

The effect of the non-native superb lyrebird (*Menura novaehollandiae*) on Tasmanian forest ecosystems

**A thesis submitted in fulfillment of the requirements for the
degree of Doctor of Philosophy**

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Abstract

Some 900 species of bird have been introduced throughout the world but the research effort regarding their ecological impact as non-native species has been minimal and largely based on *ad hoc* observations. In particular, the impact of non-native birds on non-avian components of native biota and ecosystem function are poorly understood. I addressed this knowledge gap by investigating the effect of the non-native superb lyrebird (*Menura novaehollandiae*) on native soil- and leaf litter-dwelling forest invertebrates, seedling survival and ecosystem processes within the wet eucalypt forests of Tasmania, Australia. The superb lyrebird is a predator of invertebrates and is an ecosystem engineer capable of turning over hundreds of tonnes of soil and leaf litter per hectare every year. The absence of any native equivalent-sized predator of invertebrates or native species capable of such large-scale habitat modification within Tasmanian wet forest means that the superb lyrebird may have a significant negative effect on Tasmanian forest ecosystems.

I used a multifactorial approach consisting of field surveys and manipulative experiments to examine the impact of the superb lyrebirds at a number of spatial and temporal scales. Firstly, I surveyed six sites, three invaded by lyrebirds and three without lyrebirds to investigate the patterns of association between macroinvertebrate assemblage structure and abundance and the presence of superb lyrebirds. I found that the presence of superb lyrebirds was associated with lower abundance and taxonomic richness of invertebrates, higher evenness and altered assemblage composition but the magnitude of this relationship was strongly dependent on small-scale variation in microhabitat.

To establish any causal link between the presence of lyrebirds and patterns in invertebrate assemblages and seedling numbers, I conducted two manipulative field experiments that examined the short and long term influence of superb lyrebird disturbance. The physical disturbance of soil and leaf litter immediately reduced the abundance and taxonomic richness of macroinvertebrates, those that inhabit leaf litter being more affected than generalists and soil dwelling taxa. However, the influence was short-lived: the abundance of generalist and soil dwelling taxa was similar to that of individuals in undisturbed areas within 21 days. Similarly, a longer-term experiment

found no evidence of impact on invertebrates after approximately two months. Next, I used a multi-scale survey to determine how the magnitude of the effect of superb lyrebirds on invertebrate assemblages varied across different spatial scales. While their effects on invertebrates were profound at small spatial scales and short timeframes, they were weaker over longer timeframes and at intermediate and landscape scales. In general, mesoinvertebrates showed a weaker response to the presence of superb lyrebirds than did macroinvertebrates. Thus, although superb lyrebird scratching causes obvious changes to the structure of the forest floor of Tasmanian wet eucalypt forests; it appears that their disturbance is neither frequent nor intense enough to result in lasting changes in biotic communities. Finally, I tested the influence of superb lyrebirds on ecosystem function through experiments on the effect of their activity on several ecosystem processes (decomposition, nitrogen cycling and soil respiration). Superb lyrebirds increased decomposer potential but did not appear to influence soil respiration or pH. The concentration of inorganic nitrogen was lower at lyrebird sites; this may have been linked to their disturbance but the lack of any experimental treatment effects weakens the strength of this inference. Overall, it is unlikely that the presence of superb lyrebirds will significantly affect functioning of mature forest ecosystems, as they are resilient to all but extreme perturbation such as wildfire. This thesis represents an integrated and holistic examination of the ecological impact of a non-native bird. In doing so it makes a substantial contribution to global understanding by demonstrating that non-native birds can have an influence, albeit a limited one in this case, on native biota and ecosystem function.

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Chapter 1: General introduction

1.1 Introduction

Non-native species are recognised as major threats to the integrity of native ecosystems worldwide (Sala *et al.* 2000, Vilá *et al.* 2010, Lambertini *et al.* 2011). However, only a small proportion of non-native species cause significant ecological, economic and social problems, with the majority having little or no impact (Williamson and Fitter 1996, Parker *et al.* 1999, Pimentel *et al.* 2005). Assessing the degree of threat posed by non-native species allows conservation and environmental management agencies to prioritise the allocation of limited resources for controlling or eradicating those species which have the most severe impact (Parker *et al.* 1999, Ross *et al.* 2003). The need for quantitative impact data to inform policy and assist managers has seen research on non-native species grow exponentially in the last 30 years (Mack *et al.* 2000, Simberloff 2004, Simberloff *et al.* 2013). However, some significant gaps in our understanding of their ecological impacts remain (Kumschick and Nentwig 2010, Shine 2010, Jeschke *et al.* 2012). Notably, the ecological impact of non-native species of an entire vertebrate taxon, namely birds, is poorly understood (Sol *et al.* 2005, Lavers *et al.* 2010, MacGregor-Fors *et al.* 2010).

The lack of information on the ecological impacts of non-native birds is surprising because a large number of bird species (at least 900) have been introduced into new areas throughout the world, approximately 440 of which have established successfully (Long 1981, Lever 2005, Sol *et al.* 2005, Blackburn *et al.* 2009, Dyer and Blackburn unpublished data 2012). Moreover, due to the availability of high quality data on the distribution and abundance of non-native birds, the early stages of the invasion process (establishment and dispersal) in birds are well studied (Duncan *et al.* 2003, Blackburn *et al.* 2009, Bauer and Woog 2011). There is also a large body of research on other forms of non-native bird impacts such as the economic losses associated with crop and infrastructure damage (Long 1981, Pimentel 2000, 2005, Lever 2005). However, very few non-native bird species have been the subject of quantitative ecological impact studies (Parker *et al.* 1999, Lever 2005, Wright *et al.* 2010, Kumschick *et al.* 2013). Instead, much of the information on the ecological impact of non-native birds is anecdotal, consisting of *ad hoc* observations and often only published in “grey”

literature (Chase and Walsh 2006, Shirley and Kark 2009, Bauer and Woog 2011, Strubbe *et al.* 2011).

The limited research effort directed towards the impacts of non-native birds to date is probably due in part to the general perception that they pose little threat to native biota and ecosystems, particularly in comparison with non-native mammals such as rabbits, rodents, goats and pigs (Diamond and Veitch 1981, Long 1981, Ebenhard 1988, Duncan *et al.* 2003, Simberloff 2006, Kumschick and Nentwig 2010, Strubbe *et al.* 2011). It may be that these perceptions of non-native birds have developed because many non-native birds were largely restricted to urban or agricultural landscapes, and consequently thought unlikely to pose a threat to native ecosystems (Case 1996, Duncan *et al.* 2003, Sol *et al.* 2005). In addition, until recently native birds were generally thought to have a limited capacity to influence communities and ecosystem functioning even within their native range (Sekercioglu 2006, Whelan *et al.* 2008) and this view appears to have been extended to non-native birds. Finally, a large proportion of bird introductions have been deliberate (Duncan *et al.* 2003, Lever 2005, Blackburn *et al.* 2010), so the public has often regarded their presence as positive or benign rather than as a potential threat to native species and ecosystems (Temple 1992, Bremner and Park 2007, Ellis and Elphick 2007, Strubbe *et al.* 2011).

The historical perceptions of non-native birds as largely benign and the likelihood that attempts to control or eradicate non-native birds may be met with public resistance have probably contributed to the limited impetus for conducting quantitative research on the ecological impacts of non-native birds (e.g. Bremner and Park 2007). The lack of rigorous studies presents challenges for assessing the true magnitude of the threat posed by non-native birds (Wright *et al.* 2010, Bauer and Woog 2011). Impacts may be underestimated, undetected or in some cases, overestimated. To date, there is little evidence that non-native birds have major ecological impacts (Blackburn *et al.* 2009, Strubbe *et al.* 2011) (but see Green 1996, Rhymer and Simberloff 1996). Equally, the number of studies demonstrating an absence of impact is also limited (e.g. Lowe *et al.* 2011, Newson *et al.* 2011, Orchan *et al.* 2013). Without comprehensive evidence it is somewhat presumptuous to believe that non-native birds generally have little ecological impact, particularly given that many non-native bird species are currently suspected of having adverse ecological effects (Wright *et al.* 2010).

While evidence of large-scale impacts is not yet forthcoming, a growing number of quantitative studies have demonstrated that some non-native birds are capable of having considerable effects at small and medium spatial scales. Non-native birds compete with native birds for nesting holes (Pell and Tidemann 1996, Ingold 1998, Blanvillain *et al.* 2003) and food (Freed and Cann 2009), hybridise with native species (Rhymer and Simberloff 1996, Allendorf *et al.* 2001, Barilani *et al.* 2007, Muñoz-Fuentes *et al.* 2007, 2012), prey on native birds (Lever 2005, Harper 2007), facilitate the spread of exotic plants (Best and Arcese 2009, Linnebjerg *et al.* 2010, Chimera and Drake 2010), carry exotic avian diseases (van Riper *et al.* 1986, Carrete *et al.* 2009) and modify habitat (Tatu *et al.* 2007, Best and Arcese 2009, Dixon 2009). These studies highlight a range of impacts, but until more research is undertaken it is difficult ascertain whether the threat of non-native birds has, in general, been underestimated because of the lack of research or because the impacts are difficult to detect, or whether such negative impacts are actually rare.

Although the impacts of some non-native birds may currently be underestimated, there are also cases where the popular perception of the threat posed by non-native species may be overstated, or at least exceed the current scientific evidence available (Shine and Doody 2011). For example, the common or Indian myna (*Acridotheres tristis*) is one of only three bird species on the International Union for Conservation of Nature (IUCN) list of the “100 of the World’s Worst Invasive Species” (Lowe *et al.* 2000). The myna is listed because of its economic, social and ecological impacts (the latter due to competition with native fauna for food and nesting resources). Public opinion of mynas is negative: for example, a survey in Australia found that the community ranked the myna alongside species such as the cane toad (*Rhinella marina*) and the red fox (*Vulpes vulpes*) (ABC Wildwatch Australia Survey 2005). However, most of the information on the ecological impact of mynas is based on observational records. The few studies that have attempted to quantify the impact of the myna have been contradictory regarding the significance of their impact on native species (Lowe *et al.* 2011, Garrock *et al.* 2012, Haythorpe *et al.* 2012, Pell and Tidemann 1997, Blanvillain *et al.* 2003), thereby raising questions regarding the prioritisation of management of mynas over other species (Garrock *et al.* 2012).

Detecting impacts of non-native species can be difficult, time consuming and expensive (Byers *et al.* 2002 Strayer *et al.* 2006, Simberloff *et al.* 2013). Furthermore, it is not always possible or desirable for managers to wait for cogent information before taking action, particularly in the case of newly introduced non-native bird populations (Simberloff 2003, Genovesi 2005, Edelaar and Tella 2012). However, research on the nature and magnitude of impact is often required to gain the public and political support necessary to implement intervention measures (Bomford and O'Brien 1995, Shine and Doody 2011). Muñoz-Fuentes *et al.* (2012) highlighted this point in their review of the role played by genetic studies in the case of the establishment of several populations of non-native ruddy duck (*Oxyura jamaicensis*) in European countries. The genetic studies demonstrated the hybridisation occurring between the introduced ruddy duck and the critically endangered native white-headed duck (*Oxyura leucocephala*). Without this information, it is unlikely that there would have been the political momentum to drive eradication or facilitate the cooperation between multiple countries with populations of the ruddy duck, which appears to have successfully saved the white-headed duck from extinction.

1.1.1 Quantifying impacts of non-native species

Clearly, more research on the ecological impact of non-native bird species is urgently required to enable policy makers and environmental managers to make informed decisions regarding resource allocation (Edelaar and Tella 2012). In addition, managers need information on the ecology of the non-native species, their interactions with native ecosystems, and the causal mechanisms of their impacts in order to design effective amelioration plans (Bauer and Woog 2011). To date, quantitative experiments that have provided environmental managers with these data are very rare (Sol *et al.* 2005). Thus, in order to resolve the current knowledge gaps, future quantitative research on non-native birds is required, particularly on the topics detailed below.

1.1.1.1 Investigate more species and in more locations

A diverse range of bird species have been introduced throughout the world but few studies have investigated their ecological impact. While it is not possible to study all species, information on a wider range of species is necessary to develop trait-based criteria that will allow researchers to predict the threat of non-native species, as has been done with other groups of organisms such as plants and aquatic invertebrates

(Parker *et al.* 1999, Thiele *et al.* 2010). In addition, some bird species have established populations in multiple locations around the world and because ecological impacts are often highly context-dependent on the recipient ecosystems and local species (Byers *et al.* 2002, Simberloff *et al.* 2013), a species may have very different effects in different ecosystems (Valéry *et al.* 2008). Furthermore, there is a geographic bias (of both investigator and species) in research effort on non-native species in general (Pyšek *et al.* 2008, Davis 2009, Vilá *et al.* 2010, Speziale *et al.* 2012). The numbers of species and research publications on non-native birds are higher for Europe and America than elsewhere in the world (Pyšek *et al.* 2008). However, this pattern of study does not necessarily reflect the relative importance of non-native species throughout the world. It is mainly an artefact of the variable financial resources available to conduct ecological research in different regions (Leimu and Koricheva 2005).

1.1.1.2 Quantify more mechanisms of impacts and their effects on a wider range of organisms and ecosystem processes:

While some types of impact such as hybridisation have received a reasonable amount of attention (e.g. Green 1996, Rhymer and Simberloff 1996, Barilani *et al.* 2007, Muñoz-Fuentes *et al.* 2007, 2012), other forms of impact such as predation and habitat modification have only been addressed by a small number of studies (e.g. Lever 2005, Harper 2007, Best and Arcese 2009). In addition, the majority of research on non-native birds has focused on their impacts on native avifauna, while very few studies have considered impacts on other components of native biota or ecosystem function (Sol *et al.* 2005, Strubbe *et al.* 2011). Given that the impact of other groups of invasive organisms is often not restricted to native congeners but can also affect other organisms, whole communities and ecosystems (Crooks 2002, Vilá *et al.* 2010, Simberloff 2011, Strayer 2012) it is unwise to assume that birds do not affect other organisms. For example, despite the fact that many species of birds were introduced to areas for invertebrate pest control (Drummond 1907, Lever 2005, Lockwood *et al.*, 2007), there is very little information regarding their impact on native invertebrate communities (Cole *et al.* 1995, Dixon 2009, Blackburn *et al.* 2009, Strubbe *et al.* 2011). Similarly, only a handful of quantitative studies have examined the effects of non-native birds on ecosystem properties and habitat structure (e.g. Cobb and Harlin 1980, Tatu *et al.* 2007, Best 2008, Dixon unpublished data 2009).

1.1.1.3 Determine impacts at different levels of biological organisation

Parker *et al.* (1999) suggested that the impact of non-native species could be measured at five levels of biological organisation:

1. Effects on individuals (demographic, morphometric and life history characteristics)
2. Genetic effects on native species (such as hybridisation)
3. Population effects (changes in abundance and distribution of a species)
4. Community-level effects such as richness, abundance, evenness and composition
5. Effects on ecosystem functions and processes (such as nutrient cycling and community metabolism).

In the case of non-native birds, it is the community and ecosystem levels of organisation that require the most attention because most studies to date have considered the first three levels, reflecting the fact that most investigations have only examined interactions with native birds (Blackburn *et al.* 2009, Bauer and Woog 2011, Strubbe *et al.* 2011). In addition, integrative studies which use a variety of methods (both experimental and observational) at multiple levels of organisation are widely regarded as the best means of obtaining robust indications of the nature and magnitude of impacts of non-native species (Parker *et al.* 1999, Crooks 2002, Orchan *et al.* 2013, Strayer 2012). However, such studies are rare in research on non-native birds (Bauer and Woog 2011, Garrock *et al.* 2012).

1.1.1.4 Quantify impacts at different spatial and temporal scales

To date, most investigations of the impact of non-native bird species have been undertaken at local scales over short timeframes (Strubbe *et al.* 2011, Garrock *et al.* 2012). While these are often the most logistically feasible scales at which to carry out research, it is difficult for the findings of such studies to be scaled up to larger spatial scales or longer timeframes (Parker *et al.* 1999, Hewitt *et al.* 2001, Crooks 2002). This is because the impact of a non-native species is strongly influenced by the abiotic and biotic conditions prevailing in the environment in which the species establishes (Bonter *et al.* 2010, Strayer 2012). Since these conditions vary across a range of different spatial, temporal and organisational scales, it means that results of small-scale studies,

where a species is subject to local scale factors such as habitat suitability, cannot readily be scaled up (Levin 1992, Thrush *et al.* 1997, 2000, Englund and Leonardsson 2008, de Moura Queirós *et al.* 2011). Thus, the scale of field surveys and experimental design are very significant considerations for future studies on the impacts of non-native birds because it is important to understand the context dependence of impact.

Addressing issues of scale when designing studies to investigate impact is not trivial. For example, it is often costly and difficult to set up long-term projects to examine impacts (Strayer *et al.* 2006, Simberloff *et al.* 2013), but such studies can be very important. This is because the some mechanisms such as competition (e.g. reduced breeding success) are not as easy to detect over short time scales (Mooney and Cleland 2001, Davis 2003, Edelaar and Tella 2012). It is also common for time lags to occur between the establishment of a non-native species and significant impact, due to the time taken for the introduced population to grow (particularly if impacts are density dependent) (Ricciardi 2003). Changes in environmental conditions (e.g. climate) over time may also enable population growth or expansion into to new areas (Ricciardi *et al.* 2013). Finally, genetic changes in the non-native species over time may eventually allow the species to exert an impact when it once did not (Crooks and Soulé 1999, Crooks 2011, Strayer 2012).

In recent years there have been significant advances in how to incorporate scale into ecological experiments and surveys (Thomsen *et al.* 2011, Simberloff *et al.* 2013). Ideally, ecologists employ Before-After-Control-Impact (BACI) and Beyond- BACI experimental designs at a range of spatial scales, but this approach relies on comprehensive baseline data for the recipient system and biota (Underwood 1994, Parker *et al.* 1999, Hewitt *et al.* 2001). More often than not, these data are lacking so researchers must use a combination of surveys and experiments in a ‘weight of evidence’ approach to assess impact (Parker *et al.* 1999, Byers and Noonburg 2003, Ross *et al.* 2003, 2006). This often involves using hierarchically nested spatial designs that incorporate several levels of spatial scale and allow for comparison across systems (Levin 1992, Thrush *et al.* 2000, de Moura Queirós *et al.* 2011). Another approach is to use space-for-time surveys or experiments in which impact locations are compared with ecologically similar areas where the species is absent (Ross *et al.* 2006). While it is

generally not possible to demonstrate causal mechanisms in space-for-time surveys they can generate hypotheses that can then be experimentally tested.

1.1.2 Study species: the superb lyrebird (*Menura novaehollandiae*)

In this study, I investigate the ecological impact of the introduced population of the superb lyrebird (*Menura novaehollandiae*) on the forest ecosystems of Tasmania, Australia. Superb lyrebirds are large (880-1100g), terrestrial, passerine birds that are native to the temperate forests in the southeast of the mainland of the Australian continent (Reilly 1988, Higgins *et al.* 2001). The superb lyrebird is one of two extant species belonging to the family Menuridae. The other species, the Albert's lyrebird (*Menura alberti*), has a very restricted range in northeastern mainland Australia (Higgins *et al.* 2001).

1.1.2.1 Superb lyrebird ecology

Superb lyrebirds are charismatic birds that have become well known throughout the world for their elaborate courtship displays in which the males mimic other birdcalls and sounds (Smith 1988, Higgins *et al.* 2001, Attenborough 2002). They are long lived (up to 25 years in captivity) and reach sexual maturity between 5 and 8 years (Reilly 1988). Adult superb lyrebirds are strongly sexually dimorphic: males have long plumed tails and perform loud and visible courtship displays while females lack these plumes and are more cryptic in behaviour. Superb lyrebirds are predominantly solitary: both males and females hold territories for much of the year, with one male territory frequently overlapping those of several females (Robinson and Frith 1981). Territories range in size from 0.9 hectares (Robinson and Frith 1981) up to approximately 30 ha (Reilly 1988), presumably dependent on factors such as habitat availability, carrying capacity, and population density, although this has not yet been investigated thoroughly.

The superb lyrebirds breed in the austral autumn and winter and employ a kind of open lekking system whereby males cluster geographically during the breeding season to display (Robinson and Curtis 1996, Zann and Dunstan 2008). Males attract females by performing elaborate vocal and dancing displays utilising their long tail feathers and ability to mimic sounds (predominantly other birds' calls) (Zann and Dunstan 2008, Dalziell and Magrath 2012). Displays are frequently made on 'display mounds' that the males construct by raking over soil to form a bare patch of around 1 m in diameter

(Adamson *et al.* 1983, Smith 1988). After mating, males take no further part in parenting and females build a large domed nest, either on the ground or in a tree in which they typically lay a single egg (Lill 1979). After a long incubation period (6–7 weeks) the chicks hatch in late winter or early spring and typically stay with their mother until the onset of the next breeding season (Lill 1979).

Superb lyrebirds are weak flyers, and spend much of the time on the ground where they forage for food, primarily invertebrates, in leaf litter and soil (Smith 1968, Robinson and Frith 1981, Lill 1986). They feed by using their large, powerful feet and long claws (with a span of up to 150 mm) to scratch and turn over leaf litter and soil down to 150 mm in depth (Adamson *et al.* 1983, Smith 1988, Ashton and Bassett, 1997). The birds often forage up to the base of trees, logs and rocks, and are capable of displacing rocks that weigh up to 2 kg (Adamson *et al.* 1983, Tassell, S. pers. obs. 2012). Superb lyrebird feeding activity has a significant effect on the pedological and physiographic features of forest floors (Ashton 1975). For example, in some forest types within their native range, individual superb lyrebirds have been estimated to turnover 200 t/ha/yr of soil and leaf litter (Ashton and Bassett 1997). Adamson *et al.* (1983) estimated that superb lyrebirds were able to turn over the entire forest floor within 20–31 months. Superb lyrebirds have been recognised as an important source of natural disturbance, and Ashton 1975 proposed that they are a keystone species within forests in their native range.

Species such as the superb lyrebird, which are able to create, destroy, modify or maintain habitats are referred to as ‘ecosystem engineers’ (Jones *et al.* 1994). Via engineering, superb lyrebirds can directly or indirectly influence the availability of resources to other organisms and potentially affect the dynamics of ecosystem processes such as soil formation and nutrient cycling. Scratching and digging can cause colluvial creep of soil into gullies (Ellis 1971) and Ashton (1975) suggested that superb lyrebirds were likely to be a key driver of natural erosion within their native range. Furthermore, lyrebirds can affect the rate of decomposition because the burial of leaf litter and mixing of soil layers can increase the rate at which organic material breaks down, thereby influencing long term nutrient cycling and rates of soil formation (Ashton 1976, Ashton and Bassett 1997). By altering the soil structure and microclimate, superb lyrebirds may promote or suppress germination of some plants. For example, Ashton and Bassett

(1997) found that superb lyrebird scratching appeared to create the suitable microsites for young tree ferns to establish.

Predation or risk of predation coupled with habitat disturbance by superb lyrebirds is thought to drive microhabitat selection by small reptiles. For example, Webb and Whiting (2006) found that juveniles of two species of small snake preferred to hide under large rocks, even though these rocks had lower thermoregulatory benefits than small rocks, because their size provided a refuge from superb lyrebirds. There have been no quantitative studies investigating the influence of superb lyrebirds on soil and leaf litter invertebrate communities, but predation and modification of habitat structure and disturbance regimes by these birds could potentially have an effect (Ashton and Bassett 1997). Adamson *et al.* (1983) found some evidence that the excavation of soil and creation of debris heaps by superb lyrebirds creates favourable habitat for some invertebrates. However, there is not enough information to determine whether the birds effectively ‘farm’ their prey by creating suitable conditions for them, or whether non-prey species increase in number.

1.1.2.2 History of the superb lyrebird in Tasmania

Between 1934 and 1949 a total of 22 superb lyrebirds were introduced to two locations, Mount Field National Park and Hastings Caves Reserve (Fig 1.1) in an effort to save the species from the perceived threat posed by foxes and habitat loss on the Australian mainland (Sharland 1952, 1981). Recorded sightings indicate that superb lyrebirds are now established throughout much of southwestern Tasmania (Fig 1.1), while Tanner (2000) estimated that by 2010 the population could have grown as large as 16,000. Significantly, superb lyrebirds are found throughout a large proportion of the internationally important Tasmanian Wilderness World Heritage Area (TWWHA). Conservation managers are concerned that superb lyrebirds could have a significant negative impact on forest ecosystems through predation on invertebrates and habitat modification (Mallick and Driessen 2009). Given that there are many endemic species of flora and fauna within forests that the superb lyrebirds have invaded, including many invertebrates with very limited geographic ranges (Harvey 2002, Greenslade 2008, Mesibov 1994, 2011, Threatened Species Section 2009), it is possible that the superb lyrebirds pose a threat to their survival. Consequently, superb lyrebirds are described as

“high risk” under the Introduced Species Management Strategy for the TWWHA (Mallick and Driessen, 2009).

1.1.2.3 Ecological impact of the superb lyrebird in Tasmania

Very little is known about the impact of the superb lyrebird in Tasmania and prior to the present study, the only such investigation was in the form of an Honours thesis (Tanner 2000). That study investigated superb lyrebird influence on invertebrate communities by fencing out superb lyrebirds from patches of forest floor. While Tanner (2000) found no evidence of any overall influence on assemblage structure, beetles belonging to the superfamily Staphylinoidea were more abundant in the fenced exclosures than in plots open to superb lyrebirds. The timeframe of this exclosure study was limited to 11 weeks, which may preclude recovery by other invertebrate populations in the fenced areas.

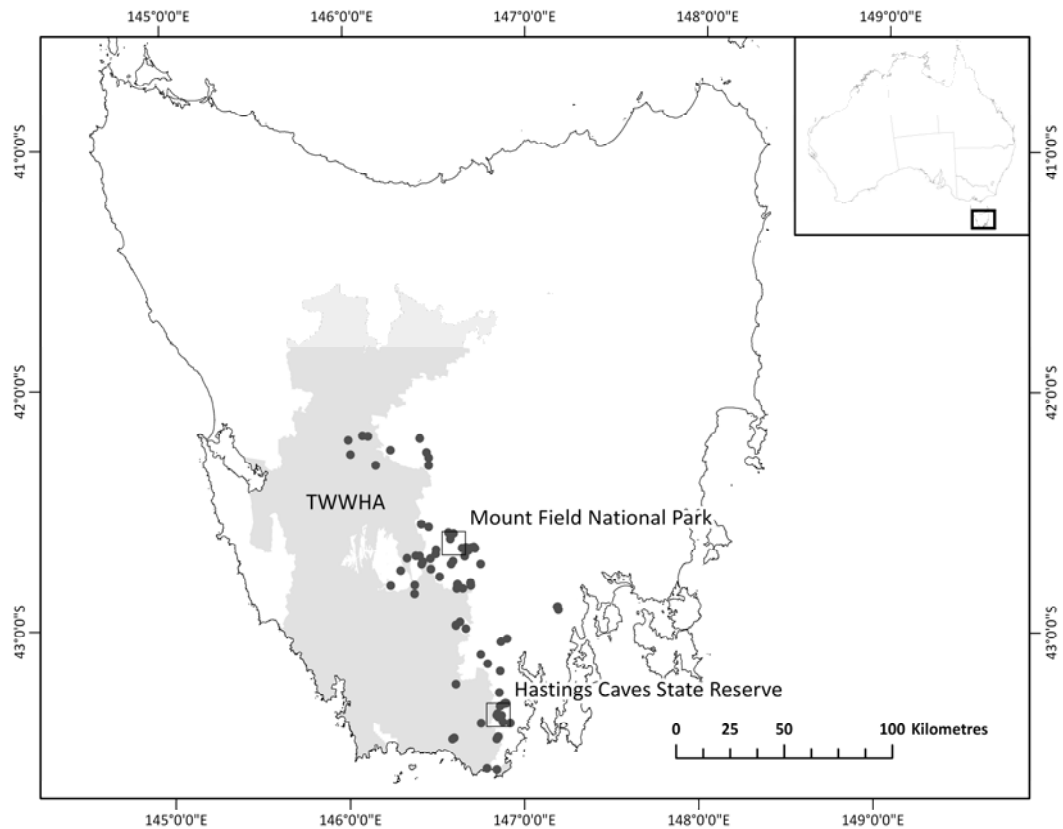


Figure 1.1: Current known distribution of the superb lyrebird (*Menura novaehollandiae*) in Tasmania based on sighting records from Tasmanian Parks and Wildlife Service Natural Values Atlas (2012) and BirdLife Tasmania (2012), and the location of the original points of introduction: Mount Field National Park and Hastings Caves Reserve. The grey shaded area denotes the Tasmanian Wilderness World Heritage Area (TWWHA). Map grid of Australia zone 55.

Anecdotal reports suggest that lyrebirds may affect germination and survival of some plants in Tasmania. Neyland (2004) observed that scratching by foraging superb lyrebirds appeared to reduce the regeneration of seedlings in experimental timber harvesting plots in southern Tasmania. Superb lyrebirds are also considered to be a potential threat to the survival of the endangered endemic myrtle elbow orchid (*Thynninorchis nothofagicola*), which is known only from a few square metres at one location in south-western Tasmania (Threatened Species Section 2009). It is thought that the birds could potentially eat tubers of *T. nothofagicola* as there are reports of superb lyrebirds within their native range eating orchid tubers (Higgins *et al.* 2001), and that scratching activity may limit recruitment of new seedlings (Threatened Species Section, 2009). Although these effects have not been demonstrated due to the rarity of the myrtle elbow orchid, a fence has been erected around the single known population to protect it from superb lyrebirds.

Given what is known about the influence of the birds on their native forest ecosystems, conservation managers have hypothesised that they may be capable of significant adverse effects on Tasmanian forests (Mallick and Driessen 2009). There is no native animal with feeding ecology equivalent to that of the superb lyrebird in Tasmanian wet forests. Firstly, there are no native ground dwelling vertebrates of a similar size inhabiting Tasmanian wet forests that feed primarily on macroinvertebrates. Secondly, while there are a number of small and medium sized mammals in Tasmania that disturb soil and leaf litter either by burrowing or digging foraging pits for subterranean foods, they are not typically found in large numbers in the preferred habitat of the superb lyrebird: wet forest with a closed understory but with a relatively open shrub layer and sparse ground cover (Ashton and Bassett 1997, Higgins *et al.* 2006). The short-beaked echidna (*Tachyglossus aculeatus*), eastern barred bandicoot (*Parameles gunii*), southern brown bandicoot (*Isodon obesulus*) and the Tasmanian bettong (*Bettongia gaimardi*) are typically found in habitats such as open dry sclerophyll forests, scrub and heath that have dense ground cover (Duffy 1991, Mallick *et al.* 1997, Johnson 1994, Claridge and Barry 2000,). Long-nosed potoroos (*Potorous tridactylus*) and wombats (*Vombatus ursinus*) occur more commonly in wet forests, but the potoroos prefer dense scrub and ground cover while wombats prefer an open canopy and grassy groundcover (Kershaw 1971, Bennett 1993, Johnson 1995, Claridge and Barry 2000). When these mammals are present, they tend to make discreet foraging pits or burrows and do not create large

expanses of continuously disturbed substrate in the same way as superb lyrebirds (Eldridge and Kwok 2008, Higgins *et al.* 2006, Triggs 2009).

There are no native large or medium-sized birds that bioturbate the soil in Tasmanian wet eucalypt forests. However, there are two species of thrush, the Bassian thrush (*Zoothera lunulata*) and the non-native European blackbird (*Turdus merula*). Although both are much smaller than the superb lyrebird, these species do turn over leaf litter when foraging for invertebrates. Both thrushes create feeding scrapes but these are shallow (typically < 50 mm, my personal observations 2008) and small in diameter (<200 mm) in comparison with the superb lyrebird scratchings which are often >500 mm in diameter (Higgins *et al.* 2006, S Tassell pers. obs. 2007). Thus, superb lyrebird feeding activity represents a novel disturbance in Tasmanian wet eucalypt forests.

Concern about the potential impact of the superb lyrebird as an ecosystem engineer is warranted as non-native ecosystem engineering organisms often have devastating and far-reaching impacts on native systems (Crooks 2002). This is because they can alter habitat and resources for a whole suite of organisms with flow on effects for the structure and function of ecosystems (Crooks 2002, Cuddington and Hastings 2004, Ehrenfeld 2010). Well known examples of the impact of non-native ecosystem engineers on native forest ecosystems include the alteration of soil chemistry and forests by the nitrogen fixing plant, *Myrica faya*, in Hawaii (Vitousek 1990, Levine *et al.* 2003), broad-scale changes to the structure of forest soils and ecosystem processes by several species of non-native earthworms in North America (Bohlen 2004) and changes to biotic communities by bioturbating feral pigs (*Sus scrofa*) (Vtorov 1993).

The likelihood of a non-native ecosystem engineer having a significant impact is generally higher if the engineered habitat is different from any that naturally occurs in the ecosystem (Ricciardi and Atkinson 2004). Likewise, if the non-native species in question introduces a new process, the effect on native ecosystems can be significant (Vitousek *et al.* 1996). This is because native species are likely to have little or no evolutionary history with that disturbance regime or the habitat created (Byers 2002, Cuddington and Hastings 2004, Ehrenfeld 2010). In the case of the superb lyrebird, it is possible that Tasmanian forest biota may not be adapted to the higher frequency and intensity of disturbance, or to the changes in the physical structure of the forest floor

habitat, that occur as a result of superb lyrebird foraging. If the native biota is unable to withstand these changes then the superb lyrebird may pose a significant threat to the integrity of Tasmanian forest ecosystems. It is imperative that the current and potential future threat of superb lyrebirds is determined as rapidly as possible because there appear to be large areas of potentially suitable habitat in Tasmania that have not yet been invaded by the birds (Tanner 2000, Higgins *et al.* 2001). Thus it is important to try to establish the current and potential threat before lyrebirds saturate all suitable habitats and the population increases further. More generally, this investigation is a useful and timely case study for investigating impacts of non-native birds on native invertebrate assemblages, seedlings and ecosystem function at multiple spatial and temporal scales: to the best of my knowledge this is the first of its kind globally.

1.2 Research objectives and structure

The overall aim of this thesis was to determine the nature and magnitude of the ecological impact of the non-native superb lyrebird on Tasmanian forest biota and ecosystem processes. Not only does this study make a significant contribution towards filling the worldwide knowledge gap concerning the ecological impact of non-native birds on native invertebrates and ecosystem functioning, but it also fulfils the need of conservation managers in Tasmania for an assessment of the current and potential future impact of the superb lyrebird in Tasmania.

Quantifying the current and potential future impact of a non-native species is difficult, particularly when, as in the case of superb lyrebirds, there is no pre-impact baseline data (Ruiz *et al.* 1999). This is because changes in the recipient ecosystem that occur as a result of the establishment of a non-native species may be confounded with concomitant environmental changes (either natural or human-induced), thereby making it extremely challenging to isolate the impact of the non-native species (Strayer 2010). Carefully controlled experiments can help to quantify impacts in the absence of baseline data but it is normally not practical to undertake them at large spatial or temporal scales (Lodge *et al.* 1998, Ross *et al.* 2003, Ims 2005). Unfortunately, many ecological processes are scale-dependent so there is no guarantee that simply extrapolating the results of small-scale experiments to larger spatial or temporal scales will give an accurate

representation of the impact of an invasive species (Thrush *et al.* 1997, Lodge *et al.* 1998).

To contend with the lack of baseline data and the shortcomings associated with relying on any one method of investigation, I used an integrated approach that combined multifactorial field surveys and manipulative field experiments to test hypotheses on the influence of the non-native superb lyrebird on native forest biota and ecosystem processes in Tasmania. Observational surveys were used in the first instance to determine if there was any indication that superb lyrebirds influenced macroinvertebrates assemblages (as this component of the fauna could potentially be affected by predation and disturbance of the forest floor). The other aims of this survey were to assess the influence of small-scale environmental heterogeneity on the nature and magnitude of impact and to set up hypotheses that could be tested experimentally. Field experiments were then conducted at small spatial scales used because they can provide a powerful test of the presence of causal relationship between the non-native species and recipient biota or ecosystem processes. Further observational surveys were then undertaken to assess whether the results of the experiments were consistent with patterns observed across a range of spatial scales.

A key consideration when designing studies to determine the impact of non-native species is that of heterogeneity (Thomsen *et al.* 2011). The effect of non-native species is typically highly context-dependent meaning that it is governed by variation in: (1) the composition and structure of the recipient biological communities (Crooks 2002), (2) the abiotic conditions and environment where the non-native species establishes, and (3) the spatial and temporal scale at which the impact is observed. Rather than trying to avoid heterogeneity, studies should encompass it because understanding when and where non-native species have an impact is a vital component of assessing the overall risk they pose (Strayer 2010). Thus, in this thesis I examined the impact of the superb lyrebird at different levels of biological organization (assemblages and ecosystems), gradients in environmental conditions, and multiple spatial and temporal scales.

The first step of my research (chapter 2) involved contending with the lack of pre-introduction data by conducting a space-for-time survey at three sites with superb lyrebirds and three ecologically similar sites immediately beyond the current range of

the birds in Tasmania. The purpose of this survey were two fold: firstly, with virtually no information regarding the impact of the superb lyrebird on invertebrates either in their native range or in Tasmania, I wanted to ascertain whether there were patterns of association between superb lyrebirds and macroinvertebrates inhabiting the forest floor. Superb lyrebirds feed predominantly on macroinvertebrates as well as disturb their habitat via scratching, so it is likely that they could influence this component of the biota. The second aim of this survey was to investigate whether the strength of any association between superb lyrebirds and macroinvertebrate assemblages differed with variation in environmental conditions at the small scale (tens of meters).

The second step of my study (chapter 3) was to identify causal links between the presence of the superb lyrebird and patterns in macroinvertebrate and mesoinvertebrate assemblages as well as on seedling survival. I conducted two manipulative field experiments that incorporated medium-term (months) and short-term (days to weeks) temporal scales. The first experiment was conducted over 8 months and used exclosures and simulated lyrebird disturbance at four locations: two with superb lyrebirds and two beyond their current range. The design also allowed the independent assessment of the relative importance of habitat modification versus predation on invertebrates. The second experiment, conducted at one location without lyrebirds, used simulated lyrebird disturbance to determine the immediate impact of a single disturbance event as well as the short-term dynamics of recovery over 3 weeks. To assess the broader relevance of the findings of the small-scale experiments conducted in chapter 3, I undertook a large-scale field survey in chapter 4 to examine the relationship between invertebrate assemblages and lyrebird foraging intensity at several spatial scales. This survey used a nested sampling strategy to examine whether the patterns observed in the small-scale experiments were reflected at large spatial scales.

Some non-native species can have a far-reaching effect on the ecosystem processes and can ultimately alter the functioning of an ecosystem as a whole (Crooks 2002). However, attempts to quantify the influence of non-native species on ecosystem function lag behind research on their impact on biological communities (Ehrenfeld 2010, Green *et al.* 2013). Therefore, in chapter 5 I investigated the capacity of superb lyrebirds to influence important ecosystem processes of decomposition, nutrient cycling, and soil respiration. I used the same experimental exclosures described in

chapter 3. Decomposition and soil respiration were measured every 3 months for 12 months to account for seasonal variation in the influence of superb lyrebirds on the processes measured. Finally, chapter 6 provides a synthesis of my findings, a discussion of the current ecological impact of the superb lyrebird population in Tasmania, their potential future impact, and the implications for management of the species in Tasmania.

1.2.1 Thesis Presentation

This thesis as written consists of four data chapters, which have been presented as a series stand-alone papers with the aim of submission to relevant journals, along with a general introduction and discussion. As a result of writing each chapter to stand-alone, there is some unavoidable repetition both in the description of the study species and the methods. When fitted into the context of the thesis, the data chapters provide the appropriate information to address the overall objectives of this study.

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Chapter 2: Patterns of association between a non-native bird and native macroinvertebrate assemblages: the importance of environmental gradients.

2.1 Abstract

The ecological impact of non-native vertebrates on native invertebrates is not well understood. In this study the non-native population of the superb lyrebird (*Menura novaehollandiae*) in the temperate forests of Tasmania, Australia, were used as a case study to evaluate the capacity of non-native birds to influence native terrestrial macroinvertebrate communities. The superb lyrebird is a predator of soil- and leaf litter-dwelling macroinvertebrates, which also modifies their habitat through digging and scratching during foraging. The macroinvertebrate assemblages at sites with and without superb lyrebirds were compared by stratifying sampling across three microhabitats (riparian, slope and ridge). Overall, there was a significant interaction between lyrebird presence/absence and microhabitat on mean abundance and taxonomic richness of macroinvertebrates. Both measures were significantly lower in slope microhabitats at sites with superb lyrebirds. In contrast, evenness did not differ significantly with superb lyrebird presence or absence. Lyrebird foraging disturbance reduced leaf litter cover and increased exposed mineral soil. This may explain why the abundance of macroinvertebrates with an affinity for leaf litter was significantly lower in slope and riparian microhabitats at sites with superb lyrebirds. There was no significant difference in the abundance of soil dwellers and generalists between sites with and without superb lyrebirds. Macroinvertebrate assemblage composition differed significantly between sites with and without lyrebirds but there was also high level of variation among assemblages within each group of sites. This study shows that the superb lyrebird is capable of influencing native macro-invertebrate communities but that the impact is context dependent.

2.2 Introduction

Some non-native species can profoundly change the distribution, structure and composition of native communities by altering food webs, the flow of nutrients, disturbance regimes and the physical structure of habitats (Vitousek 1990, Crooks 2002, Simberloff *et al.* 2013). While the impact of non-native animals on native invertebrate communities has received considerable attention in marine and freshwater environments (e.g. Bax *et al.* 2003, McCarthy *et al.* 2006, Ward and Ricciardi 2007, Crooks 2008, Strayer 2010, Nilsson *et al.* 2011), comparatively little is known about the impact of non-native animals on native terrestrial macroinvertebrates (>2 mm), particularly those living in leaf litter and soil (Mysterud *et al.* 2005, Migge-Kleian *et al.* 2006, St Clair 2011). Instead, the majority of research on the impacts of non-native animals on soil ecosystems has focused on microbial communities and ecosystem processes (Barrios-Garcia and Ballari 2012, Greiner *et al.* 2012).

It is important to understand the impact of non-native animals on soil-dwelling and leaf litter macroinvertebrates because they are major components of the decomposer subsystem and play a vital role in the cycling of carbon and other nutrients (Wardle 1995, Hunter *et al.* 2003, Lavelle *et al.* 2006, Bultman and de Witt 2008, Parker 2010). For example, in forest ecosystems around 90% of net above-ground primary production returns to the forest floor as litter (Swift *et al.* 1979). Macroinvertebrates living in the soil and leaf litter break up this litter material; the rate at which they do so mediates the speed of chemical leaching, transformation of organic matter by micro-organisms, and the transfer of nutrients into the soil (Wall 2004, Lavelle and Spain 2005, Decaëns *et al.* 2006). Thus, changes in the structure and composition of macroinvertebrate communities as a result of invasion by non-native species can have flow-on effects on ecosystem processes, and therefore the functioning of the ecosystem as a whole (Ehrenfeld *et al.* 2001, Bohlen *et al.* 2004, Dunham and Mikheyev 2010).

Despite the fact that a large number of insectivorous bird species have been specifically introduced to control terrestrial macroinvertebrate populations (Long 1981, Cassey 2002, Lever 2005, Blackburn *et al.* 2009), the impact of these birds on native terrestrial invertebrates has rarely been considered (Blackburn *et al.* 2009). Indeed, I am aware of only one study, by Cole *et al.* (1995), that consists of more than anecdotal reports

regarding the impact of non-native birds on native soil and leaf litter invertebrates. They investigated the influence of two species of non-native game birds, the ring-necked pheasant (*Phasianus colchicus*) and the chukar partridge (*Alectoris chukar*) on invertebrate fauna in Hawaii. They did not find large numbers of native macroinvertebrates in the analysis of the birds' crops, but their study area supported a depauperate native macroinvertebrate fauna due to habitat modification and the presence of several other non-native species. Furthermore, macroinvertebrates make up only a small part of the diet of the two birds, so it is possible that other species which feed primarily on macroinvertebrates may have a stronger effect. There is clearly a need to investigate the impact of non-native birds on soil and leaf litter macroinvertebrates.

The superb lyrebird (*Menura novaehollandiae*) is a ground-foraging, pheasant-sized passerine bird native to forests along the east coast of mainland Australia (Higgins *et al.* 2001). It was first introduced to Tasmania from mainland Australia in 1934 and has now spread throughout much of the forested areas in the south of the island (Sharland 1944, Smith 1988, Tanner 2000). Superb lyrebirds are generalist predators of invertebrates (Robinson and Frith 1981, Lill 1996) that can dramatically modify forest floor habitat within their native range through their foraging activity (Adamson *et al.* 1983, Ashton and Bassett 1997). By using their large feet and claws to turn over leaf litter and soil to depths of up to 150 mm in search of prey, individual superb lyrebirds have been estimated to turn over 200 tonnes of soil per hectare per annum in some forest types within their native range (Ashton and Bassett 1997). Consequently, they are considered to be an important source of natural disturbance within their native range (Ashton 1975, Webb and Whiting 2006), and have been recognised as ecosystem engineers, as defined by Jones *et al.* (1994, 1997), i.e. as organisms which are capable of destroying, modifying, maintaining or creating habitats and controlling the availability of resources to other organisms through non-trophic means.

The thick layer of leaf litter on the forest floor in wet eucalypt forests provides habitat for diverse and numerous invertebrates (Ashton 1975, Meggs and Munks 2003). In the absence of fire and windfall of trees in Tasmanian wet eucalypt forests, disturbance of the forest floor is minimal (Harris and Kitchener 2005). Disturbance by native animals (such as digging or trampling) is limited because large ground dwelling animals are absent and most small to medium vertebrates prefer either drier forests, or wet forest

with a dense shrub layer and thick ground-level vegetation (Bennett 1993, Johnson 1994, Claridge and Barry 2000). Two species of birds, the native Bassian thrush (*Zoothera lunulata*) and the European blackbird (*Turdus merula*), occur at low densities in wet forests and also forage by scratching over leaf litter, but their feeding scrapes are much smaller (150 mm diameter) and shallower (<50 mm) than those of the superb lyrebirds (approximately 500 mm–1 m diameter and up to 100–150 mm deep) (Higgins *et al.* 2006, Ashton and Bassett 1997, Tassell, S. pers. obs).

Endemicity among Tasmanian forest invertebrates is high, many have very restricted geographical ranges, and some are listed as threatened species (Bryant and Jackson 1999, Harvey 2002, Mesibov *et al.* 2002, Meggs and Munks 2003). Conservation managers are concerned that Tasmanian forest floor invertebrates may be adversely affected by the superb lyrebird because they evolved without the predation pressures of a large insectivorous vertebrate, and without such an extent and frequency of bioturbation within their habitat (Mallick and Driessen 2009). Therefore, the first aim of this study was to determine whether the superb lyrebird has the potential to have a significant negative impact on native macroinvertebrates by investigating patterns in the structure and composition of macroinvertebrate communities that were associated with the presence of superb lyrebirds in southern Tasmania. Due to the lack of ‘pre-lyrebird’ impact information on macroinvertebrates in the study area, a quantitative field survey was employed with a space-for-time design, comparing macroinvertebrate communities in forests where superb lyrebirds were present to ecologically similar forest that had not yet been invaded.

Designing surveys that maximise the likelihood of detecting the impact of non-native species on native communities can be difficult for a number of reasons. In order to identify an impact, a survey must be able to account for natural variation at different spatial scales in the recipient communities in response to environmental factors or other influences (Lortie and Cushman 2007, Thomsen *et al.* 2011). The spatial distribution of forest and leaf litter macroinvertebrate assemblages is known to vary dramatically over the scale of tens of metres in response to smaller-scale variation in topography and underlying environmental conditions (Richardson and Devitt 1984, Taylor *et al.* 1994, Catterall *et al.* 2001, Baker *et al.* 2006, Barton *et al.* 2010). Furthermore, foraging by superb lyrebirds is very likely to be habitat dependent (Adamson *et al.* 1983, Ashton

and Basset 1997). Therefore, any impact of the superb lyrebird on macroinvertebrate fauna would likely be spatially heterogeneous due to the variation in environmental conditions over small spatial scales. The second aim, therefore, was to investigate the pattern of association between lyrebird presence/absence and macroinvertebrates across different microhabitats within and between sites. To achieve this, sample collection areas were stratified into riparian, slope and ridge zones, which encompasses the variation in microhabitats.

In the absence of prior research it is difficult to predict which native macroinvertebrates are likely to be affected through their interaction with the superb lyrebirds. Dietary studies show that superb lyrebirds are generalist predators of macroinvertebrates and feed on a wide range of taxa including earthworms, fly larvae, amphipods, centipedes and spiders (Robinson and Frith 1981, Smith 1988, Lill 1996). However, non-prey species could also be affected as a result of habitat modification or indirectly as a result of altered trophic interactions with prey species. This issue was addressed by surveying the majority of macroinvertebrate taxa rather than concentrating on a limited subset of species. Further, in the forest floor environment, macroinvertebrates may dwell primarily in the soil, the leaf litter, or occur in both habitats (Friend and Richardson 1977, Blakemore 2000, Baker *et al.* 2006, Doblas-Miranda *et al.* 2007). I hypothesised that the disturbance of the forest floor as a result of superb lyrebird feeding activity would reduce the extent of the leaf litter layer and increase the extent of exposed mineral soil, which will in turn impact the taxa that are dependent these different substrate habitats. Thus, the third aim was to establish whether the presence/absence of superb lyrebirds was associated with patterns in the abundance of macroinvertebrates with different substrate habitat affinities.

2.3 Methods

2.3.1 Study area

The study was conducted at six sites (three with lyrebirds present and three control sites without lyrebirds) in southern Tasmania, Australia (Fig 2.1). This region supports large tracts of wet eucalypt forest, which is a favoured habitat for superb lyrebirds (Ashton and Bassett, 1997). The climate is temperate with average daily minimum of 6.6 °C and a maximum of 15.9 °C in 2008, and an average annual rainfall of 569 mm during 2008

(Bureau of Meteorology 2008). Records of superb lyrebird sightings since their introduction, as collated by the Tasmanian Parks and Wildlife Service Natural Values Atlas (2007) and by BirdLife Tasmania (unpublished records 2007) revealed that there are areas of forest in southeastern Tasmania that are heavily disturbed by superb lyrebirds, but which are in close proximity to very similar lyrebird-free tracts of forest. By matching sites closely, environmental variables are less likely to co-vary with the presence/absence of superb lyrebirds, and thus confound the results. Potential field sites were identified by conducting a spatial multi criteria analysis using ESRI ArcGIS software and data layers supplied by Forest Practices Authority and Forestry Tasmania. Sites were chosen for their similarity in terms of vegetation composition and structure, altitude, geology, climate, slope, aspect, and history of logging and fire (see Table 2.1). Located no more than 60 km apart, the sites were situated in areas of wet sclerophyll forest that had been selectively logged more than 30 years ago but had not been subject to modern silviculture methods, and where there was no evidence of a major fire during the previous 40 years (Stone 1998, M.J. Brown pers. comm.).

As forest type in this region varies widely and can change within tens of metres (Neyland 2001, Meggs and Munks 2003), the final position of field sites was based on local (<100m) vegetation community type and structure as identified using Tasmanian Vegetation Monitoring and Mapping Program maps (TASVEG Version 1.3, Department of Primary Industries and Water 2001, Harris and Kitchener 2005), 1:25000 Photo Interpretation (PI) maps produced by Forestry Tasmania (Stone 1998, Forestry Tasmania 2007), and my own groundtruthing field surveys.

All sites were located in wet eucalypt forest with an understorey consisting of broad-leaved shrubs and rainforest species. Vegetation communities were dominated by either *Eucalyptus obliqua* or *Eucalyptus regnans*. Other canopy and sub-canopy species included *Nothofagus cunninghamii*, *Atherosperma moschatum*, *Phyllocladus aspleniifolius* and *Acacia dealbata*. The understorey was composed of broad-leaved trees and shrubs including *Olearia argophylla*, *Pomaderris apetala*, *Bedfordia linearis* and the tree fern *Dicksonia antarctica*. Shrub and ground level cover was sparse and mainly composed of species of fern including *Grammitis billardieri* and *Histiopteris incisa*. Herbaceous ground flora and moss ground cover were limited where the forest floor was open and covered with a layer of leaf litter that was 10–70 mm deep. The

underlying geology at sites was comprised of Jurassic dolerite or Triassic sandstone (Forsyth *et al.* 1995, Spanswick and Kidd 2000). The soils under wet eucalypt forest in this area include poor to well drained mineral soils with gradational texture profiles dominated by loamy clays up to 1m in depth with a rich organic layer above (Grant *et al.* 1995, Laffan 2001).

In the Southern Hemisphere, north-facing slopes are warmer than south-facing slopes and are subject to larger daily and seasonal fluctuations in temperature and evaporation. Sites on slopes facing east, southeast and southwest were selected because they were likely to share a similarly stable climate on a local scale (Barclay *et al.* 2000). Furthermore, Adamson *et al.* (1983) reported that superb lyrebirds forage mainly on east and south facing slopes within their natural range. Likewise, all sites were located in close proximity (20 m) to a permanent stream because the microclimate (particularly humidity and soil moisture levels) was likely to be more constant at the local scale.

2.3.2 Survey Design

To examine the effect of superb lyrebird foraging on macroinvertebrates, the study design used a space-for-time substitution (Pickett 1989) whereby three forested sites where superb lyrebirds were present (henceforth referred to as lyrebird sites) were compared with three sites without superb lyrebirds (control sites). Lyrebird sites were selected on the basis that annual surveys of a 30m × 2m transect at each potential site during the previous two years had found that superb lyrebird disturbance covered more than 50% of the forest floor. Each site consisted of a square approximately 50 × 50 m that was divided into three strata (henceforth referred to as ‘riparian’, ‘slope’ and ‘ridge’) by visual assessment. These strata encompassed the variation in microclimate and vegetation communities over the scale of tens of metres that often occurs in wet sclerophyll forest in Tasmania (Neyland 2001, Meggs and Munks, 2003, Baker *et al.* 2006). The ‘riparian’ microhabitats were located in the riparian strip within 10 m of a permanent stream, ‘slope’ microhabitats were located beyond the riparian zone within 10–25 m of the stream, and the ‘ridge’ microhabitats were located approximately 25–35 m from the stream on a convex landform.

A 4 × 4 m sample plot was marked out within each microhabitat, yielding three sample plots per site. To maximise the probability of detecting lyrebird impact, plots at lyrebird

sites were located in areas that were visually assessed as having the most recent and highest level of disturbance intensity present in the microhabitat zone. Forest floor microhabitat in sample plots at control sites were then matched with those of areas that were heavily disturbed at lyrebird sites. Information on the superb lyrebird within its natural range (Ashton and Bassett 1997, Higgins *et al.* 2006) together with that from pilot surveys (2006–2007) indicated that superb lyrebirds prefer to feed in areas where there are relatively few ground ferns but with thick leaf litter. Therefore, sample plots in areas of dense fern cover or thin leaf litter were avoided at control sites.

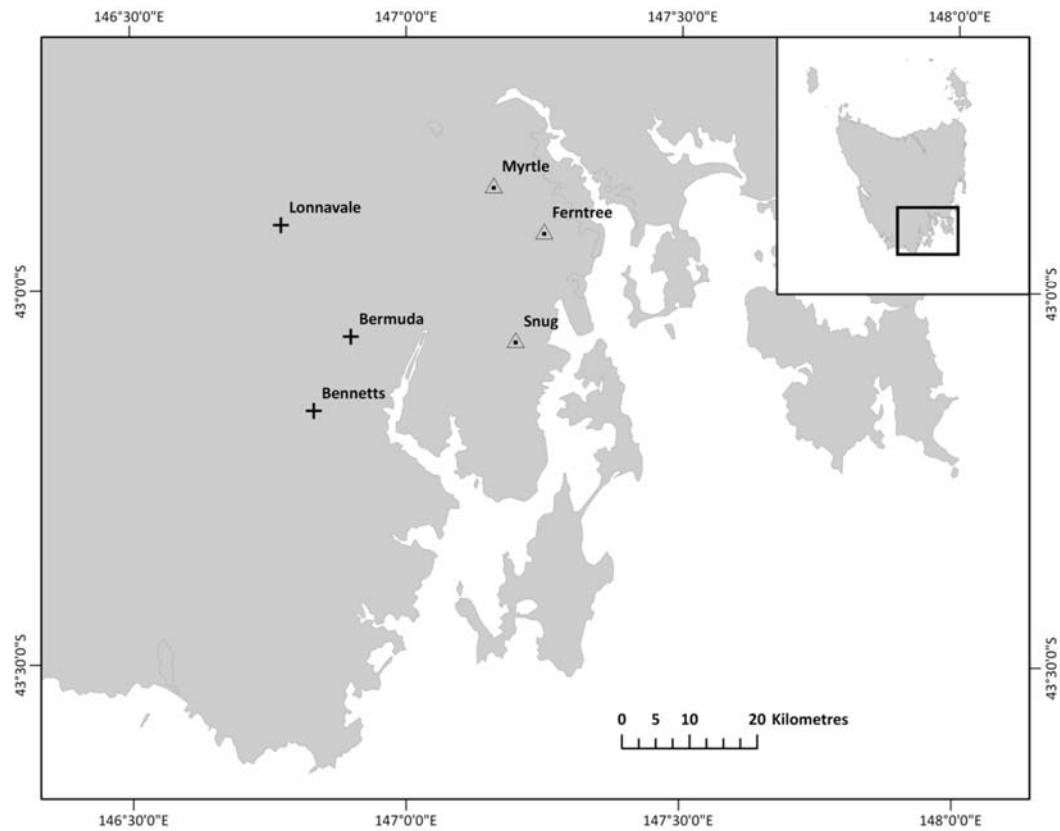


Figure 2.1: Map of southeast Tasmania, Australia showing the six sites sampled in the survey, comprising three sites where superb lyrebirds (*Menura novaehollandiae*) were present (+) and three sites beyond the current range of superb lyrebirds (△).

Table 2.1: Site environmental characteristics. Mean monthly rainfall was calculated for 2008 from the Australian Bureau of Meteorology data recorded at the meteorological station nearest to each study site. Vegetation community was determined using Tasmanian Vegetation Monitoring and Mapping Program maps (TASVEG Version 1.3, Department of Primary Industries and Water 2001, Harris and Kitchener 2005). Aspect identifies the downslope direction of the maximum rate of change in elevation. The values are the compass direction of the aspect. Hill shade analysis provides a measure of the average degree of shadow at the site by considering the effects of the local horizon in relation to the dominant sun angle and sun elevation. Areas in complete shadow have a value of zero. Areas in no shadow have a value of 255. Slope identifies the gradient in degrees, or rate of maximum change in elevation at the site. Slope, aspect code, hill shade and elevation were derived using geographical information system software (ESRI ArcGIS 10.0). †GDA 94. *No available climate data – rainfall given is from the nearest Meteorological station.

Site Control/ Lyrebird	Longitude †	Latitude †	Elevation (m)	Aspect Code (°)	Slope (°)	Hill shade	Geology	Mean Monthly Rainfall (mm)	Vegetation Community
Ferntree Control	147°15'03"E	42°55'15"S	490	252	21	133	Triassic quartz sandstone	70.2	<i>Eucalyptus regnans</i> forest and woodland
Myrtle Control	147°09'32 "E	42°51'34"S	550	282	7	178	Jurassic dolerite	44.3	<i>Eucalyptus regnans</i> forest
Snug Control	147°11'58"E	43°04'01"S	362	167	28	235	Triassic quartz sandstone	58.7	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)
Lonnavale Lyrebird	146°46'22"E	42°54'46"S	477	213	15	162	Jurassic dolerite	62.9	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)
Bermuda Lyrebird	146°53'59"E	43°03'47"S	542	76	15	144	Jurassic dolerite	62.9*	<i>Eucalyptus regnans</i> forest
Bennetts Lyrebird	146°49'49"E	43°09'34"S	436	262	17	225	Jurassic dolerite	98.1	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)

2.3.3 Data collection

2.3.3.1 Environmental variables

In each microhabitat a 30 m long \times 2 m wide transect was marked out in the immediate vicinity (within 3 m) of the sample plot. The percentage cover by each of canopy, understorey and groundcover was visually estimated and assigned to one of seven classes using a modified Braun-Blanquet index (Mueller-Dombois and Ellenberg 1974); i.e. 0 = 0% 1 = <1%, 2 = 2–5%, 3 = 6–25%, 4 = 26–50% 5 = 51–75% and 6 = 76–100%. The Braun-Blanquet index was also used to assess the percentage cover by each of the following forest floor substrate types: leaf litter layer, nonvascular plants and bryophytes, rock, and exposed mineral soil. The exposed mineral soil category incorporated both soil mixed with leaf litter by lyrebird scratching and bare areas devoid of leaf litter (which naturally occur in these forests and therefore may occur at control sites). Average leaf litter depth along each transect was visually estimated and categorised as thin <10 mm, medium 10–30 mm or deep >30 mm) (Meggs and Munks 2003, Forest Practices Authority 2005). The basal area of trees (a proxy for stand density) was recorded by using a Bitterlich basal wedge to measure the average cross-sectional area in square metres of all trees with wood >10 mm diameter at approximately 1.3 m above ground (Braithwaite *et al.* 1989, Forest Practice Authority 2005).

Prior to macroinvertebrate sampling, the cover (using the index above) of leaf litter layer and exposed mineral soil within each 4 \times 4 m sample plot was recorded. At lyrebird sites, the percentage of the total surface of each sample plot that had been disturbed was recorded, and ranked on both the age and intensity of that disturbance. Where more than one age and/or intensity were present in a plot that which covered the greatest extent was scored. Scores ranged from 0 to 3, where 0 = no disturbance, 1 = ‘old’ or ‘light’ disturbance intensity, and 3 = ‘heavy’ disturbance (for intensity) or ‘recent’ disturbance (for age) as described in detail in Table 2.2.

Table 2.2: Scores for assessing the intensity and age of superb lyrebird (*Menura novaeahollandiae*) disturbance in sample plots.

Scor	Intensity	Age
0	No disturbance	No disturbance
1	Light: -Leaf litter layer partially broken or removed. Scratching 10–40mm deep -Limited mixing of leaf litter and topsoil	Old: > 1– 2 months -Fallen leaf litter and debris has accumulated over scratching. -Seedlings may have started to germinate -Buried vegetation has turned brown
2	Medium: -Scratching 40–80 mm deep -Litter layer has been broken and mixed partially with topsoil -Some mineral soil exposed on surface	Medium: 2 weeks–1 month -Exposed mineral soil has been weathered, evidence of rain-wash -Some fallen leaf litter over diggings
3	Heavy: -Scratching to depth of 150 mm -Litter layer partially to completely broken, removed or incorporated with topsoil -Mineral soil exposed on surface	Recent: <2 weeks -Freshly turned over, moist soil on surface, not compacted, no indication of rain-wash -No mosses, shoots, or seedlings growing in scratched out patches -No fallen leaves on scratching -Displaced and buried vegetation still green

2.3.3.2 Macroinvertebrate sampling

Macroinvertebrate sampling was carried out at the six sites during October 2008 (austral spring). In order to minimise sampling bias associated with different collectors, the same two experienced researchers (ST and AMMR) carried out all fieldwork.

Researchers searched for macroinvertebrates in leaf litter and friable soil to a depth of approximately 100 mm within each 4 × 4 m sample plot. Each plot was divided into four 2 × 2 m quadrats which were marked out with tape. Soil and leaf litter in each quadrat was searched for 30 minutes, giving a total of two person hours per sample plot. With the exception of talitrid amphipods and entomobryid collembola, all macroinvertebrates >2 mm were collected with tweezers and preserved immediately in 80% ethanol and 2% glycerol. While talitrid amphipods and entomobryid collembola are sometimes abundant in Tasmanian forest soils (Friend and Richardson 1977), these groups were not collected because their ability to jump rapidly made them difficult and

time-consuming to catch by hand so that other taxa would have been under-sampled. Timed hand searches have been shown to be more efficient and effective than pitfall trapping for collecting many macroinvertebrate groups both in Tasmanian forests (Mesibov *et al.* 1995, Bonham *et al.* 2002, Meggs and Munks 2003) and elsewhere (Snyder *et al.* 2006, Carr 2010). Pitfall traps and other *in situ* trapping techniques were not appropriate because traps were likely to be damaged or destroyed by the foraging activity of the superb lyrebirds (Burrows, R. pers. comm.). In addition, pilot surveys revealed that digging or coring soil monoliths (e.g. Anderson and Ingram 1993) was difficult due to the presence of rocks and tree roots in the soil and so was likely to under represent the large macroinvertebrates which were the focus of this study.

Macroinvertebrates were identified to the lowest taxonomic level possible, usually genus, species or morphospecies, using external morphology (see Appendix 1 for a list of taxonomic keys and experts consulted). Taxonomic knowledge for some groups, particularly many of the coleopteran families, is limited, so standardised sorting codes were given to undescribed taxa. For Coleoptera, the morphospecies codes from the Forestry Tasmania Insect Collection (TFIC), now housed at the Tasmanian Museum and Art Gallery (TMAG) collection, were used. Adult and larvae of the same Coleopteran species were recorded separately because the habitat requirements and feeding ecology of many species differ with life history phase (Lavelle *et al.* 1993). Undescribed Diplopoda and Chilopoda were given standardised sorting codes as per Mesibov (2012). Diptera larvae and Oligochaete worms were sorted into size classes based on length for Diptera (5 mm, 6–10 mm and >10 mm) and width for Oligochaeta (<1 mm, 2–5 mm and >5 mm) rather than taxa. Size varied dramatically in these groups and the use of size classes made it possible to account for the possibility that larger individuals would be favoured food items for superb lyrebirds (Robinson and Frith 1981, Lill 1996). The voucher collection for this study was deposited with TMAG.

2.3.3.3 *Substrate habitat affinities of macroinvertebrates*

It was hypothesised that superb lyrebird foraging would reduce the availability of leaf litter habitat and increase exposed mineral soil habitats. Whether there was a pattern in the abundance of macroinvertebrates with affinities for either of these substrate habitats, as a result of habitat availability and/or differing vulnerability to predation by superb lyrebirds, was tested. Therefore, each taxon was assigned to one of two substrate affinity

types: ‘leaf litter-dwellers’ or ‘generalists/soil dwellers’ (the latter type included taxa that primarily dwell in soil as well as generalists which readily inhabit both soil and leaf litter) based on literature and communication with taxonomic experts (see Appendix 1).

2.3.4 Statistical Analysis

2.3.4.1 Environmental variables

To check for confounding differences in the underlying environmental factors at lyrebird and control sites and microhabitats, a Principal Components Analysis (PCA) of normalised environmental variables recorded from transects in each microhabitat was performed using PRIMER-E 6 software (Clarke and Gorley 2006). Leaf litter cover and exposed mineral soil cover were excluded from analysis, as they were likely to be directly influenced by lyrebird activity. The remaining variables were: canopy cover, understorey cover, ground vegetation cover, nonvascular plants & bryophytes cover, rock cover, leaf litter depth and stand density. To establish whether lyrebird disturbance varied across microhabitat types at the time of the survey the mean level of lyrebird disturbance (extent, age and intensity) in the sample plots within the three microhabitat types at lyrebird sites was also calculated. Mean cover of leaf litter and exposed mineral soil in sample plots within each microhabitat type at lyrebird sites were also calculated to compare the relative availability of each substrate type.

2.3.4.2 Macroinvertebrate analysis

Subsamples collected by the two researchers within each sample plot were averaged to estimate the mean abundance of individuals, taxonomic richness, Pielou’s evenness (J') in each plot. The latter metric provides a measure of the relative distribution of individuals among the taxa present in a community (Pielou 1966, Magurran 1988). Pielou’s evenness uses the ratio of observed Shannon diversity (H') to maximum diversity (H_{max}) that could occur if all species were equally abundant. An evenness value of 1 indicates that all species are equally abundant.

2.3.4.3 Univariate analyses: macroinvertebrate assemblage structure

The influence of lyrebird presence/absence and of microhabitat on macroinvertebrate community structure was investigated using generalised linear mixed models (GLMMs) to account for the presence of random factors and non-normal data, without the need to

transform the data prior to analysis (Faraway 2005, Zuur *et al.* 2009). The response variables for the models were mean macroinvertebrate richness, taxonomic abundance and evenness. Models with a Poisson error distribution and log-link function were fitted for abundance and richness counts data, while a Gaussian error distribution and identity-link function were most appropriate for evenness. Lyrebird status (two levels: presence and absence of lyrebirds) and microhabitat (three levels: riparian, slope and ridge) were crossed fixed factors, with sites and researcher identity treated as random effects. Poisson models were checked for over dispersion following Zuur *et al.* (2009) and Wetherill and Brown (1991), and the standard diagnostic plots of residuals were inspected to assess conformation to assumptions. Fixed effects were tested using likelihood ratio tests (χ^2) on models fitted via maximum likelihood; once fixed effects were simplified, final models were fitted using restricted estimate maximum likelihood (REML) following Zuur *et al.* (2009). GLMMs were also used to test whether there were differences in the mean abundance of leaf litter dwellers and generalist/soil dwellers. Poisson distributions and log-link functions were fitted to mean abundance data for these two substrate habitat affinity types and the models used the same design as the assemblage structure GLMMs described above. All univariate analyses were conducted using the function 'glmer' in the 'lme4' library (Bates *et al.* 2011) for the R software package version R 2.15.2 (R Development Core Team 2012).

2.3.4.4 *Multivariate analyses: macroinvertebrate assemblage composition*

Singletons were excluded from analysis because they do not contribute to general patterns across sites (McCune and Grace 2002). Abundance data was square-root transformed to reduce the influence of numerically dominant taxa (Clarke 1993). All multivariate statistical analyses were conducted using PRIMER-E 6 (Clarke and Gorley 2006) with the PERMANOVA + add-on package (Anderson *et al.* 2008). Permutational multivariate analysis of variance (PERMANOVA) was used based on the same mixed model design as the univariate analyses to test for significant differences in overall macroinvertebrate assemblage composition between lyrebird and control sites. However, high taxonomic richness and the large number of rare taxa recorded at single sites could potentially obscure any signal of superb lyrebird influence on assemblage composition. Therefore, taxa were also pooled together as leaf litter dwellers or generalist/soil dwellers and a second PERMANOVA test was conducted.

Each PERMANOVA was based on a Bray-Curtis similarity matrix of square-root transformed abundance data (total abundance for the first PERMANOVA and abundance of leaf litter and generalist/soil dwellers in the second) and used 9999 unrestricted permutations under a reduced model (Anderson *et al.* 2008). As the number of unique permutations in this design was relatively small, I used the Monte Carlo asymptotic *P*-value for the test statistic (Anderson and Robinson 2003). PERMDISP (Anderson 2004), a distance based test, was then used to test the homogeneity of multivariate dispersion, or scatter, between samples from each lyrebird status group and their group centroids (Anderson *et al.* 2006). PERMDISP makes it possible to distinguish the relative influence of the centroids versus dispersion of samples around their centroid in driving any differences between lyrebird and control site assemblages. A nonmetric multidimensional scaling (nMDS) ordination based on the Bray-Curtis similarity matrix was used to visually inspect the pattern of macroinvertebrate composition. The individual taxa that contributed the most to the overall dissimilarity between assemblages at lyrebird and control sites were identified using the similarity percentage procedure (SIMPER) (Clarke and Gorley 2006).

The Distance-based Linear Modelling (DISTLM) routine was used to determine which environmental variables best explained the variation in the macroinvertebrate data (Legendre and Anderson 1999, McArdle and Anderson 2001). DISTLM allows for significance testing of explanatory environmental variables for a multivariate response variable in the form of a resemblance matrix, in this case the same Bray-Curtis similarity matrix of macroinvertebrate abundance data, generated as above (Anderson *et al.* 2004, Anderson *et al.* 2008). Prior to conducting the DISTLM, a draftsman plot of environmental variables was examined to check whether any environmental variables required transformation. The presence of highly correlated variables ($r > 0.8$, Clark and Gorley 2006) was also checked, and depending on their ecological meaning, all but one of the correlated variables was removed in order to avoid biases associated with multicollinearity (Clarke and Gorley 2006). As expected, several variables related to lyrebird disturbance were highly correlated: plot leaf litter, plot exposed mineral soil, transect leaf litter cover, transect leaf litter depth, lyrebird disturbance extent, lyrebird disturbance age and lyrebird disturbance intensity. Therefore, all except for plot leaf litter cover were omitted, which serves as a proxy for the other variables in the analysis. The DISTLM was then fitted using the BEST selection procedure, and the Akaike

Information Criterion (AIC) was used as a measure of goodness-of-fit to identify the most parsimonious explanatory model (the smaller the AIC value, the better the fit). DISTLM analysis was then repeated using only the subset of variables included in the most parsimonious model (Anderson *et al.* 2008).

To examine the relationship between macroinvertebrate assemblages and environmental factors, both constrained and unconstrained ordinations of macroinvertebrate assemblages were conducted. A distance-based redundancy analysis (dbRDA) was used to specify the relationship between macroinvertebrate communities and the optimal model predictors, based on the multivariate regression model generated by the DISTLM (Legendre and Anderson 1999, McArdle and Anderson 2001). In addition, the unconstrained ordination technique, nMDS, was used to validate the pattern displayed in the dbRDA analysis because the nMDS technique is based on the assumption that the relationship between the dependent (macroinvertebrate) and independent (environmental) variables is linear. The spatial arrangement of samples in the nMDS would therefore be similar to that shown in the dbRDA if the relationship is indeed linear.

2.4 Results

2.4.1 Environmental variables

The PCA of microhabitat-level environmental variables (excluding ground cover classes that were likely to be directly affected by lyrebird scratching) indicated that leaf litter depth and stand density loaded positively on PC1 while rock cover loaded positively and canopy cover loaded negatively on PC2 (Fig 2.2). Although there was considerable variation in vegetation structure and ground cover both between and within sites, there were no consistent differences between lyrebird and control sites (Fig 2.2). This indicated that any patterns in macroinvertebrate assemblages that were associated with the presence of superb lyrebirds were unlikely due to underlying co-varying environmental factors. In addition, the lack of grouping of samples from the same site indicated there is substantial variation in environmental variables within sites. The PCA also indicated that microhabitats of the same type were not particularly similar in terms of vegetation structure.

Examination of lyrebird disturbance in sample plots revealed that lyrebird disturbance typically covered 50–100% of each plot at lyrebird sites but was highest in slope microhabitats (Table 2.3). Intensity of lyrebird disturbance in plots was similar across microhabitats at lyrebird sites, being largely ‘medium’ or ‘heavy’, and mainly two weeks to a month old (i.e. ‘medium’ age). Mean cover of leaf litter was lower in all microhabitats at lyrebird sites than at control sites, with the reverse being true for the cover of exposed mineral soil (Table 2.3). This suggests that, in the absence of lyrebirds, the leaf litter layer is more or less continuous in wet forest of this kind, and that lyrebird disturbance leads to an increase in the extent of exposed mineral soil.

2.4.2 Univariate analyses: macroinvertebrate assemblage structure

A total of 2,465 individuals from 125 taxa were collected in this study. Of the taxa collected, 46 were collected only at control sites compared to 25 that were only collected at lyrebird sites. More than half of the taxa collected (79) were represented by five or fewer individuals and 38 of these taxa were singletons. Four taxonomic groups accounted for over 70% of all captures: Oligochaeta (29.1%), Diplopoda (22.5%), Diptera (10.6%) and Chilopoda (9%).

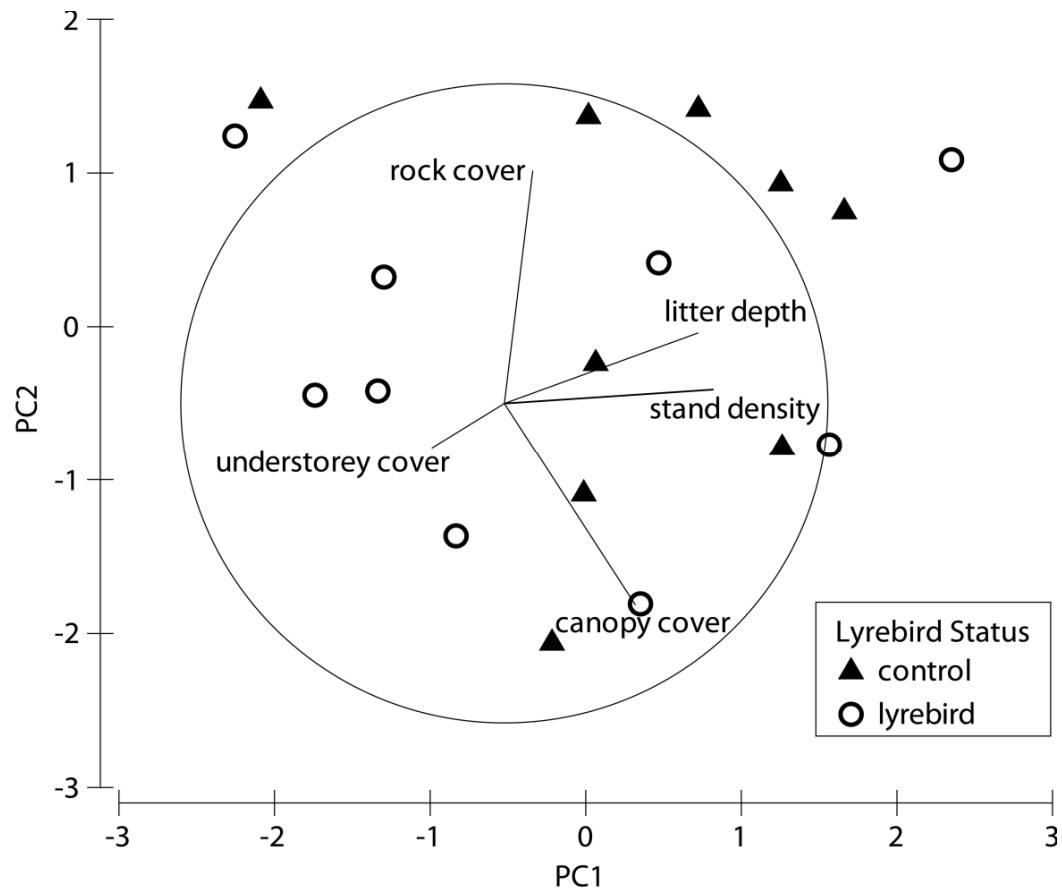


Figure 2.2: Principal component analysis (PCA) analysis of site-level environmental parameters (not influenced directly by superb lyrebirds, *Menura novaehollandiae*). The first two principal components accounted for 63.7 % of the total variation (PC1 = 37.0%, PC2 = 26.7%).

There was a significant interaction between lyrebird status and microhabitat for mean richness and abundance (abundance $df = 2$ $\chi^2 = 102.69$ $P < 0.001$ and richness $df = 2$ $\chi^2 = 11.70$ $P < 0.002$). Simple effects tests showed that richness and abundance only differed between lyrebird and control sites within slope microhabitats (Table 2.4). Mean richness was two times higher in slope microhabitats at control sites than in slopes at lyrebird sites (mean: 24.5 and 12.5 respectively). Similarly, mean abundance was almost three times higher in slope microhabitats at control sites than in slope samples at lyrebird sites (mean: 102 and 35 respectively) (Fig 2.3). There were no significant factors or interactions in the evenness models (Table 2.4) but evenness values were more variable at lyrebird sites (shown by large confidence intervals in Fig 2.3).

There were significant interactions between lyrebird status and microhabitat for both leaf litter dwelling and generalist/soil dwelling affinity groups (Table 2.5). The abundance of leaf litter-dwelling individuals in slope microhabitats at control sites was almost 4 times higher (mean 69.5) than in slope microhabitats at lyrebird sites (mean 18.3) while twice the number of individuals were collected from riparian microhabitats at control sites (Fig 2.4). In contrast, there were no significant differences in abundance of generalist/soil dwellers in any of the microhabitats (Table 2.4).

Table 2.3: Mean (\pm SE) of substrate habitat cover (leaf litter versus exposed mineral soil) and superb lyrebird (*Menura novaehollandiae*) disturbance in riparian, slope and ridge microhabitats at lyrebird and control sites. Extent of superb lyrebird disturbance, exposed mineral soil and intact leaf litter layer are presented as modified Braun-Blanquet scores: 0 = 0%, 1 = < 1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75% and 6 = 76–100%. Intensity and age of lyrebird disturbance are scored as 0 = no disturbance, 1 = light intensity/ old, 2 = medium intensity/ medium, 3 = heavy intensity /recent. NA = not applicable due to absence of superb lyrebirds.

Variable	Riparian		Slope		Ridge	
	Lyrebird	Control	Lyrebird	Control	Lyrebird	Control
Intensity	3 \pm 0	NA	2 \pm 0.5	NA	1 \pm 0.3	NA
Age	2 \pm 0	NA	2.6 \pm 0.3	NA	2 \pm 0.5	NA
Extent	5.3 \pm 0.3	NA	5.6 \pm 0.3	NA	5.6 \pm 0.3	NA
Exposed mineral soil	5.3 \pm 0.3	1 \pm 1	5.6 \pm 0.3	2.3 \pm 1.2	5.3 \pm 0.3	0 \pm 0
Intact leaf-litter	3.3 \pm 0.6	6 \pm 0	3.0 \pm 0.5	6 \pm 0	3.6 \pm 0.3	6 \pm 0

Table 2.4: Generalised linear mixed model (GLMM) likelihood ratio tests of the interaction between the two experimental factors, superb lyrebird (*Menura novaehollandiae*) status and microhabitat, on macroinvertebrate assemblage structure (mean abundance, taxonomic richness and evenness J'). Simple effect tests are given for microhabitat where there was a significant interaction between lyrebird status and microhabitat. *P*-values <0.05 are in bold and indicate a significant effect. NS = nonsignificant.

	Abundance			Richness			Evenness J'		
	df	χ^2	<i>P</i>	df	χ^2	<i>P</i>	df	χ^2	<i>P</i>
<i>Lyrebird status x Microhabitat</i>	2	102.69	<0.001	2	11.70	0.002	2	0.869	0.647
Riparian	1	0.402	0.524	1	0.506	0.476	-	NS	NS
Slope	1	5.901	0.015	1	10.03	0.001	-	NS	NS
<i>Ridge</i>	1	0.312	0.576	1	0.219	0.639	-	NS	NS

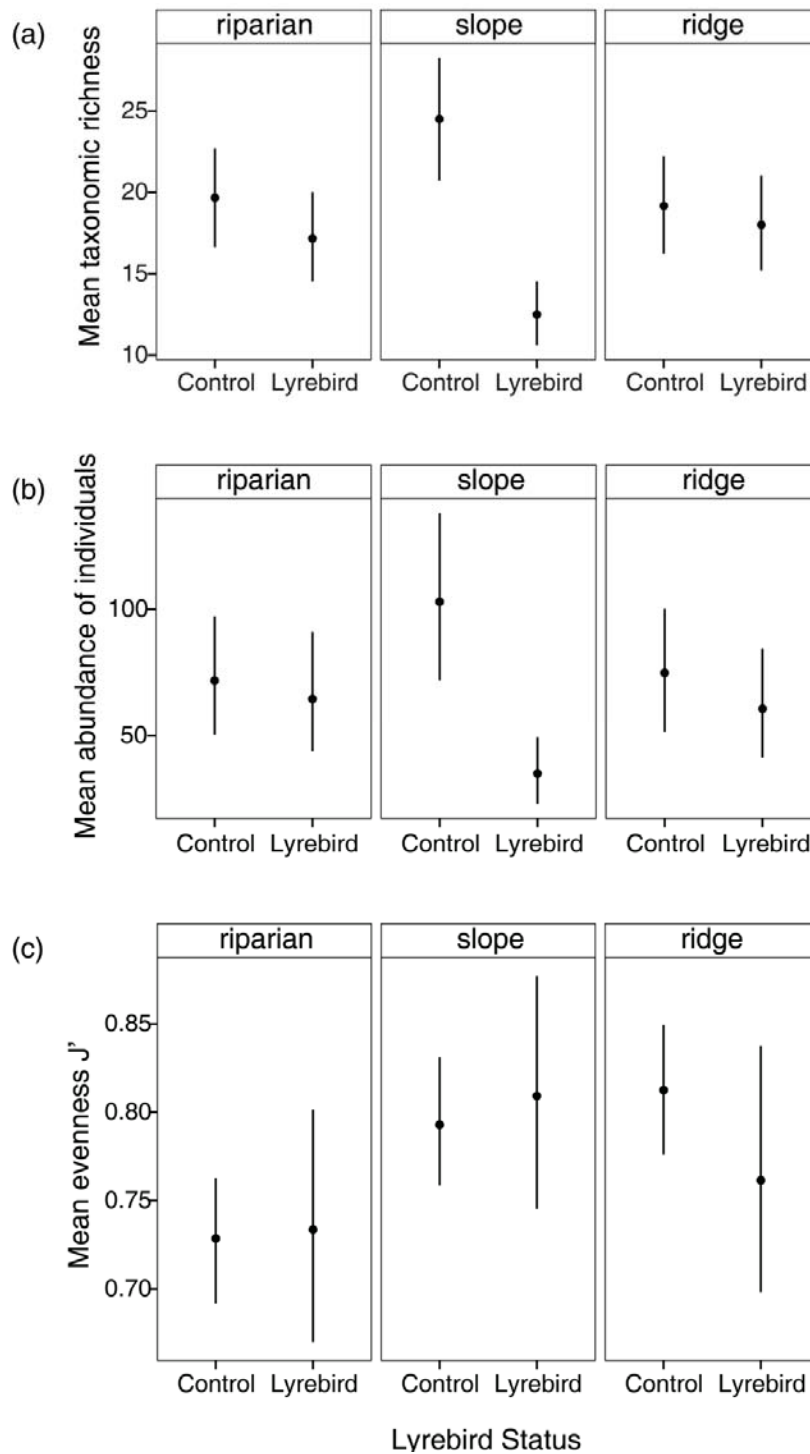


Figure 2.3: Mean taxonomic richness (a), abundance (b), and evenness (c) of macroinvertebrates in different microhabitats (riparian, slope and ridge) at sites with superb lyrebirds (*Menura novaehollandiae*) and control sites without. Plots are mean fitted values with 95% bootstrapped confidence intervals. All values are means from $n=3$ replicate microhabitat plots at lyrebird and control sites.

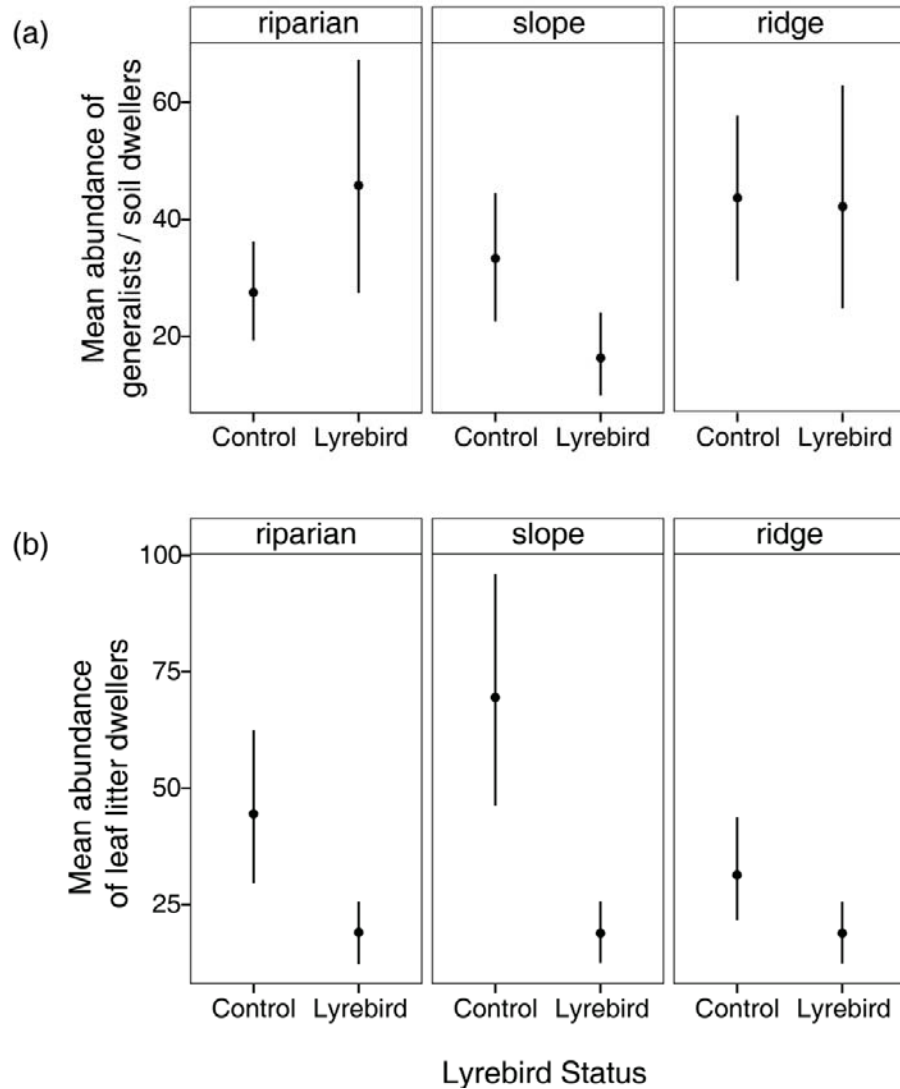


Figure 2.4: Mean abundance of a) generalist/soil-dwelling individuals and b) leaf litter-dwelling individuals in three microhabitats (riparian, slope and ridge) in the presence/absence of the superb lyrebird (*Menura novaehollandiae*). Plots are mean fitted values with 95% bootstrapped confidence intervals. All values are means from $n=3$ replicate microhabitat plots at lyrebird and control sites.

Table 2.5: Generalised linear mixed models (GLMMs) likelihood ratio tests of the interactions between the presence/absence of the superb lyrebird (*Menura novaehollandiae*) and microhabitat (riparian, slope ridge) on mean abundance of leaf litter-dwelling and generalist/soil-dwelling macroinvertebrates. Simple effect tests between lyrebird and control treatments are then given for each microhabitat. P-values <0.05 are in bold and indicate a significant effect on that response variable of macroinvertebrate substrate habitat affinities.

	Leaf litter dwellers			Generalists /soil dwellers		
	df	χ^2	P	df	χ^2	P
<i>Lyrebird status x Microhabitat</i>	2	25.902	<0.001	2	63.579	<0.001
Riparian	1	4.538	0.033	1	0.854	0.355
Slope	1	5.279	0.021	1	2.633	0.104
<i>Ridge</i>	<i>1</i>	1.252	0.263	1	0.045	0.831

2.4.3 Multivariate analyses: macroinvertebrate assemblage composition

There was a significant difference in assemblage composition between lyrebird and control sites when abundance data was pooled by habitat affinity (PERMANOVA $F_{1,4} = 4.8$ $P = 0.04$) (Table 2.6). The pair-wise test showed that the only significant difference in abundance between lyrebird and control sites occurred in slope microhabitats (PERMANOVA *a-posteriori* comparison for slope $t = 2.84$ $P = 0.02$). There was no difference in the degree of dispersion among samples between lyrebird and control sites (PERMDISP $F_{1,16} = 3.7755 \times 10^{-2}$ $P = 0.85$). As expected due to high taxonomic richness, the large number of rare taxa, and the small number of unique permutations possible, overall taxonomic composition did not vary significantly between lyrebird and control sites (PERMANOVA $F_{1,4} = 1.46$, $P = 0.21$ PERMDISP $F_{1,16} = 0.13$, $P = 0.71$). The nMDS ordination revealed that samples from lyrebird and control sites formed distinct groups but also showed that there was considerable spread among samples within each lyrebird status group (Fig 2.5).

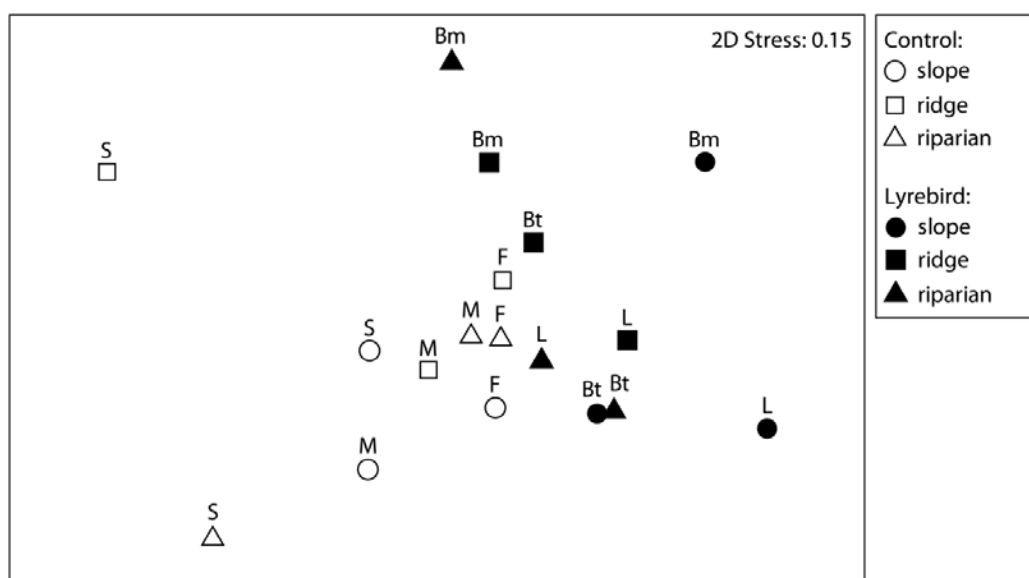


Figure 2.5: Non-metric multidimensional scaling (nMDS) ordination based on a Bray-Curtis similarity matrix of square-root transformed macroinvertebrate abundance data from microhabitats (slope, ridge, riparian) at sites with superb lyrebird (*Menura novaehollandiae*) and control sites without them. Site abbreviations: S = Snug, M = Myrtle, F = Ferntree, Bt = Bennetts, Bm = Bermuda and L = Lonnale.

The SIMPER revealed that there was an average dissimilarity of 61.63% between the assemblages of lyrebird and control sites (Table 2.7). Ten taxa contributed 38.63% of the dissimilarity and seven of these taxa were less abundant at lyrebird sites than at control sites. Two millipede taxa (*Spirostreptida* spp. and *Austroleuma jeekeli*) and small Oligochaeta contributed the most to the observed dissimilarity. Oligochaetes (categorised as generalists/soil dwellers) were more abundant at lyrebird sites while the two millipede taxa, which were categorised as leaf litter dwellers, were most numerous at control sites. No taxon contributed more than 6.21% to the dissimilarity between lyrebird and control sites, indicating that differences in composition were largely due to the relative abundance of a subset of relatively common taxonomic groups. The results highlight that few individual taxa occurred across all the sites, or were insufficiently abundant across multiple sites to drive differences in assemblages.

2.4.4 Relationship between environmental parameters, lyrebird presence/absence and macroinvertebrates

The most parsimonious DISTLM model ($R^2 = 0.121$, $AIC = 141.37$) consisted of only one variable: plot leaf litter cover ($F = 2.1981$, $P = 0.0004$). However, plot leaf litter cover was a proxy for plot exposed mineral soil cover, plot leaf litter depth, transect leaf litter cover, and the measures of lyrebird disturbance: intensity, age and extent. Only 12.08 % of the total variation among macroinvertebrate samples was explained by plot leaf litter cover: lyrebird plots generally had less leaf litter cover than control plots, as shown in the nMDS ordination of macroinvertebrate similarity with bubble plot projection of the extent of plot leaf litter cover (Fig 2.6).

Table 2.6: Results of the three-factor multivariate PERMANOVA comparing macroinvertebrate assemblage composition at sites with superb lyrebirds (*Menura novaehollandiae*) and control sites. Based on Bray-Curtis similarity matrix of square-root transformed macroinvertebrate abundance data pooled by habitat affinity (leaf litter dwellers, generalist/soil dwellers). SS: sum of Squares, MS: mean square, P (MC): Monte Carlo asymptotic P-value (statistically significant values of <0.05 are listed in bold).

Factors	df	SS	MS	pseudo-F	permutations	P(MC)
<i>Between Sites</i>						
Lyrebird status	1	1426.5	1426.5	4.81	10	0.04
Residuals	4	1188.2	297.1	1.31	-	-
<i>Within Sites</i>						
Microhabitat	2	131.01	65.51	0.29	9961	0.798
Lyrebird status X Microhabitat	2	635.61	317.81	1.4	9953	0.27
Residuals	8	1815.1	226.88	-	-	-
Total	17	5196.4	-	-	-	-

Table 2.7: Summary of SIMPER showing the average abundances of the taxa that contributed the most to the dissimilarity between sites with superb lyrebirds (*Menura novaehollandiae*) and control sites. Average dissimilarity between lyrebird status groups was 61.63%. Habitat affinity abbreviations: G/S = generalist/soil dwellers, L= leaf litter dwellers.

Class/Order	Taxa	Habitat Affinity	Control Sites	Lyrebird Sites	% Contribution to Assemblage Differences	% Cumulative
			Average Abundance	Average Abundance		
Diplopoda	Spirostrepsida spp.	L	2.65	0.04	6.21	6.21
Diplopoda	<i>Austroleuma jeekeli</i> .	L	3.88	0.03	5.88	12.09
Annelida	<1 mm Oligochaeta	G/S	0.98	2.62	5.63	17.72
Diptera	6-10 mm Diptera larvae	G/S	2.22	0.16	4.24	21.96
Chilopoda	<i>Steneurytion</i> sp.	G/S	0.28	0.96	3.61	25.58
Annelida	2-5 mm Oligochaeta	G/S	5.07	4.45	3.30	28.88
Platyhelminthes	Turbellaria sp.	L	1.93	0.88	2.81	31.68
Acari	Mesostigmata sp.	L	1.87	0.56	2.45	34.13
Formicidae	<i>Prolasius</i> sp.	G/S	0.51	0.82	2.25	36.38
Araneae	<i>Araneae</i> sp. 03	L	0.51	0.03	2.25	38.63

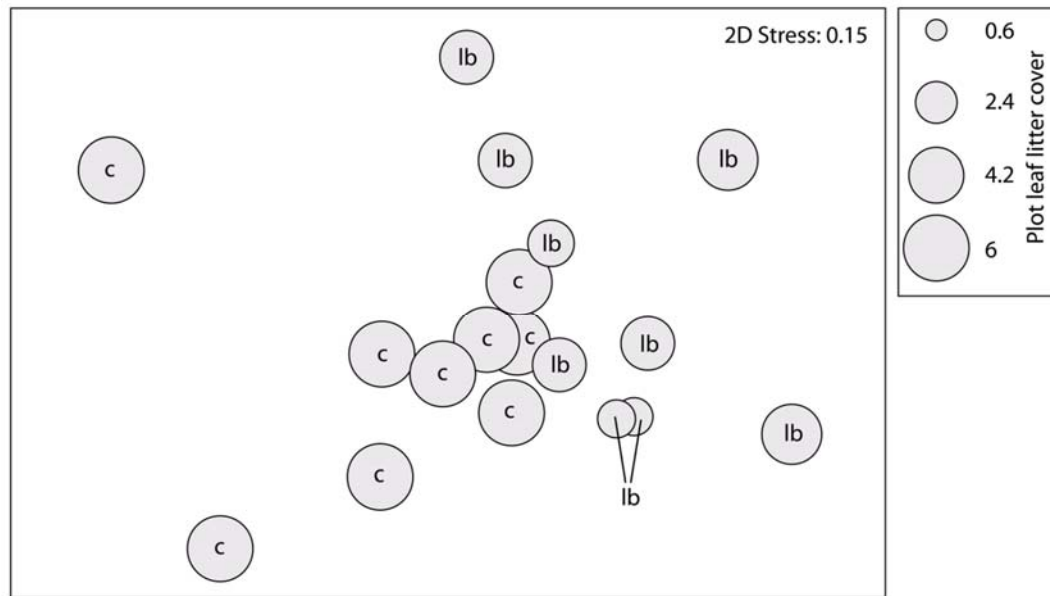


Figure 2.6: Non-metric multidimensional scaling (nMDS) ordination based on a Bray-Curtis similarity matrix of untransformed macroinvertebrate abundance data from plots (slope, ridge, riparian) at sites with superb lyrebird (*Menura novaehollandiae*) (lb) and control sites (c). Sizes of circles denote the extent of leaf litter in plots based on the Braun-Blanquet index where 1 < 1% and 6 = 76-100% cover.

2.5 Discussion

While other non-native animals are known to influence native terrestrial macroinvertebrates (Fukami *et al.* 2006, Migge-Kleian *et al.* 2006, Choi and Beard 2012,), the impact of non-native birds has only been investigated once prior to the present study (see Cole *et al.* 1992). This knowledge gap was addressed by using a space-for-time survey to compare macroinvertebrate assemblages at sites where the non-native superb lyrebird was present with sites immediately beyond its current range. There were two major findings: firstly, there were patterns in the structure and composition of macroinvertebrate assemblages across sites and microhabitats that were associated with the presence of superb lyrebirds in spite of substantial within- and between-site variation. Secondly, the response to the presence of superb lyrebirds varied between macroinvertebrates with different substrate habitat affinities.

Before discussing the results of the influence of superb lyrebirds on macroinvertebrates it is important to outline the inherent variability in macroinvertebrate assemblage

structure and composition identified at different spatial scales. Soil and leaf litter communities are typically highly variable at a spatial scales ranging from centimetres to hundreds of kilometres (Mesibov 1998, Ettema and Wardle 2002, Barton *et al.* 2010). This natural variation was accommodated by (a) selecting sites that were ecologically as similar as possible and within close proximity to each other (thereby minimising differences in fauna due to historical biogeographic influences on species distribution) and (b) stratifying sampling across microhabitats within sites in order to encompass small-scale environmental gradients that often exist in wet forests (Richardson and Devitt 1984, Taylor *et al.* 1994, Catterall *et al.* 2001, Baker *et al.* 2006, 2007). Despite selecting sites with no significant differences in environmental conditions, considerable variation in assemblages was found between sites regardless of the presence or absence of superb lyrebirds. Mesibov (1998) also found that Tasmanian forests of the same vegetation composition and structure, subject to similar environmental conditions, could support very different macroinvertebrate assemblages. Although eliminating inter-site variation was impossible, there were no consistent differences in environmental conditions that co-occurred with the presence/absence of lyrebirds.

As anticipated, assemblages in the three microhabitats differed from one another within sites (most likely due to differences in microclimatic conditions). However, assemblages from the same microhabitat did not closely resemble each other across sites, either in the presence of superb lyrebirds or without them. This indicates that while microhabitats support distinct assemblages within sites, the assemblages are also influenced by site-level (geographical factors). Baker *et al.* (2007) also found that site-level effects outweighed the more subtle effects of riparian and upslope microhabitats in wet forest in Tasmania, but studies conducted elsewhere, such as Catterall *et al.* (2001) and Brenner (2000), found the opposite. The relative importance of site versus microhabitat factors probably depends in part on the strength of the local environmental gradients. For example, factors such as moisture level may differ more between slope and riparian microhabitats in the warmer and drier subtropical forests investigated by Catterall *et al.* (2001) than in the temperate wet forests of Tasmania (Baker *et al.* 2007).

While macroinvertebrate assemblages were inherently heterogeneous on both small and large spatial scales, there were also distinct patterns of association between macroinvertebrate assemblages and the presence of superb lyrebirds. Although causal

links cannot be demonstrated, this survey provided a good test of impact as all sites with superb lyrebirds were heavily impacted and individual plots all contained medium and/or high intensity disturbance that was recent or medium in age. Furthermore, there was evidence that superb lyrebirds were at least partially responsible for some of the patterns in macroinvertebrate assemblages. For example, control site slope samples had the highest number of individuals and taxa, therefore the low abundance and richness recorded in slope microhabitats at lyrebird sites was very likely a result of superb lyrebird foraging activity rather than inherently low numbers on slopes at those sites. Similar patterns of low abundance and richness of macroinvertebrates have also been identified in other soil communities as a response to interaction with non-native predators (Cole *et al.* 1992, Hoffman *et al.* 1999) and ecosystem engineers (Snyder *et al.* 2013, Taylor *et al.* 2011).

Interestingly, my results contrast with those of Adamson *et al.* (1983) who observed that, within the natural range of the superb lyrebird, the abundance of invertebrates appeared to be higher in patches of forest floor disturbed by superb lyrebirds. This may be because the invertebrate fauna in Tasmanian forests has a large endemic component (Bryant and Jackson 1999), and endemism on islands often makes fauna more vulnerable to non-native species (Berglund *et al.* 2009). This is thought to be because native species in isolated areas may evolve in the absence of any species that is functionally similar to a newly arrived non-native species and therefore have not developed any adaptations to withstand it (Diamond and Case 1986, Vitousek 1990). In this case, the lack of exposure to high levels of predation or frequent disturbance may explain why Tasmanian soil and leaf litter macroinvertebrates responded in the opposite direction to macroinvertebrates that evolved within the native range of superb lyrebirds.

The differences in abundance and richness between lyrebird and control sites were not uniform across the three microhabitats; that is, there were notable differences in the strength of the association between lyrebird presence and macroinvertebrate assemblages. So while abundance and richness were lower in all microhabitats in the presence of lyrebirds, they were only significantly lower in slope microhabitats. This finding is in agreement with the general principle in invasion ecology that the impact of a non-native species is heterogeneous as a result of spatial variation in environmental conditions and biological communities (Crooks 2002, de Moura Queirós *et al.* 2011,

Thomsen *et al.* 2011). Differences in environmental factors such as soil moisture between the microhabitats could help or hinder the ability of the superb lyrebird to capture prey. For example, when soils are moist, macroinvertebrates tend to occur in high numbers close to the soil surface (Robinson and Frith 1981, Frouz *et al.* 2004). However, in drier conditions, fewer taxa and individuals are able to survive and those that can tend to migrate down deeper into the soil (Friend and Richardson 1977, Bromham 1999, Ashton and Bassett 1997) which is likely to make them more difficult and energetically more expensive for superb lyrebirds to catch (Campbell and Grey 1942, Littlejohns 1947, Lill 1996). Superb lyrebirds are selective about where they feed (Ashton and Bassett 1997, Lill 1996), probably in order to optimise the efficiency of foraging by seeking out areas where it is relatively easy to capture their food (Robinson and Frith 1981, Lill 1996). Therefore, the association between superb lyrebirds and macroinvertebrates on slopes and riparian areas may have been stronger than on ridges because superb lyrebird feeding (and associated habitat modification) was concentrated in those areas due to the abundance and accessibility of macroinvertebrate prey. The extent of superb lyrebird disturbance was higher in slope microhabitats than ridges or riparian areas which supports this explanation.

As hypothesised, the presence of superb lyrebirds was associated with low leaf litter cover and a greater extent of exposed mineral soil within plots as a result of their scratching. The expectation that the abundance of individuals with affinities for leaf litter or soil would be affected by the presence of lyrebirds was also supported, as the abundance of leaf litter dwellers was lower at lyrebird sites. In contrast, there was little evidence that superb lyrebirds adversely affected generalists and soil dwellers as they occurred in similar numbers across both groups of sites. This may be because the latter are better able to avoid predation or possibly because their habitat is modified but not destroyed by superb lyrebird scratching. Other investigators have reported similar findings; for example the impact of the non-native Puerto Rican coqui frog (*Eleutherodactylus coqui*) on Hawaiian invertebrates was greater for leaf litter dwellers than for foliage dwelling taxa because the latter group was more able to escape the reach of the frogs (Choi and Beard 2012).

The reduction of habitat availability could limit the number of leaf litter dwellers in several ways. Firstly, scratching by superb lyrebirds mixes the leaf litter layer into the

mineral soil, producing one homogenous layer, thereby reducing structural complexity. Complex habitats provide a greater range of microhabitats than structurally simple ones, thereby reducing interspecies competition and facilitating the coexistence of greater numbers of species (Bromham *et al.* 1999, Crooks 2002). In an analogous example, invasive earthworms in naturally earthworm free forests in North America dramatically reduce habitat complexity by incorporating the leaf litter layer into the mineral soil with associated declines in invertebrate abundance and richness (Bohlen *et al.* 2004, Migge-Klein *et al.* 2006). Secondly, leaf litter provides an insulating layer at the soil surface, protecting it and inhabitants from the extremes of temperature (Bromham *et al.* 1999). Leaf litter also reduces water loss and insolation (Migge-Kleian *et al.* 2006), so a decrease in leaf litter coverage would likely mean a decrease in humidity, soil moisture and an increase in insolation. As many soil and leaf litter dwelling invertebrates are susceptible to desiccation (Coleman *et al.* 2004), the change in microclimatic conditions as a result of superb lyrebird scratching could cause invertebrate numbers to decline. Thirdly, the leaf litter layer is also a source of food for many invertebrates, so a reduction in this resource could alter the abundance and richness of the taxa that depend on it (Migge-Klien *et al.* 2006, Robson *et al.* 2009). Finally, the frequency and intensity of the disturbance itself could affect macroinvertebrate abundance and richness. Frequent disturbance, particularly if it is intense, is often associated with low abundance and richness because fewer species are able to persist or able to recolonize the area during short intervals between disturbances (Wardle *et al.* 2001, Wardle and Bardgett 2004, Bohlen 2006). Thus, the frequency of superb lyrebird disturbance may prevent some taxa from establishing in disturbed areas, thereby reducing abundance and richness of the assemblage.

Overall, while there were strong variations in macroinvertebrate assemblages both within sites and between sites, there was nonetheless a distinct signal of impact in the invertebrate assemblages at sites with superb lyrebirds. While the evidence presented here is inferential, it does indicate that non-native birds can influence native macroinvertebrates. The results also highlight the context-dependent nature of impact of non-native species on recipient native communities as a product of both the local environmental conditions and the inherent identity of the native biological community itself. Clearly, experimental studies and surveys which incorporate more replication within sites and microhabitats are now required to confirm the causal link between the

presence of superb lyrebirds and patterns in macroinvertebrate assemblages. Furthermore, any such attempts should account for the scale-dependent nature of impact when designing experiments. Estimations of the impact of superb lyrebirds at the landscape scale will need to take into account the variation of impact across smaller-scale microhabitats and the relative proportion of the landscape that these cover. More generally, further research on the impact of non-native birds on native macroinvertebrates and other non-avian fauna is clearly warranted.

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Chapter 3: Impacts of a non-native ecosystem engineer on invertebrate assemblages and seedling survival

3.1 Abstract

Quantitative data on the effects of non-native species on native biota is crucial for the accurate assessment and successful mitigation of their impact. Currently, however, the information regarding the impact of non-native birds on non-avian native fauna is largely anecdotal. In this study two complementary field experiments were used to investigate the impact of a non-native bird, the superb lyrebird (*Menura novaehollandiae*), on native forest invertebrate assemblages and seedlings in Tasmania, Australia. This ground-feeding bird is an ecosystem engineer, turning over large amounts of leaf litter and soil while foraging for invertebrate prey. An 8-month exclosure experiment was conducted at two sites with superb lyrebirds and two sites without. A second experiment examined the immediate response and short-term recovery trajectory (over 21 days) of macroinvertebrate assemblages following simulated superb lyrebird disturbance. While disturbance of soil and leaf litter profoundly reduced macroinvertebrate abundance and richness and altered assemblage composition, the effect was short-lived. The short-term recovery experiment showed that some components of the fauna were able to recover significantly within three weeks and the exclosure experiment demonstrated that the whole macroinvertebrate assemblage was able to recover within approximately 2 months. While there was no difference in mesoinvertebrate assemblages between treatments in the exclosure study that could be attributed to superb lyrebirds, overall abundance was far lower at sites with superb lyrebirds than at control locations, which may indicate that the birds have a long-term effect. Artificial superb lyrebird scratching appeared to stimulate germination of new seedlings but overall numbers in areas with and without superb lyrebird disturbance were the same. This was probably because scratching also killed many existing individual seedlings; thus if superb lyrebird disturbance is frequent, few seedlings survive long term. Overall, recruitment in mature wet eucalypt forests is probably more strongly driven by disturbance events that reduce canopy cover and increase light levels (such as tree-fall and fire) than by superb lyrebird scratching. This study demonstrates that while superb lyrebirds are capable of exerting an influence on native biota, their impact is generally short-lived and spatially restricted

3.2 Introduction

Great advances have been made in the last 20 years in our understanding of the ecological impacts of non-native species and the mechanisms by which they exert an influence on the native ecosystems they invade (Mack *et al.* 2000, Simberloff *et al.* 2013). Carefully designed manipulative field and laboratory experiments have been an integral part of this process as they make it possible to identify causal links and to understand the direct and indirect pathways by which non-native species can effect recipient ecosystems (Parker *et al.* 1999, Crooks 2002, Byers *et al.* 2002). Although manipulative experiments are acknowledged as being the most powerful way to identify causal links between non-native species and native biota (Ross *et al.* 2003, 2006, Strayer 2006), some groups of non-native organisms, particularly birds, have rarely been the subject of quantitative experiments (Lever 2005, Blackburn *et al.* 2009, Kumschick and Nentwig 2010, Bauer and Woog 2011).

Very few studies have examined the effect of non-native birds on non-avian components of native fauna such as invertebrates (Blackburn *et al.* 2009), which is surprising given that many non-native birds are insectivorous, and were deliberately introduced to combat insect pests (Drummond 1907, Lever 2005, Lockwood *et al.* 2007). More is known about the interactions of non-native birds with plants. For example, some non-native birds are known to spread the seeds and fruit of both native and non-native plants (Simberloff and von Holle 1999, Linnebjerg *et al.* 2010). Herbivory and nutrient addition (via faeces) by non-native birds can also change plant community composition and facilitate the growth of non-native plants (Tatu *et al.* 2007, Best 2008, Best and Arcese 2009). Thus, it seems very likely that with a more concerted research effort, more interactions between non-native birds and recipient biota will be uncovered (Blackburn *et al.* 2009).

In this study the ecological impact of a non-native bird, the superb lyrebird (*Menura novaehollandiae*), on native macroinvertebrates, mesoinvertebrates and seedling survival was examined in the wet eucalypt forests of Tasmania, Australia. The superb lyrebird is native to the forests of eastern mainland Australia, and is well known throughout the world because of its spectacular ability to mimic sounds during courtship, as popularised by documentaries (Attenborough 2002). Any attempt to

control the bird in Tasmania would likely be met with public opposition and would therefore require a clear demonstration of ecological impact to justify any management action.

Superb lyrebirds were deliberately introduced to Tasmania in 1934 to protect them from the perceived threat of habitat loss and predation by the European fox (*Vulpes vulpes*), and they have spread throughout much of the forested areas in the south of Tasmania (Sharland 1952, Smith 1988, Tanner 2000). The superb lyrebird feeds on terrestrial invertebrates in forests by scratching over leaf litter and soil to depths of 150 mm using its large feet and claws (approx. 150 mm span) (Ashton and Bassett 1997). The amount of soil and leaf litter moved by lyrebirds is not trivial: an individual bird is capable of turning over the entire forest floor annually within their home range (usually several hectares) which can amount to hundreds of tonnes per bird every year (Ashton 1975, Adamson *et al.* 1983, Ashton and Bassett 1997). Therefore, although little is known about the ecological impact of the superb lyrebird in Tasmania, it is regarded as a potential threat both as a predator and as an ecosystem engineer (*sensu* Jones *et al.* 1994, 1997), and has been classified as a ‘high risk’ non-native species within the Tasmanian Wilderness World Heritage Area by conservation managers (Mallick and Driessen 2009).

Not only may superb lyrebirds affect the taxonomic richness, abundance and composition of native biotic assemblages, but there are a large number of endemic species within Tasmanian forests that have very restricted geographic ranges which may be particularly vulnerable to predation or habitat modification by superb lyrebirds (Mesibov 1994, Threatened Species Section 2009). For example, superb lyrebirds are thought to pose a risk to the long-term survival of the endemic and critically endangered myrtle elbow orchid (*Thynninorchis nothofagicola*), which is known only from one locality (Threatened Species Section 2009). Although the impact of the superb lyrebird on *T. nothofagicola* has not been demonstrated, they are known to eat orchid tubers within their native range (Higgins *et al.* 2001). In addition, superb lyrebirds could potentially limit the recruitment of new orchid seedlings because their scratching could kill them or provide unsuitable conditions for germination. Moreover, even widely distributed plants and invertebrates may be affected; for example, it has been suggested that frequent bioturbation by superb lyrebirds may reduce the germination and survival

of seedlings of some tree species such as sassafras (*Atherosperma moschatum*) and myrtle (*Nothofagus cunninghami*) (Howard 1973, McKenny and Kirkpatrick 1999, Neyland 2004). Read and Brown (1996) proposed that the absence of the superb lyrebird from parts of Tasmania might explain the greater rate of seedling establishment in those places than within the native range of the bird. Conversely, Ashton and Bassett (1997) argued that superb lyrebirds might facilitate the successful establishment of tree ferns (*Cyathea cunninghamii*) by creating microsites devoid of leaf litter where fern prothalli can germinate.

If superb lyrebirds alter soil and leaf litter dwelling invertebrate communities there may be repercussions on several important processes in soil ecosystems that are mediated by these invertebrates, including nutrient cycling and decomposition (Wardle 1995, Lavelle *et al.* 2006, Bultman and de Witt 2008, Parker 2010), potentially altering the functioning of the forest soil ecosystem as a whole. Therefore, quantifying the impact that the superb lyrebird has on Tasmanian forest invertebrates is essential. Thus, the aims of this study were to test for differences in macroinvertebrate and mesoinvertebrate assemblage composition and structure as well as seedling survival following superb lyrebird disturbance or simulated lyrebird disturbance. Two experiments were conducted; the first used exclosures to determine the longer-term effects of lyrebird foraging on biota, while the second examined the immediate impact on macroinvertebrates and their subsequent short-term recovery.

An exclosure experiment was conducted at two sites where superb lyrebirds were present ('lyrebird sites') and at two sites beyond the current range ('control sites') to determine the responses of macroinvertebrates, mesoinvertebrates and seedling recruitment to lyrebird foraging in Tasmanian forests. Invertebrate assemblages and seedling numbers were compared in fenced exclosure plots and unfenced plots. A difference between treatments at lyrebird sites may indicate a lyrebird effect on biota, while the comparison between the two treatments at control sites provided a test for the presence of a caging effect not related to the presence of lyrebirds. To separate the effects of habitat modification and disturbance from those of predation, fenced plots were compared with plots that were hand-raked and fenced. Given that studies within the native range of the superb lyrebird (Ashton 1975, Adamson *et al.* 1983, Ashton and Bassett 1997) have shown that lyrebird disturbance tends to reduce the extent of leaf

litter cover, I expected that macroinvertebrates that live primarily in the leaf litter were more likely to be strongly affected by the presence of the superb lyrebird than those invertebrates that live in the soil or in both soil and leaf litter layers (generalists). Therefore, I also examined whether the presence or absence of superb lyrebirds was associated with low abundance of leaf litter dwelling macroinvertebrates.

The time frame of the exclosure experiment (8 months) was based on information from Australian mainland studies that indicated that birds do not revisit disturbed areas until the leaf litter layer has reformed (Robinson and Frith 1981, Lill 1996, Ashton and Bassett 1997). However, during the course of the exclosure study, superb lyrebirds were observed revisiting areas frequently (in a matter of weeks), which potentially meant that any impact of an individual disturbance event was short lived. Thus, it was possible that the exclosure study design may over- or under-estimate the impact of superb lyrebirds depending on how recently the superb lyrebirds had disturbed the unfenced treatment plots. Therefore, a second experiment at one field site beyond the current range of superb lyrebirds was conducted specifically to document the immediate response to, and recovery from, simulated lyrebird disturbance over 21 days.

3.3 Methods: Exclosure experiment

3.3.1 Study sites

The experiment was conducted between April 2008 (Austral autumn) and November 2008 (Austral spring) in the southern forests of Tasmania, Australia (Fig 3.1). This area of Tasmania is heavily forested and has a temperate climate with mean minimum temperature of 6.6° C and maximum of 15.9° C during 2008 (Bureau of Meteorology 2008). Average annual rainfall in the region during 2008 was 569 mm (Bureau of Meteorology 2008). The study region was selected because it contains areas of forest where superb lyrebirds are present that are in close proximity to forest immediately beyond their current range. Four sites were selected (two sites with superb lyrebirds and two control sites immediately beyond the current range of superb lyrebirds) in wet sclerophyll forest located a maximum of 60 km apart. A spatial multi criteria analysis was performed using ESRI ArcGIS software to identify areas that were similar in terms of: vegetation community composition and structure, forest history (forestry and fire), geology, climate, elevation, slope, aspect, and road accessibility. The forest at each site

consisted of either *Eucalyptus obliqua* or *Eucalyptus regnans* overstorey with a mixed canopy and understorey of thamnic rainforest and broad-leaved species including *Atherosperma moschatum*, *Phyllocladus aspleniifolius*, *Olearia argophylla*, *Pomaderris apetala*, *Bedfordia linearis* and *Dicksonia antarctica* (Reid *et al.* 1999, Neyland 2001). Shrub and ground cover were sparse, with the latter comprising of forbs and bryophytes (Neyland 2001). Soils were well to poorly drained, had gradational texture profiles and were a mixture of loams and clays derived from Jurassic dolerite and Triassic sedimentary parent material (Laffan 2001, Laffan and McIntosh 2005). Selective logging occurred before 1960 but no logging had occurred since and there was no evidence of major fire in the last 40 years (Stone 1998, Brown, M.J, pers. comm.). To maximise the likelihood of superb lyrebirds disturbing open plots, sites were located in an area where annual monitoring of a 30m x 2m transect in the previous 2 years had shown that superb lyrebirds disturbance covered more than 50% of the forest floor. A summary of site environmental characteristics is provided in Table 3.1.

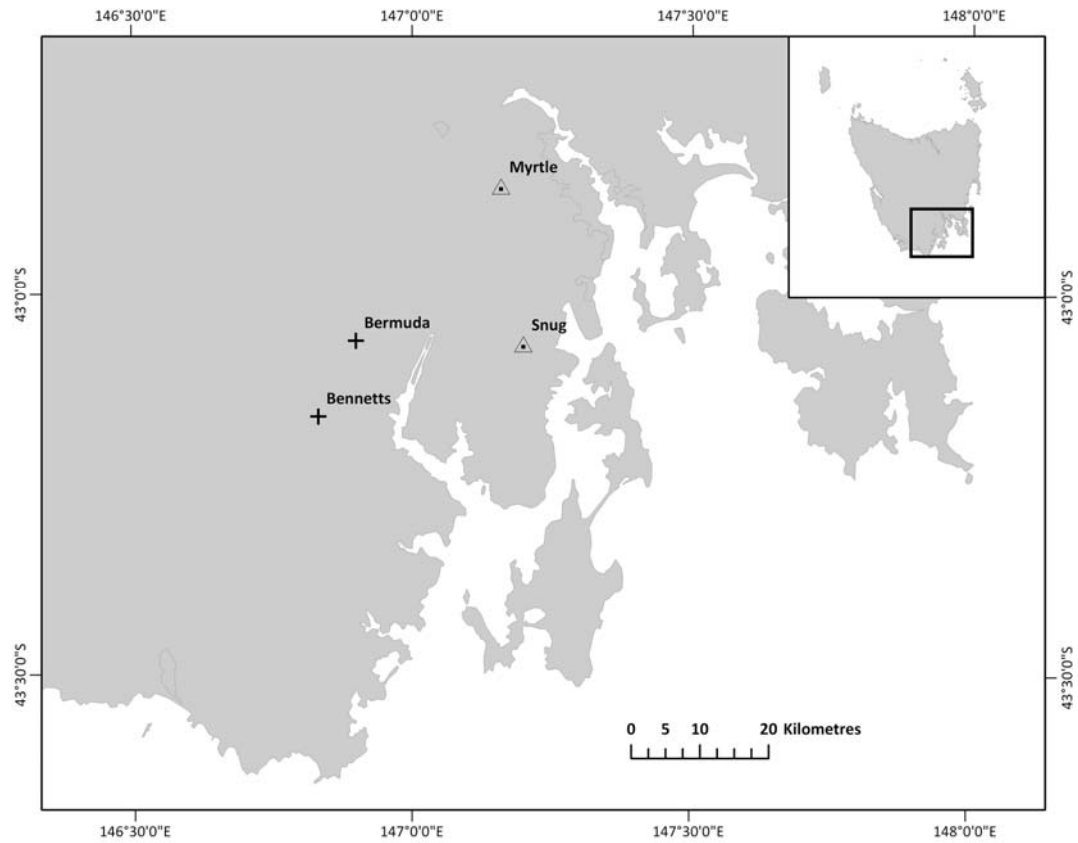


Figure 3.1: Map of southern Tasmania, Australia showing the locations of the four field sites: two sites where superb lyrebirds (*Menura novahollandiae*) were present (+) and two control sites where superb lyrebirds were absent (\triangle).

Table 3.1: Site environmental characteristics. Mean monthly rainfall was calculated for 2008 from the Australian Bureau of Meteorology data recorded at the meteorological station nearest to each study site. Vegetation community was determined using Tasmanian Vegetation Monitoring and Mapping Program maps (TASVEG Version 1.3, Department of Primary Industries and Water 2001, Harris and Kitchener 2005). Aspect identifies the downslope direction of the maximum rate of change in elevation. The values are the compass direction of the aspect. Hill shade analysis provides a measure of the average degree of shadow at the site by considering the effects of the local horizon in relation to the dominant sun angle and sun elevation. Areas in complete shadow have a value of zero. Areas in no shadow have a value of 255. Slope identifies the gradient in degrees, or rate of maximum change in elevation at the site. Slope, aspect code, hill shade and elevation were derived using geographical information system software (ESRI ArcGIS 10.0). †GDA 94.

Site Control/ Lyrebird	Longitude †	Latitude†	Elevation (m) †	Aspect (°)	Slope (°)	Hill Shade	Geology	Mean Monthly Rainfall (mm)	Vegetation Community
Myrtle Control	147°09'32 "E	42°51'34"S	550	282	7	178	Jurassic dolerite	44.3	<i>Eucalyptus regnans</i> forest
Snug Control	147°11'58"E	43°04'01"S	362	167	28	235	Triassic quartz sandstone	58.7	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)
Bermuda Lyrebird	146°53'59"E	43°03'47"S	542	76	15	144	Jurassic dolerite	62.9	<i>Eucalyptus regnans</i> forest
Bennetts Lyrebird	146°49'49"E	43°09'34"S	436	262	17	225	Jurassic dolerite	98.1	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)

The location of plots within each site at the local scale was determined by several factors. Firstly, in forest of this type there is often variation in microclimate, vegetation and invertebrate communities over the scale of tens of metres (Neyland 2001, Meggs and Munks 2003, Baker *et al.* 2006). Therefore, in order to minimise local scale variability that may lead to inherent differences between treatment plots, all plots were placed within 10–25 m of a permanent stream in what was identified as ‘slope’ microhabitat, i.e. between the riparian zone and convex landforms (ridges). This was because research on superb lyrebird microhabitat usage within their native range indicated that their activity was heaviest in slope microhabitats during the months that the experiment was undertaken (autumn to spring) (Robinson and Frith 1981, Adamson *et al.* 1983, Ashton and Bassett 1997). Secondly, all sites were south, southeast or southwest facing to standardise the local climatic conditions across sites, and because lyrebirds preferentially forage on south facing slopes as they provide better conditions for desiccation-prone invertebrate prey (Adamson *et al.* 1983, Robinson and Frith 1981, Barclay *et al.* 2000). All sites were located close to a permanent stream because the microclimate (particularly humidity and soil moisture levels) was likely to be more constant at the local scale. Finally, sites were chosen such that environmental conditions including vegetation species composition and cover were as uniform as was possible across the 30 × 20 m area required for the experiment.

3.3.2 Experimental design

A multi-stratum design was employed consisting of four sites, two of which were located in areas with superb lyrebirds (lyrebird sites) and two in areas not yet invaded by the birds (control sites). At each of the four sites (each 30 m × 20 m, treated as a random effect nested with lyrebird status), four blocks (random effect) were set up, within which were nested three 2 × 2 m experimental plots, with each plot allocated at random to one of three treatments (fixed effect): ‘fenced’ enclosure (which excluded lyrebirds), ‘hand-raked + fenced’ enclosure (simulating lyrebird disturbance but not predation) and ‘unfenced’ (which allowed lyrebirds free access). Thus the design was a randomised complete block with respect to enclosure treatments.

A pilot study conducted at the sites showed that assemblages in plots up to 5 m away were similar to one another but plots 10–20 m away were not. Therefore, plots within each block were no more than 5 m away from each other while blocks were no more than 20 m away from each other. To ensure comparable conditions within plots across sites, all plots were placed in

areas of medium to deep leaf litter with sparse ground-level plant cover, which are preferred feeding areas of superb lyrebirds (Robinson and Frith 1981, Ashton and Bassett 1997). To reduce differences in the initial level of superb lyrebird disturbance in plots at lyrebird sites, it was ensured that all plots contained at least 50% cover of recent disturbance of medium or heavy intensity (which was assessed using an ordinal score; 0–3: Table 3.2).

The corners of unfenced plots were marked out with metal markers while the fenced plots were constructed using 1 m high wire mesh (with a gauge of 10×10 mm) and star pickets. A gap of 100 mm was left below the fence to prevent litter building up against the fence and to enable invertebrates and small vertebrates to enter the plots. As superb lyrebirds are poor fliers, high visibility flagging tape criss-crossed over the plots successfully excluded them and there was no evidence of lyrebirds feeding in the fenced enclosure plots during the experiment. To simulate lyrebird foraging disturbance in the hand-raked + fenced treatments, a three-pronged hand-rake with a span of 150 mm (which is similar to a lyrebird foot) was used to rake over the leaf litter and soil to a depth of approximately 100 mm. This disturbance was designed to mimic the scratching of lyrebirds as described by Higgins *et al.* 2001 and based on my own observations of feeding lyrebirds. Kotanen (1997) and Mohr *et al.* (2005) successfully used a similar strategy of mimicking wild boar foraging disturbance to investigate impacts on invertebrates.

Table 3.2: Scores for assessing the intensity and age of superb lyrebird (*Menura novaeollandiae*) disturbance in sample plots.

Score	Intensity	Age
0	No disturbance	No disturbance
1	Light: -Leaf litter layer partially broken or removed. Scratching 10–40 cm deep -Limited mixing of leaf litter and topsoil	Old: > 1–2 months -Fallen leaf litter and debris has accumulated over scratching. -Seedlings may have started to germinate -Buried vegetation has turned brown
2	Medium: -Scratching 4-8 cm deep -Litter layer has been broken and mixed partially with topsoil -Some mineral soil exposed on surface	Medium: 2 weeks-1 month -Exposed mineral soil has been weathered, evidence of rain-wash -Some fallen leaf litter over diggings
3	Heavy: -Scratching to depth of 15cm -Litter layer partially to completely broken, removed or incorporated with topsoil -Mineral soil exposed on surface	Recent: <2 weeks -Freshly turned over, moist soil on surface, not compacted, no indication of rain-wash -No mosses, shoots, or seedlings growing in scratched out patches -No fallen leaves on scratching -Displaced and buried vegetation still green

3.3.2.1 Environmental variables

A range of physical and environmental parameters were recorded along a 30 m long × 2 m wide transect running through each site. Specifically, the percentage cover of the canopy, midstorey and understorey strata were visually estimated according to seven classes using a modified Braun-Blanquet index (Mueller-Dombois and Ellenberg 1974) where 0 = 0%, 1 = <1%, 2 = 2–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75% and 6 = 76–100%. The Braun-Blanquet index was also used to assess the proportion of the following ground cover types: leaf litter, nonvascular plants and bryophytes, rock and exposed mineral soil. The latter category incorporated both soil mixed with leaf litter by lyrebird scratching and bare areas devoid of leaf litter. Average leaf litter depth along each transect was visually estimated using the Tasmanian Forest Practices Authority classification codes (Meggs and Munks 2003, Forest Practices Authority 2005): thin = <

1 cm, medium= 1–3 cm, deep= >3 cm). The basal area of trees (an index for stand density and size structure of the forest community) was recorded with a Bitterlich basal wedge following Braithwaite *et al.* (1989) and the Forest Practices Authority (2005). At sites with superb lyrebirds the extent of lyrebird disturbance along the entire transect was visually estimated (using the Braun-Blanquet index described above). The age and intensity of superb lyrebird disturbance was recorded using an ordinal score (0 to 3: Table 3.2).

To accurately quantify relevant environmental variables in plots at the conclusion of the experiment, each plot was divided into four 1 × 1 m quadrats with flagging tape and the mean values were computed for each plot (Table 3.3). Cover of intact leaf litter, exposed mineral soil and extent of superb lyrebird disturbance (at lyrebird sites only) were estimated using the Braun-Blanquet index. The age and intensity of superb lyrebird disturbance were assessed as above (Table 3.2). The depth of leaf litter in each 1 × 1 m quadrat was measured in two randomly selected positions with a ruler and then averaged to provide a mean for each plot. Canopy closure (a proxy for the light regime and microclimate) was measured in each plot and was measured by using a vertical sighting tube with a central wire cross hair (Brown, M.J. pers. comm., Jennings *et al.* 1999). Presence or absence of canopy at the point of intercept of the cross wires was recorded for nine points on each plot (i.e. at the corners of each 1 m quadrat within each plot). Percentage plot canopy closure was then calculated as the number of points on each plot where the sky was obscured by (vegetation / 9) × 100 (Ganey and Block 1994).

The frequency and extent of lyrebird foraging in unfenced plots over the course of the experiment was recorded by measuring the extent of ‘recent’ disturbance (<two weeks old: Table 3.2) in each unfenced plot every month. This information was necessary to avoid erroneously assuming a long-term effect of disturbance if, for example, superb lyrebirds had scratched open plots immediately before sampling invertebrates and seedlings.

3.3.2.2 Macroinvertebrate sampling

At the conclusion of the experiment all leaf litter and loose soil was collected from a randomly selected 1 m × 1 m quadrat in each plot. Litter and soil was hand searched in

white trays on site for invertebrates > 2 mm for 30 minutes by two workers (giving a total of 60 minutes per plot). Hand sorting of soil and litter samples in this way provides an efficient, cost effective means of processing large samples and gives a reliable indication of macroinvertebrate populations (Snyder *et al.* 2006, Smith *et al.* 2008, Hedde *et al.* 2012). Specimens were preserved immediately in 80% alcohol with 2% glycerol. Invertebrates were sorted to the lowest taxonomic level feasible, generally species or genus using relevant keys and consultation with taxonomic specialists (see Appendix 1 for list of resources). Taxonomic knowledge of many soil invertebrates in Australia is poor, particularly coleopteran families, so identification to species was not always possible in which case morphospecies were used. Coleoptera were ascribed to the morphospecies codes used by the Tasmania Forestry Insect Collection (TFIC, now housed at the Tasmanian Museum and Art Gallery (TMAG) collection). Adults and larvae of the same coleopteran species were recorded separately because the habitat requirements and feeding ecology differ with life history phase in many species (Lavelle *et al.* 1993). Undescribed Diplopoda and Chilopoda were given standardised sorting codes as per Mesibov (2012). Dipteran larvae, Oligochaeta and Araneae were not classified further but were sorted into size classes based on length for Diptera and Araneae (5 mm, 6-10 mm and >10 mm) and diameter for Oligochaeta (<1 mm, 1-5 mm and >5 mm). As there was substantial variation in size within these groups, size classes made it possible to account for the possibility that larger individuals would be more likely to be eaten by superb lyrebirds than very small individuals (Robinson and Frith 1981, Lill 1996). A voucher collection of specimens from this study has been deposited with TMAG.

3.3.2.3 *Substrate habitat affinity of macroinvertebrates*

I predicted that taxa reliant on leaf litter would be less abundant at lyrebird sites than those that inhabit soil because superb lyrebird foraging reduces the cover of intact leaf litter (Adamson *et al.* 1983, Ashton and Bassett 1996). With the aid of literature and taxonomic experts (see Appendix 1), all macroinvertebrates were assigned to one of two habitat affinity classes based on their microhabitat associations: leaf litter dwellers (those taxa that are known to be epigeic, occurring predominantly in leaf litter or at the interface between litter and topsoil), or generalist and soil dwelling taxa (those taxa that inhabit mineral soil or are capable of living in and moving between both mineral soil and leaf litter). An attempt was not made to separate taxa that live in both leaf litter and

soil from those that only live in soil because taxonomic resolution and/or information on specific habitat affinities for local species were not available. For example, some species of earthworm only live in topsoil while others are litter dwellers, but because the ecology of Tasmanian earthworms is poorly understood (Blakemore 2000) all earthworms were assigned to the ‘generalist/soil dwelling’ group.

3.3.2.4 Mesoinvertebrates sampling

Mesoinvertebrates (i.e. Collembola and Acari: Decaëns 2006), were collected by taking a 150 mm diameter × 100 mm deep core of leaf litter and soil in each plot prior to collecting macroinvertebrates. Cores were stored in Ziplock bags for transport back to the laboratory where they were placed (within 12 hours of collection) in Tullgren funnels under 40 W incandescent light globes for 7 days (Behan-Pelletier 1999, Bromham *et al.* 1999, Nakamura *et al.* 2007). After extraction, the mesoinvertebrates were identified to family for Collembola and oribatid Acari. All other adult Acari were identified to suborder while immature Acari were identified to subclass (see Appendix 3 for list of taxonomic keys used).

3.3.2.5 Seedling survival

A count of the total number of seedlings (<150 mm in height) in each plot was made at the beginning of the experiment in April 2008 and once again at the conclusion of the experiment in November 2008. Seedlings were recognised by the presence of cotyledons and were not identified to species, as accurate identification of species at the seedlings stage is difficult (Brown, M.J pers. comm.). Small ferns including young tree ferns (*Dicksonia antarctica*) (<100 mm in height) were also recorded but were too low in number for meaningful analysis.

3.3.3 Statistical analysis

3.3.3.1 Environmental variables

A Principal Components Analysis (PCA) was used to explore relationships between vegetation and ground cover variables, based on a correlation matrix of environmental variable data and Euclidian distances (PRIMER E version 6.1. Clarke and Gorley 2006). Before conducting the PCA, understorey cover was excluded because it did not vary across sites, as were leaf litter cover and exposed mineral soil cover, which were likely

to be directly affected by the lyrebirds. Means and standard errors of the extent of substrate habitat cover, canopy closure, litter depth and superb lyrebird disturbance for each treatment for lyrebird sites and control sites were calculated. The percentage cover of recent lyrebird disturbance in each unfenced plot at lyrebird sites was also calculated for every month of the experiment.

3.3.3.2 Invertebrate analysis

Differences in invertebrate assemblage structure were assessed using analysis of variance (ANOVA). Two sets of hypotheses were of interest in the randomised complete block design. First, the interaction term tested whether the responses across treatments differed between lyrebird sites and control sites. Second, the responses to the treatments were analysed including two orthogonal *a priori* planned contrasts to determine (1) whether the fenced undisturbed plots differed from unfenced controls (which would correspond to caging artefact at control sites and a recovery from lyrebird impact at lyrebird sites), and (2) whether the two fenced treatments differed from each other (which tested for a disturbance effect in the absence of lyrebird predation). These tests were carried out for several suites of response variables: univariate descriptors of assemblage structure (abundance, taxonomic richness, evenness (Pielou's J' : Pielou 1966, Magurran 1988). These analyses were carried out on three sets of the invertebrate data: (1) macroinvertebrates assemblage structure, (2) mesoinvertebrate assemblage structure, and (3) macroinvertebrate habitat affinities (the abundance of 'leaf litter dwellers' and 'generalists/soil dwellers'). These univariate analyses were carried out using the 'lme4' package (Bates *et al.* 2011) in the R software package version R 2.15.2 (R Development Core Team 2012), with assumptions checked using standard procedures, and transformations applied where necessary (Quinn and Keogh 2002).

Differences in community composition were tested using the same design via permutational multivariate analysis of variance (PERMANOVA, Anderson 2001, Anderson *et al.* 2008). Prior to computing the Bray-Curtis similarities, all singletons were removed and abundance data were square-root transformed to down-weight the contribution of numerically dominant taxa (Clarke 1993). All tests used 9999 unrestricted permutations of residuals under a reduced model, and the data were fully balanced with no missing values (Anderson *et al.* 2008). The Monte Carlo asymptotic *P*-value was referred to for the *a priori* contrasts, as there were few unique values for

the test statistic (Anderson 2005). Differences in the degree of dispersion among groups were tested using PERMDISP (Anderson 2004). This distance-based test determines the homogeneity of multivariate dispersion (i.e. the degree of scatter) between samples and their group centroids (Anderson *et al.* 2006, Anderson *et al.* 2008). The relationship between samples was visualised using a nonmetric multidimensional scaling (nMDS, Clarke 1993) ordination. The taxa that contributed most to the dissimilarities between lyrebird sites and control sites were identified using the similarity percentages routine (SIMPER) (Clarke and Warwick 2001). The survival of seedlings in treatment plots in the presence and absence of lyrebirds was compared using the same basic ANOVA design used to analyse invertebrate assemblage structure, but the added the number of seedlings in April 2008 (beginning of experiment) as an additional factor in order to account for initial differences in the number of seedlings in plots.

3.4 Methods: Short-term recovery experiment

To establish if there was an immediate but short-lived impact of physical disturbance on invertebrates that may have been undetected in the exclosure experiment, a short-term recovery experiment was conducted over a period of 21 days. Superb lyrebirds create two types of disturbed patches when foraging: bare patches where leaf litter has been scratched away exposing the mineral soil, and patches of mixed leaf litter and mineral soil that are created as the birds kick dislodged material behind them thereby burying leaf litter as well as mixing it with mineral soil (Adamson *et al.* 1983, Mitchell and Humphreys 1987, Ashton and Bassett 1997). Both patch types were included in the experiment to determine whether impact on and subsequent recovery of macroinvertebrate assemblages varied between the two patch types.

3.4.1 Study Site

The experiment was carried out at one location beyond the current range of the superb lyrebird on the Snug Tiers, southern Tasmania 43° 3'36. 02"S 147° 11'53. 43"E in October 2008 (Austral spring). The site was on a southeast-facing slope at an elevation of 420 m and vegetated by uniform wet eucalypt forest dominated by an even-aged stand of *Eucalyptus regnans*, as well as silver wattle *Acacia dealbata*. The understorey was comprised of *Olearia argophylla* and the tree fern *Dickonsia antarctica*. Ground cover vegetation was very sparse and the forest floor was covered in a medium (1-3 cm)

to deep (>3 cm) layer of leaf litter (Meggs and Munks 2003, Forest Practices Authority 2005). Underlying geology was a mixture of Jurassic dolerite and Permian/Triassic sandstone and mudstone. Soil was mottled grey/brown with a gradational texture of sandy loam over clayey loam (Derose 2001, Laffan and McIntosh 2005).

The likelihood of confounded results due to inherent variability in environmental conditions was reduced as much as possible by undertaking this experiment at a single field site that supported a vegetation community that was uniform in structure and composition and with a forest floor that was evenly covered in leaf litter. It was necessary to select a site where superb lyrebirds were absent in order to control for differences in disturbance history of the forest floor that would occur if lyrebirds were present and thus potentially confound results.

3.4.2 Experimental design

The experiment used a randomised complete block design consisting of 27 blocks (1.5 m × 1.5 m) within which were nested three 50 × 50 cm plots assigned at random to three levels of treatment: ‘bare’ (leaf litter removed leaving mineral soil exposed), ‘mixed’ (leaf litter layer combined with mineral soil), and ‘control’ (unmanipulated). The simulated disturbance of mixed and bare treatment plots occurred on the 20 September 2008. The two types of disturbance were created using the same three-pronged 15 cm diameter hand-rake that was used in the exclosure experiment. The size of the treatment plots was based on the average size of superb lyrebird scratchings recorded from mainland studies (Robinson and Frith 1981, Ashton and Bassett 1997). On each of the three sampling events (at 7, 14 and 21 days), nine randomly selected treatment blocks were destructively sampled. All surface litter and soil in plots was collected into zip lock bags for transport to lab where they were processed within 12 hours by tipping each sample into a white tray, hand sorting all macroinvertebrates >2 mm in length. Specimens were preserved, sorted and identified as described above.

3.4.3 Statistical analysis

To determine whether there were differences in mean abundance, richness and evenness of macroinvertebrates over time and between treatments, a three-factor analysis of variance (ANOVA) was used with ‘Days’ (fixed with three levels: 7, 14, 21 days)

‘Block’ (n=27 random) and ‘Treatment’ (fixed with three levels: mixed, bare, control). Two *a priori* contrasts were used to test for differences between (1) mixed treatments and control treatments and (2) bare treatments and control treatments. Assumptions were tested as above. The same model design was used to determine whether there were differences in the abundance of leaf litter dwellers and generalist/soil dwellers.

PERMANOVA was used to test the macroinvertebrate assemblage composition response to disturbance over time using the same factorial design described above for assemblage structure. ‘Days’ and ‘Treatment’ were tested with 9999 permutations of residuals under a reduced model using square-root transformed abundance data. As with the enclosure experiment, a PERMDISP function was used to test for differences in dispersion around group centroids, nMDS to visualise the relationships between assemblages from different treatments through time and a SIMPER routine to identify the taxa responsible for driving the patterns observed in the nMDS.

3.5 Results: Exclosure experiment

3.5.1 Environmental variables

The PCA showed that, while environmental variables and abiotic condition varied substantially between sites, there were no consistent differences between lyrebird and control sites that were likely to confound results of the exclosure experiment (Fig 3.2). PC1 had positive loadings for canopy cover and leaf litter depth and negative loadings for hill shade and rainfall and explained 53.7% of the variation. PC2 had positive loadings for ground level vegetation cover and aspect code and negative loadings for slope and stand density and explained a further 33.6% of the variation. As predicted, leaf litter cover was higher in the unfenced plots at control sites than in unfenced plots at lyrebird sites and the exclusion of superb lyrebirds resulted in higher mean coverage of leaf litter than in unfenced plots at lyrebird sites (Table 3.3). All unfenced treatment plots at lyrebird sites were disturbed at least once during the course of the experiment, but there was little new disturbance in most of the unfenced plots in the two months prior to the end of the experiment (Fig 3.3).

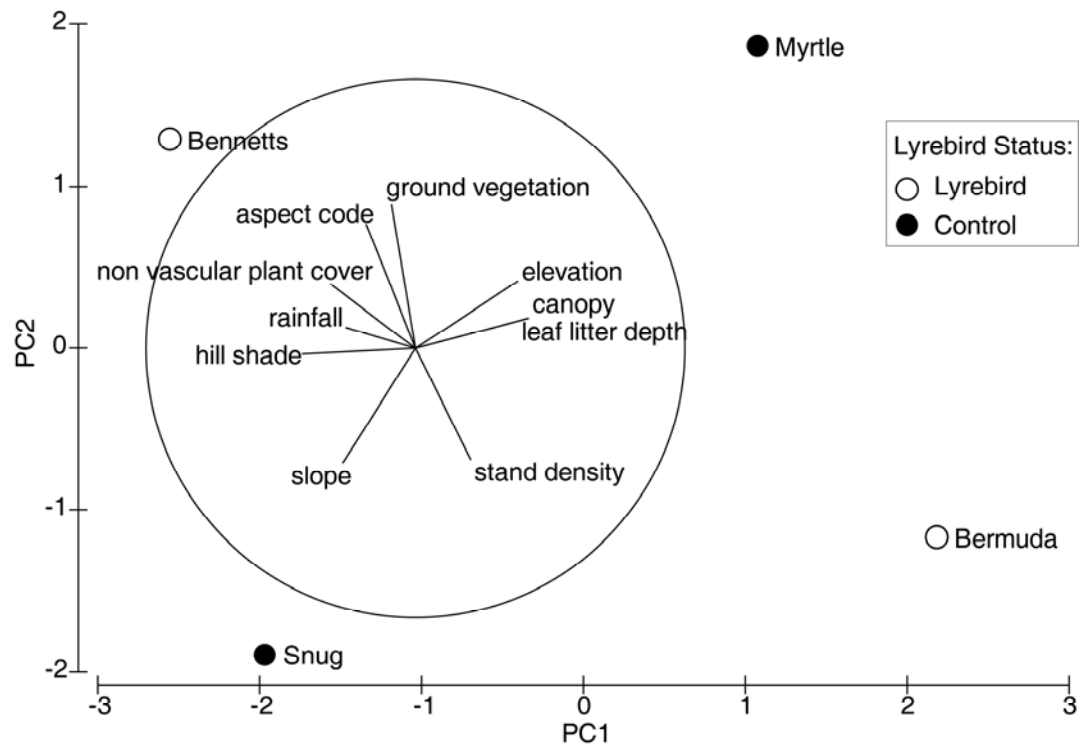


Figure 3.2: Principal Components Analysis (PCA) of site-level environmental parameters. Factors that were likely to be directly affected by superb lyrebirds (*Menura novaehollandiae*) were not included. Vector length represents their relative importance in accounting for variation between sites (i.e. longer = more important).

Table 3.3: Mean (\pm 1 SE) (n=8) substrate habitat cover (leaf litter versus exposed mineral soil) and superb lyrebird (*Menura novaehollandiae*) disturbance in sample plots. Extent of lyrebird disturbance, exposed mineral soil and intact leaf litter layer are given as modified Braun-Blanquet scores: 0 = 0%, 1 = <1%, 2 = 1-5%, 3 = 6-25%, 4 = 26-50%, 5 = 51-75% and 6 = 76-100%. Intensity and age of lyrebird disturbance are scored as 0 = no disturbance, 1 = light intensity/ old (>2 month), 2 = medium intensity/medium age, 3 = heavy intensity/recent (<2 weeks). NA = not applicable, no birds present at control sites.

Variable	Lyrebird Sites			Control Sites		
	Fenced	Hand-raked & Fenced	Unfenced	Fenced	Hand-raked & Fenced	Unfenced
Intact leaf-litter	4.3 \pm 0.1	3.8 \pm 0.2	3.25 \pm 0.3	6.0 \pm 0.0	4 \pm 0.1	6 \pm 0.0
Exposed mineral soil	4.7 \pm 0.2	5 \pm 0.2	5.2 \pm 0.16	0.0 \pm 0.0	4.3 \pm 0.2	0 \pm 0.0
Extent of simulated disturbance	0.0 \pm 0.0	5.2 \pm 0.2	0.0 \pm 0.0	0.0 \pm 0.0	4.8 \pm 0.1	0 \pm 0
Extent of lyrebird disturbance	5.0 \pm 0.1	0.0 \pm 0.0	5.7 \pm 0.1	NA	NA	NA
Lyrebird disturbance Age	1.0 \pm 0.0	0.0 \pm 0.0	1.8 \pm 0.2	NA	NA	NA
Lyrebird disturbance Intensity	1.6 \pm 0.1	0.0 \pm 0.0	2.6 \pm 0.1	NA	NA	NA
Leaf litter depth	1.6 \pm 0.1	2.1 \pm 0.3	2.3 \pm 0.3	2 \pm 0.3	2.1 \pm 0.13	2.5 \pm 0.2
Canopy closure	94.4 \pm 4.1	95.0 \pm 2.9	93.0 \pm 3.5	84.7 \pm 5.5	95.8 \pm 2.9	94.4 \pm 4.1

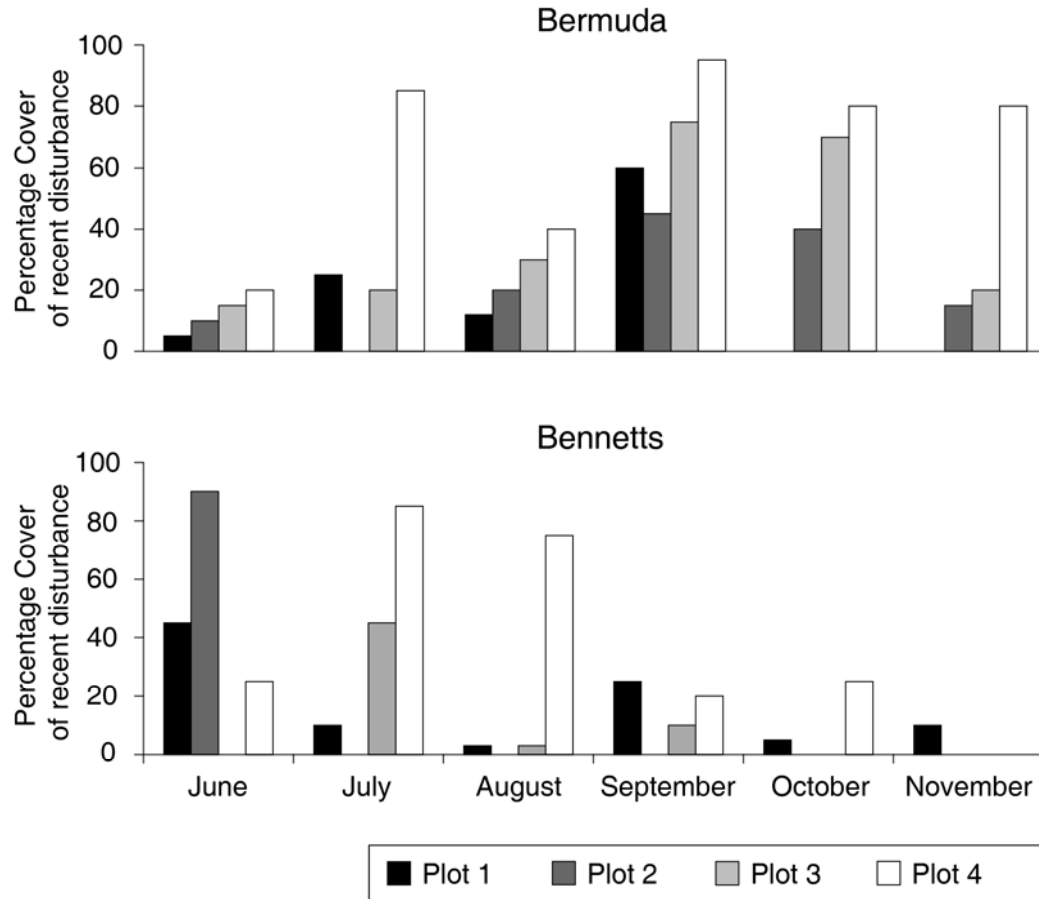


Figure 3.3: Monthly percentage cover of recent disturbance (<2 weeks) by superb lyrebirds (*Menura novaehollandiae*) in each of the unfenced treatment plots (n=4) at each of the two sites with superb lyrebirds (Bermuda and Bennetts).

3.5.2 Macroinvertebrate assemblage

In total, 4,425 individuals from 127 macroinvertebrate taxa were collected from the exclosures at the four sites, a third (42) of which were represented by a single individual. Thirty-six taxa were unique to lyrebird sites while 35 taxa were unique to control sites. Five taxonomic groups accounted for 79% of the fauna: Amphipods (49.2%), Oligochaeta (8.9%), Araneae (7.9%), Coleoptera (7.07%) and Diptera (6.8%).

There were no significant interactions between lyrebird status and treatment for taxonomic richness, abundance or evenness (all $P > 0.5$). Taxonomic richness differed significantly between treatments (ANOVA $F_{1,28} = 4.44$ $P = 0.04$); this was driven by a higher number of taxa in fenced plots compared to unfenced plots (17.72 versus 14.46

respectively, Fig 3.4a)—weak evidence of a caging effect. Neither of the main effects (lyrebird status or treatment) influenced macroinvertebrate abundance or evenness (all $P > 0.2$, Fig 3.4b and c). Contrary to predictions, there was also no interaction between lyrebird status and treatment on the abundance of leaf litter dwellers or generalist/soil dwellers nor were there any significant main effects (all $P > 0.2$, Fig 3.5).

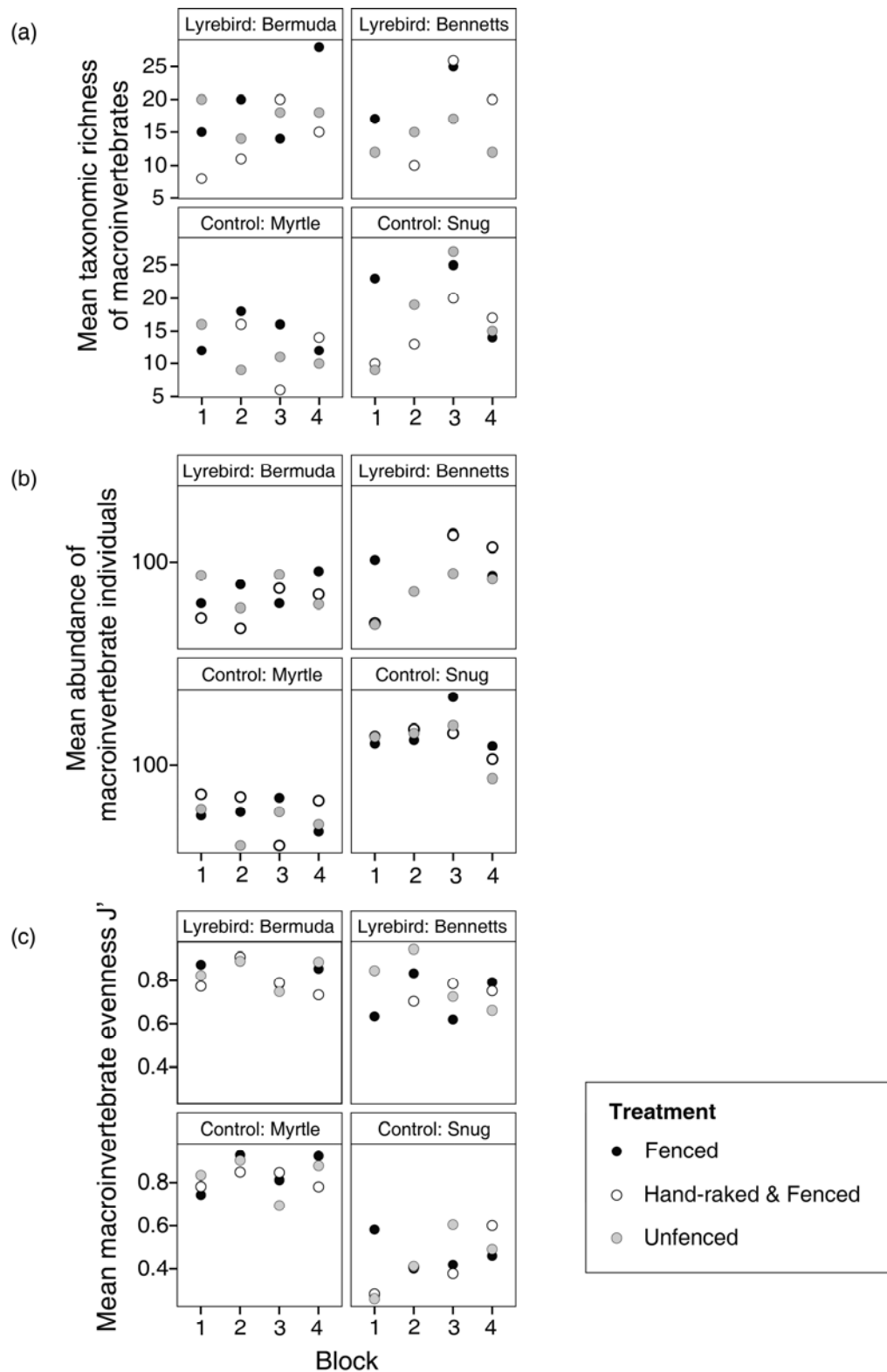


Figure 3.4: Macroinvertebrate taxonomic richness (a), abundance (b), and evenness J' (c) in the three experimental treatments (fenced, hand-raked & fenced and unfenced) at sites with superb lyrebirds (*Menura novaehollandiae*) and control sites (no superb lyrebirds).

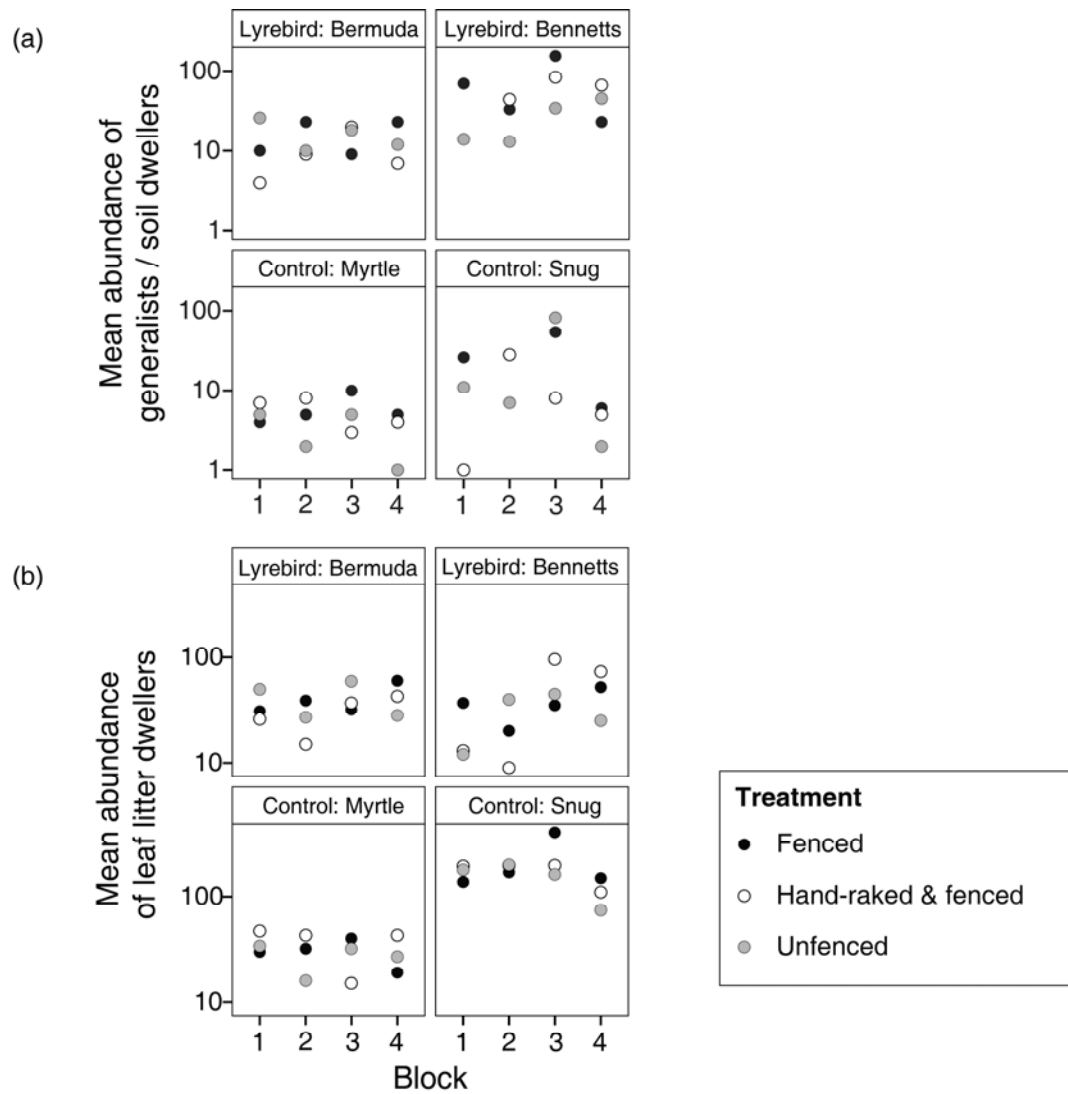


Figure 3.5: Abundance of (a) generalist/soil dwelling (b) leaf litter dwelling macroinvertebrates in three treatments (Fenced, Hand-raked & Fenced and Unfenced) at sites with superb lyrebirds (*Menura novaehollandiae*) and control sites beyond their current range.

There was no interaction effect of lyrebird status and treatment on macroinvertebrate assemblage composition (PERMANOVA $F_{2, 24} = 1.441$, $P = 0.44$). Macroinvertebrate assemblage composition did vary between lyrebird and control sites (PERMANOVA $F_{1, 2} = 2.982$, $P = 0.05$), but treatment had no influence on assemblage composition (PERMANOVA $F_{2, 24} = 1.1575$, $P = 0.33$). The SIMPER comparing lyrebird and control sites found that the overall level of dissimilarity between lyrebird and control assemblages was high (83.91%, Table 3.4), with eleven taxa explaining 51% of the variation between lyrebird status groups. Two species of amphipod, *Mysticotalitrus tasmaniae* and *Keratroides vulgaris*, contributed the most to differences between groups, with the former species only found at control sites and the latter only present at lyrebird sites. Generalist/soil dwellers including worms, ants and dipteran larvae were generally more common at lyrebird sites while leaf litter dwellers such as spiders and mites were more common at control sites. The nMDS ordination showed that while there was strong separation of samples from lyrebird and control sites, the samples were also distinctly clustered by site (Fig 3.6).

Table 3.4: Summary of SIMPER on abundance data showing the taxa which contributed most to the dissimilarity between sites with superb lyrebirds (*Menura novaehollandiae*) and control sites. Overall dissimilarity between lyrebird and control sites was 83.91%. L = leaf litter dwelling G/S = Generalist soil dwelling.

Class/Order/Family	Taxa	Habitat Affinity	Control Sites	Lyrebird Sites	% Contribution to Assemblage Differences	% Cumulative Contribution
			Average Abundance	Average Abundance		
Amphipoda	<i>Mysticotalitrus tasmaniae</i>	L	49.28	0.00	14.31	14.31
Amphipoda	<i>Keratroides vulgaris</i>	L	0.00	12.18	7.44	21.75
Annelida	<1 mm Oligochaeta	G/S	0.21	3.64	4.00	25.75
Acari	> 5 mm Prostigmata	L	5.06	0.39	4.00	29.75
Annelida	1 – 5 mm Oligochaeta	G/S	0.07	3.13	3.66	33.41
Amphipoda	<i>Mysticotalitrus cryptus</i>	L	0.00	2.59	3.59	37.00
Araneae	5mm Araneae	L	4.16	1.16	3.51	40.50
Formicidae	<i>Prolasius</i> sp	G/S	0.08	2.28	3.17	43.68
Diptera	10 mm Diptera	G/S	1.25	2.28	2.86	46.53
Araneae	6-10 mm Araneae	L	3.09	0.42	2.85	49.39
Diptera	6-10 mm Diptera	G/S	0.84	0.28	2.15	51.54

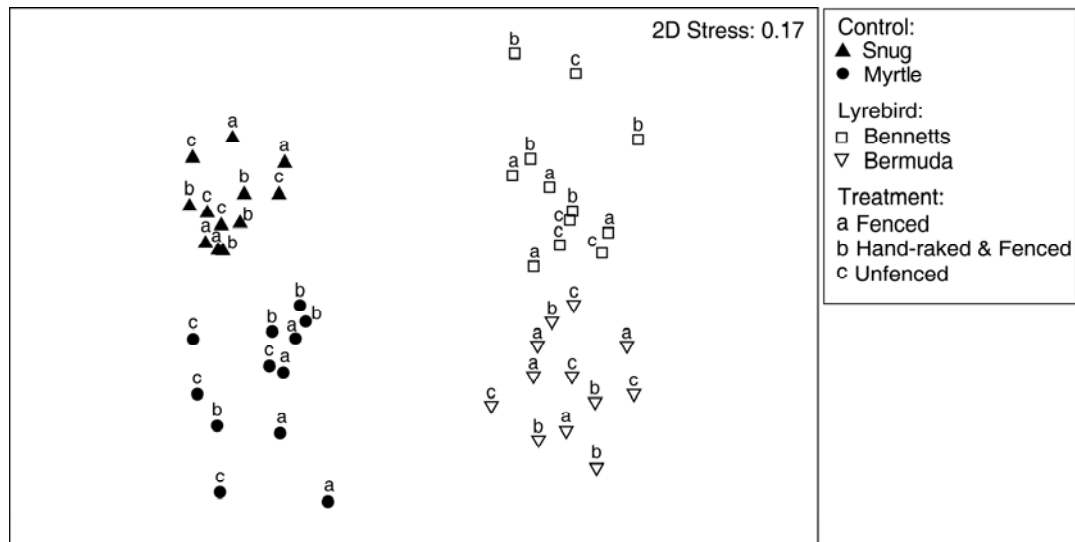


Figure 3.6: NMDS ordination based on a Bray-Curtis similarity matrix of square-root transformed macroinvertebrate abundance data from three experimental treatments at four sites = two with superb lyrebirds (*Menura novaehollandiae*) (lyrebird sites) and two sites without them (control sites). The stress level (0.17) indicated that the two-dimensional plot was a reasonable representation of the relationship between samples.

3.5.3 Mesoinvertebrate assemblage

A total of 3,724 individuals from 16 mesoinvertebrate taxonomic groups were collected at the four study sites. These included three families of Collembola (Poduridae, Sminthuridae and Entomobryidae), eight groups of detritivorous oribatid Acari (including a group of unidentified immature oribatids), three groups of predatory Acari from the mesostigmatid and prostigmatid orders, and one group of holothyrids. Two taxonomic groups, the oppid oribatid Acari and podurid Collembolans, accounted for 53% of all individuals collected. There was no significant interaction between lyrebird status and treatment for any measure of assemblage structure (all $P > 0.3$). However, there was a highly significant difference in the abundance of individuals between lyrebird and control sites (ANOVA $F_{1,2} = 2.392$, $P = 0.0004$, Fig 3.7). The mean number of individuals in plots at control sites was more than three times higher (73.19 individuals) than in plots at lyrebird sites (20.31 individuals). Taxonomic richness did not vary between lyrebird and control sites ($F_{1,2} = 1.5$ $P = 0.34$), but these taxa were not identified below family. As a result of the large differences in abundance but similar

number of taxa present at sites, evenness was significantly higher at lyrebird sites (0.86) than control sites (0.71) (ANOVA $F_{1,2} = 136.3$ $P = 0.007$, Fig 3.7).

There was no significant interaction between lyrebird status and treatment on mesoinvertebrate assemblage composition (PERMANOVA $F_{2,24} = 1.87$ $P = 0.11$).

However, there was a difference in the composition of mesoinvertebrate assemblages at lyrebird and control sites irrespective of treatment (PERMANOVA $F_{1,2} = 4.368$ $P = 0.02$). Because there were no significant differences in dispersion (PERMDISP $F_{1,46} = 1.457$ $P = 0.279$), these differences in composition are not artefacts of heteroscedasticity. The nMDS showed that while samples formed clusters based on lyrebird presence or absence, there was some overlap between the two groups (Fig 3.8). There was a significant treatment effect (PERMANOVA $F_{2,24} = 2.382$ $P = 0.04$), which was driven by weak effects due to fenced versus hand-raked + fenced ($F_{1,24} = 2.71$ $P = 0.09$) and fenced versus unfenced ($F_{1,24} = 3.12$ $P = 0.06$).

SIMPER results showed that overall dissimilarity between lyrebird and control site assemblages was low, at only 52.73% and this was driven primarily by differences in relative abundance of taxa rather than differences in the presence or absence of taxa (Table 3.5). However, taxonomic resolution was low for mesoinvertebrates. All taxa responsible for explaining 75% of the difference in macroinvertebrate assemblage composition between lyrebird and control sites were more abundant at control sites (Table 3.5). Oppid oribatids were the largest contributor, accounting for 25.47% of the difference between control and lyrebird assemblages.

3.5.4 Seedling abundance

The interaction between lyrebird status and treatment did not strongly affect the number of seedlings in plots (ANOVA $F_{2,27} = 1.869$ $P = 0.11$). The only main effect that was significant was treatment (ANOVA $F_{2,27} = 3.543$ $P = 0.04$). The *a priori* contrast between fenced treatments and the hand-raked + fenced treatments was significant ($F_{1,27} = 5.098$ $P = 0.03$) because the number of seedlings in the latter treatment was higher (45) than in fenced treatments (34) (Fig 3.9). However there was no difference in seedling abundance in the fenced and unfenced treatments ($F_{1,27} = 1.97$ $P = 0.17$).

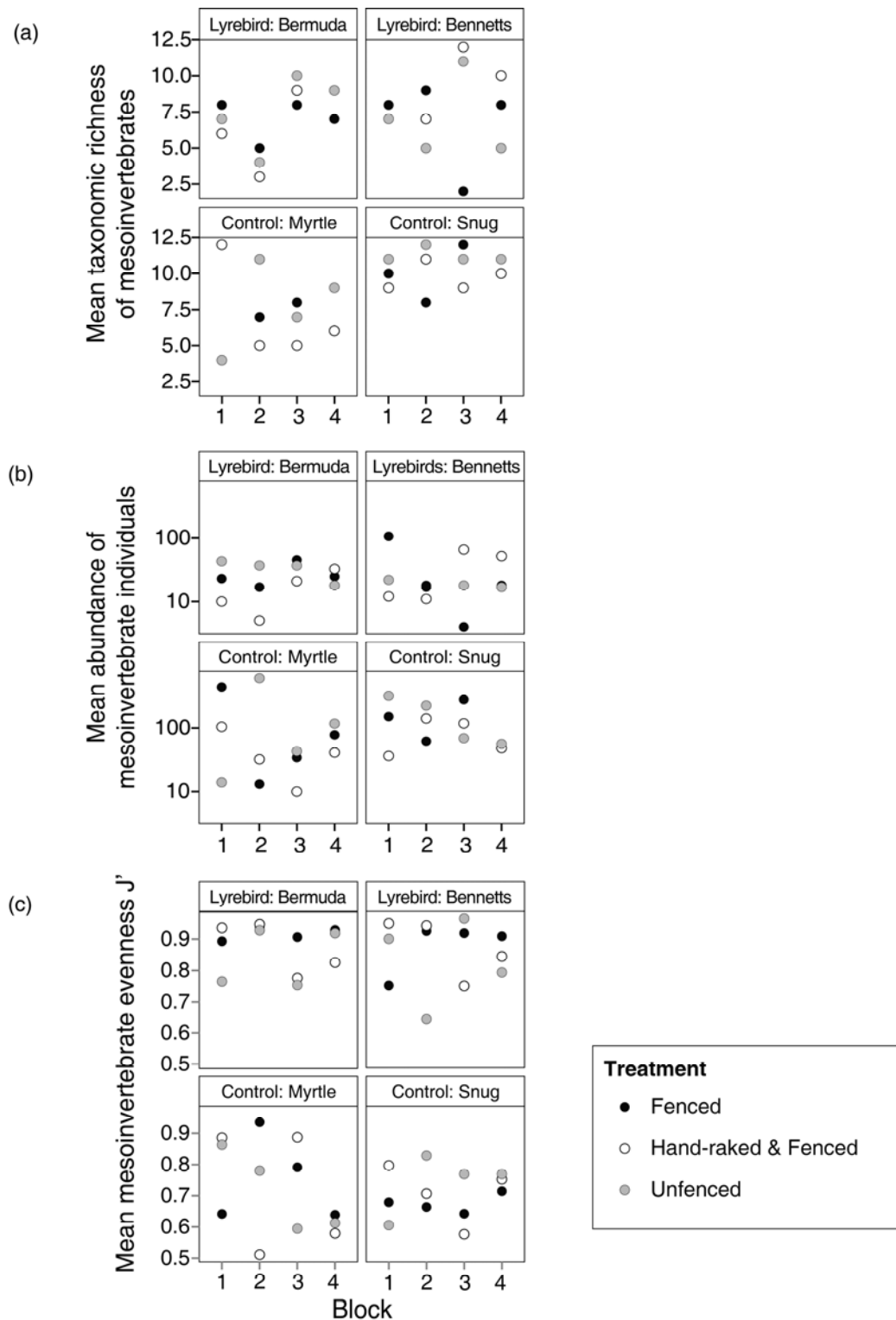


Figure 3.7: taxonomic richness (a), abundance (b) and evenness J' (c) of mesoinvertebrates in three treatments (Fenced, Hand-raked & Fenced and Unfenced) at sites with superb lyrebirds (*Menura novaehollandiae*) and control sites beyond their current range.

Table 3.5: Summary of SIMPER on mesoinvertebrate abundance data showing the taxa that contributed most to the dissimilarity between sites with superb lyrebirds (*Menura novaehollandiae*) and control sites without. Overall dissimilarity between lyrebird and control sites was 52.73%.

Class	Taxa	Control Sites	Lyrebird Sites	% Contribution to Assemblage Differences	% Cumulative contribution
		Average Abundance	Average Abundance		
Acari	Oribatid: oppid	35.40	1.41	25.47	25.47
Collembola	Poduridae	18.6	4.66	12.22	37.69
Acari	Oribatid: macropylina	4.75	0.56	8.54	46.23
Collembola	Entomobryidae	4.75	1.69	8.06	54.29
Acari	Prostigmata	4.45	2.68	7.49	61.78
Acari	Mesostigmata	6.15	2.52	7.39	69.18
Acari	Oribatid: teromorph	3.13	0.08	6.62	75.80

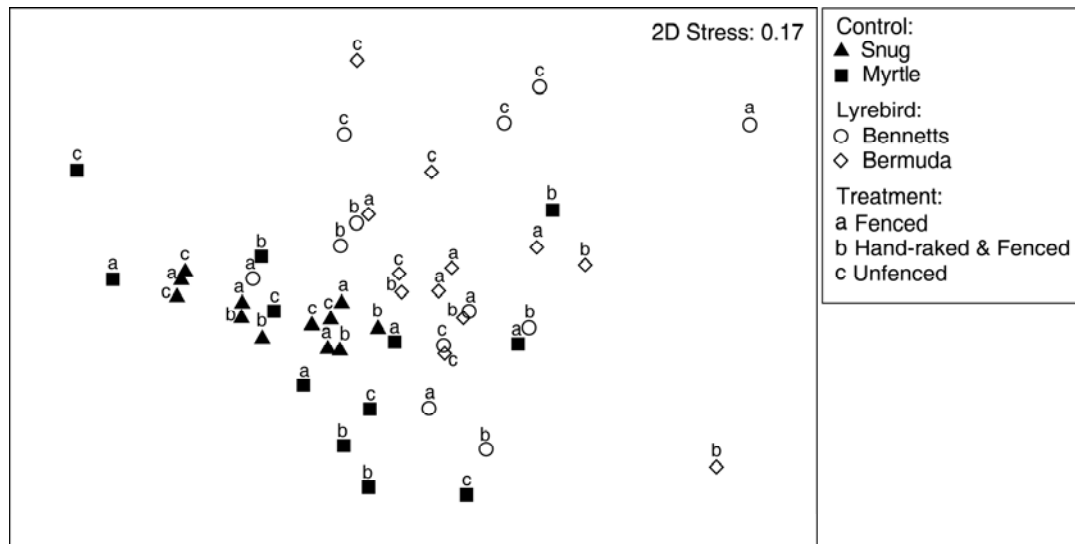


Figure 3.8: NMDS ordination based on a Bray-Curtis similarity matrix of square-root transformed mesoinvertebrate abundance data from three experimental treatments at four sites, two with superb lyrebirds (*Menura novaehollandiae*) (lyrebird sites) and two without (control sites). The stress level (0.17) indicated that the two-dimensional plot was a reasonable representation of the relationship between samples.

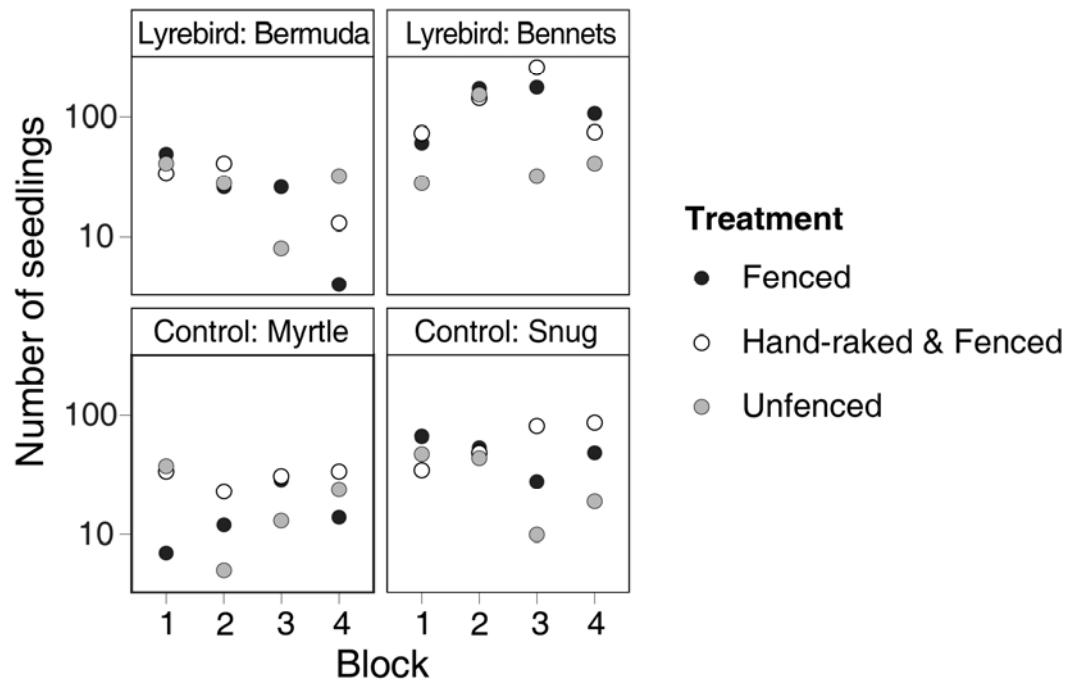


Figure 3.9: Abundance of seedlings in three treatments (fenced, hand-raked + fenced and unfenced) at sites with superb lyrebirds (*Menura novaehollandiae*) and control sites where they were absent.

3.6 Results: Short-term recovery experiment

Nearly 7,000 (6,936) individuals in 112 taxa were collected, of which 28 were singletons. *Mysticotalitrus tasmaniae* (Amphipoda) dominated the fauna, accounting for 30.5% of the total number of individuals. A further 40.5% of the individuals belonged to five other groups (small Araneae, small and medium dipteran larvae, oecophid moth larvae, and a species of staphylinid beetle - *Atheta* TFIC morphospecies 02). There was no significant interaction between treatment and time for mean macroinvertebrate taxonomic richness, abundance and evenness (Table 3.6, Fig 3.10). However, there was a significant treatment effect for all three measures and all *a priori* contrasts between treatments were highly significant (all $P < 0.0001$). Specifically, mean taxonomic richness and abundance were highest in undisturbed control treatments (mean richness = 21.81, mean abundance = 122) and lowest in bare treatments (mean richness = 9, mean abundance = 24, Fig 3.10), while the reverse was true for evenness (bare treatments = 0.845, control treatments = 0.745).

The mean abundance of generalist/soil dwellers varied with treatment and days (ANOVA $F_{2,50} = 4.442$ $P = 0.016$). Their abundance increased in mixed treatments over the time (from a mean of 26 at 7 days to a mean of 37 individuals at 21 days, Fig 3.11), indicating that some recovery from disturbance occurred. However, numbers in undisturbed controls fell slightly (from a mean of 49 to 37) and numbers in bare treatments remained constant (from a mean of 8 to 7). In contrast, the abundance of leaf litter dwellers in treatments did not vary over time (ANOVA $F_{2,50} = 1.159$ $P = 0.228$) but there was a highly significant difference in abundance among treatments (ANOVA $F_{2,50} = 75.38$ $P < 0.0001$). Both *a priori* contrasts showed that there were fewer individuals in bare (15) and mixed (63) treatments than in the controls (79) (all $P < 0.004$).

There was a weak interaction between treatment and days in macroinvertebrate assemblage composition (PERMANOVA $F_{4,48} = 1.3157$ $P = 0.059$). The main effects and two *a priori* contrasts were all significant (Table 3.7). Examination of the nMDS plot (Fig 3.12) showed that samples from mixed and control treatments overlapped, while bare treatment plots formed a more distinct but much more dispersed group. This difference in dispersion was confirmed by PERMDISP ($F_{2,78} = 38.235$ $P = 0.001$).

SIMPER showed that the overall dissimilarity between the bare and control assemblages was 66.29% (Table 3.7). Four taxa individually contributed more than 5% of the dissimilarity between the treatments with all four occurring in much higher numbers in control treatments (Table 3.7). The amphipod *Mysticotalitrus tasmaniae*, a leaf litter dweller, accounted for the around 10% of the variation between assemblages. The overall dissimilarity between mixed and control assemblages was only 45% and no individual taxa contributed more than 5% to the dissimilarity between assemblages. Of the four taxa that contributed the most to assemblage dissimilarity, three were more abundant in control treatments but one, the staphylinid beetle *Atheta* sp. TFIC 02, was more abundant in mixed treatments and may be a disturbance specialist despite being a leaf litter dweller.

Table 3.6: Results from the two-way ANOVA examining the effect of simulated superb lyrebird (*Menura novaehollandiae*) disturbance on macroinvertebrate taxonomic richness, abundance and evenness (J') over 21 days.

	Richness				Abundance				Evenness			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
Days	1	0.109	1.558	0.224	1	0.009	0.044	0.835	1	0.002	0.483	0.494
Residuals	25	0.070	-	-	25	0.219	-	-	25	0.004	-	-
Treatment	2	5.885	126.73	<0.0001	2	20.054	115.773	<0.0001	2	0.070	18.981	<0.0001
Control v bare	1	4.547	97.56	<0.0001	1	15.29	88.274	<0.0001	1	0.067	18.203	<0.0001
Control v mixed	1	7.223	154.98	<0.0001	1	24.817	143.272	<0.0001	1	0.073	19.758	<0.0001
Treatment: Days	2	0.061	1.315	0.277	2	0.250	1.443	0.246	2	0.002	0.801	0.455
Residuals	50	0.047	-	-	50	0.173	-	-	50	0.003	-	-

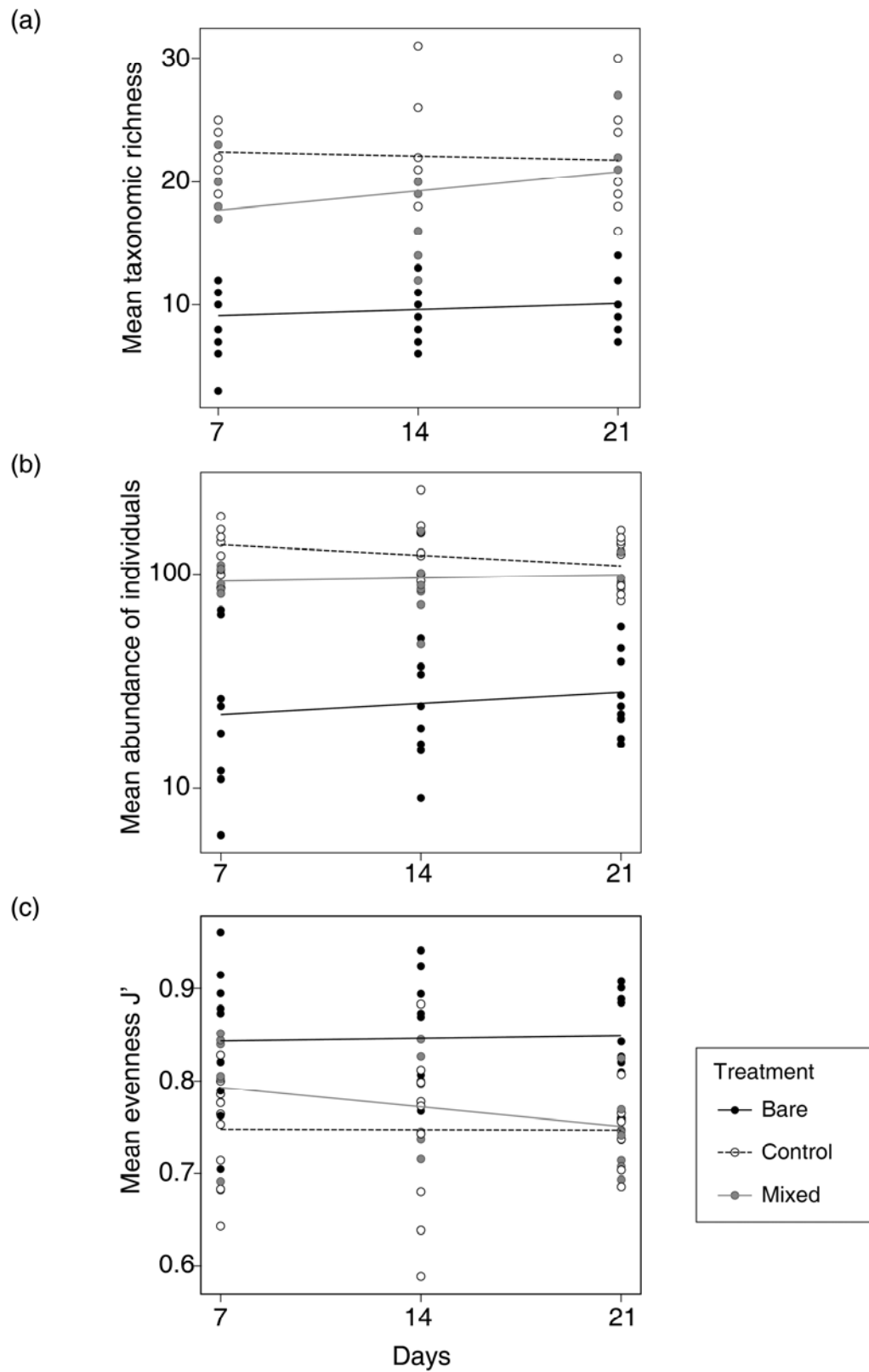


Figure 3.10: Mean taxonomic richness (a), abundance (b) and evenness J' (c) of mesoinvertebrates in three treatments (bare, control and mixed) in the 21 days following simulated superb lyrebird (*Menura novaehollandiae*) disturbance.

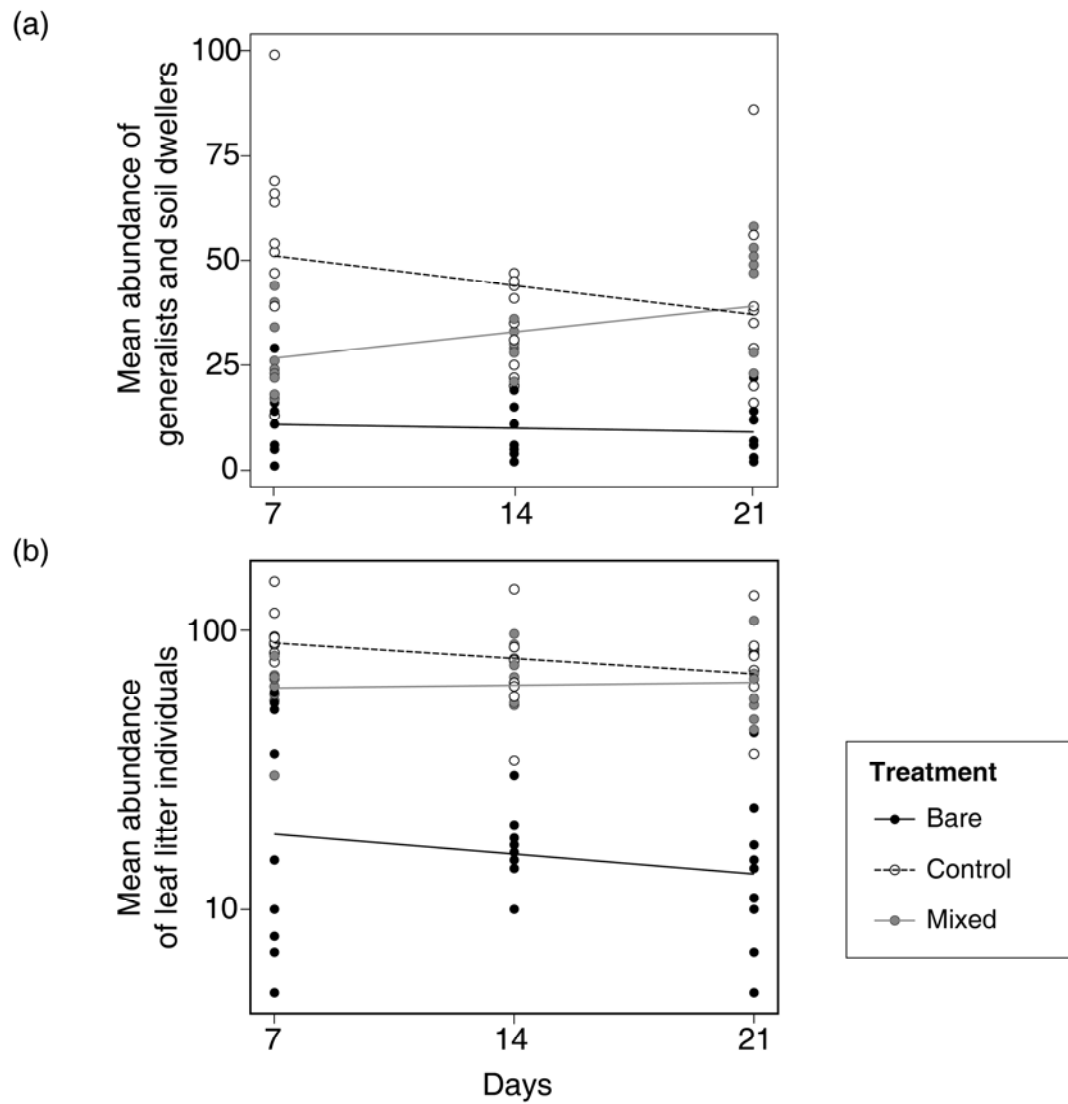


Figure 3.11: Mean abundance of (a) generalist/soil dwelling and (b) leaf litter dwelling macroinvertebrates in three treatments (bare, mixed and control) over 21 days following simulated superb lyrebird (*Menura novaehollandiae*) disturbance.

Table 3.7: Results of the PERMANOVA of square-root transformed macroinvertebrate abundance data examining the effect of simulated superb lyrebird (*Menura novaehollandiae*) disturbance on macroinvertebrate assemblage composition over 21 days. P (MC) = Monte Carlo asymptotic *P*-value (significant *P* values <0.05 are listed in bold).

Source	df	SS	MS	Pseudo-F	Unique permutations	P(MC)
Between Days						
Days	2	4306.1	2153.1	1.33	9890	0.12
Residuals	24	38572	1607.2	1.436	-	-
Within Days						
Treatment	2	28979	14490	12.952	9901	0.0001
Mixed vs Control	1	2700	2700	3.3903	9929	0.0001
Bare vs Control	1	23572	23572	17.229	9919	0.0001
Days: Treatment	4	5887.6	1471.9	1.3157	9864	0.08
Residuals	48	53699	1118.7	-	-	-
Total	80	1.3144x10 ⁻⁵				

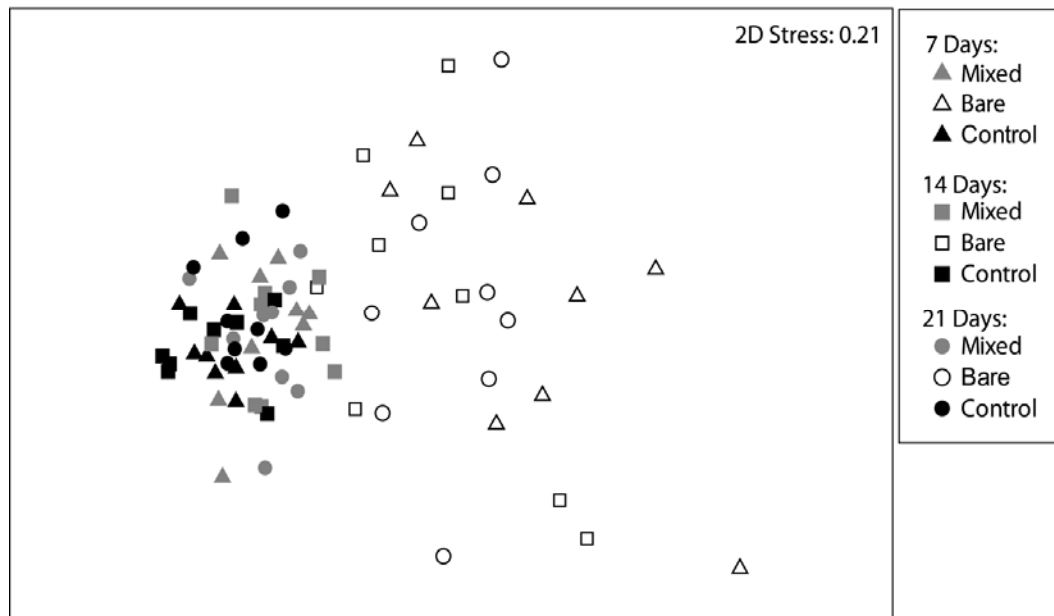


Figure 3.12: NMDS ordination based on square-root transformed macroinvertebrate abundance data from three treatment plots (n=9) on three sample days (7,14 and 21) following simulated superb lyrebird (*Menura novaehollandiae*) disturbance.

Table 3.7: Summary of the SIMPER on macroinvertebrate abundance data showing the taxa that contributed most to the dissimilarity between (a) Bare and Control treatments (overall dissimilarity: 66.29%) and (b) Mixed and Control treatments (overall dissimilarity: 45.52%). L = leaf litter dwelling G/S = Generalist soil dwelling.

Order/family	Taxa	Habitat affinity	Average Abundance	Average Abundance	% Contribution to Assemblage Differences	% Cumulative
(a)			Bare	Control		
Amphipoda	<i>Mysticotalitrus tasmaniae</i>	L	5.52	38.93	10.58	10.58
Insecta	5 mm Diptera	G/S	2.19	12.11	6.09	16.67
Araneae	5 mm Araneae	L	1.36	10.30	6.00	22.67
Diptera	6-10 mm Diptera	G/S	0.34	5.01	5.19	27.86
(b)			Mixed	Control		
Diptera	5 mm Diptera	G/S	5.52	12.11	4.97	4.97
Araneae	5 mm Araneae	L	4.20	10.30	4.83	9.80
Coleoptera	<i>Atheta</i> sp. TFIC 02	L	7.61	2.68	4.62	14.42
Amphipoda	<i>Mysticotalitrus tasmaniae</i>	L	28.19	38.93	4.52	18.94

3.7 Discussion

The paucity of information regarding the impact of non-native birds on native biota has hampered attempts to assess the threat they pose and to develop effective strategies for their management (Blackburn *et al.* 2009, Bauer and Woog 2011, Strubbe *et al.* 2011). Experimental studies, while acknowledged as crucial tools for determining the ecological impact of non-native species (Ross *et al.* 2006, Strayer *et al.* 2006, Byers *et al.* 2010), have been infrequent for non-native birds (Kumschick and Nentwig 2010, Bauer and Woog 2011). This investigation is the first to use field experiments to test the impact of a non-native bird on native invertebrates. It revealed that the superb lyrebird is capable of influencing native macroinvertebrate and mesoinvertebrate assemblages, especially over short time frames, but may have little impact on seedling survival.

3.7.1 Short-term recovery experiment

Disturbance of the forest floor significantly reduced both macroinvertebrate abundance and richness and altered assemblage composition immediately (seven days) after disturbance. However, the magnitude of this impact depended on the specific nature of the disturbance: leaf litter removal had a much stronger effect than the mixing of leaf litter and soil. This is not surprising given that invertebrate richness and abundance is generally much higher in leaf litter than in soil (Evans *et al.* 2003), and therefore much of the fauna would have been removed in the process of scratching away the leaf litter, and was probably unable to return rapidly due to a lack of food and/or habitat. For example, the amphipod *Mysticotalitrus tasmaniae* (which feeds on and resides in leaf litter; Friend and Richardson 1977, Walsh *et al.* 1994) dominated the fauna in undisturbed areas and was also abundant when soil and leaf litter were mixed but was uncommon where there was no leaf litter. The fact that abundance and richness were still lower when soil and leaf litter were mixed together (but no litter was removed) than in undisturbed areas indicates that some individuals and taxa must either have left the disturbed area or perished *in situ* as a result of the disturbance. The majority of taxa that contributed to compositional differences between assemblages in the disturbed and undisturbed areas were much less abundant in disturbed areas. The only exception was the staphylinid beetle *Atheta* TFIC sp. 02, which was more common when leaf litter was mixed with soil, suggesting that it may be a disturbance specialist and had preferentially moved into these areas. *Atheta* TFIC sp. 02 is known to be associated with young forest

that is regenerating from large-scale disturbance in the form of fire and forestry (N. Fountain Jones, UTAS pers. coms.), supporting the current finding.

Overall assemblage structure and composition and the abundance of leaf litter dwellers did not recover from either type of disturbance within 21 days. However, the abundance of generalist/soil dwellers did increase significantly in areas where leaf litter was mixed with soil, probably because they are less dependent than leaf litter dwellers on the structure offered by an intact leaf litter layer (York 1999, Teasdale *et al.* 2013). Similarly, soil macroinvertebrates recover more quickly than leaf litter invertebrates from disturbances such as fire where soil remains intact but the leaf litter is removed (York 1999, Dawes-Gromadzki 2007). The short-term recovery experiment indicated that the magnitude of the impact of superb lyrebird disturbance and the speed of recovery are likely to vary among invertebrate taxa and also with the specific type of disturbance.

3.7.2 Exclosure experiment

The findings of the exclosure experiment regarding the influence of superb lyrebirds on invertebrate assemblages were complex. There were no differences in the structure and composition of mesoinvertebrate and macroinvertebrate assemblages between the three treatments (fenced exclosures, hand-raked + fenced exclosure, and unfenced areas) that could be attributed to the presence of superb lyrebirds. However, when the data were examined at the site level, there were some significant differences in the structure (mesoinvertebrate abundance and evenness, and the composition of both meso and macroinvertebrate assemblages) between sites with and without superb lyrebirds. Several factors may explain the seemingly paradoxical results of this experiment (i.e. differences in the invertebrate assemblages between sites that were associated with the presence or absence of lyrebirds but a lack of evidence of superb lyrebird impact differing between treatments).

Firstly, the absence of any observed effect of superb lyrebirds between treatments (the fenced exclosure, and unfenced areas disturbed by the birds) and very few differences between the fenced exclosures and the hand-raked + fenced exclosures is probably due to the speed at which the invertebrate assemblages are able to recover. As discussed above, the short-term recovery experiment demonstrated that generalists/soil dwelling

macroinvertebrates increased in abundance to a level similar to adjacent undisturbed areas within three weeks of disturbance. This means that in the exclosure experiment, invertebrates in the hand-raked exclosures may have had sufficient time during the eight-month period since hand-raking occurred for assemblages to return to their pre-disturbance state. Moreover, because monthly monitoring showed that there was very little new disturbance in the unfenced areas at lyrebird sites in the final two months of the experiment, the timeframe for recovery is probably in the vicinity of eight to ten weeks. This means that even though the two lyrebird sites were heavily disturbed, foraging activity in the unfenced plots was not sufficiently frequent or intense to affect invertebrates in the longer term. Similarly, experimental studies on feral pigs (*Sus scrofa*), which also turn over leaf litter and soil and feed on invertebrates, have found little evidence of impact on macroinvertebrates (Vtorov 1993, Mitchell *et al.* 2007, Elledge 2011; but see Taylor, 2010). Both feral pigs and superb lyrebirds are highly mobile, so their feeding activity tends to be very patchily distributed across both landscape and local scales (Higgins *et al.* 2001, Elledge *et al.* 2012). This kind of foraging creates a mosaic of disturbed patches at different stages of recovery as well as relatively undisturbed areas. This may enable invertebrates to survive in adjacent undisturbed patches and then quickly recolonise recently disturbed areas.

While speed of recovery explains the general lack of significant effects between treatments, there was a difference in macroinvertebrate taxonomic richness in fenced exclosures and unfenced exclosures across all sites (suggesting a caging artefact). A possible explanation for the caging effect is that the exclosures prevented other insectivores from entering. Although there was a gap between the fencing and the ground that allowed access for invertebrates and small vertebrates, the flagging tape across the exclosures may have deterred other insectivorous birds such as the Bassian thrush (*Zoothra lunulata*) from entering the plots to feed, thereby lowering predation and increasing invertebrate taxonomic richness.

The differences in macroinvertebrate assemblage composition between sites with superb lyrebirds and sites without were largely driven by two species of amphipod (*Mysticotalitrus tasmaniae*, found only at control sites and *Keratroides vulgaris*, found only at lyrebird sites). These species of amphipod have wide and overlapping distributions in Tasmania, but where they co-occur they usually partition the habitat,

with *K. vulgaris* dominating in wetter microhabitats (Richardson and Devitt 1984, Friend 1987). Amphipods are important prey for superb lyrebirds (Yen 2001) and it seems unlikely that these two species would be differently affected by predation or disturbance by the birds. Both are large and therefore likely to be eaten (Friend 1987), and inhabit leaf litter (Richardson and Devitt 1984), and so would be negatively affected by reduction in leaf litter cover. Thus, the most likely reason for the difference in amphipod species across the sites is past or present environmental conditions—particularly rainfall (which was lower at control sites than at lyrebird sites during 2008). However, surveys of more locations are required to assess whether superb lyrebirds are influencing amphipod distribution, or whether this is indeed driven by environmental conditions.

Not only did mesoinvertebrate assemblage composition differ between sites with and without superb lyrebirds, but their abundance was also significantly lower at sites in the presence of the lyrebirds than at control sites. It is difficult to determine the factors responsible for these findings. On the one hand it is possible that environmental conditions such as rainfall may be responsible. However, the groups that dominated assemblages, the podurid collembolans and oribatid Acari, are known to be sensitive to disturbance of leaf litter and soil (Behan-Pelletier 1999, Greenslade 2007). For example Vtorov (1993) found that ground disturbance by feral pigs in Hawaiian forests severely reduced the abundance and richness of Collembola and Acari. Many oribatids have limited dispersal abilities and life cycles that last several years (Lindberg *et al.* 2002); this may mean that while the mesoinvertebrate fauna in the unfenced and hand-raked experimental treatments at sites with superb lyrebirds were able to recover to some degree, their abundance at the sites overall was depressed as a result of broader disturbance by the lyrebirds. Vtorov (1993) found that Acari and Collembola did recover from pig disturbance but that was after exclusion from pigs for 7 years. Therefore, the possibility that superb lyrebirds are capable of changing mesoinvertebrate assemblages in the long term cannot be ruled out.

There were no differences in the number of seedlings in the exclosure experiment treatments that could be attributed to superb lyrebirds. This was surprising because within the native range of the birds, they are known to promote (Ashton and Bassett 1997) or in some cases reduce the survival of some plant species (Howard 1973, Read

and Brown 1996). In this study, the numbers of seedlings in exclosures that had been artificially disturbed were higher than in undisturbed exclosures, irrespective of the presence or absence of superb lyrebirds. This suggests that a low frequency of disturbance (once in 8 months) may promote seedling germination. However, there was no difference between the number of seedlings in undisturbed exclosures and in unfenced plots that were disturbed by superb lyrebirds throughout the experiment. This indicates that disturbance also kills many existing seedlings and therefore, more frequent disturbance (i.e. more than once in 8 months, as was the case when lyrebirds were present) probably kills seedlings that germinate so that numbers stay similar to undisturbed areas. Overall, the long term survival of seedlings in mature wet eucalypt forest is probably more strongly influenced by disturbance events such as tree-fall and fire, which open the canopy, increase light levels and allow seedlings to establish (Ashton 1976, Ashton and Attiwell 1994, Facell *et al.* 1999) than by superb lyrebird activity.

Although superb lyrebirds may have a limited effect on seedling survival in an intact forest, they may have the capacity to significantly alter species establishment following forestry operations. Anecdotal evidence suggests that repeated disturbance by superb lyrebirds inhibits regeneration of tree seedlings following timber harvesting (Neyland 2004). It is also possible that superb lyrebirds could have an impact on rare plants as is currently suspected for the myrtle elbow orchid (*Thynninorchis nothofagicola*) (Threatened Species Section 2009). However, species-specific studies would be required to test such impacts given these taxa occur at low densities and are unlikely to be detected in investigations of community-level impacts, such as the present study.

Taken together, the results of the two experiments demonstrate that the ecosystem engineering activities of the superb lyrebird are capable of altering native invertebrate assemblage structure and composition but that these effects are mainly short lived and spatially limited. Thus, superb lyrebirds will only affect macroinvertebrates in a small proportion of the forest floor at any one time. Seeding survival within established forest also appears to be unaffected by the birds. However, the long-term effect of the birds on mesoinvertebrates remains unclear and requires further research. These findings highlight the value of employing a multifaceted research approach at different temporal scales. The use of manipulative field experiments in this study represents a step towards

improving the rigour of investigations of the impact of non-native birds on native biota after years of speculation based on largely anecdotal observations.

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Chapter 4: Scale-dependent effects of a non-native bird on native invertebrate assemblages

4.1 Abstract

Multi-scale studies offer an effective means of understanding the spatial dependency of the ecological impact of non-native species but have rarely been used to investigate the impact of non-native animals on terrestrial invertebrates. The superb lyrebird (*Menura novaehollandiae*), introduced to Tasmania last century, substantially modifies the structure of forest floors by moving hundreds of tonnes of soil and leaf litter per hectare every year while foraging for invertebrate prey, but its impact on native invertebrates is unknown. A multi-scale survey was used to investigate the impact of this ecosystem engineer on native soil- and leaf litter-dwelling invertebrates in the wet eucalypt forests of southern Tasmania at small (within 1 m² patches), local (within sites across tens of metres) and landscape scales (between sites across tens of kilometres). Superb lyrebird activity was associated with reductions in invertebrate abundance and taxonomic richness, increased taxonomic evenness, and altered assemblage composition. The negative influence of the birds was greater on macroinvertebrates than on mesoinvertebrates; within the former group, leaf litter dwellers were more affected than generalists and soil dwellers. However, the superb lyrebirds' impact on invertebrate assemblage structure and composition varied greatly across different spatial and temporal scales: the impact was profound at the smallest spatial scale (patch), but depended on whether or not the patch had been recently disturbed. At the local scale (within sites), the magnitude of impact was influenced by the amount of disturbance across the site. There was less difference between patch types at sites with medium disturbance (< 50% forest floor disturbed) than at sites where more than 50% of the forest floor was disturbed. At the landscape scale, when all samples were considered, the impact of superb lyrebirds was discernible for some measures but not others. However, these patterns were almost entirely driven by the assemblages in recently disturbed patches, while assemblages in patches that had not been disturbed in a year did not differ from those at sites without superb lyrebirds. Thus while impact was detectable at large spatial scales, the patchy nature of superb lyrebird foraging and the speed at which invertebrate assemblages recover means that the birds are unlikely to

have significant deleterious impacts on native invertebrate assemblages at the landscape scale.

4.2 Introduction

Limited funding means that conservation managers must prioritise the allocation of resources for the management of established non-native species based on the severity of their current and predicted future impact (Byers *et al.* 2010, Thrush and Lohrer 2012). However, if the nature or magnitude of impact of a non-native species varies in space or time, it can be difficult to accurately assess the risk posed because their actual and perceived impact will depend on the scale of observation (Lodge *et al.* 1998, Ross *et al.* 2003, Powell *et al.* 2013). There are three reasons for this: firstly, biotic patterns may be apparent at one scale but not at others, secondly the influence of environmental factors on ecosystems and biota may only operate at certain spatial scales and thirdly probability of detecting impact varies at different scales (Sandel and Smith 2009). For example, studies of the impact of non-native species conducted at small spatial scales often demonstrate that native species richness is far lower in locations where a non-native species is established than in locations without the non-native species. However, when studies include larger areas such impacts are rarely observed (Powell *et al.* 2013). This occurs because non-native species often reduce the population sizes of native species making them harder to detect at small spatial scales, but at large sampling scales the chances of detecting the native species increases so that the overall perception of impact is reduced (Powell *et al.* 2013). This is not to say that small-scale studies are unimportant or unnecessary: they are, because there is a big difference in the threat posed by a species that has a significant impact at small scales and a species that has no discernible influence at any spatial scale. While some non-native species may not, in themselves, cause extinctions at large spatial scales, they can reduce the resilience and increase the susceptibility of native species to others stressors by reducing population sizes and by causing localised extinctions that then restrict native species to refugia where their long term survival may be limited (Gilbert and Levine 2013).

While the importance of scale—both spatial and temporal—to our understanding of the impact of non-native species on the structure and dynamics of ecological communities has been highlighted in recent years (Strayer *et al.* 2006, Sandel and Smith 2009, Powell

et al. 2013), it is uncommon for scale to be explicitly incorporated into studies investigating the impact of non-native species (Parker *et al.* 1999, Ujvari *et al.* 2011, Grarock *et al.* 2012). Instead of ignoring the potential spatial dependency of impact, studies which link patterns and process across multiple spatial scales offer a means of understanding any spatial dependency, and in turn, potentially provide a more holistic understanding of the impact of a non-native species than investigations performed at a single spatial scale (Lodge *et al.* 1998, Sandel and Smith 2009). Multi-scale approaches have been used successfully in aquatic systems to determine the impacts of non-native animals on native invertebrate assemblages (e.g. Lodge *et al.* 1998, Mayer *et al.* 2002, Ross *et al.* 2003, Townsend 2003). However, they have rarely been employed to investigate the impacts of non-native animals on terrestrial invertebrate communities, particularly outside of agricultural landscapes.

Identifying the impacts of non-native species on terrestrial invertebrates, especially those that dwell in leaf litter or soil, is particularly challenging (York 1999, Sileshi *et al.* 2008). Soil and leaf litter communities are renowned as being highly heterogeneous at a range of spatial and temporal scales (Ettema and Wardle 2002). Populations may be aggregated (Ettema and Wardle 2002, Sileshi 2008) or over-dispersed (Traniello and Levings 1986). Adequate sampling of these communities can be hard to achieve and studies are often hampered by high sample variance, making it difficult to detect even large impacts (Lavelle and Spain 2001, Sileshi 2008). In addition, soil and leaf litter invertebrate communities are typically highly diverse, but taxonomic knowledge (especially in the Southern Hemisphere) is often limited (Bardgett and Anderson 2005, Decaëns *et al.* 2006), meaning that studies must often rely on order or family level data and run the risk of missing genus and species level differences in response (Teasdale *et al.* 2013). None-the-less, soil and leaf litter invertebrate communities represent the majority of animal biodiversity in most terrestrial ecosystems (Bardgett and Anderson 2005, Decaëns *et al.* 2006), and through their activities as decomposers, they are vital to the functioning of most terrestrial ecosystems (Ettema and Wardle 2002, Decaëns *et al.* 2006, Parker 2010). Therefore, non-native species that interact with these communities could greatly influence ecosystem function. Explicitly addressing scale in both observational and experimental studies in soil ecosystems offers a powerful but as yet under-utilised means of assessing impact of non-native species on this component of native ecosystems.

In this study, the Tasmanian population of the superb lyrebird (*Menura novaehollandiae*) was used as a case study to examine the impact of a non-native animal on soil and leaf litter assemblages across a range of spatial and temporal scales. The superb lyrebird is a medium-sized bird weighing approximately 1 kg (Higgins *et al.* 2001), native to the temperate forests of the south-eastern mainland of Australia. The species was introduced to Tasmania in the 1930s in an attempt to save it from the perceived threat of habitat loss and predation from the introduced European fox (*Vulpes vulpes*) within its native range. The superb lyrebird is a predator of invertebrates and significantly modifies forest floor habitat through scratching and digging when searching for invertebrate prey (Robinson and Frith 1981, Lill 1996, Ashton and Bassett 1997). Ashton and Bassett (1997) estimated that an individual bird could move around 200 tonnes of soil and leaf litter per hectare annually, and it is thought that superb lyrebirds constitute a significant form of natural disturbance within their native range (Ashton 1975, Webb and Whiting 1975). There are no native equivalents of the superb lyrebird in Tasmanian wet forests (Bennett 1993, Johnson 1994, Claridge and Barry 2000, Harris and Kitchener 2005). Thus, the presence of a large insectivore, together with the physical disturbance of the forest floor, represent both a novel predator and process in Tasmanian wet forests. As the superb lyrebird has now spread throughout much of southern Tasmania, including parts of the Tasmanian Wilderness World Heritage Area, conservation managers are concerned that the ecosystem engineering activities of the superb lyrebird, in combination with their predation on invertebrates, could threaten native forest biota (Mallick and Driessen 2009).

Superb lyrebirds are highly mobile and forage in a patchy manner over local scales (tens to hundreds of metres) (Ashton and Bassett 1997). The average size of a single scratching event ranges between 0.25 m² to 0.50 m² (Ashton and Bassett 1997). Each feeding event is usually discrete, and in heavily disturbed areas they are spaced approximately 1–2 metres apart (Ashton and Bassett 1997). Occasionally feeding patches will join together to form larger scratched areas several square metres in size (Tassell pers. obs.). Typically, at any one time part of the forest floor will be covered with recently disturbed patches and a mosaic of other disturbed patches of various ages (Ashton and Bassett 1997). Whether or not superb lyrebirds have a significant impact on invertebrate communities at large spatial scales (site and landscape) will depend the

following: the magnitude of impact on invertebrates within an individual disturbed patch, the length of time that impact lasts, and the frequency and extent of disturbance across sites and landscape (Crooks 2002). If disturbance is spatially heterogeneous or the effect of the disturbance on invertebrates is small and short lived, then the impact will probably be restricted to the scale of individual disturbed patches (Crooks 2002, Cuddington and Hastings 2004). This is because the cumulative effect of individual patches is unlikely to have significant impact at intermediate and large spatial scales. Conversely, if disturbed patches are common or their effect is substantial and long-lived, then the combined impact at larger spatial scales could be high (Hall *et al.* 1993).

To determine the impact of the superb lyrebird, invertebrate assemblages were compared at (1) small spatial scales (1 m² patches), (2) local scales (within sites, 10 m²) and (3) landscape scale (between sites, across tens of kilometres). The survey incorporated control sites beyond the current range of the superb lyrebirds and sites with either high or medium levels of lyrebird foraging activity (based on the extent and the intensity of foraging across the site). These different levels of disturbance intensity were included because the speed at which the assemblage within an individual disturbed patch recovers will be influenced by the availability and proximity of refugia (i.e. relatively undisturbed zones) in the surrounding area from which individuals can recolonise (Leibold *et al.* 2004, Sandal and Smith 2009). High levels of disturbance generally result in fewer refugia and potentially slow the speed of recovery more than medium levels of disturbance (Gilbert and Levine 2013). At sites with superb lyrebirds, patches that had been recently disturbed by superb lyrebirds and those that had not been disturbed for around a year were compared to assess the duration of the effect of lyrebird disturbance.

This study investigated three main questions: (1) does invertebrate assemblage structure and composition vary between sites with and without superb lyrebirds? (2) do patches that have not been disturbed by lyrebirds for around a year support different assemblages than assemblages at control sites that have never been disturbed by lyrebirds? (3) does the magnitude and direction of the effect of superb lyrebirds vary with the level of lyrebird activity (disturbance intensity) at sites or with different components of the invertebrate fauna (mesoinvertebrates and macroinvertebrates)? The hypotheses were that (1) superb lyrebirds will effect species richness and abundance of

taxa, due to the considerable differences in disturbance regime, habitat structure and predation pressure between areas with and without the birds; (2) the effect of superb lyrebirds on invertebrates will be greater in recently disturbed patches than patches that have not been disturbed for around a year; (3) the difference between undisturbed and disturbed patches will be greater at high intensity disturbance sites; (4) superb lyrebirds will reduce the abundance of macroinvertebrates that are dependent on leaf litter for food or habitat (leaf litter dwellers) more than the abundance of macroinvertebrates that primarily live in the soil (generalists and soil dwellers) because lyrebird foraging activity reduces the extent of the leaf litter layer but not soil (Ashton and Bassett 1997).

4.3 Methods

4.3.1 Study region and study sites

This study was carried out during October and November (Austral Spring) 2009 in southern Tasmania, Australia (Fig 4.1). This region supports extensive temperate forests, which are the preferred habitat for the superb lyrebird (Higgins *et al.* 2001, Ashton and Bassett 1997). The study area was selected because it contains locations where superb lyrebirds are present that are in close proximity to suitable habitat that is immediately beyond their current range but share the same forest type, geology and faunal species composition.

Twelve sites were selected (three sites with high levels of superb lyrebird foraging activity, three sites with medium levels of superb lyrebird activity and six control sites where lyrebirds were absent) in wet sclerophyll forest located a maximum of 60 km apart. A spatial multi criteria analysis (using ESRI ArcGIS software) was used to select sites on the basis of the following: similarity of vegetation community composition and structure, forest history (forestry and fire), geology, climate, elevation, slope, aspect, and road accessibility. Each comprised wet sclerophyll forest with a canopy dominated by either *Eucalyptus obliqua* or *E. regnans*. Other canopy and sub-canopy species included *Nothofagus cunninghamii*, *Atherosperma moschatum*, *Phyllocladus aspleniifolius* and *Acacia dealbata*. The understorey was dominated by broad-leaved species including *Olearia argophylla*, *Pomaderris apetala*, *Bedfordia linearis* and the treefern *Dicksonia antarctica*. Cover of shrub and ground level vegetation was sparse (Neyland 2001). Soils had gradational texture profiles comprised of loams or clayey

loams above loam or clayey subsoils and ranged from poor to well drained (Laffan 2001, Laffan and McIntosh 2005). Underlying geology at sites was a combination of Jurassic dolerite and Permian to Triassic sedimentary parent material (Forsyth *et al.* 1995, Spanswick and Kidd 2000). All sites had been selectively logged over thirty years ago but had not been subject to modern silvicultural practices or major fire in the last 40 years (Forestry Tasmania GIS maps, Stone 1998, Brown, M.J. pers. comm.). Sites with superb lyrebirds were selected because annual monitoring of the extent of lyrebird disturbance along a 30m x 2m transect line at each site had shown that there was either high (>50% disturbance) or medium (30-50% disturbance) during the previous three years. A summary of site environmental characteristics is provided in Table 4.1.

4.3.2 Survey Design

To minimise confounding environmental factors, within each of the 12 sites a 10 × 10 m area in which to sample was chosen on the basis of the following: (a) located within 10–25 m of a permanent stream in what was identified as a ‘slope’ microhabitat, i.e. between the riparian zone and convex landforms (ridges); (b) south, southeast or southwest-facing slopes; (c) uniform vegetation species composition and cover, and (d) leaf litter 10–40 mm deep and with very sparse cover of ground level plants (identified as the main criterion for small-scale habitat selection by foraging lyrebirds) (Ashton and Bassett 1997, Higgins *et al.* 2001).

Six 1 × 1 m ‘patches’ were selected within each site in which to sample for invertebrates. At control sites these patches were selected on the basis that they were highly suitable for superb lyrebirds to forage (see criterion (d) above). At lyrebird sites, three patches were selected where there were visible signs of lyrebird scratching and digging (disturbed patches). To provide a strong test of the effects of lyrebird presence, the most recent and heavily disturbed areas present at the site were selected using an ordinal score (0 to 3: Table 4.2). Three patches with no visible lyrebird disturbance on the surface and covered by an intact leaf litter layer were also selected. Both Ashton and Bassett (1997) and the results from Chapter 3 showed that it takes around a year for the leaf litter layer to reform in this forest type. Although these patches are henceforth referred to as ‘undisturbed’ to distinguish them from the recently disturbed patches, the lack of distinct separation between the humus layer and the mineral topsoil layer and

loose cultivated soil in these patches indicated that they had been disturbed in the past (Ashton and Bassett 1997, Ashton and Attiwell 1994). The fact that they had been previously disturbed meant that these patches provided an appropriate test for the magnitude of impact at the site level and were not simply areas that were avoided by superb lyrebirds as unsuitable for foraging. They also provide a test of the duration of the effect of lyrebird disturbance on invertebrate assemblages.

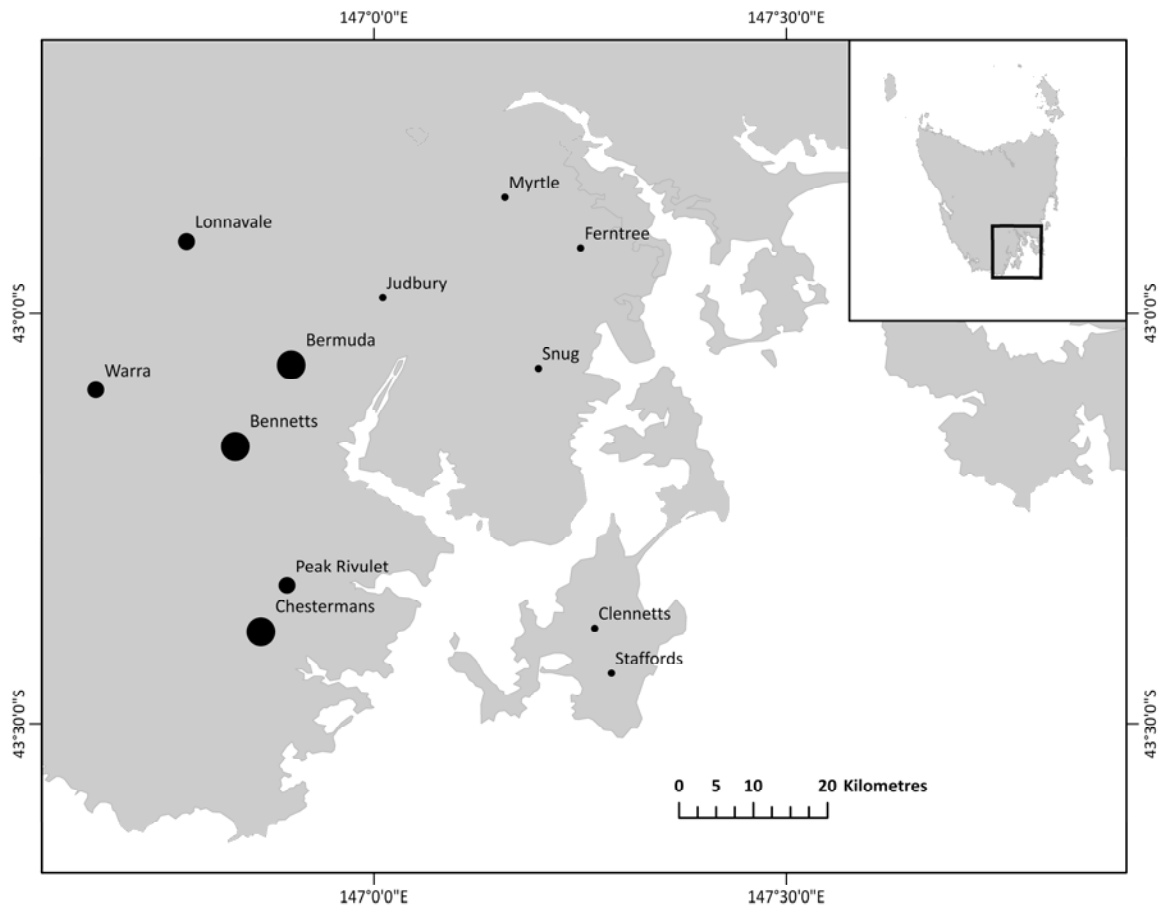


Figure 4.1: Map of southeastern Tasmania, Australia showing the locations of the twelve field sites: three sites with high intensity disturbance by superb lyrebirds (*Menura novahollandiae*) (●) three sites where medium disturbance by superb lyrebirds (●) and six sites where superb lyrebirds were absent (●).

Table 4.1: Site environmental characteristics. Mean monthly rainfall was calculated for 2009 from the Australian Bureau of Meteorology data recorded at the meteorological station nearest to each study site. Vegetation community was determined using Tasmanian Vegetation Monitoring and Mapping Program maps (TASVEG Version 1.3, Department of Primary Industries and Water 2001, Harris and Kitchener 2005). Aspect identifies the downslope direction of the maximum rate of change in elevation. The values are the compass direction of the aspect. Hill shade analysis provides a measure of the average degree of shadow at the site by considering the effects of the local horizon in relation to the dominant sun angle and sun elevation. Areas in complete shadow have a value of zero. Areas in no shadow have a value of 255. Slope identifies the gradient in degrees, or rate of maximum change in elevation at the site. Slope, aspect code, hill shade and elevation were derived using geographical information system software (ESRI ArcGIS 10.0). †GDA 94.

Site Control/ Lyrebird	Longitude †	Latitude †	Elevation (m) †	Aspect Code (°)	Slope (°)	Hill shade	Geology	Mean Monthly Rainfall (mm)	Vegetation Community
Ferntree Control	147°15'03"E	42°55'15"S	490	252	21	133	Triassic quartz sandstone	149.5	<i>Eucalyptus regnans</i> forest and woodland
Myrtle Control	147°09'32 "E	42°51'34"S	550	282	7	178	Jurassic dolerite	100.8	<i>Eucalyptus regnans</i> forest
Snug Control	147°11'58"E	43°04'01"S	362	167	28	235	Triassic quartz sandstone	118.3	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)
Judbury Control	147°00'39"E	42° 58'51"S	400	272	22	105	Jurassic dolerite	93.7	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)
Staffords Control	147°17'17"E	43°26'17"S	210	115	7	189	Jurassic dolerite / Triassic siltstone	107.2*	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)

Site Control/ Lyrebird	Longitude †	Latitude †	Elevation (m) †	Aspect Code (°)	Slope (°)	Hill shade	Geology	Mean Monthly Rainfall (mm)	Vegetation Community
Clennetts Control	147° 16' 04"E	43° 23' 01"S	110	120	14	202	Jurassic dolerite / Triassic quartz sandstone	107.2*	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)
Lonnavale Lyrebird	146°46'22"E	42°54'46"S	477	213	15	162	Jurassic dolerite	74.4	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)
Peak Rivulet Lyrebird	146°53'41"E	43°19'54"S	160	272	26	99	Triassic lithic sandstone	126.1*	<i>Eucalyptus obliqua</i> with broad leaf shrubs
Warra Lyrebird	146°39' 47"E	43°05'35"S	171	133	21	103	Jurassic dolerite / Permian Sandstone	169.2	<i>Eucalyptus obliqua</i> with broad leaf shrubs
Chestermans Lyrebird	146°51' 47"E	43°23'17"S	220	84	34	88	Permian sandstone	126.1*	<i>Eucalyptus obliqua</i> with broad leaf shrubs
Bermuda Lyrebird	146°53'59"E	43°03'47"S	542	76	15	144	Jurassic dolerite	70.4*	<i>Eucalyptus regnans</i> forest
Bennetts Lyrebird	146°49'49"E	43°09'34"S	436	262	17	225	Jurassic dolerite	104.6	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)

4.3.2.1 Environmental variables

At each site, the environmental variables considered most likely to affect both superb lyrebirds and the invertebrate assemblages were quantified along a 30×2 m transect as follows. The percentage cover of the canopy, midstorey and understorey strata were visually estimated using a modified Braun-Blanquet index (Mueller-Dombois and Ellenberg 1974); specifically, 0 = 0% 1 = <1%, 2 = 2–5%, 3 = 6–25%, 4 = 26–50% 5 = 51–75% and 6 = 76–100%. The Braun-Blanquet index was also used to assess the proportion of the following ground cover types: nonvascular plants + bryophytes, and rock. Average leaf litter depth along transects was visually estimated using the Tasmanian Forest Practices Authority classification codes: thin = < 10 mm, medium = 10–30 mm, deep > 30 mm (Meggs and Munks 2003, Forest Practices Authority 2005). Basal area of trees was used as a proxy for stand density and size structure of the forest community, and was recorded using a Bitterlich basal wedge. The average cross-sectional area in square metres of all trees with wood greater than 10 mm diameter was determined by measuring approximately 1.3 m above ground using the angle count sampling method at the middle of the transect (Braithwaite *et al.* 1989, Forest Practice Authority 2005). Within each patch selected for sampling, I recorded the litter depth (average from two measurements made with a ruler) and soil and litter moisture (calculated as weight loss after oven drying at 70°C for 48 hours).

Table 4.2: Scores for assessing the intensity and age of superb lyrebird (*Menura novaehollandiae*) disturbance in sample plots.

Score	Intensity	Age
0	No disturbance	No disturbance
1	Light: -Leaf litter layer partially broken or removed. -Scratching 10-40 mm deep -Limited mixing of leaf litter and topsoil	Old: > 1– 2 months -Fallen leaf litter and debris has accumulated over scratching -Seedlings may have started to germinate -Buried vegetation has turned brown
2	Medium: -Scratching 40-80 mm deep -Litter layer has been broken and mixed partially with topsoil -Some mineral soil exposed on surface	Medium: 2 weeks-1 month -Exposed mineral soil has been weathered, evidence of rain-wash -Some fallen leaf litter over diggings
3	Heavy: -Scratching to depth of 150 mm -Litter layer partially to completely broken, removed or incorporated with topsoil -Mineral soil exposed on surface	Recent: <2 weeks -Freshly turned over, moist soil on surface, not compacted, no indication of rain-wash -No mosses, shoots, or seedlings growing in scratched out patches -No fallen leaves on scratching -Displaced and buried vegetation still green

4.3.2.2 Invertebrate Sampling

Within each of the six 1×1 m patches at a site, two samples of leaf litter and soil (each from an area of approximately 0.5×0.5 m) were collected for the extraction of macroinvertebrates and mesoinvertebrates into 2 L Ziploc bags, yielding a total of 12 samples per site. Superb lyrebirds create two types of disturbance when foraging: bare areas where leaf litter has been scratched away exposing the mineral soil, and areas of mixed leaf litter and mineral soil that are created as the birds kick dislodged material behind them. (Adamson *et al.* 1983, Robinson and Frith *et al.* 1981, Ashton and Bassett 1997; see Chapter 3). Hence equal amounts of material from both types of disturbance were collected in each sample. Samples were placed in cool boxes for transport to the laboratory where they were hand sorted for macroinvertebrates (> 2 mm) in white plastic trays within 8 hours of collection. Specimens were preserved immediately in 80% alcohol with 2% glycerol. After hand sorting for macroinvertebrates, samples were placed in Tullgren funnels under 40W incandescent light globes for 7 days (Behan-Pelletier 1999, Bromham *et al.* 1999, Nakamura *et al.* 2007) to extract mesoinvertebrates (Acari and Collembola) and any remaining macroinvertebrates. Hand sorting was used in conjunction with the Tullgren funnels because heat gradient extraction methods are not an effective means of extracting some groups, such as Mollusca and Diplopoda (Krell *et al.* 2005).

Macroinvertebrates were sorted to the lowest taxonomic level feasible, generally species or genus, using relevant keys and consultation with taxonomic specialists (see Appendix 1 for list of resources). Taxonomic knowledge of many soil invertebrates in Australia is poor so morphospecies are commonly used in place of species (Harris *et al.* 2003), particularly for the Coleoptera, Diplopoda and Chilopoda. For Coleoptera, the morphospecies codes used were those of the Forestry Tasmania Insect Collection (TFIC, now housed at the Tasmanian Museum and Art Gallery (TMAG) collection). In addition, the adults and larvae of the same Coleopteran taxa were recorded separately as the habitat preferences and diet of many species differ with life history phase (Lavelle *et al.* 1993). Undescribed Diplopoda and Chilopoda were given standardised sorting codes as per Mesibov (2012). Dipteran larvae, Oligochaeta and Araneae were sorted into size classes based on length for Diptera and Araneae (5 mm, 6–10 mm and >10 mm) and diameter for Oligochaeta (<1 mm, 1–5 mm and >5 mm). Individuals can vary widely in size within these groups: the use of size classes accounted for the possibility that larger

individuals would be more likely to be eaten by superb lyrebirds than very small individuals (Robinson and Frith 1981, Lill 1996). A reference collection of specimens from this study has been deposited with TMAG.

To investigate whether the responses of different components of the macroinvertebrate fauna to the presence of lyrebirds varied, all taxa were classified by their habitat affinities based on literature and expert opinion (see Appendix 1). Those taxa that commonly occur only in leaf litter were classified as leaf litter dwelling specialists, while taxa that occur in the soil or have no clear preference for either habitat were classified as generalist/soil dwellers. Generalists were not separated from soil dwellers because taxonomic resolution and information on specific habitat affinities for local species were inadequate. For example, some species of earthworm only live in topsoil while others are leaf litter dwellers, but because the ecology of Tasmanian earthworms is poorly understood (Blakemore 2000), and earthworms were not identified to species, all earthworms were assigned to the ‘generalist/soil dwelling’ group. Mesoinvertebrates were identified to family for Collembola and oribatid mites. All other mites were identified to suborder with the exception of immature Acari, which were identified to subclass (see Appendix 1 for list of habitat classification of macroinvertebrates).

4.3.3 Statistical analysis

4.3.3.1 Environmental parameters

To establish if any environmental variables co-varied with the presence or absence of lyrebirds, a Principal Components Analysis (PCA) of normalised environmental variables recorded from each site transect was undertaken using PRIMER-E 6 software (Clarke and Gorley 2006). Because underlying environmental conditions might be confounded with lyrebird activity, all measures of lyrebird disturbance were excluded from analysis as well as cover of leaf litter and exposed mineral soil as they were likely to be directly influenced by lyrebird activity. Canopy cover was also excluded because values were the same at every site.

4.3.3.2 *Invertebrate analyses*

Invertebrates assemblages were analysed in three data sets: (1) measures of macroinvertebrate assemblage structure (taxonomic richness, abundance and evenness (Pielou's J' : Pielou 1966, Magurran 1988); (2) the abundance of leaf litter dwelling and generalist/soil dwelling macroinvertebrates; (3) descriptors of mesoinvertebrate assemblage structure (as for macroinvertebrate assemblage). Firstly, this established whether there was a difference between response variables at lyrebird and control sites using a two factor Analysis of Variance (ANOVA) to examine all response variables (with the exception of species richness) using the following design: 'Lyrebird Status' (fixed factor with 2 levels: 'lyrebird' and 'control'), with 'Site' (random, $n = 6$) nested within each level of Lyrebird Status. Because species richness was positively linearly related with the logarithm of abundance, log abundance was added as a covariate to this design using Analysis of Covariance (ANCOVA). Secondly, all disturbed patches at lyrebird sites were excluded from the data sets and assessed whether assemblages in undisturbed patches at lyrebird sites differed from assemblages at control sites using the same design as above. Thirdly, data from lyrebird sites only was used to test whether assemblages at undisturbed and disturbed patch types at lyrebird sites differed. If there were significant differences, the interaction between disturbance intensity and patch type was examined to establish whether the nature or magnitude of lyrebird impact on invertebrate assemblages in patches was dependent on site-level disturbance intensity. The three-factor ANOVA/ANCOVA design included 'Disturbance Intensity' (fixed factor with 2 levels: 'medium' and 'high') with Site (random $n = 3$) nested in Disturbance Intensity and 'Patch Type' (fixed with 2 levels: 'undisturbed' and 'disturbed'). Prior to conducting analyses, abundance was logarithmically transformed and species richness was square root transformed to meet the assumptions of normality and variance. Assumptions were checked using standard diagnostics (Quinn and Keough 2002). All univariate analyses were performed in statistical platform R version 2.15.2 (R Development Core Team, 2012).

Permutational Multivariate Analyses of Variance (PERMANOVA) (Anderson 2001) were used to assess differences in macroinvertebrate and mesoinvertebrate assemblage composition between lyrebird and control sites and to compare composition of undisturbed and disturbed patches at the high and low intensity lyrebird sites. In addition, PERMANOVA analyses were conducted based on macroinvertebrate habitat

affinity data because the assemblages contained a large number of rare taxa that were only found at single sites and which could potentially mask a lyrebird effect. The design was the same as described for the univariate analyses and was based on Bray-Curtis similarity matrices calculated from square root transformed abundance data (with all singletons removed) for macroinvertebrates or fourth root transformed data for mesoinvertebrate data in order to down weight the influence of numerically dominant taxa. The PERMANOVA was run over 9999 permutations under a reduced model. Where there were few unique values, the Monte Carlo asymptotic *P*-value was referred to for the test statistic (Anderson 2005). These and all subsequent multivariate analyses were performed using the statistical software package PRIMER v 6.1 (Clarke and Gorley 2006). The PERMDISP function (Anderson 2004) was used to test the homogeneity of multivariate dispersion among samples and their group centroids (Anderson *et al.* 2006, Anderson *et al.* 2008). The taxa that contributed most to the dissimilarities between lyrebird sites and control sites, disturbance intensities and patch types were identified using a similarity percentages routine (SIMPER) (Clarke and Warwick 2001). The overall relationship between assemblages was then visually examined using a nonmetric multidimensional scaling ordination (nMDS, Clarke 1993).

4.4 Results

4.4.1 Environmental variables

The PCA showed that there was considerable variation between sites but there was no indication of any consistent underlying differences in environmental conditions between lyrebird and control sites that could potentially confound the results of the invertebrate analyses (Fig 4.2). PC1 (which explained 24.4% of the variation) had positive loadings for hill shade, understorey and site level litter cover and negative loadings for slope, rainfall and rock cover. PC2 explained 18.9% of the variation and had positive loadings for site level litter depth, elevation, shrub cover and negative loadings for understorey cover, non-vascular cover and slope.

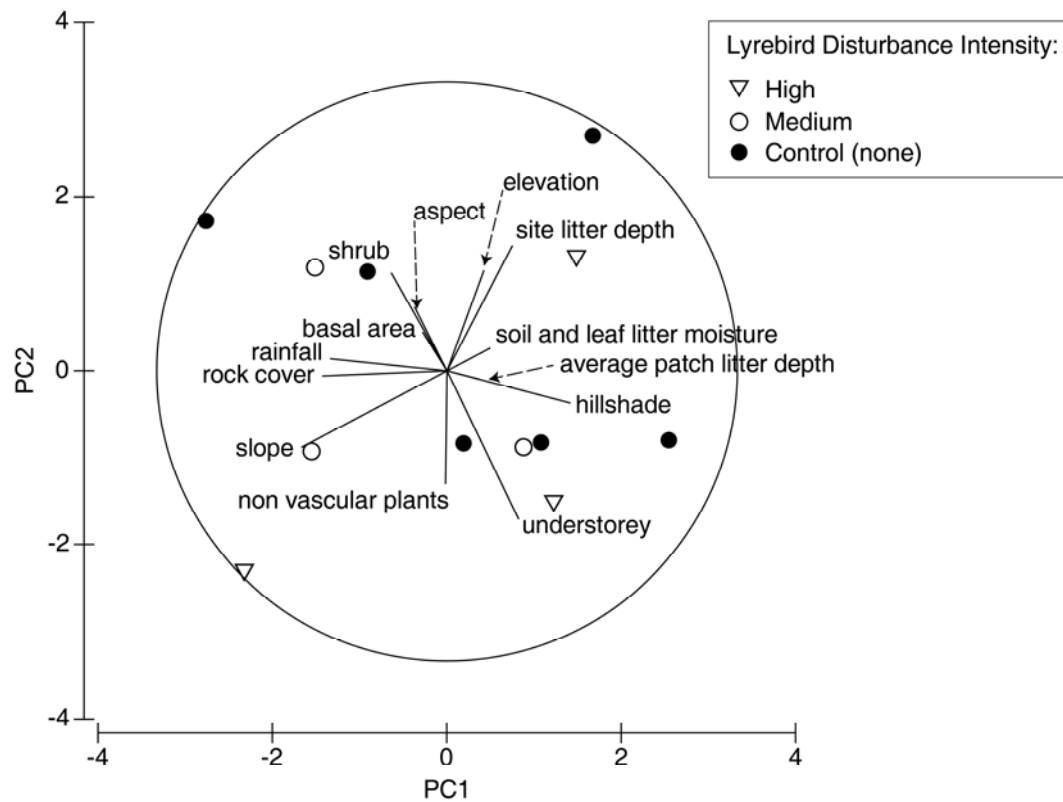


Figure 4.2: Principal Components Analysis (PCA) of site-level environmental parameters. Factors that were likely to be directly affected by superb lyrebirds (*Menura novaehollandiae*) were excluded. PC1 explained 24.4% of the total variation and PC2 explained 18.9% of the total variation). Vector length represents their relative importance in accounting for variation between sites (i.e. longer = more important).

4.4.2 Univariate analysis

4.4.2.1 Macroinvertebrates

A total of 11,593 individuals belonging to 213 macroinvertebrate taxa were collected, of which just under a quarter of taxa were singletons (51). Forty-six taxa were found exclusively at control sites while 47 were found only at lyrebird sites. Six higher taxonomic groups accounted for 72% of total abundance: Diptera larvae (19.2%), Coleoptera (17.1%), Amphipoda (13.46%), Oligochaeta (8.4%), Hemiptera (7.62%) and Araneae (5.9%). All invertebrate groups collected were present in both lyrebird and control groups, with the exception of the neanurid Collembola, which were absent from the control group. However, only four neanurid individuals were collected overall, and only from one lyrebird site, so it was impossible to make any inferences about the distribution of this group in response to the presence of superb lyrebirds. Similarly, when taxa from all disturbed and undisturbed patches at all lyrebird sites were compared, all but two higher taxonomic groups were collected in both patch types across sites. Nemertea and Plecoptera were both absent from disturbed patches but again, only a handful of individuals (<5) of each were collected in total.

Overall, taxonomic richness was significantly higher at control sites than at lyrebird sites (mean richness 23.3 and 19.6 respectively) (ANCOVA $F_{1,10} = 5.07$ $P = 0.045$). However, this difference was driven by the disturbed samples at lyrebird sites, as the comparison between undisturbed patches and control site samples was non-significant (ANCOVA $F_{1,8} = 0.25$ $P = 0.628$). Similarly, the difference in the abundance of macroinvertebrates across all samples from lyrebird and control sites approached significance (ANOVA $F_{1,10} = 3.61$ $P = 0.086$), but samples from control sites and undisturbed patches at lyrebird sites did not differ (ANOVA $F_{1,10} = 0.76$ $P = 0.404$). Conversely, evenness did not vary when all samples were considered (ANOVA $F_{1,10} = 1.61$ $P = 0.234$), but the difference between undisturbed samples at lyrebird sites and control site samples did approach significance (ANOVA $F_{1,10} = 3.40$ $P = 0.095$). This was because distribution of individuals across taxa was more similar at lyrebird sites (i.e. more even) than at control sites (lyrebird sites mean=0.86 versus control sites mean=0.82).

Within lyrebird sites, the interaction between site disturbance intensity, patch type (disturbed, undisturbed) and the relationship between log abundance and taxonomic

richness was significant (ANCOVA $F_{1,64} = 4.65$ $P = 0.034$). Simple effects tests showed that richness was significantly lower in disturbed patches than in undisturbed patches at high disturbance sites (ANCOVA: $F_{1,31} = 75.79$ $P < 0.0001$) and medium disturbance sites (ANCOVA: $F_{1,31} = 7.60$ $P = 0.009$). However, the difference between the patch types was much greater at high disturbance sites (disturbed patch mean = 15.5, undisturbed patch mean = 25.6, Fig 4.3a) than at medium disturbance sites (disturbed patch mean = 15.4, undisturbed patch mean = 18.1). Interestingly however, there were more taxa present in relation to the number of individuals in disturbed patches at medium disturbance intensities (Fig 4.3a).

The interaction between site disturbance intensity and patch type approached significance for abundance (ANOVA: $F_{1,64} = 2.85$ $P = 0.09$) and the simple effects showed that undisturbed patch types contained many more individuals than disturbed patches. At high disturbance intensity sites there were almost twice as many individuals in undisturbed patches (ANOVA $F_{1,32} = 75.79$ $P = 0.0003$, disturbed mean = 53.2, undisturbed mean = 99.4, Fig 4.3b). The same pattern occurred at medium disturbance intensities but was less pronounced (ANOVA $F_{1,32} = 5.33$ $P = 0.027$, disturbed mean = 36.3, undisturbed mean = 49.2). For evenness, neither the interaction between site disturbance intensity and patch type nor the main effects were significant, although evenness was slightly higher at medium intensity disturbance sites (ANOVA $F_{1,32} = 0.94$ $P = 0.337$, mean disturbed: 0.87, undisturbed 0.88) than at high intensity disturbance sites (ANOVA $F_{1,32} = 1.86$ $P = 0.181$, mean disturbed: 0.81, undisturbed 0.84, Fig 4.3c).

Generalist/soil dwellers did not differ significantly between lyrebird and control sites (ANOVA $F_{1,10} = 0.001$ $P = 0.976$). When only the undisturbed patches from lyrebird sites were compared with control sites, there was also no difference (ANOVA: $F_{1,10} = 1.09$ $P = 0.321$). Among lyrebird sites, there was a weak interaction between disturbance intensity and patch type (ANOVA $F_{1,64} = 3.27$ $P = 0.075$). Disturbance intensity did not have a significant effect on abundance (ANOVA $F_{1,4} = 1.42$ $P = 0.299$), but there was a strong difference in abundance between patch types (ANOVA $F_{1,64} = 17.27$ $P < 0.0001$). The simple effects tests showed that at both high and medium disturbance intensities, disturbed patches supported far fewer generalist/soil dwellers than undisturbed patches. The difference was largest at high disturbance intensities

(ANOVA $F_{1,32} = 13.54$ $P = 0.0008$) where mean abundance in undisturbed patches was more than double that of disturbed patches (45 and 21 respectively). The effect size of patch type was smaller at medium intensity sites (ANOVA $F_{1,32} = 4.01$ $P = 0.053$) and abundances in both patch types (disturbed: 16.6, undisturbed: 22.3, Fig 4.4a) were lower than at high disturbance intensity sites.

Leaf litter dwellers were strongly affected by the presence of lyrebirds. The mean number of leaf litter dwellers in samples from control sites was around twice that in samples at lyrebird sites (mean: 57.4 and 28.5 respectively) (ANOVA $F_{1,10} = 9.69$ $P = 0.011$). There was also a significant difference in the abundance of leaf litter dwellers between undisturbed patches from lyrebird sites and control sites (ANOVA $F_{1,10} = 4.87$ $P = 0.05$), which was driven by much higher numbers of individuals at control sites (control sites mean: 57, lyrebird sites mean: 35, Fig 4.4b). Among lyrebird sites, the interaction between site disturbance intensity and patch type was not significant but there was a significant difference between the two patch types (ANOVA $F_{1,64} = 17.27$ $P = 0.0006$). There were close to twice as many individuals in the undisturbed patches as in the disturbed patches (undisturbed mean: 50, disturbed mean: 28, Fig 4.4b). At high disturbance intensities, the number of leaf litter dwellers in undisturbed patches differed from undisturbed patches (ANOVA $F_{1,32} = 10.38$ $P = 0.002$) but at medium intensity sites the relationship only approached significance (ANOVA $F_{1,32} = 3.39$ $P = 0.07$). Overall, the numbers of leaf litter dwellers were higher in both patch types at high disturbance intensity sites (disturbed mean = 28.2 undisturbed mean = 50.2) than in either patch type at medium intensity sites (disturbed mean = 18, undisturbed mean = 25).

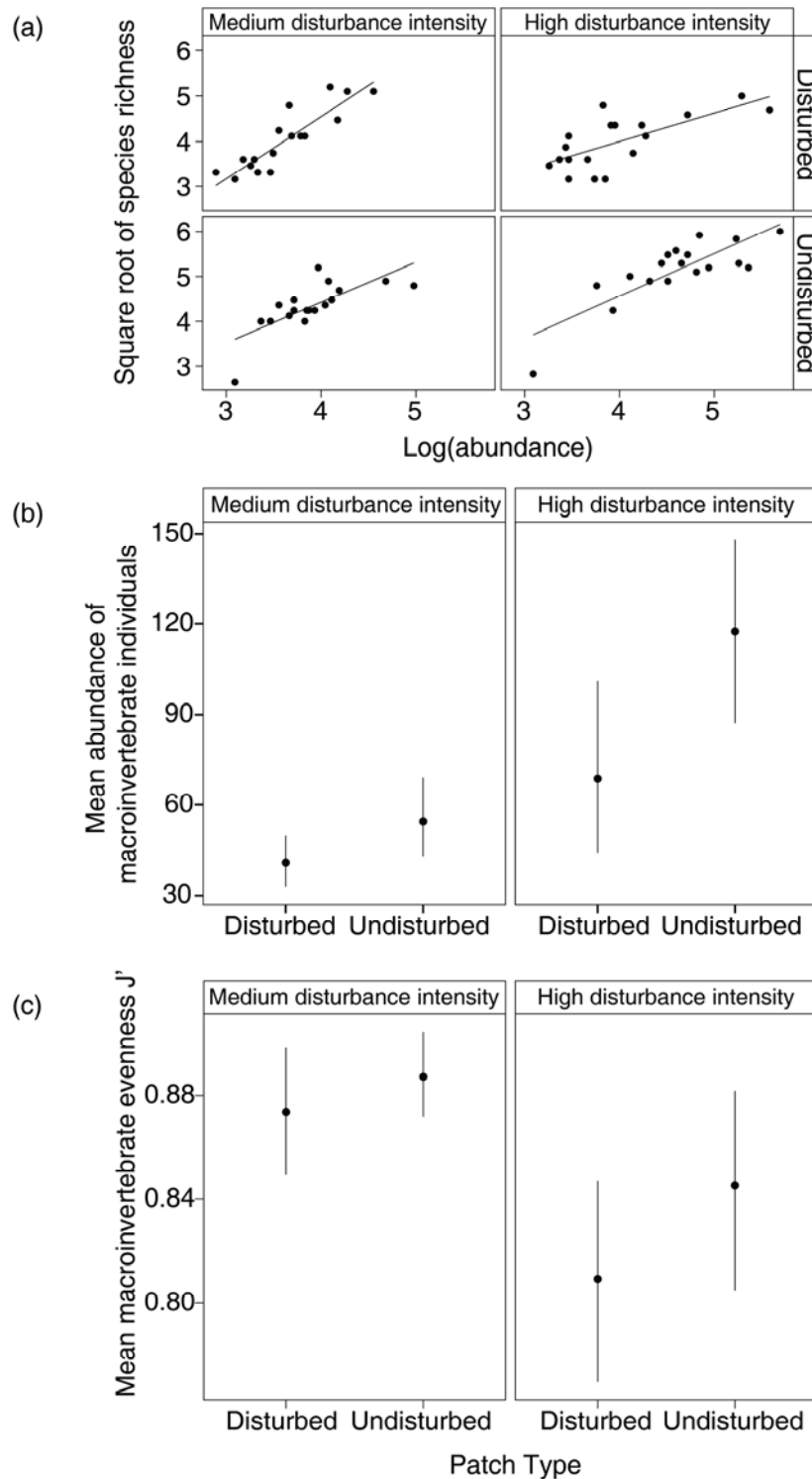


Figure 4.3: Plots of mean taxonomic richness (a) abundance (b) and evenness (c) of macroinvertebrates in disturbed and undisturbed patches at sites with medium and high intensity of disturbance by superb lyrebirds (*Menura novaehollandiae*). Plots are mean fitted values with 95% bootstrapped confidence intervals.

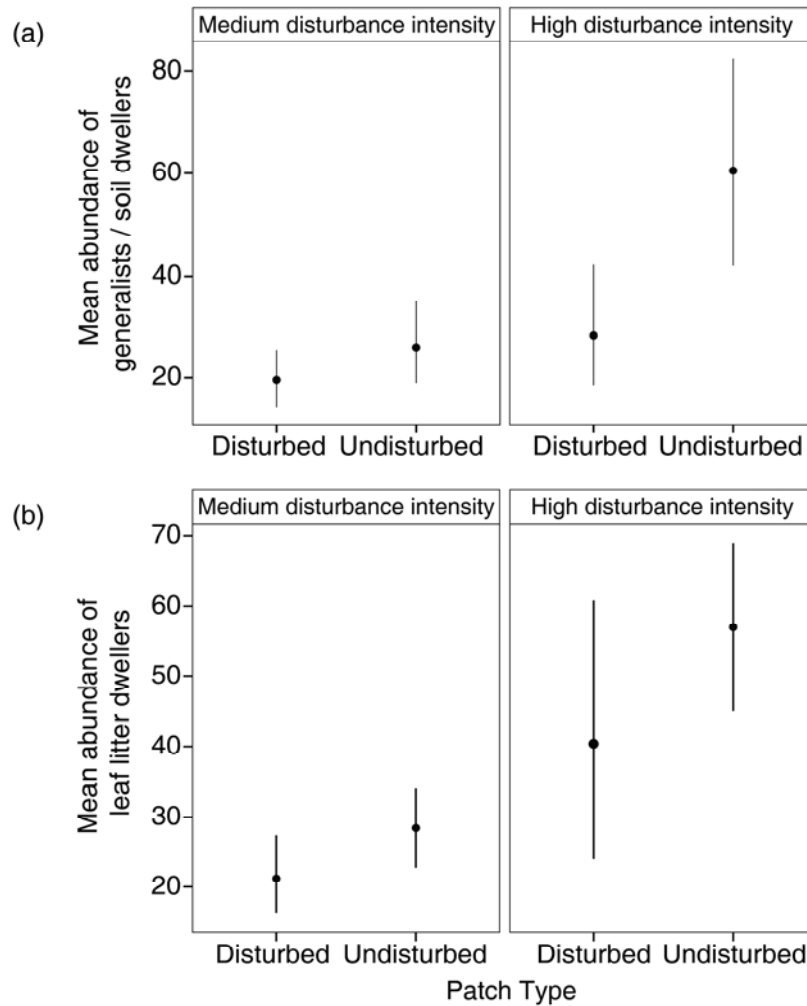


Figure 4.4: Mean abundance of generalist/soil dwelling macroinvertebrates (a) and leaf litter dwelling macroinvertebrates (b) in disturbed and undisturbed patches at sites with medium and high intensities of disturbance by superb lyrebirds (*Menura novaehollandiae*). Plots are mean fitted values with 95% bootstrapped confidence intervals.

4.4.2.2 Mesoinvertebrates

A total of 15,518 individuals from 15 taxonomic groups were collected from the study sites including three families of Collembola (Poduridae, Sminthuridae and Entomobryidae) along with six families of detritivorous oribatid Acari (including a group of unidentified immature oribatids), four groups of predatory Acari from the mesostigmatid and prostigmatid suborders and one primitive group, *Stomacarus*. Podurid Collembolans accounted for about a third (5,745) of all individuals. All taxonomic groups were collected from both lyrebird and control sites with the exception of *Stomacarus*, which was found only at lyrebird sites. However, as only four individuals were collected in the whole survey it is not possible to draw any conclusions about factors controlling distribution of the group. Within lyrebird sites, all taxonomic groups were present in each patch type.

When all samples from lyrebird and control sites were considered, there were no differences in taxonomic richness, abundance or evenness associated with the presence or absence of lyrebirds (richness: ANOVA $F_{1,10} = 0.43$ $P = 0.526$, abundance: ANOVA $F_{1,10} = 0.57$ $P = 0.467$, evenness ANOVA: $F_{1,10} = 0.24$ $P = 0.631$). Likewise, there was no variation in any measure of assemblage structure between control sites and undisturbed patches at lyrebird sites (taxonomic richness ANCOVA: $F_{1,10} = 0.34$ $P = 0.571$, abundance ANOVA: $F_{1,10} = 0.076$ $P = 0.78$, ANOVA evenness: $F_{1,10} = 0.038$ $P = 0.849$).

Within lyrebird sites, the interaction between disturbance intensity, patch type and log abundance for taxonomic richness was also non-significant (Fig 4.5a, ANCOVA $F_{1,64} = 0.374$ $P = 0.543$). Further, there were no significant differences for either main effects, but this was to be expected because taxonomic resolution for mesoinvertebrates was low. In contrast, there was a significant interaction between site disturbance intensity and patch type for abundance (ANOVA $F_{1,64} = 6.231$ $P = 0.015$) as well as for the main effect of patch type ($F_{1,64} = 5.558$ $P = 0.021$). Mean abundance at high disturbance intensity sites was more than twice that in undisturbed patches (Fig 4.5b mean 73 and 31 respectively) (ANOVA $F_{1,64} = 8.383$ $P = 0.006$). However, at medium disturbance sites, the mean number of individuals in patches of each type was almost identical ($F_{1,64} = 0.016$ $P = 0.941$; undisturbed mean = 60.7 versus disturbed mean = 61.2). Finally, the interaction between site disturbance intensity and patch type for

evenness approached significance ($F_{1, 64} = 4.145$ $P = 0.094$) because evenness in the two patch types at high disturbance intensity sites differed significantly (Fig 4.5c, ANOVA $F_{1, 32} = 4.63$ $P = 0.039$; disturbed = 0.8, undisturbed 0.7) while there was no difference between patches at medium intensity sites (ANOVA $F_{1, 32} = 0.115$ $P = 0.737$; mean of 0.8 in both patch types).

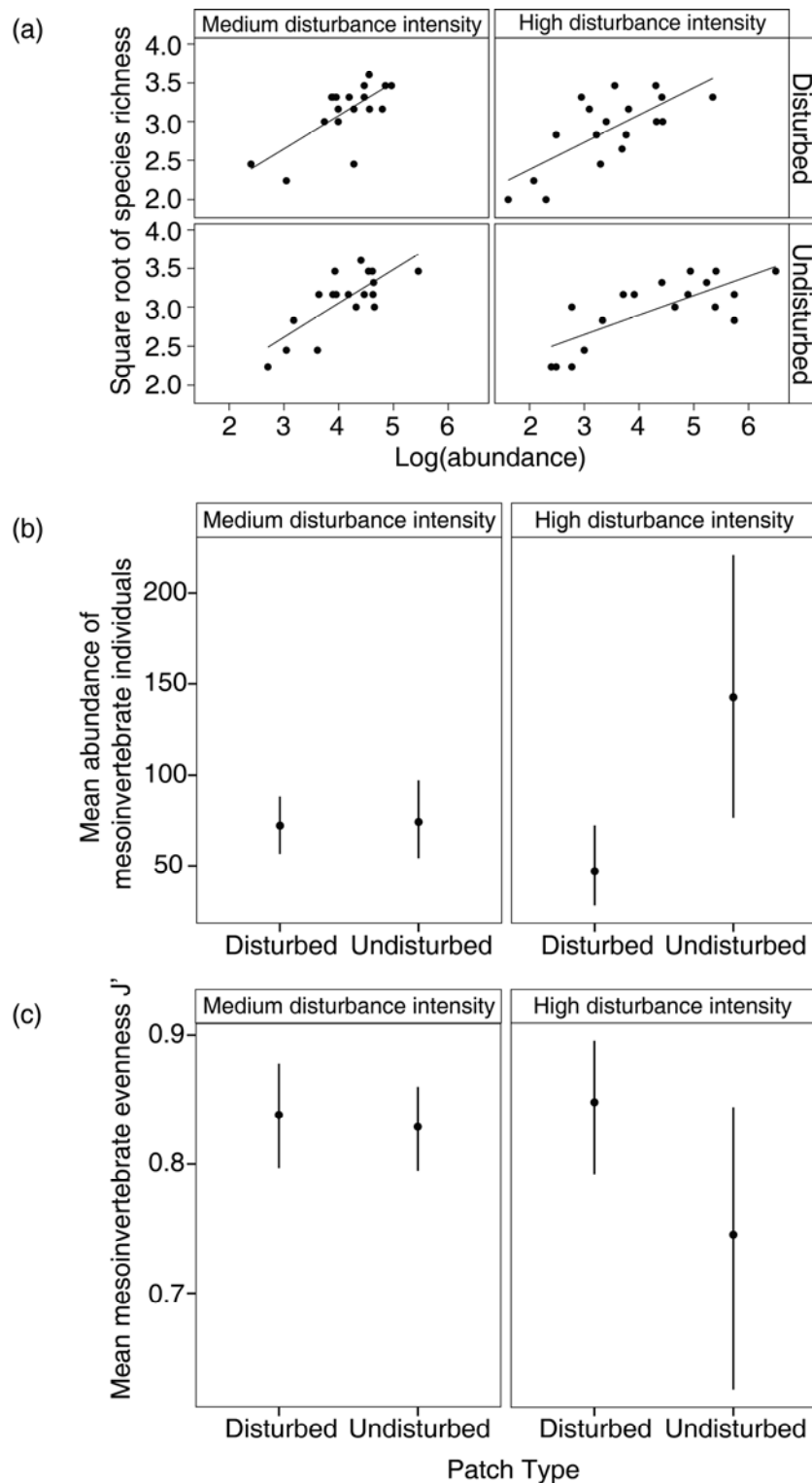


Figure 4.5: Mean taxonomic richness (a), abundance (b) and evenness J' (c) of mesoinvertebrates in disturbed and undisturbed patches at sites with medium intensity disturbance by superb lyrebirds (*Menura novaehollandiae*) and high intensity superb lyrebird disturbance. Plots are mean fitted values with 95% bootstrapped confidence intervals.

4.4.3 Multivariate analysis

4.4.3.1 Macroinvertebrates

Overall, there was a significant difference between lyrebird and control sites (PERMANOVA $F_{1,132} = 1.71$ $P = 0.036$) and the PERMDISP showed that the level of dispersion within each group of sites differed significantly ($F_{1,142} = 36.74$ $P = 0.0001$). The disturbed patches at lyrebird sites drove the overall difference between assemblages because there was no strong difference when only samples from undisturbed patches at lyrebird sites were compared to control samples (PERMANOVA $F_{1,10} = 1.48$ $P = 0.098$). The PERMDISP showed a significant difference in the amount of variation among assemblages within the groups of lyrebird and control sites ($F_{1,106} = 7.0602$ $P = 0.014$). The average distance from the group centroid at control sites (43.8 SE 0.6) was less than at lyrebird sites (46.1 SE 1.08). The higher level of dispersion at lyrebird sites indicated that there were probably differences between assemblages at high and medium intensity sites.

There was no significant interaction between the two main effects of site disturbance intensity (medium, high) and patch type (disturbed, undisturbed) (PERMANOVA $F_{1,60} = 1.009$ $P = 0.455$). The analysis of lyrebird sites showed that there was a significant difference between undisturbed and disturbed patch types (PERMANOVA $F_{1,60} = 2.22$ $P = 0.01$). The PERMDISP comparing the average distance from the group centroids of the samples from undisturbed and disturbed patches was significant, which supported this interpretation (PERMDISP $F_{3,68} = 3.12$ $P = 0.05$). The difference between medium and high disturbance intensity sites approached significance (PERMANOVA $F_{1,4} = 1.66$ $P = 0.08$). The PERMANOVA comparing patch types at high intensity sites was significant (PERMANOVA $F_{1,30} = 2.37$ $P = 0.021$), but there was no difference between patch types at medium intensity sites (PERMANOVA $F_{1,30} = 0.93$ $P = 0.528$). The nMDS of lyrebird sites showed some grouping of samples from high and medium intensity sites as well as considerable variation among the samples from each patch type within the two groups (reflected by the relatively high stress level of 0.24, Fig 4.6).

The SIMPER routine found that only four taxa contributed more than 3% each to the overall differences between differences between samples from control sites and from undisturbed samples at lyrebird sites (Table 4.3). This reflected the prevalence of rare taxa and the fact that few individual taxonomic groups were found in high numbers

across multiple sites. Of the four taxa, two, *Keratroides vulgaris* (Amphipoda), a leaf litter dweller, and a species of Coccoidea (Hemiptera), a generalist/soil dweller, were more abundant at control sites. The remaining two taxa, large and small Diptera larvae (generalist/soil dwellers) were most common at lyrebird sites. Similarly, the SIMPER identifying the taxa contributing to differences between undisturbed and disturbed patches at lyrebird sites found that all of the taxa that contributed more than 3% to dissimilarity were soil dwellers and were more common in undisturbed patches than disturbed patches (Table 4.4). When the remainder of the taxa that contributed to the dissimilarity were examined, a small number of taxa were more common in recently disturbed patches than in undisturbed patches. These included two species of staphylinid beetle (*Atheta* TFIC sp. 03 and *Osirius* TFIC sp. 1), staphylinid larvae and *Stenurytion* centipedes, suggesting that these taxa may be disturbance specialists (for full list see Appendix 2).

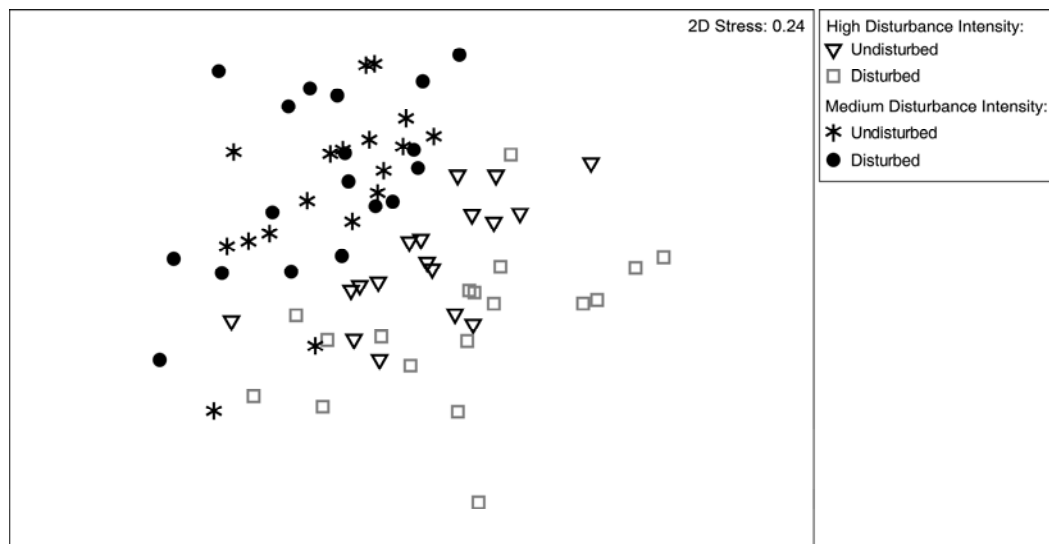


Figure 4.6: Non-metric multidimensional scaling (nMDS) ordination based on a Bray-Curtis similarity matrix of square-root transformed macroinvertebrate abundance data from undisturbed and disturbed patches of the forest floor at sites with medium and high intensity disturbance by foraging superb lyrebirds (*Menura novaehollandiae*).

Table 4.3: Summary of SIMPER on abundance data showing the macroinvertebrate taxa which contributed most (more than 3%) to the dissimilarity between sites with superb lyrebirds (*Menura novaehollandiae*) and control sites without. Overall dissimilarity between lyrebird and control sites was 71.03%. L = leaf litter dwelling G/S = generalist /soil dwelling. Higher abundances are in bold.

Class/Order	Taxa	Habitat Affinity	Control Sites	Lyrebird Sites	% Contribution to Assemblage Differences	% Cumulative Contribution
			Average Abundance	Average Abundance		
Amphipoda	<i>Keratroides vulgaris</i>	L	5.48	1.28	4.43	4.43
Diptera	5 mm Diptera	G/S	4.37	6.15	3.83	8.26
Hemiptera	Coccoidea sp.	G/S	3.42	0.20	3.25	11.52
Diptera	10 mm Diptera	G/S	0.85	3.50	3.20	14.72

Table 4.4: Summary of SIMPER on macroinvertebrate abundance data showing the taxa which contributed most to the dissimilarity between disturbed and undisturbed patches from sites with superb lyrebirds (*Menura novaehollandiae*) and samples from control sites without. Overall average dissimilarity between assemblages in disturbed and undisturbed patches was 72.05. L = leaf litter dwelling G/S = Generalist soil dwelling. Higher abundances are in bold.

Class/Order	Taxa	Habitat Affinity	Undisturbed Patches	Disturbed Patches	% Contribution to Assemblage Differences	% Cumulative Contribution
			Average Abundance	Average Abundance		
Diptera	<5 mm Diptera	G/S	6.15	2.89	4.30	4.30
Diptera	>10 mm Diptera	G/S	3.50	0.76	3.64	7.93
Diptera	6-10 mm Diptera	G/S	4.00	1.64	3.59	11.52
Annelida	1 mm Oligochaeta	G/S	1.82	1.37	3.30	14.82
Annelida	2-5 mm Oligochaeta	G/S	2.56	0.69	3.01	17.83

4.4.3.2 Mesoinvertebrates

Overall, the composition of mesoinvertebrate assemblages among control sites did not differ significantly (PERMANOVA $F_{1,132} = 0.63$ $P = 0.688$). Control samples and

samples from undisturbed patches at lyrebird sites also did not vary significantly

(PERMANOVA $F_{1,10} = 0.767$ $P = 0.738$, PERMDISP: $F_{1,106} = 1.028$ $P = 0.372$).

Within the lyrebird sites, the interaction between disturbance intensity and patch type was significant (PERMANOVA $F_{1,4} = 0.076$ $P = 0.04$) and examination of patches

within high and medium intensity groups of sites revealed that the difference in composition between disturbed and undisturbed patches was weakly significant at sites

with high disturbance intensity (PERMANOVA $F_{1,30} = 3.32$ $P = 0.07$) but not at

medium disturbance intensity sites (PERMANOVA $F_{1,30} = 0.31$ $P = 0.371$).

Unsurprisingly, the nMDS of samples from high and medium disturbance intensity sites showed considerable overlap between samples from the two patch types (Fig 4.7).

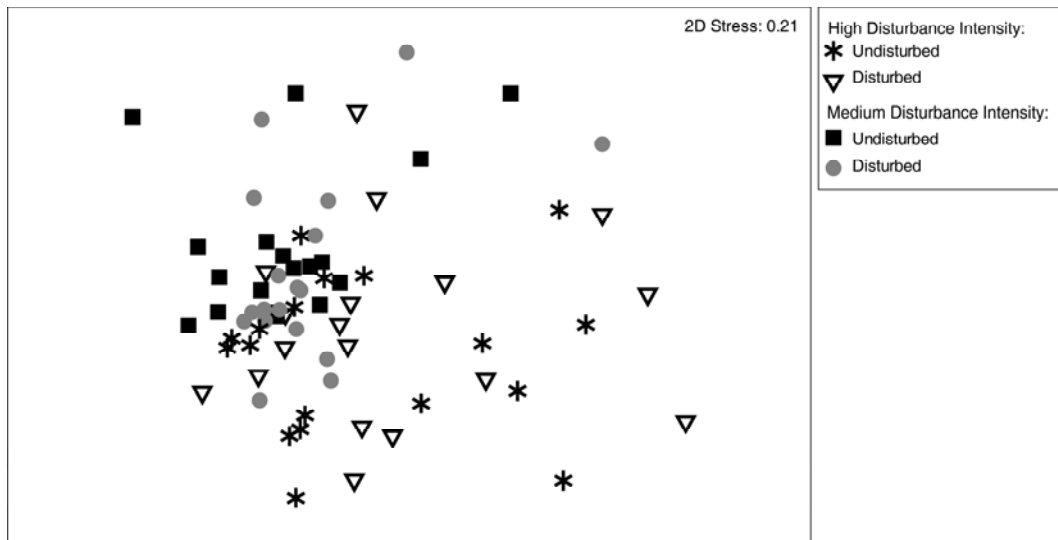


Figure 4.7: Non-metric multidimensional scaling (nMDS) ordination based on a Bray-Curtis similarity matrix of square-root transformed mesoinvertebrate abundance data from undisturbed and disturbed patches of the forest floor at sites with medium and high intensity disturbance by foraging superb lyrebirds (*Menura novaehollandiae*).

4.5 Discussion

Understanding the effects of non-native species on native biota at different spatial scales is essential for the accurate assessment of their current and future impact (Ross *et al.*

2003, Ujvari *et al.* 2011). Despite the fact that soil and leaf litter invertebrate

communities are characterised by high spatial variability in structure and composition (Ettema and Wardle 2002), few studies to date have explicitly examined the impact of non-native animals on these communities at different spatial scales. The results of this study showed that presence of superb lyrebirds was associated with distinct patterns in invertebrate assemblage structure and composition that varied across different spatial scales, disturbance intensities and components of the invertebrate fauna.

As this was an observational survey it is not possible to establish a definitive causal link between the activities of superb lyrebirds and the observed patterns in invertebrate assemblages. However, by carefully selecting similar sites in terms of environmental conditions and biota the likelihood of confounding factors that may be responsible for the results are greatly reduced. It was not possible to predict where the birds would feed so I could not sample before and after disturbance. However, I ensured that patches from which samples were collected were able to provide a strong test of superb lyrebird effect by (a) selecting the positions to take samples at control sites based on the microhabitat criteria thought to be responsible for the selection of foraging points by superb lyrebirds (Robinson and Frith 1981, Ashton and Bassett 1997) and (b) comparing recently disturbed patches at lyrebird sites with patches that had been disturbed in the past. Therefore, it was unlikely that the patches at control sites and the undisturbed samples at lyrebird sites were in some way unsuitable for superb lyrebirds to feed in or supported dramatically different fauna from that of recently disturbed patches prior to that disturbance.

4.5.1 Assemblage structure and composition

The presence of superb lyrebirds was associated with reduced abundance and richness of invertebrates at small spatial scales. While predation may partially explain these results, the effects of habitat modification and disturbance are likely to be important. When habitat is destroyed or substantially modified by ecosystem engineers the effect on resident biota is often negative, at least at small spatial scales (Crooks 2002). Ecosystem engineering of the forest floor by other non-native species has been found to alter invertebrate assemblages. For example, invasive earthworms in North American forests remove large areas of the leaf litter layer from the forest floors, thereby homogenising the forest floor environment and reducing the abundance of litter dwelling invertebrates (Migge-Kliean *et al.* 2006).

At larger spatial scales, taxonomic richness may increase in the presence of an ecosystem engineer because the net effect of the engineer is to create a mosaic of engineered and non-engineered habitat patches where, in addition to the species contained in the non-engineered patches, additional species capable of exploiting the new habitat may also establish (Crooks 2002, Wright 2009). In fact, a small number of taxa did appear to respond positively to superb lyrebird disturbance or the resulting new habitat: two species of staphylinid beetle (*Atheta* TFIC sp. 03 and *Osirus* TFIC sp. 01), immature staphylinid beetles, and *Steneurytion* centipedes were more common in disturbed patches than in undisturbed patches at lyrebird sites. Although ecological knowledge regarding Tasmanian staphylinids is limited, some species are known to be disturbance specialists, and so could explain the higher number of the three staphylinid groups in disturbed patches. These taxa feed on mesoinvertebrates and possibly benefit from reduced competition for food due to the low numbers of other macroinvertebrate predators (Fountain-Jones, N. UTAS pers comm). *Steneurytion* centipedes that inhabit both leaf litter and soil (Mesibov 2012) may have benefited from disturbed soil because scratching is likely to increase soil porosity and reduce bulk density, thereby making it easier to burrow (Bromham 1999, Schon *et al.* 2010). However, these few exceptions aside, there was no evidence of significant increases in taxonomic richness at any spatial scale.

Overall, macroinvertebrates were more strongly affected by the presence of superb lyrebirds than mesoinvertebrates, which was unsurprising for three reasons. Firstly, predation as well as the effects of disturbance and habitat modification may directly affect macroinvertebrates whereas mesoinvertebrates are generally too small to be directly affected by predation (Lill 1996). Secondly, several studies of the impact of stock grazing, tillage and other forms of soil disturbance on invertebrates have found that small-bodied taxa are better able to cope with the disturbance, compaction and turnover of soil than larger invertebrates that can be damaged or killed by disturbance or are unable to burrow in the compacted soil (e.g. Abbott 1979, Wardle 1995, Bromham *et al.* 1999, Wardle *et al.* 2001). Thirdly, the absence of a significant difference in mesoinvertebrate taxonomic richness between sites with and without lyrebirds may simply be a reflection of the fact that taxonomic resolution for this group was low (because taxonomic information, particularly for Tasmanian Acari, is limited). Further research may reveal that there are species-level differences in mesoinvertebrate

assemblages: other non-native species such as feral pigs and introduced earthworms that modify the structure of forest soil and leaf litter in similar ways to the superb lyrebird are known to reduce species richness of Collembola (Vtorov 1993) and oribatid mites (Burke *et al.* 2011).

Community evenness in many ecosystems is reduced by invasive species and other environmental impacts because the altered conditions tend to favour only a small number of species that are then able to exploit modified conditions and, in the absence of many competitors or predators, are able to reach high numbers (Wardle 2002). In contrast, while evenness in the assemblages in this study was high overall, evenness of both macroinvertebrate and mesoinvertebrates assemblages actually increased in the presence of superb lyrebirds. This pattern may reflect that under natural conditions, the highly diverse soil and leaf litter assemblages are typically categorised by a small number of very abundant species and a large number of rare species (Bardgett *et al.* 2005). Superb lyrebird foraging had the effect of reducing the abundances of common taxa thereby making the distribution of individuals across the taxa present more equal.

As predicted, leaf litter dwelling macroinvertebrates were more strongly affected by the presence of superb lyrebirds than were generalists and soil dwellers. This could be a reflection of predation on animals such as amphipods (thought to be a favoured prey; Lill 1996, Yen 2001), which dominated the macroinvertebrate fauna at sites without lyrebirds. However, many generalist/soil dwellers such as earthworms and Dipteran larvae are also important prey (Robinson and Frith 1981, Smith 1988, Lill 1996), so it is more likely that the low numbers of leaf litter dwellers were due to the reduction in the cover of leaf litter habitat that occurs as a result of lyrebird foraging. In analogous studies, researchers have found that feral pig predation and soil disturbance did not significantly reduce earthworm populations despite representing an important source of food for feral pigs (Mitchell *et al.* 2007, Elledge 2011, Taylor *et al.* 2011).

4.5.2 Scale-dependence of impact

The relationship between superb lyrebirds and invertebrate assemblages was strongest at the smallest spatial scale (patches), but the magnitude of impact depended on whether or not the patch had been disturbed recently. In fact, assemblages in undisturbed patches at sites with superb lyrebirds were generally more similar to assemblages at other sites without lyrebirds than to disturbed patches only a matter of metres away. While the impact was extreme across small spatial scales it was detectable but far less intense at local and landscape scales. At the local scale (within sites) the magnitude of impact was linked to the intensity of lyrebird disturbance across the site. As predicted, when sites with medium and high levels of superb lyrebird disturbance at the site level were compared, the differences in structure and composition between undisturbed and disturbed patches were greatest at high disturbance intensity sites. However, abundance and richness were lower in both patch types at medium intensity sites than at high intensity sites. This was unexpected because in general, intermediate disturbance intensity and engineering activity are thought to enhance abundance and richness (Badano *et al.* 2006, Wright 2009 but see Wardle 1995).

Two possible explanations for the patterns in invertebrate assemblages observed at local scales are as follows: firstly, that the intensity of superb lyrebirds activity at the sites in this study was driven by the amount of invertebrate prey available at sites. Thus, medium intensity sites may have naturally supported lower numbers of invertebrates than high intensity sites. A second possibility is that superb lyrebirds actually increase numbers of invertebrates by disturbance (in effect farming them) following an initial decline in recently disturbed patches. This scenario has been suggested to occur in the natural range of the superb lyrebird (Adamson *et al.* 1983) but has not been demonstrated experimentally. However, if ‘farming’ occurred, higher abundances would be expected in the patches that had not been recently disturbed by lyrebirds than were present at sites without superb lyrebirds, but this was not the case. Thus, it is more likely that the lower abundance and richness recorded at medium disturbance intensity sites reflect the lower numbers of invertebrates that these sites supported compared to high intensity sites. It is unclear why this is the case given that there were no obvious consistent differences in environmental conditions between groups of sites at the time of sampling. One possibility is that past events such as drought at some sites may have influenced the invertebrate assemblages present at the medium intensity sites.

At the broader spatial scale that is, between sites, the magnitude of impact depended on which component of the assemblage was considered. Only the abundance of leaf litter dwellers differed significantly between undisturbed samples and control sites (the strongest test of a large-scale impact). In all other respects, patches that had not been disturbed for some time supported assemblages that were similar to those at sites without lyrebirds. This indicates that it is unlikely that superb lyrebirds would, by themselves, have a serious large-scale impact on invertebrate assemblages in this forest type. In part, these findings support those of a number of recent studies on the impacts of non-native plants that have found that significant reductions in species abundance and richness at local scales are often not manifested at larger (landscape) spatial scales and may rarely lead to extinction in the short term (Gurevitch and Padilla 2004, Powell *et al.* 2013). The reason behind this pattern is largely a sampling effect; simply, that more species will be encountered as the area sampled increases (Gilbert and Levine 2013, Powell *et al.* 2013). In addition, because sampling in this study was stratified between patches that had not been disturbed for some time and recently disturbed patches, it is possible to observe the duration of the impact of superb lyrebirds. The impact on invertebrates appears to be relatively short-lived, generally lasting less than 12 months.

Given the extent of foraging disturbance, even at high intensity disturbance sites there appear to be sufficient areas at varying degrees of recovery for the majority of species to persist. However, it remains to be seen whether the reduction in abundance and richness at small scales reduces the overall resilience and persistence of invertebrates in the face of other stressors such as forestry activity in what is known as an extinction debt (Tilman *et al.* 1994, Vellend *et al.* 2006). Threatened endemic fauna with restricted geographic ranges may be at particular risk of extinction via this process, and warrant targeted investigation. In addition, this study was necessarily restricted (for logistical reasons) to one forest type occurring on similar bedrock: wet sclerophyll forest on dolerite and or sandstone, but superb lyrebirds are able to inhabit a wide range of forest types including dry sclerophyll forest and rainforest growing on limestone parent material (Higgins *et al.* 2001). It is possible that the magnitude of lyrebird impact on invertebrate communities could vary with environmental factors. Thus, further research of the effect of lyrebirds on invertebrate communities across a range of forest types in Tasmania is needed to determine their impact on the scale of the island. Finally, even if

the impact of superb lyrebirds on biota is relatively small, this does not preclude the possibility that their disturbance of the forest floor alters ecosystem processes such as decomposition and nutrient cycling. A quantitative assessment of the impact of the superb lyrebird on soil ecosystem functioning is required before the magnitude of the impact this species has on Tasmanian forest ecosystems, as a whole can be determined.

In conclusion, this study highlights the importance of including multiple scales in order to detect patterns of impact of non-native species. If sampling had only been carried out at large spatial scales, it is unlikely that the important small-scale patterns among patch types would have been detected. Likewise, if the study had only been conducted across small spatial scales it is possible that the impact of superb lyrebirds at larger spatial scales may have been over estimated. Linking the fine scale inter-patch dynamics to landscape patterns was the key to understanding the capacity of the superb lyrebird to influence native invertebrates. Therefore, given the inherent spatial variability of soil communities, it is perhaps more critical here than in many other ecosystems to incorporate spatial scale into observational or experimental designs in order to understand the threat posed by non-native species.

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Chapter 5: Effects of a non-native bird on ecosystem processes

5.1 Abstract

In terrestrial ecosystems the majority of studies that have investigated the influence of non-native species on ecosystem function have concerned non-native plants. Much less is known about the effects of non-native animals, particularly birds. This study examined the effect of the non-native superb lyrebird (*Menura novaehollandiae*) on soil ecosystem processes in the temperate forests of Tasmania, Australia. The superb lyrebird is a forest-dwelling predator of detritivorous invertebrates and also conspicuously alters the forest floor habitat through widespread disturbance of leaf litter and soil when foraging. Thus the superb lyrebird could potentially alter soil ecosystem processes through direct effects such as modification of the physical structure of soil and distribution of organic matter and indirect effects such as changing the abundance and richness of invertebrates. The influence of the superb lyrebird on decomposition potential, soil respiration (CO₂ efflux) and soil nitrogen availability (ammonium, nitrate and total inorganic nitrogen) was assessed using a two year exclosure experiment at two sites with superb lyrebirds and two sites beyond their current range (control sites). The only process clearly influenced by superb lyrebirds was decomposition, which was greater in areas scratched by superb lyrebirds than areas from which they were excluded. The availability of ammonium, nitrate and total inorganic nitrogen was lower at sites with superb lyrebirds than at sites without them. While there were no differences in nitrogen availability between the three experimental treatments (unfenced plots, fenced exclosures, fenced + hand-raked exclosures), it is possible that superb lyrebirds have a long-term effect on nutrient availability at sites and that the two year period of exclusion was not sufficiently long for concentrations within exclosures to increase. In contrast, soil respiration and pH did not vary with the presence or absence of superb lyrebirds although the former was strongly influenced by season. While this study demonstrates that non-native birds are capable of altering at least some ecosystem processes, it is argued that in the case of the superb lyrebird, the overall effect on ecosystem function is likely to be limited.

5.2 Introduction

Some non-native species can alter the structure and function of entire ecosystems; although their effects on native biota have been extensively studied (Vitousek 1990, Simberloff 2011), quantitative assessment of effects on ecosystem function are comparatively rare (Crooks 2002, Ehrenfeld 2010). In terrestrial ecosystems, most of the work regarding impact of non-native organisms on ecosystem functioning has focused on non-native plants (see reviews by Ehrenfeld 2003, Liao *et al.* 2008, Vilà *et al.* 2011) while studies on the impacts of non-native animals are uncommon (Wardle *et al.* 2009). Nonetheless, a small but growing body of research has demonstrated that non-native animals can influence ecosystem functioning by altering processes such as biogeochemical cycling (Fukami *et al.* 2006), decomposition (Krull *et al.* 2013) and community respiration (Bohlen *et al.* 2004a) through a number of direct and indirect pathways (Ehrenfeld 2010).

Non-native animals can indirectly influence ecosystem processes through trophic interactions such as predation or competition. For example, Fukami *et al.* (2006) and Wardle *et al.* (2009) found that introduced rats on offshore islands profoundly changed nutrient dynamics through predation on seabirds, which reduced the input of nutrients to the islands. Similarly, non-native populations of the little red fire ant (*Wasmannia auropunctata*) reduced the abundance of native macroinvertebrate detritivores, thereby slowing the rate of leaf litter decomposition (Dunham and Mikheyev 2010). Introduced herbivores such as moths (Lovett *et al.* 2006) and ungulates (Wardle *et al.* 2001, Stritar *et al.* 2009) can, through selective feeding, reduce plant biomass and community composition, which in turn can alter the quality, quantity and decomposability of leaf litter with flow-on effects on nutrient cycling (Siemann *et al.* 2009.)

Some non-native animals can directly influence ecosystem processes by ecosystem engineering, i.e. altering the physical structure of the environment, the availability and quality of resources and the frequency and intensity of disturbance regimes (*sensu* Jones *et al.* 1994, 1997). For example, ecosystem engineering by non-native earthworms in previously worm-free forest soils in North America have dramatically modified a number of ecosystem processes (Burtelow *et al.* 1998, Bohlen *et al.* 2004b). Earthworms change the physical structure of the forest floor and alter the availability of

resources to the decomposer community by incorporating leaf litter into the mineral soil profile which changes microclimatic conditions in the soil, infiltration capacity and bulk density (Fisk *et al.* 2004, Straube *et al.* 2009). These changes have been shown to improve conditions for the microbial community with a subsequent increase in the speed of decomposition, soil respiration and nutrient cycling (Bohlen *et al.* 2004b). Trophic effects and ecosystem engineering are not mutually exclusive: some species may influence ecosystem processes through a combination of both mechanisms (Simberloff 2011). For example, browsing ungulates can not only influence soil processes through the effects of herbivory on plant communities but also alter the structure of the soil environment through trampling and soil compaction (which can reduce infiltration and decrease soil oxygen levels) and alter nutrient input and distribution through their urine and faeces (Wardle *et al.* 2001).

Despite the introduction of around 900 species of bird to areas beyond their natural range worldwide (Dyer and Duncan unpublished data 2012), there has been little investigation of their impact on ecosystem function (Temple 1992, Blackburn *et al.* 2009). For example, even though populations of non-native waterfowl can have visually obvious impacts on ecosystem structure through grazing on plants and nutrient input via faeces deposition (Allin and Husband 2003, Tatu *et al.* 2007), the ramifications of their activities on ecosystem processes have rarely been examined (but see Best 2008). The present study addresses this knowledge gap by investigating the influence of the non-native superb lyrebird (*Menura novaehollandiae*) on ecosystem processes in the temperate forests of Tasmania, Australia. The superb lyrebird was introduced to Tasmania in the 1930s in an effort to conserve it from the perceived threat of predation by the European fox (*Vulpes vulpes*) and habitat loss within its natural range in eastern mainland Australia (Sharland 1952). Since then, the bird has spread throughout much of the forest area in the south of the state (Smith 1988, Tasmanian Parks and Wildlife Service Natural Values Atlas unpublished data 2012, BirdLife Tasmania unpublished data 2012).

Superb lyrebirds are generalist predators of invertebrates that forage for prey by scratching and digging leaf litter and soil with their powerful feet and claws to depths of 150 mm (Adamson *et al.* 1983, Ashton and Bassett 1997). Disturbance incorporates leaf litter into the mineral soil, thereby increasing the level of organic material in the soil

and reducing bulk density and increasing porosity (Adamson *et al.* 1983, Mitchell and Humphreys 1987, Ashton and Bassett 1997). Ashton and Bassett (1997) estimated that in some forest types within their native range, individual superb lyrebirds could turnover 200 tonnes per hectare per years of soil. This incorporates leaf litter into the mineral soil, increasing its availability to the soil microbial community and hence its rate of decomposition. They suggested that increased decomposition might accelerate nutrient cycling in forests where superb lyrebirds were present. Because large native insectivores and soil bioturbators are uncommon in wet eucalypt forest in Tasmania (Claridge and Barry 2000, Mallick and Dreissen 2009), the superb lyrebird has the potential to alter ecosystem processes by disturbing the forest floor and preying on detritivorous invertebrates. There is particular concern that the superb lyrebirds may alter ecosystem functioning of the forests whose natural values contributed to the establishment of the Tasmanian Wilderness World Heritage Area (TWWHA). (Mallick and Dreissen 2009).

Researchers have recommended that studies on the effects of non-native species on ecosystem function are most informative when they investigate several indicators of ecosystems processes at once (Ehrenfeld 2010, Strayer 2012). A species may influence some but not all processes so that a multifactorial approach is the best way to detect impact. Thus, I used a two-year field exclosure experiment to measure the magnitude and direction of the effect of superb lyrebirds on decomposer community potential, soil respiration, soil pH and nitrogen availability. Differences between fenced and unfenced treatments at lyrebird sites may indicate a lyrebird effect on processes, while the comparison between the two treatments at control sites provided a test for the presence of a caging effect not related to the presence of lyrebirds. To separate the effects of ongoing disturbance by superb lyrebirds from a single recent disturbance event, fenced plots were compared with plots that were hand-raked and fenced.

Based on the evidence from native populations of superb lyrebirds, I hypothesised that the birds would increase the rate of decomposition, the availability of nitrogen and alter pH. In addition, I hypothesised that soil respiration (CO₂ efflux) would increase in plots that were disturbed either by lyrebirds or simulated lyrebird disturbance (hand-raking) because disturbance of soil stimulates microbial activity (Luo and Zhou 2006), a major contributor to respiration. Finally, I predicted that there would be large seasonal effects

on respiration and decomposition because both are strongly influenced by temperature and soil moisture (Sigurdsson and Magnusson 2010).

5.3 Methods

5.3.1 Study area

The experiment was conducted between February and November 2009 using experimental plots that had been set up in April 2008 as part of another study on superb lyrebirds (see Chapter 3) in wet sclerophyll forests of southern Tasmania, Australia (Fig 5.1). The region has a temperate climate (mean daily minimum of 7.5 ° C and maximum of 16 ° C in 2009 (Bureau of Meteorology 2009) and average rainfall in the region was approximately 1200 mm during 2009 (Bureau of Meteorology 2009). The study area contains locations where superb lyrebirds are present that are in close proximity to suitable habitat that is immediately beyond their current range but share the same forest type, geology and faunal species composition. I selected four sites (two sites with superb lyrebirds and two control sites immediately beyond the current range of superb lyrebirds) located no more than 60 km apart.

To reduce variation in environmental conditions between sites, a spatial multi criteria analysis (using ESRI ArcGIS software) was conducted to choose sites that were similar in terms of vegetation community composition and structure, forest history (forestry and fire), geology, climate, elevation, slope, aspect and accessibility. The forests at each site consisted of an overstorey consisting of *Eucalyptus obliqua* or *Eucalyptus regnans* with a mixed canopy and understorey of thamnian rainforest and broad-leaved species; the shrub layer and ground cover of forbs and bryophytes were very sparse (Reid *et al.* 1999, Neyland 2001). Underlying geology at sites was either Jurassic dolerite or Triassic sedimentary material (Forsyth *et al.* 1995, Spanswick and Kidd 2000). Soils were well to poorly drained and had gradational texture profiles comprised of loams and clays (Laffan 2001, Laffan and McIntosh 2005). Although there was evidence of selective logging before 1960, the sites had not been subject to clear felling and there was no evidence of major fire in the last 40 years (Stone 1998, Brown, M.J, pers. comm.). A summary of environmental characteristics at each site is provided in Table 5.1. To ensure that open plots were likely to be disturbed by lyrebirds, I selected sites where there had been consistently high levels of lyrebird disturbance in the previous

two years. This was assessed by annual monitoring of a 30m x 2m transect line at each potential site. Sites where >50% of the forest floor along the transect line had been disturbed each year were chosen.

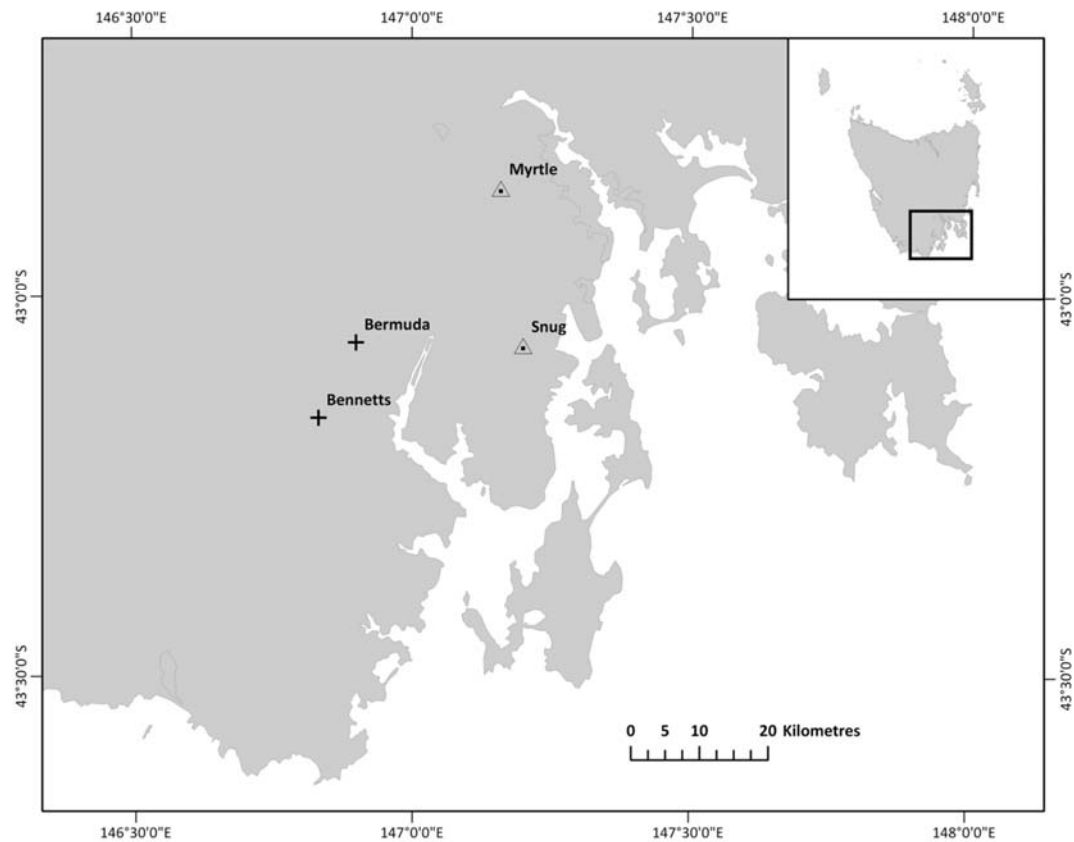


Figure 5.1: Southern Tasmania, Australia showing the locations of the four field sites: two sites where superb lyrebirds (*Menura novahollandiae*) were present (+) and two control sites where superb lyrebirds were absent (Δ).

Table 5.1: Site environmental characteristics. Mean monthly rainfall was calculated for 2009 from the Australian Bureau of Meteorology data recorded at the meteorological station nearest to each study site. Vegetation community was determined using Tasmanian Vegetation Monitoring and Mapping Program maps (TASVEG Version 1.3, Department of Primary Industries and Water 2001, Harris and Kitchener 2005). Aspect identifies the downslope direction of the maximum rate of change in elevation. The values are the compass direction of the aspect. Hill shade analysis provides a measure of the average degree of shadow at the site by considering the effects of the local horizon in relation to the dominant sun angle and sun elevation. Areas in complete shadow have a value of zero. Areas in no shadow have a value of 255. Slope identifies the gradient in degrees, or rate of maximum change in elevation at the site. Slope, aspect code, hill shade and elevation were derived using geographical information system software (ESRI ArcGIS 10.0). †GDA 94.

Site Control/ Lyrebird	Longitude †	Latitude†	Elevation (m) †	Aspect (°)	Slope (°)	Hill Shade	Geology	Mean Monthly Rainfall (mm)	Vegetation Community
Myrtle Control	147°09'32 "E	42°51'34"S	550	282	7	178	Jurassic dolerite	44.3	<i>Eucalyptus regnans</i> forest
Snug Control	147°11'58"E	43°04'01"S	362	167	28	235	Triassic quartz sandstone	58.7	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)
Bermuda Lyrebird	146°53'59"E	43°03'47"S	542	76	15	144	Jurassic dolerite	62.9	<i>Eucalyptus regnans</i> forest
Bennetts Lyrebird	146°49'49"E	43°09'34"S	436	262	17	225	Jurassic dolerite	98.1	<i>Eucalyptus obliqua</i> wet forest (undifferentiated)

Within each site, the location of plots was determined by several factors. Firstly, in forest of this type there is often significant strong variation in microclimate, vegetation and invertebrate communities over the scale of tens of metres (Neyland 2001, Meggs and Munks 2003, Baker *et al.* 2006). Therefore, to minimise local-scale variability (particularly in temperature and moisture) that may lead to inherent differences in ecosystem processes between treatment plots, all plots were located within 10-25 m of a permanent stream in what was identified as ‘slope’ microhabitat, i.e. between the riparian zone and convex landforms (ridges). Observations from mainland studies of superb lyrebirds (Adamson *et al.* 1983, Robinson and Frith 1981) showed that activity was generally heaviest for most of the year in slope microhabitats. Secondly, local climatic conditions at sites were standardised by selecting sites so that all were south, southeast or southwest facing. Finally, I chose sites where vegetation community species composition and cover were as uniform as was possible across the 30 × 20 m area required for the experiment.

5.3.2 Experimental design

The randomised complete block design consisted of four sites, two of which were located in areas with superb lyrebirds (‘lyrebird’ sites) and two in locations not yet invaded by the birds (‘control’ sites). At each of the four sites (each 30 × 20 m, treated as random effects), four blocks (random effects) were set up, within which were nested three 2 × 2 m experimental plots. One quarter of each plot (1 × 1 m) had previously been destructively sampled the previous year and so was excluded from sampling. Plots in each experimental block were randomly allocated to one of three treatments (fixed effect): fenced exclosure, unfenced, and fenced + hand-raked exclosure (simulating lyrebird disturbance). The latter treatment was hand-raked in April 2008.

All plots were set up in areas of medium to deep leaf litter with sparse plant cover at ground-level to ensure conditions were both comparable and of the kind that superb lyrebirds are known to prefer feeding (Robinson and Frith 1981, Ashton and Bassett 1997). In 2008 all plots at lyrebird sites initially contained at least 50% cover of recent medium intensity superb lyrebird disturbance. The age and intensity of lyrebird disturbance was assessed using an ordinal score (0–3: Table 5.2). Unfenced plots were marked at the corners with metal markers while the fenced plots were constructed using 1 m high wire mesh (with a gauge of 10 × 10 mm) and star picket corner posts. A gap of

100 mm was left below the fence to prevent litter building up against the fence and to enable invertebrates and small vertebrates to enter the plots; some larger species may have been excluded. High visibility flagging tape criss-crossed over the plots was used to exclude superb lyrebirds (which are poor flyers) from entering them. In 2008, lyrebird feeding disturbance was simulated in the hand raked and fenced treatments using a three-pronged hand-rake with a span of 150 mm (which is similar to a lyrebird foot) to rake over the leaf litter and soil to a depth of approximately 100 mm in the raked enclosure plots. This disturbance was designed to mimic the scratching of lyrebirds (see Kotanen 1997, Mohr *et al.* 2005 for similar strategies of mimicking soil disturbance by pigs).

Table 5.2: Scores for assessing the intensity and age of superb lyrebird (*Menura novaehollandiae*) disturbance in sample plots.

Score	Intensity	Age
0	No disturbance	No disturbance
1	Light: -Leaf litter layer partially broken or removed. Scratching 10–40 mm deep -Limited mixing of leaf litter and topsoil	Old: > 1–2 months -Fallen leaf litter and debris has accumulated over scratching -Seedlings may have started to germinate -Buried vegetation has turned brown
2	Medium: -Scratching 40–80 mm deep -Litter layer has been broken and mixed partially with topsoil -Some mineral soil exposed on surface	Medium: 2 weeks–1 month -Exposed mineral soil has been weathered, evidence of rain-wash -Some fallen leaf litter over diggings
3	Heavy: -Scratching to depth of 150 mm -Litter layer partially to completely broken, removed or incorporated with topsoil -Mineral soil exposed on surface	Recent: <2 weeks -Freshly turned over, moist soil on surface, not compacted, no indication of rain-wash -No mosses, shoots, or seedlings growing in scratched out patches -No fallen leaves on scratching -Displaced and buried vegetation still green

5.3.2.1 *Decomposition potential*

Cotton strip assays (where a standardised cotton material is placed directly in the soil) were used for measuring the relative activity of soil decomposer organisms, particularly microorganisms, across treatments (Latter and Howson 1977). The advantage of using a standardised form of organic matter such as cotton is that broad-scale comparisons between sites with differing climatic conditions, soil and vegetation can be made (Latter and Walton 1988, Correll *et al.* 1997). A standardised soil burial test fabric (EMPA, St Gallen Switzerland) of unbleached cotton (96% cellulose) with a standard thread count, was used for the assays. Three 35 × 60 mm (100 thread width) cotton strips were cut and inserted horizontally next to each other at the interface between the leaf litter and soil using a broad knife at a randomly selected position within each plot. In the fenced + hand-raked treatments, a hand-rake was used to disturb the soil and leaf litter in the position where strips were about to be placed. After four weeks, the strips were retrieved, washed carefully and air-dried. At the same time, replicate control strips of the same dimensions and also of other widths were washed and air-dried as procedural controls. Tensile strength loss was measured using a tensiometer (University of Tasmania) with digital hand held scales (Salter ElectroSamson, UK) following Latter and Howson (1977). Cotton tensile strength (kg) was measured as the initial breaking point of the cotton strip and reported as the relative tensile strength loss by deducting the tensile strength of the incubated strips from that of the procedural control strips (Clapcott and Barmuta 2009, 2010). Replicate strips from each plot were pooled to obtain a mean value per season for each plot.

5.3.2.2 *Soil respiration*

Soil respiration was measured using the adsorption of CO₂ by soda lime (Grogan 1998) in closed chambers following Keith and Wong (2006). Soda lime is a mixture of sodium and calcium hydroxides that reacts with CO₂ to form carbonates. The difference in weight of the soda lime after 24-hour exposure to CO₂ in a closed chamber can be converted to net CO₂ efflux (a proxy for soil respiration rate). This measurement includes heterotrophic respiration from both soil and litter and autotrophic respiration from fine roots (Luo and Zhou 2006). Soil respiration was recorded in each plot once in autumn, winter, spring and summer in order to account for seasonal variation because respiration is strongly influenced by both temperature and soil moisture (Sigurdsson and

Magnusson 2010). Full details of the technique can be found in Keith and Wong (2006); in brief, an uncovered PVC plastic chamber with a surface area of 0.08 m²) was inserted into the ground in each plot seven days prior to sampling thereby allowing time for any spike in respiration (following the disturbance associated with placing the chambers) to subside. At the same time, the soil and leaf litter in the position where the chamber was to be placed in hand-raked + disturbed plots was hand-raked to simulate recent lyrebird disturbance. After 7 days, respiration was measured over a 24-hour period: a glass petri dish containing 50g of oven dried (105°C for 14 hours) soda lime pellets (SofnoDive 797, granule size 1.0-2.5 mm, Molecular Products, UK) that had been rewetted with 8 ml of water was placed on a raised wire mesh stand (so as not to obstruct CO₂ efflux) in each chamber before attaching the gas tight lid. After 24 hours the dishes were collected and sealed for transport to the laboratory where they were once again oven dried. Three blank chambers with sealed bases were used at each site at the time of measurement to assess absorption of atmospheric CO₂ by soda lime during the procedure and subsequent drying and reweighing of the soda lime. Average weight gain by the soda lime in blanks was averaged and then subtracted from the weight of lime in each chamber to provide a measure of daily CO₂ adsorption.

5.3.2.3 Nutrient availability

The availability of ammonium, nitrate and total inorganic nitrogen (the sum of ammonium and nitrate; TIN) of soils in treatment plots was determined using the ion exchange resin (IER) bag method (Hart and Firestone 1989). Thirty grams of mixed bed ion exchange resin beads (J.T. Baker, Phillipsburg, NJ, USA; Hart *et al.* 1994) was placed into individual nylon stocking bags; three bags were buried at a depth of 10cm in each plot. After a four-month incubation the bags were retrieved and placed in individual paper bags and air dried before extraction using 100 ml 2M KCl. The filtered extracts were then frozen until analysis of ammonium and nitrate on a Lachat AE flow-injection auto-analyser (Hart *et al.* 1994; Lachat Industries, Inc., Loveland, CO, USA). In addition a sample of air-dried resin that had not been incubated was oven dried at 70° C for 48 hours so that final data could be expressed as oven dried mass. To determine pH within each plot, two 500 g soil samples were randomly collected, homogenised and air dried before mixing with 0.01M CaCl₂ and measured with a pH meter (Hendershot *et al.* 1993; Orion 720A series Thermo Fisher Scientific, Inc., Waltham, MA, USA).

5.3.3 Statistical analysis

Four sites (randomly selected) were nested within 'Lyrebird Status' (fixed factor, two levels: 'Lyrebird' and 'Control'). Within each site were four randomly selected blocks, each block divided into three plots. Each plot within each block was then assigned at random to one of three treatments (fixed factor, three levels: 'Fenced ', 'Fenced + hand-raked ' and 'Unfenced'). For decomposition potential and soil respiration, each plot was sampled once in each of four seasons (fixed, levels: 'Autumn', 'Winter', 'Spring' and 'Summer') so 'Season' was treated as a repeated measure. For measuring decomposition, three replicate cotton strips were placed together within each plot on each occasion. For nutrient variables measured using ion exchange resin balls, there were no repeated measures, with three replicates placed in each plot in November 2009 and removed after a four-month incubation. Values from replicates within plots were averaged prior to analysis, and the analyses were performed using standard mixed model procedures as implemented in the R package 'nlme' (Pinheiro and Bates 2000). Using this procedure accommodated the occasional missing value resulting from a tree-fall over two exclosures (which was removed and exclosures repaired), lost test materials or spilt soda lime granules. All analyses were conducted using the R software package version R 2.15.2 (R Development Core Team 2012), with assumptions being checked using standard procedures and transformations applied where necessary (Pinheiro and Bates 2000, Quinn and Keough 2002).

Two sets of hypotheses were of interest in the randomised complete block design. Firstly, the interaction term tested whether the responses across treatments differed between lyrebird sites and control sites. Secondly, the responses to the treatments were analysed including two orthogonal *a priori* planned contrasts to determine (1) whether the fenced plots differed from unfenced controls (*i.e.* a caging artefact at control sites and a recovery from lyrebird impact at lyrebird sites) and (2) whether the two fenced treatments differed from each other, which tested for the effect of a once-off recent disturbance effect versus the effect of multiple disturbance events.

5.4 Results

5.4.1 Decomposition potential

Neither of the interactions between season and the other main factors (lyrebird status and treatment) was significant for decomposition potential (both $P > 0.25$) and so any differences between levels of the other factors were consistent over time. The interaction between lyrebird status and treatment was significant ($L_2 = 2.78$, $P = 0.02$); therefore, the differences between the treatments were assessed separately for each level of lyrebird status (i.e. lyrebird versus control). Within control sites, the planned contrast tests showed that there were no significant differences in tensile strength between fenced and fenced + hand-raked or unfenced treatments (all $P \geq 0.10$). However, at lyrebird sites, tensile strength in the unfenced treatments was only about 0.71 of the tensile strength in fenced ($t = 2.07$ $P = 0.05$) (Fig 5.2). There was no difference in tensile strength between fenced and the fenced + hand-raked treatments ($t = 1.10$ $P = 0.29$).

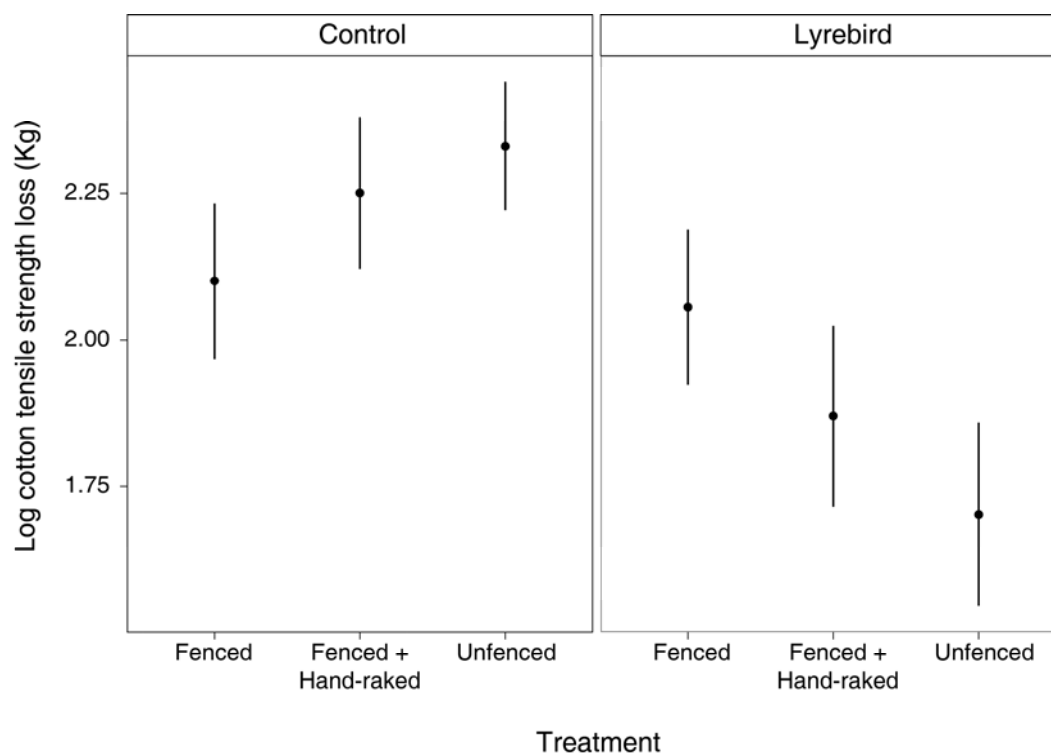


Figure 5.2: Average cotton tensile strength loss in the three treatments (Fenced, Fenced and Hand-raked, and Unfenced) at two sites with superb lyrebirds (*Menura novaehollandiae*) and two sites without them (controls). Error bars indicate the lower and upper 95% confidence intervals of the means.

5.4.2 Soil respiration

Soil respiration was not influenced by the interaction between the presence of superb lyrebirds and treatment and there were no detectable difference in soil respiration across sites with and without lyrebirds and across treatments ($F_{2,42} = 1.19$ $P = 0.31$). However, the rate of soil respiration varied significantly across season ($F_{3,120} = 19.51$ $P < 0.001$) being highest in spring and lowest in winter (mean = 3.84 and 2.29 g C m⁻²day⁻¹ respectively) (Fig 5.3).

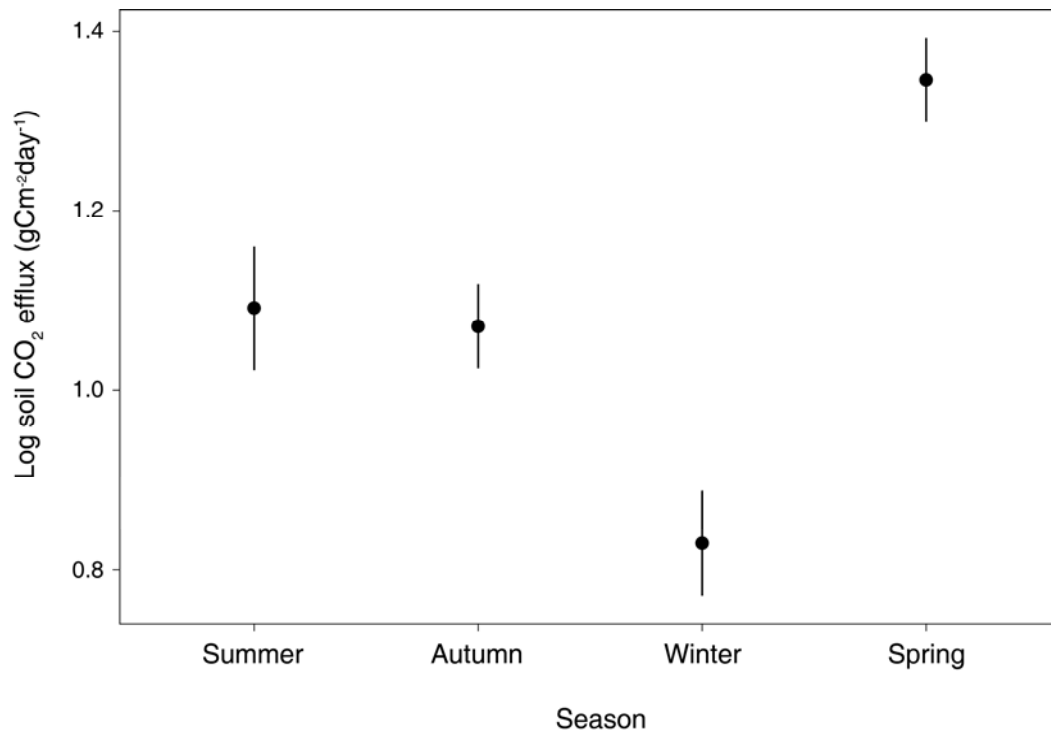


Figure 5.3: Seasonal Mean CO₂ efflux across all sites. The error bars indicate the lower and upper 95% confidence intervals of the means.

5.4.3 Soil nutrients

All measures of nitrogen compounds were significantly higher in concentration at control sites than at lyrebird sites (NH₄: $L_1 = 9.42$, $P = < 0.01$, NO₃: $L_1 = 4.77$, $P = 0.03$, TIN: $L_1 = 7.76$, $P = 0.005$; see Fig 5.4); however, there were no interactions between treatment and lyrebird status, or any effect of treatment. The concentration of NH₄ at lyrebird sites was around a quarter of the concentration at control sites (Fig 5.4) while the concentrations of NO₃ and TIN at lyrebird sites were 60% and 40% of the

concentration at control sites respectively. Soil pH did not vary significantly with lyrebird status or with treatment ($L_5 = 4.84$ $P = 0.45$). Soils were acidic at all sites with a mean pH of 4.57 at control sites and 4.23 at lyrebird sites.

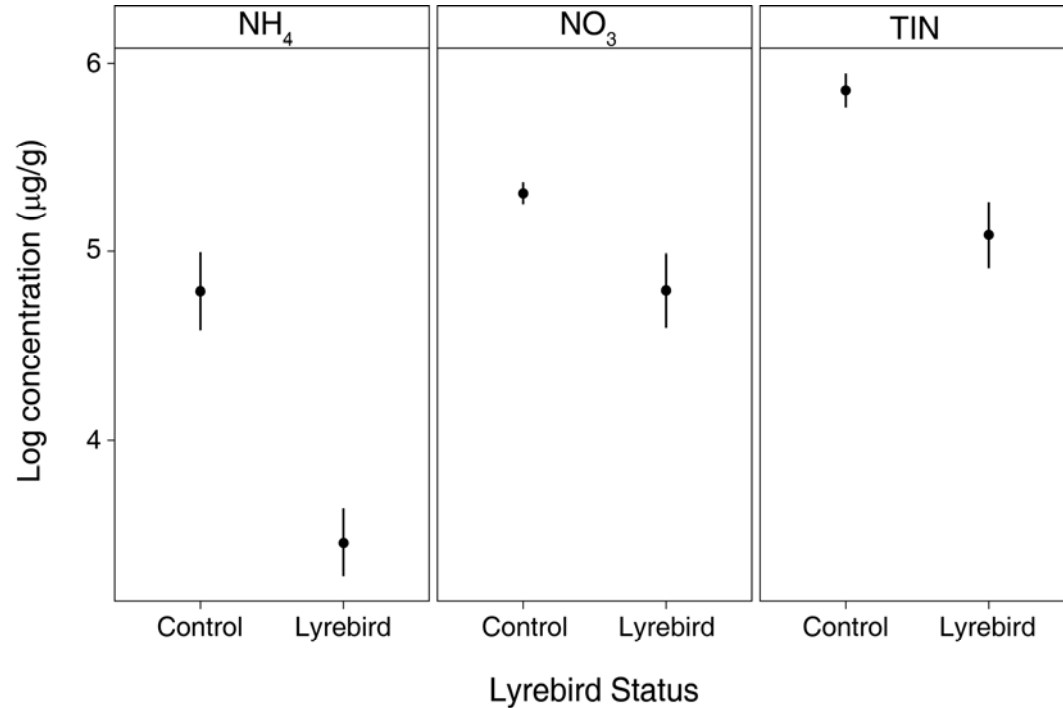


Figure 5.4: Ammonium (NH_4), Nitrate (NO_3), and Total Inorganic Nitrogen (TIN) at sites with and without superb lyrebirds (*Menura novaehollandiae*). Error bars indicate the lower and upper 95% confidence intervals of the means.

5.5 Discussion

The results of this study show that, like other non-native animals, non-native birds have the potential to alter ecosystem processes. However, the effect of superb lyrebirds on ecosystem processes was complex, making interpretation a challenge. There were three main findings. Firstly, decomposition potential increased significantly in the presence of foraging superb lyrebirds. Secondly, soil respiration and pH did not differ with the presence or absence of superb lyrebirds although respiration rates did vary strongly between seasons. Thirdly, concentrations of all forms of inorganic nitrogen were lower at sites with superb lyrebirds than at control sites but there were no differences among the three experimental treatments that could be attributed to superb lyrebirds.

Decomposition was greatest in areas where superb lyrebirds continued to be active (see Chapter 3) showing that the birds increased the activity of the decomposer community, probably by improving conditions for decomposition. Burying leaf litter makes it more accessible to soil microbes (Aggangan *et al.* 1999) while turnover of the soil reduces bulk density (Ashton and Bassett 1997) and increases soil porosity and oxygen levels, thereby providing better conditions for aerobic respiration by mineralising and nitrifying microbes (Xu and Qi 2001). The increase in decomposition in this study was consistent with the findings of Ashton and Bassett (1997) who found that, within the native range of the superb lyrebird, leaf litter decomposition was faster in areas disturbed by superb lyrebirds. These results also concur with research on other non-native bioturbating animals. For example, feral pigs incorporate leaf litter into mineral soil in a similar way to superb lyrebirds and have been shown to accelerate the speed of leaf litter decomposition in the forests they have invaded (Singer *et al.* 1994, Siemann *et al.* 2009).

Soil respiration varied seasonally, following the trend generally observed in regions with temperate or Mediterranean climates where respiration rates are lowest in winter (when temperature is low) and summer (when soil moisture is low) and highest in spring as temperature rises and soils are moist from spring rain (Keith *et al.* 1997, Epron *et al.* 1999, Luo and Zhou 2006). There were no differences in respiration associated with the presence or absence of superb lyrebirds or simulated lyrebird disturbance (hand-raking), which was surprising because both physical disturbance and the incorporation of organic material into soil stimulate the soil microbial community thereby increasing soil respiration (Vitousek and Matson 1985, Aggangan *et al.* 1999, Keith and Wong 2006).

The most obvious explanation for the absence of a difference in respiration associated with disturbance in this study is that neither lyrebird disturbance nor simulated lyrebird disturbance were great enough to result in any measurable lasting change in the rate of soil respiration. However, this explanation does not account for the observed increase in decomposition in areas where superb lyrebirds were active. Respiration by the soil microbial community as it decomposes organic material accounts for a large proportion of total soil respiration (Coleman *et al.* 2004); as decomposer potential increased in plots where superb lyrebirds were active, I would have expected that there would be a

corresponding rise in respiration. A possible explanation for the lack of change in respiration rates between treatments (unfenced, fenced, fenced + hand-raked) in this study is that while the activity of soil microbes may have been enhanced by superb lyrebird disturbance, scratching and digging may have simultaneously reduced the biomass of fine roots in the top layer of the soil and hence root respiration, which is the other major contributor to total soil respiration (Luo and Zhou 2006). In an analogous study, Fisk *et al.* (2004) found that non-native earthworms increased microbial activity through their bioturbation, worm casts and burial of leaf litter but observed no increase in overall respiration; they attributed this to the reduction in the biomass of fine roots in the surface layers of the soil as a result of disturbance by worms. Further research on the effect of superb lyrebirds on microbial activity and biomass and on fine root biomass could clarify whether superb lyrebirds do have an influence on soil respiration.

There were no differences in the concentration of any form of inorganic nitrogen or in pH between the experimental treatments that could be attributed to superb lyrebirds. This was unexpected given that, in general, an increase in the rate of decomposition (like that observed in areas where lyrebirds were active) accelerates the speed of mineralisation and nitrification resulting in higher levels of ammonium, nitrate and TIN in the soil (Singer *et al.* 1984, Adams and Attiwell 1986, Ashton and Bassett 1997). Not only was there no difference in nitrogen between fenced and unfenced exclosures at lyrebird sites but the concentration of all forms of inorganic nitrogen was much lower at sites with superb lyrebirds than at sites without them (although pH did not vary). While it is possible that underlying, co-varying environmental differences between lyrebird and control sites were responsible for the differences in nitrogen concentration between lyrebird and control sites, careful site selection ensured that there were no obvious confounding differences in environmental conditions between the groups of sites (see Chapter 3). Thus, the difference in nitrogen concentration between sites with and without lyrebirds could possibly be the result of a longer-term and large-scale effect of superb lyrebirds.

If superb lyrebirds were responsible for the lower concentrations of inorganic nitrogen, the most likely explanation is that they increased the rate of nitrogen cycling through accelerating decomposition but also simultaneously increased nitrogen leaching, surface runoff and/or immobilisation. One possible pathway through which nitrogen may have

been lost is by increased leaching of nitrate following the breaking up leaf litter into smaller pieces by the superb lyrebirds and subsequent incorporation of the fragments into the soil (Ashton and Bassett 1997). Nitrate ions will be leached more quickly from leaf fragments in the soil than from intact leaves on the soil surface because the former will have a greater surface area to volume and microbial activity levels are higher within the soil (Bohlen *et al.* 2004b, Wirthner *et al.* 2012). In addition, the reduction in soil bulk density and physical displacement of soil downhill by superb lyrebirds also increases soil erosion (Adamson *et al.* 1983, Mitchell and Humphreys 1987, Ashton and Bassett 1997), which can also exacerbate the loss of nutrients via surface runoff. A reduction in nitrate as a result of increased leaching following bioturbation by feral pigs and non-native earthworms has been reported in several studies (e.g. Bratton 1975, Siemann *et al.* 2009, Scheu and Parkinson 1994). However, while leaching may explain the low levels of nitrate observed in this study it does not account for the even lower levels of ammonium at lyrebird sites because, unlike nitrate, positive ammonium ions bind readily with soil colloids (which are typically negatively charged) and are therefore not easily leached away by water (Adams and Attiwell 1986, Weston and Attiwell 1990).

An explanation that may account for the low levels of ammonium at lyrebird sites is that uptake of nitrogen by plants and/or immobilisation of nitrogen by the microbial community increased in the presence of superb lyrebirds. Scratching by superb lyrebirds incorporates leaf litter into the mineral soil, thereby increasing resource availability for the microbial community and favouring an increase in their activity levels and biomass. Carbon is not limiting in wet eucalypt forest soils (Weston and Attiwell 1990) so there is likely to be high microbial demand for inorganic nitrogen (particularly ammonium). Thus, in the event of increased microbial biomass and activity levels, microbes may need to be scavenge nitrogen from the soil solution in order to acquire the necessary amount required for metabolic processes (Aggangan *et al.* 1999). Increased immobilisation as a result of the growing demand for nitrogen by microbes has been implicated in reduced levels of inorganic nitrogen where naturally occurring wild boar (*Sus scrofa*) have mixed organic material into soil (Wirthner *et al.* 2012). Likewise, Aggangan *et al.* (1999) found that experimental incorporation of leaf litter into soils within tree plantations resulted in a decrease in nitrogen concentrations due to increased microbial demand. It is also possible that there may have been an increase in the uptake

of nitrogen by plants. Although plant growth was not assessed in this experiment, I found no difference in the numbers of seedlings at lyrebird and control sites and no obvious differences in the amount of vegetation cover that would suggest higher plant growth rates at lyrebird sites (see Chapter 3).

While leaching, immobilisation, or a combination of the two processes could account for differences in nitrogen concentration between sites with and without superb lyrebirds, they do not explain the lack of treatment effects. A possible reason for the absence of any difference in nitrogen levels between undisturbed areas and areas that were either disturbed by superb lyrebirds or hand-raked is that while leaching and/or immobilisation can occur rapidly (in days), the replenishment of nitrogen may occur over a much longer timeframe than the two year enclosure period of the experiment. For example, it generally takes at least 12 months for the leaf litter layer to reform in wet eucalypt forest (Ashton 1975, Ashton and Attiwell 1994); meanwhile the decomposer community may have continued to process the organic material that has been previously incorporated into the soil thereby keeping nitrogen levels low. Furthermore, processes such as erosion and the percolation of water through the soil profile are likely to operate at a larger spatial scale than individual plots so that the low cover of leaf litter across the site may have affected the fenced enclosures. Conversely, at control sites, the nitrogen concentrations in hand-raked plots may have been buffered from loss of nitrogen via incorporation of leaf litter into the soil and surface runoff because of the thick leaf litter cover in the surrounding area. Likewise, the high concentration of nitrogen in the soil prior to hand-raking plots at control sites may have meant that an increase in immobilisation following the incorporation of leaf litter did not greatly reduce nitrogen concentrations.

In conclusion, this study showed that superb lyrebirds are capable of influencing the speed of decomposition of organic matter, and potentially, additional processes such as nitrogen cycling and soil respiration. However, evaluating what the presence of superb lyrebirds might mean for the functioning of Tasmanian wet eucalypt forests is not straightforward. Even if superb lyrebirds are able to alter the speed of nitrogen cycling, the significance of their influence will depend on whether they exacerbate the loss of nitrogen or increase immobilisation. If the former is true then superb lyrebirds could potentially reduce nitrogen pools in forest soils in the long term but in the case of

enhancing immobilisation there will likely be little effect on pool size. Faster nitrogen cycling could theoretically lead to a rise in forest productivity (plant growth rates) if there is an increase in immobilisation, but in practice any increase would probably be minimal because the cool climate in southern Tasmanian ultimately limits the speed of decomposition and therefore the productivity of wet eucalypt forests in the region (Ashton and Attiwell 1994).

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Chapter 6: General Discussion

As non-native species continue to establish throughout the world (Blackburn *et al.* 2010, Simberloff *et al.* 2013) the need to accurately assess and predict the threat they pose is becoming increasingly important (Ricciardi *et al.* 2013, Simberloff *et al.* 2013). Resources to tackle non-native species are finite so their allocation must be prioritised based on the severity of their current or predicted future impact (Parker *et al.* 1999, Leung *et al.* 2012). Prioritisation of funding for management and forecasting future impact relies on the accuracy of the information on which the assessments of impact are based (Byers *et al.* 2002, Shine 2010, Barney *et al.* 2013). However, in the case of non-native birds the data available are frequently insufficient for these tasks (Bauer and Woog 2011, Strubbe *et al.* 2011).

While few non-native birds are currently known to have significant, large-scale ecological impacts (Blackburn *et al.* 2009, Strubbe *et al.* 2011, Kumschick *et al.* 2013), only a small number of quantitative investigations have been conducted. Thus it is unclear whether non-native birds have a lesser effect than other groups of animals (e.g. mammals) or whether their impacts have gone undetected (Temple 1992, Wright *et al.* 2010, Bauer and Woog 2011). Most research on non-native birds has focused on competition for food (e.g. Freed and Cann 2009), nesting sites (Pell and Tidemann 1997, Ingold 1998, Blanvillain *et al.* 2003) or hybridisation with native species (Rhymer and Simberloff 1996, Muñoz-Fuentes *et al.* 2007, 2012). Little is known about their effect on other native taxa (e.g. invertebrates) or on ecosystem function (Blackburn *et al.* 2009). With almost 450 non-native bird species established worldwide (Dyer and Blackburn unpublished data 2012), there is a clear need for more quantitative information on their ecological impact.

In this thesis, I have taken the first steps towards addressing the knowledge gap regarding the impact of a non-native bird on native non-avian biota and on ecosystem function. I used the introduced population of the superb lyrebird (*Menura novaehollandiae*) in Tasmania, Australia as a study system to conduct a comprehensive multifactorial investigation of impact. The effect of the superb lyrebird (which is both a predator of soil- and leaf litter- dwelling invertebrates and an ecosystem engineer) on Tasmanian forests was unknown prior to undertaking this study. Nevertheless

conservation managers were concerned that the superb lyrebird could be causing large-scale change in Tasmanian wet sclerophyll forests, which lack any native ecosystem engineer or invertebrate predator of similar size or capacity for soil disturbance (Mallick and Dreissen 2009). Therefore, my work both makes a significant contribution to the understanding of the ecological impact of non-native birds and addresses the particular needs of conservation managers within Tasmania for information on the nature and magnitude of superb lyrebird impact.

Designing studies to assess the impact of non-native species is challenging when, as is the case with superb lyrebird, there is no pre-introduction data. Other anthropogenic stressors or co-varying environmental differences affecting the ecosystem can make it difficult to isolate the influence of the non-native species in question (Ruiz *et al.* 1999). It is also clear that impacts of non-native species are generally context-dependent, varying in both strength and direction over a range of spatial, temporal and organisational scales (Thomsen *et al.* 2011). Integrative and multifactorial studies are generally accepted as being the most thorough means of evaluating impact (Byers *et al.* 2002, Strayer 2012, Barney *et al.* 2013) but prior to this study, such approaches have rarely been employed to investigate the impact of non-native birds (Strubbe *et al.* 2011). My research combined field-based experiments (Chapters 3 and 5) and observational surveys (Chapters 2 and 4) to investigate the nature and magnitude of the effect of superb lyrebirds on various components of native biota and on ecosystem function over a range of temporal and spatial scales and environmental gradients.

6.1 What is the nature and direction of the effect of superb lyrebirds on native biota?

A central objective of this study was to determine the effects that the superb lyrebird has on native invertebrate assemblages and on seedling survival. The field surveys and experiments reported in Chapters 2, 3 and 4 all showed that the soil and leaf litter invertebrate assemblages were inherently variable at a range of spatial and temporal scales. This finding is consistent with other research conducted on forests soil invertebrates in Tasmania and elsewhere (Mesibov 1998, Catterall *et al.* 2001, Ettema and Wardle 2002, Baker *et al.* 2006). Despite this heterogeneity, a consistent pattern emerged in the structure of invertebrate assemblages that was associated with the

presence of superb lyrebirds. Specifically, the first key finding was that macroinvertebrate abundance and richness were generally lower in the presence of superb lyrebirds while evenness was either unchanged or higher (Chapters 2, 3 and 4). With the exception of higher evenness, these results concur with those of many studies conducted on the effect of non-native animals on soil biota to date: namely, that non-native animals typically have a negative influence on the abundance and richness of native soil and leaf litter invertebrates (Vtorov 1993, Wardle *et al.* 2001, Fukami *et al.* 2006, Dunham and Mikheyev 2010, Choi and Beard 2012). However, this differs from the effects of most non-native plants, which typically have a positive effect on both abundance and richness of soil biota (Pyšek *et al.* 2012).

In contrast to my findings, taxonomic evenness of native assemblages often decreases following the establishment of non-native animals because the new conditions imposed by the non-native species cause most native taxa to decline, while a small subset may actually benefit, becoming more abundant as a result of reduced competition and predation (Wardle 2002). However, the natural structure of some soil and leaf litter assemblages appears to prevent a decline in evenness because they are highly diverse and are comprised of a large number of species that are only present in low numbers, together with only a small number of taxa that are abundant (Bardgett *et al.* 2005, Coleman and Rieske 2006). Superb lyrebirds were associated with both lower invertebrate taxonomic richness and much lower abundance, particularly of numerically dominant taxa such as amphipods (Chapters 3 and 4) than at sites without them. Therefore, the net effect of the birds was to make the numbers of individuals belonging to each invertebrate taxon more equal, thereby increasing evenness. Although this response to non-native animals appears to be uncommon in soil invertebrate assemblages, other perturbations such as forest fire are known to increase the evenness of soil and leaf litter invertebrate assemblages in this way (e.g. Coleman and Rieske 2006).

The second important finding was that mesoinvertebrate abundance and evenness followed the same patterns as macroinvertebrates in the presence of superb lyrebirds (lower abundance and higher evenness), but richness varied very little (Chapters 3 and 4). The lack of variation in richness may reflect the limited taxonomic resolution for this group (as taxonomic information for mesoinvertebrates in Tasmanian forests is

limited, particularly for Acari), which could potentially have masked any impact at the genus or species level. Indeed, the few studies to examine the impact of non-native animals on forest soil mesoinvertebrates showed that they could be strongly affected (e.g. Vtorov 1993, Burke *et al.* 2011). However, it is also possible that mesoinvertebrates, due to their small size, are less affected by physical disturbance and/or predation by superb lyrebirds. Mesoinvertebrates can be more resistant than larger invertebrates to impacts such as tilling and grazing that disturb or compact the soil (Abbott *et al.* 1979, Wardle 1995, Bromham *et al.* 1999, Wardle *et al.* 2001). I suggest that future research using recognisable taxonomic units or morphospecies would make it possible to determine the extent to which this component of the native fauna is influenced by superb lyrebirds.

A third key finding relates to different habitat affinities of macroinvertebrate taxa. Within native communities, the response of individual species to the presence of a non-native species often varies in direction (positive, negative or neutral) and magnitude, depending on whether the non-native species increases, decreases or has no effect on the strength of the regulatory processes such as competition and predation that control native species (Ehrenfeld 2003, Byers *et al.* 2010). In the case of the superb lyrebird, macroinvertebrates with an affinity for leaf litter were consistently less abundant in areas with superb lyrebirds than areas without them, implying that superb lyrebirds had a strong negative effect on their abundance (Chapters 2, 3 and 4). In contrast, the birds appeared to have a weaker influence on generalists and soil dwellers, which occurred in similar numbers across sites with and without lyrebirds (Chapter 2). The numbers of generalists and soil dwellers did decline following disturbance (see Chapter 3 and 4) but unlike leaf litter dwellers, they were able to recolonise disturbed areas rapidly (within 21 days; Chapter 3).

The difference in the abundance of leaf litter dwellers and the generalists/soil dwellers may reflect higher predation by the superb lyrebirds on leaf litter invertebrates than on generalists and soil dwellers. However, both earthworms and Diptera larvae (which I classed as soil dwellers and generalists) are important prey for superb lyrebirds (Robinson and Frith 1981, Smith 1988, Lill 1996). Since earthworms and Diptera larvae generally dominated the fauna in areas disturbed by lyrebirds, I argue that it is likely that habitat modification and disturbance by the superb lyrebirds rather than predation

were responsible for the reduction in leaf litter dwellers. This explanation is supported by the short-term recovery experiment (Chapter 3), which demonstrated that physical disturbance and modification of soil and leaf litter habitat was sufficient to strongly reduce invertebrate abundance even without predation. While superb lyrebird scratching alters soil structure to some extent by reducing bulk density, increasing organic matter content and increasing soil porosity (Ashton and Bassett 1997), the leaf litter layer habitat is largely destroyed and is incorporated into the soil (Ashton and Bassett 1997). Thus, the greater influence of superb lyrebirds on leaf litter dwellers was probably driven by the reduced availability of leaf litter habitat (Chapters 2, 3). Studies on other bioturbating non-natives species (such as invasive earthworms, Migge-Kleian *et al.* 2006) and other forms of disturbance such as fire and forestry have also found that the reduction in leaf litter associated with the disturbance meant that leaf litter dwelling taxa were much more affected than soil dwellers (York 1999, Coleman and Rieske 2006, Pryke *et al.* 2012).

In contrast to invertebrate assemblages, there was no difference in the number of seedlings between areas with and without superb lyrebirds (Chapter 3). This was an unexpected result because within their native range, superb lyrebirds are thought to have both positive and negative effects on seedling establishment (Howard 1973, Read and Brown 1996, Ashton and Bassett 1997). Interestingly, a once-off simulated lyrebird scratching in an eight-month period resulted in higher seedling numbers than areas with or without superb lyrebirds. It appears that disturbance of the soil and leaf litter can promote germination of new seedlings but kills many existing seedlings. Thus, seedling survival depends on the frequency disturbance. If it is too frequent (i.e. more than once in 8 months, as was the case when lyrebirds were present) few seedlings survive long-term, meaning that the overall numbers will be equivalent to numbers in undisturbed areas. Overall, the activities of superb lyrebirds are unlikely to have a strong influence on recruitment rates in mature wet eucalypt forest because the long-term survival of seedlings is limited by low light levels at ground level (Attiwill 1994). Successful recruitment mainly occurs following disturbance events unrelated to superb lyrebirds, such as tree-fall and fire, which open the canopy thereby increasing light levels and allow seedlings to establish (Ashton 1976, Ashton and Attiwill 1994, Facelli *et al.* 1999).

Determining whether non-native species affect any ecosystem processes is important because they can potentially change the functioning of entire ecosystems, particularly if the species in question is an ecosystem engineer (Jones *et al.* 1994, Cuddington and Hastings 2004). Such species frequently have profound impacts on ecosystem function as they can directly alter biological communities as well as physical ecosystem properties (Crooks 2002). The effects of superb lyrebird foraging on ecosystem processes were complex: on the one hand the capacity of the decomposer community to process leaf litter was higher in areas where lyrebirds were active than in areas without them. On the other hand there was no difference in the rate of soil respiration (CO₂ efflux), which was surprising because a more active decomposer community is expected to produce more carbon dioxide as a by-product of metabolic activity (Coleman *et al.* 2004). One possible explanation for the absence of a rise in respiration is that superb lyrebird scratching destroys fine roots, counteracting the stimulating effect that their disturbance has on the microbial community. Because respiration by fine roots comprises a significant proportion of total soil respiration (Coleman *et al.* 2004), a reduction in their biomass at the same time as an increase in microbial respiration could result in overall soil respiration remaining constant.

An increase in decomposition was also expected to be associated with an increase in the speed of nitrogen cycling because the breakdown of organic material by microbes involves the transformation of organic nitrogen into inorganic nitrogen (Singer *et al.* 1984, Adams and Attiwill 1986, Ashton and Bassett 1997). While all forms of inorganic nitrogen were lower at sites with superb lyrebirds (Chapter 5) there were no differences in the levels between treatments. The low levels of nitrogen at lyrebird sites may indicate that nitrogen cycling was accelerated with a corresponding increase in the rate of uptake by microbes and plants and/or higher loss of nitrogen via leaching and runoff (see Chapter 5), but it was not possible to definitively link the low levels to superb lyrebirds. Overall, although I was able to demonstrate that superb lyrebirds are at least capable of altering decomposition rates, the extent to which they influence other ecosystem processes and ecosystem function remains unclear. Future research on the influence of superb lyrebirds should investigate any changes in soil microbial community composition, enzyme activity and fine root biomass.

6.2 Variability and context dependence of impact

Having determined the nature and direction of the effects that a non-native species has on native biota and ecosystems, the next logical question to ask is ‘what is the size and strength of their impact?’ All non-native species are likely to have an effect of some kind on the receiving ecosystem (Barney *et al.* 2013) but the magnitude of that effect could fall anywhere along a spectrum ranging from benign to high impact. Furthermore, the impact of non-native species is often context-dependent, i.e. the effect of the same non-native species may vary in magnitude and direction in time and space depending on factors such as environmental conditions, resource availability, the density of the non-native species and the identity of the native species in the receiving community (de Moura Queirós *et al.* 2011, Thomsen *et al.* 2011, Barney *et al.* 2013). For this reason, I examined three sources of heterogeneity that were likely to influence the magnitude of superb lyrebird impact on invertebrate assemblages: environmental gradients (microhabitat type, Chapter 2), the intensity of lyrebird activity (Chapter 4) and the identity and habitat affinity of native invertebrate taxa (as discussed above, Chapters 2, 3 and 4). In addition, I investigated the response of invertebrate assemblages to the presence of superb lyrebirds across a range of spatial and temporal scales (Chapters 3 and 4).

As anticipated, I found that the size of the effect of the superb lyrebird on invertebrate assemblages varied greatly both spatially and temporally. Importantly, the three sources of context dependence listed above all appeared to be both influential and interrelated. Chapter 2, which focused on environmental spatial variability of impact, showed that macroinvertebrate assemblages were inherently variable between riparian, slope and ridge microhabitats within sites. The differences between the assemblages were most likely driven by heterogeneity in environmental conditions such as moisture and humidity that typically vary across these microhabitats (Richardson and Devitt 1984, Taylor *et al.* 1994, Catterall *et al.* 2001, Baker *et al.* 2006, 2007). My results showed that although macroinvertebrate abundance and richness were highest in slope microhabitats at control sites, they were lowest in slope habitats at lyrebird sites. I argue that this was probably because the extent of superb lyrebird foraging was higher in slopes due to the abundance and accessibility of macroinvertebrate prey. Superb lyrebirds are selective about where they feed (Ashton and Bassett 1997, Lill 1996), presumably because they

optimise the efficiency of foraging. Consequently, individuals concentrate their foraging activity on areas (slopes) where it is relatively easy to capture invertebrate prey (Campbell and Grey 1942, Littlejohns 1947, Robinson and Frith 1981, Lill 1996), and therefore their impact is greater here than in areas with lower resource availability. Conditions in slope microhabitats were probably the most suitable for invertebrates at the time of sampling (austral spring) because moisture levels are typically higher on slopes than on ridges (Ashton and Bassett 1997, Catteral *et al.* 2001) and they are not subject to the winter flooding that can drown invertebrates that occur in the riparian habitats in wet eucalypt forests (Baker *et al.* 2006, 2007).

The magnitude of the effect of non-native species can also vary temporally in response to changing environmental conditions and resource availability (Strayer *et al.* 2006). Research on native populations of the superb lyrebirds has found that individuals show temporal variation in their preference for feeding in certain microhabitats, probably in response to seasonal variation in moisture levels and presumably the availability of prey (Ashton and Bassett 1997, Robinson and Frith 1981). Native superb lyrebirds have been observed to concentrate their foraging effort on ridges during the winter months, moving to the mid-slopes in autumn and spring, and into gullies during the summer (Ashton and Bassett 1997, Campbell and Grey 1942). This behaviour is thought to be in response to changes in the relative ease of capturing prey (Campbell and Grey 1942, Littlejohns 1947, Lill 1996). For example, superb lyrebirds probably avoid dry ridges during the summer months because invertebrates move deeper into the soil making them more difficult and energetically more expensive to catch (Campbell and Grey 1942, Littlejohns 1947, Lill 1996). From my observations it appears likely that superb lyrebirds in Tasmania follow a similar pattern, meaning that impact within different microhabitats tends to vary in magnitude over time.

The strength of the interaction between non-native species and recipient biota is often related to the density, biomass or the geographic extent of the non-native species (Thomsen *et al.* 2011, Barney *et al.* 2013). In the case of non-native ecosystem engineers that alter disturbance regimes and the physical structure of habitat (such as the superb lyrebird), the speed at which native assemblages in disturbed areas recover will be influenced by the availability and proximity of refugia from which individuals can recolonise (Crooks 2002, Leibold *et al.* 2004, Sandel and Smith 2009). As the size of

the area affected by an ecosystem engineer increases, the distance to refugia also increases and can slow the speed of recovery (McCabe and Gotelli 2000, Gilbert and Levine 2013). I examined the relative effect of two levels of superb lyrebird activity: medium (<30% of forest floor disturbed) and high (>50% of the forest floor disturbed) on invertebrate assemblages within one microhabitat type (slopes) across multiple sites (Chapter 4). When superb lyrebirds feed they typically create discrete scratched areas of around 0.25 m² to 0.50 m² (Ashton and Bassett 1997). The result is a matrix of disturbed areas at varying stages of recovery depending on time since disturbance. I compared recently disturbed patches (<2 weeks old) with patches that had not been disturbed for around 12 months. As expected, the difference in abundance and richness between the two patch types was greater at high disturbance sites than at medium disturbance sites. Interestingly, however, the number of individuals and taxa were lower in both patch types (i.e. irrespective of how recently disturbed) at medium disturbance sites than at high disturbance sites. Based on the findings from Chapter 2, it appears that resource availability (i.e. invertebrates) may have been inherently lower at the sites with medium disturbance (possibly in response to previous drought conditions or small scale differences in drainage patterns) and that this in turn influenced the extent of superb lyrebird foraging activity. Therefore, limited resource levels appear to dampen the impact of superb lyrebirds because they feed there less. In contrast, where resource levels are high, assemblages in recently disturbed patches in highly productive areas are more strongly affected. This finding corroborates with the “habitat-filtering” hypothesis proposed by Weiher and Keddy (1999), which posits that the impact of non-native species will be limited by suboptimal conditions and greater when conditions are good.

In addition to heterogeneity in environmental conditions and resource availability, I found that the patchy nature of superb lyrebird foraging also influenced the magnitude of their impact in space and time (Chapters 3 and 4). This is because the overall net effect of any form of biogenic disturbance will depend in part on how much of the landscape is disturbed at any one time, the frequency of disturbance and the duration of its effect (in this case, the impact of an individual scratching event) on the recipient community (Hall *et al.* 1993, Crooks 2002, Cuddington and Hastings 2004). Consequently, if disturbance is uncommon and it is short-lived, then the impact will probably be restricted to the scale of individual disturbed patches because the combined effects of individual patches will rarely result in a significant impact at larger spatial

scales (Hall *et al.* 1993, Crooks 2002, Cuddington and Hastings 2004). However, if disturbed patches are widespread or their effect is substantial and long-lived, then the combined impact at larger spatial scales could be high (Hall *et al.* 1993). I found that the impact of superb lyrebirds on invertebrate assemblages was strongest at the smallest spatial scale (0.25 m² to 0.50 m² patches), but the magnitude of impact depended on whether or not the patch had been disturbed recently (i.e. within 1 month). At the larger scales (local and landscape) the impact was detectable but far less intense while the effect was undetectable over long time frames (12 months). Thus, my results indicate that even at sites with high levels of disturbance (where over 50% of the forest floor was disturbed), superb lyrebird activity resulted primarily in short-lived and spatially restricted impacts on invertebrate assemblages (Chapter 4).

6.3 Significance of the immediate and potential future effect of the superb lyrebird in Tasmania

The overall aim of this thesis was to determine whether or not superb lyrebirds have or are likely to have a significant, large-scale impact on biological communities and ecosystem functioning of wet eucalypt forests in Tasmania. The short answer to this question is ‘probably not’. While superb lyrebirds do have a demonstrable effect on biota and some ecosystem processes, their impact appears to be largely restricted to small spatial and temporal scales. As outlined above, this can in part be explained by environmental variability and the patchy foraging behaviour of the lyrebirds. However, there are also some features of Tasmanian wet eucalypt forest ecosystems and their biological communities that may make them inherently resilient to the effects of the superb lyrebird.

The main form of natural disturbance in Tasmanian wet eucalypt forests is wildfire (Attiwill 1994, Baker *et al.* 2004); this has led to strong selective processes among plants and invertebrates towards those that can either survive or rapidly recolonise burnt areas following fire (Attiwill 1994, Baker *et al.* 2004). The capacity of the native plant and invertebrate communities to survive this larger-scale and more intense form of perturbation may help them to cope with smaller-scale and less intense (albeit more frequent) disturbance in the form of superb lyrebird foraging. In the case of plants, seedling germination may or may not benefit from superb lyrebird scratching depending on its frequency (Chapter 3), but overall vegetation communities are unlikely to be

affected because the majority of successful recruitment occurs following events such as wildfire and tree fall (Ashton 1976, Attiwill 1994, Facelli *et al.* 1999). Likewise, many invertebrates are able to recover within a few years following fire, either by surviving by moving downwards in the soil profile or recolonisation from adjacent unburnt areas. For example, Collett (2000) found that beetle assemblages recovered within two years of wildfire with little change in the proportional abundances of the families present. Like fire, superb lyrebird scratching removes the leaf litter on which many invertebrates rely, but the removal of leaf litter is much patchier and affects much smaller areas than is typical for fire. Thus, the distances that must be covered by individuals in order to recolonise areas scratched by lyrebirds are unlikely to pose a barrier to species that are capable of recolonising after fire.

Assessing the significance of the threat that superb lyrebirds pose to ecosystem processes is more challenging given the mixed evidence regarding their impact reported in this thesis (Chapter 5). Clearly, they are capable of influencing decomposition but whether this has large-scale repercussions in terms of the rate of nutrient cycling, the size of nutrient pools and soil respiration is unclear. However, the inherent resilience of wet eucalypt forest ecosystems to fire (Attiwill 1994) means that these ecosystems contain internal feedback mechanisms that allow them to respond to large-scale perturbation, thereby retaining the same functions and structures. In particular, these ecosystems rapidly and efficiently retain nutrients such as nitrogen following fire, preventing loss by leaching or volatilisation (Ashton and Attiwill 1994). Consequently nutrient pools can return to pre-fire levels within two years (Weston and Attiwill 1990). These same mechanisms may also enable these ecosystems to absorb changes to ecosystem processing that occur as a result of superb lyrebird activity.

Overall, there is probably only a low current or future risk that superb lyrebirds may force wet eucalypt ecosystems beyond their steady state (or resilience) threshold, thereby causing a regime shift, given their natural resistance to all but catastrophic disturbance. However, superb lyrebirds may have significant impacts on a subset of native species and features. Certain threatened endemic species with limited geographic distribution will potentially be put at further risk by the presence of the superb lyrebirds. The critically endangered myrtle orchid (*Thynninorchis nothofagicola*) is a case in point as it is highly sensitive to disturbance of the forest floor and has a known range of only

a few hundred square metres of forest (Threatened Species Section 2009). Likewise, certain geomorphological features such as karst landscapes, which can be sensitive to changes in colluvial creep (downhill movement of soil) and in the balance between water infiltration and runoff, may be affected by an increase in soil disturbance (Mitchell and Humphreys 1987). Headwater streams are another feature of the landscape that may be affected. Anecdotal observations suggest that scratching by superb lyrebirds can substantially alter the path that these streams take across the landscape and may also alter the speed of decomposition and nutrient cycling within them (Burrows 2013). Headwater streams are abundant across the landscape (Bryant *et al.* 2007), so if superb lyrebirds do significantly modify the structure and function of headwater streams there could be serious ramifications for down stream ecosystems and water quality.

The superb lyrebird population in Tasmania appears to be spreading (Tasmanian Parks and Wildlife Service unpublished records 2012, BirdLife Tasmania unpublished records 2012); based on habitat modelling by Tanner (2000), there appear to be large areas of potentially suitable habitat in Tasmania that could be colonised in the future. In this thesis, I focused on the impact of superb lyrebirds in wet eucalypt forest because this is both a preferred habitat of native populations of superb lyrebirds (Higgins *et al.* 2001) and a dominant forest type within their current range in Tasmania. However, superb lyrebirds can inhabit other forest types within their native range including dry sclerophyll forest and temperate rainforest (Higgins *et al.* 2001). Thus, it is possible that the impact of non-native superb lyrebirds could vary in magnitude and direction across different forest types in Tasmania. Examining the influence of the superb lyrebird on temperate rainforest is an important area for future research because there are extensive tracts of this forest type on the western side of the island. However, I posit that impact may be minimal because much of this forest occurs on low nutrient soils (Grant *et al.* 1995, Cotching *et al.* 2009) and so is likely to support fewer invertebrate prey. I found that the effect of superb lyrebirds was dampened at sites with limited food resources because foraging was less intense than those with higher resource availability (Chapter 4), therefore it is possible that impact in temperate rainforest would be lower than in the more productive wet eucalypt forest.

While superb lyrebirds may not in isolation cause large-scale change to Tasmanian biotic communities and ecosystems, it remains to be seen whether the observed reduction in invertebrate abundance and richness at small scales reduces the overall resilience and persistence of invertebrates in the face of other stressors, such as forestry activity, in what is known as an extinction debt (Tilman *et al.* 1994, Vellend *et al.* 2006). For example, there are anecdotal reports that suggest that superb lyrebirds may affect the trajectory of forest regeneration following logging. Neyland (2001) observed that scratching by foraging superb lyrebirds appeared to reduce the regeneration of seedlings in experimental timber harvesting plots in southern Tasmania. This could have significant repercussions for slow-growing trees such as *Nothofagus cunninghamii* and *Phyllocladus aspleniifolius*.

6.4 Management implications

Continuing to monitor the superb lyrebird and its distribution in Tasmania should be central to the ongoing management of this species. Identifying native species and particular habitats that are likely to be at risk from superb lyrebirds either now or in the future should be a priority for management. Given that large-scale impacts are unlikely and that eradication or prevention of further spread of superb lyrebirds throughout the state would be logistically challenging and prohibitively expensive, mitigating impact is the most pragmatic approach to managing this species. Where native species are identified as being at risk, the most viable option would be to setup small-scale exclusion areas as for the myrtle elbow orchid (Threatened Species Section 2009).

In conclusion, addressing the knowledge gap regarding the ecological impact of non-native birds is important for two reasons. Firstly, in cases such as the superb lyrebird, if the impact is indeed minimal then resources can be safely directed elsewhere. Secondly, if non-native birds do exert strong but as yet unidentified impacts, this may change the way in which they are managed. This is not trivial because at present the funding directed towards the management of non-native birds is typically far less than is directed towards other non-native vertebrates, particularly mammals (Kumschick and Nentwig 2010). More generally, if non-native birds typically do not have a significant impact, determining why this is the case may provide valuable insights into one of the central questions of invasion ecology: why do some non-native species have profound

impacts while others are benign? Given that many hundreds of bird species from a broad range of families and representing many life history characteristics have been introduced throughout the world, non-native birds offer an opportunity to elucidate the factors that determine the impact of non-native species more broadly. In the same way that the study of the process of invasion has been progressed by examining the establishment success and spread of non-native birds (Blackburn *et al.* 2009), birds may also help us to understand and ultimately predict the magnitude of impact of non-native species.

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Appendix 1

List of taxonomic references by invertebrate group and habitat affinity

Invertebrate group		Habitat Affinity	Taxonomic References
Oligochaeta	Haplotaxida	Generalist/soil dweller	<p>Blakemore, R. Blakemore, R. J. (2007). A Series of Searchable Texts on Earthworm Biodiversity, Ecology and Systematics from Various Regions of the World. 2nd Edition (2006) and Supplemental March, 2007." Retrieved 20 Dec, 2011, from http://bio-eco.eis.ynu.ac.jp/eng/database/earthworm/</p> <p>Blakemore, R. 2000. Tasmanian Earthworms. CD-ROM Monograph with Review of World Families. 'VermEcology', PO BOX 414 Kippax 2615. Canberra, December, 2000. Pp. 800 (incl. 222 figs).</p>
Hirudinea	Arhynchobdellida	Leaf litter dweller	Harvey, M.S. and Yen, A.L. 1990. Worms to wasps: an illustrated guide to Australia's terrestrial invertebrates. Oxford University Press. USA.
Turbellaria		Leaf litter dweller	Harvey, M.S. and Yen, A.L. 1990. Worms to wasps: an illustrated guide to Australia's terrestrial invertebrates. Oxford University Press. USA.
Nemertea	<i>Geonmertes australiensis</i>	Leaf litter dweller	<p>Hickman, V.V. 1963. The occurrence in Tasmania of the land nemertine, <i>Geonemertes australiensis</i> Dendy, with some account of its distribution, habits, variation and development. Papers and Proceedings of the Royal Society of Tasmania. 97: 63-77+ plates,</p> <p>Moore, J 1975. Land nemertines of Australia. Zoological Journal of the Linean Society. 56: 23-43</p>

Gastropoda		Leaf litter dweller	Kevin Bonham, University of Tasmania, Smith, B.J. & Kershaw, R.C. 1981. <i>Tasmanian land and freshwater molluscs</i> . Hobart: University of Tasmania.
onychophora	Ooperipatellus sp.	Leaf litter dweller	Mesibov, R. 2012. Tasmanian multipedes. http://www.polydesmida.info/tasmanianmultipedes/ 20 January 2012.
Diplopoda		Leaf litter dweller	Mesibov, R. 2012. Tasmanian multipedes. http://www.polydesmida.info/tasmanianmultipedes/ 20 January 2012.
Chilopoda			
Craterostigmomorpha	Craterostigmus tasmanicanus	Leaf litter dweller	Colloff, M.J., Hastings, A. M., Spier, F. and Devonshire, J. (2005). Centipedes of Australia. Canberra, CSIRO Entomology and Australian Biological Resources Study. Mesibov, R. 2012. Tasmanian multipedes. http://www.polydesmida.info/tasmanianmultipedes/ 20 January 2012. Minelli, A. 2011. Treatise on Zoology-Anatomy, Biology. The Myriapoda.Vol 1. Brill. Netherlands
Geophilomorpha	Steneurytion sp.	Generalist/soil dweller	
	Tasmanophilus sp.	Generalist/soil dweller	
	geophilomorph sp.	Generalist/soil dweller	
Lithobiomorpha	Henicops maculatus	Leaf litter dweller	
	Anopsobinnae	Leaf litter dweller	
Scolopendromorpha	Cryptops sp.	Leaf litter dweller	

Symphyla	Hanseniella sp	Generalist/soil dweller	Mesibov, R. 2012. Tasmanian multipedes. http://www.polydesmida.info/tasmanianmultipedes/ 20 January 2012.
Arachnida			
Araneae	Araneomorph	Leaf litter dweller	Lynne Forster, University of Tasmania, Spiders of Australia - Interactive Identification to Subfamily (CD-ROM) - Raven, Baehr & Harvey. CSIRO Publishing (c) Commonwealth of Australia 2002.
	Mygalomorph	Generalist/soil dweller	Lynne Forster, University of Tasmania, Spiders of Australia - Interactive Identification to Subfamily (CD-ROM) - Raven, Baehr & Harvey. CSIRO Publishing (c) Commonwealth of Australia 2002.
Opiliones		Leaf	Harvey, M.S. and Yen, A.L. 1990. Worms to wasps: an illustrated guide to Australia's terrestrial invertebrates. Oxford University Press. USA.
Pseudoscorpiones		Generalist/soil dweller	Harvey, M.S. and Yen, A.L. 1990. Worms to wasps: an illustrated guide to Australia's terrestrial invertebrates. Oxford University Press. USA.
Acari	>2 mm Mesostigmata	Leaf litter dweller	David Green, University of Tasmania
	< 2 mm Acari	Mesoinvertebrates	

Crustacea		
Amphipoda	Leaf litter dweller	Alastair Richardson, University of Tasmania, Friend, J.A. 1987. The terrestrial amphipods (Amphipoda: Talitridae) of Tasmania: systematics and zoogeography. Records of the Australian Museum Supplement. 7: 1-87.
Isopoda	Leaf litter dweller	Alastair Richardson, University of Tasmania, Green, A. J. A. 1961. A study of Tasmanian Oniscoidea (Crustacea: Isopoda). Australian Journal of Zoology 9: 258-365.
Insecta		
		<i>The Insects of Australia: a textbook for students and research workers. 2nd Ed. 1991.</i> The Division of Entomology, Commonwealth Scientific and Industrial Research Organisation. Melbourne University Press. Carlton South, Vic, 1991.
Coleoptera (adult)	Leaf litter dweller	Grove, S.J. (2012). <i>Tasmanian Forest Insect Collection website and database</i> (Hobart: Forestry Tasmania)
Coleoptera(larvae)	Generalist/soil dweller	Grove, S.J. (2012). <i>Tasmanian Forest Insect Collection website and database</i> (Hobart: Forestry Tasmania)
Diptera (adult)	Leaf litter dweller	<i>On The Fly - The Interactive Atlas and Key to Australian Fly Families</i> (CD-ROM) - Hamilton, Yeates, Hastings, Colless, McAlpine, Bickel, Daniels, Schneider, Cranston & Marshall. Published by Australian Biological Resources Study and Centre For Biological Information Technology.

Diptera (larvae)	Generalist/soil dweller	<i>On The Fly - The Interactive Atlas and Key to Australian Fly Families</i> (CD-ROM) - Hamilton, Yeates, Hastings, Colless, McAlpine, Bickel, Daniels, Schneider, Cranston & Marshall. Published by Australian Biological Resources Study and Centre For Biological Information Technology.
Formicidae	Generalist/soil dweller	Peter McQuillan, University of Tasmania
Lepidoptera larvae		Peter McQuillan, University of Tasmania
Blattodea		<i>The Insects of Australia: a textbook for students and research workers. 2nd Ed. 1991.</i> The Division of Entomology, Commonwealth Scientific and Industrial Research Organisation. Melbourne University Press. Carlton South, Vic, 1991.
Plecoptera	Leaf litter dweller	Lawrence Cook, University of Tasmania. Hynes, H.B.N. Hyes. 1989. Tasmanian Plecoptera. Australian Society for Limnology. Special Publication. No. 8.
Trichoptera	Leaf litter dweller	Lawrence Cook, University of Tasmania; Neboiss, A. 1979. A terrestrial caddis-fly larva from Tasmania (Calocidae: Trichoptera). <i>Australian Entomological Magazine</i> , 5, 90–93; Jackson, J.E. 1998. <i>Preliminary guide to the identification of late instar larvae of Australian Calocidae, Helicophidae and Conoesucidae (Insecta: Trichoptera)</i> . Co-operative Research Centre for Freshwater Ecology Identification Guide, 16, 1–81.

Hemiptera	Rhyparochromidae	Leaf litter dweller	Peter McQuillan, University of Tasmania.
	Pscoridae	Leaf litter dweller	
	Cydnidae	Leaf litter dweller	
	Peloriidae	Leaf litter dweller	
	Coccoidea	Generalist/soil dweller	
	Gelastocoridae	Leaf litter dweller	
	unidentified homopteran nymphs	Leaf litter dweller	
	Encicocephalidae	Leaf litter dweller	
	Schizopteridae	Leaf litter dweller	
	Fulgoridae	Leaf litter dweller	
Collembola	Neonuridae	Leaf litter dweller	Greenslade, P. J. 1991. Collembola. Insects of Australia. CSIRO. Melbourne, CSIRO and Melbourne University Press: 252-264.
	< 2 mm Collembola	Mesoinvertebrates	

Appendix 2

SIMPER on macroinvertebrate abundance data showing the taxa which contributed most to the dissimilarity between disturbed and undisturbed patches from sites with superb lyrebirds (*Menura novaehollandiae*) and samples from control sites without. Overall average dissimilarity between assemblages in disturbed and undisturbed patches was 72.05. L = Leaf Litter dwelling G/S = Generalist soil dwelling. Higher abundances are in bold.

Class/Order	Taxa	Habitat affinity	Average abundance	Average abundance	% Contribution to assemblage differences	% Cumulative contribution
			undisturbed patches	disturbed patches		
Diptera	<5 mm Diptera	G/S	6.1504	2.89	4.3	4.3
Diptera	10 mm Diptera	G/S	3.4969	0.7569	3.64	7.93
Diptera	6-10 mm Diptera	G/S	4	1.6384	3.59	11.52
Annelida	10 mm Oligochaeta	G/S	1.8225	1.3689	3.3	14.82
Annelida	2-5 mm Oligochaeta	G/S	2.56	0.6889	3.01	17.83
Hemiptera	Rhyparochromidae	L	1.3456	0.4624	2.96	20.8
Amphipoda	<i>Keratroides vulgaris</i>	L	1.2769	0.7396	2.94	23.74
Coleoptera	Staphylinid larvae	G/S	0.9216	1.1025	2.86	26.6
Coleoptera	Ptilidae	L	1.2321	0.7056	2.79	29.4

Coleoptera	<i>Atheta</i> TFIC sp 03	L	0.81	1.0404	2.74	32.13
Isopoda	<i>Styloniscus</i> sp	L	1.8496	0.3721	2.58	34.71
Diplopoda	unknown small polydesmid	L	0.7225	0.5184	2.29	37
Hemiptera	Pschoridae	L	0.7921	0.1681	2.15	39.15
Araneae	<5 mm Araneae	L	0.7921	0.36	2.14	41.29
Trichoptera	Calocidae	L	0.6084	0.3481	2.12	43.41
Araneae	6-10 mm Araneae	L	0.7744	0.1296	2.08	45.49
Amphipoda	<i>Mysticotalitrus cryptus</i>	L	0.5329	0.25	2.01	47.5
Coleoptera	<i>Osirus</i> TFIC sp1	L	0.1369	0.6561	1.9	49.4
Lepidoptera	Oecophoridae	G/S	0.6561	0.3481	1.88	51.28
Platyhelminthes	Turbellaria	L	0.9216	0.4489	1.83	53.11
Diplopoda	<i>Paredrodesmus purpensius</i>	L	0.5476	0.2025	1.81	54.92
Coleoptera	Lycidae larvae	G/S	0.4489	0.3721	1.72	56.64
Pseudoscorpiones	Pseudoscorpion	G/S	0.3364	0.0729	1.68	58.32
Opiliones	Palpatories	L	0.3969	0.0729	1.59	59.91
Diplopoda	Procyliosoma	L	0.2601	0.0841	1.51	61.43
Lepidoptera	Tortricidae	G/S	0.4225	0.0121	1.5	62.92

Chilopoda	Steneurytion sp	G/S	0.1521	0.2704	1.48	64.41
Hemiptera	Coccoidea	G/S	0.2025	0.1089	1.48	65.88
Coleoptera	Tenebrionid larvae	G/S	0.0121	0.0256	0.4	87.1
Diplopoda	Polydesmid sp ER3	L	0.0144	0.0064	0.39	87.49
Mollusca	<i>Caryodes dufresnii</i>	L	0.0196	0	0.33	87.83
Mollusca	<i>Pernagera kingstonensis</i>	L	0.0081	0.0036	0.33	88.15
Mollusca	<i>Thryasona marchianae</i>	L	0.0064	0.0036	0.32	88.47
Mollusca	<i>Paralaona halli</i>	L	0.0081	0.0064	0.31	88.78
Coleoptera	<i>Pselaphaulax</i>	L	0.0016	0.0064	0.31	89.09
	CHANDLER Tasmania TFIC sp 1					
Coleoptera	<i>Nargomorphus globulus</i>	L	0.0064	0.0036	0.3	89.38
Mollusca	<i>Mulathena fordei</i>	L	0.0196	0	0.29	89.67
Amphipoda	<i>Mysticotalitrus tasmaniae</i>	L	0.01	0.0009	0.28	89.95
Coleoptera	<i>Rybaxis variabilis</i>	L	0.0064	0.0036	0.27	90.22