual. The most rapid turnover in ~45 year old sites related to litter cover. Consistent with the NCAP analysis results, the distance curves for the ~7 and ~27 year old communities' showed most of the species turnover occurs within 50m of the forest boundary, but in the old forest there was only a shallow gradual change.

Only two of the environmental parameters ranking among the top five in the GFM models were significantly associated with distance from mature forest using linear and non-linear regression (Only significant regressions are presented in Appendix B Fig. B.4.1-B.4.3). Litter depth was negatively correlated with distance, but only in the ~7 year old age class. In this age-class, litter depth was also correlated with total beetle abundance. LAI was correlated with distance in each age class, with mature forest LAI rapidly declining at the edge into secondary forest. There was no relationship between C:N, pH, nitrogen, plant diversity/cover or litter cover with distance from edge in any age class.

The average midday temperature data showed positive relationships with distance from mature forest in ~7 and ~27 year old regeneration but not in ~45 year old regeneration. There was no correlation between total beetle abundance and temperature.

3.5 Discussion

3.5.1 Edge gradients and succession

Our results showed not only that the beetle communities showed strong succession, with composition approaching that of mature forest by ~45 years (Figs 3.4 and 3.5),

forest influence also persisted until at least that stage, albeit with decreasing magnitude. Associated with this declining magnitude was an increase in the estimated depth of forest influence (DFI) from ~13 m in the youngest forest class to ~175-200 m in the oldest forest (Fig. 3.2). Even though the estimated DFI in the young forest was less than the distance to the first plot in the clearfell, CAP ordination confirmed that the 15 m plots were associated with the gradient of species composition within the harvested area (N Fountain-Jones, unpublished data). As indicated by the wide confidence intervals associated with the NCAP, there is uncertainty associated with the distance estimate of DFI, which may be greater than 13 m. It is also possible that the DFI actually extends beyond our 200 m transect length, although testing this is difficult because the maximum length of transects is limited by the size of clearcuts in these forests. These distances are all greater than that reported for beetles by Roume et al. (2011), possibly because the eucalypt forests on either side of our boundaries showed greater biotic and abiotic similarities than the woodland and agricultural fields in the French study. For example, even ~7 after logging, emerging eucalypts provide some shade and litter resources that may lessen the severity of the gradient. Furthermore, unlike in agricultural fields, the substantial coarse woody debris remaining after logging may aid species recovery since many of the species we collected are known to be saproxylic. Our results also indicate that mature forest species continue to occur in secondary forest, although their abundance declines with distance from mature forest. This illustrates that forest edges are permeable boundaries for beetles (Ries et al., 2004) even when there are large differences in habitat conditions, as for instance occurs soon after harvesting.

The longer but much weaker forest influence gradients in older (~45 year old) secondary forest (Fig. 3.2) indicate that either mature forest is still acting as a source population for beetle re-colonisation or mature forest affiliated beetles are gradually moving further into harvested areas with time. Although the latter process could be due to constraints on mobility of mature forest beetles, it could also reflect other aspects of forest influence, such as a greater density of regenerating rainforest tree species nearer the edge (Tabor et al., 2007). By ~45 years these trees will approach maturity and provide litter and shade.

Our observations that ~45 year old forest beetle communities were relatively similar to those of mature forest (Figures 3.4 and 3.5) are broadly consistent with the 35-50 years suggested for near complete beetle assemblage recovery in Atlantic forest in Brazil (Hopp et al., 2010) and 60 (±10) years for carabids in boreal forests (Koivula et al., 2002; Buddle et al., 2006). However, the persistence of edge gradients shows that this rate of ecological re-assembly of mature forest source communities is constrained by how close the secondary forest is to mature forest. This relatively long edge gradient is comparable to estimated dispersal distances from mature into long established secondary forest for Scandinavian beetle fungivores (Jonsson & Nordlander, 2006). Thus, it would be worthwhile to investigate whether differences between secondary forest and mature forest beetle communities may be persistent, as found in hemlock forests (Latty et al., 2006).

3.5.2 Species responses to succession

This study clearly demonstrates distinct beetle successional assemblages in each forest age. In Tasmania, most species considered indicators of young (~3 year old) forest by Baker (2006) were also indicators in our ~7 year old plots (see Appendix B.4). These species may be pyrophilic, or responding to the changed habitat conditions such as increased light or altered food resources. For example, the early seral indicator *Mecyclothorax ambiguus* (Carabidae: Psydrinae) has also been collected in native grassland (Michaels, 1999), which may suggest a preference for open conditions. As observed in other studies in Tasmanian wet forests, young seral species were uncommon in ~27 year old forest, and not collected at all at the ~45 year old sites (Michaels & McQuillan, 1995; Baker, 2006). The overall change in community gradient in the ~27 year old regenerating forest appears to be mainly driven by mid-successional specialist species, including *Microsilpha ANIC Thayer sp 15* (Staphylinidae: Microsilphinae) and *Decilaus TFIC sp 03* (Curculionidae: Cryptorynchinae) (see Appendix B.4 for species abundance data). However, mature forest specialists are generally more abundant in the ~27 year old regenerating forest than in ~7 year old forests and the slope of their decline in abundance with distance from edge is shallower (Fig. 3.3).

3.5.3 Environmental modelling

The observation that leaf litter attributes were the most important explanatory variables in ~7 and ~45 year old sites (Fig. 3.6) makes sense, because leaf litter is the primary habitat for forest ground-dwelling beetle species and affects the micro-spatial distribution of some species that prefer open ground (Magura et al., 2005). The decline in litter depth with distance in the ~7 year old sites suggests that mature forest is providing additional inputs of leaf litter near edges and this habitat provision might be significant for facilitating beetle re-colonisation. These results are consistent with previous studies indicating that litter is an important predictor of beetle re-colonisation and succession (Michaels & McQuillan, 1995; Magura et al., 2005; Nakamura et al., 2009).

The importance of plant diversity as an explanatory variable for forest influence in young and intermediate edges may reflect its relationship with diversity of leaf litter chemistry (Bardgett & Shine, 1999). Since monotypic litter contains lower abundance and diversity of micro-arthropods than litter from several plant species, plant diversity is likely to have cascading effects on arthropods (Hansen, 2000). The increased structural diversity supplied by rainforest plants typically present near mature edges (Tabor et al. 2007; J Balmer, unpublished data) may also facilitate re-colonisation of mature forest beetle species.

The importance of soil C:N ratio in the community gradient model for each forest age class as well as the beetle succession model (Fig. 3.6) may reflect impacts on predatory beetles resulting from the sensitivity of common prey (e.g. mites and springtails) to this ratio (Noti et al., 2003; Jensen et al., 2006). The lack of a relationship between distance and C:N ratio, may be due to high spatial variability in levels of both C and N (Shaw et al., 2008). C:N was affected by forest age, with ~7 year old stands having a higher C:N than the older secondary forest, presumably due to the migration of nitrogen from the soil into the canopy as the forest ages (Finzi et al., 1998). Few studies have measured beetle community responses to soil C:N ratio, yet other soil variables are known to be important (Schwerk & Szyszko, 2007;

Antvogel & Bonn, 2008). Soil pH affects carabid communities (McCracken, 1994; Schwerk & Szyszko, 2007; Antvogel & Bonn, 2008) and was an explanatory factor in the GFM. However, as with all variables, the association of beetle communities with pH may not be causal, it may simply reflect a strong link between pH, soil moisture and LAI (Antvogel & Bonn, 2008).

The strong predictive power of LAI (Fig. 3.6) suggests that forest cover has significant impact on beetle communities, presumably mediated by effects on microclimate. High LAI results in significantly lower temperatures and evaporative demand in these forests (Baker et al., 2014).There were strong temperature and LAI gradients across the ~7 year old edges, but the gradients in later successional stages were less pronounced. Even ~7 years after harvest, the 15 m and 35 m plots had a greater LAI and were cooler compared to plots further away from the boundary, showing a strong forest influence effect. In the GF model, increasing LAI explains species turnover predominantly in the early and intermediate age sites and little in ~45 year old sites. LAI was also important in explaining the beetle community successional changes. Canopy closure occurs in this forest type at around 20 years after harvest and clearly had an impact on community composition in both our older regrowth age classes. Canopy closure facilitates increased moisture content of the surface soil and a decrease in temperature and humidity fluctuations (Entling et al., 2007). For some mature-forest species, canopy closure may therefore be the most important factor enabling successful re-colonisation beyond shaded edge conditions (Koivula et al., 2002; Grimbacher et al., 2006; Nakamura et al., 2009). However, collinearity of variables in the model results in some ambiguity about which factors drive the patterns observed here. Experimental work on the effects of environmental variables on beetle re-colonisation would help resolve this ambiguity.

3.5.4 Conservation and management outcomes

This study clearly illustrates the importance of maintaining mature forest in production forest landscapes through its impacts on the successional trajectory of beetle communities in adjacent secondary forest. Not only do these mature forests

have ecologically important effects on leaf litter inputs, microclimate and shading on nearby regenerating forest, but they also provide sources of mature forest species. The nearly complete reassembly of mature forest communities within ~175-200 m by ~45 years after harvest shows how retained mature forest can assist species re-establishment and persistence in regrowth forest landscapes (Chazdon et al., 2009; Hopp et al., 2010).

Our results are relevant to forest managers looking to build connectivity into fragmented landscapes, as secondary forests with mature forest boundaries may harbour a comparable beetle community over time. Maintaining sufficient mature forest embedded within harvested landscapes should be a high priority, since our study demonstrates that as well as providing habitat for species requiring this successional stage, they appear to influence successional dynamics of the entire landscape. Furthermore, this study shows the conservation potential of retention forestry approaches like aggregated retention where unlogged patches are retained within harvested areas (Baker et al., 2009a). Current practices for designing aggregated retention harvests sometimes require that the harvested area is no more than one mature tree height from retained mature forest (forest influence target (Baker & Read, 2011)). The almost complete recovery of mature forest beetle assemblages up to 200 m from mature forest by ~45 years indicate that this one-tree height target is relatively conservative for beetles, at least for this age class, although the estimated DFI was substantially less than one mature forest tree height for ~7 and ~27 year old age classes. However, since our study surveyed clearcut edges rather than gradients from small isolated aggregates, the poorly understood effects of mature forest patch-size or total quantity of mature forest in the surrounding landscape may also be important limitations to the re-establishment of beetles that require further study.

This study was one of the first to analyse the long term impacts of forest influence on forest biodiversity. The relatively rapid recovery of mature forest successional communities was driven by edge re-colonisation coupled with litter input and microclimate factors. Mature forest stands are not necessarily ‘islands’ in a

secondary forest mosaic, but instead are critical components facilitating connectivity and succession in fragmented landscapes.

Acknowledgements

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Chapter 4

Beetle trophic groups show differential effects of phylogeny and environment along a successional gradient

This chapter contains material from a manuscript under review with Axios Review with the intention of submission to *Ecology Letters*.

Fountain-Jones, N.M,, Jordan, G.J.,, Baker, T.P., Burridge, C., Petersfeld, M., Wardlaw, T.J., Forster, L. and Baker, S.C. (2014). 'Beetle trophic groups show differential effects of phylogeny and environment along a successional gradient.' (in preparation).

4.1 Summary

Evolutionary,environmental and biotic forces drive community assembly, yet how these forces co-vary across trophic groups is unknown. As beetles are trophically diverse, the effects of phylogeny and environment can be determined across multiple co-occuring trophic groups. Using a novel combination of functional trait and phylogenetic approaches, we assessed the role of environmental filtering, neutral processes and biotic interactions in determining predator and decomposer/primary consumer assembly patterns across forest succession. We also compared phylogenetic signals of these communities and tested whether phylogenetic niche conservatism helped explain the successional patterns. Environmental filtering was the dominant assembly pattern for both groups, but this pattern, and the phylogenetic signal, changed substantially across forest succession. We demonstrate that individual trait responses of one trophic group may not be a surrogate for another, even within clades. Here, we provide the first insights into the differential evolutionary and environmental forces acting on co-occuring trophic groups.

4.2 Introduction

Rapid environmental change, including widespread ecological disturbance, creates an increasing imperative to predict how ecological communities will respond to these changes, and to use these predictions to manipulate conditions to favour beneficial community composition and function. Community assembly processes provides a conceptual foundation for understanding the dynamics of how coexisting species respond to disturbance in the short and long term. In recent decades, functional trait approaches have transformed our understanding of community assembly, particularly for plants (Hodgson et al., 1999) but also for animals (Southwood, 1977; Ribera et al., 2001; Vandewalle et al., 2010). As an example, habitat template theory (Southwood, 1977; Greenslade, 1983) has enabled researchers to predict how environmental shifts filter animal species traits (environmental filtering). This theory assumes that the combined effects of evolutionary processes and the fit of species' traits to environment determine the occurrence of species. Understanding the

interplay between environmental filtering and evolutionary forces on animal traits has greatly increased our comprehension of community responses to environmental shifts, such as those initiated by disturbance (Southwood, 1977; Greenslade, 1983; Ribera et al., 2001).

Community functional trait composition can illustrate how evolution has shaped communities over multiple temporal and spatial scales (Pillar & Duarte, 2010; Barton et al., 2011). Thus, different patterns of community functional traits along environmental gradients can indicate different processes of community assembly. Convergence in community functional traits (trait convergence assembly patterns) indicates that the position along an environmental gradient favours certain trait states. Alternatively, biotic interactions (e.g. competition) leading to niche differentiation result in divergence of traits during community assembly (trait divergence assembly patterns). Finally, stochastic functional trait patterns are best explained by neutral theory (Hubbell, 2001). Trait convergence and divergence assembly patterns have rarely been explicitly investigated for animal communities, particularly at the metacommunity level (i.e. the local set of communities connected by dispersal) (Leibold et al., 2004; Pillar & Duarte, 2010; Podgaiski et al., 2013).

Knowledge of phylogenetic relationships is also important because it can be used to untangle the relative importance of short term and evolutionary processes in guiding community assembly. Species that are closely related are expected to have greater trait similarity than distantly related species (phylogenetic signal). Convergence in community functional traits, in particular, is expected to involve traits with high phylogenetic signal (Webb et al., 2002; Silvertown et al., 2006). Phylogenetic signal is most commonly measured at the species level by correlating trait and phylogenetic distance (Blomberg & Garland, 2002), but can also be measured at a metacommunity level (Pillar & Duarte, 2010) where communities that have similar phylogenetic structure also have similar trait values (Pillar & Duarte, 2010). If metacommunity phylogenetic signal mediates the link between environment and traits, phylogenetic niche conservatism is likely to be important for community assembly (Pillar & Duarte, 2010). In contrast, phylogenetically independent correlations between

environment and traits provide evidence for evolutionary convergence (niche lability). Even though phylogenetic niche conservatism is often considered to dominate community assembly (Wiens & Graham, 2005), recent work suggests considerable niche lability for some groups (Silvertown et al., 2006; Losos, 2008; Segar et al., 2013).

Trait weighted species composition (species abundance weighted by functional trait mean values) can demonstrate differences in assembly patterns between communities, and thereby help explain the mechanism for community recovery after disturbance (Podgaiski et al., 2013). For example, trait weighted species composition can indicate whether a forest has recovered to a pre-disturbance state based on trait values rather than species composition alone. If traits are phylogenetically conserved, it is likely that phylogenetically weighted species composition (species abundance weighted by phylogenetic distance) will illustrate similar patterns to trait weighted species composition, and show which clades are driving recovery (Pillar & Duarte, 2010).

Forest succession – the changes in species composition of a forest following disturbance – provides an ideal system for investigating community assembly processes because it represents systems with more-or-less complete assembly within observable time scales (Lebrija-Trejos et al., 2010). However, relatively little is known about the factors driving animal community assembly during succession. Studies of beetles in forests of known disturbance history provide an opportunity to address this knowledge gap (e.g. Fountain-Jones et al. in press (b)). For example, while beetle species composition tends to largely recover to a pre-disturbance state ~50 years after logging (Hopp et al., 2010; Fountain-Jones et al., in press (b)), the underlying assembly processes, and whether they vary with trophic position, are unknown.

Successional gradients reflect temporal changes in environmental variables that will affect beetle community assembly in different ways (Ribera et al., 2001; Hopp et al., 2010; Fountain-Jones et al., in press (b)). However, other environmental variables

unrelated to the successional gradient may also be influential. For instance, elevation as well as disturbance history were both important in determining predatory beetle trait responses to disturbance (Ribera et al., 2001). Furthermore, knowing which particular environmental filters act on which traits can provide a deeper understanding of community assembly for each trophic group, and enhance the predictive capacity of a disturbance model.

How individual trait values (community weighted means) vary over succession can provide complementary evidence to trait composition, and furthermore can allow development of predictive frameworks (Vandewalle et al., 2010; Lasky et al., 2014). The capacity to estimate time since forest disturbance from animal traits has rarely been explored, and might vary between trophic groups. For example, in some systems, robustness is important for microhabitat use in herbivore but not predator clades (Barton et al., 2011). In contrast, responses of dispersal traits following disturbance are thought to be similar across trophic groups, with the habitat template theory predicting dispersal-limited species are more likely to occur in less disturbed habitats (Southwood, 1977; Greenslade, 1983). Beetle colour traits also respond to disturbance (Ribera et al., 2001), yet these traits have been rarely quantified even though there are clear functional links to variation in colour, such as thermoregulation and crypsis (Harris & Weatherall, 1990; Ribera et al., 2001). While there are clear functional links to variation in colour, such as thermoregulation and crypsis that are important (Harris & Weatherall, 1990; Ribera et al., 2001), community variation in colour has not been quantified in response to disturbance.

Here we use the latest quantitative methods that integrate functional trait and community phylogenetic approaches to understand ecological and evolutionary contributions to community assembly (Pillar & Duarte, 2010; Pavoine et al., 2011; Diniz-Filho et al., 2012; Segar et al., 2013). We compare the roles of environmental filtering and biotic interactions on the assembly of predator and decomposer/primary consumer beetle metacommunities across a successional gradient from recently logged to mature forest. Additionally, we characterise predator and decomposer/primary consumer functional trait syndromes in this system, and identify

broader phylogenetically-corrected trait-environment relationships for each trophic group. Since functional trait evidence has rarely been used to formally explore terrestrial invertebrate community assembly specifically, we answer four linked questions: (I) is community assembly is better explained by environmental filtering or biotic interactions than neutral processes? (II) Are the patterns influenced equally by phylogenetic signal in both trophic groups? (III) Is phylogenetic niche conservatism (e.g. beetle niches are labile across succession) important? (IV) Is community assembly underlain by significant but differing trait-environment relationships among beetle trophic groups? We also investigate to what extent species, trait and phylogenetically weighted species composition is similar to mature forest, ~7, ~27 and ~45 years after logging, and develop a trait-based tool to quantify recovery following disturbance

4.3 Materials and methods

4.3.1 Data collection

Our study uses beetle species composition, abundance and environmental datasets from 15 sites (180 plots) in mature forest and adjacent clear-cut harvested secondary forest in three logging age classes in southern Tasmania (see detailed description and a map of study sites in Appendix C.1, trapping methodology in Appendix C.2.1 and environmental data collection in Appendix C.2.2). The three age classes comprised sites averaging 45 years (harvested between 1966 and 1970), 27 years (1983 to 1989), and 7 years (2002 to 2007) post-harvest. Plots were sub-sampled from a broader transect-based study across mature forest clear-cut boundaries (Fountain-Jones et al., in press (b)). Here we employ plots located 120 m and 200 m into secondary forest from the forest edge and mature forest plots 15 m and 35 m from the forest edge. In previous work edge effects into mature forest were found to extend between 10-25 m into mature forest from adjacent clear cut forest (Baker et al. 2006), suggesting that at least the 35 m plot was not affected by the edge.

We collected beetles using pitfall traps over three trapping periods (spring, summer and autumn 2011/2012). All beetles were identified to species or morphospecies

level, but functional trait measurements and molecular data were only collected from common species (≥6 individuals; 133 species out of 271 in total), and all subsequent analyses was performed on these species.

For each species, we calculated and analysed 14 functional traits, including12 morphological traits, one phenological and one ecological performance trait (Table 4.1). For each morphological trait, measurements from six individuals of each species were averaged, following preliminary investigations indicating that this was sufficient to account for most within-species variation. Phenological and ecological performance traits were measured using species distribution data (see Appendix C.2.2 for calculation details). Trophic group was determined at the sub-family level from Lawrence *et al.*. (1999). We focused on traits which have previously been found to vary with disturbance (Ribera et al., 2001; Vandewalle et al., 2010; Fountain-Jones et al., in press (a)). We also focused on comparing patterns in predators versus decomposer/primary consumer species because preliminary analysis (Appendix C.5) demonstrated that this broad trophic classification represented a major functional contrast in our system.

A molecular phylogeny was developed for the 133 beetle species based on one mitochondrial (COI) and one nuclear (28S D3) region sequenced from one individual of each species. See Appendix C.2.4 for phylogenetic method details and Appendix C.3 for the phylogeny.

We analysed 16 environmental parameters that were collected at each plot (Appendix C2, Table C.2.1). These variables are considered important in filtering beetle species post-disturbance in this system and elsewhere (Michaels & McQuillan, 1995; Ribera et al., 2001; Vandewalle et al., 2010) and were not strongly collinear.

Table 4.1. Traits of beetles measured in this study.

Trait	Trait type	Data type	Functional links	Units	Measurement details
Body Length	M	Qn	Fecundity, foraging capability dispersal	Log(mm)	Total length from anterior of head to posterior of abdomen.
Antennae Length	M	Qn	Predator avoidance, habitat preference	Log(mm)	Total length of antennae from base to apex.
Eye size	M	Qn	Habitat preference, hunting capability	PCA PC 1 scores	PCA of eye width and eye length.
Eye Width				Log(mm)	From point closest to dorsal surface of head to point closest to ventral surface of head on eye.
Eye Length				Log(mm)	From point closest to anterior of head to point closest to potsreior of head on eye.
Wings?	M	Bi	Dispersal capability	Binary	Presence or absence
Elytra Length	M	Qn	Dispersal, microhabitat use	Log(mm)	Maximum dorsal length of elytra along medial line.
Average leg length & Back leg to front leg ratio	M	Qn	Dispersal capability, microhabitat use	Average and ratio (mm)	
Front Leg Length					Maximum length of femur, tibia and tarsi of a front leg
Back Leg Length					Maximum length of femur, tibia and tarsi of a back leg
Robustness	M	Qn	Defensive, microhabitat use, dispersal	PCA PC1 score	PCA of head width, pronutum length/width, prothorax depth, abdomen width/length/depth. See Barton et al., (2011)
Head Width				Log(mm)	Maximum dorsal width of head (not including eyes)
Pronotum Width				Log(mm)	Maximum dorsal width of pronotum
Pronotum Length				Log(mm)	Maximum dorsal length of pronotum along medial line
Prothorax Depth				Log(mm)	Maximum depth of prothorax
Abdomen Width				Log(mm)	Maximum dorsal width of abdomen
Abdomen Length				Log(mm)	Maximum dorsal length of abdomen along medial line
Abdomen Depth				Log(mm)	Maximum depth of abdomen
CIE L (lightness)	M	Qn	Predator avoidance, thermal maintenance	Co-ord	USB 4000 spectrophotometer
CIE A (red/green)	M	Qn	Predator avoidance	Co-ord	USB 4000 spectrophotometer
CIE B (blue/yellow)	M	Qn	Predator avoidance	Co-ord	USB 4000 spectrophotometer
Dominant wavelength	M	Qn	Predator avoidance, thermal maintenance	nm	USB 4000 spectrophotometer
Seasonal activity	Ph	Qu	Thermal tolerance, fecundity	ratio	
Habitat occupation	E	Qu	Resource use, thermal tolerance	ratio	

Bold trait are the traits used in the study, traits in italics were used to generate a particular trait score. M: Morphological trait, P: Physiological traits, Ph: Phenological trait, E: Ecological performance trait. Data type: Qu: Qualitative, Qn: Quantitative, Bi: Binary. Co-ord: Colour co-ordinate in International Commission on Illumination (CIE) colour space.

4.2.2 Statistical approaches

We tested our four hypotheses using combined phylogenetic and traits-based analysis of functional trait, phylogenetic distance, species abundance and environment data sets. We adapted the Pillar & Duarte (2010) metacommunity framework to analyse trait divergence and convergence community assembly patterns and phylogenetic signal for both trophic groups. To assess trait convergence and trait divergence assembly patterns for each trophic group, a series of mantel correlations was performed, first on the complete trait set and then on reduced sets of traits that maximised the expression of trait convergence and trait divergence assembly patterns. We also applied the Pillar & Duarte (2010) framework to test for phylogenetic signal at both species and metacommunity levels using mantel tests also. These correlations were then tested against null models using permutation tests. These analyses were conducted using the R package 'SYNCSA' (Debastiani & Pillar, 2012). See Appendix C.2.5 for matrix calculation and permutation test details.

To assess trait-environment relationships for both trophic groups, we applied a combined RLQ and fourth corner approach to the complete set of environmental variables and functional traits (Dray & Legendre, 2008; Dray et al., 2014). Because our trait data showed phylogenetic signal (as indicated by Abouheif's test (Abouheif, 1999), we followed the approach of Dray et al. (2014) of basing our analyses on phylogenetically independent species values derived from phylogenetic eigenvector regression (Diniz-Filho et al., 2012). Unlike phylogenetic-independent contrasts, which only provide scores for internal nodes of the phylogeny (Garland et al., 1992), phylogenetic eigenvector regression provides scores for terminal nodes (i.e. species), making the RLQ and fourth corner analyses possible. The overall analyses then involved a two step permuation method testing the links between species and environment (model 2 of Dray & Legendre (2008)) and between species and traits (model 4 of Dray & Legendre (2008)). Models were tested against the null model that species were distributed randomly across the sites. If both were significant then the global model linking traits to environment through species composition was

tested (model 6 of Dray & Legendre (2008)), and pairwise trait-environment realtionships plotted on RLQ ordination axes. See Appendix C2.5 for more details.

To visualise and assess metacommunity relationships between successional stages for both trophic levels, canonical analysis of principal coordinates (CAP) ordination (Anderson & Willis, 2003) and PERMANOVA (Anderson, 2001) were performed on three datasets for a) unadjusted, b) trait weighted and c) phylogenetically weighted beetle species abundance data. Ordinations were constrained by successional stage; species vectors were overlaid using Pearson correlations. Tests for difference in community composition among successional stages were conducted using one-way PERMANOVAs for each dataset. Due to the lack of independence between mature forest and adjacent secondary forest plots, separate analyses compared mature plots with each individual successional stage. One-way PERMANOVA was then used to test for differences between the three secondary forest age classes with site as a nested random factor. CAP and PERMANOVA analyses were conducted using 9,999 permutations in PERMANOVA+ in PRIMER 6 (Anderson et al., 2008).

Phylogenetically adjusted traits were also used to generate community weighted trait values (matrix T in the framework of Pillar *et al.*. (2009); see Appendix C.2.5). Community weighted trait values can help predict system-specific responses to disturbance (Charvet et al., 2000; Vandewalle et al., 2010). However, controlling for phylogenetic autocorrelation can provide trait values comparable with other systems with different evolutionary histories of beetle lineages (Poff et al., 2006). Individual community weighted trait values were analysed using a two-way factorial ANOVA (successional stage × trophic group) and post-hoc Holm-Sidak pair-wise comparisons.

4.4 Results

4.4.1 Trait convergence, divergence and phylogenetic signal and structure

For both predator (60 species) and decomposer/primary consumer (73 species) communities, trait convergence patterns dominated assembly across the successional gradient (Question I). Decomposers/primary consumers showed significant trait convergence both for all traits combined and for the subset optimised for trait convergence (Table 4.2). Predators only showed significant trait convergence using the convergence-optimised subset of traits (Table 4.2). Trait divergence was not significant for either trophic group, even with when divergence-optimised traits were used (Table 4.2). For predator traits, there was significant species-level phylogenetic signal for all trait sets (Appendix C.4); however, species level phylogenetic signal was not significant for decomposer/primary consumer traits (including optimised trait sets) (Question II). There was a significant metacommunity phylogenetic signal for the complete and optimised predator trait sets and the decomposer/primary consumer convergence optimised traits (Table 4.2). For all sets of traits in both trophic groups that displayed convergence, the correlation was independent of phylogeny (Table 4.2), suggesting that convergent evolution was more important than phylogenetic niche conservatism in community assembly (Question III). Only decomposer/primary consumer communities demonstrated significant successional phylogenetic structure.

Table 4.2. Successional filtering/trait divergence patterns and phylogenetic signal/structure for both predators and decomposer/primary consumer communities across a forest successional gradient. Numbers are correlation coefficients from the mantel/partial mantel tests.

	Predators			**Decomposers and primary consumers**		
	All traits	Optimal TCAP°	Optimal TDAP†	All traits	Optimal TCAP°°	Optimal TDAP††
Environmental filtering	0.15	**0.19****	0.15	**0.23***	**0.27*****	0.14
Trait divergence	-0.01	-0.001	0.05	0.008	-0.07	0.16
Phylogenetic signal (species pool)	**0.55*****	**0.42*****	**0.41*****	0.005	0.11	0.49
Phylogenetic signal (metacommunity, PSM) (PT)	**0.44 *****	**0.35*****	**0.32*****	0.24	**0.45***	0.15
Phylogenetic structure (PE)	0.05	0.05	0.05	**0.24***	**0.24***	**0.24***
Environmental filtering (removing phylogeny) (TE.P)	0.13	**0.18****	0.14	**0.18***	**0.19***	0.11
Phylogenetic niche conservatism likely?	No	No	No	No	No	No

*°Trait subset: Habitat occupation, CIE L, eye size; °°Trait subset: CIE A, seasonality, robustness, elytra length, wings; † Trait subset: CIE L; †† Trait subset: CIE B. Phylogenetic niche conservatism was deduced according to the method developed by Pillar & Duarte (2010). * P < 0.05, **P < 0.01, ***P < 0.001.*

4.4.2 Trait-environment relationships

Predator species composition corresponded to environment (model 2 P < 0.001) but not significantly for traits (model 4 P = 0.066) (Question IV). As both fourth corner models were not significant, trait-environment relationships were not assessed for predators. Analyses of non-phylogenetically corrected data showed qualititively similar results (Appendix C.4, Fig. C.4). Even though model 4 was only just non-significant, after false discovery rate there were no significant individual trait-environment relationships. In contrast, both models were significant for decomposer/primary consumers (model 2 P < 0.001, model 4 P < 0.001), suggesting

strong trait environment relationships, and thus significant individual trait-environment relationships were overlaid on RLQ axes for decomposer/primary consumers (Fig. 4.1 II)). RLQ axis 1 (explaining 66% of the covariance) separated species characteristic of mature forest from ~7 year old communities (Fig. 4.1 Ic), whereas axis 2 (explaining 25% of the covariance) separated ~27 and ~45 year old decomposer/primary consumer species from the other groups. There were significant positive correlations between successional stage and both robustness and average leg length (Fig. 4.1). Leaf area index and litter depth were positively correlated to average leg length, as were moss cover and CIE A. There were significant negative correlations between successional stage and elytra length and wings, as well as between wings and litter depth and soil carbon (Fig. 4.1).

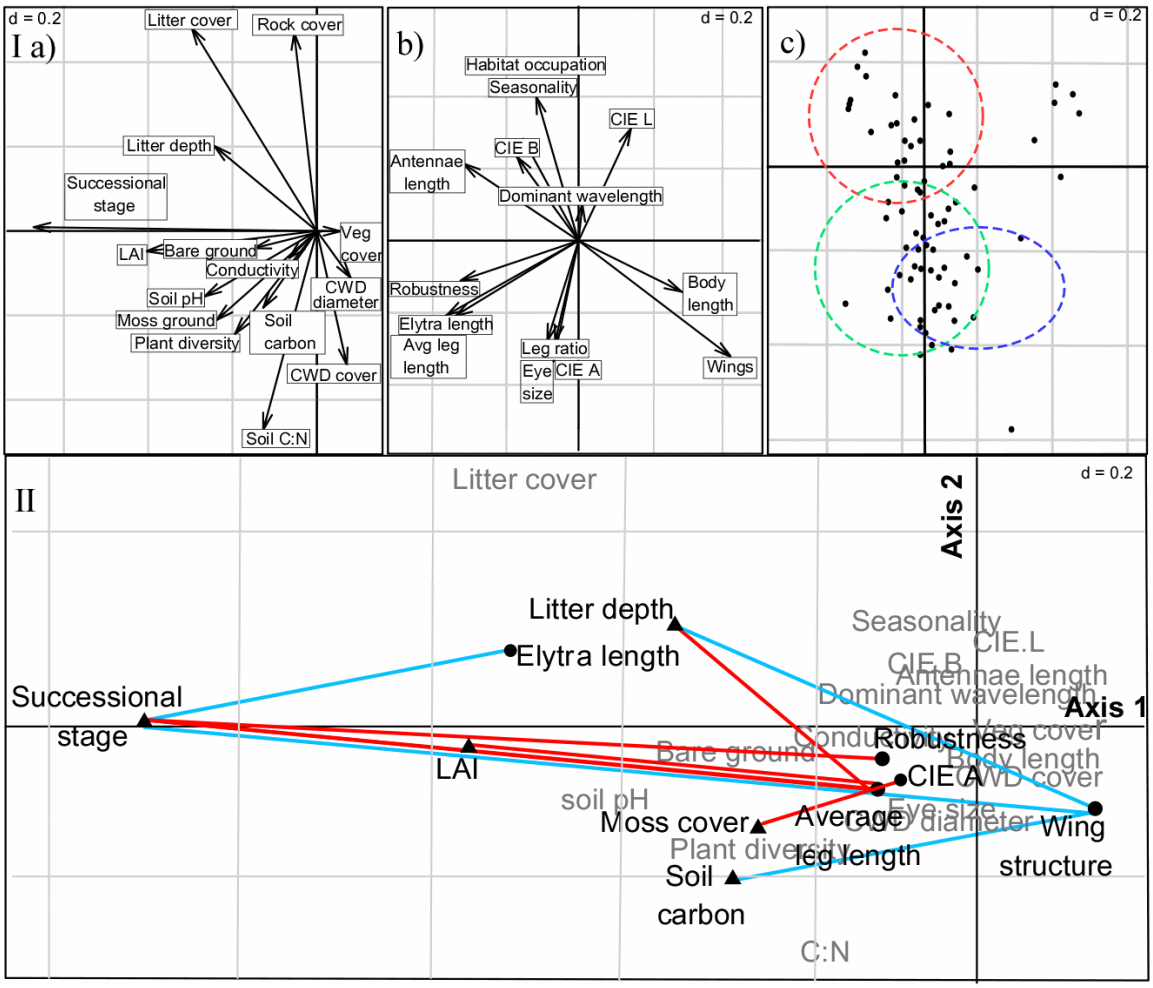

Figure 4.1. Comparison of ordinations of different datasets presented within the same ordination space and RLQ and fourth corner results showing significant trait-environment relationships for decomposer/primary consumer species. I(a) Environmental variables PCA, (b) Functional trait PCA, and (c) species CA. In I(c), the blue circle indicates species common in ~7 year old forests, the red circle indicates species associated with ~27 and ~45 year old forest and the green circle indicates mature forest (Appendix C.3). II: Combined RLQ and fourth corner analysis for decomposers/primary consumers across successional stages (fourth corner model 6). Permutation tests showed significant global trait-environment relationships (P = 0.003). Significantly inter-related traits and environmental variables are displayed in black rather than grey text. Light blue lines indicate a significant negative relationship between variables whereas red lines indicate positive relationships (P < 0.05).

4.4.3 Species, trait and phylogenetic composition

The CAP ordination and PERMANOVA pair-wise tests also showed that both trophic groups responded differently to the succession gradient. Pair-wise comparisons found unadjusted species composition for predators differed among three groups – ~7, ~27 and ~45 year old, and mature forest (Fig. 4.2 I(a)), yet only ~7 year old beetle trait-weighted composition was distinct (Fig. 4.2 II(a)). In contrast, decomposer/primary consumer species assemblages were distinct for each of the four age classes for both species and trait weighted species composition (Fig. 4.2 I (b), II(b)). Succession was not a significant factor for predator phylogenetic structure. For decomposers/primary consumers, unlike ~ 7 and ~ 27 year old forest, ~ 45 year old phylogenetic structure was not significantly different from mature forest – a result driven primarily by the association of Curculionidae with older age classes, whereas a variety of decomposer/primary consumer families were correlated with early successional stages (Fig. 4.2 III(a)).

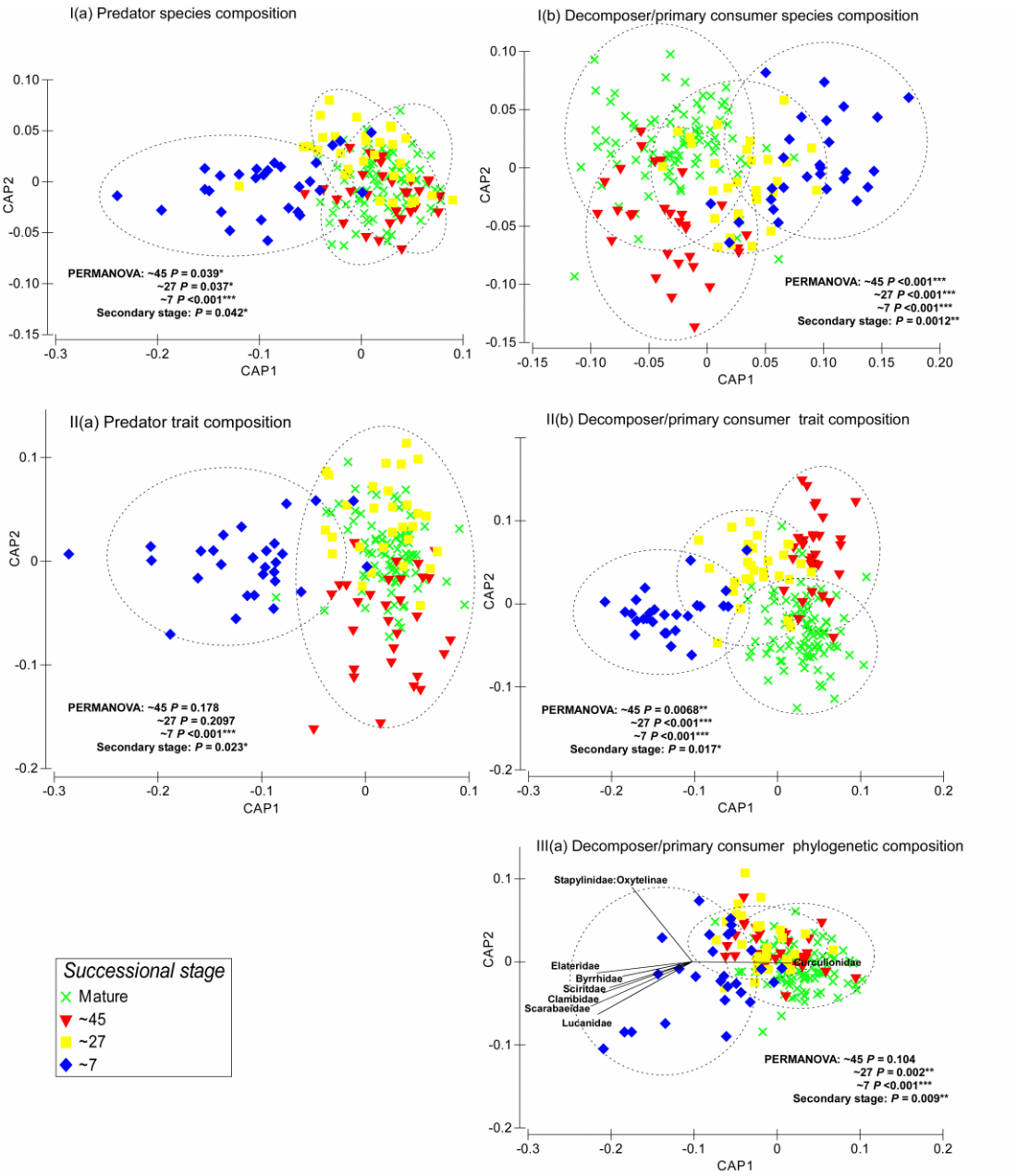

Figure 4.2. CAP ordination and PERMANOVA tests for species composition and trait/phylogenetic weighted species composition for each trophic group. CAP ordination and PERMANOVA tests for species composition and trait/phylogenetic-weighted species composition for each trophic group. P-values are from one-way PERMANOVAs assessing differences between mature and secondary forest for each age (~45, ~27, ~7 year-old regrowth). Secondary stage P-values are from one-way PERMANOVA looking for differences between secondary forest species composition among age classes. I: Species composition CAP, II: Trait-weighted species composition CAP. Dotted lines represent groups distinguished by PERMANOVA pair-wise tests. III. Phylogenetic distance-weighted species composition. (a): Predators, (b): Decomposer/primary consumers. There was not a significant succession effect (P = 0.33) for predator phylogenetic distance weighted composition, therefore it is not shown. * P < 0.05, **P < 0.01, ***P < 0.001.

4.4.4 Individual trait-succession relationships

Individual phylogenetically-corrected community-weighted trait relationships demonstrated further similarities and differences in functional responses of both trophic groups and helped characterise beetle functional trait combinations. Seasonal activity, habitat use, eye size, dominant wavelength traits and presence of wings responded to succession in similar ways in both trophic groups: beetles in the younger secondary forest were active in fewer seasons (Fig. 4.3c), occupied fewer habitats, had larger eyes (Fig. 4.3g), had longer dominant colour wavelengths (more yellow) and were more likely to be winged than beetles in the older successional communities. Average leg length was not significantly different between trophic groups for secondary forest communities, yet mature forest decomposer/primary consumer species had a greater leg length compared to other stages while the predators in this age class did not (Fig. 4.3d). The remaining trait scores were quite distinct for predators and decomposers/primary consumers. Varying successional relationships were evident, although predator traits generally varied less among successional stages. Regardless of successional stage, predatory beetles were longer (Fig. 4.3a), less robust (Fig. 4.3i), less dark (i.e. have higher CIE L values) and greener (i.e. lower CIE A values) than decomposer/primary consumers (Fig. 4.3j/k), and also had shorter elytra (Fig.4.3f), and longer antennae (Fig. 4.3h). Generally, however, predator communities were more likely to be winged and restricted in habitat occupancy. Decomposer/primary consumers had more successional shifts for more traits overall with, for example, longer elytra in mature and ~45 year old forests compared to the younger forests. Mature forest beetles were more robust, darker and less green than beetles of early successional stages (Figs. 4.3i/k).

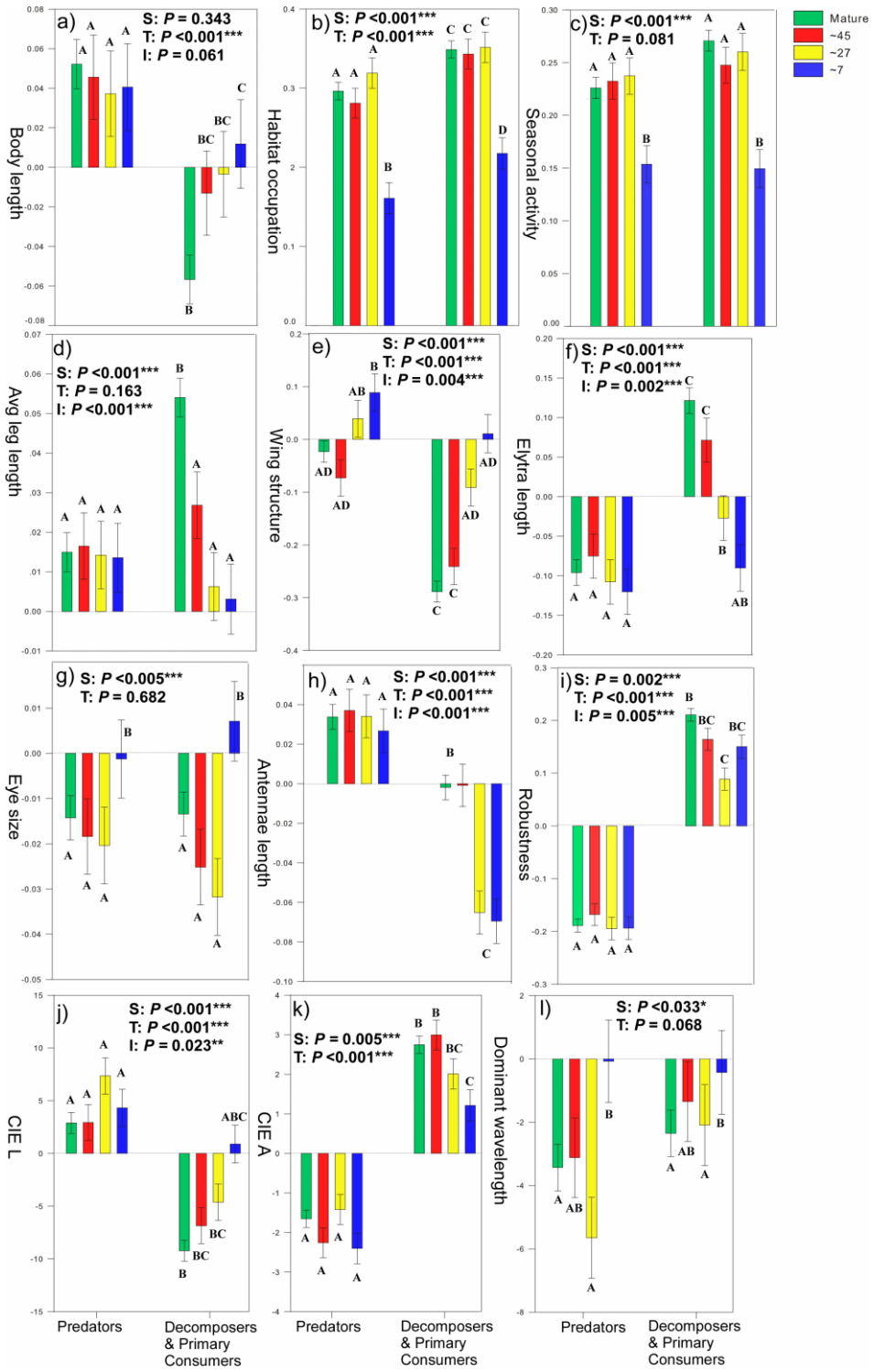

Figure 4.3. Individual trait-succession relationships using trait phylogenetically corrected community weighted means scores. S: Succession, T: Trophic group, I: Succession × trophic group interaction. The X axis for each graph is on a phylogenetically-independent scale * P < 0.05, **P < 0.01, ***P < 0.001.

4.5 Discussion

This study shows that the community assembly of sympatric beetle trophic groups (decomposers/primary consumers, predators) are influenced by differential evolutionary and environmental forces. For both groups, metacommunity assembly was mostly driven by environmental filtering rather than biotic interactions or neutral processes. However convergent traits assembly processes were important but the traits involved were different for the two trophic groups. All decomposer/primary consumer traits demonstrated strong successional effects and links to environmental gradients. However, predator traits were more evolutionarily-constrained across succession than decomposer/primary consumers, for which community phylogenetic signal was only demonstrated for a subset of strongly convergent traits. Each successional stage also had a unique trait syndrome.

4.5.1 Environmental filtering drives community assembly

Although environmental filtering of beetle traits was important for both trophic groups this effect was weaker for predator traits than for decomposer/primary consumers. Hunting strategy rather than habitat is thought to be more important for carabid community assembly (e.g. Forsythe, 1987) and this may also be true for other beetle predator groups. For predators, only the trait set optimised for convergence demonstrated environmental filtering, whereas environmental filtering was demonstrated for decomposers/primary consumers in both the complete and convergent-optimised trait sets (Table 4.2). The traits making up the optimal sets varied substantially between the trophic groups. Although this result should be expected considering the divergent feeding strategies and habitat requirements of each trophic group (Lawrence et al., 1999; Ribera et al., 2001) it has not been demonstrated previously. For example, robustness showed strong convergence for decomposers/primary consumers, but was neither divergent nor convergent for predators (Table 4.2).

Divergence patterns were absent for predators and decomposer/primary consumers, suggesting that biotic interactions such as competition are generally less important

than environmental filtering in community assembly. However, trait divergence assembly patterns have been found for spiders along a plant functional diversity gradient (Podgaiski et al., 2013), and for some water beetle communities (Juliano & Lawton, 1990). Although it is conceivable that the lack of trait divergence was due to measurement of inappropriate traits or spatial/temporal scales (Pillar et al., 2009b), the effects of biotic interactions such as inter-specific competition have been difficult to demonstrate for beetles even when measured directly for both trophic groups (e.g. Niemelä 1993).

4.5.2 Phylogenetic signal of traits varies with respect to trophic group

Phylogenetic signal and structure also varied substantially for traits between trophic groups (Table 4.2). At the species level, traits were much more constrained by phylogeny for predators than for decomposers/primary consumers. This is likely to be related to staphylinid and carabid families dominating the beetle leaf litter faunas, as observed in many parts of the world (e.g. Koivula et al., 2002; Hopp et al., 2010). Carabids, in particular, are known to have a conserved body plan that is adaptable to varying habitats (e.g. Lövei & Sunderland, 1996). Conversely, decomposers/primary consumers were less constrained by phylogeny, with non-significant species-level phylogenetic signal for all trait combinations. It is possible that this group has more labile niches or finer scale niche partitioning than predators (Cunningham & Murray, 2007). This study clearly demonstrates that phylogenetic signal varies between trophic groups even within the same family (e.g. within the Staphylinidae), and this should be considered in future arthropod functional trait studies.

4.5.3 No evidence for phylogenetic niche conservatism

At the metacommunity level, both predators and decomposer/primary consumers showed phylogenetic signal, but for decomposers/primary consumers this was restricted to the most convergent traits. However, there was little evidence for phylogenetic niche conservatism for either trophic group, and evolutionary convergence was more likely to be important for beetle community assembly during succession. This highlights that environment and phylogeny act independently to

shape beetle traits. This study provides evidence that phylogenetic niche conservatism cannot be assumed to be the dominant mechanism for community assembly and that niches in general are relatively labile (Losos, 2008; Pillar & Duarte, 2010; Segar et al., 2013).

4.5.4 Which environmental filters?

Trait–environment relationships also exhibited contrasting patterns between trophic groups and identified which environmental filters drove the successional shifts. For decomposers/primary consumers, canopy cover (as assessed by leaf area index), leaf litter depth and soil carbon were important trait filters, and are known to be important factors in determining beetle species distributions (Ribera et al., 2001; Fountain-Jones et al., in press (b)). The finding that beetles with stronger red spectra (Fig. 4.3k) were linked to plots with increased moss cover is curious and warrants further investigation. The combined RLQ and fourth-corner approach also gave further evidence for weaker trait-environment relationships in predators than decomposers/primary consumers. Environment was important for predator species distribution, but for this trophic group traits were not significantly linked to environment. Carabids, for example, can have a rather generalist morphology not linked to habitat, yet can be specialists physiologically (Lövei & Sunderland, 1996). Collecting detailed diet and physiological trait data, possibly via metagenomics or metabolomics (e.g. Nota et al. 2013), may reveal additional important trait-environment relationships. Another possibility is that changes in environment over larger spatial scales may be better predictors of predator trait states.

4.5.4 Succession and recovery

The CAP ordinations and pair-wise tests showed differential composition recovery patterns for trophic groups across succession. The large differences in species composition between young secondary forest and mature forest are consistent with patterns in many other systems (Koivula et al., 2002; Baker, 2006). However, for predators, trait composition did not change significantly beyond ~27 year old secondary forest communities (Figure 4.2). Thus, predator trait recovery precedes

species composition recovery in this system. It was also notable that traits and species recovered after logging to levels comparable with mature forest much more quickly for predators than for decomposer/primary consumers. This may relate to traits associated with relatively high mobility for predators, especially considering that we sampled within 200 m of nearby mature forest. For predators, canopy cover may be a more important environmental filter than successional stage, as canopy cover greatly increases in ~27 year old sites and is maintained in the latter stages (Fountain-Jones et al., in press (b)).

4.5.6 Individual trait relationships as predictors of time since disturbance

Successional relationships for phylogenetically-corrected individual trait values offer further insights into the forces acting on both trophic groups (Figure 4.3), and allow us to predict how relative trait states change as forest succession proceeds (Figure 4.4). As in similar studies, individual trait values responded strongly to succession (Ribera et al., 2001; Moretti & Legg, 2009; Vandewalle et al., 2010), but our study is the first to show that the response varies with trophic position. Traits from carabids (mostly predators) can predict time since disturbance over broad spatial scales (Ribera et al., 2001; Vandewalle et al., 2010), but our study found no trait responses to fine-scale environmental changes in predatory beetles. In other systems, predatory species (and decomposers/primary consumers) of recently disturbed habitat had larger eyes (Ribera et al., 2001) and had a greater proportion of winged species than beetles of undisturbed habitat (Ribera et al., 2001; Vandewalle et al., 2010; Pakeman & Stockan, 2014). Predator antennae length has also been shown not to respond to succession (Ribera et al., 2001). However, other predator traits such as leg length have been shown to significantly increase in older successional stages (Ribera et al., 2001; Vandewalle et al., 2010), yet this was a only weak trend in our study (Figure 4.3). This may be explained by the wider variety of predators (e.g. the staphylinids) included in our analysis, or possibly that our gradient was not as severe, as our youngest sites had not been disturbed for ~7 years.

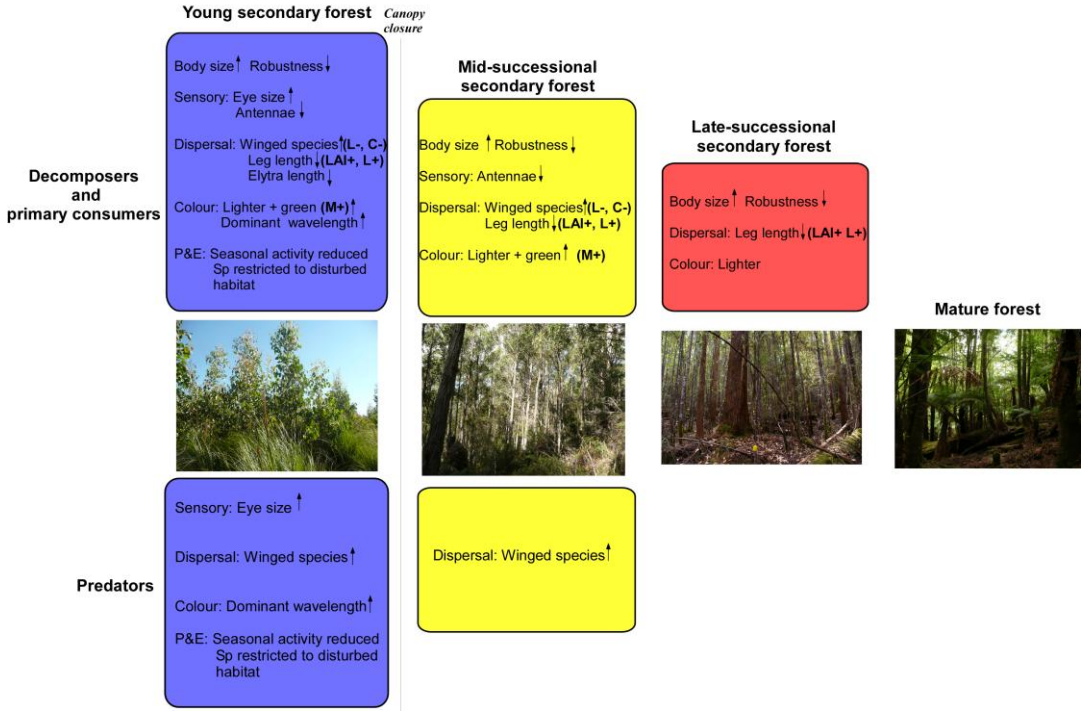

Figure 4.4. Predictive framework based on our data for species traits across four forest successional stages for both decomposers/primary consumers and predators. Arrows indicate direction of the trend in relation to mature forest trait values. Environmental variables (besides succession) are shown that that have significant positive (+) or negative (-) relationships with particular traits; generated from Fig.4.3. L: Litter depth, LAI: Leaf Area Index, C: Soil Carbon, M: Moss cover, P&E: Phenology and ecological performance traits. The size of the coloured boxes is relative to overall trait compositional differences.

In comparison, decomposers/primary consumer traits were much more sensitive to succession than predators. Thus, members of this trophic group showed a significant successional transition from a trait associated with flying (presence of wings) to a trait associated with walking (longer leg length), as has also been reported for flightless predatory carabids at broader scales (Ribera et al., 2001; Vandewalle et al., 2010). The colour shifts we detected, with paler beetles in younger forest and darker beetles in mature forest, is likely to relate to canopy closure and the darker habitat conditions in older forests (Ribera et al., 2001; Vandewalle et al., 2010). The colour shift from red to green with succession for decomposers/primary consumers has never previously been demonstrated, and we hypothesise that differences in crypsis

are responsible. Older successional forest litter has a higher red/blue ratio compared to young forest litter (N. Fountain-Jones, unpublished data). Colour traits have clear functional importance and could help explain beetle preference for particular habitat conditions.

Studies assessing animal responses to disturbance have typically combined trophic groups. However, it is clear from our results that trophic groups have differential responses to disturbance. Therefore, just assessing predator trait responses, for example just carabids (Ribera et al., 2001; Gerisch et al., 2011), is an inadequate surrogate for other trophic groups.

4.6 Implications and Conclusions

This study demonstrates the utility of functional traits, phylogeny and environmental variables to understand community assembly. A key observation was that trait composition of predator communities had largely recovered ~27 years post-logging but decomposer/primary consumers had not recovered by ~45 years, even though there was near complete recovery of phylogenetic composition of both trophic groups at this time. This demonstrates that recovery of phylogenetic composition with succession does not necessarily translate to the functional characteristics of the species. This relationship is a topic worthy of future research. Furthermore, changes in species composition relate, to an extent, to changes in phylogenetic composition, with some beetle families having preferences for older or younger forests while others are common in both, but with different species present in each. We also show that the functional characteristics of beetles have a significant component that is independent of phylogeny. Our study demonstrates the value of maintaining a variety of forest successional stages, not only to ensure habitat availability for the full range of native species, but also for conservation of functional characteristics that they provide. An important caveat on our results is that only relatively common species were analysed, so the pattern may have been different if rare species were included.

We also characterised successional functional trait syndromes for predators and decomposer/primary consumer species independent of phylogeny in different successional stages (Fig. 4.4). This could provide the basis for similar predictive frameworks for trait responses during succession in other systems. However, trait responses from one trophic group cannot be considered analogous to another, even within the same taxon and traits. This study not only increases our understanding of community assembly, but provides a foundation for developing an effective bio-monitoring model using beetle traits.

This study provides novel insights into the differential effects of environment and phylogeny on two trophic groups from Earth's most hyper-diverse invertebrate clade. Evolutionary history constrains predator metacommunity assembly in particular; yet phylogenetic niche conservatism was unlikely to be acting. Environmental filtering was the key assembly process for both trophic groups, yet this study demonstrates that the environment can shape trophic groups within the same lineage in contrasting ways.

Acknowledgements

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Chapter 5

Environment, evolution or biotic interactions? Beetle metacommunity responses to leaf litter and shade

This chapter is currently submitted to *Animal Ecology*.

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5.1 Summary

To disentagle mechanisms of recolonisation of secondary forest by beetles we experimentally tested the effects of litter addition and shade modification on beetle community composition and assembly processes.We used a replicated randomised block design with four litter treatments (control, artificial plastic litter, mixed and wet sclerophyll forest litter) and two shade treatments (shaded and unshaded). Using datasets of abundance, functional trait and phylogenetic data for the 31 most common beetle species observed in our experiment, we assessed species abundance, and composition. Furthermore, we integrated recently developed metatacommunity analyses coupling functional and phylogenetic approaches to examine the roles of niche (environmental filtering and biotic interactions) and neutral processes in community assembly.

Litter addition and shade modification greatly altered species abundance, diversity and composition; and facilitated colonisation by species indicative of older successional forest. Litter and shade also changed the community assembly patterns, phylogenetic structure and shifted community trait values. Environmental filtering processes operated on shaded and litter plots, whereas biotic interactions were more important for open unshaded plots.

Our study is the first to explicitly demonstrate that habitat manipulation affects animal community assembly processes. Niche processes were more important than neutral processes and we hypothesise that increased habitat heterogeneity under litter treatments caused finer niche partitioning and coexistence of functionally similar species. Adding litter and shade altered beetle abundance and species composition but also shifted the forces driving community assembly from biotic to environmental. Experimental manipulation combined with analysis of phylogeny and functional traits illuminated the complex mechanisms underlying species recolonisation in ways impossible with traditional observational studies of species patterning.

5.2 Introduction

How environmental and historical forces impact community assembly is a central question in community ecology. Niche-based models assume that community patterns are strictly related to underlying variability in ecological parameters such as habitat (environment) and competition (biotic) (Thompson & Townsend, 2006). Neutral theory, in contrast, argues that much of community assembly can be explained by differences in dispersal and evolutionary factors without needing to invoke niche differentiation (Hubbell, 2001). It is now widely considered that both niche differentiation and neutral processes are important for community assembly (Thompson & Townsend, 2006; Kitching, 2013). Furthermore, the relative contributions of biotic interactions and abiotic effects on community assembly remain unclear. Experiments manipulating habitat variables and analysing recolonisation can test which of these sets of assembly processes best explains real systems. However, studies analysing the forces behind terrestrial invertebrate assembly are rare (Kitching, 2013). Beetle communities are hyper-diverse, functionally rich, and sensitive to fine-scale processes, making them an ideal study model for testing the impacts of habitat modification on community assembly.

Observational studies and manipulative experiments show that leaf litter and shade are key factors affecting beetle community composition and abundance (e.g. Koivula et al., 1999; Mazía et al., 2006; Nakamura et al., 2009; Fountain-Jones et al., in press (b)). Leaf litter addition increases habitat complexity and alters microclimate (Koivula et al., 1999; Sayer, 2006) in ways that may allow species adapted to mature forest to recolonise disturbed habitat (Nakamura et al., 2009). litter and shade have varied impacts on arthropod abundance and community composition in a variety of systems across the world. For example, effects of leaf litter addition in coniferous forests have varied from minor impacts on a few ground beetle (family: Carabidae) species (Koivula et al., 1999), to substantial increases in diversity of both forest generalists and specialists (Magura et al., 2005). Different types of leaf litter can be distinct structurally and chemically (Barbour et al., 2009), however, it is not known to what extent these changes in diversity and compostion can be attributed to litter

structure or to the food sources litter provides beetles. To our knowledge the impact of these differences on beetle communities has not been experimentally tested in terrestrial systems.

Understanding the role of leaf litter and shade in structuring invertebrate communities has broad conservation relevance. Anthropogenic landscape modification has resulted in boundaries between forest types and successional stages becoming increasingly common (e.g. Ewers & Didham, 2008). Nearby undisturbed habitat potentially acts as primary sources for plants and animals to re-colonise disturbed areas, and therefore is fundamental for ecological viability of forest landscapes (Baker et al., 2013a). Adjacent mature forest contribute both shade (Baker et al., 2014) and leaf litter to secondary forest, both of which are important for beetle distribution (Fountain-Jones et al., in press (b)).

Functional trait patterns can reveal the relative importance of niche-based processes, such as environmental filtering and biotic interactions, versus neutral processes, on community assembly along an environmental gradient. Environmental filtering is likely when the change in communities resulting from shifts in environment lead to similar functional trait values— 'trait convergence assembly patterns' (Pillar et al., 2009). Biotic interactions are important for assembly processes when community traits are also linked with environment, but trait values are divergent— 'trait divergence assembly patterns' (Pillar et al., 2009b). Divergent traits are considered a response to biotic forces, as species with similar traits are more likely to compete for niche space — 'limiting similarity' (e.g. Diamond, 1975). A lack of association between traits and environment can indicate that neutral processes dominate community assembly (Hubbell, 2001).

Understanding the interplay between species, functional traits and environment within an evolutionary context is also important in understanding community assembly patterns. Trait variation includes both phylogenetic and environmental effects. Trait values can be phylogenetically conserved, as closely related species can have more similar phenotypes than distantly related species. This phylogenetic signal

(Blomberg et al., 2003) can be identified at both species and metacommunity levels (Pillar & Duarte, 2010). At a species level, phylogenetic signal can be used to assess the strength of evolutionary pressure on traits (e.g. Blomberg et al., 2003; Pavoine et al., 2013). At a metacommunity level, phylogenetic signal identifies communities that have more similar levels of trait convergence or divergence than expected by chance (i.e. a null model) (Pillar & Duarte, 2010). Metacommunities can also be phylogenetically structured; for example, we found some beetle clades were only present in recently disturbed habitats and were filtered out as succession proceeds (Chapter 4).

This project uses an experimental approach to test the effects of litter type and shade on beetle communities using a combination of species, phylogenetic and functional trait approaches. Specifically, we tested three linked hypothesis: (Ia) Total beetle abundance increases and species composition becomes more similar to mature forest with shading and litter addition. (Ib) Artificial plastic litter (structure without chemistry) changes species abundance and composition compared to control plots (II) Environmental filtering is the dominant metacommunity assembly pattern across both litter and shade treatments. (III) Overall trait values in mixed forest litter and shade experimental treatments are comparable to undisturbed mature forest.

5.3 Materials and methods

5.3.1 Study design and beetle collection

This study was conducted in 2012-2013 in wet forest in southern Tasmania that had been clearcut, burnt and sown with eucalypt seed (see Hickey & Wilkinson, 1999 for more details) in 2011. The clearcut site was surrounded by mature wet forest dominated by tall eucalypts. This mature forest comprised two general types; mixed forest, an older successional forest stage in which the eucalypts overtop a rainforest sub-canopy, and wet sclerophyll forest, a mid-successional forest type with a sub-canopy of broad-leaved, disturbance-dependent species. In the short term, clearcutting dramatically increases light intensity and the regeneration burn removes leaf litter (Neyland & Jarman, 2008). Within the harvested area, eight treatments

were employed to experimentally test the effects of shade and leaf litter on beetle community assemblage.

In total, 80 1 m×1 m plots were established in a strip approximately 40 m - 55 m from a mature forest edge (see Fig. 5.1). The experiment used a factorial design, with four litter treatments by two shade treatments (shade or non-shade) arrayed in a randomised design.

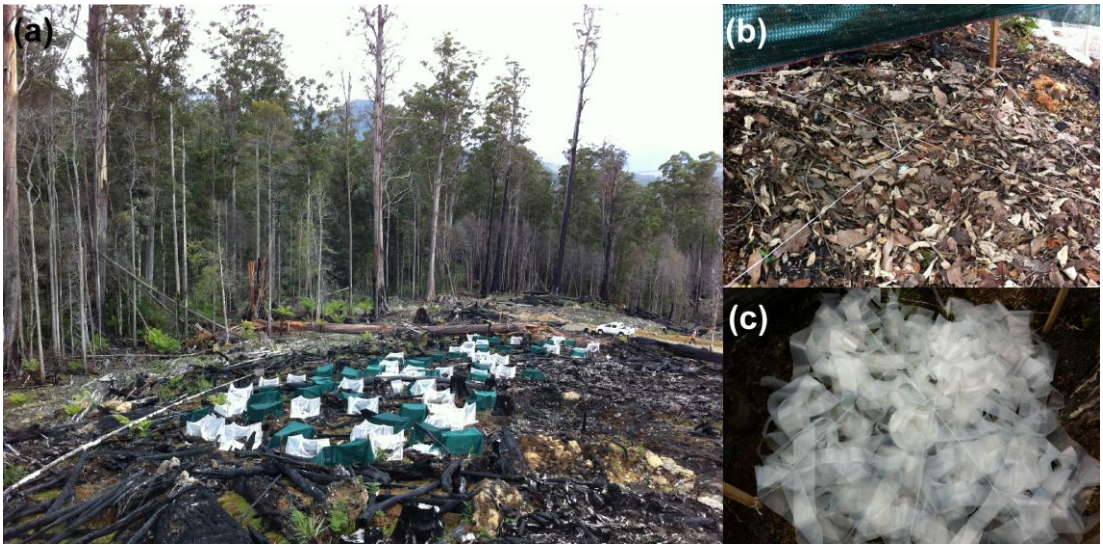

Fig. 5.1. Photos illustrating plot layout and design. (a): Overall plot set up, (b): Wet sclerophyll litter treatment, (c): Plastic litter treatment.

The four litter treatments were selected to compare the effects of two major litter types (wet sclerophyll and mixed forest litter – representing different plant communities and different leaf chemistry), raw litter structure (plastic 'litter') and a control (no litter). Wet sclerophyll and mixed forest litter were collected from nearby unlogged sites. Plastic litter was generated by cutting industrial grade ethylene film into narrow irregular strips to mimic litter structure but without directly providing food resources. To ensure that insects were not brought in with leaf litter, the wet sclerophyll and mixed forest litter was sterilized using methyl bromide fumigation, which eradicates protozoa, nematodes and insects (Thomas, 1996). The litter was fumigated in a closed chamber at 21°C for 8 h at a concentration of 32g m^{-3}. The artificial and natural litter was then laid out in the plots to create a layer

approximately 40 mm deep and was replaced to mimic fresh litter fall halfway through the experiment.

Wooden pegs were placed in each of the four plot corners. These were 1 m high, and supported either 70% ultra violet blocking shade cloth (shade treatment) or bird mesh (open treatment) covers. These extended across the top and down the sides to exclude browsing mammals and to ensure shading at any sun angle (Fig. 5.1). Bird netting extended all the way to ground level while shade cloth extended to approximately 30 cm above ground and a band of bird netting was placed at ground level below this to prevent litter being blown away. A single pitfall trap was placed in the centre of each treated area. Traps consisted of 750 mm diameter plastic cups inserted into PVC tubes dug into the soil. Propylene glycol (100%) was used as a preservative in the traps. To protect against rainfall, traps were covered by a plastic lid supported by three sticks. Two autumn pitfall trapping sessions were undertaken – once in March-April 2012, approximately 1 month after creation of the plots, and once in March-April 2013. The pitfall traps were collected after 30 trapping days and specimens were immediately transferred to 96% ethanol and sorted to species or morphospecies. Only species collected in at least two traps and with >6 individuals across all plots were used for further analysis.

Functional traits and phylogenetic data

In total, 15 functional traits (11 morphological, one phenological and three ecological performance traits) were measured for each species (Table 5.1). See Fountain-Jones et al. (in press (a)) for trait selection criteria. We focussed on response traits because we were primarily interested in how species responded to habitat manipulation. For each morphological trait, a species average was generated by measuring six individuals of each species. These traits were measured using a calibrated microscope camera or, for colour-related traits, a spectrophotometer. Trophic group was assigned to each species based on published knowledge of subfamily (Lawrence et al., 1999). Seasonal activity for each species was determined based on previous

work (Fountain-Jones et al., in press (b)) and habitat occupation was based on species occurrence from our study.

Table 5.1. Traits of beetles measured in this study.

Trait	Trait type	Functional links	Units	Measurement details
Body Length	M	Fecundity, foraging capability, dispersal	Log(mm)	Total length from anterior of head to posterior of abdomen.
Antennae Length	M	Predator avoidance, habitat preference	Log(mm)	Total length of antennae from base to apex.
Eye size	M	Habitat preference, hunting capability		PCA of eye width and eye length.
Eye Width			Log(mm)	From point closest to dorsal surface of head to point closest to ventral surface of head on eye.
Eye Length			Log(mm)	From point closest to anterior of head to point closest to posterior of head on eye.
Wings	M	Dispersal capability	Binary	Presence or absence
Elytra Length	M	Dispersal, microhabitat use	Log(mm)	Maximum dorsal length of elytra along medial line.
Average leg length & Back leg to front leg ratio	M	Dispersal capability, microhabitat use	Average and ratio	
Front Leg Length			Log(mm)	Maximum length of femur, tibia and tarsi of a front leg.
Back Leg Length			Log(mm)	Maximum length of femur, tibia and tarsi of a back leg.
Robustness	M	Defensive, microhabitat use, dispersal		PCA of head width, pronutum length/width, prothorax depth, abdomen width/length/depth. See Barton et al. (2011).
Head Width			Log(mm)	Maximum dorsal width of head (not including eyes).
Pronotum Width			Log(mm)	Maximum dorsal width of pronutum.
Pronotum Length			Log(mm)	Maximum dorsal length of pronotum along medial line.
Prothorax Depth			Log(mm)	Maximum depth of prothorax.
Abdomen Width			Log(mm)	Maximum dorsal width of abdomen.
Abdomen Length			Log(mm)	Maximum dorsal length of abdomen along medial line.
Abdomen Depth			Log(mm)	Maximum depth of abdomen.
CIE L (lightness)	M	Predator avoidance, thermal maintenance	Co-ord	USB 4000 spectrophotometer.
CIE A (red/green)	M	Predator avoidance	Co-ord	USB 4000 spectrophotometer.
CIE B (blue/yellow)	M	Predator avoidance	Co-ord	USB 4000 spectrophotometer.
Dominant wavelength	M	Camouflage, thermal maintenance	Nm	USB 4000 spectrophotometer.
Seasonal activity	Ph	Thermal tolerance, fecundity	Ratio	
Habitat occupation	E	Resource use, thermal tolerance	Ratio	
Predator guild	E	Resource use	Binary	Derived from the literature (Lawrence et al., 1999).
Decomposer/Primary consumer guilds	E	Resource use	Binary	Derived from the literature (Lawrence et al., 1999).

Bold-highlighted traits were used in the study, others were used to generate a particular trait score. M: Morphological, Ph: Phenological, E: Ecological performance trait. Co-ord: Colour coordinates in CIE colour space.

As the phylogenetic relationships between the species in this study were poorly known, a working molecular phylogeny was developed from one mitochondrial marker (cytochrome oxidase subunit 1) and one ribosomal marker (28 S D3 region). See Appendix D.1.2 for laboratory protocol and phylogenetic method details and Appendix D.2 for the resulting phylogeny.

5.3.2 Statistical approaches

Data from both sampling periods were combined during analysis because the beetle numbers were insufficient to provide a robust comparison from year to year.

We assessed treatment effects on abundance (Hypothesis Ia, b) on the full data set using fully factorial ANOVAs with litter type and shade as factors, followed by Holm-Sidak pair-wise comparisons. To identify treatment effects on metacommunity assembly patterns (Hypothesis II), we adapted the Pillar & Duarte (2010) approach to test for trait convergence, divergence and phylogenetic signal and structure (see Appendix D.1.3 for details). For this approach, we generated trait-weighted and phylogenetically-weighted community distance matrices and community-weighted trait means from community abundance, species trait, phylogenetic distance and environmental datasets. Community abundance data was square root transformed to down-weight abundant species. Morphological traits (excluding colour and body length) were expressed relative to body length and log transformed (Table 5.1). As traits were on different scales, the complete set was standardised prior to analysis. The environment was coded as one of eight combinations of litter and shade for each plot. Mantel and partial Mantel tests were then performed to assess correlations between pairs of matrices, and then permutation tests were conducted against a null model (no convergence, divergence or phylogenetic signal at a metacommunity or species level) to test for each pattern. This analysis was done using the complete dataset and then, as various traits are likely to respond differently to treatments (Pillar et al., 2009b), on two reduced sets of up to five traits that maximised trait convergence and divergence patterns (calculated using an iterative algorithm developed by Pillar & Sosinski (2003)). These analyses were conducted in R (R

Development Core Team, 2013) using package 'SYNCSA' (Debastiani & Pillar, 2012).

PERMANOVA (Anderson, 2001) with post-hoc pair-wise tests and constrained ordination with canonical analysis of principal coordinates (CAP) (Anderson & Willis, 2003) constrained by treatment group were used to assess among-treatment metacommunity responses. Two-way factorial PERMANOVA with litter and shade as fixed factors was conducted on a species abundance Bray-Curtis matrix, trait-weighted and phylogenetically-weighted Euclidean distance matrices using 9999 permutations of residuals under the reduced model.

To assess if beetle trait values in mixed forest leaf litter and under shaded conditions were approaching values found in mature mixed forest (Hypothesis III), we compared community-weighted means from the manipulated plots with values for plots located in undisturbed mature forest in the same region. The mature forest community-weighted means were generated from the same trait set from 30 plots from five sites. These mature mixed forest plots were within 35 m of a ~7 year old secondary forest boundary, and were sampled in autumn (see Fountain-Jones et al. (in press (b)) for site details). Both were analysed using two separate one-way PERMANOVAs testing for the effects of litter and shade respectively using 9999 permutations under the reduced model. CAP ordination constrained by treatment group was used to visualise the patterns, and as a model to test for misclassification error between groups using leave-one-out analysis as a way to help disentangle community assembly patterns between plots (Anderson & Willis, 2003). For example, if a plot type was expressing trait convergence patterns, the plot misclassification rate would be low. Both of these analyses were conducted using PRIMER 6 PERMANOVA+ (Anderson et al., 2008).

As beetle traits have previously been found to have strong but varying phylogenetic signals (Ribera et al., 1999), phylogenetic signal was quantified for each trait using Bloomberg's K (Blomberg et al., 2003), calculated using package 'Picante' in R (Kembel et al., 2010). To control for phylogenetic signal, the trait dataset was

transformed using phylogenetic eigenvector regression (PVR) implemented in the R package 'PVR' (Santos et al., 2014) following the method of Diniz-Filho et al. (2012). The regression residuals account for environment and unexplained variation (Diniz-Filho et al., 2012) and were used to assess individual trait responses

To understand how each treatment affected trait patterns independent of phylogeny, individual trait-treatment relationships were analysed using community-weighted means generated from both phylogenetically-transformed and untransformed trait data. As trophic group (predator and detritivore/primary consumer) was determined from subfamily groupings it was not phylogenetically transformed. As with abundance, treatment effects on individual trait values were tested with factorial two-way ANOVAs. As we performed this procedure for 14 different traits, false discovery rate adjustment was applied to correct overall P-value (Benjamini, 1995).

5.4 Results

5.4.1 Beetle abundance and species composition

We collected 1014 beetles from 89 species from all of the treatments (643 in year 1 and 371 in year 2) (see Appendix D.3 for species abundance data). There was a significant litter effect for average beetle abundance, and pair-wise tests revealed that mixed and wet sclerophyll plots had significantly more beetles than control plots but not plastic litter plots (Fig. 5.2). Plastic litter had higher numbers of beetles than control plots, but this difference was just insignificant (P=0.061) after Holm-Sidak adjustment. Restricting the data to species with >6 individuals and which occurred in more than two plots reduced this data set to 510 beetles from 31 species. Species composition had a significant litter by shade interaction (Fig. 5.3(a)), with mixed forest litter metacommunity being significantly different from those of all other treatments only under shade (Table 5.2). Also, under both shade and no-shade treatments, control plot metacommunities were significantly different in species composition from those of wet sclerophyll and mixed litter metacommunities. Wet

sclerophyll litter species composition was different to plastic litter for open plots but not under shaded plots (Table 5.2).

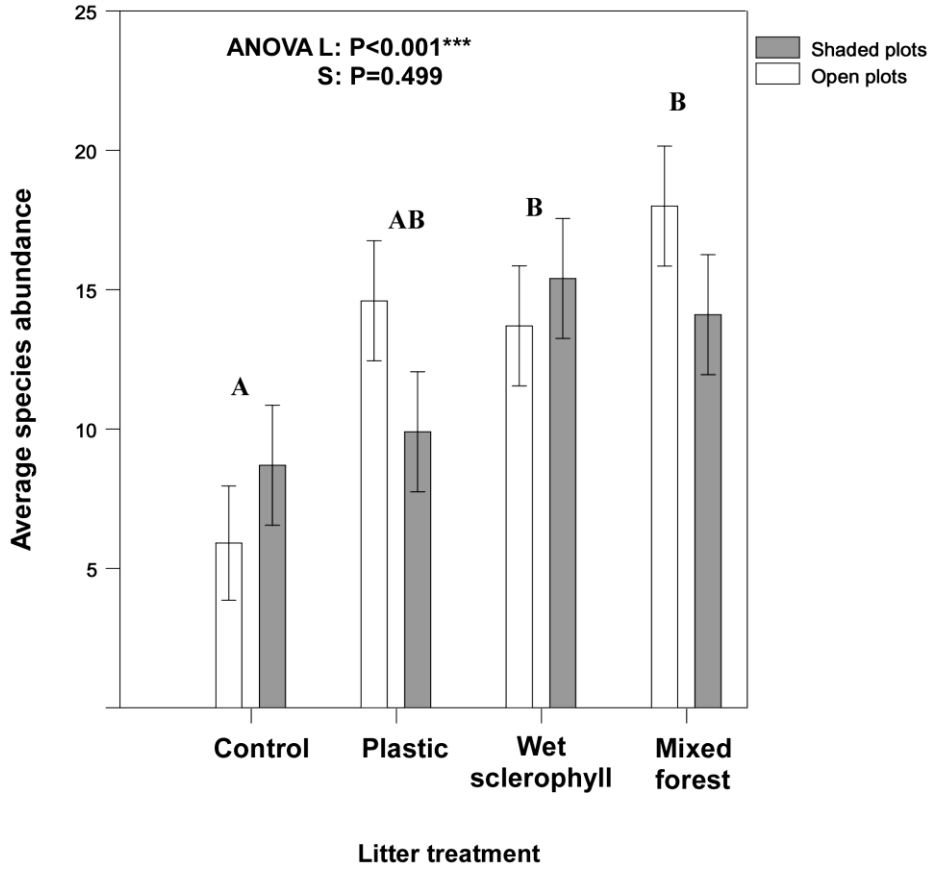

Fig.5.2. Bar graph of average beetle abundance across treatment types. L: Litter effect, S: Shade effect. There was no significant interaction effect. Letters indicate significant groupings according to Holm-Sidak pair-wise tests. ******* P < 0.001.

5.4.2 Trait convergence, divergence snd phylogenetic signal

Both trait convergence and trait divergence across the treatment gradient were found for sets of traits selected to optimise these two assembly patterns (Hypothesis II), but not for the complete dataset (Table 5.3). Thus, significant convergence patterns (environmental filtering) were present both with and without filtering-out phylogenetic effects for the optimal convergent trait subset, comprising of robustness, wings, and average leg, body and elytra lengths. Significant trait divergence occurred for the trait subset consisting of wings, body length, antennae length, CIE A (red-green spectra) and seasonal activity.

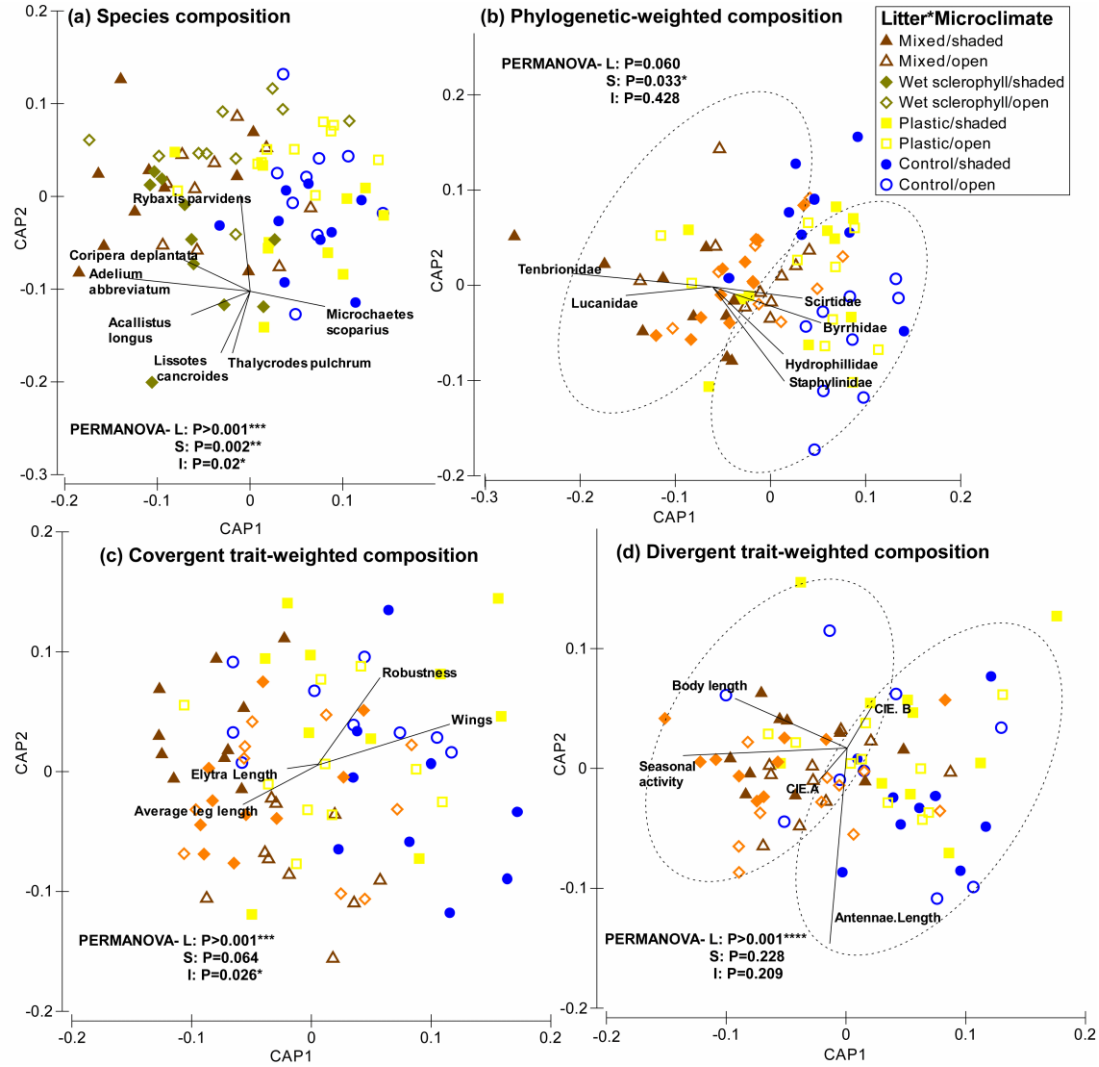

Fig. 5.3 Canonical analysis of principal coordinate (CAP) ordinations of species composition, phylogenetic-weighted and trait-weighted (both convergent and divergent traits) species composition responses to shade and leaf litter treatments constrained by treatment group. L: Litter treatment, S: Shade, I: Interaction L×S. Where there was not a significant interaction effect, dotted circles indicate groupings indicated by PERMANOVA pair-wise tests. See Table 4 for PERMANOVA pair-wise results for (a, c). Vectors show how individual species, traits and clades drive each respective pattern. *P < 0.05, **P < 0.01, ***P < 0.001.

Table 5.2. PERMANOVA interaction table for pair-wise comparison P-values for each litter type and shade treatment combination for species composition and convergent trait-weighted species composition (italics in brackets).

	Microclimate	
Litter treatment	***Open***	***Shaded***
Control/Plastic	0.104 *[0.161]*	0.529 *[0.134]*
Control/Wet sclerophyll	**0.001**** *[0.082]*	**0.011*** ***[0.001**]***
Control/Mixed forest	**<0.001***** ***[0.017*]***	**<0.001***** ***[0.006**]***
Plastic/Wet sclerophyll	0.16 *[0.664]*	**0.023*** *[0.022*]*
Plastic/Mixed forest	**0.037*** *[0.077]*	**0.002**** ***[0.026*]***
Wet sclerophyll/Mixed forest	0.283 *[0.191]*	**0.036*** *[0.189]*

*Key: *P < 0.05, **P < 0.01, ***P < 0.001. Significant pair-wise differences are in bold.*

Trait- and phylogenetic-weighted species composition demonstrated variable responses to litter and shade treatments. Phylogenetic-weighted species composition had a significant shade but non-significant litter effect, with the CAP 1 axis separating open from shaded plots (Fig. 5.3(b)). Convergent and divergent trait-weighted species composition gave contrasting results. Convergent traits showed a similar pattern to species composition with significant interaction between litter and shade (Fig. 5.3(c)). Analogous to species composition, plastic and control plots were not distinct in either shade or unshaded treatments (Table 5.2); yet unlike with species composition, wet sclerophyll trait-weighted composition was not significantly different to plastic in open plots only (Table 5.2). In contrast, there was a litter effect but no shade effect for divergent trait-weighted species composition. This trait set was convergent in metacommunities in mixed forest/wet sclerophyll and in shaded control/plastic plots but was divergent in open control and plastic. In the CAP model (Fig. 5.3(d)), mixed forest/shade, control/open and plastic/open treatments plots were allocated less than 12.5% to the correct treatment (out of eight possible treatments) using leave-one-out analysis. All other treatments were allocated correctly between 40-60% of this time, indicating that even divergence optimised

traits were still convergent in the majority of treatments. Mixed forest/shade plots were mis-allocated to mixed forest/open and wet sclerophyll/open or shaded treatments 60% of the time, whereas control and plastic plots were misallocated evenly across treatments and were not clustered at all, therefore indicating biotic interactions may be more important in these metacommunities.

Table 5.3. Trait convergence, divergence and phylogenetic signal and structure across the litter and shade gradients.

	All traits	*Optimal for convergence°*	*Optimal for divergence°°*
Environmental filtering (TE)	0.16	**0.21****	0.14
Trait divergence (XE.T)	0.14	0.004	**0.18****
Phylogenetic signal (species pool, PSS) (PdTd)	**0.18***	-0.05	0.15
Phylogenetic signal (metacommunity, PSM) (PT)	0.24	0.02	0.12
Phylogenetic structure(PE)	0.07	0.07	0.07
Successional filtering (removing phylogeny) (TE.P)	0.12	**0.20****	0.12

°*Trait subset: Robustness, average leg length, elytra length, body length and wings.*
°°*Trait subset: Seasonal activity, body length, wings, antennae length and CIE A.*
*, *P < 0.05, **P < 0.01, ***P < 0.001.*

There was no significant phylogenetic signal at a metacommunity level or phylogenetic structure associated with the treatment gradient (Table 5.3). Significant phylogenetic signal at a species level was found in the complete dataset, but not for either optimised trait set. Blomberg's K also showed similar results with an average of 0.643 for convergent traits and 0.472 for divergent traits, yet phylogenetic signal varied between traits (see Appendix D.4, Table D.4).

Wings, average leg length, antennae length and predator mean abundance all had significant but variable treatment effects after adjustment for false discovery rate (Fig. 5.4 (a-d)). Wings and antennae length both responded to leaf litter manipulation, with longer antennae length and increased number of winged individuals in control and plastic plots compared to wet sclerophyll and mixed forest litter plots (Fig. 5.4 (a, c)). Even though the interaction effect was non-significant, wet sclerophyll communities' wings and mixed forest litter antennae length differed with shade treatment. Average leg length and the number of predators only

responded to shade, with both being greater in open plots than in shaded plots (Fig. 5.4 (b, d)). However, even though the interaction effect was non-significant, average leg length was similar in shaded and open mixed forest litter plots. The number of predators in control plots was similar in both shade and unshaded treatments. See Appendix D.4 for all phylogenetically unadjusted individual trait comparisons.

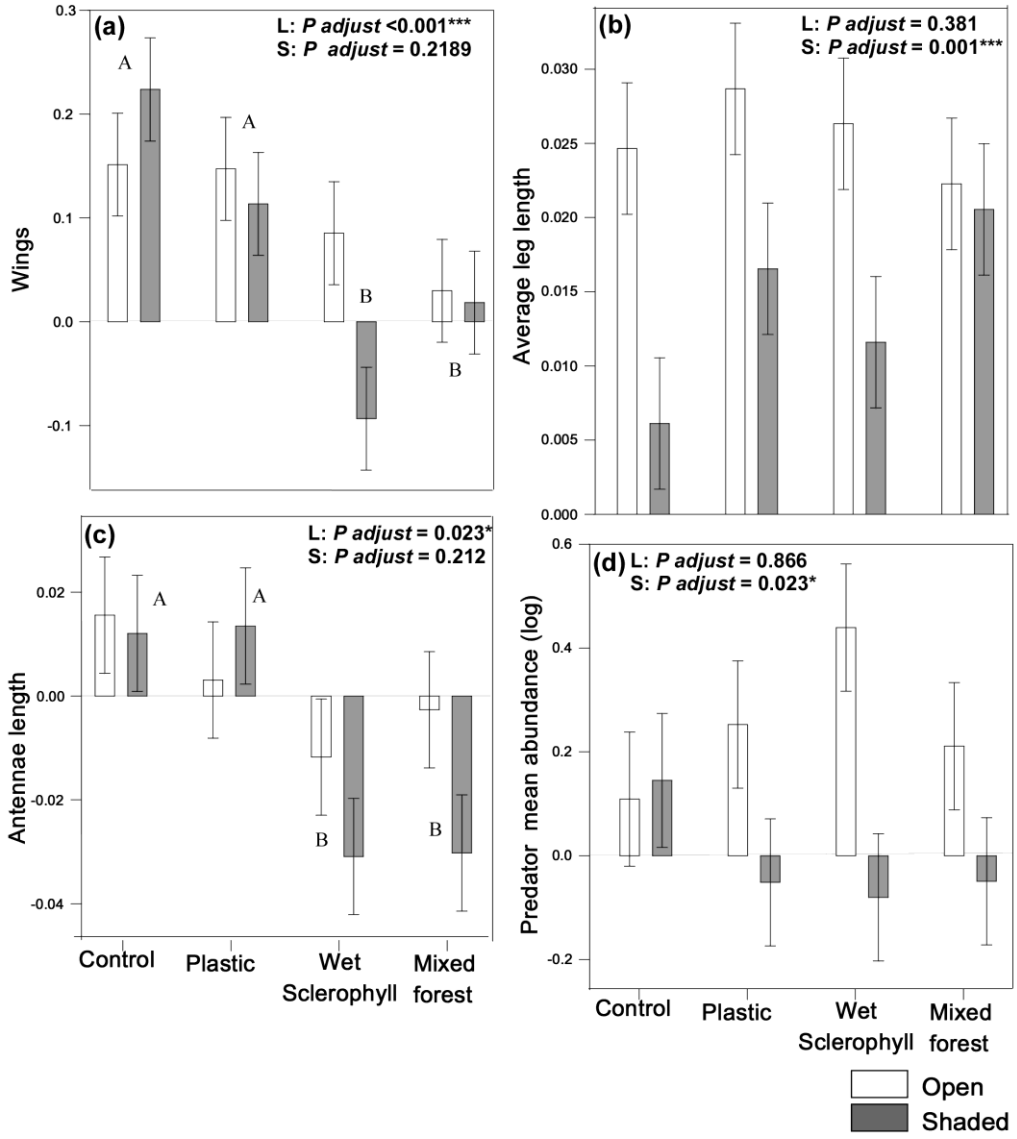

Fig. 5.4. Phylogenetically-adjusted individual abundance-weighted traits with significant treatment effects after the P-value adjustment for false discovery rates. (a): winged species, (b): average leg length, (c): antennae length, (d): predator mean abundance (log transformed). With the exception of predators, the Y-axis scale is adjusted to control for phylogenetic autocorrelation. Letters indicate significant groupings according to Holm-Sidak pair-wise tests. L: Litter treatment, S: Shaded. There were no significant interaction effects for these traits. *P < 0.05, **P < 0.01, ***P < 0.001.

5.4.3 Species and trait recovery

Species considered as mature forest indicators in Tasmanian wet forest (see Baker et al., 2007), such as *Decilaus lateralis* (Curculionidae), were only found in either wet sclerophyll or mixed forest litter. *Adelium abbreviatum* (Tenebrionidae), *Acallistus*

longus (Carabidae) and *Thalycrodes pulchrum* (Nitidulidae) are indicators of ~45 year old secondary forest (Fountain-Jones et al., in press (b)) and were common in all treatments except the control. Several young forest indicators, such as *Scopodes sigillatus* (Carabidae) occurred throughout the treatments, but others, such as *Microchaetes scoparius* (Byrrhidae) were only found in either control or plastic litter treatments (see Appendix D.3 for species abundance data). The species *M. scoparius*, *A longus, A. abbreviatum* and *T. pulchrum* were also important in the compositional response to the treatments (Fig. 5.3(a)).

Overall trait space showed that habitat manipulation led to trait community-weighted means recovering to values similar to undisturbed mature forest (Fig. 5.5). Metacommunity trait community-weighted means in mixed forest and wet sclerophyll litter treatments were not significantly different from values in mature forest, whereas plastic and control plots were distinct and grouped together on the CAP 1 axis (Fig. 5.5 (a)). Control and plastic plots tended to have more winged species and species with a smaller back leg to front leg ratio. CAP 2 distinguished mature forest from mixed forest/wet sclerophyll metacommunities, with mature forest having species with longer average antennae length and darker colours (smaller CIE L values), but shorter leg length. Metacommunity traits in shaded plots were also similar to mature forest plot values, but open plots were significantly different from mature forest. Average leg length and the predator trophic group helped distinguish open plots on the CAP 2 axis (Fig. 5.5 (b)) and antennae length and back to front leg length ratios also distinguished the mature forest plots on the CAP 1 axis.

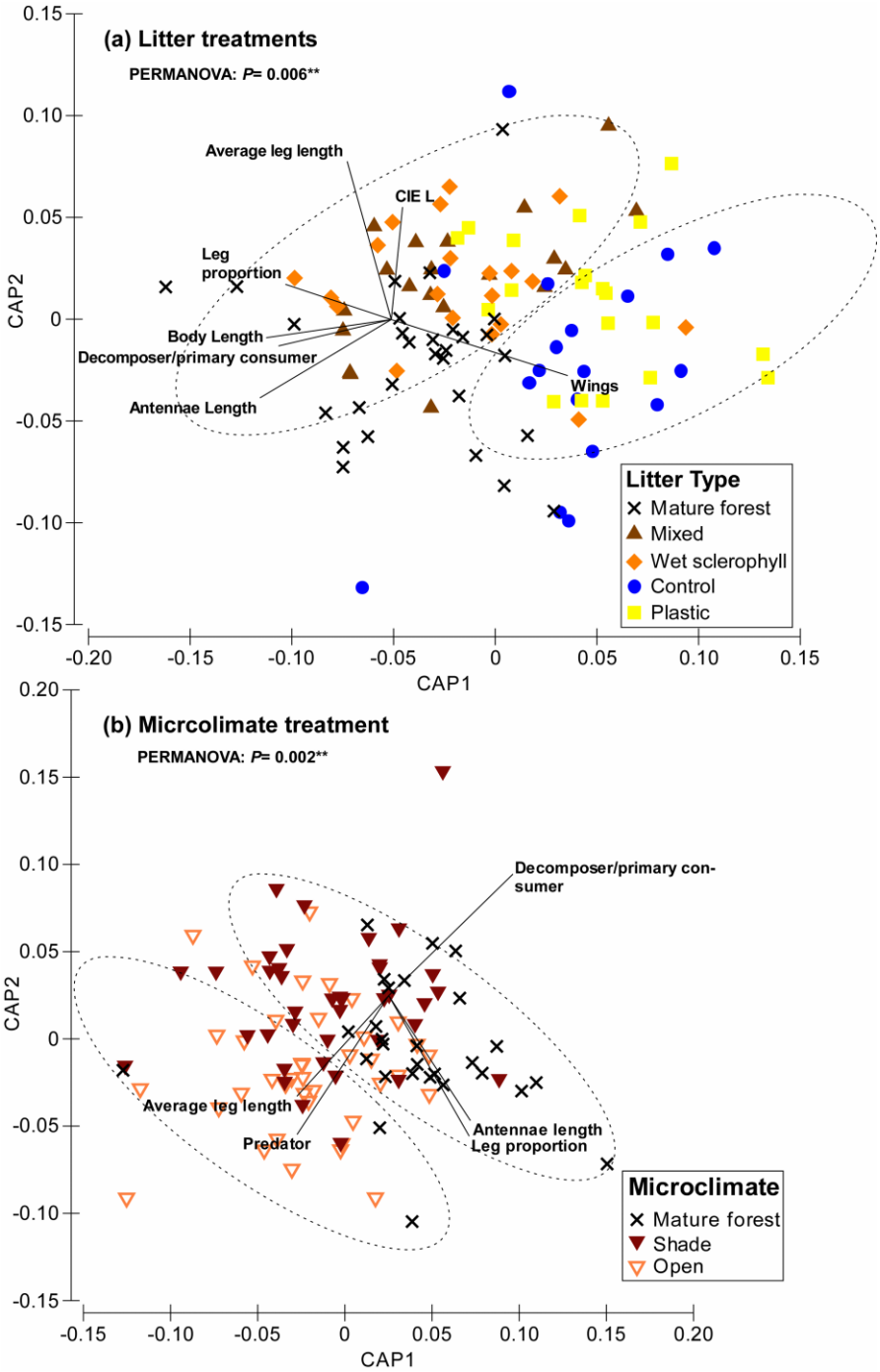

Fig. 5. 5. Canonical analysis of principal co-ordinates (CAP) ordinations of trait community-weighted means; (a) constrained by litter type, and (b) constrained by shade. The experimental litter/shade habitats are compared to plots from nearby undisturbed mature forest. One-way PERMANOVA results test for shade and litter treatment effects. Dotted circles represent grouping detected by PERMANOVA pair-wise tests. Vectors indicate which traits drive the groupings.
**P < 0.01

5.5 Discussion

This is one of the first studies to directly investigate the effects of habitat manipulation on community assembly using a combined functional and phylogenetic approach and the first using beetles. Litter addition and shade not only increased beetle abundance and altered species composition; it also changed the underlying community assembly pattern. Furthermore, adding either wet sclerophyll or mixed forest litter and shade increased the speed of succession, as it allowed species associated with later successional stages of native forest to recolonise and for trait values to be comparable to communities from mature forest.

Our findings partially supported our first hypothesis, but contrast with those of other leaf litter addition experiments in boreal forest (Koivula et al., 1999; Magura et al., 2003), where leaf litter addition did not affect beetle abundance or species composition. Leaf litter addition typically increases habitat complexity (Koivula et al., 1999), which is often associated with greater beetle abundance (e.g. Lassau et al., 2005). In our study, adding just plastic litter (i.e. increasing structural complexity without adding food sources) increased beetle abundance. Adding food resources and increased habitat heterogeneity with natural leaf litter addition caused further increases in beetle abundance. These results show that leaf litter has both structural and non-structural impacts on beetle communities. Even though abundance did not differ significantly between wet sclerophyll and mixed forest litter plots, these two types had different beetle community composition in the shade treatments (Table 5.2), which suggests an effect of leaf litter chemistry. Contrary to the hypothesis, the effect of shade on beetle abundance in our study was not significant. In contrast, other studies found the effects of litter addition were trivial compared to those of shade; e.g. beetles in arid areas (Mazía et al., 2006) and arthropods in the tropics (Nakamura et al., 2009). Shading may be relatively more important under the harsher humidity gradients experienced in arid and tropical systems.

As found for tropical and arid beetle communities (Mazía et al., 2006; Nakamura et al., 2009), shading affected species composition in our study by causing turnover to

species adapted to older successional stages. This turnover was augmented by changes to litter type. Species composition was altered significantly between mixed and wet sclerophyll forest litter when coupled with shade, as these treatments more closely reflected undisturbed wet sclerophyll and mixed forest conditions, allowing specialist species to recolonise. Specialist species were also responsible for compositional change in response to litter addition in boreal forest (Magura et al., 2003). Plastic litter, whilst having similar beetle abundance to both mixed forest litter and wet sclerophyll in both shade treatments, was only similar in terms of species composition to open/wet sclerophyll plots. Specialist species in these communities are therefore likely to require more than structure alone for colonisation to occur.

5.5.1 Environmental filtering and biotic interactions both affect assembly patterns and individual traits

Niche-based processes were important in explaining beetle community assembly response to habitat manipulation. Dispersal limitation was likely to play some role, yet in contradiction to neutral theory, species recolonising plots were clearly not ecological equivalents and community assembly was not random. Of the niche processes, contrary to our expectations, both environmental filtering (trait convergence) and biotic interactions (trait divergence) were both important for beetle community assembly patterns across treatments (Hypothesis II). Environmental filtering may be the dominant assembly factor in leaf litter/shaded plots via increased habitat heterogeneity, possibly allowing finer niche partitioning for the coexistance of functionally similar species. In particular, the convergent traits (robustness, elytra length, wings, body length and leg length) were directly or indirectly related to locomotion and protection. This is logically linked to habitat complexity, because different defensive and locomotory strategies can be favoured in habitats of different complexity, e.g. moving through leaf litter may require longer legs than moving in open spaces (Barton et al., 2011).

As predicted (Hypothesis II), shade and litter treatments induced distinct compositional responses (Fig. 5.3). Not only did leaf litter alter species composition,

it also altered convergent trait-weighted species composition in a similar way. Increased numbers of winged species in control/plastic plots helped formulate the trait compositional patterns and a higher proportion of wing presence has been shown to be a characteristic of young successional forest where high mobility is beneficial to take advantage of temporally-restricted habitat (Southwood, 1977; Ribera et al., 2001). Similar wing presence in plastic litter compared to control suggests that litter structure alone does not restrict winged species, and it is possible that flightless beetles adapted to living in natural leaf litter may out-compete winged species. This may be linked to elytra length, as there a trend for longer elytra in natural litter plots (see Appendix D.4). Longer elytra provide increased protection to move through dense habitats at the cost of aerodynamic efficiency (Johansson et al., 2012). Beetle dispersal strategy shifted to increased leg length in mixed forest litter plots in particular, though this appears to be related to phylogenetic signal, as controlling for phylogeny removed the effect. Beetle leg length was greater in the open plots compared to shaded plots, possibly because faster walking speeds provided by longer legs (Krasnov et al., 1996) may enhance predator avoidance, which is beneficial in open habitats (e.g. Barton et al., 2011). Robustness also drove compositional changes, with increased robustness possibly a response to less cover in control plots, though this pattern was influenced by the highly robust pill beetle *Microchates scoparius* being abundant in open plots.

Biotic interactions maybe more important in open/control and open/plastic plots due to the restricted niche space compared to shaded and natural litter plots, though the mechanisms for animal community trait divergence are poorly known. Another hypothesis is that, as with plants (e.g. Grime, 2006), relatively stable habitat may allow species with different trait values to coexist. For example, open plots in this experiment experienced more extreme microclimate fluctuations (T. Baker, unpublished data) and plastic may lack microclimate buffering qualities analogous to real leaf litter.

The traits showing divergence patterns (seasonal activity, colour traits (CIE A (red/green) and B (blue/yellow)), body and antennae length) are linked to a broader

set of performance currencies. Differences in seasonal activity can facilitate the avoidance of competition (Brooks et al., 2012), making this trait an obvious candidate for divergent assembly patterns. Different beetle body sizes provide access to different resources (e.g. Nichols et al., 2013) and thus competition may alter body size distributions. Divergence in colour traits in this study may be attributed to differences in trophic group, as decomposer/primary consumers and predators have different spectral signals (Chapter 4).

5.5.2 Phylogenetic patterns

There was no phylogenetic signal at species or metacommunity levels for either convergent or divergent traits along the treatment gradient. As beetle predators were found to be more constrained by phylogeny compared to other trophic groups (Chapter 4), combining trophic groups for analysis may have reduced the signal. Nonetheless, even though there was no significant phylogenetic structure overall, shade had a significant effect on phylogenetic composition. As predators in this study were taxonomically restricted to the Staphylinidae and Carabidae families, the overall increase in community-weighted predator abundance in open plots (Fig. 5.4 (d)) was a likely mechanism for this structure. Predatory beetle preference for open plots is perhaps due to increased hunting efficiency in open plots with increased light saturation.

5.5.3 Trait recovery precedes species recovery

The high representation of mid-successional species in natural litter plots (Appendix D.3) supports Hypothesis III, which suggests that a lack of suitable habitat rather than poor dispersal may be the main limiting factor for these species recolonising disturbed habitat. However, dispersal limitation may have been significant for mature forest indicator species, which were collected only in low numbers in the experimental plots and are often flightless (Baker, 2006). Recolonisation by mature forest species may also be constrained by other environmental characteristics such as

soil carbon to nitrogen ratio (Fountain-Jones et al., in press (b)) or lack of suitable (e.g. not recently burned) coarse woody debris (Gibb et al., 2012). Further experimental work is necessary to assess the importance these mechanisms. The species present in shaded wet sclerophyll and mixed forest litter experimental plots were different from undisturbed mature forest, but the community-weighted trait composition was not. Trait recovery therefore appeared to precede species recovery. Therefore, even though mature forest species had not fully recolonised the leaf litter habitat, the litter and shade niche space is constrained by similar evolutionary forces.

5.6 Conclusion

Our results show that increased leaf litter and shading can change beetle recolonising patterns. Adding leaf litter and shade not only altered allowed species associated with older successional stages to recolonise, it also selected for species with traits similar to mature forest habitat. This artificial system has significant similarities to areas of secondary forest close to mature forest edges which can provide both shade and litter. Our data therefore suggests that proximity to mature forest or 'forest influence' (Beese et al., 2003; Baker et al., 2013a) may alter the successional trajectory of secondary forest areas. This study provides a causal mechanism for recolonisation patterns observed in other work (Fountain-Jones et al., in press (b)). Furthermore, litter structure alone did not alter species and trait compostion, although the plastic litter treatment did increase beetle species abundance. Beetle community recovery and succession is limited by habitat suitability and perhaps also by poor dispersal capabilities of some species. One caveat is that we did not consider rare species in this study, and species that are rare can be unique both functionally (Bihn et al., 2010) and phylogenetically (Mi et al., 2012).

More broadly, if biotic interactions are more important in animal community assembly in increasingly unstable habitats, and increased habitat heterogeneity allows functionally similar species to coexist, this may change our understanding of how disturbance affects animal communities. Our study has demonstrated that leaf

litter and shade manipulation not only alters species abundance and composition, it changes the forces that shape community assembly and alters the successional trajectory of beetle metacommunities.

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Chapter 6
General discussion and synthesis

6.1 General discussion

The overall aims of this thesis were to assess whether beetles responded to proximity to nearby mature forest (forest influence), to understand the underlying forces acting on beetle recolonisation and to understand whether these forces were dynamic over forest succession. To do this, I examined beetle community ecology using a traditional species based approach coupled with both functional trait and phylogenetic methodologies; to gain insights into community assembly and the interplay between short term and evolutionary processes. At an applied level, this thesis also provides a new set of tools to understand the impact of disturbance on beetle communities and helps provide justification for forest influence to be incorporated into management planning for fragmented landscapes. This chapter will synthesize these in terms their relevance for forest management, indicator species, and more theoretical aspects of community assembly. Finally, I will suggest some directions for future research.

6.1.1 Implications for forest management

How beetles respond to disturbances such as logging, is complex, but it is clear that maintaining sufficient mature forest embedded within harvested landscapes should be a high priority for forest managers. The fact that forest influences is important for beetles (Chapter 3), silvicultural techniques such as aggregated retention or retention of mature forest adjacent to clearcuts, are not only beneficial for biodiversity in the short term (Beese et al., 2003; Baker et al., 2009b), but are also likely to have mid to long term benefits, particularly for beetles. Mature forest specialists are likely to be able to recolonise successfully from retained stands over time. Aggregates, therefore, can act as population sources for dispersal as well as alter adjacent secondary forest conditions. The changed conditions provide suitable habitat characteristics such as

leaf litter and shade that drive changes in ground active beetle abundance, composition and community assembly and facilitate successional turnover. Chapter 5 proves this point as experimental manipulation of leaf litter and shade does alter community composition and allows species indicative of older forest to recolonise.

If forest influence is incorporated into harvest planning, aggregates are unlikely to be isolated 'life boats' (Rosenvald & Lohmus, 2008) for mature forest species in the mid-term (Fig. 6.1). The current forest influence targets used to design aggregated retention harvests stipulate that 50% of the harvested area must be within one mature tree height from retained mature forest (Beese et al., 2003; Baker & Read, 2011). Even though the estimated depth of forest influence (DFI) was substantially less than one mature forest tree height (~40 m) for ~7 and ~27 year old age classes, the extended DFI of 176 m and the near complete recovery of mature beetle species and function by ~45 years illustrates the complex nature of forest influence, even for a single taxonomic group. However, it is currently not known if long term recolonisation success from aggregates matches the continuous edges used in this study, and this should be assessed in the future.

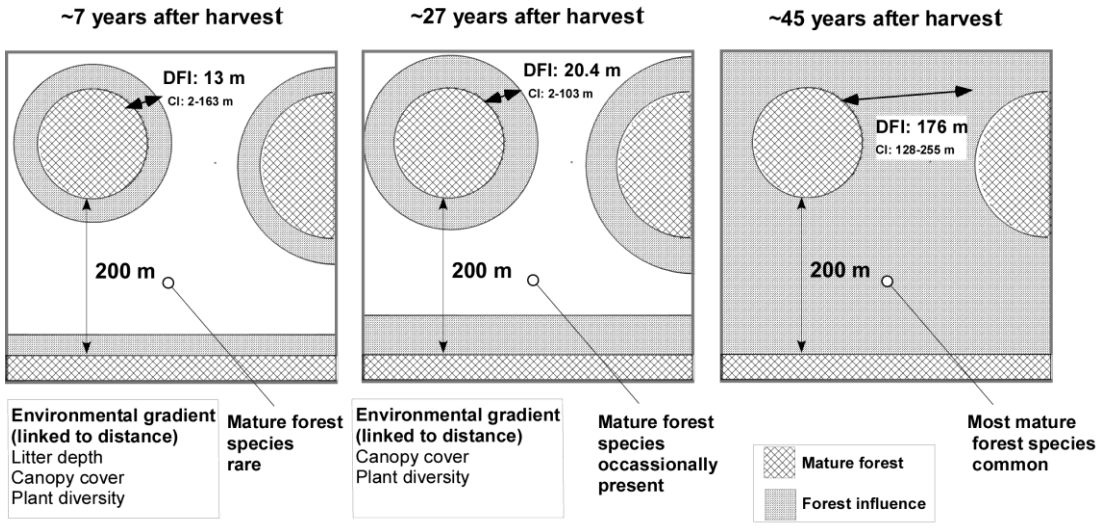

Figure 6.1. How depth of forest influence (DFI) changes over forest succession and how this can help build habitat connectivity in a VR context. Thatched circles indicate retained mature forest aggregates**.** Thatched narrow rectangle represents part of an undisturbed mature forest stand. The DFI and environmental gradient variables associated with distance are from Chapter 3.

With widespread loss of mature forest across the globe, secondary forest has been increasingly recognized to be of conservation value (Chazdon et al., 2009; Melo et al., 2013). Forest influence should be considered when assessing the conservation potential of secondary forests, and forest influence targets into conservation planning may also be useful in fragmented landscapes more broadly. Secondary forests with mature forest boundaries not only harbour a comparable community in terms of species present, but also are similar to mature forest functionally and phylogenetically ~45 years after logging (Fig 6.2). Similar timescales for beetle species recovery after logging has been found in Brazilian Atlantic forest (Hopp et al., 2010) and in boreal forest (e.g. Niemela et al. 1993; Koivula et al. 2002). The functional and phylogenetic dimensions to community recovery, however, have never previously been explored, yet these dimensions can provide additional insights into the recovery of these complex systems.

Beetle community recovery varied with trophic position, with decomposers/ primary consumers slower to recover compared to predatory beetles (Fig. 6.2). After ~45 years, for example, nearly the complete set of predatory carabids was present in secondary forest 200 m away from mature forest. Even though predator species composition had not recovered ~27 years after logging, as in other studies (Niemela et al., 1993; Koivula et al., 2002), predator trait values were already comparable to that of mature forest. Predator phylogenetic composition was even less sensitive to forest succession as it did not vary in any successional stage. For decomposers/primary consumers, only phylogenetic composition was comparable to that of mature forest ~45 years after harvest. Even though predatory species and carabids in particular, have been the focus of bio-monitoring schemes across the world (e.g. Michaels & McQuillan, 1995; Rykken et al., 1997; Vandewalle et al., 2010), in this system predatory species compostion, phylogeny and traits may not be the best surrogate to assess impacts of forest management on beetles.

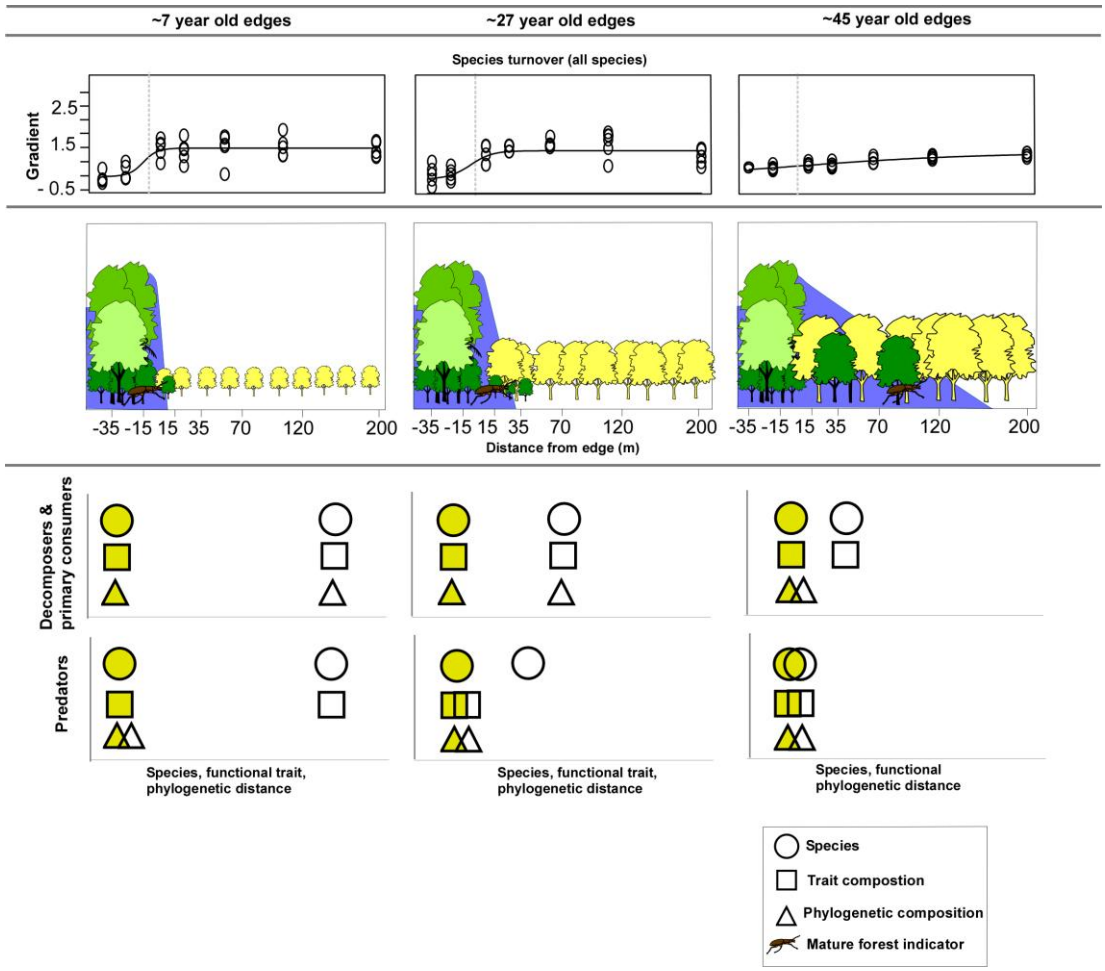

Figure 6.2. Graphic model of how species turnover with distance from mature forest over forest succession and how species, trait and phylogenetic composition changes over forest succession. The coloured circles, squares and triangles represent mature forest compositional values, whilst the open symbols are secondary forest values. The closer each symbol is to each other the more similar the composition is. Symbols overlapping each other reflect that there is no significant difference between the communities.

6.1.2 Indicator species over distance and succession

For forest managers and ecologists, indicator species can provide a useful tool to understand recovery. Undertaking ecologically sensitive logging practices, such as variable retention, are much more laborious and expensive compared to clear cutting (Mitchell & Beese, 2003), so having indicators that these practices are actually having positive biological outcomes is important.

Of the species considered indicators of successional stage and distance from edge (mature forest, near or far) in Chapter 3, only two were carabids (Table 6.1). This further supports the idea that just focussing on carabids as indicators of forest succession of beetles may be undesirable (Baker et al., 2007). Predator species in general, however, are useful as indicators of forest successional stage in Tasmanian wet forest. Of the predators, the Staphylinidae were clearly sensitive to successional stage and distance, but are often overlooked in studies due the difficulty in identification (Thormann et al., 2011). Staphylinds in Tasmania are cryptic, diverse and abundant and thus time consuming to correctly delimit as morphospecies. However, with the decreasing cost of molecular analysis, DNA barcoding (Hebert & Gregory, 2005) may provide a way for ecologists to quickly overcome the taxonomic impediment associated with this taxon. My reference COI barcodes for this taxon will be particularly useful for future taxonomic and ecological work on this important group in Tasmania.

Synthesizing indicator species trophic level and trait values are also informative in understanding the dynamics of succession. Staphylinids were also the only beetle family to have indicator species from both trophic levels (Table 6.1), further demonstrating the importance of the group in Tasmanian wet forest. All of the staphylinid indicator species possessed wings (Table 6.1), so perhaps these species are not dispersal limited but restricted instead by suitable habitat. For predators this sensitivity may be related to prey preference for a particular forest successional stage. Scydmaenin beetles, such as from the genus *Horaemorphus*, are restricted to certain armoured mite species (Molleman & Walter, 2001). Only one predatory indicator species (a carabid) was functionally flightless, whereas this was the case for over half of the decomposers/primary consumer indicators (Table 6.1). As the analysis of overall phylogenetic composition demonstrated (Chapter 4), there is clearly a phylogenetic component with all of the indicator weevil species being flightless along with all species (except *Exeiratus TFIC sp 07*) from the subfamily Cryptorynchinae (Curculionidae). Cryptorynchine weevils are known to be useful mature forest indicators (Baker, 2006), and were also the most important indicators of mature forest and ~45 year old secondary forest in my work. This indicator

species lists builds on the list developed by Baker (2006) who compared mature forest and young forest ~2.5 years post logging. My study provides a useful extension to this previous work as it fills in the indicator species gap in the intermediate successional stages in Tasmania. Coupled with the trait-based monitoring outlined in Chapter 4, this thesis provides valuable tools for forest managers assessing wet forest recovery in Tasmania.

Table 6.1. Indicator species for each distance category and each age.

Species	Family	Wings?	Indicator
Decomposers & primary consumers			
Spaerothorax pubientris	Clambidae	✓	~7 secondary forest (edge avoiding)
Arsipoda variegate	Chrysomelidae	✓	~7 y.o. secondary forest (edge avoiding)
Decilaus nigronotatus	Curculionidae		~45 y.o. secondary forest (edge avoiding)
Decilaus striatus	Curculionidae		Mature forest edge (all ages)
Decilaus TFIC sp 01	Curculionidae		Mature forest edge (all ages)
Decilaus TFIC sp 04	Curculionidae		~27 y.o. secondary forest (edge preference)
Exeiratus TFIC sp 07	Curculionidae		Mature forest edge (all ages)
Mandalotus arciferus	Curculionidae		Mature forest edge (all ages)
Roptoperus tasmaniensis	Curculionidae		~45 secondary forest (edge preference)
Choleva TFIC sp 01	Leiodidae	✓	Mature forest edge (all ages)
Nargiotes gordoni (id uncertain)	Leiodidae	✓	~7 y.o. mature forest edge
Adelium abbreviatum	Tenebrionidae		~45 y.o. secondary forest (edge avoiding)
Anotylus TFIC sp 02	Staphylinidae	✓	~27 y.o. secondary forest (edge avoiding)
Anotylus TFIC sp 03	Staphylinidae	✓	~45 y.o. secondary forest (edge avoiding)
Predators			
Chylnus ater	Carabidae		Mature forest edge (all ages)
Mecyclothorax ambiguus	Carabidae	✓	~7 y.o. secondary forest (edge avoiding)
Anabaxis CHANDLER type 1	Staphylinidae	✓	~7 y.o. secondary forest (edge preference)
Atheta TFIC sp 01	Staphylinidae	✓	~7 y.o. mature forest edge
Falagria TFIC sp 05	Staphylinidae	✓	~45 y.o. secondary forest (edge avoiding)
Horaemorphus TFIC sp 10	Staphylinidae	✓	~27 y.o. secondary forest (edge avoiding)
Palimbolus victoriae	Staphylinidae	✓	~7 secondary forest (edge preference)
Philonthus TFIC sp 010	Staphylinidae	✓	~27 y.o. secondary forest (edge avoiding)
Quedius inaequalipennis	Staphylinidae	✓	~45 y.o. secondary forest (edge avoiding)
Sagola ruggicornis	Staphylinidae	✓	~45 y.o. secondary forest (edge avoiding)
Spanioda carissima	Staphylinidae	✓	~45 y.o. secondary forest (edge avoiding)
Tasmanityrus newtoni	Staphylinidae	✓	~7 y.o. secondary forest (edge preference)
within Aleocharinae TFIC sp 007	Staphylinidae	✓	~7 y.o. mature forest edge
within Aleocharinae TFIC sp 100	Staphylinidae	✓	~45/27 y.o. secondary forest (edge preference)
Zyras TFIC sp 01	Staphylinidae	✓	~7 y.o. secondary forest (edge avoiding)
Zyras TFIC sp 02	Staphylinidae	✓	~45 y.o. secondary forest (edge avoiding)
Zyras TFIC sp 05	Staphylinidae	✓	~7 y.o. mature forest edge

Mature forest edge species were indicators from -35, -15 m into mature forest, species with an edge preference were indicators of +15, +35 m into secondary forest and edge-avoiding species were indicators of 120 and 200 m plots.

6.1.3 Understanding beetle community assembly

This thesis adds further support to the importance of niche-based models in explaining community assembly over a succession gradient (Lebrija-Trejos et al., 2010; Lohbeck et al., 2013). Niche-based processes were also dominant in community assembly in the experiment manipulating litter and shade. However, components of neutral theory, such as dispersal limitation play some role in forest influence (Fig. 6.2) (Chapter 3), and ecological drift still likely to have of some importance in determining species assembly, and the niche/neutral dichotomy may not be a realistic one (Thompson & Townsend, 2006; Kitching, 2013).

Of the niche processes, environmental filtering was the dominant process explaining community assembly both as a response to succession and to manipulated habitat. Across succession, functional trait values were convergent for both trophic groups; likewise, traits were also convergent in communities occupying leaf litter and shaded plots. Since ground active beetles species following logging and wildfire are comparable (Baker et al., 2004), I hypothesise that environmental filtering may act across a wildfire initiated succession gradient as well. If that is the case, the dynamic and fire regulated nature of Australian forests for the last 40 000 years (Bowman, 2008), environmental filtering of beetle communities may have had a long history. The significant metacommunity phylogenetic signal related to the convergence pattern over succession for both trophic groups is further evidence that this maybe the case.

Biotic interactions were only found to be important for beetle assembly in recently (<1 year old) logged experimental open control plots, but not at any stage of the successional gradient from ~7 years post harvest to mature forest. I hypothesised in Chapter 5 that this was due to the open plots experiencing the most extreme microclimate gradients, and that the open exposed conditions are the most short-lived

of any successional stage (e.g. see Gerisch, 2014). It is possible that this is because the youngest forest sites I sampled were ~7 years after logging, and competition is only important for assembly in open temporally-restricted habitat. After ~7 years, open habitat had largely disappeared and the sedge layer was dominant. Even though leaf litter was sparse, the sedge layer may stabilise ground active beetle habitat sufficiently to mask the early effects of competition. This topic is clearly ripe for investigation and beetle responses to logging offer an ideal system for future research.

6.2 Future research directions

The studies described in his thesis are certainly the first to explore concurrently the evolutionary, environmental and biotic forces that shape beetle community assembly and distribution, and are among the few that have assessed how beetles recolonise secondary forest habitat across the world. In a world where habitats are becoming increasingly fragmented these types of studies are going to become even more important. My thesis has barely scratched the surface in terms of understanding the complex forces operating on beetles. There are of course large knowledge gaps, but some general areas that seem particularly worthy for future research relate to beetle taxonomy and habitat requirements, forest management, future development of the beetle functional trait paradigm and expanding our understanding of community assembly. Filling these knowledge gaps will not only allow for more effective management of this diverse group of organisms, but also may help generate assembly rules that can help further understand and predict how communities responds to disturbance.

6.2.1 The taxonomic impediment and habitat requirements

Some of the biggest challenges faced by invertebrate conservation biologists across the world, but particularly outside of Europe, include the difficulty in species identification and the lack of species-level knowledge about habitat requirements and distribution. For example, even in this relatively well studied system (for Australian standards) the majority of species lack formal description and very little is known

about their habitat requirements and distribution. Using molecular data to delimit and identify species has the potential to help overcome the taxonomic impediment (Monaghan et al., 2005; Pons et al., 2006). Coupled with thorough DNA inventory using metagenomic approaches (e.g. Zhou et al., 2013) to identify both beetle species and other invertebrates in wet forests, our knowledge of beetle distribution and diversity would greatly increase. Considering the large number of beetle species even in this temperate system, gaining insights into species habitat requirements and life history may be a more difficult proposition. As I mentioned in Chapter 1, molecular and metabolomic approaches may offer a shortcut to gain insights into the habitat requirements and life history aspects of a species. For example, quantitative trait approaches can identify particular genes associated with insect fecundity (Leips et al., 2006). However, in the short term at least, increased autecological work is required. Such knowledge can help determine which species may decline in response to forest management (Didham et al., 1998; Henle et al., 2004; Baker et al., 2007).

6.2.2 Forest management

As forest influence is still a relatively new concept there are wide gaps in our understanding. The optimal size of retained mature forest remnants, for example, is likely to be important for beetle recolonisation in the long term but is currently unknown. Within beetle metapopulations, for example, local patch size has been shown to determine beetle colonisation into burnt habitat, with larger patch sizes leading to higher colonisation of burnt forest (Ranius et al., 2014). If small mature forest aggregates reduce recolonisation success, forest influence may not extend as far as I have suggested. Understanding how mature forest patch size impacts forest influence will be important for designing effective aggregated retention systems.

As beetles communities exhibit strong fluctuations in species compostion throughout the year, understanding how forest influence may change temporally is also apotentially significant. For example, the microclimate gradient across forest edges is most extreme during the summer months, even ~45 years after logging (Baker, in press), and this may follow on to differential forest influence effects on beetles. Also,

forest edges may be less permeable in summer and species that disperse at this time maybe more restricted to mature forest habitat.

Perhaps more importantly, how forest influence impacts ecosystem processes is also an open question. Beetles are key components of the leaf litter biome and play an important role in ecosystem processes such as nutrient cycling (Nichols et al., 2009; Zhao et al., 2013). Nutrient cycling is known to change as forest succession proceeds (e.g. Vitousek, 1984), but assessing how differences in invertebrate communities can alter this process is unknown. If forest influence does have an effect on ecosystem processes, this would suggest that there is more to aggregated retention than just biodiversity conservation alone. An increased understanding of beetle 'effect traits' (Díaz et al., 2013) could be one approach to answering this question.

6.2.3 Future functional trait work and community assembly

I have demonstrated how functional trait syndromes change during forest succession in Tasmanian wet forest, but understanding to what extent this pattern is more general for similar trophic groups across the world is an important next step. In deciduous forest, for example, I expect the pattern may be quite different due to the seasonal fluctuations in canopy coverand leaf litter inputs. Also understanding if 'hard' traits or different trait sets lead to different results is also important step for arthropod trait studies. Nonetheless, As plant studies have demonstrated (e.g. López-Martínez et al., 2013), functional trait syndromes applicable across a variety of ecosystems are both a useful short cut to understand ecosystem recovery, but may also give insight to what evolutionary and environmental forces may be shaping species.

Finally, developing consistent trait approaches for other arthropod groups would also provide greater insights into their ecology, and would test how general these syndromes are. For example, as most of the traits used in this thesis are applicable to other arthropod groups, it is possible that some traits may respond in a similar fashion e.g. relative leg length and eye size. Furthermore, applying a combined functional trait and phylogenetic approach to other animal taxa would also test if

similar environmental and evolutionary forces act on all communities living amongst the undergrowth.

6.3 Conclusions

Extending traditional community ecology to incorporate functional trait and evolutionary approaches has the power to transform our understanding of how communities operate and may enable this discipline to become a more predictive science. Species based approaches are still essential, yet lack the generality of functional trait methods as they are confined by species pool of the region of interest. Functional traits approaches facilitate worldwide comparisons of communities and, if done quantitatively, can be used to build predictive models as was the case in this study. I envision that the functional trait methodology and analysis approaches used in this thesis can serve as a template for future studies on community recovery and succession. Furthermore, functional trait-environment models can help better understand the forces that underlie how these communities assemble and how disturbance can alter them. As I have demonstrated, understanding the evolutionary context of these patterns provides further insights and coupling trait studies to phylogenetics can help disentangle the extent in which environment and evolution shape community dynamics. Coupling all three has greatly increased our understanding of how succession operates on forest beetle communities and how recolonisation proceeds. Applied more broadly, these methods will increase our understanding and provide new insights into these highly diverse and important communities.

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Appendix A
Supplementary material to Chapter 2

Table A1. Summary of studies of functional, ecomorphological and life history traits in beetles.

	Study															
Traits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Body length/mass/size	✓	✓	✓	✓	C	C	C		✓	✓	✓	C	C		✓	C
Head width				C			C	✓	C							
Head length						C		✓								
Antennae length		C		C			✓		C		C					
Maxillary palp length						C										
Mandible length				✓												
Eye diameter											C					
Eye width				✓												
Eye protrusion				✓					✓							
Eye surface area				✓					✓							
Ommatidia number/density				C					C							
Pronutum width		✓				✓	C	✓								
Pronutum depth		✓									C					
Pronutum shape		*														
Prothorax depth							C									
Elytra length						✓		✓			C					
Elytra depth		✓						✓								
Elytra width		✓									C					
Wing development		*	*C		C				C	*	*					C
Front leg length							✓									
Rear leg length				✓			✓									
Metatrochanter length		✓							✓							
Length of tarsi								✓								
Metatarsi length		C									C					
Metafemur length		C														
Femur length		✓				✓		✓								
Femur width								C			C					
Tibia length		✓														
Tibia area								✓			C					
Abdomen length							✓									
Abdomen width							C									
Abdomen depth								✓	✓							
Last abdominal sternite length		✓				C										
Leg colour		*									*					

Body colour		*				*C					
Pubescence		*				*					
Foraging technique							*		*	*	
Food of adult/ trophic level		*					*C	*C		*C	✓
Habitat/feeding specificity								*		*	
Daily activity		*							*		✓
Breeding season		*					*C		C		✓
Emergence time		*									
Overwintering		*		C		*					
Main activity time		*					*C				✓
Shading/moisture/temperature preference				*				*			✓
Niche breadth				*C			*				
Primary habitat position			*				*C	*C	*	*C	
Species isolation	*C										
Natural abundance/rarity	*C						*C				
Anthropomorphic association						*C					
Fecundity							✓				
Migration pattern/dispersal ability							*	*C	*	*	

+ = study included other arthropod groups; ✓= quantitative data,; = qualitative/ordinal data; C= quantitative data positively/negatively correlated with an environmental variable (if not listed as 'Cor' no correlation was found); *Cor: Qualitative/ordinal data positively/negatively correlated with an environmental variable.*

Sources- 1 = Davies et al. (2000); 2 = Ribera et al. (2001); 3 = Driscoll and Weir (2005); 4 = Talarico et al. (2007); 5 = Lambeets et al. (2008); 6 = Laparie et al. (2010); 7 = Barton et al. (2011); 8 = Inward et al. (2011); 9 = Talarico et al. (2011); 10 = Gerisch et al. (2011); 11= Vandewalle et al. (2010); 12 = Barbaro and van Halder (2009); 13= Moretti and Legg (2009) 14: Bell et al. (2011);15: Rzanny and Voigt (2012); 16:Pakeman and Stockan (2014).

Appendix B
Supplementary material to Chapter 3

B.1. Site characteristics

Table B.1. Summary of the regeneration age, altitude, geology and position relative to streams of study sites.

Age class	Harvest year	Mean altitude (m)	Site	Geology	Riparian habitat?
~45	1966	267	AR075E	Jurassic dolerite	No
	1966	371	AR012E	Jurassic dolerite	Stream beyond -35 m plots
	1967	191	FN032C	Jurassic dolerite with some Permian pebbly mudstone	Stream beyond -35 m plots
	1968	363	KD043H	Jurassic dolerite	No
	1970	350	KD009I	Jurassic dolerite	No
~27	1983	235	AR050G	Triassic Sandstone	Stream beyond -35 m plots
	1983	247	WR017E	Jurassic dolerite derived talus	Stream beyond -35 m plots
	1984	249	KD009J	Jurassic dolerite	No
	1986	146	PC039F	Jurassic dolerite with some Permian pebbly mudstone	No
	1987	159	FN009B	Jurassic dolerite, with some dolerite talus	Stream beyond -35 m plots
~7	2003	213	PC022A	Permian mudstones	No
	2004	191	FN023E	Triassic Sandstone	No
	2005	319	EP024A	Permian mudstones	Stream beyond -35 m plots
	2006	388	DN007A	Jurassic dolerite, with some dolerite talus	Stream beyond -35 m plots
	2007	260	PC034D	Jurassic dolerite, mostly as talus	Stream beyond -35 m plots

B.2. Environmental variables important in understanding beetle succession.

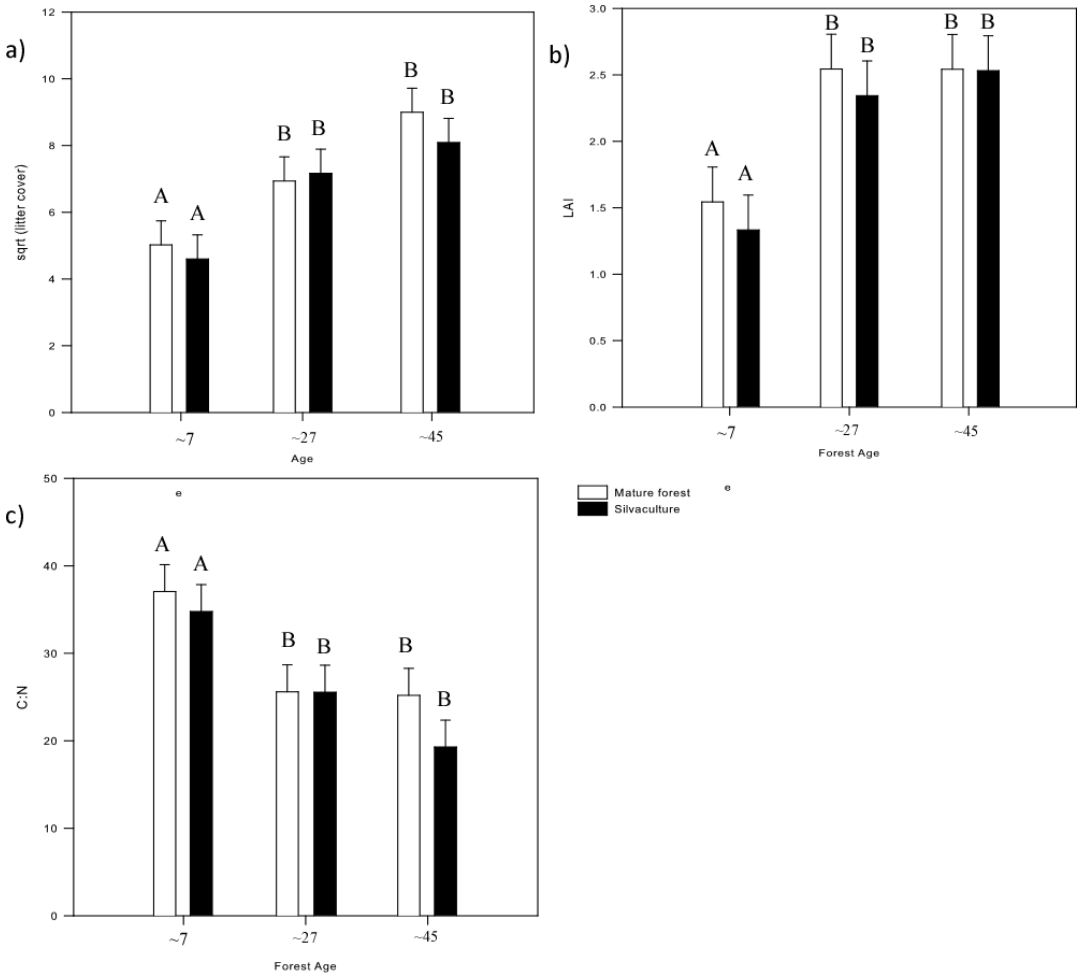

Fig. B.2. Bar plots of each environmental variable that is significant according to the beetle succession DISTLM model. a) Litter cover varied between ages (ANOVA $F_{(2,54)} = 13.502$, $P < 0.001$) but there was no difference between the secondary forest and the adjacent mature forest. b) LAI was significantly greater in ~45 and ~27 year old forest ($F_{(2,54)} = 10.791$, $P < 0.001$) than compared to ~7, but again there was no difference between the secondary forest and the adjacent mature forest. c) The C:N ratio was highest in the ~7 year old forest compared to the older successional stages ($F_{(2,54)} = 10.70$, $P < 0.001$), again with no difference with the adjacent mature forest. A/B indicate significant groupings found using Holm-Sidak multiple comparisons

B.3. Gradient forest output for each forest age.

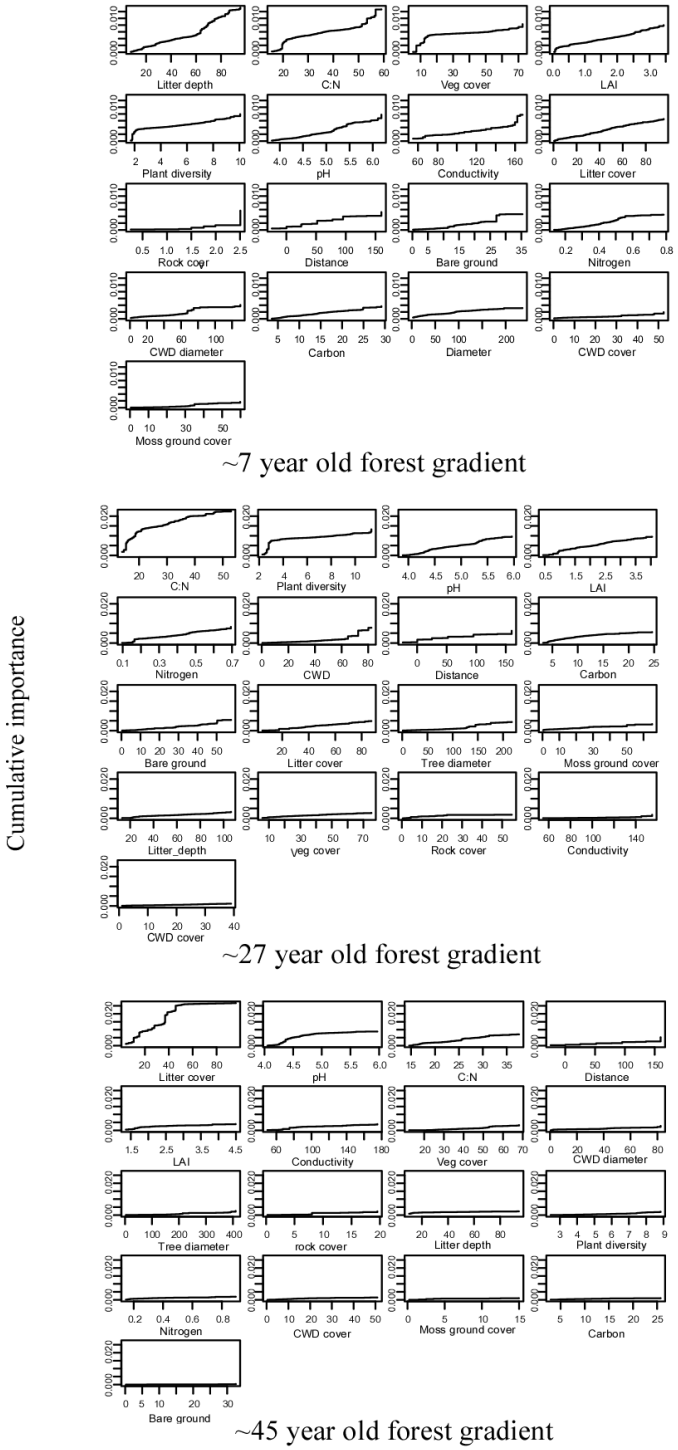

Fig. B.3. Cumulative importance curves of 17 variables modelled using Gradient Forests. Each small graph illustrates how much community turnover is associated with corresponding increases of each individual environmental variable.

B.4. Non-linear and linear regressions of individual environmental variables with distance and species abundance data.

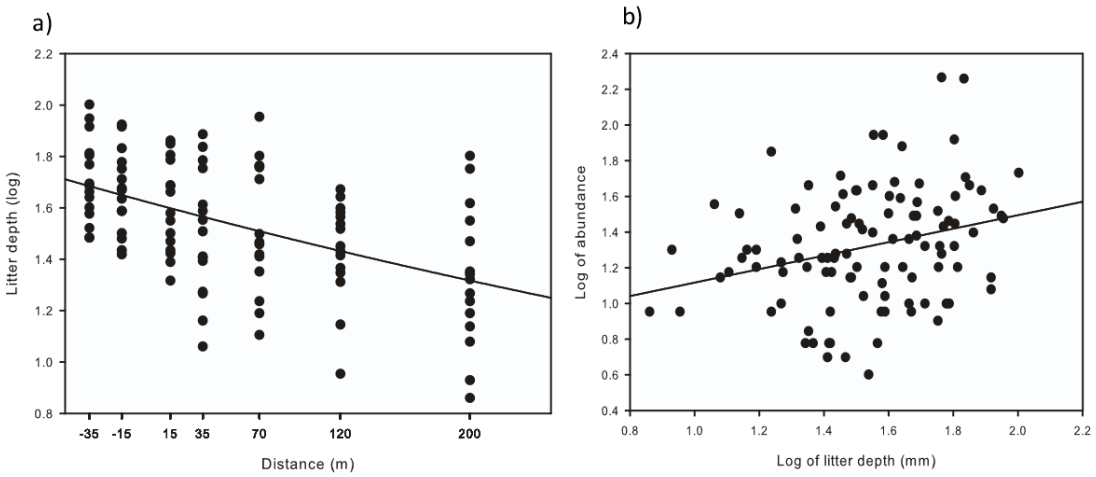

Fig. B.4.1 Linear regression for ~7 year old forest a) litter depth and distance from edge (Adj R^2 = 0.1851, P < 0.001), b) Litter depth and beetle abundance (Adj R^2 = 0.0699, P = 0.0037).

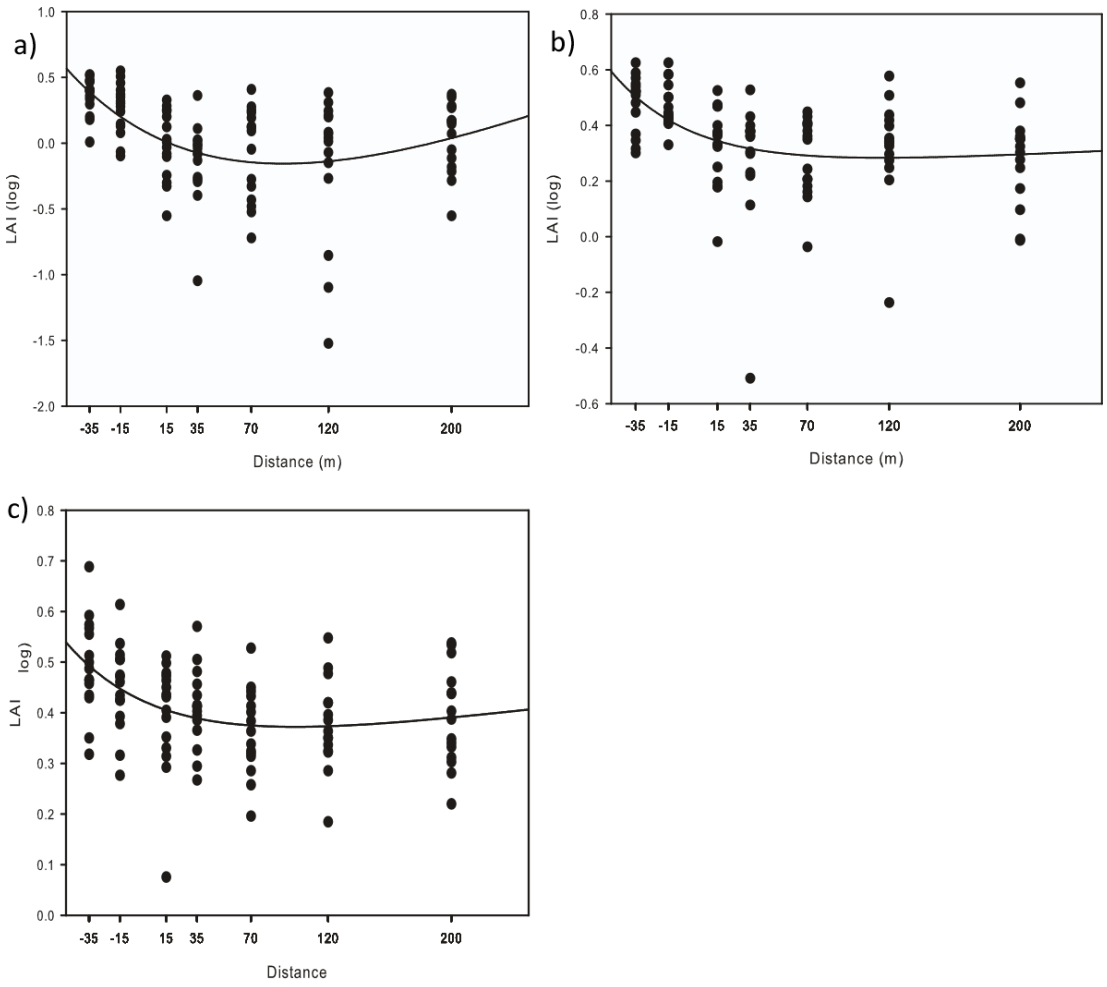

Fig. B.4.2 Non-linear regressions for LAI vs. distance from edge at a) ~7 year old forest (Adj $R^2 = 0.22$, $P < 0.0001$), b) ~27 year old forest (Adj $R^2 = 0.1680$, $P < 0.0001$), c) ~45 year old forest (Adj $R^2 = 0.1475$, $P = 0.003$).

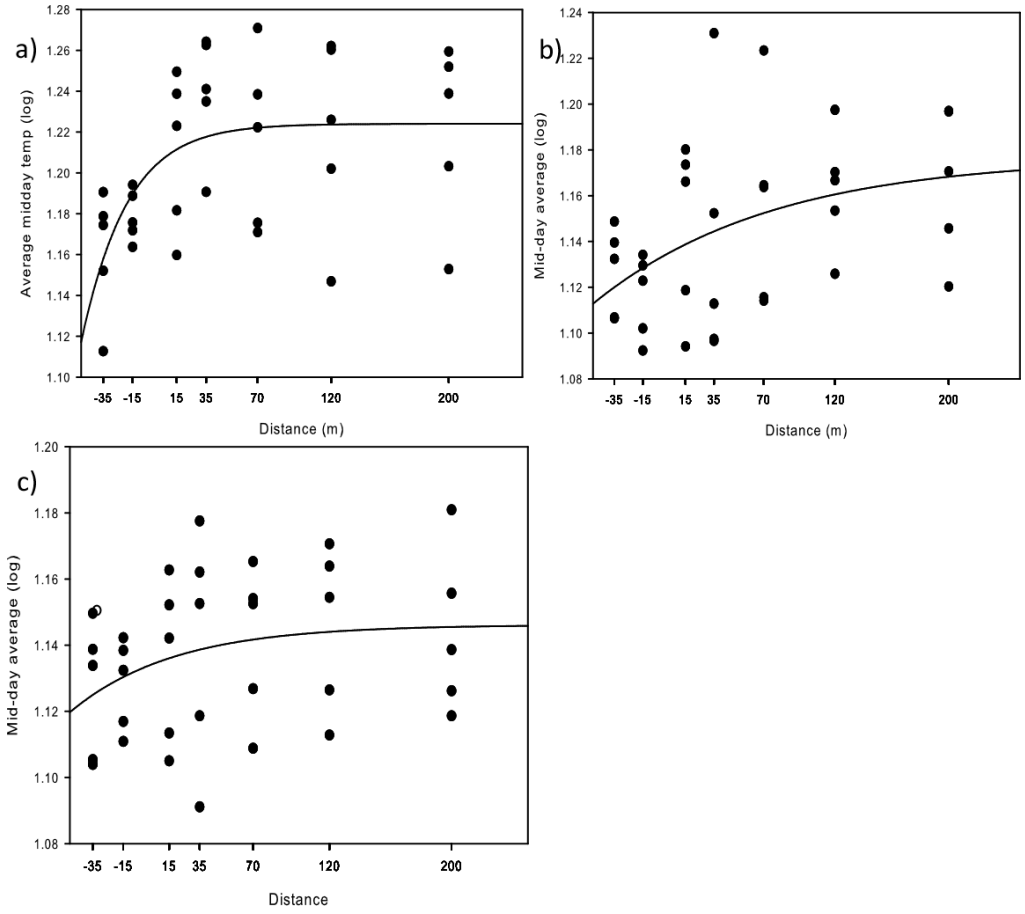

Fig. B.4.3 Non-linear regressions —— for mid-day average temperature vs. distance from edge at: a) ~7 year old forest (Adj $R^2 = 0.2941$, $P = 0.0080$), b) ~27 year old forest (Adj $R^2 = 0.1593$, $P = 0.0151$), c) ~45 year old forest (Adj $R^2 = 0.07210$, $P = 0.1834$).

Table B.4. Abundance and indicator species status for common (>5 individuals) beetle species for each distance and each age.

Species	Family	Total	~7 year old boundary							~27year old boundary							~45 year old boundary						
			-35	-15	15	35	70	120	200	-35	-15	15	35	70	120	200	-35	-15	15	35	70	120	200
Microchaetes hystricosus	Byrrhidae	27	0	0	0	0	0	0	0	1	2	1	1	1	2	0	12	0	1	1	3	0	2
Microchaetes scoparius	Byrrhidae	10	0	0	3	0	2	1	0	0	1	2	0	0	0	1	0	0	0	0	0	0	0
Heteromastix nigripes	Cantharidae	22	0	0	0	0	0	0	1	0	2	1	0	5	0	3	6	1	0	1	2	0	0
Acallistus longus	Carabidae	335	1	11	2	0	0	2	1	8	3	2	7	9	6	7	143	18	25	19	16	37	18
Chylnus ater ^{M}	**Carabidae**	87	5	2	1	0	0	0	0	2	5	0	0	0	4	1	37	11	6	3	2	0	8
Homethes elegans	Carabidae	39	0	0	0	2	0	1	4	0	1	4	2	1	0	3	11	2	2	0	1	2	3
Lestignathus foveatus	Carabidae	48	1	1	1	1	0	2	1	0	0	2	5	4	0	0	15	3	2	3	0	3	4
Mecyclothorax ambiguus $^{\sim 7F}$	**Carabidae**	19	1	1	1	3	0	5	7	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Notonomus politulus	Carabidae	155	9	2	1	5	6	3	0	3	1	5	15	20	8	1	41	0	15	5	3	10	2
Percosoma carenoides	Carabidae	69	0	0	0	3	1	1	0	1	1	2	1	0	3	4	26	7	7	3	4	2	3
Rhabdotus reflexus	Carabidae	839	20	21	19	20	30	13	5	19	22	29	20	21	21	41	286	14	72	48	39	37	42
Scopodes sigillatus	Carabidae	6	0	0	0	0	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sloaneana tasmaniae	Carabidae	181	3	1	9	25	9	24	7	4	7	6	3	2	4	2	42	6	0	5	3	13	6
Stichonotus piceus	Carabidae	17	0	0	0	0	0	0	0	6	1	0	1	0	0	0	5	0	1	0	0	2	1
Trechinae TFIC sp 08	Carabidae	13	0	0	0	0	0	0	0	0	0	1	0	0	0	0	6	1	5	0	0	0	0
Trechistus terricola	Carabidae	95	0	0	0	0	0	0	0	11	1	31	19	31	0	0	1	0	1	0	0	0	0
Arsipoda TFIC sp 04	Chrysomelidae	18	0	0	0	0	0	0	0	1	0	0	1	1	0	0	8	0	0	1	2	4	0
Arsipoda variegate $^{\sim 7F}$	**Chrysomelidae**	5	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geomela TFIC sp 01	Chrysomelidae	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0
Clambus bornemisszai	Clambidae	5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	1	0	0	0
Spaerothorax pubientris $^{\sim 7F}$	**Clambidae**	9	0	0	1	1	1	1	3	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Decilaus bryophilus	Curculionidae	16	1	0	0	0	0	0	0	0	3	0	1	0	0	1	5	0	0	1	1	3	0
Decilaus lateralis	Curculionidae	187	17	7	0	14	1	0	1	3	1	2	4	1	1	4	70	4	9	21	6	8	13
Decilaus nigronotatus $^{M,\sim 45F}$	**Curculionidae**	142	7	11	14	10	3	1	1	4	26	5	9	2	0	2	27	1	2	3	7	1	6
Decilaus striatus ^{M}	**Curculionidae**	499	22	7	3	22	6	0	0	26	27	41	20	19	18	16	142	22	38	24	12	21	13
Decilaus TFIC sp 01 ^{M}	Curculionidae	113	7	4	0	3	1	2	0	4	7	0	0	4	0	0	44	5	7	4	9	7	5
Decilaus TFIC sp 02	Curculionidae	28	0	0	0	0	0	0	0	0	1	3	3	0	0	3	12	0	0	4	0	0	2
Decilaus TFIC sp 03	Curculionidae	34	3	3	0	0	0	0	0	0	0	1	5	3	1	0	9	0	2	4	0	3	0
Decilaus TFIC sp 04 $^{\sim 27N}$	**Curculionidae**	45	6	2	2	0	1	0	0	3	5	0	6	0	1	1	10	0	3	1	0	1	3
Decilaus TFIC sp 22	Curculionidae	11	0	2	2	5	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Dinichus terreus	Curculionidae	37	3	2	0	1	1	0	0	2	0	1	0	1	0	0	14	1	2	2	2	3	2
Dryopthorus ECZ sp 02	Curculionidae	6	0	0	0	0	0	0	0	0	0	2	1	3	0	0	0	0	0	0	0	0	0
Exeiratus TFIC sp 04	Curculionidae	5	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
Exeiratus TFIC sp 07 ^{M}	**Curculionidae**	38	0	0	0	0	0	0	0	1	3	2	0	0	0	0	16	6	5	1	1	1	2
Exithius capucnicus	Curculionidae	8	0	1	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	0	1	0	1
Exithius TFIC sp 01	Curculionidae	5	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0	0	0	1

Exithius TFIC sp 03	Curculionidae	10	4	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	2	1
Mandalotus arciferus [M]	**Curculionidae**	218	13	2	0	0	0	0	2	16	19	3	0	0	0	10	81	25	19	14	4	9	1
Mandalotus blackburni	Curculionidae	318	1	0	0	0	0	0	0	10	18	38	28	23	17	9	98	5	14	9	13	9	26
Mandalotus muscivorus	Curculionidae	54	15	6	2	4	9	5	2	0	0	0	0	0	0	0	6	0	0	0	0	4	1
Pachyroptoperus satyrus	Curculionidae	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	2	3	1	3	0	0
Roptoperus tasmaniensis [~7N]	**Curculionidae**	379	2	1	14	13	2	5	3	3	6	28	18	23	18	19	114	15	33	20	8	13	21
within Cryptorhynchinae TFIC sp 07	Curculionidae	217	9	8	3	2	2	2	0	5	2	7	13	10	1	0	84	4	20	10	13	12	10
within Cryptorhynchinae TFIC sp 20	Curculionidae	8	0	0	0	0	0	0	0	0	3	0	0	0	0	0	4	0	0	0	0	1	0
Conoderus australiasiae	Elateridae	6	0	0	1	1	2	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Hobartius eucalypti	Hobartiidae	12	0	0	0	0	0	0	10	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Aridius nodifer	Latridiidae	90	5	2	1	2	3	3	0	5	3	6	3	0	7	1	25	15	2	3	2	1	1
Austronemadus TFIC sp 03	Leiodidae	249	24	7	2	8	11	2	6	25	27	28	22	10	19	15	22	3	2	12	2	1	1
Catposchema tasmaniae	Leiodidae	61	1	0	1	0	0	0	0	4	2	0	0	2	0	0	26	12	10	0	2	1	0
Choleva TFIC sp 01 [M]	**Leiodidae**	89	5	15	5	1	0	0	1	10	24	4	3	9	1	3	4	0	0	1	1	0	2
Colenisia TFIC sp 01	Leiodidae	23	0	0	4	3	3	4	1	0	0	2	1	0	1	0	2	0	0	0	0	0	2
Eublackburniella TFIC sp 01	Leiodidae	21	0	0	1	0	0	7	3	0	0	0	4	0	4	0	1	0	0	1	0	0	0
Nargiotes gordoni (id uncertain) [~7 M]	**Leiodidae**	25	0	0	0	0	0	0	0	4	1	0	0	7	1	0	6	1	1	0	0	2	2
Nargomorphus globulus	Leiodidae	1126	19	45	5	7	24	16	10	57	57	47	64	45	57	42	336	42	99	73	33	31	17
Sogdini ANIC Gen B	Leiodidae	22	0	2	0	0	0	0	0	1	0	0	0	0	0	1	9	4	3	0	1	0	1
Sogdini SEAGO Gen A	Leiodidae	30	1	13	0	1	1	0	1	0	0	0	4	0	0	1	4	0	2	0	1	1	0
Talayra TFIC sp 01	Leiodidae	6	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	1	0	0	0	1	0
Zeadolopus TFIC sp 01	Leiodidae	15	0	4	0	0	1	4	0	0	0	0	0	0	0	0	3	0	0	1	1	0	1
Zeadolopus TFIC sp 02	Leiodidae	93	1	80	0	0	3	0	1	1	1	1	2	0	1	1	1	0	0	0	0	0	0
Lissotes cancroides	Lucanidae	42	0	1	1	1	3	5	13	0	3	1	1	1	0	3	5	0	1	1	1	0	1
Lissotes curvicornis	Lucanidae	9	0	0	1	1	0	3	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0
Lissotes rodwayi	Lucanidae	11	2	0	1	0	0	1	0	1	1	0	2	1	0	0	1	0	0	0	1	0	0
Lissotes subcaeruleus	Lucanidae	22	3	0	0	0	0	2	2	0	4	3	1	2	2	1	1	0	1	0	0	0	0
Orchesia alphabetica [M]	Melandryidae	154	5	8	2	5	2	0	0	5	3	2	19	7	5	1	47	5	22	7	5	2	2
Orchesia TFIC sp 01	Melandryidae	22	1	1	0	0	0	0	0	1	0	1	5	1	2	1	6	0	0	1	0	0	2
Orchesia TFIC sp 06	Melandryidae	11	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5	1	2	0	0	2	0
Orchesia TFIC sp 07	Melandryidae	12	0	0	0	0	0	0	0	0	0	0	1	0	0	0	7	0	1	0	0	2	1
Thalycrodes cylindricum [~45F]	**Nitidulidae**	269	40	3	1	1	1	4	0	0	2	7	13	18	5	9	110	3	1	6	7	14	24
Thalycrodes pulchrum	Nitidulidae	243	6	9	12	31	29	23	40	3	4	15	3	4	15	5	23	2	4	4	2	3	6
within Ptillidae TFIC sp 01	Ptillidae	24	0	2	1	0	0	0	0	0	0	0	0	0	1	0	10	1	0	2	3	3	1
within Ptillidae TFIC sp 06	Ptillidae	16	0	0	2	0	0	0	0	0	0	2	2	1	3	0	3	1	0	0	0	2	0
within Ptillidae TFIC sp 16	Ptillidae	15	0	0	0	0	0	1	1	0	0	0	1	0	0	0	7	0	1	1	2	0	1
within Ptillidae TFIC sp 21	Ptillidae	7	0	0	2	0	0	0	0	0	0	1	0	2	0	0	1	0	0	0	0	0	1
Telura vitticollis	Scarabaeidae	21	0	0	4	2	1	1	7	0	2	1	0	0	0	1	1	0	0	0	1	0	0
Hetronyx pubescens	Scarabeidae	8	0	0	0	0	0	0	0	0	0	1	0	0	1	0	3	1	1	0	1	0	0
Cyphon TFIC sp 05	Scirtidae	7	3	0	1	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptmorpha TFIC sp 01	Silvanidae	7	0	0	0	0	0	0	0	0	0	3	0	1	3	0	0	0	0	0	0	0	0

Cryptmorpha victoriae	Silvanidae	3	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aspidiphorus humeralis	Sphindidae	9	1	1	1	2	0	2	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
Anabaxis CHANDLER type 1 ***~7N***	**Staphylinidae**	48	0	0	18	5	4	4	6	0	0	0	0	0	0	0	6	0	3	0	2	0	0
Anotylus TFIC sp 02 ***~27F***	Staphylinidae	710	2	4	28	21	86	19	82	14	1	7	9	22	13	16	220	12	5	24	20	74	31
Anotylus TFIC sp 03 ***~45F***	Staphylinidae	794	28	27	30	30	42	30	37	12	30	133	79	54	155	105	1	1	0	0	0	0	0
Anotylus TFIC sp 04	Staphylinidae	936	1	2	0	0	0	0	1	14	16	322	40	11	39	73	213	60	10	18	87	22	7
Anotylus TFIC sp 05	Staphylinidae	132	17	3	0	1	3	3	8	2	1	8	6	5	10	8	33	6	2	1	6	3	6
Anotylus TFIC sp 07	Staphylinidae	23	0	0	1	1	3	1	2	0	0	1	2	3	0	3	5	0	1	0	0	0	0
Atheta TFIC sp 01 ***~7 M***	**Staphylinidae**	89	3	1	0	1	1	1	2	3	2	0	0	2	0	3	36	22	8	2	0	2	0
Atheta TFIC sp 02	Staphylinidae	14	0	0	1	0	2	1	0	0	0	0	0	0	0	1	5	0	3	0	0	1	0
Atheta TFIC sp 03	Staphylinidae	2392	34	33	68	27	88	17	26	189	144	170	130	157	84	76	606	122	107	112	85	62	55
Aulaxus CHANDLER Type 1	Staphylinidae	32	5	1	0	0	0	2	0	0	2	3	0	2	0	1	9	0	3	3	0	1	0
Austrorhysus TFIC sp 01	Staphylinidae	5	0	1	0	0	0	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	0
Baeocera TFIC sp 01	Staphylinidae	21	0	0	1	4	0	0	0	0	1	1	2	0	0	0	6	0	0	2	2	1	1
Baeocera TFIC sp 02	Staphylinidae	194	0	0	7	3	7	11	1	5	3	92	5	3	4	10	24	1	5	3	2	2	6
Blepharyhymenus sp nr apicornis	Staphylinidae	19	0	1	0	0	0	0	0	1	0	1	2	2	0	0	6	1	1	1	2	1	0
Chichester CHANDLER Tasmania 1	Staphylinidae	8	0	1	0	0	0	0	0	0	0	0	0	1	0	0	3	1	1	0	1	0	0
Euconnus TFIC sp 07	Staphylinidae	152	2	3	0	0	0	0	3	12	5	18	2	11	8	9	44	6	6	4	6	2	11
Euplectops CHANDLER Tasmania 1	Staphylinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euplectops TFIC sp 01	Staphylinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Falagria TFIC sp 01	Staphylinidae	45	0	1	20	0	1	0	2	0	0	0	1	1	0	0	10	0	1	1	0	2	5
Falagria TFIC sp 05 ***~45F***	**Staphylinidae**	103	0	0	0	0	1	0	5	0	0	0	0	0	0	1	50	0	0	0	0	1	45
Hetrothops TFIC sp 03	Staphylinidae	42	1	1	3	0	3	0	1	0	0	6	0	1	1	5	10	0	1	3	2	1	3
Horaemorphus TFIC sp 10 ***~27F***	**Staphylinidae**	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyperomma bryophilum	Staphylinidae	58	0	1	4	0	0	0	0	0	0	0	3	2	7	3	23	1	2	2	4	4	2
Hyperomma bryophilum	Staphylinidae	19	0	1	0	4	0	0	0	1	1	0	0	1	0	1	5	1	1	1	1	0	1
Hyperomma TFIC sp 05	Staphylinidae	3	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0
Ischnosoma TFIC sp 01	Staphylinidae	8	1	0	2	0	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	1	0
Macroplectus CHANDLER Type 1	Staphylinidae	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	2	2	0	1	0
Microsilpha ANIC Thayer sp 15	Staphylinidae	129	13	45	1	13	0	1	14	0	0	1	3	0	0	0	19	2	7	1	8	0	1
Osirius TFIC sp 01	Staphylinidae	17	0	0	0	0	0	0	0	0	0	1	0	0	0	0	8	1	0	1	4	2	0
Palimbolus victoriae ***~7N***	**Staphylinidae**	29	1	1	0	0	0	0	0	0	1	7	6	7	6	0	0	0	0	0	0	0	0
Philonthus TFIC sp 0102 ***~27F***	**Staphylinidae**	59	0	2	1	5	2	1	2	0	0	0	0	0	1	6	22	3	1	2	8	3	0
Pselaphaulax CHANDLER Tasmania 1	Staphylinidae	63	2	0	1	0	0	1	0	2	3	3	0	0	1	2	24	4	4	4	3	7	2
Quedius baldiensis	Staphylinidae	13	1	0	1	2	2	2	0	0	0	0	1	0	0	0	2	0	1	1	0	0	0
Quedius duplopunctatus	Staphylinidae	17	0	1	0	0	0	1	0	0	0	1	1	1	0	0	6	1	1	2	0	0	2
Quedius inaequalipennis ***~45F***	**Staphylinidae**	30	1	0	2	2	5	8	1	0	2	1	0	0	1	1	3	2	1	0	0	0	0
Quedius stenocephalus	Staphylinidae	21	1	0	1	0	0	0	1	3	0	0	0	1	1	1	6	2	1	1	1	1	0
Quedius subopaceous	Staphylinidae	7	0	0	1	0	1	0	2	0	0	1	0	0	0	0	1	0	0	1	0	0	0
Quedius TFIC sp 04	Staphylinidae	34	3	0	4	1	2	3	7	0	2	1	1	1	0	4	3	0	0	0	0	1	1
Quedius TFIC sp 07	Staphylinidae	10	0	0	0	0	0	0	0	1	0	0	1	0	1	0	4	2	0	0	0	0	1

Rybaxis parvidens	Staphylinidae	31	0	0	17	0	10	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Rybaxis variabilis	Staphylinidae	28	0	0	3	0	0	0	0	1	5	3	1	6	0	1	5	0	0	0	0	1	2
Sagola ruggicornis $^{\sim 45F}$	**Staphylinidae**	88	0	0	3	0	70	0	1	3	0	1	2	2	0	2	2	0	1	0	0	0	1
Sagola TFIC sp 02	Staphylinidae	7	0	0	2	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spanioda carissima $^{\sim 45F}$	**Staphylinidae**	231	3	2	5	4	6	3	3	16	17	27	18	9	11	0	58	13	15	5	9	2	5
Tasmanityrus newtoni $^{\sim 7N}$	**Staphylinidae**	210	5	3	11	1	1	0	0	9	7	42	15	10	4	12	46	10	4	8	6	8	8
Tetrabothrus claviger	Staphylinidae	56	3	10	4	20	3	2	2	0	0	0	1	0	2	5	2	1	0	0	1	0	0
within Aleocharinae TFIC sp 007 $^{\sim 7M,\sim 27N}$	**Staphylinidae**	23	0	0	0	0	0	0	0	1	6	0	0	0	0	0	8	2	2	1	3	0	0
within Aleocharinae TFIC sp 014	Staphylinidae	23	0	0	0	0	0	0	0	3	0	0	1	1	0	0	10	0	0	2	2	3	1
within Aleocharinae TFIC sp 015	Staphylinidae	10	0	0	0	0	0	0	0	0	0	1	0	1	0	0	4	0	0	0	1	1	2
within Aleocharinae TFIC sp 032	Staphylinidae	13	4	2	0	0	0	0	0	0	2	0	0	0	0	1	2	2	0	0	0	0	0
within Aleocharinae TFIC sp 066	Staphylinidae	10	2	0	1	1	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1
within Aleocharinae TFIC sp 100 $^{\sim N}$	**Staphylinidae**	82	0	0	0	0	0	0	0	0	6	22	7	17	2	0	14	5	1	3	4	0	1
within Aleocharinae TFIC sp 156	Staphylinidae	50	0	0	7	6	10	5	1	0	0	1	3	2	9	1	3	0	1	1	0	0	0
within Aleocharinae TFIC sp 162	Staphylinidae	5	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
within Oxypodiini TFIC sp 03	Staphylinidae	7	0	1	1	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0
within Oxypodiini TFIC sp 05	Staphylinidae	13	1	0	0	1	5	0	1	0	0	0	1	0	0	0	2	0	0	1	0	0	1
within Oxypodiini TFIC sp 06	Staphylinidae	6	0	0	0	0	0	0	0	0	0	0	1	4	1	0	0	0	0	0	0	0	0
within PselaphinaeTFIC sp 06	Staphylinidae	5	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0
within PselaphinaeTFIC sp 12	Staphylinidae	10	0	0	0	0	0	0	0	0	0	0	1	6	0	1	1	0	0	0	0	0	1
Zyras TFIC sp 01 $^{\sim 7F}$	**Staphylinidae**	112	11	6	2	13	5	36	8	0	0	1	0	2	3	0	14	3	1	2	3	0	2
Zyras TFIC sp 02 $^{\sim 45F}$	**Staphylinidae**	72	0	4	2	8	3	6	7	0	0	2	1	6	0	4	18	2	0	0	0	2	7
Zyras TFIC sp 03	Staphylinidae	27	0	1	0	0	2	0	5	0	1	1	2	1	4	0	5	1	2	2	0	0	0
Zyras TFIC sp 04	Staphylinidae	136	5	4	0	6	2	3	5	4	4	14	4	1	2	6	41	3	10	3	2	12	5
Zyras TFIC sp 05 $^{\sim 7M}$	**Staphylinidae**	55	1	3	0	2	0	0	0	1	4	1	0	0	0	0	22	15	3	2	1	0	0
Adelium abbreviatum $^{\sim 45F}$	**Tenebrionidae**	112	5	0	0	1	0	5	2	2	3	1	7	0	1	0	45	4	6	7	10	7	6
Brycopia coeloides	Tenebrionidae	14	1	1	0	1	1	1	0	0	1	0	2	0	1	0	3	1	1	0	0	0	0
Coripera deplanata	Tenebrionidae	17	0	0	7	5	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diemenoma commoda	Tenebrionidae	3	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Ciconissus gibbicollis	Zopheridae	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	1
Enhypnon tuberculatus	Zopheridae	13	0	0	0	1	0	0	1	0	0	2	0	1	1	1	3	0	1	0	1	1	0

Significant indicator species ($P \leq 0.1$, indicator value >30)) are in bold. $^{(age)M}$*: mature forest indicator species.* $^{\sim(forest\ age)E}$*: Indicator species for edge plots (15 m and 35 m from the edge).* $^{\sim(forest\ age)F}$*: Indicator species for plots 120 and 200 m from the edge. Only M or N means that the species had a significant indicator value for more than one age. TFIC sp: Tasmanian Forest Insect Collection morphospecies. 'Within' indicates that genus is unknown for this species.*

Appendix C
Supplementary material to Chapter 4

C.1. Site details and map

Table C.1. Summary of the regeneration age, altitude, geology and position relative to streams of study sites.

Age class	Harvest year	Mean altitude (m)	Site	Geology	Riparian habitat?
~45	1966	267	AR075E	Jurassic dolerite	No
	1966	371	AR012E	Jurassic dolerite	Stream beyond -35 m plots
	1967	191	FN032C	Jurassic dolerite with some Permian pebbly mudstone	Stream beyond -35 m plots
	1968	363	KD043H	Jurassic dolerite	No
	1970	350	KD009I	Jurassic dolerite	No
~27	1983	235	AR050G	Triassic Sandstone	Stream beyond -35 m plots
	1983	247	WR017E	Jurassic dolerite derived talus	Stream beyond -35 m plots
	1984	249	KD009J	Jurassic dolerite	No
	1986	146	PC039F	Jurassic dolerite with some Permian pebbly mudstone	No
	1987	159	FN009B	Jurassic dolerite, with some dolerite talus	Stream beyond -35 m plots
~7	2003	213	PC022A	Permian mudstones	No
	2004	191	FN023E	Triassic Sandstone	No
	2005	319	EP024A	Permian mudstones	Stream beyond -35 m plots
	2006	388	DN007A	Jurassic dolerite, with some dolerite talus	Stream beyond -35 m plots
	2007	260	PC034D	Jurassic dolerite, mostly as talus	Stream beyond -35 m plots

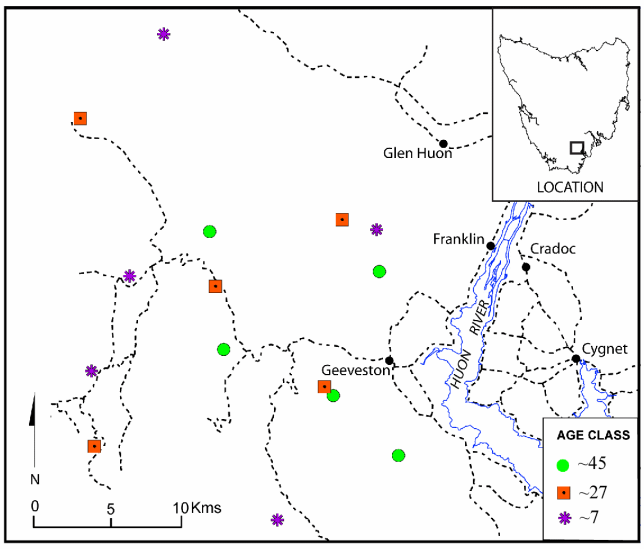

Figure C.1. Location of study sites (from Fountain-Jones, (in press (a)).

C.2. Method details

C.2.1 Site details and trapping methodology.

In total, fifteen sites were selected in southern Tasmania within and adjacent to the Warra Long Term Ecological Research (LTER) area (see Brown et al., 2001). Each site was established to contain a boundary between mature unlogged forest and a harvested area in its first rotation after clearfell, burn and sow silviculture (clearcutting) (see Hickey 1994 for details). We used a balanced design with five replicate sites for each of three age classes of silviculturally-regenerated forest. The three age classes comprised sites averaging approximately 45 years (harvested between 1966 and 1970), 27 years (harvested between 1983 and 1989), and 7 years (harvested between 2002 and 2007) post disturbance. At each site, three transects were established perpendicular to the boundary between mature and silvicultural regeneration forest, starting 35 m within mature forest and ending 200 m inside the harvested site. Plots were established in the mature forest at -35 and -15 metres from the boundary and into the harvested areas at 15, 35, 70, 120 and 200 metres to assess edge gradients(Fountain-Jones *et al.*. in press (b)). However, for this part of the study, only plots at -35, -15, 120 and 200 m were used; thus there were 180 plots (15 sites by 3 transects by 4 distances). However, data from other distances were used in some trait calculations (see C.2.2).

We collected beetles from single pitfall trap in each of the plots. Pitfall trapping is a common method of collecting beetle community data in wet forests (Niemela *et al.*. 1993; Baker *et al.*. 2007, 2009). Each trap was constructed from 150 mm lengths of 8.5 cm diameter PVC pipe buried into the soil, with plastic cups (diameter = 8.6 mm, height = 12.2 mm) inside the pipe, flush with the soil surface. Approximately 200 ml of 100% propylene glycol was added to each trap as preservative. A protective plastic plate (diameter 180 mm) was positioned 2 cm above the trap to prevent flooding and disturbance. Traps were operational for exactly 30 days for each of three sampling periods (spring, summer and autumn 2011/2012). Traps were then collected and the contents transferred immediately to 96% ethanol. Spatial

autocorrelation and pitfall trap depletion effects on beetles are not significant for our scale of sampling in this forest type (Baker & Barmuta 2006). Species had to be collected at least six times to be included in this study. This provided six specimens of each species for trait measurements, and excludes species from analysis that may have been collected by chance.

C.2.2 Trait calculations.

Morphological measurements were made using a calibrated USB microscope camera (Luminoptic ©CMOS-IS 500) mounted on a Leica ©MZ6 dissecting microscope using a range of magnifications (a maximum of 40x). Calibration was performed regularly for each microscope magnification. Images were analysed using Luminoptic IS capture ©. How morphological traits were measured is listed in Table 1 (in the main text) and the location of measurements is shown in Fig. C2.1.

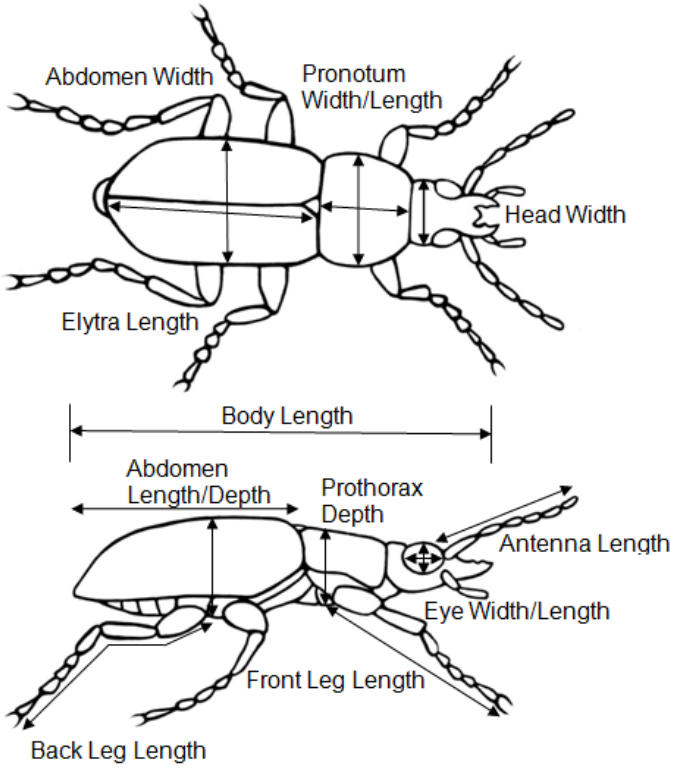

Figure C2.1. Morphological functional traits of beetles measured in this study.

Colour was measured using a Ocean Optics USB 4000 spectrophotometer optimised for near infrared measurement (~250µM-1000µM), a 200 µm reflectance probe with a white LED with constant current power supply. Measurements were conducted in controlled light conditions with the reflectance probe held in place at a 90° angle, 4 mm from the beetle. The spectrophotometer was calibrated before measurement was conducted each day using the WS 1 diffuse reflectance standard. Measurements were taken using 2° observer angle and D65 illuminant (standard daylight). Measurements were processed using Ocean Optics Spectra-Suite © spectroscopy platform.

Habitat occupation and seasonal activity were calculated using the transect dataset excluding the 70 m plot. Plots were divided into three habitats; mature forest (-15, -35 m in mature forest), near edge (15 and 35 m into secondary forest) and far away from edge (120 and 200 m into secondary forest) for each age (~7, ~27, ~45 and mature) for a total of 9 habitats. Then the ratio ——————— was calculated for each species. Sampling was conducted in spring, summer and autumn and seasonality was calculated similarly ———————.

C.2.3 Environmental data

We measured 17 environmental and biotic variables from all plots. Vegetation cover, plant species diversity, average tree diameter and percentage litter, moss, and coarse woody debris (CWD) cover were measured in10×10 m quadrats adjacent to the pitfall trap. Maximum diameter of woody material was also measured at each quadrat (minimum diameter 5 mm). At each quadrat, four 0-10 cm depth soil cores were taken and combined together. Within 48 hours of collection, each sample was stored in a paper bag in a cool dry area until ready for analysis. Soil was sieved using a 2mm sieve to remove leaf litter, roots and rocks and then ground in a mortar and pestle. The soil pH and conductivity were measured using a Palintest pH meter and an Elmetron CPC-411 conductivity meter, calibrated on each day of testing. We followed the Palintest Ltd procedure of shaking a 1:4 solution of soil to distilled water for one minute prior to taking the pH meter reading. For conductivity, we used a 1:5 solution of soil to distilled water shaken for 2 minutes and allowed this to settle

before reading as per the manufacturer's instructions. Nitrogen and carbon were analysed using a Perkins Elmer Series II 2400 CHNS/O Elemental Analyser following the manufacturer's protocol.

Litter depth was also recorded, with four measurements taken to the nearest mm with vernier calipers within one metre of pitfall traps and averaged. Leaf area index (LAI) was measured directly over the trap using hemispherical photography and analysed using Scion© Image (Bréda, 2003). Variable collinearity was screened using draftsmans plots and nitrogen was excluded as it was strongly correlated with carbon, reducing the environmental datset to 16 variables (Table C2.1).

Table C2.1. Environmental variables.

Variable	Unit	Sampling details
Carbon	%	4 soil sub-samples within 5 m of the pitfall trap
Soil C:N ratio		4 soil sub-samples within 5 m of the pitfall trap
Soil pH		4 soil sub-samples within 5 m of the pitfall trap
Conductivity	µS/cm	4 soil sub-samples within 5 m of the pitfall trap
Rock cover	%	cover within the quadrat
Bare ground	%	cover within the quadrat
Vegetation cover	%	cover within the quadrat
Litter cover	%	cover within the quadrat
Moss ground cover	%	cover within the quadrat
CWD cover	%	cover within the quadrat
Litter depth	mm	Average of 6 measurements around the pitfall trap
Plant diversity	N1	Exponential first Hill number (Chao et al., 2013) of plant species within the quadrat
Leaf Area Index		Hemispherical photo directly above the pitfall trap
CWD diameter	mm	Largest diameter of coarse woody debris within a 5 m radius of the pitfall trap
Succession	1-4	1:~7 y.o. forest, 2:~27 y.o forest 3: ~45 y.o. forest, 4: Mature forest

Quadrat is the 10 x10m quadrat associated with each pitfall trap.

C.2.4 Phylogenetic methods

DNA was extracted from one individual of each common species (≥6 individuals collected) using Qiagen DNeasy© Blood and Tissue Kit, with modification to enable DNA extraction without external damage to the specimen. Whole specimens were placed in 2 mL Eppendorf tubes and immersed in Qiagen ATL buffer (volume dependent on specimen size) and 40 µL of proteinase K, and incubated at 56°C with gentle agitation for 24 h. Specimens were then removed and placed in 100% EtOH

for 4 h to stop further digestion. Specimens were then air dried and re-pinned to facilitate functional trait analysis. Subsequent DNA extraction steps followed the standard Qiagen DNeasy protocol as per manufacturer's instructions.

Amplification of the ~700 bp mitochondrial COI (Cytochrome Oxidase subunit 1) (Folmer et al., 1994) and the 180 bp ribosomal 28S D3 (Thormann et al., 2011) regions were conducted using QIAGEN Multiplex PCR Mastermix following the protocol developed by Thormann *et al.*. (2011). See Table C2.2 for primer details. Samples were then purified and bi-directionally sequenced by Macrogen Inc. (Seoul, Republic of Korea; www.macrogen.com).

DNA sequences were assembled using Genious© software and each region was aligned using the MUSCLE procedure (Edgar, 2004), with a gap open score of -150, but otherwise using the default settings. Both regions were concatenated and jModelTest 2 (Darriba et al., 2012) was employed to find the best fit nucleotide substitution model for each region independently amongst a set of candidates. The GTR+ Γ distribution was the best fit for both alignments, but each partition ran the model independently. MrBayes (Huelsenbeck & Ronquist, 2001) was used to generate the phylogenetic tree using two million Monte Carlo generations. Species were constrained by their superfamily groups based on the phylogeny of Hunt et al., (2007).

Table C2.2. Primers used in this study.

Primer name	Region	Primer sequence 5'3	Reference
LCO1490	COI	GGT CAA CAA ATC ATA AAG ATA TTG G	Folmer et al. (1994)
HCO2198	COI	TAA ACT TCA GGG TGA CCA AAA AAT CA	Folmer et al. (1994)
CD3F	28SD3	GGACCC GTC TTG AAA CAC	Raupach et al. (2010)
CD3R	28SD3	GCA TAG TTC ACCATC TTT	Raupach et al. (2010)

C.2.5 Statistical methods

TDAP/TCAP

Trait convergence assembly pattern (TCAP) and trait divergence assembly patterns (TDAP) (see Table C2.3 for definitions and ecological significance of these and other terms) were calculated using four input datasets for phylogeny, traits, beetle species abundances and environmental variables. The complete trait dataset **Tr** and then a reduced dataset of traits that maximised either TCAP or TDAP (using an iterative method developed by Pillar & Sosinski (2003)) were used to test Hypotheses I-III. See Figure C2.3 for explanation of input data sets and calculation approaches. Matrix $\mathbf{T_d}$ (the abundance-weighted trait means or community-weighted means) is generated by matrix multiplication of **Tr** (standardized trait data) and **Sp** (square root transformed beetle species abundance data) for each plot using Euclidean distance.

Table C.2.3. Common acronyms used in the text and their ecological significance (modified from Pillar & Duarte (2010)).

Acronym	Definition
PE	**Phylogenetic structure:** The correlation between phylogenetic fuzzy-weighted species composition (P) and the environmental gradient (E) (succession in this study); referred to as ρ(PE). Significant PE suggests that the successional gradient and phylogenetic structure are linked; i.e. evidence of phylogenetic filtering.
PSM	**Phylogenetic Signal at a Metacommunity level:** The correlation between phylogenetic fuzzy-weighted species composition (P) and trait values (T); referred to as ρ(PT). If PT is significant, metacommunities with similar trait values also share similar phylogenetic structure, indicating potential phylogenetic niche conservatism.
PSS	**Phylogenetic Signal at a Species pool level:** The Mantel correlation between traits (Td) and phylogenetic distance (Pd) or ρ(Pd, Td). Significant PSS suggests that phylogeny is constraining species traits.
TCAP (TE)	**Trait Convergence Assembly Patterns:** The Mantel correlation between community-weighted trait values (T) and the succession gradient (E) or ρ(TE). Significant TE is indicative of successional filtering processes being important.
TDAP (XE.T)	**Trait Divergence Assembly Patterns:** The Mantel correlation of trait fuzzy-weighted species composition (X) and the succession gradient (E) with the convergence pattern removed (.T) using partial Mantel correlation ρ(XE.T). Significant XE.T is evidence for biotic interactions shaping trait values.
TE.P	**Trait convergence with the effect of phylogeny removed:** The Mantel correlation between community-weighted trait values (T) and the succession gradient (E) with phylogenetic distance (.P) removed using partial Mantel correlation ρ(TE.P). If significant, it demonstrates that successional filtering is independent of phylogeny.

TCAP patterns are distinguished via the mantel correlations of the distance matrices $\mathbf{T_d}$ and $\mathbf{E_d}$ to give ρ(**TE**). TDAP is assessed by computing a further matrix correlation ρ(**XE.T)** which is a partial mantel correlation between X and E removing the convergence signal of **T**. Matrix **X** is generated by assessing the degree of belonging to each trait fuzzy group for each individual beetle using fuzzy group approach (Pillar & Orlóci, 1991). The fuzzy trait allocation approach assigns traits into multiple functional groups based on trait similarity. For each species, the degree of belonging (between 0-1) to each functional group is calculated (dataset **Tf**) (see Pillar et al., 2009 for calculation details). Tf is then multiplied by Sp to generate

matrix X_d. The **ρ(XE)** expresses both TCAP and TDAP, so the convergence component is removed via partial Mantel correlation to generate ρ(**XE.T**) which is used to assess TDAP. Both TDAP and TCAP are tested the same way against a null model (i.e. that there is no assembly pattern) by permuting the row vectors (species) of **Tr** and **Tf**. The species composition dataset was unchanged to preserve real data structures. For TCAP, for example, matrix multiplication $\mathbf{T_{(random)}} = \mathbf{Tr_{(random)}} \times \mathbf{Sp}$ defines one possible null trait average. The environmental matrix ($\mathbf{E_d}$) was also not randomised to preserve the gradient data structure. Then ρ($\mathbf{T_{random}E_D}$) was recalculated for 10000 permutations to compare to the observed ρ(**TE**) to test if the proportion of ρ($\mathbf{T_{random}E}$) were not less than the observed value or ρ($\mathbf{T_{(perm)}}$; $\mathbf{E_D}$)≥ρ(**TE**) (Pillar et al., 2009)**.**

Using Euclidean phylogenetic distance, phylogenetic signal at a metacommunity level (PSM) was calculated in an analogous way to matrix **X** using permutation tests based on the randomization of **Pf**. A significant ρ**(PT)** suggests that communities that are phylogenetically similar also have similar trait values. Phylogenetic signal at a species pool level (PSS) was analysed in this framework by testing for correlation between the phylogenetic ($\mathbf{Ph_d}$) and trait ($\mathbf{Tr_d}$) similarity matrices to generate ρ($\mathbf{Ph_dTr_d}$). Phylogenetic structure related to successional stage ρ(**PE**) was also assessed for both trophic groups. See Pillar & Duarte, (2010) for further details. These analyses were conducted in R (R Development Core Team,) using packages SYNCSA (Debastiani & Pillar, 2012) and Picante (Kembel et al., 2010)

RLQ and fourth corner analysis

The combined RLQ and fourth corner analysis approach aims to assess how functional traits and environmental characteristics co-vary with species composion and each other (RLQ), and then test for individual trait-environment realtionships (fourth corner). Initially, variable collinearity was screened using draftsmans plots and nitrogen was excluded since it was strongly correlated with carbon, resulting in a environmental dataset of 16 parameters. As the functional traits were not independent of phylogeny, phylogenetic eigenvector regression (PEV) was

performed on each functional trait to control for phylogenetic autocorrelation (see Diniz-Filho et al. 2012 for details).

Using RLQ analysis, (Dolédec et al., 1996) the trait PEV residuals or $\mathbf{T_{-P}}$ were tested against the complete set of environmental variables (**E**) mediated by species compostion (**Sp**) (Figure C2.3). Using this technique, correspondance analysis was applied to **Sp** (categorical data), and, as **E** and **Tr** were quantitative, principle components analysis (PCA) was used. Co-inertia analysis is a multivariate method for coupling the three ordinations (Dolédec et al., 1996). This summarises the costructure of **E**, **Sp** and $\mathbf{T_P}$ on one set of axes and graphically presents it as an ordination plot.

Coupled with this, we analysed individual bivariate trait-environment relationships using the fourth corner routine outlined by Dray et al., (2014). This technique computes beetle trait-environment correlations using **E**, **Sp** and $\mathbf{T_{-P}}$. The null hypothesis H_o is that species assemblages are randomly attributed to sites, irrespective of both the environnmental characteristics and the beetle functional traits. Rejecting the null hypothesis is a two-step process concerning two different alternative hypotheses, H_1 and H_2. H_1 is that there is not a link between beetle composition and function traits, and that environment is the likely driver of species composition (**E**→**Sp**). This is tested by permuting *rows* (sites) of matrix **Sp** (permutation model 2 of Dray & Legendre (2008)). H_2 is that there is not a link between beetle composition and environment, therefore traits of beetles are likely to be important in structuring species composition ($\mathbf{T_{-P}}$ →**Sp**), for example because of species' interactions. This is tested by permuting *columns* (species) of matrix **Sp** (permutation model 4 of Dray & Legendre (2008)). H_o can only be rejected if $P \geq 0.05$ for both H_1 and H_2, and then then the combined approach (permutation model 6 of Dray & Legendre (2008)) can assess trait-environment relationships. As there were a large number of bivariate relationships tested, 50000 permutations were run, and the false discovery rate (False Discovery Rate (FDR) (Benjamini, 1995)) was used to adjust P-values such that only relationships with an $P \leq 0.1$ were overlaid on

the RLQ analysis. This analysis was done using ‘ade4’ package in R (Thioulouse et al., 1997).

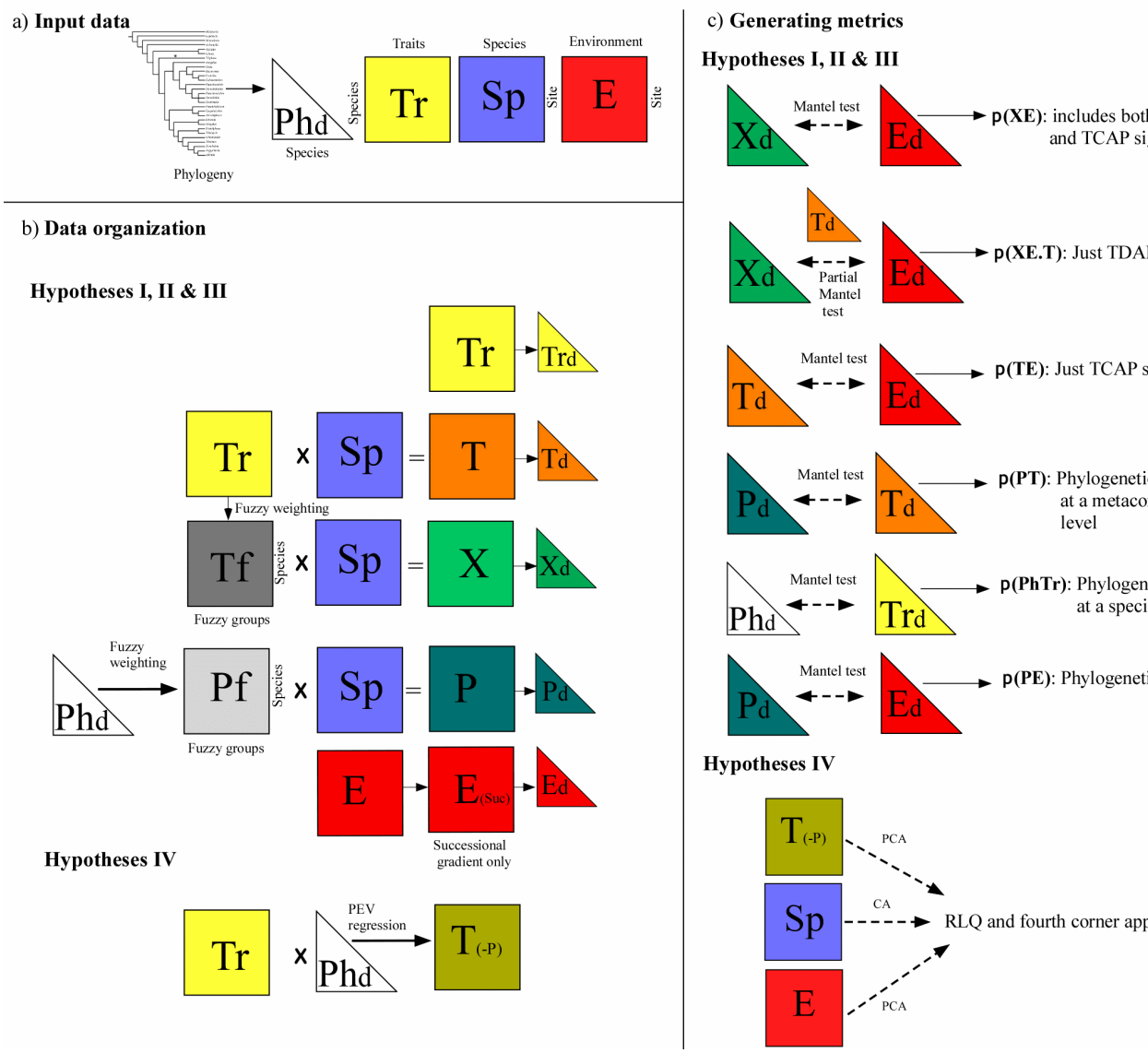

Fig.C.2.3. Input data and schematic summary of the analysis pathway used to address study hypotheses. The approach and symbols are modified from Pillar et al. 2009 and Pillar & Duarte (2010). a): The input data, b): data organization, c): tests used to generate metrics. Squares are datasets and triangles are Euclidean distance matrixes. Analysis pathways were conducted separately for detrivores/primary consumers and predators. Both unmodified Tr and TCAP- or TDAP-optimised trait sets were used to adress Hyptheses I-III.

C.3. Phylogenetic tree of beetlespecies and summaries ofspecies traits and indicator values in this study.

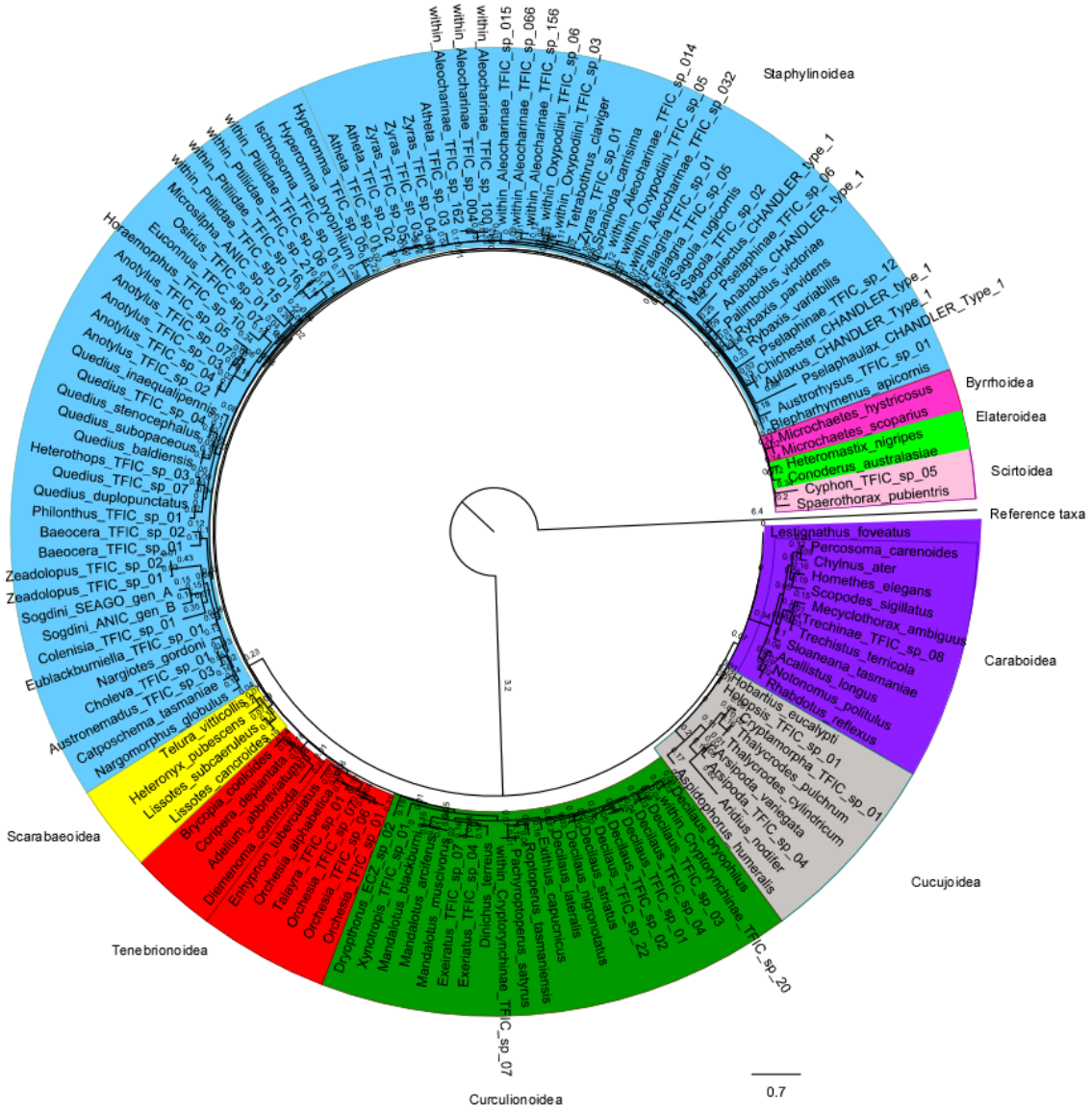

Figure C.3. Phylogenetic tree based on COI and 28SD3 regions for the species used in this study. Different colours refer to different beetle super-families based on Hunt *et al.*.(2007).

Table C.3.1. Detritvore/primary consumer species' functional traits and significant indicator species of forest succession from Baker (2006) and Fountain-Jones et al. (in press (b)). Values have not been phylogenetically corrected. See Table 4.1 in the main text for measurement details.

Species	Body length†	Antennae length†*	Eye Size ††*	Elytra length†*	Wings	Average leg length†*	Leg ratio°	Robustness††*	Seasonal activity°	Habitat occupation°	Dominant wavelength°°	CIE Lø	CIE Aø	CIE Bø
CHRYSOMELIDAE														
Arsipoda TFIC sp 04	2.138	0.486	0.140	0.689	1	1.184	-0.431	-0.484	0.667	0.222	557.600	56.167	4.983	-4.167
Arsipoda variegate (~7)	2.335	0.476	0.274	0.717	1	1.213	0.388	-0.233	0.333	0.111	521.600	49.760	4.440	-1.660
SPHINDIDAE														
Aspidophorus humeralis	1.915	0.237	0.166	0.549	1	1.118	-0.439	-0.285	0.333	0.333	562.033	78.667	13.317	-16.700
SILVANIDAE														
Cryptamorpha TFIC sp 01	2.854	0.483	0.098	0.657	1	0.945	-0.198	0.173	0.333	0.222	553.420	57.800	4.120	40.900
HOBARTIIDAE														
Hobartius eucalypti	2.331	0.261	0.128	0.621	1	1.178	-0.042	-0.282	0.333	0.111	557.400	53.533	3.150	-27.867
CORYLOPHIDAE														
Holopsis TFIC sp 01	1.742	0.219	0.098	0.790	1	1.045	-0.026	-0.417	0.667	0.444	563.500	78.250	13.650	-15.800
NITIDULIDAE														
Thalycrodes cylindricum	2.654	0.224	0.022	0.687	1	1.180	1.683	-0.187	0.667	1.000	558.633	37.117	22.433	-19.983
Thalycrodes pulchrum	2.906	0.228	-0.002	0.596	1	1.176	-0.333	-0.347	1.000	1.000	562.283	35.283	21.633	-22.817
CURCULIONIDAE														
Decilaus bryophilus	2.104	1.000	0.055	0.624	0	1.426	-0.314	-0.455	1.000	0.333	558.800	62.200	4.967	-1.133
Decilaus lateralis	2.604	0.320	0.021	0.662	0	1.328	-0.060	-0.398	1.000	1.000	588.950	29.033	10.050	-1.283
Decilaus nigronotatus (Mature)	2.137	0.364	-0.012	0.515	0	1.086	-0.337	-0.364	1.000	1.000	543.967	59.417	6.667	-4.750
Decilaus striatus (Mature)	2.175	0.283	0.075	0.619	0	1.274	-0.567	-0.419	1.000	1.000	547.767	57.533	6.383	-5.300
Decilaus TFIC sp 01 (~45)	3.566	1.000	-0.169	0.575	0	1.204	-0.668	-0.266	1.000	0.889	560.483	41.717	8.033	-8.267
Decilaus TFIC sp 02	2.802	1.000	-0.214	0.610	0	1.152	-0.724	-0.445	1.000	0.556	550.833	52.367	6.283	-4.917
Decilaus TFIC sp 03	2.474	1.000	0.033	0.612	0	1.403	-0.648	-0.396	1.000	0.667	552.800	49.000	6.133	-5.483
Decilaus TFIC sp 04	3.011	1.000	-0.186	0.615	0	1.405	-0.585	-0.388	1.000	0.778	553.117	60.317	5.400	-4.717
Decilaus TFIC sp 22	2.464	0.366	0.025	0.557	0	1.267	-0.598	-0.389	0.333	0.222	562.600	35.717	6.767	-6.533
Dinichus terreus	9.316	0.247	-0.243	0.677	0	1.317	-0.236	-0.253	1.000	0.556	554.167	24.533	16.500	-14.000
Exeriatus TFIC sp 04	5.756	0.426	-0.022	0.646	0	1.380	-0.576	-0.165	0.000	0.111	562.780	20.060	9.680	-7.800
Exeiratus TFIC sp 07	2.751	0.322	-0.049	0.625	0	1.129	-0.556	-0.354	0.667	0.556	544.767	50.383	7.600	-6.000
Exithius capucnicus	5.382	0.347	0.026	0.660	0	1.410	-0.477	-0.386	0.333	0.111	559.117	27.100	16.533	-11.533
Mandalotus arciferus	5.108	0.347	0.010	0.572	0	1.329	-0.308	-0.249	1.000	0.889	541.050	30.167	15.583	-8.783
Mandalotus blackburni	6.822	0.361	0.020	0.517	0	1.232	-0.448	-0.241	0.333	0.111	547.850	29.200	16.933	-9.533
Mandalotus muscivorus	3.940	0.363	0.038	0.573	0	1.276	-0.424	-0.039	1.000	1.000	557.967	30.133	12.550	-11.033
Pachyroptoperus satyrus	16.581	1.000	-0.124	0.650	1	1.809	-0.509	0.482	0.333	0.333	557.917	22.900	14.500	-14.617
Roptoperus tasmaniensis	3.416	0.299	-0.208	0.635	0	1.192	0.288	-0.246	1.000	1.000	557.067	28.333	11.350	-10.133

within Cryptorynchinae TFIC sp 07 (~45)	4.496	1.000	-0.166	0.643	0	0.870	-0.086	-0.370	1.000	1.000	526.133	31.017	15.033	-7.133
within Cryptorynchinae TFIC sp 20	1.661	0.356	0.028	0.599	0	0.697	-0.497	-0.443	0.333	0.222	532.750	66.650	9.550	-5.283
ANTHRIBIDAE														
Xynotropis TFIC sp 01	2.000	0.385	0.109	0.635	1	1.257	-0.346	-0.346	0.333	0.222	542.820	52.060	8.140	-5.280
TENEBRIONIDAE														
Adelium abbreviatum (~45)	11.458	0.331	-0.107	0.646	0	1.239	0.234	-0.129	1.000	0.778	573.833	32.367	4.417	7.900
Brycopia coeloides	6.228	0.290	-0.163	0.650	0	0.976	-0.389	-0.118	0.667	0.556	609.667	26.700	6.433	3.533
Coripera deplantata	17.604	0.269	-0.093	0.662	0	1.163	0.117	-0.087	0.333	0.222	583.333	25.983	3.667	6.217
Diemenoma commoda	8.951	0.325	-0.099	0.658	0	1.019	0.092	-0.033	0.000	0.222	562.940	19.860	11.680	8.740
ZOPHERIDAE														
Enhypnon tuberculatus	2.252	0.198	-0.072	0.581	1	0.834	-0.622	-0.271	0.667	0.333	551.350	51.700	7.817	-5.733
MELANDRYIDAE														
Orchesia alphabetica	3.379	0.244	-0.028	0.778	1	1.102	0.003	-0.021	1.000	1.000	564.550	39.133	17.217	-20.850
Orchesia TFIC sp 01	3.107	0.252	0.038	0.760	1	1.227	1.111	-0.019	1.000	0.333	562.633	39.433	18.967	-20.967
Orchesia TFIC sp 06	2.313	0.246	0.062	0.811	1	1.097	0.413	-0.115	0.333	0.222	559.333	46.833	14.717	-17.117
Orchesia TFIC sp 07	3.168	0.239	0.048	0.699	1	1.065	0.524	-0.069	0.333	0.111	565.480	43.720	15.020	-20.460
Talayra TFIC sp 01	2.758	0.307	0.077	0.792	1	0.773	-4.854	-0.108	0.333	0.222	563.650	46.350	15.667	-18.583
SCARBAEIDAE														
Heteronyx pubescens	11.345	0.083	-0.126	0.674	1	1.060	0.222	-0.007	0.667	0.111	633.400	38.500	12.080	7.980
Telura vitticollis	11.544	0.189	0.133	0.805	1	0.812	-0.753	-0.044	0.333	0.333	615.500	34.983	6.617	8.500
LUCANIDAE														
Lissotes cancroides	12.509	0.184	-0.091	0.550	0	1.016	-0.120	-0.193	0.667	0.889	621.167	27.200	5.133	0.183
Lissotes subcaeruleus (~7)	12.778	0.193	-0.028	0.557	0	1.101	-0.156	-0.237	0.333	0.556	472.400	19.100	5.360	-45.960
STAPHYLINIDAE														
Anotylus TFIC sp 02	4.799	0.219	-0.105	0.199	1	0.746	-0.490	0.370	1.000	0.889	546.933	66.317	7.333	-5.833
Anotylus TFIC sp 03	3.808	0.233	-0.066	0.169	1	0.776	-0.237	0.350	1.000	1.000	547.183	74.267	6.483	-5.050
Anotylus TFIC sp 04	3.893	0.168	0.013	0.253	1	0.905	-0.167	0.131	1.000	0.778	548.067	69.167	7.267	-5.233
Anotylus TFIC sp 05	4.186	0.224	-0.067	0.149	1	0.726	-0.659	0.447	1.000	0.889	533.000	82.050	9.975	-5.225
Anotylus TFIC sp 07	5.176	0.208	-0.115	0.166	1	0.704	-0.936	0.452	1.000	0.556	533.717	82.183	10.733	-5.267
Austronemadus TFIC sp 03	3.543	0.333	-0.116	0.739	1	1.376	0.984	-0.234	1.000	1.000	538.200	28.833	16.867	-11.950
Austrorhysus TFIC sp 01	2.403	0.334	0.036	0.414	1	0.750	-0.824	0.029	0.333	0.222	561.425	43.150	5.100	-46.775
Baeocera TFIC sp 01	1.743	0.321	0.199	0.547	1	1.041	-0.226	-0.436	0.667	0.444	556.067	76.350	8.117	-7.600
Baeocera TFIC sp 02	1.953	0.273	0.135	0.479	1	0.905	-0.129	-0.298	1.000	0.889	558.750	74.817	7.333	-6.600
Osirius TFIC sp 01	5.260	0.166	-0.226	0.206	1	0.619	-0.752	0.052	0.333	0.222	552.000	79.133	6.917	-5.867
LEIODIDAE														
Catposchema tasmaniae	4.879	0.270	0.220	0.759	1	1.237	3.810	-0.155	0.667	0.333	565.367	23.967	16.517	-23.183
Choleva TFIC sp 01	2.414	0.209	0.104	0.775	1	1.239	2.302	-0.254	1.000	0.889	565.250	34.017	19.733	-23.283
Colenisia TFIC sp 01	1.456	0.203	0.211	0.730	1	1.127	1.207	-0.491	0.667	0.444	562.617	54.017	4.533	-47.767
Eublackburniella TFIC sp 01	3.228	0.445	0.186	0.773	1	1.178	0.184	-0.364	0.667	0.333	565.483	22.150	16.567	-21.350
Nargiotes gordoni	3.074	0.384	0.054	0.744	1	1.445	1.229	-0.128	0.333	0.444	580.483	34.633	19.567	-24.600
Nargomorphus globulus	1.959	0.287	0.031	0.759	1	1.123	0.511	-0.319	1.000	1.000	559.517	31.867	12.467	-8.400

Sogdini ANIC gen B	2.716	0.282	0.225	0.673	1	0.792	-2.664	-0.274	0.333	0.222	565.667	31.483	16.417	-20.767
Sogdini SEAGO gen A	3.026	0.269	0.200	0.659	1	0.829	0.465	-0.291	0.667	0.444	560.267	34.250	21.300	-20.450
Zeadolopus TFIC sp 01	2.068	0.225	0.169	0.593	1	0.731	-0.544	-0.349	0.333	0.222	561.560	50.880	7.640	-7.660
Zeadolopus TFIC sp 02	1.670	0.218	0.216	0.689	1	1.032	-0.195	-0.567	0.667	0.667	548.267	43.650	8.533	-6.467
PTILIDAE														
within Ptiliidae TFIC sp 01	0.899	0.342	0.132	0.687	1	0.708	-0.536	-0.433	1.000	0.444	551.900	78.917	4.550	-3.483
within Ptiliidae TFIC sp 06	0.775	0.462	0.132	0.529	1	0.713	-0.371	-0.370	1.000	0.444	550.560	69.040	6.000	-4.940
within Ptiliidae TFIC sp 16	0.950	0.391	0.159	0.506	1	0.666	-0.172	-0.345	0.667	0.222	551.533	76.817	5.483	-3.667
within Ptiliidae TFIC sp 21	0.899	0.391	0.132	0.687	1	0.797	-0.115	-0.345	0.000	0.222	551.900	78.917	4.550	-3.483
BYRRHIDAE														
Microchaetes hystricosus	2.614	0.184	-0.008	0.735	1	1.225	-0.558	-0.544	0.667	0.667	572.433	18.200	-3.867	29.583
Microchaetes scoparius (~7)	3.806	0.120	0.147	0.805	1	1.133	-0.454	-0.408	0.333	0.333	569.733	13.700	-0.883	28.417
ELATERIDAE														
Conoderus australasiae	14.615	0.289	-0.106	0.640	1	0.713	0.142	0.197	0.333	0.111	562.720	31.960	7.880	-76.720
CANTHARIDAE														
Heteromastix nigripes	3.576	1.176	-0.311	0.840	1	0.839	-0.355	0.129	0.333	0.444	568.550	28.650	-6.233	16.050
SCIRTIDAE														
Cyphon TFIC sp 05	2.578	0.284	0.092	0.723	1	0.778	-0.199	-0.002	0.000	0.333	571.017	26.850	-6.333	31.467
CLAMBIDAE														
Spaerothorax pubientris (~7)	1.364	1.000	0.251	0.801	1	0.946	0.597	-0.524	0.333	0.222	556.250	50.917	19.300	-16.133

*Species names shown in bold type indicate significant indicator species ( ) brackets beside the species indicate which successional stage the species is an indicator. Measurement units- †: Log mm, ††: PCA score, †††: Presence/absence, °: Ratio, °°: Nanometers, ø: Colour coordinates. *measurement relative to body length.*

Table C.3.2. Predator species' functional traits and significant indicator species of forest succession from Baker (2006) and Fountain-Jones et al. (in press (b)).

Values have not been phylogenetically corrected. See Table 4.1 in the main text for measurement details.

Species	Body length†	Antennae length†*	Eye Size †**	Elytra length†*	Wings	Average leg length†*	Leg ratio°	Robustness†**	Seasonal activity°	Habitat occupation°	Dominant wavelength°°	CIE Lø	CIE Aø	CIE Bø
CARABIDAE														
Acallistus longus (~45)	11.792	1.054	-0.516	0.559	0	1.089	0.067	0.053	1.000	1.000	573.833	32.367	4.417	7.900
Chylnus ater (~45)	17.008	0.848	-0.597	0.537	0	0.996	-0.491	0.050	1.000	0.667	557.000	37.650	0.867	-1.417
Homethes elegans	7.594	1.141	-0.377	0.607	1	1.197	0.288	0.162	0.333	0.222	568.320	11.340	-10.360	19.660
Lestignathus foveatus	7.010	0.932	-0.242	0.654	0	1.201	1.130	0.032	1.000	0.889	576.067	16.433	1.200	6.750
Mecyclothorax ambiguous (~7)	5.082	1.235	-0.403	0.626	1	1.177	0.246	-0.059	0.667	0.333	585.733	9.967	2.483	8.350
Notonomus politulus	15.250	1.051	-0.360	0.605	1	1.388	0.781	-0.160	1.000	1.000	535.000	35.417	1.767	-0.767
Percosoma carenoides	23.229	0.758	-0.530	0.552	1	1.068	-0.226	0.117	1.000	0.889	500.833	47.433	0.900	-2.650
Rhabdotus reflexus	16.828	0.889	-0.313	0.607	0	1.182	0.597	-0.067	1.000	1.000	570.000	36.750	1.950	-0.617
Scopodes sigillatus	4.782	2.380	-0.537	0.553	1	0.894	0.103	0.177	0.667	0.556	581.783	2.850	1.200	4.850
Sloaneana tasmaniae	4.305	1.060	-0.423	0.666	1	0.932	-0.125	-0.153	1.000	1.000	577.933	6.150	0.483	9.283
Trechinae TFIC sp 08	5.137	1.019	-0.293	0.642	1	0.795	-0.124	-0.065	0.333	0.111	565.460	60.040	15.860	-22.340
Trechistus terricola	3.915	0.964	-0.377	0.622	1	0.838	-0.578	-0.094	1.000	0.444	576.417	13.050	-0.817	41.033
STAPHYLINIDAE														
Anabaxis CHANDLER type 1 (~7)	1.586	1.231	-0.446	0.360	1	1.328	0.281	-0.038	1.000	0.222	559.667	76.733	8.883	-10.217
Atheta TFIC sp 01	3.393	1.054	-0.560	0.207	1	0.795	-0.332	0.500	1.000	0.778	531.250	82.100	9.633	-5.017
Atheta TFIC sp 02	2.901	0.598	-0.666	0.135	1	0.765	-0.441	0.712	0.333	0.333	559.467	87.283	10.350	-10.100
Atheta TFIC sp 03	2.566	1.075	-0.490	0.256	1	0.938	-0.223	0.314	1.000	1.000	543.600	79.500	8.950	-2.900
Aulaxus CHANDLER Type 1	1.639	1.090	-0.341	0.332	0	1.698	0.625	-0.133	1.000	0.889	555.133	73.617	8.783	-7.883
Blepharhymenus apicornis	3.247	0.610	-0.627	0.193	1	0.762	0.189	0.643	0.667	0.444	547.160	79.540	10.740	-9.180
Chichester CHANDLER type 1	1.332	0.928	-0.493	0.299	0	0.995	0.742	0.061	0.333	0.111	563.880	83.900	12.640	-16.220
Euconnus TFIC sp 07	1.688	1.070	-0.364	0.566	1	1.300	-0.268	-0.194	1.000	0.889	539.950	73.350	9.000	-5.183
Falagria TFIC sp 01	3.104	0.837	-0.398	0.191	1	1.093	0.697	0.461	0.667	0.333	563.500	49.100	3.700	-1.300
Falagria TFIC sp 05	3.104	0.718	-0.408	0.193	1	0.908	0.283	0.534	0.667	0.222	507.783	80.950	6.317	-2.050
Heterothops TFIC sp 03	5.733	0.688	-0.565	0.205	1	0.674	-0.257	0.630	0.333	0.778	521.220	72.460	9.680	-2.840
Horaemorphus TFIC sp 10	1.602	0.978	-0.406	0.568	1	1.129	-0.129	-0.098	1.000	0.556	546.483	71.500	8.733	-6.267
Hyperomma bryophilum	8.648	0.498	-0.706	0.132	1	0.714	-0.287	0.843	0.333	0.222	542.350	64.333	11.250	-7.500
Hyperomma TFIC sp 05	6.838	0.670	-0.608	0.162	1	0.704	-0.088	0.737	0.333	0.444	540.740	75.800	12.080	-6.620
Ischnosoma TFIC sp 01	6.773	0.688	-0.656	0.219	1	0.679	0.217	0.701	0.333	0.222	555.433	72.433	6.733	-6.350
Macroplectus CHANDLER type 1	1.784	0.935	-0.426	0.330	1	0.961	0.071	0.011	0.333	0.333	553.200	52.060	3.480	-1.480
Microsilpha ANIC sp 15	1.512	1.504	-0.556	0.679	1	0.952	-0.196	-0.191	0.667	0.667	557.150	74.633	13.800	-11.433
Palimbolus victoriae	2.920	1.115	-0.356	0.298	1	1.311	-0.355	-0.226	1.000	0.333	578.050	82.767	10.167	-10.733
Philonthus TFIC sp 01	2.807	0.663	-0.561	0.157	0	0.854	-0.530	0.049	0.333	0.778	556.260	82.760	12.160	-12.900

Pselaphaulax CHANDLER Type 1	2.243	0.907	-0.359	0.288	1	1.033	-0.051	0.615	1.000	0.778	562.783	82.050	12.500	-14.883
Pselaphinae TFIC sp 06	2.146	1.098	-0.315	0.333	1	0.581	-0.387	-0.033	0.333	0.111	565.583	74.950	5.317	-2.050
Quedius baldiensis	5.613	0.818	-0.607	0.194	0	0.782	-0.615	0.240	1.000	0.222	559.317	40.767	8.000	-7.717
Quedius duplopunctatus	5.939	1.469	-0.630	0.174	1	0.758	-0.302	0.555	0.667	0.444	551.683	28.717	5.267	-4.467
Quedius inaequalipennis	6.297	0.996	-0.609	0.188	1	0.699	-0.487	0.466	1.000	0.556	553.217	32.917	7.383	-5.983
Quedius stenocephalus	4.430	0.713	-0.638	0.184	1	0.835	-0.334	0.612	0.667	0.444	563.233	25.967	11.933	-11.967
Quedius subopaceous	5.238	0.818	-0.607	0.194	1	0.808	-0.450	0.579	0.333	0.111	563.233	25.967	11.933	-11.967
Quedius TFIC sp 04	6.762	1.242	-0.687	0.194	1	1.684	0.943	0.461	0.667	0.778	564.033	27.267	5.900	-5.883
Quedius TFIC sp 07	7.700	1.058	-0.598	0.210	1	1.593	-1.059	0.416	0.333	0.222	558.633	28.700	7.217	-4.633
Rybaxis parvidens	2.166	1.071	-0.449	0.355	1	1.090	0.364	-0.102	0.333	0.333	554.417	75.083	8.667	-7.200
Rybaxis variabilis	2.243	1.138	-0.350	0.334	1	0.882	-0.143	-0.088	0.667	0.444	555.517	72.333	9.150	-8.750
Sagola rugicornis	2.828	0.935	-0.426	0.330	1	0.952	0.546	0.021	0.667	0.222	553.200	52.060	3.480	-1.480
Sagola TFIC sp 02	2.246	0.923	-0.426	0.330	1	1.002	0.751	0.013	0.333	0.111	559.200	54.060	5.480	-2.450
Spanioda carrisima	3.807	0.979	-0.503	0.237	1	1.552	11.590	0.386	1.000	1.000	539.833	72.350	6.683	-4.283
Tetrabothrus claviger	3.903	0.612	-0.694	0.177	1	0.896	1.908	0.514	0.333	0.444	555.660	72.660	7.380	-7.200
within Aleocharinae TFIC sp 004	1.746	1.056	-0.490	0.287	1	0.755	-0.094	0.230	0.333	0.333	553.580	85.040	10.020	-7.920
within Aleocharinae TFIC sp 014	1.933	1.071	-0.558	0.231	1	0.758	0.545	0.186	0.667	0.333	553.580	85.040	10.020	-8.920
within Aleocharinae TFIC sp 015	1.933	1.071	-0.558	0.231	1	0.885	0.508	0.352	0.333	0.222	556.150	82.650	10.517	-9.933
within Aleocharinae TFIC sp 032	3.948	0.730	-0.711	0.193	1	0.986	-0.145	0.523	0.333	0.333	557.020	79.940	12.100	-11.020
within Aleocharinae TFIC sp 066	2.287	1.330	-0.534	0.215	1	0.983	-0.395	0.200	0.333	0.444	561.483	53.217	5.200	-5.050
within Aleocharinae TFIC sp 100	1.746	1.056	-0.490	0.287	1	0.970	0.255	0.230	0.667	0.444	556.150	82.650	10.517	-9.933
within Aleocharinae TFIC sp 156	1.771	1.165	-0.519	0.241	1	1.424	-1.067	0.352	0.667	0.667	558.083	84.933	10.550	-10.450
within Oxypodiini TFIC sp 03	3.977	1.063	-0.658	0.223	1	0.669	0.220	0.413	0.333	0.222	549.480	45.860	4.540	-3.340
within Oxypodiini TFIC sp 05	3.963	0.505	-0.668	0.180	1	1.422	0.775	0.654	0.333	0.111	516.200	83.180	8.700	-3.160
within Pselaphinae TFIC sp 12	0.757	0.342	0.148	0.484	1	0.746	-0.448	-0.237	0.333	0.111	551.533	76.816	5.483	-3.666
Zyras TFIC sp 01 (~7)	4.693	0.682	-0.493	0.177	1	0.765	0.510	0.455	0.667	0.778	554.840	50.920	6.220	-4.480
Zyras TFIC sp 03	3.348	0.781	-0.654	0.192	1	0.994	-0.345	0.547	1.000	0.556	551.520	87.180	7.320	-6.000
Zyras TFIC sp 04	2.873	0.748	-0.612	0.183	1	0.780	-0.848	0.579	1.000	1.000	551.200	78.367	10.667	-7.833
Zyras TFIC sp 05	2.667	1.077	-0.471	0.243	1	0.783	-0.335	0.329	1.000	0.556	556.500	79.880	11.120	-10.160

*Species names shown in bold type indicate significant indicator species; ( ) brackets beside the species indicate which successional stage the species is an indicator of. Measurement units- †: Log mm, ††: PCA score, †††: Presence/absence, °: Ratio, °°: Nanometers, ø: Colour coordinates. *measurement relative to body length.*

C.4. Within-trait phylogenetic signal and phylogenetically-untransformed RLQ/fourth corner analysis.

Table C.4. Within-trait phylogenetic signal variation for both predators and decomposers/primary consumers.

	Predators		*Decomposers and primary consumers*	
Trait	**Bloomberg's K**	**P**	**Bloomberg's K**	**P**
Body length	0.904	***	0.591968	***
Eye size	0.205	*	0.424643	***
Antennae length	0.439	***	0.610701	***
Elytra length	1.459	***	1.754249	***
Wings	0.183	NS	0.347975	***
Average leg.length	0.143	NS	0.063624	***
Leg ratio	0.246	NS	0.161755	***
Robustness	0.500	***	0.231969	*
Seasonality	0.151	NS	0.481101	NS
Niche breadth	0.190	*	0.45348	*
Dominant wavelength	0.144	NS	0.495555	*
CIE. L	0.325	***	0.434838	***
CIE. A	0.237	*	0.230852	***
CIE. B	0.136	NS	0.241048	*

NS – not significant- P≥0.05, * P<0.05, **P<0.01, ***P<0.001.

K values around 1 indicate traits evolved under Brownian motion. K values greater than 1 indicate strong phylogenetic conservatism (Blomberg et al., 2003). Traits with significant ($\alpha = 0.05$) values have non-random phylogenetic signal.

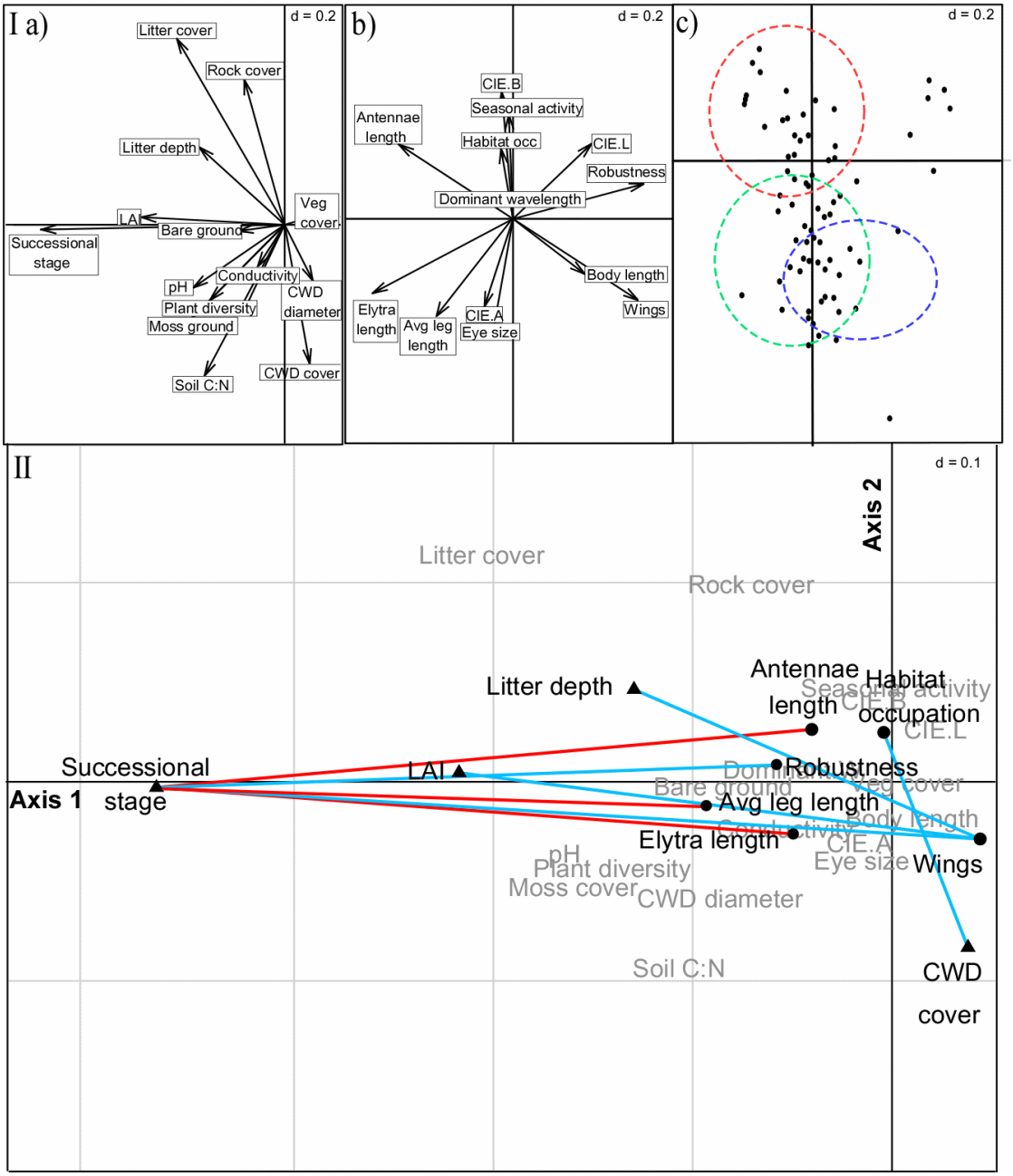

Figure C.4. Phylogenetically-untransformed RLQ/fourth corner analysis for decomposers/primary consumers. I) (a) Environmental variables PCA, (b) Functional trait PCA and (c) species PCOA results showing individual trait, environment and species variation. The blue circle indicates species common in ~7 year old forests, the green circle indicates mature forest species and the red circle indicates species associated with ~45 and ~27 year-old forest (see Appendix C.3). II) Combined RLQ and fourth corner analysis for decomposers/primary consumers across successional stages (fourth corner model 6). Permutation tests showed that there are significant global trait-environment relationships (P = 0.00012). Light blue lines indicate a significant negative relationship (P < 0.05) between the variables whereas red indicates a positive relationship.

C.5. Ordination of trait data for all three trophic groups.

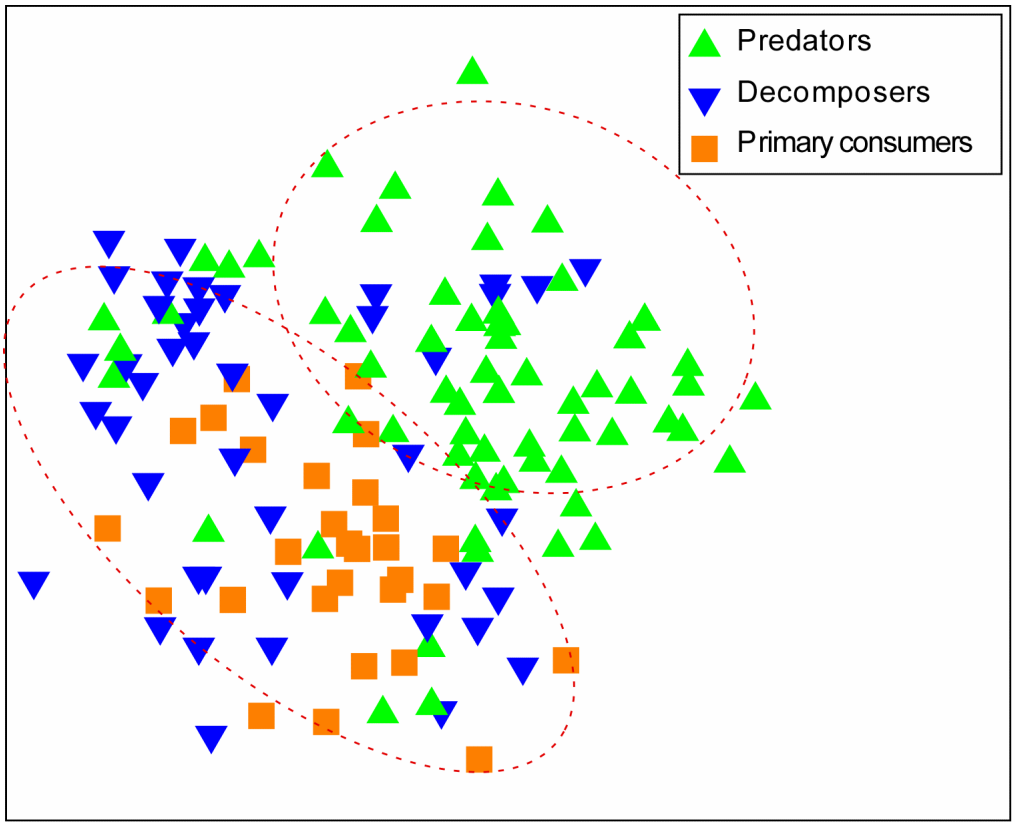

Figure C.5. Multidimensional scaling (MDS) ordination of phylogenetically corrected trait data using a Gower dissimilarity measure for the three major trophic groups (exluding habitat occupation and seasonal activity). Predators trait-space is separated from decomposers/primary consumers.

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Appendix D
Supplementary material to Chapter 5

D.1. Detailed functional and phylogenetic method details

D.1.1 Trait calculations

Morphological measurements were made using a calibrated USB microscope camera (Luminoptic ©CMOS-IS 500) mounted on a Leica ©MZ6 dissecting microscope down to 40x magnification. Calibration was performed regularly for each microscope magnification. Images were analysed using Luminoptic IS capture ©.

Colour was measured using ocean optics USB 4000 optimised for near infrared measurement (~250µM - 1000µM), 200 µm reflectance probe and white LED with constant current power supply. Measurements were conducted in controlled light conditions with the reflectance probe held in place at 90° 4 mm from the beetle. The spectrophotometer was calibrated before measurement was conducted each day using the WS 1 diffuse reflectance standard. Measurements were taken using 2° observer angle and D65 illuminant (standard daylight). Measurements were processed using Ocean Optics Spectra-Suite © spectroscopy platform.

Habitat occupation was calculated by counting how many plot types a species was collected. As there were 8 plot types (habitats) in our randomised block design, the ratio ——————————was calculated for each species. Seasonal activity was assigned to each species on the basis of a previous study (Fountain-Jones et al., in press (b)) that collected over multiple seasons, as there was significant species crossover with this study. In our previous study, sampling was conducted in spring (September - October 2011), summer (December - January, 2011/2012) and autumn (March - April 2012), and seasonality was calculated similarly ——————————. There were only five species that were unique to this study and these were given a score of 0.33 (collected in one season only).

D.1.2 Phylogenetic methods

DNA was extracted from one individual of each common species (≥6 individuals) using Qiagen DNeasy© Blood and Tissue Kit, with modification to enable DNA extraction without external damage to the specimen. Whole specimens were placed in 2 mL Eppendorf tubes and immersed in Qiagen ATL buffer (volume dependent on specimen size) and 40 µL of proteinase K, and incubated at 56°C with gentle agitation for 24 hours. Specimens were then removed and placed in 100% EtOH for 4 hours to stop further digestion. Specimens were then air dried and re-pinned to facilitate functional trait measurement. Subsequent DNA extraction steps followed the standard Qiagen DNeasy protocol as per manufacturer's instructions.

Amplification of the ~700 bp mitochondrial COI (Cytochrome Oxidase subunit 1) (Folmer et al., 1994) and the 180 bp ribosomal 28S D3 (Thormann et al., 2011) regions were conducted using QIAGEN Multiplex PCR Mastermix following the protocol developed by Thormann *et al.*. (2011). See Table D1 for primer details. Samples were then purified and bi-directionally sequenced by Macrogen Inc. (Seoul, Republic of Korea; www.macrogen.com).

DNA sequences were assembled using Genious© software and each region was aligned using the MUSCLE procedure (Edgar, 2004), with a gap open score of -150, but otherwise using the default settings. Both regions were concatenated and jModelTest 2 (Darriba et al., 2012) was employed to find the best fit nucleotide substitution model for each region independently amongst a set of candidates. The GTR+ Γ distribution was the best fit for both alignments, but each partition ran the model independently. MrBayes (Huelsenbeck & Ronquist, 2001) was used to generate the phylogenetic tree using two million Monte Carlo generations. Species were constrained by their superfamily groups based on the phylogeny of Hunt et al. (2007).

Table D.1. Primers used in this study.

Primer name	Region	Primer sequence 5'3	Reference
LCO1490	COI	GGT CAA CAA ATC ATA AAG ATA TTG G	Folmer et al., (1994)
HCO2198	COI	TAA ACT TCA GGG TGA CCA AAA AAT CA	Folmer et al., (1994)
CD3F	28SD3	GGACCC GTC TTG AAA CAC	Raupach et al.,(2010)
CD3R	28SD3	GCA TAG TTC ACCATC TTT	Raupach et al.,(2010)

D.1.3 Statistical methods

Trait convergence assembly pattern (TCAP) and trait divergence assembly patterns (TDAP) were calculated using four input datasets for phylogeny, traits, beetle species abundances and environmental variables. The complete trait dataset **Tr** and then a reduced dataset of traits that maximised either TCAP or TDAP was calculated using an iterative method developed by Pillar & Sosinski, (2003)). See Table D.2 for a list of abbreviations used, and Fig. D.1 for explanation of input data sets and calculation approaches. Matrix $\mathbf{T_d}$ (the abundance weighted trait means or community weighted means) is generated by matrix multiplication of **Tr** (standardized trait data) and **Sp** (square root transformed beetle species abundance data) for each plot using Euclidean distance.

Table D.2. Common acronyms used in the text and their ecological significance (modified from Pillar & Duarte, (2010)).

Acronym	Definition
PE	**Phylogenetic structure:** The correlation between phylogenetic fuzzy-weighted species composition (P) and the environmental gradient (E) (succession in this study); referred to as ρ(PE). Significant PE suggests that the successional gradient and phylogenetic structure are linked; i.e. evidence of phylogenetic filtering.
PSM	**Phylogenetic Signal at a Metacommunity level:** The correlation between phylogenetic fuzzy-weighted species composition (P) and trait values (T); referred to as ρ(PT). If PT is significant, metacommunities with similar trait values also share similar phylogenetic structure, indicating potential phylogenetic niche conservatism.
PSS	**Phylogenetic Signal at a Species pool level:** The Mantel correlation between traits (Td) and phylogenetic distance (Pd) or ρ(Pd, Td). Significant PSS suggests that phylogeny is constraining species traits.
TCAP (TE)	**Trait Convergence Assembly Patterns:** The Mantel correlation between community-weighted trait values (T) and the succession gradient (E) or ρ(TE). Significant TE is indicative of successional filtering processes being important.
TDAP (XE.T)	**Trait Divergence Assembly Patterns:** The Mantel correlation of trait fuzzy-weighted species composition (X) and the succession gradient (E) with the convergence pattern removed (.T) using partial Mantel correlation ρ(XE.T). Significant XE.T is evidence for biotic interactions in shaping trait values.
TE.P	**Trait convergence with the effect of phylogeny removed:** The Mantel correlation between community-weighted trait values (T) and the succession gradient (E) with phylogenetic distance (.P) removed using partial Mantel correlation ρ(TE.P). If significant, it demonstrates that successional filtering is independent of phylogeny.

TCAP patterns are distinguished via the mantel correlations of the distance matrices Td and Ed to give ρ(TE). TDAP is assessed by computing a further matrix correlation ρ(XE.T) which is a partial mantel correlation between X and E removing the convergence signal of T. Matrix X is generated by assessing the degree of belonging to each trait fuzzy group for each individual beetle using fuzzy group approach (Pillar & Orlóci, 1991). The fuzzy trait allocation approach assigns traits into multiple functional groups based on trait similarity. For each species, the degree of belonging (between 0-1) to each functional group is calculated (dataset **Tf**) (see Pillar et al. 2009 for calculation details). **Tf** is then multiplied by Sp to generate matrix $\mathbf{X_d}$. The **ρ(XE)** expresses both TCAP and TDAP, so the convergence component is removed via partial Mantel correlation to generate ρ(**XE.T**) which is used to assess TDAP. Both TDAP and TCAP are tested the same way against a null model (i.e. no assembly pattern) by permuting the row vectors (species) of **Tr** and **Tf**. The species composition dataset was unchanged to preserve real data structures.

For TCAP, for example, matrix multiplication $\mathbf{T_{(random)}} = \mathbf{Tr_{(random)}} \times \mathbf{Sp}$ defines one possible null trait average. The environmental matrix ($\mathbf{E_d}$) was also not randomised to preserve the gradient data structure. Then $\rho(\mathbf{T_{random}E_D})$ was recalculated for 10000 permutations to compare to the observed $\rho(\mathbf{TE})$ to test if the proportion of $\rho(\mathbf{T_{random}E})$ were not less than the observed value or $\rho(\mathbf{T_{(perm)}}; E_{\mathbf{D}}) \geq \rho(\mathbf{TE})$ (Pillar et al., 2009).

Using Euclidean phylogenetic distance, phylogenetic signal at a metacommunity level (PSM) was calculated in an analogous way to matrix **X** using permutation tests based on the randomization of **Pf**. A significant $\rho(\mathbf{PT})$ suggests that communities that are phylogenetically similar also have similar trait values**.** Phylogenetic signal at a species pool level (PSS) was analysed in this framework by testing for correlation between the phylogenetic ($\mathbf{Ph_d}$) and trait ($\mathbf{Tr_d}$) similarity matrices to generate $\rho(\mathbf{Ph_dTr_d})$. Phylogenetic structure related to successional stage $\rho(\mathbf{PE})$ was also assessed for both trophic groups. See Pillar & Duarte, (2010) for further details. These analyses were conducted in R (R Development Core Team) using packages SYNCSA (Debastiani & Pillar, 2012) and Picante (Kembel et al., 2010).

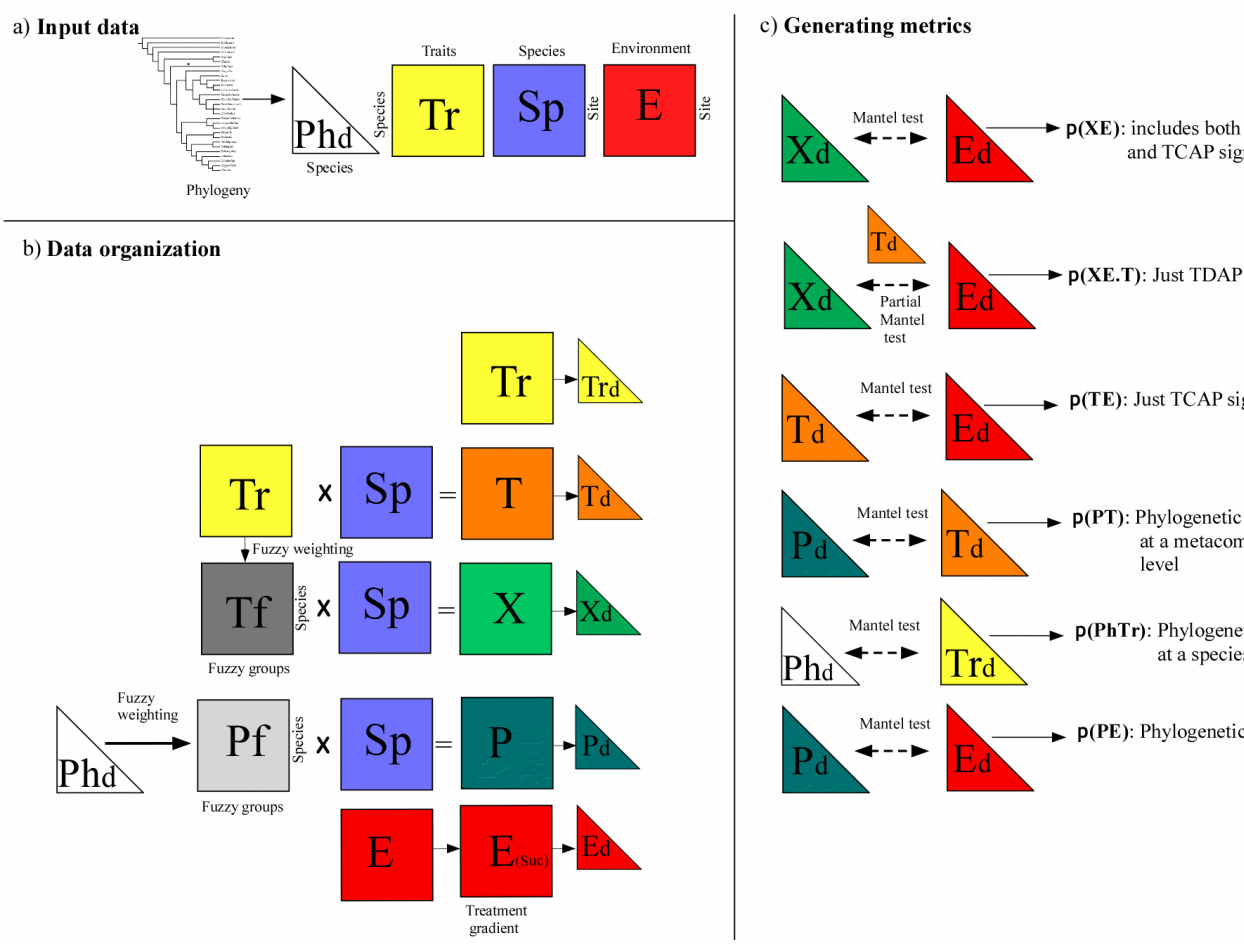

Fig. D.1. Input data and schematic summary of the analysis path used used to calculate trait divergence and convergence patterns. The approach and symbols are modified from Pillar et al. 2009; Pillar & Duarte (2010). a): The input data, b): data organization, c): tests used to generate metrics. Squares are datasets and triangles are Euclidean distance matrixes. Both unmodified **Tr** and TCAP- or TDAP-optimised trait sets were used to adress Hyptheses I-III.

D.2. Phylogenetic tree of species and species traits and indicator values in this study.

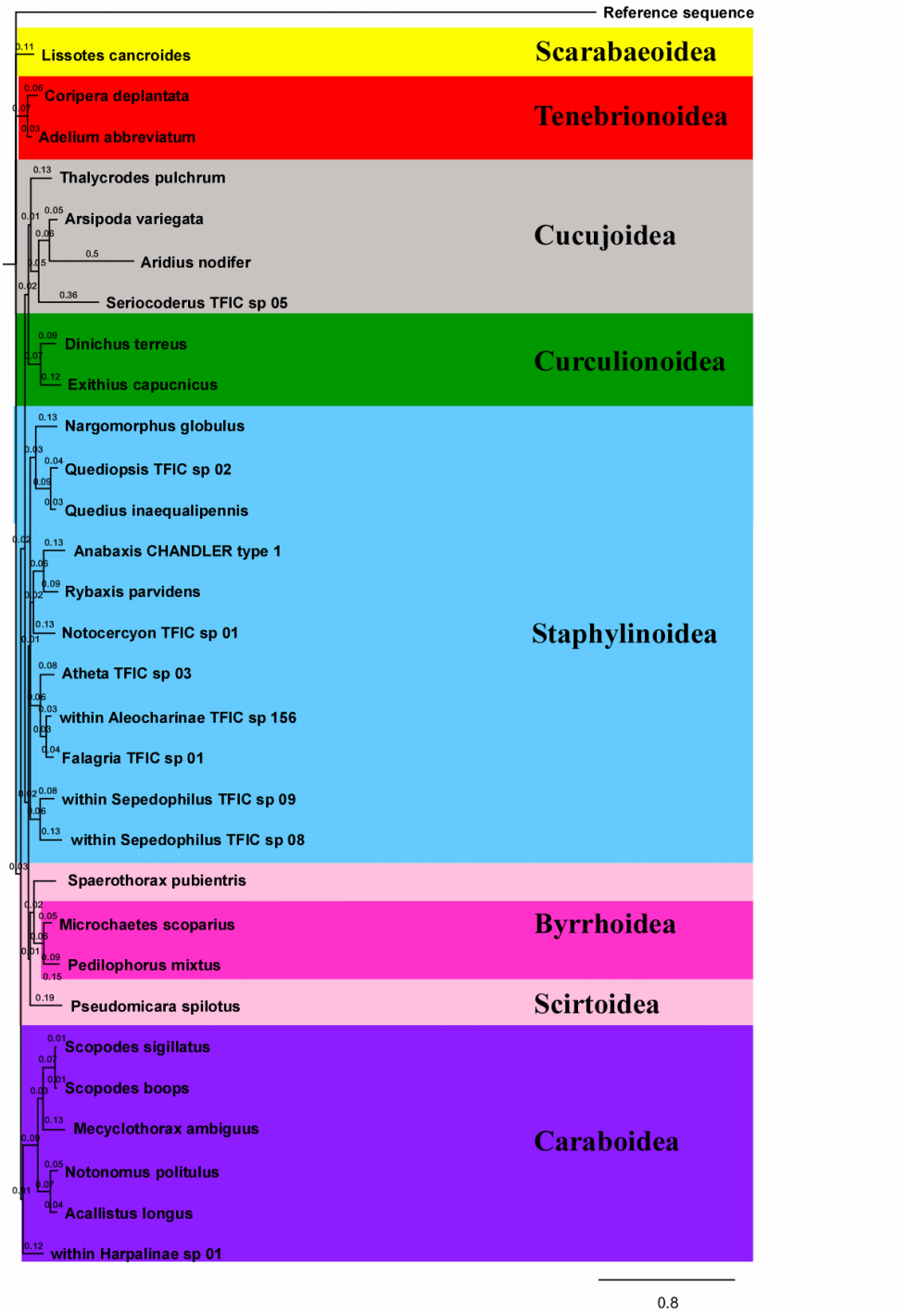

Fig D.2. Phylogenetic tree based on COI and 28SD3 regions for the species used in this study. Different colours refer to different super families. Super-family groupings were taken from (Hunt et al. 2007).

Table D.2. **Beetle functional traits values for species used in this study.** Values have not been phylogenetically-corrected. See Appendix D.1 for measurement details.

Species	Body Length †*	Antennae Length†*	Eye size ††*	Elytra Length†*	Wings †††	Average leg length†*	Leg ratio°*	Robust-ness††*	Dominant Wavelength°°	CIE Lø	CIE Aø	CIE Bø	Habitat occupation °	Seasonal activity°	PC^G	PR^G	D^G
LUCANIDAE																	
Lissotes cancroides	1.10	-0.74	-0.27	-0.26	0	0.43	1.36	0.03	621.17	27.	5.13	0.18	0.50	0.67	0	0	1
TENEBRIONIDAE																	
Coripera deplantata	1.25	-0.57	-0.08	-0.18	0	0.51	1.34	-0.02	583.33	25.	3.67	6.22	0.50	0.67	0	0	1
Adelium abbreviatum	1.06	-0.48	0.00	-0.19	0	0.52	1.39	0.07	573.83	32.	4.42	7.90	0.50	1.00	0	0	1
NITIDULIDAE																	
Thalycrodes pulchrum	0.46	-0.64	-0.14	-0.22	1	0.40	1.32	0.17	550.50	45.	7.72	-8.30	0.00	0.33	0	0	1
CHRYSOMELIDAE																	
Arsipoda variegata	0.37	-0.32	0.19	-0.14	1	0.50	1.68	0.17	521.60	49.	4.44	-1.66	0.13	0.33	1	0	0
LATRIDIIDAE																	
Aridius nodifer	0.28	-0.66	-0.21	-0.20	1	0.44	1.20	-0.09	563.35	78.	13.6	-15.70	0.63	0.33	1	0	0
CORYLOPHIDAE																	
Seriocoderus TFIC sp 05	0.01	-0.55	-0.33	-0.12	1	0.45	1.51	-0.40	562.28	35.	21.6	-22.82	0.50	0.67	0	0	1
CURCULIONIDAE																	
Dinichus terreus	0.73	-0.46	0.03	-0.18	0	0.63	1.24	0.13	559.12	27.	16.5	-11.53	0.25	0.67	0	0	1
Exithius capucnicus	0.97	-0.61	-0.21	-0.17	0	0.45	1.09	0.24	554.17	24.	16.5	-14.00	0.38	0.33	0	0	1
LEIODIDAE																	
Nargomorphus globulus	0.29	-0.54	-0.01	-0.12	1	0.49	1.82	0.05	559.52	31.	12.4	-8.40	0.13	1.00	0	0	0
STAPHYLINIDAE																	
Quediopsis TFIC sp 02	0.55	-0.49	-0.06	-0.77	1	0.26	0.92	0.14	556.60	30.	12.8	-5.28	0.63	0.33	0	1	0
Quedius inaequalipennis	0.80	-0.61	-0.20	-0.73	1	0.29	1.04	-0.38	553.22	32.	7.38	-5.98	0.88	0.67	0	1	0
Anabaxis CHANDLER type 1	0.20	-0.45	0.00	-0.44	1	0.57	1.37	-0.02	559.67	76.	8.88	-10.22	1.00	1.00	0	1	0
Rybaxis parvidens	0.34	-0.45	-0.03	-0.45	1	0.55	1.57	0.22	554.42	75.	8.67	-7.20	1.00	0.67	0	1	0
Atheta TFIC sp 03	0.41	-0.49	-0.05	-0.59	1	0.39	1.49	-0.36	543.60	79.	8.95	-2.90	0.38	1.00	0	1	0
within Aleocharinae TFIC sp 156	0.25	-0.52	-0.03	-0.62	1	0.39	1.14	0.17	563.64	54. 18	4.82	-4.62	0.38	0.33	0	1	0

Falagria TFIC sp 01	0.49	-0.40	0.01	-0.72	1	0.53	1.75	-0.54	563.50	49.	3.70	-1.30	0.25	0.67	0	1	0
within Sepedophilus sp 08	0.68	-0.59	-0.17	-0.58	1	0.35	1.76	-0.42	555.73	54.	-2.78	-16.88	0.50	0.33	1	0	0
within Sepedophilus sp 09	0.58	-0.47	-0.01	-0.51	1	0.42	1.76	0.47	556.25	50.	19.3	-16.13	0.75	0.67	1	0	0
HYDROPHILIDAE																	
Notocercyon TFIC sp 01	0.40	-0.78	-0.27	-0.20	1	0.40	1.51	-0.06	581.50	49.	2.04	4.74	0.50	0.33	0	0	1
CLAMBIDAE																	
Spaerothorax pubientris	0.13	0.00	0.49	-0.10	1	0.36	1.57	-0.29	558.08	84.	10.5	-10.45	0.13	0.67	0	1	0
BYRRHIDAE																	
Microchaetes scoparius	0.58	-0.92	-0.20	-0.09	1	0.43	1.14	0.16	569.73	13.	-0.88	28.42	1.00	0.67	1	0	0
Pedilophorus mixtus	0.60	-0.05	0.37	-0.27	1	0.32	1.20	0.34	550.22	44.	16.7	-11.14	0.50	0.33	1	0	0
SCIRTIDAE																	
Pseudomicara spilotus	0.57	0.13	0.58	-0.49	1	0.40	1.50	0.47	581.02	26.	6.18	12.56	0.38	0.33	0	0	1
CARABIDAE																	
Scopodes sigillatus	0.60	-0.03	0.29	-0.62	1	0.55	1.55	0.21	581.78	2.8	1.20	4.85	0.50	0.33	0	1	0
Scopodes boops	0.68	-0.54	-0.04	-0.26	1	0.56	1.76	-0.30	549.76	8.4	4.82	-3.82	0.63	0.33	0	1	0
Mecyclothorax ambiguus	0.71	-0.40	0.10	-0.20	1	0.53	1.48	-0.03	585.73	9.9	2.48	8.35	0.75	1.00	0	1	0
Notonomus politulus	1.18	-0.36	0.06	-0.22	0	0.54	1.64	-0.15	535.00	35.	1.77	-0.77	0.25	1.00	0	1	0
Acallistus longus	1.07	-0.52	-0.08	-0.25	0	0.45	1.38	-0.12	557.00	37.	0.87	-1.42	0.50	1.00	0	1	0
within Harpalinae sp 01	0.28	-0.28	0.26	-0.63	1	0.46	1.16	0.17	560.60	60.	4.55	-4.30	0.50	0.33	0	1	0

*Measurement units- †: Log mm, ††: PCA score, †††: Presence/absence, °: Ratio, °°: Nanometers, ø: Colour co-ordinates. *measurement relative to body length,*
[G]: Guild; PC: Primary consumers, PR: predators, D: Decomposers.

D.3. Species abundance for each treatment and indicator species status.

Table D.3. Species abundance for each treatment and indicator status, organized by beetle family in alphabetical order.

	OC	SC	OP	SP	OW	SW	OM	SM	Total
ANTHRIBIDAE									
within Anthribidae 01	0	0	1	0	1	0	0	0	2
BYRRHIDAE									
***Microchaetes scoparius**^{Y}*	6	7	12	15	7	7	4	2	60
Notolion mixtus	2	3	6	6	1	1	0	0	19
CARABIDAE									
***Acalistus longus**$^{\sim 45}$*	0	1	1	0	4	5	9	4	24
Chylnus ater^{M}*	0	0	0	0	0	2	0	1	3
Lecanomerus tasmanicus	0	1	0	0	0	1	0	0	2
***Mecyclothorax ambiguus**^{Y}*	1	2	2	3	5	6	4	0	23
Notonomus politulus	1	1	1	0	0	3	3	0	9
Pentagonica vittipennis	0	0	0	0	3	0	0	0	3
Percosoma carenoides	0	2	0	0	0	1	0	0	3
Pterocyrtus globosus	0	0	0	0	0	0	1	0	1
Rhabdotus reflexus	0	0	0	1	0	1	0	1	3
***Scopodes boops**^{Y}*		4	5	5	6	3	11	0	34
***Scopodes sigillatus**^{Y}*	*1*	1	0	2	5	3	2	1	15
Scopodes tasmanicus	*0*	0	1	0	0	0	0	0	1
Sloaneana tasmaniae	*0*	5	3	3	1	4	1	0	17
within Harpalinae TFIC sp 01	*0*	0	1	0	0	0	0	1	1
CHRYSOMELIDAE									
***Arsipoda variegata**$^{\sim Y}$*	0	1	0	1	0	0	2	1	5
within Chrysomelidae 01	0	0	0	0	0	0	0	1	1
within Chrysomelidae 02	0	0	0	0	1	0	0	0	1
within Chrysomelidae 03	0	0	0	0	0	1	0	0	1
Sericoderus TFIC sp 05	5	0	1	0	2	3	5	0	16
CLAMBIDAE									
Clambus bornemisszai	0	0	1	0	0	0	1	0	2
Spaerothorax pubientris^{Y}*	0	0	1	0	0	0	1	0	2
CORYLOPHIDAE									
Holopsis TFIC sp 01	0	0	0	0	0	2	0	0	2
CRYPTOPHAGIDAE									
Cryptophagus gibbipennis	0	0	0	0	1	0	0	0	0
CURCULIONIDAE									
Decilaus lateralis^{M}*	0	0	0	0	0	0	1	0	1
Decilaus nigronotatus$^{M, \sim 45}$*	0	0	0	0	0	1	1	0	2
Decilaus striatus^{M}*	0	0	0	0	0	1	0	0	1
Decilaus TFIC sp 04$^{\sim 27}$*	0	0	0	0	0	0	0	1	1
Dinichus terreus	1	0	0	1	1	6	2	1	12
Exithius capucinus	2	0	0	1	0	2	3	1	9
Mandalotus arciferus^{M}*	0	0	0	0	0	0	1	0	1
Mandalotus muscivorus	0	1	0	0	0	0	0	0	1
Pachyporopterus satyrus	0	0	0	0	0	0	0	1	1
Poropterus melancholicus	0	0	0	0	2	0	0	0	2
Prostomus murinus	2	0	0	0	0	1	1	0	4
Rhadinosomus TFIC sp 01	0	0	0	0	0	0	0	1	1
Roptoperus tasmaniensis^{Y}*	0	0	0	0	0	1	0	0	1
HYDROPHILIDAE									

Notocercyon TFIC sp 01	3	0	3	1	0	0	26	5	38
LATRIDIIDAE									
Aridius nodifer	0	5	5	5	1	4	4	10	34
Cortinicara REIKE sp nov 1	0	0	1	0	0	0	0	0	1
Enicmus priopterus	0	1	0	0	0	0	0	0	1
within Latriididae 01	0	1	1	1	0	1	1	0	5
within Latriididae 02	0	1	0	0	0	0	0	0	1
LEIODIDAE									
Nargomorphus globulus	0	1	0	0	2	11	0	0	14
*Zeadolopus TFIC sp 02** [Y]	0	0	0	0	1	0	0	0	1
LUCANIDAE									
Lissotes cancroides	0	2	2	5	0	6	0	1	16
Lissotes subcaeruleus	0	1	1	0	0	0	0	0	2
LYCIDAE									
Porrostoma rhipidium	1	0	0	0	0	0	0	1	2
MORDELLIDAE									
Mordeliidae TFIC sp 03	0	0	0	0	0	1	0	0	1
NITDULIDAE									
Thalcrodes pulchrum	0	2	0	4	0	7	1	6	20
Thalycrodes cylindricum	0	0	0	0	0	0	0	2	2
OEDEMERIDAE									
Asclera sublineata	0	1	1	0	0	0	0	0	2
PTILIIDAE									
Ptiliidae TFIC sp 19	0	0	1	0	0	0	0	0	1
Ptilliidae TFIC sp 20	0	0	0	1	0	0	0	0	1
within Ptiliidae TFIC sp 21	0	0	0	0	1	0	0	0	1
SALPINGIDAE									
Neosalpingus hybridus	0	0	1	0	0	0	0	0	1
SCIRTIDAE									
Cyphon TFIC sp 05	1	0	0	1	0	0	0	0	2
Pseudomicara spilotus* [Y]	2	4	2	1	1	0	1	0	11
SILVANIDAE									
Hymaea succinifera	0	2	0	0	0	0	0	0	2
SPHINDIDAE									
Aspidiphorus humeralis	0	1	0	0	0	0	0	0	1
STAPHYLINIDAE									
Anabaxis CHANDLER Type 1* [Y]	24	7	29	20	31	17	32	17	177
*Anotylus TFIC sp 02** [~27]	0	0	0	0	0	0	0	2	2
Atheta TFIC sp 03	0	0	1	0	2	2	1	2	8
Euconnus TFIC sp 07	0	1	0	1	0	0	0	1	3
Euplectops CHANDLER Tasmania 1	0	0	1	0	0	1	1	0	3
Falagria TFIC sp 01	0	0	0	3	0	1	3	1	8
Heterothops TFIC sp 03	0	1	1	0	0	0	0	1	3
Quediopsis TFIC sp 02	1	3	3	2	3	0	3	0	15
Quedius inaequalipennis* [~45]	1	6	7	3	8	6	5	9	45
Quedius subopaceus	0	0	0	0	0	0	0	1	1
*Sagola ruggicornis** [~45]	0	0	1	0	0	1	0	0	2
Rybaxis parvidens* [7]	7	4	38	4	28	9	20	29	139
Sepedophilus TFIC sp 08	1	0	0	0	0	0	0	0	1
Sepedophilus TFIC sp 09	0	1	2	1	2	0	3	1	9
Spanioda carissima* [~45]	0	7	3	0	3	3	4	3	23
Tetrabothrus claviger	1	0	2	0	0	0	0	0	3
Thyreocephalus chalcopterus	0	1	0	0	0	4	0	0	5
within Aleocharinae TFIC sp 068	0	0	1	0	0	0	1	0	2
within Aleocharinae TFIC sp 156* [~Y]	1	2	0	0	1	0	3	0	6
*Zyras TFIC sp 02** [~45]	0	1	0	0	0	0	0	0	1

Zyras TFIC sp 03	0	0	0	0	0	0	1	0	1
Zyras TFIC sp 04	0	0	1	0	0	0	0	1	2
TENEBRIONIDAE	0								
Adelium abbreviatum**[~45]**	0	0	1	3	11	21	17	29	82
Brycopia picta	0	0	0	1	0	0	1	1	3
Coripera deplanata**[Y]**	0	0	1	2	0	3	2	4	12
ZOPHERIDAE	0								
Enhypnon tuberculatus	0	0	0	1	1	0	0	0	2
Overall abundance	65	87	146	99	137	154	180	142	1014

*Plot types- OC: Open control, SC: Shaded control, OP: Open plastic litter, SP: Shaded plastic litter, OW: Open wet sclerophyll litter, SW: Shaded wet sclerophyll litter, OM: Open mixed forest litter, SW: Shaded mixed forest litter. We collected functional trait/phylogenetic data from species highlighted in bold. Indicator species - *: Species considered an indicator by Baker (2006) and/or Fountain-Jones et al.. (in press (b)). Y: Young forest indicator (0 to ~7 years after logging), ~27: Considered an indicator of ~27 year-old secondary forest, ~45: Considered an indicator of ~45 year-old secondary forest, M: Considered a mature forest indicator.*

D.4. Phylogenetic signal and all unadjusted individual trait ANOVAs.

Table D.4. Bloomberg's *K* score for each trait used in this study. A *K* value >1 suggests that the trait has a strong phylogenetic signal and conservatism.

Trait	*Trait type*	*K Value*	P
Antennae length	Morphological	0.219	0.815
Eye size	Morphological	0.583	0.311
Body length	Morphological	0.891	0.001**
Elytra length	Morphological	0.567	0.213
Wings	Morphological	1.049	0.001**
Average leg length	Morphological	0.581	0.017*
Hind leg to fore leg proportion	Morphological	0.422	0.345
Robustness	Morphological	0.373	0.851
Dominant wavelength	Morphological	0.8355	0.618
CIE L	Morphological	0.8231	0.001*
CIE A	Morphological	0.5035	0.037*
CIE B	Morphological	0.4147	0.122
Habitat occupation	Ecological	1.1184	0.015*
Seasonal activity	Life History	0.660	0.123

* P < 0.05, **P < 0.01, ***P < 0.001.

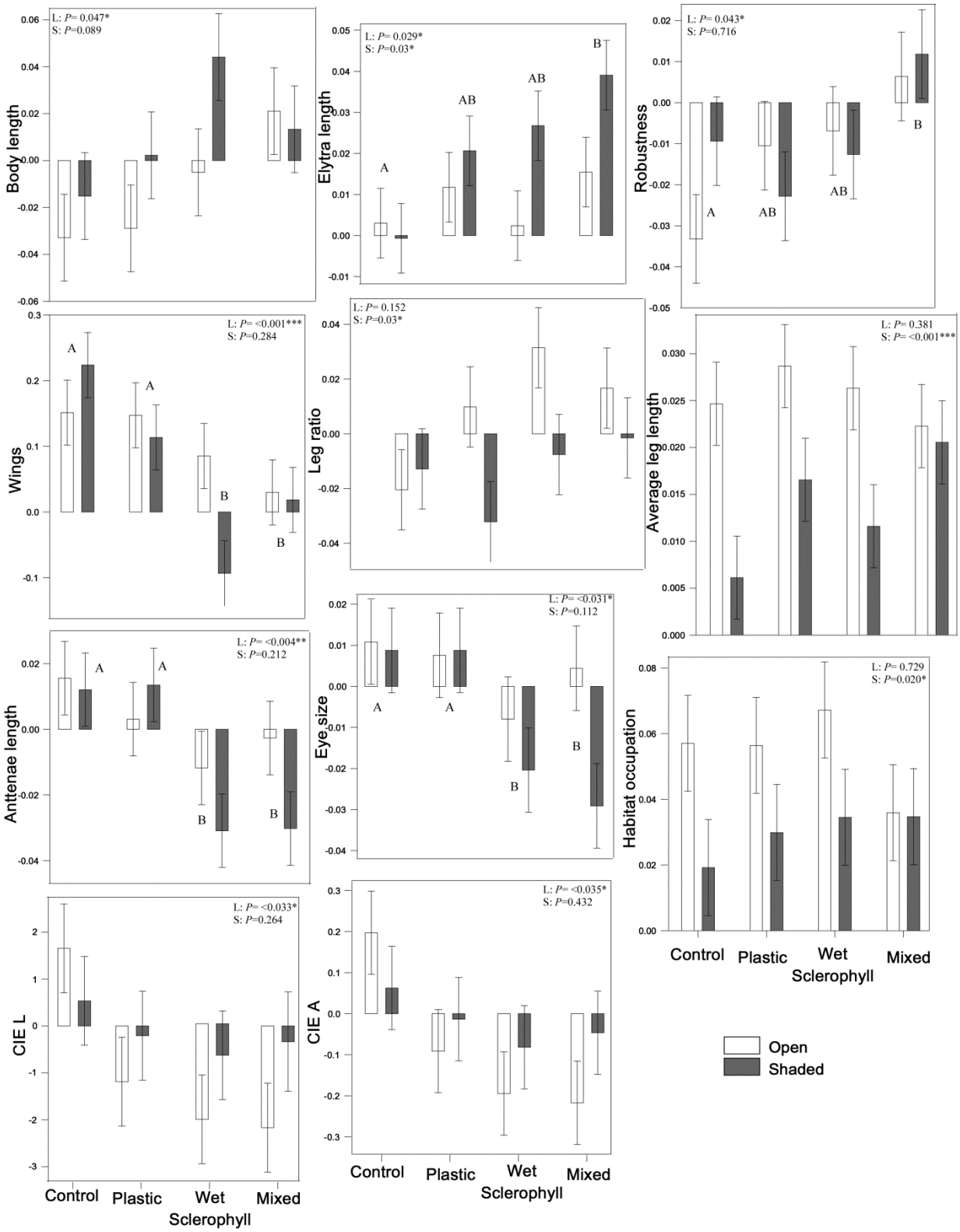

Fig. D4. Phylogenetically-adjusted individual abundance-weighted traits with significant treatment effects (not adjusted for phylogeny). With the exception of predators, the Y-axis scale is

adjusted to control for phylogenetic autocorrelation. L: Litter treatment, S: Shade. Letters indicate significant groupings according to Holm-Sidak pair-wise tests. There were no significant interaction effects for these traits. * P < 0.05, **P < 0.01, ***P < 0.001.

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Appendix E
Publications from Ph.D candidature

Reprint attachments of papers published from this thesis, in the order corresponding to Chapters 2 and 3 respectively:

Fountain-Jones, N.M., Baker, S.C. and Jordan, G.J. (in press). **'**Moving beyond the guild concept: developing a consistent functional trait framework for terrestrial beetles' *Ecological Entomology.*

Fountain-Jones, N.M., Jordan, G.J., Baker, T.P., Balmer, J. **Wardlaw, T.J.** and Baker, S.C. (in press). 'Living near the edge: Being close to mature forest increases the rate of succession in beetle communities.*' Ecological Applications.*