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The vulnerability of flightless ground beetles (Carabidae) to climate change in the Australian tropical rainforest

Thesis submitted by

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B.NSc, B.Sc (Hons)
in September 2013

For the degree of Doctor of Philosophy
In the School of Marine and Tropical Biology
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STATEMENT OF CONTRIBUTION OF OTHERS

Chapter 2 of this thesis was submitted, and in review, with a journal prior to submission of this thesis. This work is co-authored with my supervisors (Steve Williams, Simon Robson, Chris Burwell and Geoff Monteith), along with Dr April Reside. The experimental design of each chapter was developed in consultation with a combination of the above-mentioned supervisors. While undertaking this research, I was responsible for the project design, obtaining research funding and permits, collecting field and laboratory data, statistical analysis and interpretation, and synthesis and preparation of the manuscript for submission to a peer reviewed journal. I led the writing of all chapters, with corrections and contributions from Steve Williams, Simon Robson and Chris Burwell. I obtained direct financial support from James Cook University, School of Marine and Tropical Biology, the JCU Centre for Tropical Biodiversity and Climate Change and the Skyrail Rainforest Institute.

DEDICATION

I dedicate this thesis to my father Peter, and mother Jillian. Dad for all your thoughts and advice, as well as significant physical contributions to this project; Mum for always insisting on the importance of education and guiding me along the long path. This thesis is as much a product of your efforts as it is of mine.

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THESIS ABSTRACT

As climate change continues to threaten global biodiversity, knowledge of the fundamental processes influencing species' distributions is vital to determining their vulnerability. This thesis investigated the distributions of a diverse insect group, flightless ground beetles (Carabidae), in the tropical rainforests of Australia. Influences from abiotic (such as climatic) and biotic (such as lowland ant richness) factors were analysed in relation to this group and projections of future distributions, abundance and richness patterns determined under multiple climate change scenarios. This thesis is the most detailed ecological investigation into any flightless insect taxa as well as ants to date within the Australian World Heritage Wet tropics Area (hereinafter the "Wet Tropics").

Flightless ground beetle distributions were determined throughout the Wet Tropics using both spatial distribution modelling and standardised sampling across elevational gradients. The sampling of flightless ground beetles and ants occurred primarily using 210 pitfall traps across elevational transects from 5 separate mountain ranges throughout the Wet Tropics, between 2008 and 2010. Location data from this sampling was combined with data from the Queensland Museum to create spatial distribution models. Additionally, future vulnerability of flightless ground beetles was assessed in a climate change context, under multiple emissions scenarios using distribution modelling techniques. Changes in community patterns were investigated and linked to environmental factors across spatial and temporal frameworks. Finally, relationships between flightless ground beetle and ant (a suggested competitor) richness and abundance changes were investigated.

Flightless ground beetles predominantly inhabit upland areas characterised by stable, cool and wet environmental conditions. These beetles generally displayed highly restricted distributions, and therefore were most species-rich, in mountain-top habitats. Of the climatic variables modelled to best explain this taxa's species richness, maximum temperature of the warmest period contributed the most. These distribution and richness patterns supported the time-stability hypothesis (whereby, more climatically stable

habitats contain greater diversity) as this group's primary habitat, upland rainforest, is considered to be the most stable habitat within the region.

In future, flightless ground beetles throughout the Wet Tropics are projected to substantially reduce their current range sizes, population sizes and species richness under all emission scenarios. These projections were determined using multiple emissions scenarios, derived from the Intergovernmental Panel on Climate Change's Special Report on Emissions Scenarios. Future ranges are projected to contract as distributions shift upwards and subsequently species richness is expected to decline. However, the greatest impact of climate change on flightless ground beetles was indicated to be extreme reductions in abundance, with 88% of species modelled predicted to decline in population size by over 80%, for the most severe emission scenario by the year 2080. Of this taxa, species currently restricted to more marginal mountain ranges (those characterised as drier and with lower summits) are projected to be the most vulnerable to climate change impacts. Seasonal investigations also indicate that, as flightless ground beetles are inactive during dry seasons, projected increases in dry season length will negatively affect this taxa. These results suggest that flightless ground beetles are among the most vulnerable taxa to climate change impacts so far investigated in the Wet Tropics. Such findings have dramatic implications for all other flightless insect taxa and, therefore, the future biodiversity of this region.

Flightless ground beetle communities are highly distinct between subregions throughout the Wet Tropics. Such high levels of dissimilarity of flightless ground beetle assemblages between subregional blocks were attributed to factors including: low dispersal between subregions, a high level of *in situ* evolution, extinction filtering events and current climatic conditions. Regarding current climatic factors, differences between subregional assemblages were linked to changes of: temperature seasonality, maximum temperature, precipitation seasonality, wet season rainfall and minimum temperatures. Furthermore, species richness and abundance of flightless ground beetles significantly increased with elevation throughout the Wet Tropics and therefore species generally inhabit cooler, wetter locations.

Richness and abundance changes of the flightless ground beetle community were not only strongly linked spatial variance in climatic factors, but also seasonal changes.

Beetle activity increased between November and February (during the wet season) and correlated positively with changes in both temperature and precipitation. Across the Wet Tropics landscape, the precipitation seasonality of a site negatively correlated with both richness and abundance of flightless ground beetles. This pattern adds further support to influences from the time-stability hypothesis. Seasonal changes in environmental factors were strongly linked to changes in activity, richness and abundance of flightless ground beetles.

The literature suggests that flightless ground beetles display restricted mountain-top ranges due to either intolerance of lowland climatic factors or overwhelming competition from lowland ant species. Such suggestions were assessed by analysing co-located ant and flightless ground beetle data across multiple elevational transects.

Like flightless ground beetles, the ant community is strongly linked to climatic conditions. However, unlike flightless ground beetles, ants display highly similar assemblages within similar climates throughout the Wet Tropics, regardless of geographical distance, elevation, or potential barriers to dispersal. Consequently, the lowland ant community, which is highly species-rich, is expected to be able to easily migrate up mountains, as climatic conditions become favourable due to climate change. Such migrations would result in much greater species richness in future highland ant assemblages.

Negative correlations were revealed between flightless ground beetles and ant richness and abundance across the elevational gradients. However, despite such correlations, variances in both beetle abundance and richness were best-explained by climatic factors when considered in a combined statistical model. Subsequently, flightless ground beetles are considered to respond primarily to changes in climate, rather than ant richness or abundance, across the elevational gradients. Therefore, any future reductions in flightless ground beetles are expected to predominantly occur due to changes in climatic conditions rather than possible climate-induced changes in ant richness.

Flightless ground beetles are highly vulnerable to projected climate change impacts. This high sensitivity implies that similar flightless mountain-top taxa, the vast majority of which remain unstudied, may be similarly threatened by climate change. Future research must address this lack of understanding if climate change impacts on mountain-top ecosystems are to be comprehensively understood.

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Chapter 1. General Introduction

1.1 Where are species and why?

Where are species and why are they there? These two fundamental questions have driven ecological research for hundreds of years. Many theories have been developed explaining differences in distributions and diversities of taxa across both latitudinal and altitudinal gradients. Such theories often focus on effects from environmental factors such as solar energy, productivity, and physical heterogeneity (Rohde, 1992). As new theories develop, greater understanding arises linking distributional and diversity patterns to environmental factors and ultimately answering these two fundamental questions. Lately, the world's climate has been changing at an extraordinary rate with catastrophic implications to global biodiversity (Malcolm, Liu, Neilson, Hansen, & Hannah, 2006; Pereira et al., 2010; J. A. Pounds et al., 2006; Tewksbury, Huey, & Deutsch, 2008; C. D. Thomas et al., 2004). In efforts to identify the vulnerability of communities to climate change, many studies have reverted to answering these basic ecological questions of where are species and why. Only after these aspects are comprehensively understood can we adequately assess the vulnerabilities of taxa to climate change and mitigate such impacts.

1.2 How is the climate changing?

Globally, temperatures in the last century have risen from approximately the coolest to warmest expressed during the Holocene period (Marcott, Shakun, Clark, & Mix, 2013). Occurrences of local record-breaking monthly temperature extremes are now five times more frequent due to climate change (Coumou, Robinson, & Rahmstorf, 2013). Furthermore, annual maximum daily precipitation rates have significantly increased between 1900 and 2009 (Westra, Alexander, & Zwiers, 2012). Throughout Australia, average temperatures have increased by 0.9°C since 1910 (CSIRO/BoM, 2012). Australia's rainfall has varied greatly, but there is a recent trend of increasing spring and summer monsoonal rainfall across northern regions (CSIRO/BoM, 2012). Projections state that temperatures will increase between 1.1- 6.4°C by the end of this century (Meehl et al., 2007) and dry seasons are expected to become more severe (Suppiah, Macadam, & Whetton, 2007). Additionally, tropical cyclones are projected to occur less frequently, although the proportion of severe cyclones is expected to increase (CSIRO/BoM, 2012; Suppiah et al., 2007). Finally, orographic clouds are projected to form at higher elevations subsequently reducing water supplies to montane environments (Still, Foster, & Schneider, 1999). It is clear that all aspects of climates have been changing drastically and are projected to continue to do so in future.

1.3 Climate change effects on species' distribution and richness patterns

Climate change has profound implications for both the ranges and richness of species worldwide. According to Bellard *et al.* (2012) species will be affected by climate change both temporally and spatially. Temporally, phenological trends may change such as patterns of migration, and periods of growth, activity and hibernation (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Such changes will affect species survival during seasonal changes.

Spatially, terrestrial species are expected to shift ranges either polewards or upwards in elevation in order to maintain tolerable conditions within specific climatic envelopes (Hannah, 2011; Parmesan, 2006). A climatic envelope refers to the area in which suitable conditions exist to allow a species to persist, despite influences from competitors and natural enemies (C. D. Thomas et al., 2004). Species have generally, in the last three decades, shifted boundaries in directions consistent with expectations from climate change (Chris D. Thomas, 2010). Detailed studies, involving temperate species, have already revealed shifts in distribution towards higher latitudes, concurrent with climatic changes, despite barriers such as land use changes (Hickling, Roy, Hill, Fox, & Thomas, 2006; Parmesan & Yohe, 2003; Chris D. Thomas, 2010). Unfortunately, there remains a substantial lack in baseline (and subsequent) studies able to monitor shifts of tropical species' distributions (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008; Chris D. Thomas, 2010). The few tropical range shifts observed only describe movements up elevational ranges (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; J. Alan Pounds, Fogden, & Campbell, 1999; Raxworthy et al., 2008). These findings are consistent with suggestions that tropical species are more are more likely to move ranges higher in elevation rather than latitude as the small distances across elevational gradients are more easily travelled in tropical locations (Bush, 2002; Colwell et al., 2008).

Future studies will hopefully reveal further insight regarding the effects of climate change on temperate and especially tropical species' ranges.

Species richness is widely projected to decline in response to climatic changes (Malcolm et al., 2006; Pereira et al., 2010; J. A. Pounds et al., 2006; Tewksbury et al., 2008; C. D. Thomas et al., 2004). Climate change is caused by greenhouse gas emissions and the greater the emissions the further species must move to maintain their climatic envelopes. In future, when species are unable to maintain adequate climatic envelopes, they are projected to become extinct and species richness subsequently reduced. For example, as tropical habitats warm and species move upwards across elevational gradients, many organisms confined to the tops of mountains are projected to lose their habitat and die out (Williams, Bolitho, & Fox, 2003). Furthermore, organisms moving upwards from the lowlands are unlikely to be replaced resulting in species poor lowland habitats (Colwell et al., 2008). Both processes combined indicate substantial losses of montane tropical species due to climate change. Accordingly, projections indicate that greater levels of emissions are linked to greater warming and therefore higher species losses (C. D. Thomas et al., 2004).

Tropical species are suggested to be more sensitive to climate change than temperate species, despite relatively smaller changes in temperatures predicted to occur in tropical regions (Tewksbury et al., 2008). This is because tropical species currently live close to upper thermal tolerances and are highly sensitive to climatic changes such as increased temperatures (Curtis A. Deutsch et al., 2008). Malcolm et al. (2006) investigated extinctions resulting from projected habitat changes due to climate change. Species with narrow, rather than broad, habitat specificities were at much greater risk of extinction from climate change impacts (Malcolm et al., 2006). Tropical species with narrow ranges are therefore considered to be highly vulnerable to extinction from climate change.

1.4 Altitudinal gradients as climate change surrogates

Environmental gradients are useful tools for predicting climate change effects on species (Andrew & Hughes, 2004). As elevation increases in tropical mountains, temperature decreases approximately 1°C per 200 meters (L. Shoo, Williams, & Hero, 2005) and water availability can rise due to greater precipitation and cloud stripping (water deposition from clouds intercepting forests; Egger & Hoinka, 1992; McJannet, Wallace, & Reddell, 2007). In efforts to better understand the implications of climate change on communities, elevation transects are used as surrogates whereby compositional changes such as differences in species turnover and richness are linked to environmental factors (Bruhl, Mohamed, & Linsenmair, 1999; Fleishman, Fay, & Murphy, 2000; Hodkinson, 2005).

Tropical species often show higher habitat specificity or endemism than temperate species and therefore are expected to display high levels of turnover across elevational gradients (D. Olson, 1994). Species turnover measures the compositional change of assemblages across a gradient (Arita & Rodriguez, 2002). Tropical studies using elevational transects show that as elevation increases, high turnover of species assemblages occurs with highland species being distinct from lowland species (Escobar, Lobo, & Halffter, 2005; Fisher, 1999; Monteith & Davies, 1991; D. Olson, 1994). Subsequently, even tropical mountains, which may be relatively small in area, are still able to support highly diverse communities.

Species richness patterns across elevational gradients have been noted to differ greatly between taxa with three trends most commonly reported. First, generally species richness declines as elevation increases, although not always monotonically (C. Rahbek, 1995). Studies have attributed this pattern to a variety of environmental factors including changes in solar energy, water availability and primary productivity availability (Brown, 1973; B. L. Fisher, 1998; Janzen, 1967). Second, mid-elevational peaks in richness have also been recorded and attributed to overlapping distributions of highland and lowland habitat specialists (Escobar et al., 2005). Third, increases in richness with higher elevations can occur and are suggested to be driven by factors such as predation from, or competition with, lowland species as well as intolerances of lowland climatic conditions (Brehm & Fiedler, 2003; Coulson & Whittaker, 1978; Darlington, 1971; D. Olson, 1994). Investigating how patterns of species turnover and richness across elevational gradients correlate with environmental factors give much insight into suitability of habitats for species and future impacts of climatic changes on assemblage structures and biodiversity.

1.5 The Wet Tropics bioregion and associated climate change research

Within Australia, the Australian Wet Tropics World Heritage Area (hereinafter ‘the Wet Tropics’) is a mountainous region supporting Australia’s only tropical rainforest. The Wet Tropics have been listed as a World Heritage Area since 1988 due to high levels of biodiversity and endemism (Williams et al., 2003). This region is approximately 10,000 km² in area and is dominated by woodlands and rainforest (Hilbert, 2008). The Wet Tropics has been referred to as a “mesotherm archipelago” as it is composed of a series of distinct high elevational mountain ranges separated by lowland gullies or relatively dry areas (Nix, 1991; Williams et al., 2003). As elevation increases, rainforest types generally change from complex mesophyll vine forest in fertile lowlands to upland simple notophyll vine forest (Adam, 1992). High annual rainfall occurs throughout the Wet Tropics, with 2,000 – 8,000 mm annually received in coastal areas, mostly between December to March (Bonell & Callaghan, 2008). Approximately one-third of the Wet Tropics bioregion is higher than 600 m a.s.l., where annual mean temperatures are below 22°C (N. E. Stork, Goosem, & Turton, 2009). Throughout the region extreme temperatures have been noted to reach from -2°C to 45°C (Metcalfe & Ford, 2008). The presence of such high biodiversity associated with unique geography and climate have attracted a variety of studies aimed at linking patterns displayed by species to environmental factors.

Tropical rainforest species have been collected and documented since the 1860’s when the Wet Tropics region was first settled by Europeans (Yeates & Monteith, 2008). In the 20th Century species restricted to remote montane peaks were revealed during expeditions by notable biologists such as P. J. Darlington Jr, who sampled throughout the Wet Tropics both during 1931-32 and 1956-58 (Darlington, 1961). More recently, the Queensland Museum led substantial field surveys during the 1980’s and 1990’s creating a database of almost 40,000 specimens from 457 localities (Yeates & Monteith, 2008). During this time Frith and Frith (1985; 1990) investigated seasonal changes in abundance of leaf litter invertebrates in the Wet Tropics and significant work occurred linking vertebrate richness and endemism patterns to historical events (Williams, 1997; Williams & Pearson, 1997).

Climate change now poses significant threats to biodiversity and consequently studies have investigated associated environmental implications within the Wet Tropics. Hilbert *et al.* (2001) modelled climate change impacts of highland vegetation within the Wet Tropics projecting up to 50% of range lost due to only one degree of warming. Williams (2003) anticipated that 65 endemic vertebrates in the Wet Tropics would experience substantial losses of range with one degrees of warming. Additionally, almost half of these species were expected to lose their core habitats with three and a half degree of warming (Williams et al., 2003). A further study by Hilbert et al. (2004) projected that the endemic golden bowerbirds would lose 60% of their current range where temperature increased by one degree and rainfall reduced by 10%. Of 55 rainforest bird species examined by L. Shoo et al. (2005), 74% were predicted to reduce in population size to a point where they were classified as threatened (26 of which, critically endangered) due to three and a half degree of warming. Clearly vertebrates in the Wet Tropics, especially regional endemics, are projected to be highly vulnerable to climate change impacts.

Studies within the Wet Tropics concerning the responses of insects to climate change are limited to species from the dipteran sub-order Shizophora. These projections highlight extinction risks of highland schizophoran species due to warming between two to three degrees and substantial losses in richness from warming above three degrees (R. D. Wilson, 2010; Rohan D. Wilson, Trueman, Williams, & Yeates, 2007). To date insects of low vagility and endemic to the Wet Tropics, of which 274 are known to exist (Yeates & Monteith, 2008), have yet to be assessed in relation climate change impacts. However, Williams *et al.* (2008) suggest that such insects will be as vulnerable to climate change impacts as regionally endemic vertebrates.

1.6 Flightless ground beetles

Flightless ground beetles display extremely low vagility and represent a major component of invertebrate taxa endemic to the Wet Tropics (Yeates & Monteith, 2008). These beetles are of the family Carabidae, commonly known as ground beetles, for which approximately 40,000 species have been described internationally making it a major coleopteran family (Lovei & Sunderland, 1996). Ground beetles are usually separable from other beetles by their general shape, filiform antennae, prognathous head with obvious mandibles and antennal cleaners on both protibia (Lawrence & Britton, 1991).

Historically, the vast majority of ground beetle taxonomic work derived from temperate regions (Lovei & Sunderland, 1996; New, 1998). Within Australia, Castelnau and Sloane produced much of the early ground beetle taxonomic work since the 1860’s (Horne, 2007).

Following them, Darlington collected and identified a broad range of rainforest species across the eastern coast of Australia (Darlington, 1961). More recently, M. Baehr and B. P. Moore conducted a plethora of taxonomic studies of Australian ground beetles. Extensive collecting of Queensland fauna was also performed by G. B. Monteith and colleagues associated with the Queensland Museum.

Like the taxonomic work concerning ground beetles, the knowledge base regarding ecological aspects of this group is heavily biased towards temperate research (Horne, 2007; Kromp, 1999). Ground beetles are generally polyphagous and mainly predate upon other epigaeic invertebrates (Rykken, Capen, & Mahabir, 1997). A notable exception is the tribe Harpalini which is generally phytophagous (Lawrence & Britton, 1991) and have therefore been investigated in agricultural studies (Kromp, 1999). Within Australia the well-known genera *Calosoma* consume caterpillars and *Pamborus* has been documented to predate on earthworms and snails (Lawrence & Britton, 1991).

Flightless ground beetles, like other flightless insect taxa restricted to highland habitats, display a high level of endemism throughout the Wet Tropics (Yeates, Bouchard, & Monteith, 2002). Wet Tropics endemics are highly vulnerable to climate change impacts especially those displaying low vagility and are restricted to mountain-top habitats (Williams et al., 2003). To date limited knowledge exists linking the distributions of Wet Tropics ground beetles, and changes in richness and abundance, to environmental factors. Flightless ground beetles have been suggested to display restricted highland distributions in response to either intolerances from lowland climates or pressure from competition with lowland ants (Darlington, 1971; D. M. Olson, 1994). Ants are considered to be the stronger competitor and actively exclude ground beetles through either predation or competition (Darlington, 1943; Hawes, Stewart, & Evans, 2002; Reznikova & Dorosheva, 2004). Researching such relationships is a major step towards understanding the vulnerability of this group to climate change and implementing appropriate measures to reduce extinction risks.

1.7 Thesis structure

This thesis explores distributional, richness and abundance patterns of flightless ground beetles in the Wet Tropics. These trends are related to colocated abiotic and biotic environmental factors and the vulnerability of these flightless ground beetles is investigated in a climate change context. The first data chapter, Chapter 2, utilises species distribution modelling to define the extent of current distributions of individual flightless ground beetles throughout the Wet Tropics. Environmental correlates best describing beetle distributions, as well as species richness changes, throughout the Wet Tropics are further analysed and impacts of climate change on these patterns are determined.

While distributional models are extremely useful in linking theoretical distributions of organisms to environmental correlates, sufficient baseline data is also required to comprehensively assess impacts of climate change on assemblages (L. P. Shoo, Williams, & Hero, 2006). In Chapter 3, standardised data was collected, for the first time, of flightless ground beetles using pitfall traps across altitudinal transects within five subregions throughout the Wet Tropics. Compositional patterns of the flightless ground beetle community, both across elevational gradients and between subregions, were investigated. Furthermore, turnover of assemblages and changes in richness and abundance were linked to environmental factors. This standardised methodology also provides a valuable empirical data set from which patterns expressed in Chapter 2 may be reinforced.

Climate change impacts species not only spatially, but also temporally (Bellard et al., 2012). It is therefore also vital to link richness and abundance changes of flightless ground beetles within the Wet Tropics to seasonal variances in climatic conditions. Chapter 4 uses pitfall trap data from a two-year period, across multiple elevations and subregions, to describe temporal changes in richness and abundance of flightless ground beetles. Abundance changes are also related to seasonal variances of temperature and precipitation. Additionally, this chapter investigates relationships between precipitation and temperature seasonality, across the Wet Tropics landscape, and abundance and richness of flightless ground beetles.

While climate affects the range boundaries of many terrestrial species, biological interactions may also play large roles (Chris D. Thomas, 2010). Flightless ground beetles display distributions which may also be affected by competition with lowland ants (Darlington, 1971; D. Olson, 1994). If so, expected upwards migration of such lowland species, due to climate change impacts, will have serious implications for flightless ground beetles. While some preliminary studies of ant species within the Wet Tropics have been performed (Majer, Kitching, Heterick, Hurley, & Brennan, 2001; van Ingen, Campos, & Andersen, 2008; Yek, Williams, Burwell, Robson, & Crozier, 2009) much more detailed ecological studies are required to understand the patterns within this community. The final data chapter therefore investigates current distributions of ants within the Wet Tropics and determines patterns of richness across an altitudinal gradient. Variance in ant richness is then assessed against climatic factors to determine which variables best explain richness and abundance changes of flightless ground beetles in the Wet Tropics. This assessment gives an insight into the risk lowlands ant pose, compared to climatic changes, to future populations of flightless ground beetles in the Wet Tropics.

Finally, Chapter 6 is a general synthesis of the results and findings from each data chapter, outlining the main implications of this thesis and proposing directions for future research.

Chapter 2. Projected distributions and diversity of flightless ground beetles within the Wet Tropics and their environmental correlates.

Staunton, K., Robson, S. K. A., Burwell, C. J., Monteith, G. B., Reside, A. E. & Williams, S. E.

2.1 Abstract

With the impending threat of climate change, greater understanding of patterns of species distributions and richness and the environmental factors driving them are required for effective conservation efforts. Species distribution models enable us to not only estimate geographic extents of species and subsequent patterns of species richness, but also generate hypotheses regarding environmental factors determining these spatial patterns. Projected changes in climate can then be used to predict future patterns of species distributions and richness. We created distribution models for most of the flightless ground beetles (Carabidae) within the Wet Tropics World Heritage Area of Australia, a major component of regionally endemic invertebrates. Forty-three species were modelled and the environmental correlates of these distributions and resultant patterns of species richness were examined. Flightless ground beetles generally inhabit upland areas characterised by stable, cool and wet environmental conditions. These distribution and richness patterns are best explained using the time-stability hypothesis as this group's primary habitat, upland rainforest, is considered to be the most stable regional habitat. Projected changes in distributions indicate that as upward shifts in distributions occur, species currently confined to lower and drier mountain ranges will be more vulnerable to climate change impacts than those restricted to the highest and wettest mountains. Distribution models under projected future climate change suggest that there will be reductions in range size, population size and species richness under all emission scenarios. Eighty-eight per cent of species modelled are predicted to decline in population size by over 80%, for the most severe emission scenario by the year 2080. These results suggest that flightless ground beetles are among the most vulnerable taxa to climate change impacts so far investigated in the Wet Tropics World Heritage Area. These findings

have dramatic implications for all other flightless insect taxa and the future biodiversity of this region.

2.2 Introduction

Climate change is expected to negatively impact biodiversity due to increased exposure of species to deleterious climatic conditions. Many studies have raised concern that this is potentially one of the greatest threats to global biodiversity ever faced (Malcolm et al., 2006; Pereira et al., 2010; J. A. Pounds et al., 2006; Tewksbury et al., 2008; C. D. Thomas et al., 2004). Species' distributions have already shifted upwards in elevation and polewards in response to climate change (Hannah, 2011; Parmesan, 2006). Montane fauna, especially those with limited dispersal abilities, are generally unable to migrate higher than the mountain they currently inhabit and are therefore highly threatened from climate change due to projected range contractions (Hijmans & Graham, 2006). Temperatures are predicted to increase by 1.1- 6.4°C by the end of this century (Meehl et al., 2007). With the vulnerability of dispersal-limited montane fauna to climate change, a greater understanding of the links between environmental conditions and species' distributions and resultant biodiversity patterns is vital to conservation biology and biodiversity management.

Multiple factors drive the distributions of species and therefore patterns of biodiversity (Gaston, 2000). Climate is generally thought of as the primary driver of terrestrial species' distributions (Chris D. Thomas, 2010). Consequently, the climatic envelopes of species (the area in which suitable conditions exist, allowing a species to persist despite influences from competitors and natural enemies) have been modelled and used to project range shifts in response to future climatic impacts (Hijmans & Graham, 2006; Chris D. Thomas, 2010; C. D. Thomas et al., 2004).

Globally, species richness increases toward the equator, and several environmental parameters, such as solar energy, productivity and physical heterogeneity, have been suggested to drive this pattern (Rohde, 1992). These same parameters have also been used to explain changes in species richness across elevational gradients, where, for example, lowland areas exposed to higher levels of solar energy are more productive and therefore may support more species than uplands habitats (C. Rahbek, 1995). Other studies have reveal mid-elevational peaks in richness which are attributed to factors such as overlapping ranges of lowland and upland specialist fauna (B. L. Fisher, 1998; Pyrcz & Wojtusiak, 2002). Additionally, richness may peak at high elevations in response to favourable climatic conditions or greater resource availability (Coulson & Whittaker, 1978; Niemelä, Rousi, & Saarenmaa, 1987).

Often, explanations for biodiversity patterns overlook historical factors which may exert considerable influence on current assemblage structure and species richness, especially for taxa with low dispersal abilities (Graham, Moritz, & Williams, 2006). Theories incorporating the influence of historical factors on species assemblages include the time-stability hypothesis, where habitat stability affects the rate of *in situ* evolution of species (Pianka, 1966), and the species filtering effect, where changes in historical environmental conditions selectively drive local populations extinct resulting in patterns of species richness determined largely by the process of non-random extinction, rather than evolution (Graham et al., 2006; Williams & Pearson, 1997). Whether the theories which contribute to biodiversity patterns consider current or historical influences, it is important to note that changes in biodiversity are most likely caused by a variety of factors rather than simply one mechanism (Willig, Kaufman, & Stevens, 2003).

The tropical rainforests of the Wet Tropics World Heritage Area of Australia (hereafter the “Wet Tropics”) boast among the highest levels of biodiversity within Australia (1986). The mean saturated adiabatic lapse rate of temperature within the rainforest of the Wet Tropics is approximately 1°C per 200 m in altitude (L. Shoo et al., 2005). Therefore, species within this area would be expected to shift their distributions upwards by 220 – 1280 m by the year 2100. Clearly, distributional shifts of this magnitude are likely to have substantial impacts on assemblage composition and biodiversity. In fact, Williams *et al.* (2003) predicted catastrophic declines in regionally-endemic vertebrates within the Wet Tropics rainforests. Whilst much effort has been devoted to investigating the drivers of biodiversity of *vertebrates* within the Wet Tropics (Williams, Isaac, Graham, & Moritz, 2008), the vast majority of work concerning *invertebrates* has been taxonomic in nature and links between biodiversity of these taxa and environmental data remain to be comprehensively established. Invertebrate species account for 75% of biodiversity worldwide (E. O. Wilson, 1988) and are responsible for a multitude of vital ecosystem functions (Kim, 1993). Understanding environmental factors driving invertebrate distributions and richness within the Wet Tropics is, therefore, crucial to determining the ecological impacts of climate change in this region.

Among the invertebrate fauna of the Wet Topics region, flightless insects, particularly Coleoptera and Hemiptera, have been relatively well studied. Of these flightless insects, 50% of a group (containing 274 species) studied by Yeates *et al.* (2002) were endemic to single subregions (geographically distinct upland forest blocks). This is a high proportion when compared to 15% of vertebrates endemic to single subregions in rainforests of the Wet Tropics (Williams & Pearson, 1997; Yeates et al., 2002). A diverse group of flightless insects within the Wet Tropics is predatory beetles from the family Carabidae, commonly known as ground beetles. Ground beetles are well-known and highly diverse with approximately 40,000 described species globally (Lovei & Sunderland, 1996). Carabid beetles can be divided into three main habitat-specific groups; those associated with the ground (the vast majority of species), arboreal or aquatic habitats (Darlington, 1943; New, 1998). The Australian carabid fauna contains an abnormally high proportion (~45%) of species with atrophied wings (Darlington, 1961) and furthermore, about 75% of ground-associated species are flightless (Darlington, 1961). As ground beetles are generally predatory, feeding on other leaf litter invertebrates, they form an important functional group in forest-floor habitats (Rykken et al., 1997).

While the taxonomy of flightless ground beetles within the Wet Tropics is well known, few studies have addressed the environmental factors affecting their distributions and diversity. This study utilises a species distribution modelling approach to elucidate environmental factors that most significantly contribute to explaining observed spatial patterns of species distributions and richness of flightless ground beetles. We then use species distribution models, in combination with projected emission scenarios in the region, to predict the impacts of future climatic change on the distributions and diversity of this important group.

2.3 Methods

2.3.1 Study area

This study was conducted in north-eastern Australia (20° to 15°S and 147° to 145°E) within the Wet Tropics bioregion which is approximately 10,000 km² in area (Figure 2.1). The Wet Tropics has been listed as a World Heritage Area since 1988 due to the high biodiversity and endemism of the region's rainforests. This study was confined to rainforest and covered a range of structural rainforest types across elevational gradients from complex mesophyll vine forest in the fertile lowlands to upland simple notophyll vine forest and, in the case of Bellenden Ker Uplands, simple microphyll vine-fern thickets above 1,500 m a.s.l. (Adam, 1992).

Generally, annual rainfall throughout the Wet Tropics is high (2,000 – 8,000 mm per year) (Bonell & Callaghan, 2008) with approximately 75 - 90% of precipitation falling between November and April (McDonald & Lane, 2000). Additionally, rainforests located at elevations above 1,000 m a.s.l. receive up to 66% of their monthly water input from cloud stripping (McJannet et al., 2007). Rainfall estimates, therefore, under-estimate total water input. Approximately one-third of the Wet Tropics bioregion is higher than 600 m a.s.l., where annual mean temperatures are below 22°C (N. E. Stork et al., 2009).

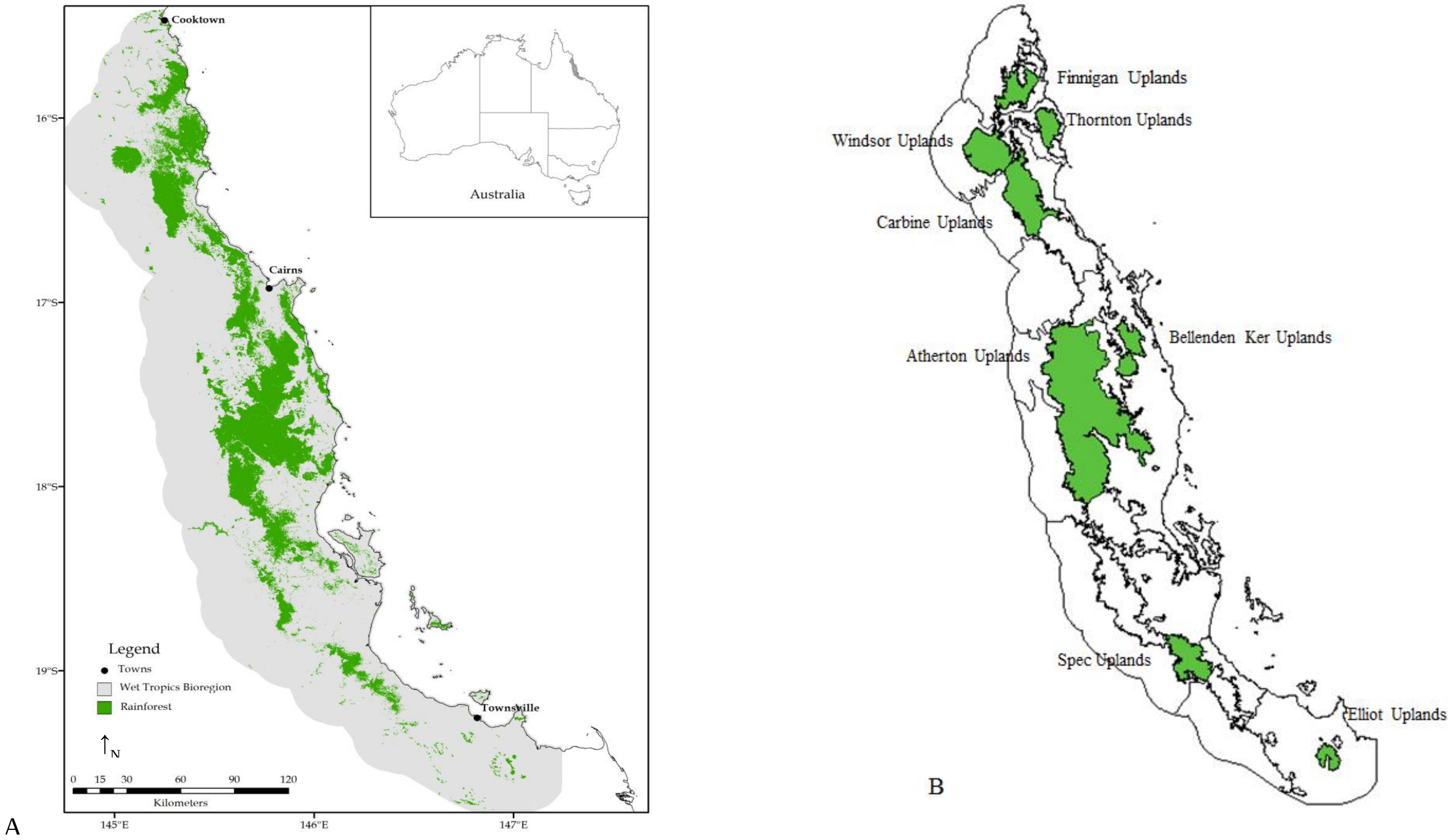


Figure 2.1. Map of the Wet Tropics bioregion: A. showing the current extent of rainforest, **B.** highlighting subregions specifically discussed in this paper.

2.3.2 Species data

Carabid beetle species data consisted of 949 geographically unique records of 43 flightless species. Locality records of species were primarily accessed from the specimen database of the Queensland Museum and additional data, obtained from specimens collected during this study, are lodged with, and available from the Centre for Tropical Biodiversity and Climate Change. These data were used to model the distributions of the 43 species within the Wet Tropics region. The number of data points varied considerably among species. The most commonly recorded species was *Castelnaudia obscuripennis* with 92 point localities while the least common was *Pamborus elegans* with only three records confirmed by the Queensland Museum. While using models derived from only three point localities is not ideal, expert inspection of the model deemed it a good representation of the extremely restricted distribution of this species and therefore warranted its use.

2.3.3 Environmental data

Bioclimatic variables used to model carabid distributions were annual mean temperature (BC01), temperature seasonality (BC04), maximum temperature of warmest period (BC05), minimum temperature of coldest period (BC06), annual precipitation (BC12), precipitation seasonality (BC15), precipitation of wettest quarter (BC16) and precipitation of driest quarter (BC17). These variables have been strongly linked to vertebrate and dipteran distributions in the Wet Tropics (J. Vanderwal, Shoo, Graham, & Williams, 2009; Jeremy VanDerWal, Shoo, Johnson, & Williams, 2009; R. D. Wilson, 2010). These climate data were used as the baseline climate, defined as a 30 year average centred around 1990 (between 1976 and 2005). The bioclimatic variables were derived using the Anuclim 5.1 software (McMahon, Hutchinson, Nix, & Ord, 1995) and a 80-m-resolution digital elevation model (DEM; resampled from GEODATA 9-second DEM, ver.2; Geoscience Australia, http://www.ga.gov.au/).

Vegetation data used were the National Vegetation Information System broad vegetation subgroups (Australian Government Department of the Environment & Water Resources, 2004) at a resolution of 250 m. These data comprise 32 major vegetation types throughout the Wet Tropics. The Wet Tropics region was delineated into subregions as defined in detail in Williams et al. (2010) (Figure 2.1B).

2.3.4 Species distribution models

Species distributions models (SDMs) were generated using Maxent, a maximum entropy algorithm (Maxent v. 3.3.3; [46]). Default settings were used (Steven J. Phillips & Dudík, 2008). Maxent is a machine learning modelling technique which utilises the concept of maximum entropy to model species distributions (S.J. Phillips, Anderson, & Schapire, 2006; Wisz et al., 2008). The explanatory variables in each of the models were the eight bioclimatic variables and 32 vegetation types. As Maxent automatically regulates effects of correlated variables, only ecologically insignificant variables need to be removed (Elith et al., 2011). The resulting potential distributions were clipped by subregions within which species are known to be present (from the occurrence records) to reduce overestimations of species distributions (R. P. Anderson, Lew, & Peterson, 2003). These realised distributions were reviewed by the expert on this insect group within this region (Geoff Monteith) and incongruous points were removed and the models rerun or inadequate models removed completely. All models presented had area under the receiver-operating characteristic curve (AUC) values greater than 0.9 and are therefore considered to perform excellently (Pearce & Ferrier, 2000). The use of the AUC metric has been criticised regarding concerns such as its: equal treatment of commission and omission errors, spatial independence and relationship to the spatial extent investigated (Jiménez-Valverde, 2012; Lobo, Jiménez-Valverde, & Real, 2008; Peterson, Papeş, & Soberón, 2008). However, Jiménez-Valverde (2012) state that all of these concerns are common to any discrimination measure used in this context, not just the AUC. Furthermore, Santika (2011) found that the AUC metric correctly identifies a model's ability to successfully capture the dominant environmental determinants. This ability of the AUC metric to successfully capture dominant environmental determinants, in combination with opinions of the expert reviewer, makes it useful in this study.

Future species distributions were generated by projecting each species model onto future climate scenarios (S.J. Phillips et al., 2006). For this model run of baseline and future projections, the same eight bioclimatic variables were used; however, vegetation type was excluded. Using vegetation type in future models is beyond the scope of this project for several reasons: 1) no future projections of vegetation type are available for use in modelling, 2) using modelled future vegetation projections would substantially increase the uncertainty of the projected species distributions, and 3) climate is a good proxy for future vegetation (Hilbert, 2008). The climate for 2080 was based on a 30 years average between 2066 and 2095. Future climate surfaces were derived from the Intergovernmental Panel on Climate Change's Special Report on Emissions Scenarios (SRES) three scenarios of B1, A1B, and A2 (Nakicenovic et al., 2000). Projections of global greenhouse gas emissions, and subsequent global temperatures, increase progressively with each scenario from B1 to A1B to A2 (IPCC, 2007a). Eight global circulation models (GCMs), from the IPPC fourth assessment report (IPCC, 2007b), were used to create future climate layers including: BCCR-BCM 2.0, CSIRO-Mk 3.0, CSIRO-Mk 3.5, GISS AOM, INM CM 3.0, MIROC 3.2 (hires), MIROC 3.2 (medres) & NCAR CCSM 3.0. Effects of each model on determining future climate layers were weighted to account for unequal numbers of realisations between GCMs and years (Reside, VanDerWal, & Kutt, 2012). Also, similar to Reside *et al.* (2012), mean projections for each year and scenario were obtained by initially summarising the multiple realisations within GCM and then across GCMs.

Multivariate analyses utilised additional environmental data considered most relevant to the ecology of these carabids including slope, aspect, distance to stream and foliage projected cover. Spatial surfaces of slope and aspect were derived from a 250 m digital elevational model obtained from Geoscience Australia (resampled from GEODATA 9S DEM Version 2; Geoscience Australia, http://www.ga.gov.au/). Both slope and aspect surfaces were created using the *r.slope* command in the GRASS package from the R statistical program v2.12.1 (R Development Core Team, 2010; Storlie, Phillips, VanDerWal, & Williams, 2013). The surface of distance to stream (ln(distance+1)), was built using Spatial Analyst in ESRI ARCGIS and maps from Geoscience Australia's Global Map Australia 1M 2001 product (http://www.ga.gov.au/nmd/products/digidat/1m.htm). Foliage projected cover was obtained from the Queensland Department of Natural Resources and Water over a 30-year average at 250 m resolution (Storlie et al., 2013).

2.3.5 Statistical analyses

A species richness layer was created as an ASCII file so that the environmental variables best correlated with changes in richness could be determined. Firstly, distribution models for each species were converted to a binary format. To do this the areas with a probability of presence either equal to or greater than a threshold value that minimizes 6 * training omission rate + 0.04 * cumulative threshold + 1.6 * fractional predicted area, were set to one (suitable). All other areas within the models were set to zero (unsuitable). This threshold has been determined to produce the most realistic distributions by experts concerning species within this region (Williams et al., 2010). All 43 species distribution models were then summed and each 80 m by 80 m cell was represented by a cumulative value.

We randomly extracted 10,000 points from the species richness layer and used best sub-set multiple linear regression to analyse correlations between richness values and co-located environmental data (bioclimatic, vegetation and other environmental factors) using the *leaps* package from the R statistical program v2.12.1 (R Development Core Team, 2010). The best models derived from any combination of the explanatory variables were determined using Bayesian Information Criterions (BICs). This statistical modelling technique differs slightly from the more standard variable selection methods of stepwise regression, as it better accounts for co-linearity problems between explanatory variables (Mac Nally, 2000). However, some removal of significantly correlated variables was still required. The final model selected used four environmental factors as addition of a fifth produced only marginal improvements in the BIC (-9490 for four factors, -9541 for five factors). To visualise the significant relationships, species richness and environmental factor residuals from this model were plotted using the *car* package from the R statistical program v2.12.1 (R Development Core Team, 2010).

The species richness layer was also weighted by endemism to visually assess which areas contained higher proportions of species with restricted ranges. Rather than using a value of one to indicate presence of a species for a given cell when overlaying individual SDMs to create a species richness model, the inverse of each species' area of range size, derived from Maxent output, was used. Therefore subregions containing a high proportion of species displaying restricted ranges expressed comparatively higher values than subregions dominated by species with larger ranges.

Projected changes in the proportion of total abundance of each species were calculated using the approach described in VanDerWal *et al*. (2009b). This approach assumes a relationship between environmental suitability and a species' abundance. Environmental suitability was derived from the probability of presence value provided by the Maxent species distribution model output. Summed environmental suitability across a species' distribution can be used as an index of total population size (Jeremy VanDerWal, Luke P Shoo, et al., 2009). Therefore, proportional changes in total abundance can be estimated from changes in environmental suitability derived from the projected future model output. Proportional changes in total abundance for each species were averaged for each model output per decade. These resulting decadal averages for all 43 species were then averaged again to give an estimate for the entire group, per emission scenario outlined above.

Best sub-set multiple linear regression was used to determine which combination of bioclimatic variables best explained variation in the proportional changes in total abundance of the 14 most vulnerable (those projected to lose >50% of current population) subregional endemic species (for simplicity, only results from the year 2080 and SRES A2 are shown). This analysis used the *leaps* package from the R statistical program v2.12.1 (R Development Core Team, 2010). A Fisher test, using the *fisher.test* function in the R statistical program v2.12.1 (R Development Core Team, 2010), was also run to determine if there was a positive association between occupation of drier habitats and higher reduction in proportional abundance for all 16 subregional endemics (year 2080, SRES A2). Species projected to lose more of their proportional abundance by 2080 were inferred to be at higher risk of extinction than those projected to maintain more of their abundance.

2.4 Results

2.4.1 Species distribution models

The distribution modelling outputs for the flightless ground beetles highlighted that almost half (20) of the 43 species are predicted to be distributed solely within the central Wet Tropics (Figures 2.2 – 2.7). Of these centrally located species five are predicted to exclusively occur within Bellenden Ker Uplands while a further 12 species had broader distributions extending into adjacent mountain ranges. Thirteen species are predicted to be restricted to the northern subregions with only small southern extensions of distributions predicted over the Black Mountain Barrier for *Leiradira opacistriatus* and *Pamborus euopacus*. Two northern species, *Notonomus NQ1* and *Pamborus elegans*, are endemic to Windsor Uplands, a western mountain range situated in the rain shadow of the Carbine

Uplands. Of the five southern species modelled, the highly restricted *Nurus rex* and *Notonomus ellioti* were only found in Mt Elliot, the most southern mountain in the Wet Tropics bioregion. Finally, five species, each from different genera, had widespread predicted distributions throughout the Wet Tropics with *Pamborus tropicus* displaying the greatest range of all flightless ground beetles examined, inhabiting such diverse sub-regions as Windsor Uplands, Bellenden Ker Uplands and south to Spec Uplands. These results are consistent with previous findings published on this group (Monteith, 1994b).

Climatic and vegetation variables used in the Maxent species distribution models were ranked according to their relative contributions to the model. The three most important environmental predictors of each species' distribution and their relative percentage contribution to each model are presented in Figures 2. 2 – 2.7. Maximum temperature of the warmest period was most frequently the most important factor contributing to the SDMs, including those of all five widespread species were most highly correlated with the maximum temperature of the warmest period. Precipitation variables contributed most to explaining distribution patterns of many species restricted to the central Wet Tropics and vegetation type made the most significant contribution to the distributions of five northern, three central and three southern species.

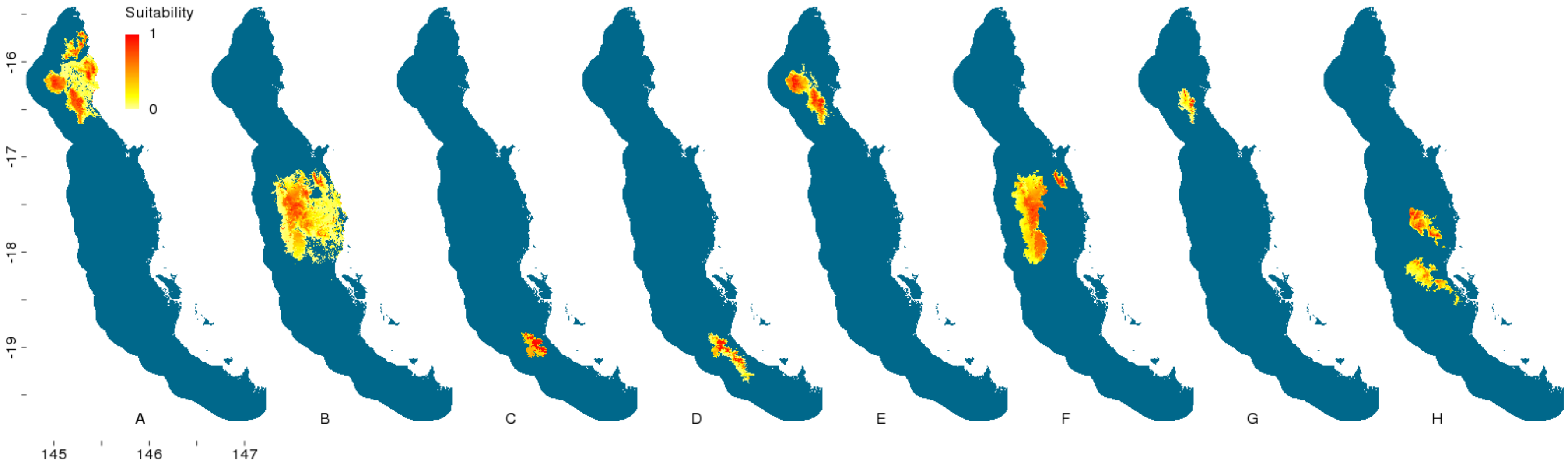


Figure	A.	B.	C.	D.
Species	*Castelnaudia obscuripennis*	*Castelnaudia setosiceps*	*Castelnaudia sp1.*	*Castelnaudia spec*
Environmental variables	temperature seasonality 38.9	precipitation seasonality 53.7	vegetation type 35.7	vegetation type 37.8
	max. temp. of warmest p. 23.8	vegetation type 21.2	temperature seasonality 34.8	temperature seasonality 15.8
	vegetation type 22.1	max. temp. of warmest p.18.5	precipitation seasonality 15.7	min. temp. of coldest p. 15.5
Figure	E.	F.	G.	H.
Species	*Coptocarpus NQ1*	*Coptocarpus philipi*	*Habutarus nitidicollis*	*Laccopterum NQ1*
Environmental variables	vegetation type 32.9	vegetation type 36.3	vegetation type 61.4	vegetation type 32.5
	temperature seasonality 28.2	precipitation seasonality 28.7	max. temp. of warmest p.18	precipitation seasonality 28.8
	max. temp. of warmest p. 24.8	annual mean temperature 23.4	temperature seasonality 9.9	max. temp. of warmest p. 17.7

Figure 2.2A-H: Distribution models of flightless ground beetle species in the Wet Tropics bioregion. Noted are the three highest-ranked environmental correlates selected by Maxent with percentage contribution of each variable to the model. Max. temp. of warmest p. = maximum temperature of the warmest period, min. temp. of coldest p. = minimum temperature of the coldest period. Habitat suitability for each species is indicated in a gradient from yellow (less suitable) to red (highly suitable). Blue areas are considered unsuitable for the species.

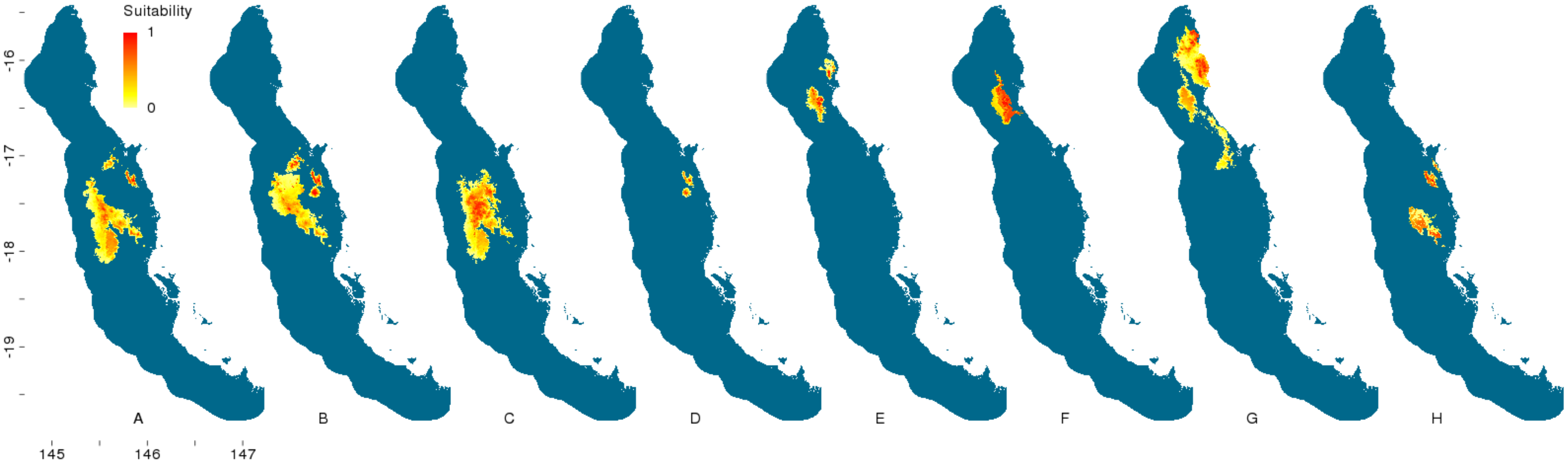


Figure	A.		B.		C.		D.	
Species	*Lacordairia NQ2*		*Lecanomerus niger*		*Leiradira alternans*		*Leiradira alticola*	
Environmental variables	annual mean temperature	40.8	max. temp. of warmest p.	66.8	vegetation type	34.3	precipitation of driest q.	47.7
	precipitation seasonality	36.1	precipitation seasonality	8.6	max. temp. of warmest p.	26.6	precipitation seasonality	17.2
	vegetation type	23	precipitation of driest q.	7.2	precipitation seasonality	21.6	max. temp. of warmest p.	14.2
Figure	E.		F.		G.		H.	
Species	*Leiradira NQ2*		*Leiradira NQ3*		*Leiradira opacistriatus*		*Leiradira soror*	
Environmental variables	vegetation type	42.5	temperature seasonality	43.3	temperature seasonality	40.6	precipitation of driest q.	54.1
	max. temp. of warmest p.	33.1	vegetation type	41.9	max. temp. of warmest p.	34.5	vegetation type	37.6
	temperature seasonality	16.1	annual precipitation	11.3	annual precipitation	16.7	precipitation seasonality	2.2

Figure 2.3A-H. Distribution models of flightless ground beetle species in the Wet Tropics bioregion. Noted are the three highest-ranked environmental correlates selected by Maxent with percentage contribution of each variable to the model. Max. temp. of warmest p. = maximum temperature of the warmest period, min. temp. of coldest p. = minimum temperature of the coldest period. Habitat suitability for each species is indicated in a gradient from yellow (less suitable) to red (highly suitable). Blue areas are considered unsuitable for the species.

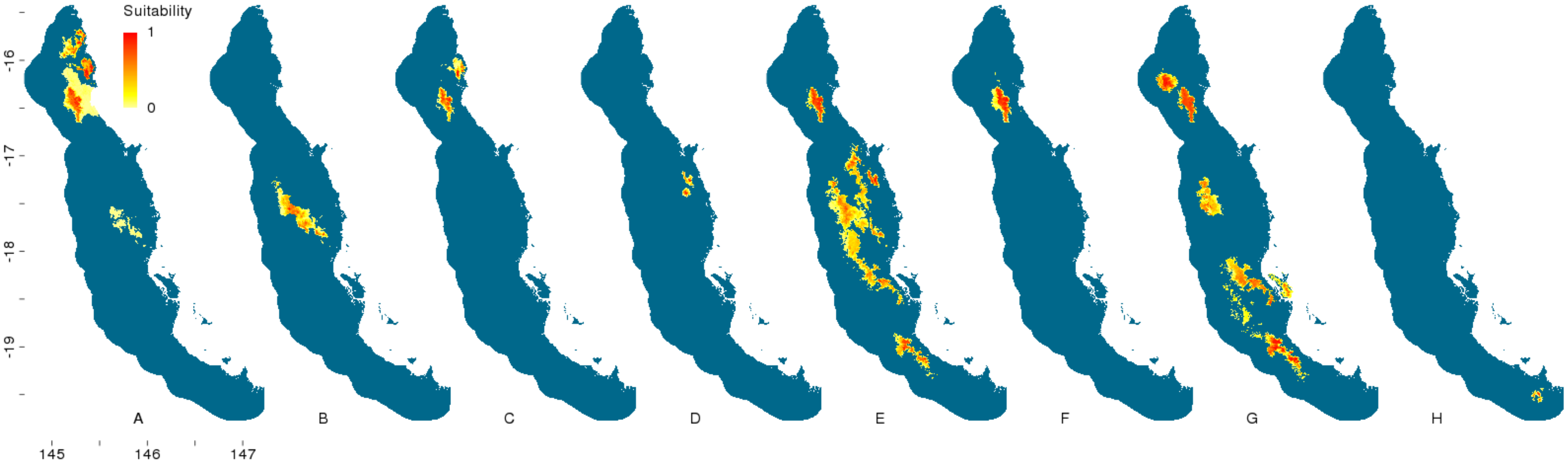


Figure	A.		B.		C.		D.	
Species	*Loxogenius opacipennis*		*Mecyclothorax inflatus*		*Mecyclothorax lewisensis*		*Mecyclothorax storeyi*	
Environmental variables	max. temp. of warmest p.	29.8	precipitation seasonality	50.9	max. temp. of warmest p.	39.3	precipitation of driest q.	53.1
	temperature seasonality	26.8	annual mean temperature	17.8	vegetation type	25.9	max. temp. of warmest p.	16.6
	vegetation type	24.9	vegetation type	17	temperature seasonality	14.9	precipitation seasonality	14.3
Figure	E.		F.		G.		H.	
Species	*Mystropomus regularis*		*Notonomus dimorphicus*		*Notonomus doddi*		*Notonomus ellioti*	
Environmental variables	max. temp. of warmest p.	70.4	vegetation type	46.8	max. temp. of warmest p.	59.8	max. temp. of warmest p.	67.2
	vegetation type	18.2	temperature seasonality	21.1	vegetation type	19.1	temperature seasonality	24.1
	annual precipitation	4.2	max. temp. of warmest p.	16.7	precipitation seasonality	13.7	vegetation type	6.5

Figure 2.4A-H. Distribution models of flightless ground beetle species in the Wet Tropics bioregion. Noted are the three highest-ranked environmental correlates selected by Maxent with percentage contribution of each variable to the model. Max. temp. of warmest p. = maximum temperature of the warmest period, min. temp. of coldest p. = minimum temperature of the coldest period. Habitat suitability for each species is indicated in a gradient from yellow (less suitable) to red (highly suitable). Blue areas are considered unsuitable for the species.

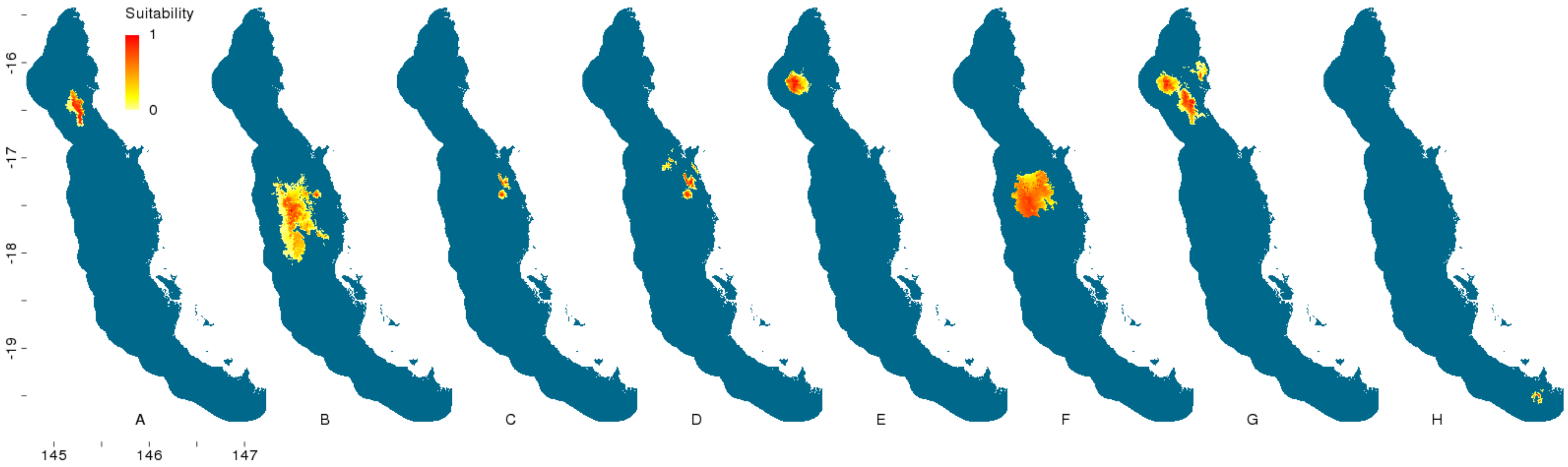


Figure	A.		B.		C.		D.	
Species	*Notonomus flos*		*Notonomus masculinus*		*Notonomus montellus*		*Notonomus montorum*	
Environmental variables	vegetation type	33.3	precipitation seasonality	27.6	precipitation seasonality	73.3	max. temp. of warmest p.	63.7
	temperature seasonality	33.2	annual mean temperature	25.6	vegetation type	18.4	precipitation seasonality	16.2
	max. temp. of warmest p.	24.7	vegetation type	18	precipitation of driest q.	5.7	precipitation of driest q.	11
Figure	E.		F.		G.		H.	
Species	*Notonomus NQ1*		*Notonomus saepistriatus*		*Notonomus spurgeoni*		*Nurus rex*	
Environmental variables	max. temp. of warmest p.	31.1	annual mean temperature	37	max. temp. of warmest p.	44.1	max. temp. of warmest p.	60.4
	temperature seasonality	30.8	vegetation type	26.3	temperature seasonality	31.3	temperature seasonality	19.3
	vegetation type	13.6	precipitation seasonality	13.2	vegetation type	14.1	vegetation type	13.9

Figure 2.5A-H. Distribution models of flightless ground beetle species in the Wet Tropics bioregion. Noted are the three highest-ranked environmental correlates selected by Maxent with percentage contribution of each variable to the model. Max. temp. of warmest p. = maximum temperature of the warmest period, min. temp. of coldest p. = minimum temperature of the coldest period. Habitat suitability for each species is indicated in a gradient from yellow (less suitable) to red (highly suitable). Blue areas are considered unsuitable for the species.

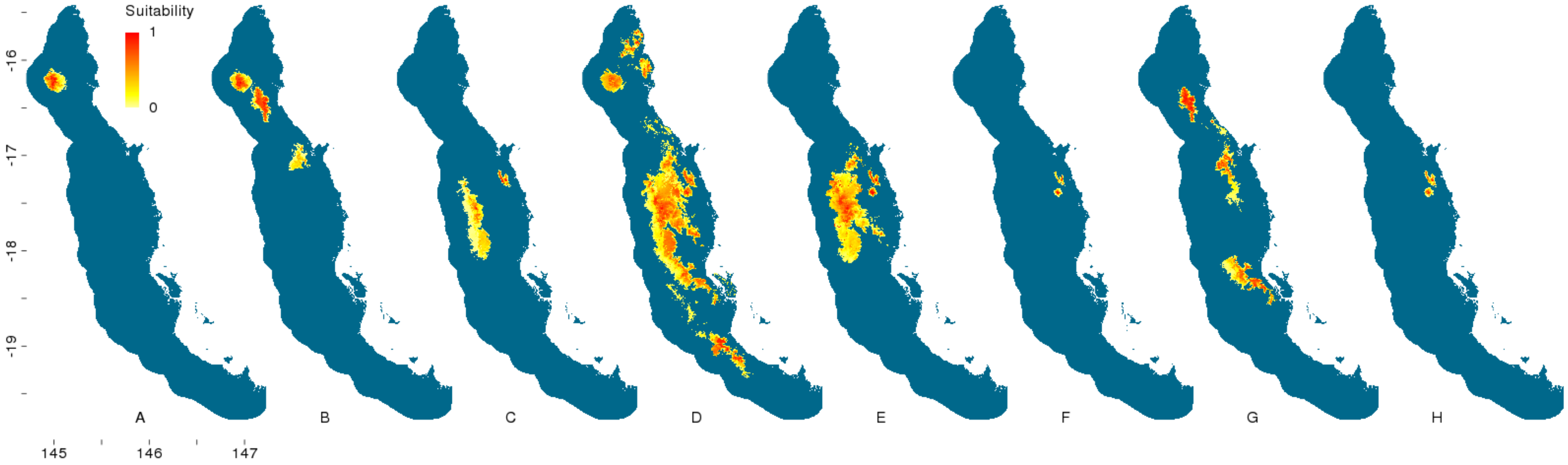


Figure	A.		B.		C.		D.	
Species	*Pamborus elegans*		*Pamborus euopacus*		*Pamborus punctatus*		*Pamborus tropicus*	
Environmental variables	temperature seasonality	28.9	max. temp. of warmest p.	45.6	precipitation seasonality	52.1	max. temp. of warmest p.	51.6
	annual mean temperature	24.5	temperature seasonality	32.3	vegetation type	38.5	vegetation type	26
	max. temp. of warmest p.	22.3	vegetation type	9.1	annual mean temperature	5.1	annual precipitation	15.5
Figure	E.		F.		G.		H.	
Species	*Setalis rubripes*		*Trichosternus fax*		*Trichosternus frater*		*Trichosternus montorum*	
Environmental variables	max. temp. of warmest p.	61	precipitation of driest q.	40.8	max. temp. of warmest p.	59.2	precipitation seasonality	74.3
	annual mean temperature	17.2	vegetation type	29.2	annual precipitation	11.1	precipitation of driest q.	13.5
	vegetation type	12.5	max. temp. of warmest p.	17.7	precipitation seasonality	8.9	vegetation type	9.1

Figure 2.6A-H. Distribution models of flightless ground beetle species in the Wet Tropics bioregion. Noted are the three highest-ranked environmental correlates selected by Maxent with percentage contribution of each variable to the model. Max. temp. of warmest p. = maximum temperature of the warmest period, min. temp. of coldest p. = minimum temperature of the coldest period. Habitat suitability for each species is indicated in a gradient from yellow (less suitable) to red (highly suitable). Blue areas are considered unsuitable for the species.

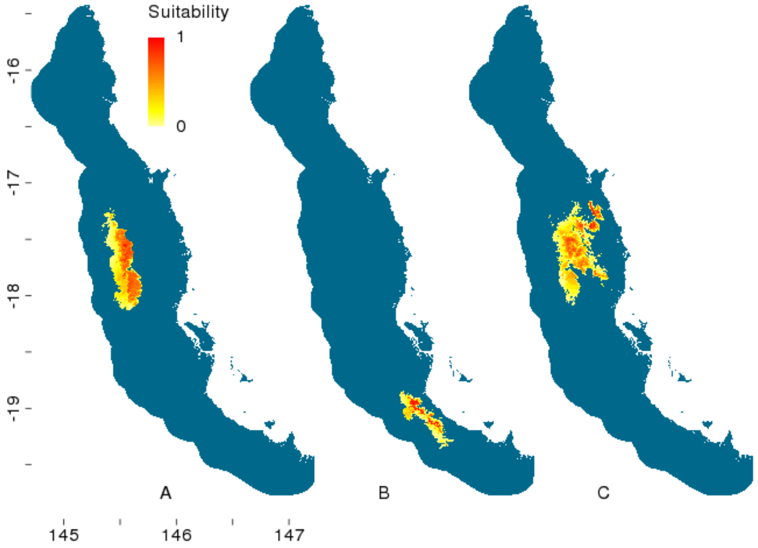


Figure	A.		B.		C.	
Species	*Trichosternus mutatus*		*Trichosternus nudipes*		*Trichosternus soror*	
Environmental variables	precipitation seasonality	37.2	vegetation type	41	precipitation seasonality	66.8
	vegetation type	35.5	precipitation seasonality	15.3	vegetation type	16.6
	min. temp. of coldest p.	27.2	min. temp. of coldest p.	14.5	max. temp. of warmest p.	10.9

Figure 2.7A-C. Distribution models of flightless ground beetle species in the Wet Tropics bioregion. Noted are the three highest-ranked environmental correlates selected by Maxent with percentage contribution of each variable to the model. Max. temp. of warmest p. = maximum temperature of the warmest period, min. temp. of coldest p. = minimum temperature of the coldest period. Habitat suitability for each species is indicated in a gradient from yellow (less suitable) to red (highly suitable). Blue areas are considered unsuitable for the species.

2.4.2 Species richness and endemism

Flightless ground beetles are predicted to be either absent or species poor throughout the vast majority of the Wet Tropics bioregion (Figure 2.8A). The subregions predicted to contain the highest species richness (15 species) of these beetles included Bellenden Ker Uplands, Carbine Uplands, and Atherton Uplands. Below approximately -18 degrees latitude the predicted species richness is noticeably lower than in the central and northern sections of the Wet Tropics bioregion.

When weighted for endemism, some subregions displayed high proportions of species with restricted distributions (Figure 2.8B). Greatest predicted endemicity was evident within the Bellenden Ker Uplands, followed by the Carbine Uplands and the southern mountain range of Mt Elliot (Figure 2.8B). Of the 43 species modelled, five are predicted to be endemic to Bellenden Ker Uplands, with a sixth species only slightly extending its range outside of these mountains. Five species were located only within the Carbine Uplands with a further five having slightly larger ranges including Windsor Uplands or Finnigan Uplands. As mentioned previously, two species were endemic to Mt Elliot, the southernmost mountain range of the Wet Tropics.

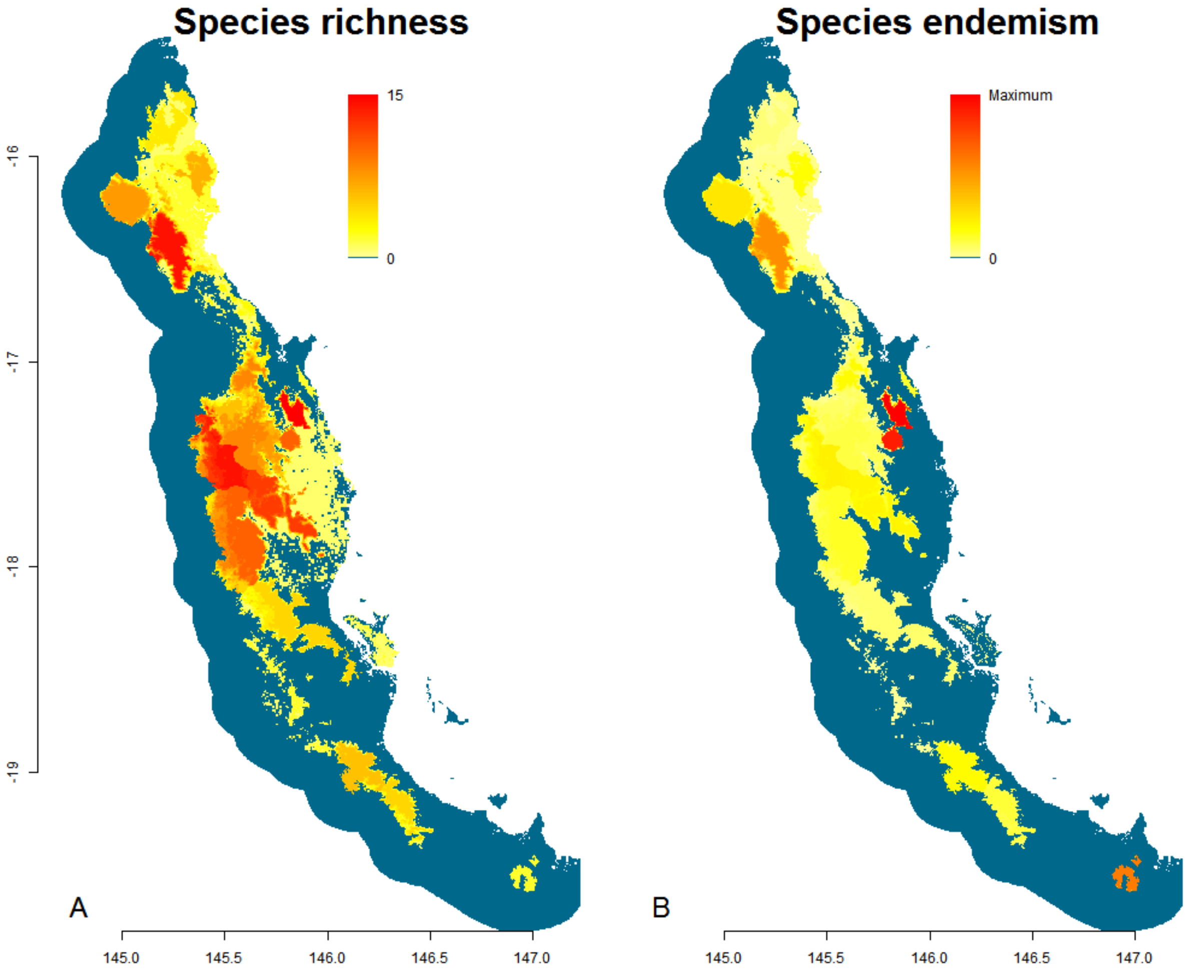
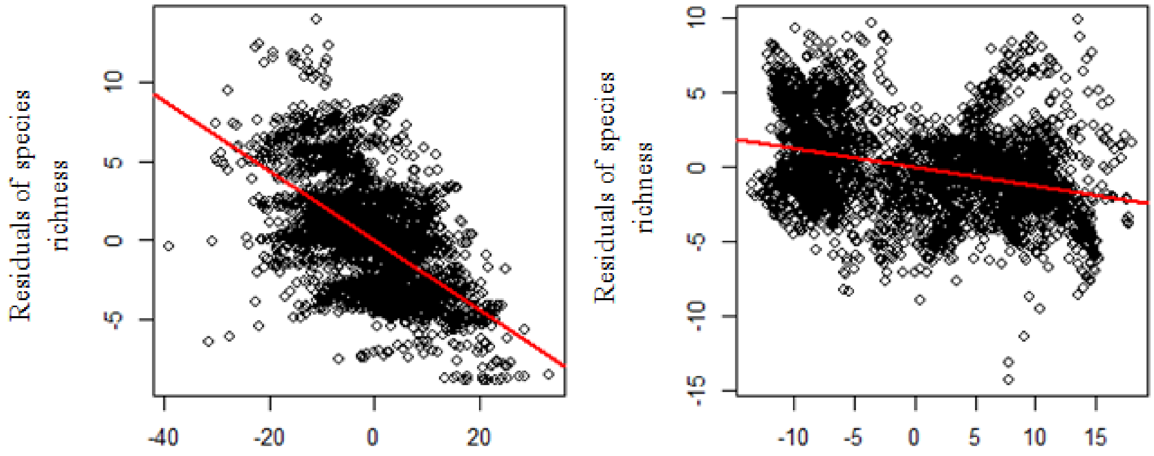


Figure 2.8. A. Models of flightless ground beetle species richness and endemism in the Wet Tropics bioregion. A. Model of the species richness, calculated by the cumulative total of the modelled distributions of 43 flightless ground beetles within the Wet Tropics. Richness is indicated in a gradient from yellow (less rich) to red (highly rich). Blue areas do not contain distributions of any species. **B.** Model of the species richness weighted for endemism. The modelled distributions of the 43 flightless ground beetles were inversely weighted by range size and summed together. Each subregion is weighted whereby yellow areas contain proportionally few endemic species and red areas display a high proportion of endemics. Blue regions lack any species.

The species richness of flightless ground beetles was explained best by a combination of four variables: maximum temperature of the warmest period, precipitation seasonality, distance to stream and notophyll vine forest (model Adj. $R^2 = 0.617$, s.e. = 2.73, n =10 000, $P < 0.001$; Table 2.1). Partial plots of these four environmental variables display significant linear correlations with species richness (Figure 2.9).

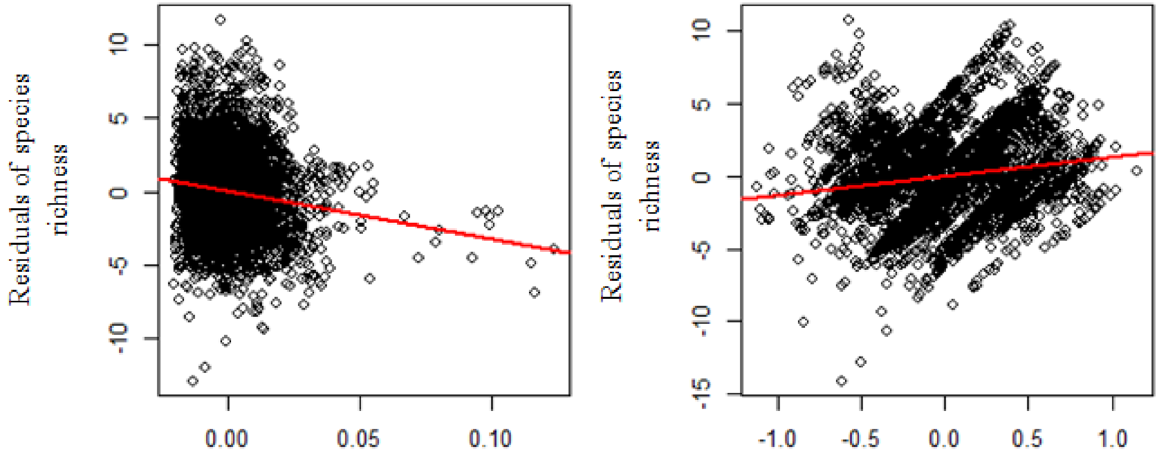
Table 2.1. Best sub-set regression models explaining modelled species richness of flightless ground beetles in the Wet Tropics. Adj. R² = Adjusted R², Std err = standard error, BIC = Bayesian information criterion, max. temp. = maximum temperature of the warmest period, precip. s. = precipitation seasonality, stream dist. = distance to the nearest stream (logx+1), veg type 5 (n. v. f.) = vegetation type 5 (notophyll vine forest). Raw output attached as Appendix 2.1.

P value	Adj. R²	Std err.	BIC	Model			
<0.001	0.556	2.94	-8054	max. temp.			
<0.001	0.592	2.82	-8868	max. temp.	precip. s.		
<0.001	0.609	2.76	-9289	max. temp.	precip. s.	stream dist.	
<0.001	0.617	2.73	-9490	max. temp.	precip. s.	stream dist.	veg type 5 (n. v. f.)



A Residuals of maximum temperature (°C)

B Residuals of precipitation seasonality (CoV)



C Residuals of distance to stream (log(x+1))

D Residuals of vegetation type 5

Figure 2.9A-D. Partial plots of the four environmental factors from the best sub-set multiple linear regression. This analysis identified the combination of environmental factors that best explained patterns of modelled species richness, based on 43 species flightless ground beetles, in the Wet Tropics bioregion. Model Adj. R^2 = 0.617, s.e. = 2.73, n =10 000, P < 0.001. A. Residuals of maximum temperature of the warmest period (t value = -45.38, s.e. = 0.004, n =10 000, Pr(>|t|) < 0.001), B. residuals of precipitation seasonality (t value = -23.43, s.e. = 0.005, n =10 000, Pr(>|t|) < 0.001), C. residuals of distance to stream (t value = -9.6, s.e. = 3.3, n =10 000, Pr(>|t|) < 0.001), D. residuals of vegetation type 5 (t value = 10.94, s.e. = 0.12, n =10 000, Pr(>|t|) < 0.001). Note raw output attached as Appendix 2.2.

2.4.3 Projected distribution modelling

Our modelling suggests that for all emission scenarios, by 2080 there will be substantial declines in the distributions of almost all 43 flightless ground beetles (Appendix 2.3) and associated declines in the species richness of this group throughout the Wet Topics (Figure 2.10). As scenarios increase in severity from B1 to A2 they are accompanied by greater losses in species richness. Range contractions are also clearly visible as lower elevations become unsuitable and connectivity between high elevational refugia decreases. However, the refugia of the Carbine Uplands, Bellenden Ker Uplands and Atherton Uplands still maintain relatively high species richness, even under the most severe scenario (A2).

All of the species modelled showed range size contractions (Table 2.2). The five most-widespread species are projected to contract their range by only 14 - 31% of their current size (Table 2.2). Three species, *Notonomus* NQ1, *Pamborus elegans* and *Trichosternus mutatus*, are predicted to go extinct by 2080 under the SRES A2 emission scenario (Table 2.2). *Notonomus* NQ1 and *Pamborus elegans* are both endemic to Windsor Uplands in the north-west of the Wet Tropics bioregion. *Trichosternus mutatus* is located in the western parts of the central Wet Tropics and is unlikely to be unable to disperse into high refugia such as the Bellenden Ker Uplands. In contrast, the five species endemic to the Bellenden Ker Uplands and Mount Bartle Frere (*Trichosternus fax*, *Mecyclothorax storeyi*, *Notonomus montellus*, *Leiradira alticola* and *Trichosternus montorum*) are predicted to occupy 40 - 50% of their current ranges (Table 2.2).

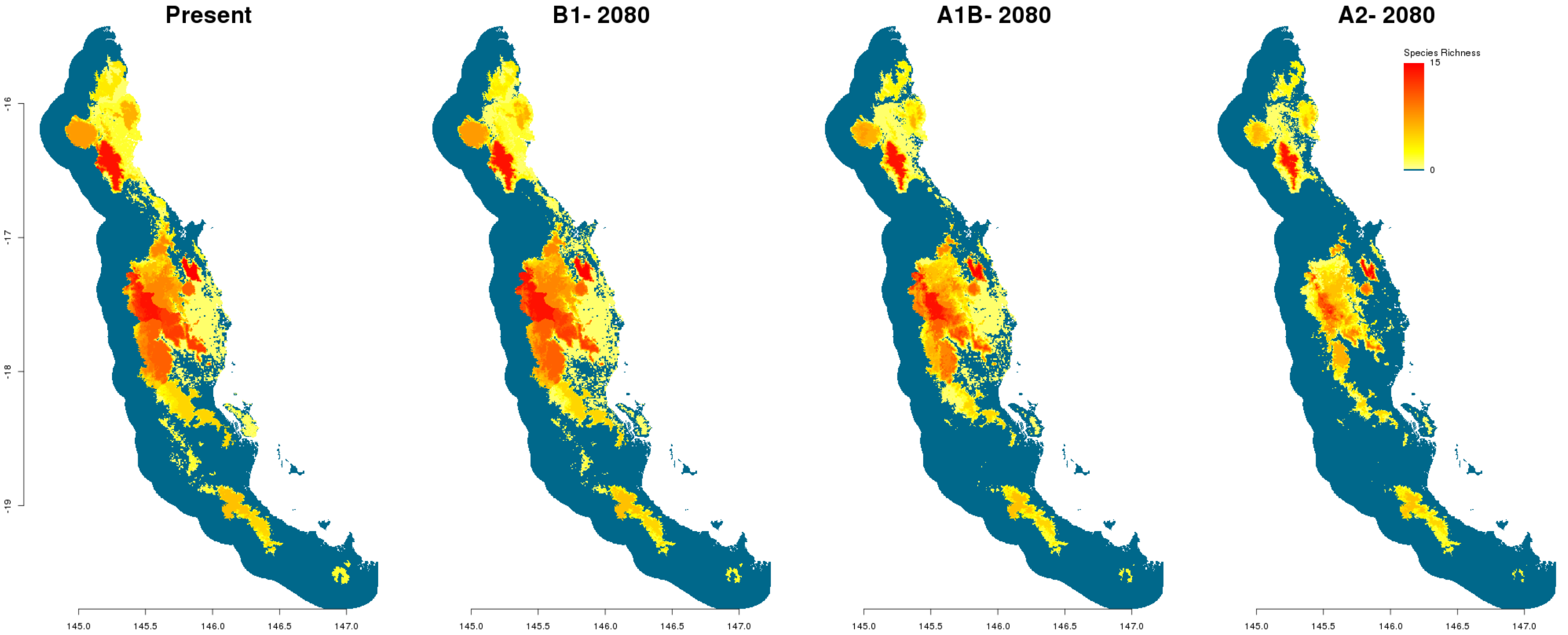


Figure 2.10. Models of species richness, both present day and future, of flightless ground beetles (n=43) in the Wet Tropics bioregion. Future models are of the year 2080, for three different emission scenarios (B1, A1B and A2). Richness is indicated in a gradient from yellow (less rich) to red (highly rich). Blue areas are not occupied by any species.

Total abundance of all flightless ground beetles is projected to greatly decrease under all three emission scenarios by the year 2080 (Figure 2.11; for individual species responses see Appendix 2.3). To demonstrate that these conclusions aren't driven only by the species for which small sample sizes were used in the models, projections were also examined using only the eight species for which more than 30 point localities were available. Declines in the abundance of this group of species were equally severe to those shown by the 43 species combined (Appendix 2.4). Loss of proportional abundance increases with severity of scenario. Eighty-eight% of species are projected to have less than 20% of their current populations by 2080 (SRES A2; Table 2.2). Although the five species endemic to the Bellenden Ker Uplands and Mount Bartle Frere are predicted to contract to 40 -50% of their current ranges, much of their distributions will be relatively unsuitable, leading to much more dramatic predicted declines in their abundances to 9 – 17% of their current population sizes (Table 2.2).

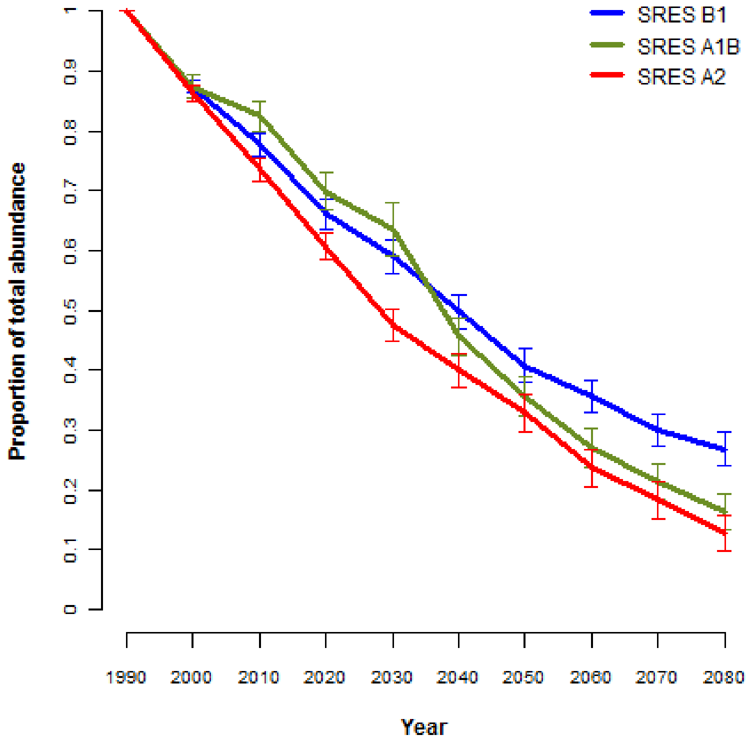


Figure 2.11. Average predicted proportional change for the total population of flightless ground beetle species (n=43) in the Wet Tropics. These projections use three emission scenarios (B1, A1B and A2) from the Special Report on Emissions Scenarios (SRES) and eight GCMs. Standard error bars are displayed representing variation between species responses. For individual species projections see Appendix 2.3.

Table 2.2. Data associated with individual species projection models. Records represent the number of point locality records used to create the model for each species. AUC is the area under the receiver-operating characteristic curve from each SDM produced. Subregion indicates the number of subregions in which species are known to currently exist and lowest elevation refers to the lowest elevation (m a.s.l.) where the species has been sampled. 2010 range represents the present day modelled range size (km²), and 2080 range is the size of the range (km²) projected for each species for 2080. 2080 population is the per cent of current population size projected to remain in the year 2080 modelled under emission scenario SRES A2. Species are ranked from the greatest to smallest loss in projected 2080 population size to order species projections from the most to the least vulnerable.

species	records	AUC	subregion	lowest elevation	2010 range	2080 range	2080 population
Notonomus NQ1	10	0.996	1	972	441	0	0
Pamborus elegans	3	0.998	1	1089	390	0	0
Trichosternus mutatus	10	0.987	1	769	1399	0	0
Lecanomerus niger	32	0.972	3	352	2229	80	1
Mecyclothorax inflatus	6	0.996	1	720	847	91	1
Nurus rex	6	1	1	834	93	11	1
Notonomus ellioti	5	1	1	834	95	15	2
Notonomus masculinus	26	0.98	2	598	2097	24	2
Pamborus euopacus	68	0.986	3	719	1152	220	2
Setalis rubripes	10	0.967	2	686	3203	188	2
Lacordairia NQ2	6	0.991	3	772	2541	440	3
Leiradira alternans	27	0.964	2	617	2459	449	3
Notonomus dimorphicus	9	0.984	1	944	451	120	3
Pamborus punctatus	19	0.991	2	769	1317	197	3
Trichosternus frater	24	0.973	5	605	1769	245	3
Castelnaudia setosiceps	34	0.964	4	101	4260	720	4
Notonomus flos	19	0.98	1	829	383	100	4
Coptocarpus NQ1	10	0.982	2	608	1072	299	5
Habutarus nitidicollis	7	0.998	1	946	420	83	5
Mystropomus regularis	68	0.96	7	239	3652	544	5
Notonomus saepistriatus	10	0.973	2	685	1661	449	6
Leiradira NQ2	16	0.988	2	944	610	190	7
Mecyclothorax lewisensis	22	0.995	2	693	564	202	7
Laccopterum NQ1	7	0.973	2	711	1380	312	8
Loxogenius opacipennis	29	0.991	4	280	2308	429	8
Notonomus spurgeoni	46	0.99	3	601	1134	444	8
Trichosternus fax	11	0.999	1	1024	184	76	9
Notonomus doddi	33	0.975	7	15	3219	998	10
Pamborus tropicus	79	0.94	11	24	6531	1594	10

species	records	AUC	subregion	lowest elevation	2010 range	2080 range	2080 population
Leiradira opacistriatus	26	0.981	5	145	2323	709	14
Mecyclothorax storeyi	15	0.999	1	987	204	95	14
Notonomus montellus	19	0.999	1	1005	216	105	14
Leiradira alticola	15	0.999	1	1005	218	108	15
Notonomus montorum	27	0.998	3	781	393	139	15
Coptocarpus philipi	7	0.964	2	693	2670	1128	16
Castelnaudia obscuripennis	92	0.978	5	19	2711	1067	17
Trichosternus montorum	22	0.999	1	987	224	115	17
Trichosternus soror	24	0.988	2	581	2150	1008	19
Castelnaudia spec	14	0.993	2	640	719	414	26
Trichosternus nudipes	16	0.993	2	640	695	459	33
Leiradira NQ3	7	0.923	1	387	771	643	55
Leiradira soror	8	0.97	3	352	890	792	83
Castelnaudia sp.1	5	0.979	1	345	435	395	90

For sixteen species endemic to a particular subregion we attempted to correlate their projected population declines with environmental factors. Two of these, *Leiradira* NQ3 and *Castelnaudia* sp.1, occur at elevations below 700 m a.s.l. (Table 2.2) and as a consequence were projected to be least vulnerable to climate change impacts (losing 45% and 10% their current populations respectively by the year 2080 under SRES A2; Figure 2.12A). The remaining 14 species were projected to decline by more than 80% of their current populations (year 2080, SRES A2). Annual mean precipitation was the environmental factor that best explained variance in the projected losses of total abundance for these 14 species (year 2080, SRES A2; model Adj. $R^2 = 0.664$, s.e. = 0.037, n =155, $P < 0.001$).

Of these 14 vulnerable subregional endemics, the five restricted to the Bellenden Ker Uplands (*Trichosternus fax*, *Mecyclothorax storeyi*, *Notonomus montellus*, *Leiradira alticola* & *Trichosternus montorum*) were predicted to experience the smallest population declines (Figure 2.12B). The remaining nine species, endemic to subregions that generally experience less annual precipitation than the Bellenden Ker Uplands, were predicted to lose 95% or more of their current population size (Figure12B). A Fisher test between annual mean precipitation values and population size reductions for all 16 endemic species confirmed a positive association between drier habitats (annual precipitation ≤3,000 mm) and projected population losses for 2080 (SRES A2, Table 2.3).

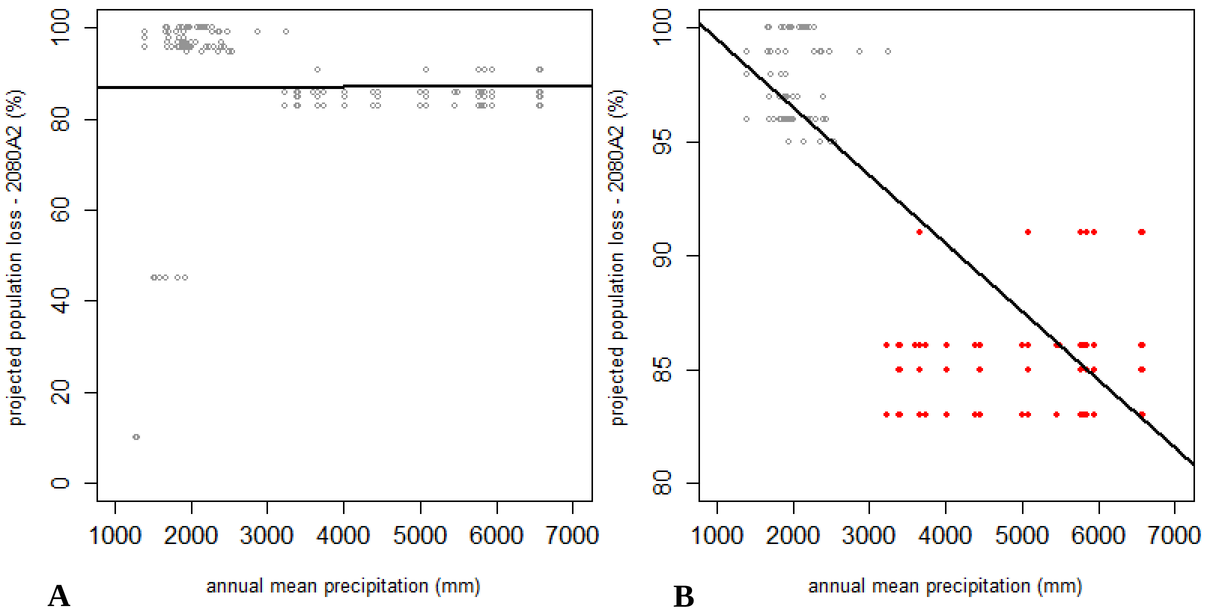


Figure 2.12. Correlation between projected proportional population loss of subregionally endemic flightless ground beetle species and precipitation. **A.** Correlation of projected proportional population loss by 2080 under SRES A2 and current annual mean precipitation experienced at point localities for all 16 subregional endemic flightless ground beetle species (Adj. $R^2 = 0$, res. s.e. = 17, n =167, P =NS). **B.** Correlation of projected proportional population loss by 2080 under SRES A2 and current annual mean precipitation experienced at point localities for the 14 most vulnerable endemics (i.e. projected population loss>80%; Adj. $R^2 = 0.66$, res. s.e. =3.8, n =146, $P < 0.001$). Data pertaining to the five species restricted to the Bellenden Ker Uplands (Trichosternus fax, Mecyclothorax storeyi, Notonomus montellus, Leiradira alticola & Trichosternus montorum) are indicated in red.

Table 2.3. Fisher test of the association of occupation of drier habitats and substantial future population declines for all 16 subregional endemic flightless ground beetles. This test determines a positive association between drier (annual precipitation ≤3,000 mm) areas and greater vulnerability to substantial population declines by 2080 (≥95% of current modelled total abundance) as a result of climate change (P value <0.005).

		wetter	drier		
extinction	lower	5	2	<95%	population
risk	higher	0	9		reduction

2.5 Discussion

2.5.1 Links between environmental correlates and distribution and species richness patterns

This study is the first to link distributional and richness patterns of a significant group of flightless invertebrate taxa in the Wet Tropics to climatic factors. Many flightless insects, including carabid beetles, have small upland ranges throughout the Wet Tropics (Yeates et al., 2002; Yeates & Monteith, 2008). Yeates *et al.* (2002) investigated the endemicity of flightless insect on both regional and subregional scales. They found that these insects display much greater levels of endemism, at both scales, than Wet Tropics vertebrates. Such highly restricted ranges are thought to have resulted from tropical ground beetles originally colonising lowland regions, then dispersing upwards into montane habitats (Darlington, 1970). Over time, living within relatively stable environmental conditions at high elevations, the beetles no longer needed to disperse long distances and the ability to fly was selected against (Darlington, 1970). Progressively, as cool wet rainforests became restricted to upland habitats in the Wet Tropics so to would have these beetles with such poor dispersal abilities. This scenario is typical of that presented by Ohlemüller *et al.* (2008) where a high proportion of Western Hemisphere birds and European butterflies with small ranges were found in areas that are higher and colder than surrounding habitats. They suggested that such regions may be interglacial refugia, which have receded over time, and where species adapted to cold conditions are able to persist during hotter interglacial periods (Ohlemüller et al., 2008). If ground beetles in the Wet Tropics were exposed to the above scenario then this would explain why they are so intimately linked to environmental conditions which are commonly found at high elevations in this region.

In the Wet Tropics bioregion, flightless ground beetles are generally confined to, and display highest richness in, cool, wet, stable upland habitats. The modelled distributions of most species are highly restricted with the highest endemism displayed in the Bellenden Ker Uplands. Maximum temperature of the warmest period was most often the environmental factor that was correlated best with individual distribution models. These beetles' strong links to specific climatic conditions becomes more apparent when examining the environmental factors which were correlated with their species richness throughout the Wet Tropics. Species richness of flightless ground beetles is higher where the rainforest has low maximum temperatures, and rainfall that is more evenly spread throughout the year. This is similar to findings regarding another mountain top taxon in this region, the microhylid frog, whereby high diversity of this group has been linked to consistent levels of moisture throughout the year (Williams & Hero, 2001). Furthermore, distance to the nearest stream negatively correlated, and the presence of notophyll vine forest positively correlated, with the richness of flightless ground beetles. The combination of these environmental correlates defines upland habitats characterised by cool, consistently wet, rainforest. In the Wet Tropics, this habitat type is predominantly confined to small mountain-top areas in and above the cloud cap, which equates to areas above approximately 1,000 m a.s.l.

Historical stability is thought to have had an important influence on current species richness patterns of taxa with low dispersal abilities that are endemic to the Wet Tropics (Graham et al., 2006). Subregions determined to have had the greatest historical stability in the Wet Tropics (Bellenden Ker Uplands and Carbine Uplands) are generally those that support the most species of both vertebrate and insect taxa, including flightless ground beetles as demonstrated in this study (Graham et al., 2006; Jeremy VanDerWal, Shoo, & Williams, 2009; Williams, 1997; Yeates & Monteith, 2008). Upland rainforest, which is associated with high species richness of flightless ground beetles, has been shown to be highly stable in the Wet Tropics during the late Quaternary (Jeremy VanDerWal, Luke P. Shoo, et al., 2009). The time-stability hypothesis postulates that stable areas enable species to evolve at a higher rate than habitats characterised by instability (Pianka, 1966; Willig et al., 2003). Previous work has implicated historical stability to be an important factor contributing to high richness of flightless invertebrate taxa throughout the Wet Tropics (Yeates & Monteith, 2008) and our findings add weight to such claims.

2.5.2 Future projections or distributions, species richness and population size

Flightless ground beetles currently confined to marginal habitats are likely to be among the species most vulnerable to climate change impacts in the Wet Tropics. Changes in the distributions flightless ground beetles due to climate change are characterised by upwards range shifts and accompanying range contractions. Worldwide, tropical montane species are expected to undergo upwards shifts in distributions (Chen et al., 2011; Colwell et al., 2008; Raxworthy et al., 2008) as are Wet Tropics species, including vertebrates (L. P. Shoo, 2005; Williams et al., 2003), schizophoran flies (R. D. Wilson, 2010) and dung beetles (Aristophanous, unpublished data).

The severity of Wet Tropic flightless ground beetle range contractions differs between subregions depending on their local climatic conditions, particularly their rainfall patterns. The two highest mountains in the Wet Tropics, Mt Bellenden Ker and Mt Bartle Frere, situated within the Bellenden Ker Uplands, display not only the lowest temperatures, but also the greatest rainfall in the region (McJannet et al., 2007). As discussed previously, flightless ground beetles are mainly restricted to, and display highest richness in, cool, wet, stable upland habitats. Such habitat is common throughout the Bellenden Ker Uplands and these mountains, therefore, offer the greatest amount of buffering of climate change impacts for flightless ground beetles. In contrast, the most vulnerable subregionally endemic ground beetles are confined to mountains outside of the Bellenden Ker Uplands that are best characterised as currently receiving lower precipitation. Species endemic to the drier mountain ranges, such as the Windsor Uplands and Elliot Uplands, are projected to be extinct by 2080 or reduced to only 1-2% of their current population sizes. This heighted vulnerability of subregionally endemic species in marginal habitats is supported by a positive association between drier habitats and higher projected population losses under the most severe emission scenario in 2080.

Projected distributional contractions of flightless ground beetles in the Wet Tropics negatively affect both the predicted species richness and abundance of this group. As richness projections are directly related to co-located distributional patterns, range contractions resulted in general declines of species richness, especially within the central Atherton Uplands for the most severe scenarios. However, the most alarming results concern the projected impacts of these range contractions on population sizes. The abundance of flightless ground beetles in the Wet Tropics is expected to dramatically decline by the year 2080 due to climate change impacts. Almost 90% of the 43 species examined here, are projected to lose 80% or more of their current populations by 2080 under the most severe emissions scenario with three species predicted to go extinct. Furthermore, dramatic declines occur under all emissions scenarios, reinforcing the sensitivity of this group to even mild levels of climate change. All species are projected to experience population reductions by 2080 with only three species projected to maintain greater than 50% of their current population sizes under the most severe scenario (A2).

These dramatic projected reductions of flightless ground beetle populations suggest that this group is among the most vulnerable to climate change impacts throughout the Wet Tropics. However, there have been very few attempts to quantify likely impacts of climate change on invertebrates in the Wet Tropics. To date only schizophoran flies have been examined in any detail with substantial declines in species richness predicted to occur with an increase in mean temperature of 3ºC (R. D. Wilson, 2010). Amongst vertebrates, climate change is projected to lead to severe declines for up to 74% of regionally endemic birds in the Wet Tropics (L. Shoo et al., 2005; Williams et al., 2003; Williams, Isaac, & Shoo, 2008). Furthermore, microhylid frogs are predicted to undergo dramatic reductions in population sizes throughout the Wet Tropics. L. P. Shoo (2005) projected population losses of microhylid frogs in relation to temperature increases in this region. Of the six frog species modelled in relation to a four degree increase, four were projected to be extinct, one almost extinct and the last had reduced in population size by over 80% (L. P. Shoo, 2005). This study confirms the prediction of Williams *et al.* (2008a) that insects of low vagility in the Wet Tropics will be similarly vulnerable to climate change impacts as regionally endemic vertebrates.

Flightless ground beetles constitute a large component, both in terms of abundance and body size, of the fauna of predatory insects found at high elevations in the Wet Tropics (Yeates et al., 2002). Consequently, the substantial reduction in carabid beetle populations projected to result from climate change has the potential to alter the community dynamics of the ground fauna. As leaf litter invertebrates perform vital roles in nutrient cycling (Heneghan, Coleman, Zou, Crossley, & Haines, 1998), suppression of this major predatory group could even potentially alter this ecosystem function. Population declines of flightless ground beetles may also have impacts at higher trophic levels as they are thought to be an important food source for many vertebrates, including mammals (Churchfield, Hollier, & Brown, 1991; Lovei & Sunderland, 1996).

Future precipitation changes are notoriously difficult to predict (Jeremy VanDerWal et al., 2013) and often limit projections of species distributions with climate change scenarios. However, this study has demonstrated strong links between ground beetle distributions, abundance and richness with precipitation levels. Therefore, it is worthwhile noting that any increase in dry season severity, rise in the level of cloud caps and subsequent reductions in cloud stripping, or other reductions in rainfall would be expected to further compromise the survival of flightless ground beetles in the Wet Tropics. Additionally, although projected changes in vegetation were not incorporated into our future scenario models, the results of Hilbert (2008) suggest that the extent of highland rainforests may decrease by 50% with only one degree of warming. In light of the relationships between ground beetle distributions and upland rainforest in the Wet Tropics, such dramatic contractions of this habitat type are likely to exacerbate future reductions in ground beetles distributions, richness and population size.

2.6 Conclusion

This study is the first to model changes in the distribution, richness and abundance of beetles under future climate change scenarios. We demonstrate that current distributions and richness of flightless ground beetles in the Wet Tropics are best correlated with high elevations, characterised by cool, moist and stable environmental conditions. These findings support the notion that differences in historical climatic stability between subregions have substantially influenced current biodiversity patterns.

Flightless ground beetles restricted to more marginal mountain ranges are projected to be the most vulnerable to climate change impacts in the Wet Tropics. Future ranges are projected to contract as distributions shift upwards and subsequently species richness is expected to decline. Ultimately however, the greatest impact on flightless ground beetles is the extreme reductions in abundance with the vast majority of species projected to lose 80% or more of their current population size.

These analyses not only describe the strong links flightless ground beetles have to climatic conditions, but also stress the negative impacts expected from future changes in these climatic correlates. The high level of sensitivity noted in this group implies that other low vagility invertebrate taxa, the vast majority of which remain unstudied, may also be similarly threatened by climate change. Future research must address this lack of understanding if climate change impacts on mountain-top ecosystems are to be comprehensively understood.

Chapter 3. Environmental influences on assemblage composition of flightless ground beetles in the Wet Tropics

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3.1 Abstract

Understanding how the environment, particularly climate, influences patterns of assemblage structure is vital for effective conservation management, especially in a changing global climate. Climate change projections suggest that tropical species are more vulnerable than their temperate counterparts as they already exist close to their thermal tolerances. Despite this, there is still a scarcity of empirical data confirming impacts of climate change on tropical species. Standardised baseline data, using replicated sampling techniques, are vital to predicting species vulnerability and monitoring change. Currently, very little standardised survey data exists for the flightless insect taxa largely confined to mountain-top refugia in the Australian Wet Topics World Heritage Area, in north-eastern Australia (herein after 'the Wet Tropics'). In this project we used standardised pitfall trapping across altitudinal transects in five subregions to capture community patterns of flightless ground beetles, a large predatory component of the flightless insect taxa in the Wet Tropics. Each subregional assemblage sampled was highly distinct, indicating a high level of compositional change between subregional blocks. Differences between subgroup assemblages were linked to temperature and precipitation changes, and the seasonality of these variables, throughout the region. Furthermore, species richness and abundance of flightless ground beetles significantly increased with elevation throughout the Wet Tropics. This study suggests that flightless ground beetles will be highly vulnerable to anticipated future climate change and conservation management strategies such as assisted migration may be required to ensure their persistence under different climate change scenarios.

3.2 Introduction

Determining the links between assemblage structure and environmental factors is fundamental to predicting responses of communities to climate change impacts. Tropical species are predicted to be more vulnerable to the negative impacts of climate change than temperate taxa (Curtis A. Deutsch et al., 2008; Laurance et al., 2011). Generally, species ranges are tracking climatic envelopes through upward shifts in elevation and polewards in response to temperature increases from climate change (Chen et al., 2011). Tropical species however, are more likely to shift upwards rather than polewards as less dispersal is required across the smaller distances of altitudinal gradients in these regions (Bush, 2002; Colwell et al., 2008). Also, as many tropical species already exist close to upper thermal tolerances, their responses to temperature increases may occur sooner than temperate species (Curtis A. Deutsch et al., 2008). Climate change is projected to have substantial effects on the distributions and abundance of montane fauna (Hodkinson, 2005; Kent, Levanoni, Banker, Pe'er, & Kark, 2013). The species confined to the tops of tropical mountains cannot display further upwards range shifts and are therefore predicted to be highly vulnerable to climate change impacts, especially those with low dispersal abilities (Williams et al., 2003). Furthermore, lowland biotic attrition is also projected to occur within altitudinal gradients when warm-adapted species move to higher locations and fail to be replaced (Colwell et al., 2008). Despite this multitude of vulnerabilities concerning tropical species, there remains a scarcity of data confirming impacts of climate change to these taxa (Chris D. Thomas, 2010). The majority of tropical taxa lack standardised baseline data. Such information is vital for appropriate determination of climate change impacts (L. P. Shoo et al., 2006).

Commonly, ecologists have replicated sampling methodology across altitudinal gradients to capture compositional changes in conjunction with environmental patterns (Kitching et al., 2011). High levels in biodiversity result from high turnovers of species within small areas. Tropical mountains often display very high turnover of species across elevational transect and subsequently such areas are often listed as hotspots of biodiversity (Fernandez, 2013; Kozak & Wiens, 2010; Lomolino, 2001). This high species turnover is often linked to changing climatic factors such as temperature and precipitation (Bruhl et al., 1999; Hodkinson, 2005). As elevation increases, temperature decreases at a rate of approximately 1°C per 200 meters in altitude (L. Shoo et al., 2005). Cloud cover also reduces temperature with significant decreases occurring within the cloud cap (Hodkinson, 2005; Sabu, Shiju, Vinod, & Nithya, 2011). Water availability increases at higher elevation due to greater precipitation and also a process known as cloud stripping (water deposited from clouds due to the physical interception of clouds and forests) which occurs at localities in the cloud cap (McJannet et al., 2007; Sabu et al., 2011). Compositional changes can be compared across elevational gradients in relation to variance of environmental factors. Therefore, transects established in these locations can be used as surrogates to investigate the effects of climate change on community patterns such as species richness and abundance (Fleishman et al., 2000).

Species richness most commonly is recorded to peak at mid elevational locations (Carsten Rahbek, 2005). This pattern is often attributed to either the mid domain effect (the effect of overlapping distributions of highland and lowland specialists; Escobar et al., 2005), as a sampling artefact from incomplete sampling of altitudinal gradients or greater human disturbance at low altitudes (McCoy, 1990; Henk Wolda, 1987). Additionally, Kozak and Wiens (2010) use the evolutionary process of the time-for-speciation effect (whereby mid-elevation habitats have accumulated more species as they have been inhabited for longer periods of time) to explain greater mid-elevational richness. Species richness also often declines with elevation although not always in a monotonic fashion (Kraft et al., 2011; C. Rahbek, 1995). This decline has commonly been attributed to reducing environmental factors, such as solar energy input, primary productivity and increases in water availability (Brown, 1973; B. L. Fisher, 1998; Janzen, 1967). Diminishing food resources with elevation have also been implicated in contributing to declines in richness at high elevations (Bruhl et al., 1999). Certain taxa also increase in richness with elevation and are suggested to do so due to lower predation and competition pressure at such locations (Brehm & Fiedler, 2003; Darlington, 1971; D. Olson, 1994). Some insects groups with soil dwelling larvae are also more species-rich at higher elevations because of a lower likelihood of desiccation in moist soil at higher locations (Coulson & Whittaker, 1978). Clearly, richness trends across elevational gradients can be taxon-specific and may correlate with a variety of environmental factors. Teasing out the relative influence of these gradients and environmental influences on assemblage structure is important to increase our understanding of biodiversity and allow better, more efficient, management of natural ecosystems.

An extremely important bioregion within Australia is the Australian World Heritage Wet Topics Area (hereinafter ‘the Wet Tropics’). This area is a tropical region characterised by its high biodiversity and is ideal for investigating climate change impacts on a wide range of communities (Williams et al., 2003). The Wet Tropics is considered a “mesotherm archipelago” as it is composed of a series of distinct high elevational mountain ranges forming isolated biogeographic and evolutionarily distant subregions, separated by lowland gullies or dry areas (Nix, 1991; Williams et al., 2003). Current compositional patterns of animals throughout the region are largely attributed to historical influences from processes such as: extinction filtering, whereby periods of intolerable environmental conditions selectively drove subregional populations to extinction (Graham et al., 2006; Williams, 1997); in situ evolution within more stable subregions (Williams & Hero, 2001; Yeates et al., 2002); and recolonisation events when subregions receive an influx of species from neighbouring refugial subregions due to climatic fluctuations (Kotze et al., 2011; Schneider, Cunningham, & Moritz, 1998; Yeates et al., 2002). However, relating compositional patterns to current processes such as climatic conditions is also vital in order to understand how communities will respond to climate change. To cope with climate change impacts, management decisions including the establishment of corridors (whereby species can disperse to more suitable habitats) and assisted migration (where people relocate species to tolerable locations) are being proposed as strategies to maintain biodiversity of regions such as the Wet Tropics (A. S. Anderson et al., 2012; Killeen, Solórzano, & Solóerzano, 2008). Insight into the links between environmental factors and community compositions is therefore vital to understanding the implications of climate change on assemblage structures within the Wet Tropics and making suitable conservation management decisions.

Insect groups often exhibit much finer patterns of assemblage structure than vertebrates and generally have higher diversity and more restricted endemism. This makes them valuable to studies examining the determinants of biodiversity patterns, assemblage structure and evolution. Among the invertebrates, an extremely biodiverse (274 species) group of flightless insect taxa populate the isolated highland areas, a staggering 50% of which are restricted to a single subregion (Yeates et al., 2002). As endemic flightless insect richness does not relate to subregional shape and size, these species have been suggested to have evolved in situ in the Wet Tropics (Yeates et al., 2002). A major predatory component of the flightless insect taxa in the Wet Tropics is the flightless ground beetles. These beetles constitute an ideal group for monitoring climate change impacts, as they not only display the high levels of endemism and poor dispersal abilities which characterise other flightless insect taxa in this region, they are also highly ubiquitous in upland rainforest habitats and relatively easy to sample. Extensive sampling of flightless ground beetles has already occurred in this region. Within the Wet

Tropics, these beetles were first intensively surveyed by Darlington during the years 1931-2 and later between 1957-8 (Darlington, 1961). Monteith built on the work performed by Darlington, through multiple surveys working for the Queensland Museum in the 1980's and 1990's (Monteith, 1995). By the 1990's, new species were rarely being collected indicating that the fauna had been comprehensively sampled (Yeates & Monteith, 2008).

To date, despite intensive sampling efforts, baseline data from which future resurveys may be compared and climate change impacts monitored do not exist for flightless ground beetles within the Wet Tropics. It has been suggested that wide scale distributional patterns may affect the interpretation of compositional changes across single altitudinal gradients (Hodkinson, 2005). Therefore, to better represent the entire community of flightless ground beetles in the Wet Tropics, as well as capture the influence of spatial heterogeneity on the assemblages investigated, we use standardised pitfall trapping across altitudinal transects within five subregions throughout the Wet Tropics. Initially, we determine the effectiveness of our standard pitfall protocol in sampling flightless ground beetle assemblages. We then examine the compositional patterns of the flightless ground beetle community, both across the elevational gradient and between subregions sampled, through investigating turnover in assemblages and changes in richness and abundance and link these trends to environmental factors.

3.3 Methods

3.3.1 Study area

This study was conducted in north-eastern Australia (between 20°S, 147°E and 15°s, 145°E) within the Wet Tropics bioregion which is approximately 10,000 km² in area and has been listed as a World Heritage Area since 1988 due to the high biodiversity and endemism of the regions rainforests (Figure 3.1). This study was confined to elevational gradients within rainforest and covered a range of structural rainforest types from the complex mesophyll vine forest in fertile lowlands to upland simple notophyll vine forest and, in the case of Bellenden Ker Uplands, simple microphyll vine-fern thickets above 1500m a.s.l. (Adam, 1992).

Generally, high annual rainfall occurs throughout the Wet Tropics (2,000-8,000 mm per year) (Bonell & Callaghan, 2008) with approximately 75-90 % of precipitation occurring between November and April (McDonald & Lane, 2000). Additionally, rainforests located at elevations above 1,000 m a.s.l. receive up to 66% of their monthly water input from cloud stripping (McJannet et al., 2007) making the rainfall estimates an under-estimate of total water input. Temperatures vary throughout the region and on average decrease at a rate of 1°C with every 200 m of increased elevation (L. Shoo et al., 2005). Approximately one-third of the Wet Tropics bioregion is higher than 600 m a.s.l., where annual mean temperatures are below 22°C (N. E. Stork et al., 2009).

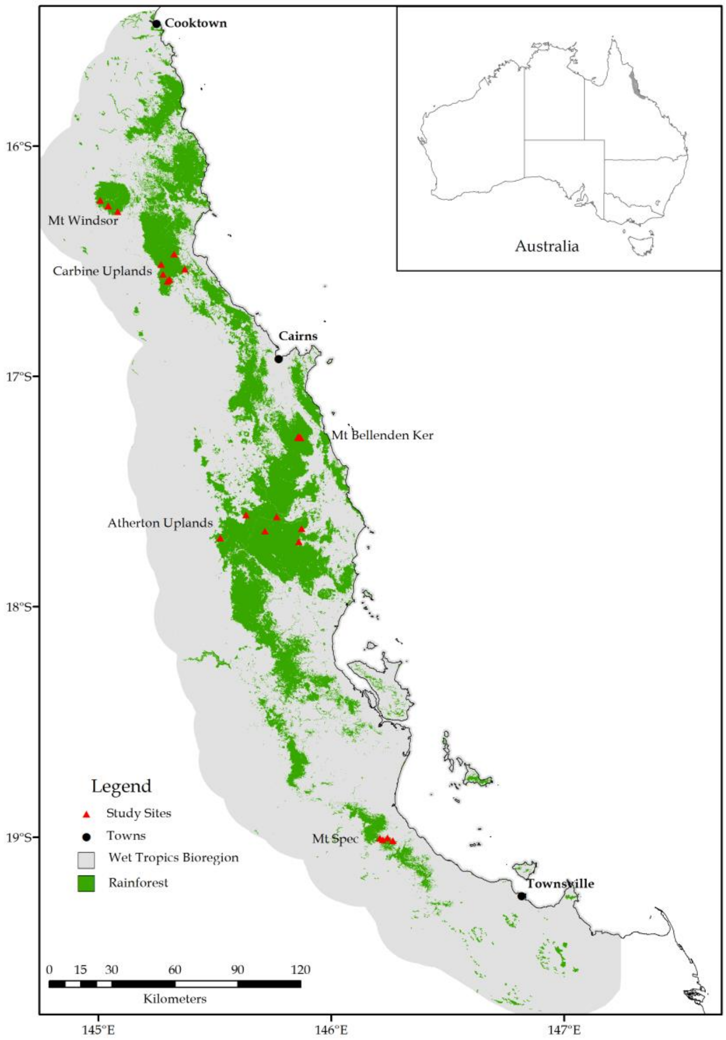

Figure 3.1. Map of the Wet Tropics bioregion showing the current extent of rainforest and study site locations.

3.3.2 Experimental design and sampling methods

The five study areas were located within the Spec Uplands, Atherton Uplands, Bellenden Ker Uplands, Carbine Uplands and Windsor Uplands subregions (Figure 3.1). The southern-most subregion is Spec Uplands with Atherton Uplands and Bellenden Ker Uplands situated in the middle of the Wet Tropics and Carbine Uplands and Windsor Uplands both located in the north. Within each subregion, the available elevational gradients within contiguous rainforest were utilised. The extent of the elevational gradient sampled varied between subregions due to differences in the availability and accessibility of rainforest habitats.

This study was designed to sample flightless ground beetles at approximately 200 m a.s.l. elevational intervals within each subregion. Elevations sampled within each subregion were: Spec Uplands - 350, 600, 800 & 1,000 m a.s.l.; Atherton Uplands - 100, 200, 400, 600, 800 & 1,000 m a.s.l.; Bellenden Ker Uplands – 1,000, 1,200, 1,400 & 1,600 m a.s.l.; Carbine Uplands - 100, 400, 600, 800, 1,000 & 1,200 m a.s.l.; Windsor Uplands - 900, 1,100 & 1,300 m a.s.l. (Chapter 3 - Appendix 3.1). At each elevation, we established three sites separated by ca. 400 m (with the exception of Spec Uplands 350 m where the sites were separated by 200 m due to there being only a small patch of rainforest). At Carbine Uplands we were unable to find suitable sites at 200 m a.s.l. due to topographical constraints. At each replicate site, three pitfall traps were set, each 15 m apart. These traps were serviced monthly and the catches were pooled together for each replicate.

Each pitfall trap consisted of two circular plastic containers (one set within the other) of diameter 11.5 cm, depth 10 cm. These were set flush with the surface of a soil mound created to prevent flooding of the trap. Traps were protected from rain by a square metal lid (length 26 cm) fixed with wire to a ring of aviary mesh (height 7.8 cm) consisting of square gaps (length 2.5 cm). Container openings were covered with the same mesh and all mesh was fixed to the trap using wire pegs. Mesh covered container openings in order to prevent frogs and skinks from falling in. All external components of the traps were metal for protection from rats, *Rattus spp.*. Propylene glycol (100%, depth 2.5 cm) was used as a preservative in traps due to its resistance to evaporation and low mammalian toxicity (Aristophanous, 2010). Some traps in drier locations (e.g. Carbine Uplands 600 m a.s.l. & Windsor Uplands 900 m a.s.l.) had to be reinforced using star pickets and wire to prevent disturbance by feral pigs, *Sus scrofa*.

3.3.3 Environmental variables

Temperature and precipitation data used in this study bioclimatic variables, derived using the Anuclim 5.1 software (McMahon et al., 1995) and a 80-m-resolution digital elevation model (DEM; resampled from GEODATA 9-second DEM, ver.2; Geoscience Australia, http://www.ga.gov.au/). Bioclimatic variables used were annual mean temperature (BC01), temperature seasonality (BC04), maximum temperature of warmest period (BC05), minimum temperature of coldest period (BC06), annual precipitation (BC12), precipitation seasonality (BC15), precipitation of wettest quarter (BC16) and precipitation of driest quarter (BC17). These variables have been strongly linked to vertebrate and dipteran distributions throughout the Wet Tropics (J. Vanderwal et al., 2009; Jeremy VanDerWal, Luke P Shoo, et al., 2009; R. D. Wilson, 2010). At each elevational site, 10 m × 50 m transects were set to determine the heterogeneity of structures on the forest floor. The proportion of forest floor within this transect covered by rocks, logs and buttress roots, was estimated and recorded using a scale from 0 to 4, where 0 = absent,

1 = 1-24%, 2 = 25-49%, 3 = 50-74% and 4 = 75-100%. Litter standing crop was also recorded using volume measurements from two sites per elevational transect during the wet season (Parsons, Shoo, & Williams, 2009).

3.3.4 Data analysis

3.3.4.1 Sampling Effort

As pitfall traps are *in situ* passive sampling devices, they only capture animals actively moving across the ground. These means that the number of animals sampled is a measure of activity density and does not necessarily estimate abundance (Greenslade, 1964; Thiele, 1977). Despite this, the term abundance is still generally used instead of activity density (Kotze et al., 2011) and this project adheres to such protocol.

In order to produce directly comparable data sets based on equal sampling effort, only 12 contiguous months of samples were analysed from each subregion. The first month of sampling was not included in any data set in an effort to remove digging-in bias whereby insects are attracted to new structures in their environment and unusually high values are recorded (Digweed, Currie, Carcamo, & Spence, 1995). A reference collection of species identified in this chapter are located in the Queensland Museum. Samples from June 2008 until June 2009 were included in the datasets from Spec Uplands, Atherton Uplands, Carbine Uplands and Windsor Uplands subregions. As Bellenden Ker Uplands was unable to be accessed until December 2009, its dataset consisted of samples from January 2009 until January 2010. Of the 2484 traps set (9 traps x 23 sites x 12 months), twenty traps were lost within Windsor Uplands 900m a.s.l. and 12 we lost in Carbine Uplands, almost all within the 600 m a.s.l. sites. The loss of traps was unlikely to influence the overall results as most of trap failures occurred during the dry season when flightless ground beetles were not caught in functioning traps within 600 m a.s.l. for Carbine Uplands or other elevations in Windsor Uplands.

Sampling efficiency was assessed by creating species accumulation curves derived from Chao 1 species richness estimator data per trap for every two month sampling unit per site, using the *adehabitat* package of the R statistical program v2.12.1(R Development Core Team, 2010). By using this rarefaction estimator of species richness, we reduce the bias caused by uneven numbers of individuals across samples and better include the influence of rare species thereby reducing negative bias with incomplete sampling of sites (Chao, Chazdon, Colwell, & Shen, 2005). Two-monthly sampling units were chosen to equalise replication of effort between all sites, as during certain months some sites could not be accessed. The resulting sampling efforts therefore derived from 6 (two-monthly samples) x 9 traps per elevation within each subregion x 3 – 5 elevational sites for each subregion (only elevational sites where species were recorded were included).

The observed species richness sampled in this project, for each subregion, was compared with the observed species richness from Queensland Museum data-base records of flightless ground beetles in the Wet Tropics for the same subregions. Further records regarding species locations of the genus *Feronista* were acquired through consultation with Kipling Will (University of California, Berkeley).

3.3.4.2 Species richness and abundance across elevation

To determine variations in species richness across the elevational gradients, species richness was analysed using the *fossil* package from the R statistical program v2.12.1 (R Development

Core Team, 2010). Chao1 estimates of species richness were calculated based on data derived from the same two-monthly sample units as above, per elevational site (points 2, 4, and 6), for the total year. Furthermore, species richness and abundance values were also averaged from these three elevational sites per elevation of every subregion.

Changes in species richness and abundances, as elevation increased, were investigated by creating generalised linear mixed models fit by Laplace approximation, with elevation as the single explanatory variable, using the lme4 package in the R statistical program v2.12.1. The entire community data was used and subregion was included as a random factor to control for the effects of these areas on the data. This random effects model was appropriate as the observed clusters (subregional assemblages) were regarded as random samples from a large pool (entire Wet Tropics) of possible clusters (Broström & Holmberg, 2011). Poisson distributions were utilised as count data was analysed and overdispersion was accounted for by adding the number of observations as a second random factor for both the richness and abundance models (Broström & Holmberg, 2011; Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

3.3.4.3 Compositional patterns of community data

Compositional variations between subregion assemblages were investigated with non-metric multi-dimensional scaling ordination (NMDS). All multivariate analyses were performed using the *vegan* package from the R statistical program v2.12.1 (Clarke, 1993; R Development Core Team, 2010). Only sites where a total of more than 5 individual ground beetles were sampled, were used. Abundance data were square-root transformed prior to analyses to increase normality as is suggested for count data (Crawley, 2003). The ordination was constructed from a matrix of Bray-Curtis dissimilarity values between all pairs of sites for each elevation. In order to determine any correlations between environmental data and assemblage patterns, BIOCLIM data and habitat heterogeneity variables were correlated with the ordination pattern of ground beetle assemblages. Relevant levels of significance were based on 1,000 permutations of variable data. Furthermore, the relationships between the community composition and the significantly correlated environmental factors, including BIOCLIM data, forest floor heterogeneity (all three structures assessed individually and combined), leaf litter depth and elevation, were investigated through analysis by permutational multivariate analysis of variance using distance matrices (1,000 permutations).

This analysis calculated *F* statistics (pseudo-*F*) using a semi-metric distance measure (Bray-Curtis) to relate variation in a matrix, in this case, species abundance data at each site, to predictor variables, thereby obtaining *P* values using permutation techniques (1000 unrestricted permutations of raw data; Zapala & Schork, 2006).

Levels of similarity between subregional assemblages were investigated through pairwise comparisons using Analysis of Similarities (ANOSIM). This program executes multivariate ANOVA, using 999 permutations, to calculate *P* values derived from pseudo *F* statistics of the distance measures (M. J. Anderson, 2005). ANOSIM produces an R statistic, ranging from -1 to +1, based on the difference of mean ranks between subregional assemblages where +1 equals a complete dissimilarity of assemblages. Zero represents completely random assemblage structures whereas any departure from zero indicates that dissimilarities among different subregions are greater than dissimilarities within each subregion (M. J. Anderson, 2005).

The patterns displayed within the NMDS were further analysed. This was performed using best sub-set multiple linear regressions between the values where sites were positioned, across both Dimension 1 and 2 axes, and co-located environmental data using the *leaps* package from the R statistical program v2.12.1 (R Development Core Team, 2010). The best models, derived from any combination of the explanatory variables, were determined using Bayesian Information Coefficients (BICs). Whilst, this statistical modelling technique is slightly different from the more standard variable selection methods of stepwise regression, as it better accounts for co-linearity problems between explanatory variables (Mac Nally, 2000), some removal of significantly cross-correlated variables was still required.

For the model determined by best sub-set regression, the influence of each environmental factor on the variance of each axis (Dimension 1 and 2) were plotted as partial-regression plots using the *car* package from the R statistical program v2.12.1 (R Development Core Team, 2010). When multiple independent variables (X1, X2) predict one dependant variable (Y), the effect of X1 on Y can be seen after removing the (linear) effect of X2 on Y. This was achieved by using the 'avplots' function in the *car* package which regresses Y against X2, X1 against X2 and creates partial-regression plots of the residuals of the former against those of the latter (Weisberg, 2005). For ease of interpretation, the independent variable (X1) reported on in each partial-regression plot is referred to as "Residuals of X1" and dependent variable (Y) referred to as "Residuals of Y".

3.4 Results

3.4.1 Taxonomic summary

A total of 4,529 flightless ground beetles were captured, belonging to 16 genera and 43 species, including 14 (33%) subregional endemic species (Table 3.1). Tribes dominating the communities included Pterostichini, Pamborini and Ozaenini. The most abundant species was *Notonomus montorum* representing 18% of the total individuals, followed by *Mystropomus regularis* (16%) and *Pamborus euopacus* (14%; Table 3.1). With all five subregional sampled combined, there were relatively few rare species sampled with only five singletons and two doubletons. Individuals from Bellenden Ker Uplands accounted for more than half the total abundance of ground beetles sampled. Species richness was about two and a half times greater at Atherton Uplands and Bellenden Ker Uplands than Spec Uplands and Windsor Uplands.

Table 3.1. Table of species sampled indicating subregion endemics Y=Yes, N=No, total abundance and elevational range (‘00m a.s.l.) of species sampled within each subregion. Spec Uplands (SU), Atherton Uplands (AU), Bellenden Ker Uplands (BK), Carbine Uplands (CU), Windsor Uplands (WU).

Species	Subregion Endemic	SU	Range	AU	Range	BK	Range	CU	Range	WU	Range
Castelnaudia obscuripennis	N							45	4-12	165	9-13
Castelnaudia setosiceps	N			7	4-10	63	10-12				
Castelnaudia sp.1	Y	16	3.5-6								
Castelnaudia spec	N	46	6-10								
Coptocarpus NQ1	N							1	12.		
Coptocarpus philipi	N					1	12.				
Craspedophorus sp.1	Y			6	2-4						
Feronista sp.1	Y					4	12-16				
Feronista sp.2	Y							6	10-12		
Feronista sp.3	Y					3	12.				
Laccopterum sp.1	N			19	8.						
Laccopterum sp.2	N			3	4.						
Lecanomerus limbatus	N			2	8.						
Lecanomerus niger	N			1	8.	7	10-14				
Lecanomerus sp.1	N							1	12.		
Leiradira alternans	N			8	6-10						
Leiradira alticola	Y					217	10-16				
Leiradira NQ2	N							6	10-12		
Leiradira opacistiatus	N			5	6.						

Species	Subregion Endemic	SU	Range	AU	Range	BK	Range	CU	Range	WU	Range
Leiradira soror	N					8	12.				
Mecyclothorax storeyi	N					2	14.				
Mystropomus regularis	N	73	8-10	20	6-10	507	10-16	140	8-12		
Notonomus dimorphicus	Y							46	10-12		
Notonomus doddi	N	5	8-10					1	8.	13	11-13
Notonomus flos	Y							77	10-12		
Notonomus masculinus	N			71	6-10						
Notonomus montellus	Y					28	10-16				
Notonomus montorum	N					811	10-16				
Notonomus NQ1	Y									17	9-13
Notonomus spurgeoni	N							26	10-12		
Oodes sp.1	N			14	2-4			1	6.		
Pamborus euopacus	N							418	10-12	221	11-13
Pamborus punctatus	N			1	10.	64	10-16				
Pamborus tropicus	N	150	8-10	258	4-10					1	9.
Pheropsophus verticalis	N			59	2.						
Prosopogmus sp. 2	Y									1	9.
Setalis rubripes	N					1	12.				
Trichosternus fax	Y					297	14-16				
Trichosternus frater	N							24	10-12		

Species	Subregion Endemic	SU	Range	AU	Range	BK	Range	CU	Range	WU	Range
Trichosternus montorum	Y					337	10-16				
Trichosternus mutatus	Y			56	10.						
Trichosternus nudipes	N	50	6-10								
Trichosternus soror	N			21	6-8	78	10-12				
Total abundance		340		551		2,428		792		418	

3.4.2 Sampling effort

Generally, accumulation curves for each subregion were stabilising or had already reached asymptote at 54 samples (Figure 3.2). Samples from 600 m a.s.l. and 800 m a.s.l. at Carbine Uplands contained only single specimens of a very few species, which accounted for the accumulation curves of these subregions not achieving asymptotes, indicating further sampling is required at these locations.

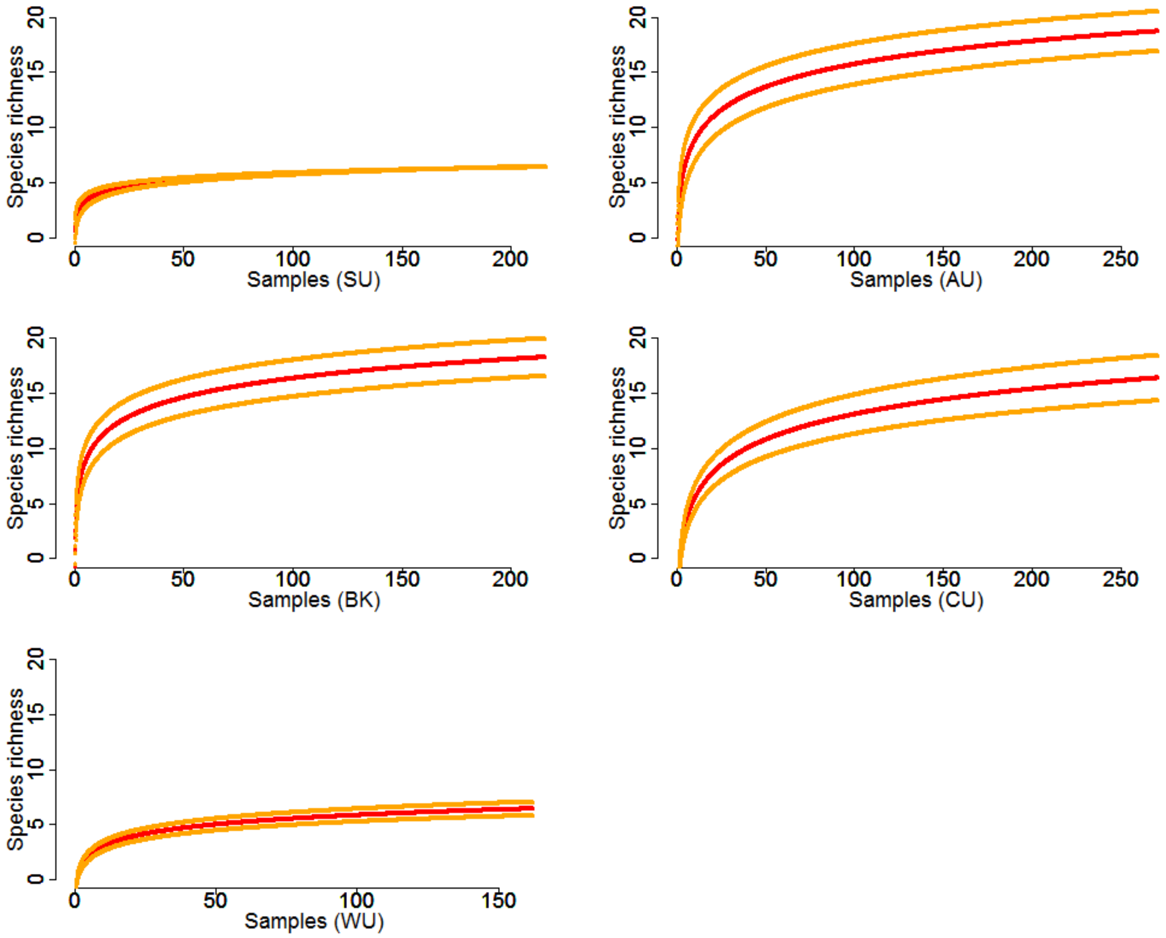

Figure 3.2. Accumulation curves using Chao1 species richness from two monthly sampling units are displayed for each subregion with 95% confidence intervals. Spec Uplands (SU), Atherton Uplands (AU), Bellenden Ker Uplands (BK), Carbine Uplands (CU), Windsor Uplands (WU).

Of the 61 flightless ground beetle species known to exist throughout all five subregions of the Wet Tropics, 43 (70%) were collected in this study. For each subregional assemblage, the majority of species known to exist were represented by this methodology (Figure 3.3). Species not sampled predominantly derived from genera *Feronista, Leiradira* and *Notonomus*.

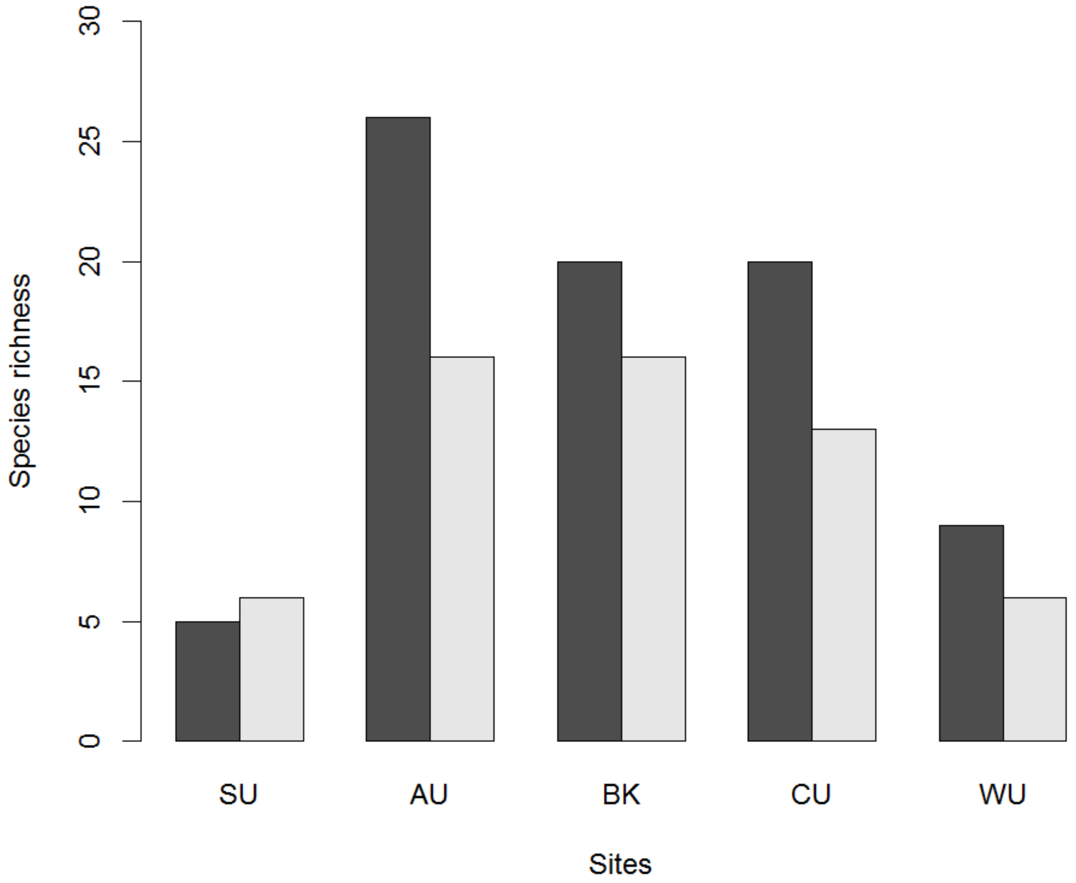

Figure 3.3. Total species richness of flightless beetles known from the existing literature (charcoal bars; see methods for more details) and species richness observed from this study (light grey bars). Spec Uplands (SU), Atherton Uplands (AU), Bellenden Ker Uplands (BK), Carbine Uplands (CU) & Windsor Uplands (WU). At Spec Uplands a new species was recorded (Castelnaudia sp.1).

3.4.3 Species richness and abundance across elevation

Species richness and abundance increased with elevation for flightless ground beetles in the Wet Tropics (Figure 3.4). Species richness was highest at the 1,000 and 1,200 m a.s.l. sites in the Carbine Uplands and Bellenden Ker Uplands, for both observed and estimated richness values. Abundance was consistently low below 1,000 m a.s.l., with Bellenden Ker Uplands displaying the highest values (Figure 3.4).

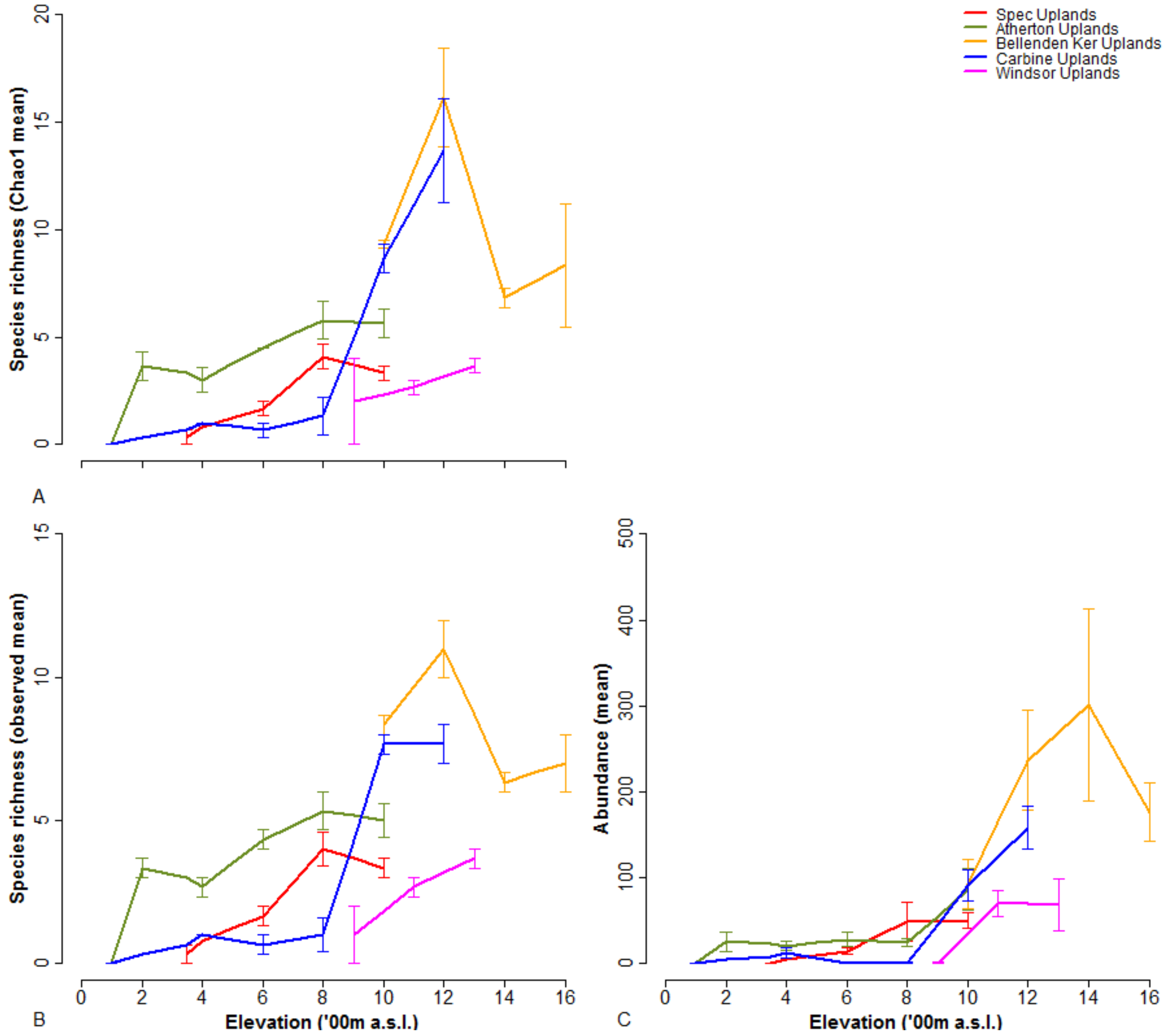

Figure 3.4A-C. Flightless ground beetle species richness and abundance changes with increasing elevation. (A) Estimated species richness (Chao1 mean (±SE, n=3)), (B) observed species richness (±SE, n=3) and (C) abundance of ground beetle communities (±SE, n=3) across elevational gradients for Spec Uplands (SU), Bellenden Ker Uplands (BK), Atherton Uplands (AU), Carbine Uplands (CU) & Windsor Uplands (WU) subregions.

Both species richness and abundance of flightless ground beetles increase with elevation in the Wet Tropics (Pr(>|z|) <0.05; Table 3.2).

Table 3.2. Generalised linear mixed model of species richness and abundance, of the entire flightless ground beetles community sampled, correlated positively with elevation as the only explanatory variable (Pr(>|z|)<0.05). Subregion was included as a random factor to control for its effect on the richness model (variance = 0.1132, standard deviation = 0.3365) and abundance model (variance = 0.4832, standard deviation = 0.6951). Pr(>|z|) values represented by * are significant Pr(>|z|)<0.05.

dependent variable	independent variable	estimate	standard error	z	n	Pr(>|z|)
richness	elevation	0.0048	0.0006	7.759	69	*
abundance	elevation	0.0017	0.0003	5.972	69	*

3.4.4 Compositional patterns of community data

The community of flightless ground displayed highly distinct assemblages within each subregion sampled (Figure 3.5; Appendix 3.2). The compositional pattern correlated with a distinct climatic gradient ranging from hotter and drier to cooler and wetter conditions. The high elevation Bellenden Ker Uplands assemblage is positioned directly at the cool-wet end of this gradient, while low elevational sites such as Spec Uplands 600 m a.s.l., Atherton Uplands 400 m a.sl. and Carbine Uplands 400 m a.s.l., are correlated with relatively hotter, drier and more seasonal environmental conditions (Figure 3.5; Appendix 3.2). Further separation of subregional assemblages correlate with temperature and precipitation seasonality (Figure 3.5; Appendix 3.2).

Sites represented by more than 5 individuals were displayed in the ordination and areas which were exceptionally species poor (Carbine Uplands 100, 600 and 800 m a.s.l., Atherton Uplands 100 m a.s.l and Spec Uplands 350 m a.s.l.) were excluded. One Spec Uplands 600 m a.s.l. site was only represented by *Castelnaudia sp.1* and was highly distinct to all other points and therefore removed as an outlier. The Atherton Uplands 200 m a.s.l. site was distinctly positioned in the centre of the ordination due to dominance by *Pheropsophus verticalis*. This site was situated within riparian habitat resulting in a high representation of *P. verticalis*, which is known to inhabit sandy creek beds throughout Australia (Baehr, 1986). Also, two Carbine Uplands 400 m a.s.l. sites differed to the high elevational sites as they were only represented by the species *Castelnaudia obscuripennis*.

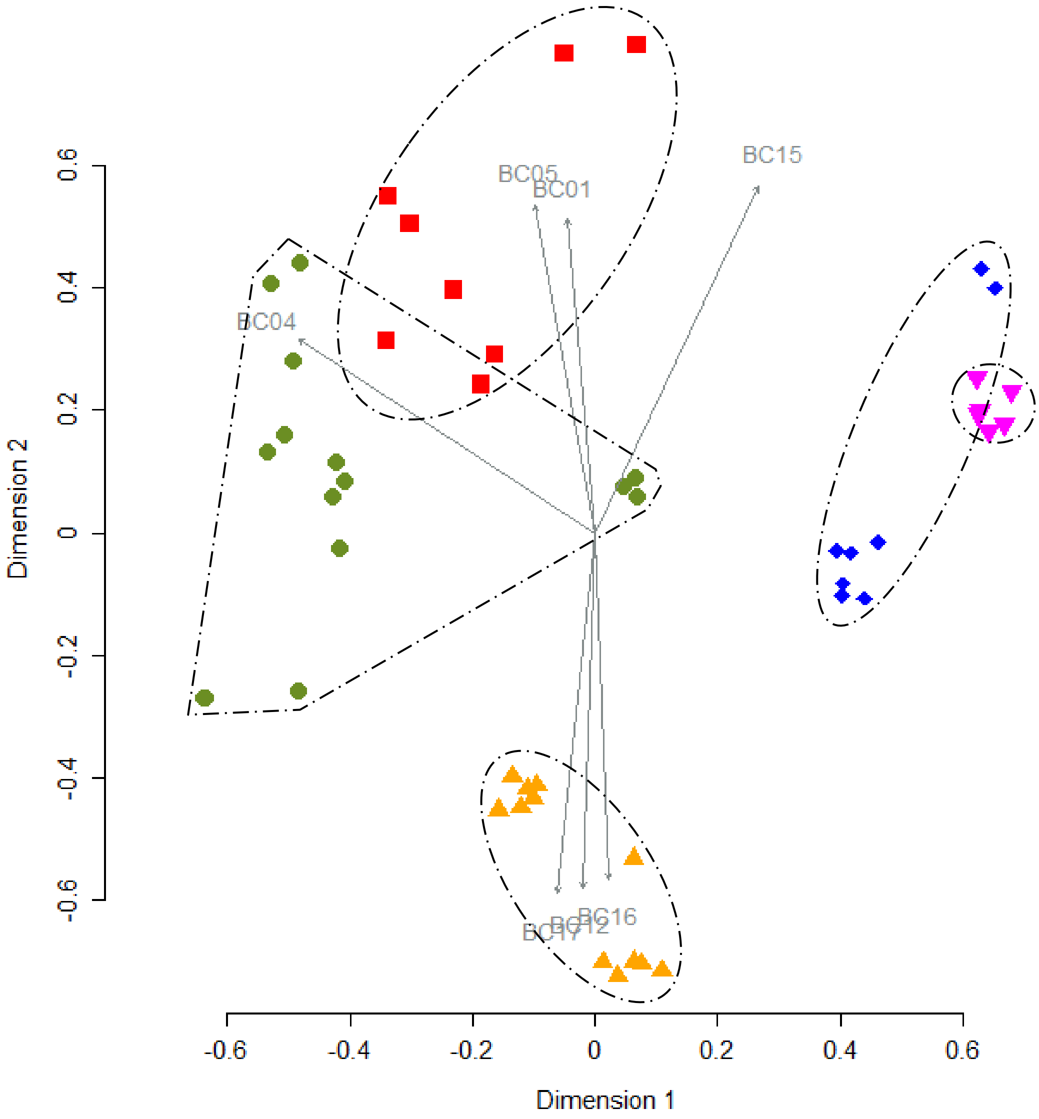

Figure 3.5. Assemblage structure of carabid beetle assemblages as described by ordination of ground beetle assemblages from each elevation within subregions of the Wet Tropics; based on Bray Curtis similarities derived from square-root transformed abundance data from pitfall traps (stress=0.21). Vectors of site environmental variables displaying significant correlations (*P*<0.001) with species data are overlayed. BC01= annual mean temperature, BC04= temperature seasonality, BC05= maximum temperature of warmest period, BC12= annual precipitation, BC15= precipitation seasonality, BC16= precipitation of wettest quarter, BC17= precipitation of driest quarter. ■ = Spec Uplands; ● = Atherton Uplands;▲ = Bellenden Ker Uplands;◆ = Carbine Uplands; ▼ = Windsor Uplands. Sites with less than 5 individuals not presented. Subregional assemblages are encircled by dashed-lines.

The community composition significantly changes in relation to variance of all seven climate variables and elevation when analysed using permutational multivariate analysis (Table 3.3).

Table 3.3. Permutational multivariate analyses of assemblage compositional change in relation to the seven significant environmental variables displayed on the ordination as well as elevation. BC01= annual mean temperature, BC04= temperature seasonality, BC05= maximum temperature of warmest period, BC12= annual precipitation, BC15= precipitation seasonality, BC16= precipitation of wettest quarter, BC17= precipitation of driest quarter.

independent variable	pseudo-$F_{1,49}$	P value
BC01	4.7	$P < 0.001$
BC04	7.5	$P < 0.001$
BC05	5.6	$P < 0.001$
BC12	6.7	$P < 0.001$
BC15	5.3	$P < 0.001$
BC16	6.6	$P < 0.001$
BC17	6.9	$P < 0.001$
Elevation	5.1	$P < 0.001$

All subregional assemblages were significantly different to each other (P<0.05) using ANOSIM (Table 3.4). Atherton Uplands and Spec Uplands, and Carbine Uplands and Windsor Uplands were less dissimilar than the other pairwise comparisons. Bellenden Ker Uplands and Windsor Uplands were entirely dissimilar as no species were shared between these assemblages. The greatest number of shared species between any two subregional assemblages was found in Atherton Uplands and Bellenden Ker Uplands. However, both these assemblages were represented by the highest unique species and were therefore still highly dissimilar to each other.

Table 3.4. Numbers of shared species between subregions (above the diagonal). Total numbers of species for each subregion with unique species to each subregion (in the diagonal). Values below the diagonal are ANOSIM R statistics indicating the degree of difference between subregions. All pairwise comparisons of subregions using ANOSIM were significant at *P*<0.05. All values are based on observed sample data from: Spec Uplands (SU), Atherton Uplands (AU), Bellenden Ker Uplands (BK), Carbine Uplands (CU) & Windsor Uplands (WU) subregions.

	SU	AU	BK	CU	WU
SU	**6 (3)**	2	1	2	2
AU	0.27	**16 (9)**	5	2	1
BK	0.81	0.69	**16 (11)**	1	0
CU	0.59	0.61	0.77	**13 (8)**	3
WU	0.81	0.73	1	0.26	**6 (2)**

Compositional changes, displayed across dimension one of the above ordination, were distinct between subregions and best explained by temperature and precipitation seasonality changes and precipitation of the wettest quarter (Table 3.5; Figure 3.6A – B; Appendix 3).

Table 3.5. Model determining which environmental correlates best describe variance in Dimension 1 axis of the ordination presented as Figure 3.5. Model performed using best sub-set regression. Adj. R^2 = Adjusted R^2, Std. err. = standard error, n =49. BC04 = temperature seasonality, BC15 = precipitation seasonality, BC16 = preciptation of the wettest quarter.

Predicted variable	Variable	T value	*P* (variables)	Model Adj. R^2	Model *P*	Std. err.	BIC
Dimension 1	(Intercept)	1.6	0.118	0.90	<0.0001	0.116	-100.7
	BC04	-15.96	<0.0001				
	BC15	14.51	<0.0001				
	BC16	4.93	<0.0001				

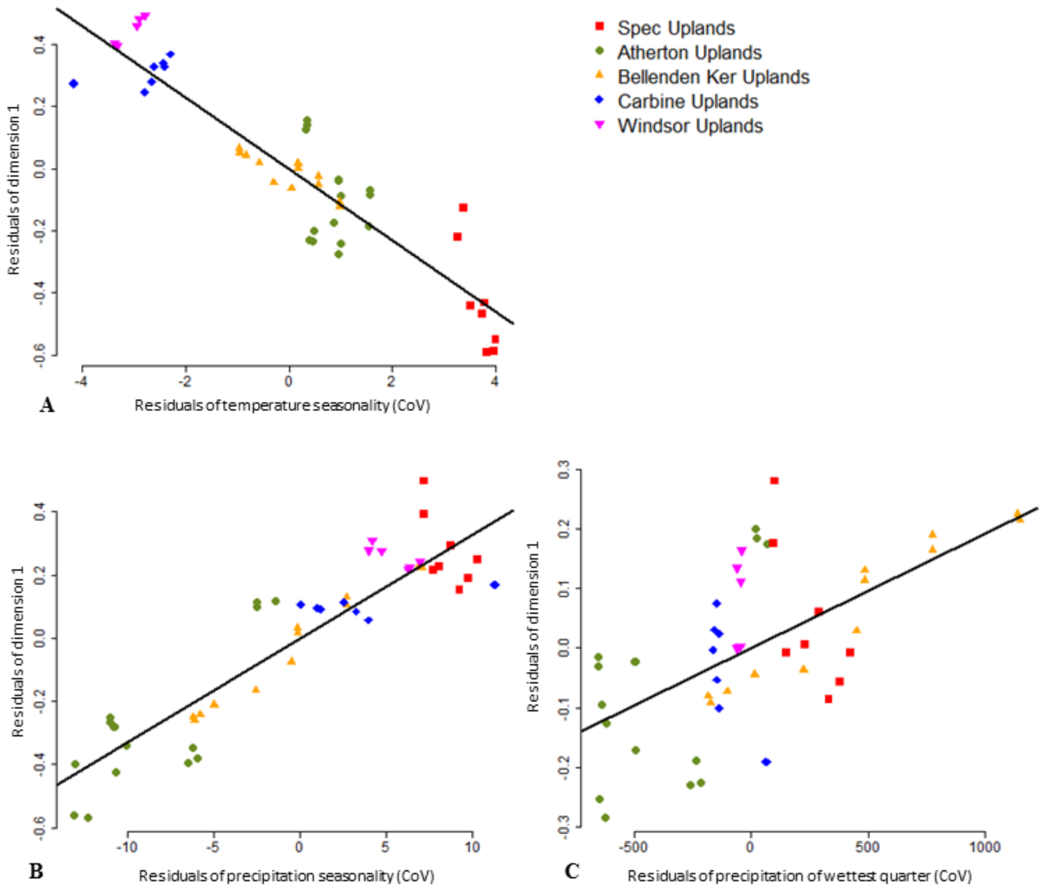

Figure 3.6A-C. The environmental factors best explaining variation of point across Dimension 1 of the NMDS of the flightless ground beetles throughout the Wet Tropics. These partial-regression plots derive from the best model selected using best sub-set multiple linear regression analysis.. Model Adj. $R^2 = 0.901$, s.e. = 0.116, n = 49, $P < 0.0001$. A. Residuals of temperature seasonality (t value = -15.96, s.e. = 0.007, n =49, Pr(>|t|) < 0.0001), B. residuals of precipitation seasonality (t value = 14.51, s.e. = 0.002, n =49, Pr(>|t|) < 0.0001), C. residuals of precipitation of the wettest quarter (t value = 4.93, s.e. = 0.00004, n =49, Pr(>|t|) < 0.0001),

Across dimension two of the ordination, variation between subregion assemblages changed significantly and was best explained by differences in maximum temperature, precipitation seasonality and minimum temperature values (Table 3.6; Figure 3.7A – C; Appendix 4).

Table 3.6. Model determining which environmental correlates best describe variance in Dimension 2 axis of the NMDS. Model performed using best sub-set regression. Adj. R² = Adjusted R², Std. err. = standard error, n =49. BC05 = maximum temperature of the warmest period, BC15 = precipitation seasonality, BC06 = minimum temperature of the coldest period.

Predicted variable	Variable	T value	*P* (variables)	Model Adj. R²	Model *P*	Std. err.	BIC
Dimension 2	(Intercept)	14.83	<0.0001	0.86	<0.0001	0.123	-85.3
	BC05	-10.18	<0.0001				
	BC15	-7.68	<0.0001				
	BC06	5.05	<0.0001				

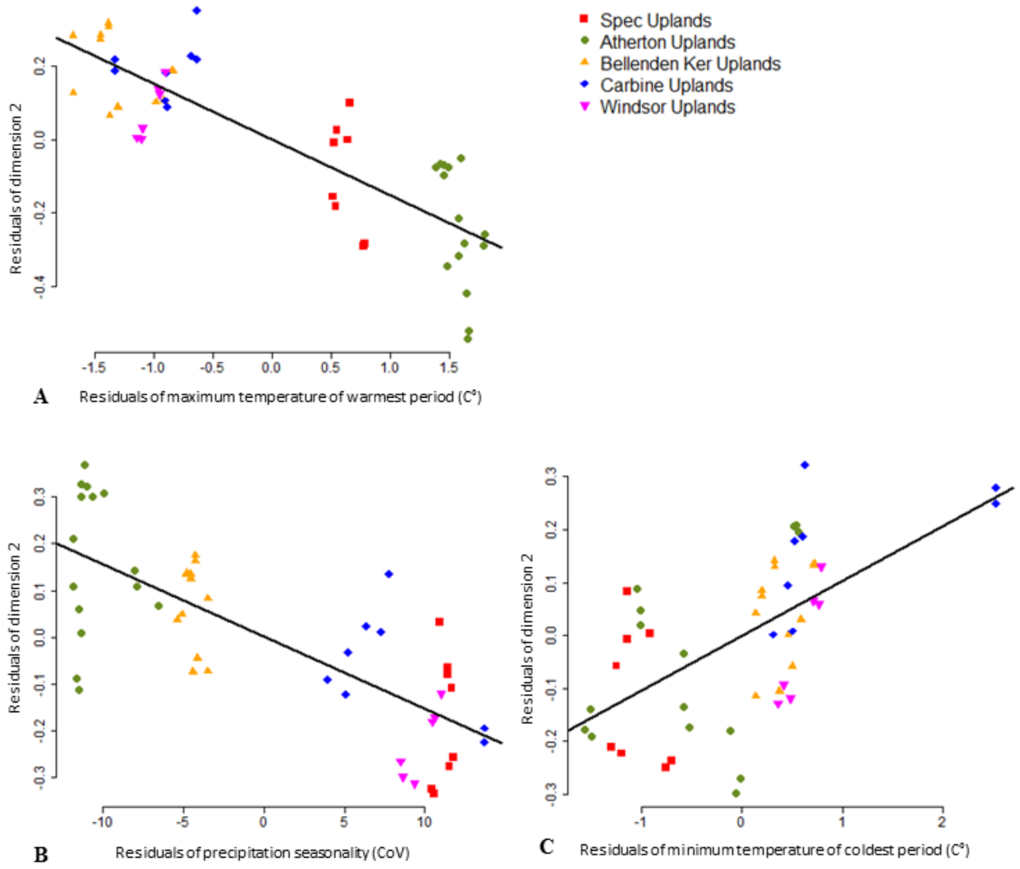

Figure 3.7A-C. The environmental factors best explaining variation of point across Dimension 2 of the NMDS of the flightless ground beetles throughout the Wet Tropics. These partial-regression plots derive from the best model selected using best sub-set multiple linear regression analysis. Model Adj. R² = 0.86, s.e. = 0.123, n =49, $P < 0.0001$. A. of maximum temperature of the warmest period (t value = -10.18, s.e. = 0.015, n =49, Pr(>|t|) < 0.0001), B. residuals of precipitation seasonality (t value = -7.68, s.e. = 0.002, n =49, Pr(>|t|) < 0.0001), C. residuals of minimum temperature of the coldest period (t value = 5.05, s.e. = 0.02, n =49, Pr(>|t|) < 0.0001).

3.5 Discussion

3.5.1 Compositional patterns relating to environmental data

These findings suggest that there are strong correlations between compositional changes of flightless ground beetles between subregions in the Wet Tropics and climatic factors. Temperature and precipitation values changes, from cool and wetter to hotter and drier conditions, correlated with differences between the Bellenden Ker Upland assemblage and the four other subregional groups, especially Spec Uplands. Differences between subregional assemblages were best explained by changes in temperature seasonality, maximum temperature, precipitation seasonality, wet season rainfall and minimum temperatures.

These results imply that the turnover of flightless ground beetle subregional assemblages is intimately linked to multiple climatic changes. This adds additional insight to the literature determining differences between subregional assemblages of animals within the Wet Tropics. High levels of compositional turnover between subregional blocks in the Wet Topics of low-vagility insects have been reported by Yeates and Monteith (2007). The extremely high proportion of subregional endemics of these insects is suggested to have resulted from *in situ* evolution without subsequent dispersal to other subregional blocks (Yeates et al., 2002). Differences in the proportion of subregional endemism of mammals throughout the Wet Tropics was related to area and shape of the subregions in which they inhabit whereby more convoluted, smaller subregions expressed lower proportions of endemics (Williams & Pearson, 1997). Therefore, like insects with low vagility, compositional turnover of mammals was related to historical factors and not present-day environmental correlates. Research performed by Wilson (2010), however, did relate variances in assemblages of Schizophoran flies between sites to changes in annual mean temperature and precipitation seasonality. Through analysing links between current climatic factors and compositional turnover of flightless ground beetles between subregions, this study therefore contributes to previous research by correlating various assemblages with environmental factors projected to change.

These results highlight that flightless ground beetles, while confined to similar habitats, are not all exposed to exactly the same climatic conditions throughout the Wet Tropics. In future, temperatures are projected to increase in this region and dry seasons are thought to become more severe (Suppiah et al., 2007). Currently there are significant differences between the temperature and precipitation and the seasonality of these factors between the five subregions sampled. Bellenden Ker Uplands contains some of the coolest and wettest conditions. Therefore, as climatic factors exacerbate in future, the assemblage within this subregion is expected to be more buffered to changes. On the other hand, the assemblage within Spec Uplands is currently exposed to the hottest temperatures during the warmest period. We would therefore expect this assemblage to be more vulnerable to the effects of climate change and therefore require more immediate conservation interventions.

3.5.2 Compositional patterns between subregions

These results suggest that there are highly distinct assemblages of flightless ground beetles within subregional areas of the Wet Tropics. Differences between Bellenden Ker Uplands and all others are clear, whereas the Carbine Uplands assemblage overlaps slightly with the group in Windsor Uplands and likewise for those in Atherton Uplands with Spec Uplands. This high level of distinction between each subregion is reinforced by the analysis of similarity whereby each subregional group is unique. In the comparison between Bellenden Ker Uplands and Windsor Uplands, a total turnover of fauna, whereby no species were shared, was seen.

The high levels of dissimilarity of flightless ground beetle assemblages between subregional blocks may be attributed to a variety of factors including low dispersal between subregions, a high level of *in situ* evolution and extinction filtering events. Darlington (1970) suggested that tropical carabids first colonised lowland regions, then dispersed into upland habitats, after which they lost their ability to fly. If this process has occurred throughout the Wet Tropics then perhaps a high level of *in situ* speciation would have occurred due to difficulty dispersing between subregions without suitable corridors connecting subregions. Upland rainforest is considered to have been highly stable within the Wet Tropics since the last glacial maximum (Jeremy VanDerWal, Luke P. Shoo, et al., 2009). If flightless ground beetles are restricted to upland rainforest habitats, as this high turnover of subregional assemblages suggests, then the stability of this vegetation may well reflect limited availability of habitat corridors between subregions which were separated by low dry barriers. Previous research has attributed high levels of endemism among flightless insects within the Wet Tropics to *in situ* speciation (Yeates et al., 2002). This process is also considered to largely affect microhylids frogs, characterised by low vagility and sensitivity to dry climates, within the Wet Tropics (Williams & Hero, 2001). This differs to the vast majority of mammals throughout the Wet Tropics for which species filter events are suggested to have shaped current community patterns (Williams & Pearson, 1997). The proportion of subregional endemics captured within this study is 33% which, while not as high as that for all flightless insect taxa in the Wet Tropics (50%; Yeates et al., 2002), is more than twice that of vertebrates (15%; Williams & Pearson, 1997). This high proportion of endemism among flightless ground beetles, and therefore compositional turnover between subregions, is a reflection of the small spatial scale at which these beetles exist in the Wet Tropics.

Such high levels of compositional turnover between subregional blocks suggest that lowland habitats may act as barriers for dispersal for flightless ground beetles in the Wet Tropics. This strongly suggests that these beetles are highly unlikely to disperse across a latitudinal gradient in response to climate and are therefore expected to only move upwards in elevation. Therefore, these assemblages are expected to become increasingly fragmented, with ranges becoming even more restricted, in response to climate change.

3.5.3 Species richness and abundance patterns across elevation

Flightless ground beetles are most species-rich and abundant in high elevations (i.e. at or above the cloud cap which is from 800 to 1,000 m a.s.l.) throughout the Wet Tropics. Of all five subregions, the highest richness values were displayed in Carbine and Bellenden Ker Uplands at 1,200 m a.s.l. Additionally, the highest abundances occurred in the higher Bellenden Ker and Carbine Upland sites. Samples from the lowest sites, both Carbine and Atherton Uplands 100 m a.s.l., contained no flightless ground beetles at all over the entire study period. It is worth noting however, that a relatively high abundance of flightless ground beetles was sampled in Atherton Uplands at 200 m a.s.l. This site was positioned within riparian habitat and the assemblage sampled was dominated by *Pheropsophus verticalis*, which is known to inhabit sandy creek beds throughout Australia (Baehr, 1986). The finding that both richness and abundance of flightless ground beetles increase with elevation is further supported by positive correlations from generalised linear mixed model analyses.

Flightless ground beetles generally inhabit the highest elevational ranges within each subregion sampled of the Wet Tropics. This result differs to the majority of insects throughout the Wet Topics which display mid elevational peaks in species richness (Yeates &

Monteith, 2008). Vertebrates within this region display greatest richness in upland habitats although birds are most species-rich and abundant around 600 - 800 m a.s.l. (Williams, 2006). Peaks in richness at mid elevational heights have been related to either suitability of environmental conditions at this height, overlapping distributions of species, and sampling artefacts (Escobar et al., 2005; Fisher, 1999; Hodkinson, 2005). However, the current project's findings are consistent with previous research showing flightless ground beetles generally occurring at higher elevations throughout the Wet Tropics (Monteith, 1989, 1994a). Internationally, greater richness and abundance of ground beetles at high elevations have been attributed to more consistent moisture levels and reduced competition from lowland ants (D. Olson, 1994; Sota, 1996; N. Stork & Brendell, 1990). Such factors could also influence the distributions of the flightless ground beetles within the Wet Tropics.

Many flightless ground beetles in the Wet Tropics are most abundant and species-rich at the highest elevations of each subregion sampled. Therefore, these beetles have already reached the highest possible extent of their distributions. Climate change is predicted to drive species distributions to higher up mountain ranges in order to maintain their current climatic envelopes change (Walther et al., 2002). However, for the vast majority of this group, which has already reached the mountain tops, further migration is impossible and therefore management interventions such as habitat corridors may offer limited benefit. Without drastic measures such as assisted migration (Peters & Darling, 1985), whereby species could be relocated to alternate mountains, reductions in richness and abundance of flightless ground beetles within the Wet Tropics are likely to occur in future.

3.5.4 Methodological efficacy

These results suggest that the methodology used in this study captures the majority of flightless ground beetles known to inhabit these subregions. This is shown by the accumulation curves either reaching or tending towards asymptote for each subregion and the result that 70% of flightless ground beetle species recorded by the Queensland Museum were sampled in this study. Furthermore, this methodology sufficiently captures the main patterns of richness and compositional change displayed by flightless ground beetles in the Wet Tropics in previous work (Monteith, 1989, 1994a; Yeates et al., 2002; Yeates & Monteith, 2008), in a standardised manner. Flightless ground beetles that were not collected in this study were either very small, and therefore subjected to trap bias (*Illaphanus NQ1*, *Sitaphe* *rotunda*, *Anomotarus NQ1* and *Feronista* spp.), or rare, or known to prefer ecotonal habitats (*Notonomus saepistriatus*, *Pamborus elegans*) and therefore unlikely to be sampled with this methodology. Therefore, replicating these experimental designs and sampling methods is suggested to be an effective technique for monitoring future compositional changes of this group in light of climate change implications.

3.6 Conclusion

This community of flightless ground beetles, within the Wet Tropics, is characterised by highly distinct subregional assemblages. Differences between these subregional assemblages are strongly linked to changes in climatic factors such as temperature and precipitation. Therefore, future climate change impacts are expected to be unequal among subregional assemblages. The assemblage in Bellenden Ker Uplands is expected to be more buffered to climate change impacts than the other four subregional assemblages due to current wetter cooler conditions. Whereas, the assemblage in Spec Uplands may be highly vulnerable to climate change as already these species are exposed to hotter, drier and more seasonal conditions. These findings support those presented in Chapter 2, using modelling techniques based on presence only data, whereby individuals endemic to drier, more marginal habitat were suggested to be the most vulnerable to climate change impacts. Conservation management concerned with helping flightless insect taxa within the Wet Topics to withstand negative climate change impacts should first focus on preserving assemblages environmentally similar to Spec Uplands.

Flightless ground beetles are more species-rich and abundant in mountain-top habitats. This community is therefore expected to undergo extremely limited dispersal in response to climate change. As these beetles are unable to disperse between mountains, management options such as assisted migration may be required to assist populations to persist under future climate change conditions. These findings are the first to relate compositional changes of a flightless insect community in the Wet Tropics to climatic factors. This study clearly highlights the sensitivity of such insects to environmental factors and warrants that further research is required in order to understand the vulnerability of flightless insects to climate change impacts.

Chapter 4. Seasonality affects both temporal and spatial variance of adult flightless ground beetle richness and abundance in the Wet Tropics.

Staunton, K., Aristophanous, M. & Williams, S. E.

4.1 Abstract

Seasonal changes in the richness and abundance of species are mostly attributed to temporal variance of climatic factors. Climate change is not only projected to the change the severity of climatic factors, but also when, throughout the year, various climates are experienced. Therefore, understanding the links between environmental factors and assemblage patterns in a seasonal context is a vital step towards comprehensively determining climate change impacts on communities. We investigated changes in richness and abundance of adult flightless ground beetles in the Wet Tropics World Heritage Area in Australia, in relation to both temporal seasonal trends and differences in seasonality displayed between locations. Richness and abundance changes of the flightless ground beetle community were strongly linked to annual seasonal variance. Abundance increased between November and February (during the wet season) and correlated positively with variances in both temperature and precipitation. Across the Wet Tropics landscape, the precipitation seasonality of a site negatively correlated with both richness and abundance of flightless ground beetles. Seasonal variations of climatic factors not only coincide with changes in abundance patterns temporally, but also relate to spatial differences in richness and abundance in flightless ground beetle assemblages. As climate change projections for the Wet Tropics bioregion suggest that dry seasons will increase in severity, future declines in richness and abundance of flightless ground beetles are expected.

4.2 Introduction

From changes in phenology and trophic interactions to range boundary shifts, climate change is predicted to have a multitude of effects on assemblages (Parmesan, 2006; Chris D. Thomas, 2010). Tropical rainforest communities contain high levels of biodiversity and are highly vulnerable to climate change impacts due to great sensitivity to further environmental changes (C. A. Deutsch et al., 2008). To date, many advances have been made to understand interactions within rainforests, such as herbivory and biodiversity of the most biodiverse animals of all, the insects (Bale et al., 2002; Kitching, 2006). One aspect that still remains largely unexamined within rainforest ecosystems is the seasonal variability of insect assemblages (Grimbacher & Stork, 2009). Such trends are often difficult to monitor as they require intensive sampling techniques to be employed for multiple years (Henk Wolda, 1983). As a result, there are few assemblage-based descriptive studies of patterns of seasonality of rainforest insects (Vojtech Novotny & Basset, 1998). Knowledge of richness and abundance patterns, and how they link to changes in seasonality, is vital for effectively monitoring and predicting climate change impacts on assemblages.

Seasonal fluctuations in insect abundance are greater in temperate rather than tropical assemblages (Vojtech Novotny & Basset, 1998). In high latitudes the period of seasonal abundance of insects is often very short with many species taking several years to complete one generation (H. Wolda, 1988). On the other hand, southern-hemisphere climatic conditions are relatively mild and unpredictable resulting in such insect assemblages displaying less distinct seasonal trends (Sinclair, Addo-Bediako, & Chown, 2003). Despite belonging to less-seasonal habitats compared to high-latitude forests, insects within tropical rainforests, which have distinct dry and wet seasons, can still exhibit notable fluctuations in abundance throughout the year (H. Wolda, 1988). Abundances, in these locations, commonly peak during the wet season and diminish during dry months (C. Frith & Frith, 1985; D. Frith & Frith, 1990; Hammond, 1990; Janzen, 1983; Vojtech Novotny & Basset, 1998; Henk Wolda, 1980).

Spatial variances in the seasonality of habitats may also affect changes in species richness and abundance throughout regions. Changes in the levels of seasonality (temperature and precipitation coefficients of variation) across a landscape have been suggested to significantly affect bird richness from dry season depletions of food availability (Williams & Middleton, 2008). Ants, even from the hottest regions in the world, are less species rich in drier localities (Jenkins et al., 2011). Changes in climatic seasonality has been linked to significant changes in dung beetle abundance and richness recorded (Andresen, 2005). Therefore, in a seasonal context, it is worthwhile noting not only how species richness and abundance values change temporally, but also spatially.

The level of seasonality characterising a region is an indicator of the area's climatic stability. A theory explaining species richness patterns is the climatic-stability-diversity, or time-stability hypothesis, whereby greater levels of speciation occur in regions which are more climatically stable (Fjeldsaå & Lovett, 1997; Graham et al., 2006; Klopfer, 1959; Pianka, 1966). Despite numerous areas characterised by high levels of stability existing throughout tropical regions, this theory still lacks supports from empirical studies (Rohde, 1992). However, as climate change is not only projected to raise temperature, but also increase seasonal severity, investigations into the impacts of seasonality on spatial distributions are imperative for interpreting and predicting climate change impacts on species.

The Australian Wet Tropics World Heritage Area (herein after "the Wet Tropics"), is a region characterised by large tracts of rainforest exposed to varying degrees of seasonality with distinct five to six month dry season (Metcalfe & Ford, 2008; Williams & Middleton, 2008). Leaf litter invertebrate fauna have been shown to display seasonal changes in abundance in this region (D. Frith & Frith, 1990; Holt, 1985), although one recent study, investigating lowland coleopterans, showed slight, if any, seasonal trends (Grimbacher & Stork, 2009). Temperature increases and greater dry-season severity are projected to occur in the Wet Tropics due to climate change effects (Suppiah et al., 2007). Flightless insect taxa, isolated on mountain-top refugia in this region, are generally considered to be highly vulnerable to such climate change impacts (Yeates & Monteith, 2008). Within this group, flightless ground beetles are the major predatory taxa. This group of beetles are not only thought to exert significant predatory pressure on other leaf litter invertebrates but are also an important food source for a variety of vertebrates (Churchfield et al., 1991; Lovei & Sunderland, 1996; Parmenter & MacMahon, 1988). To date, few ecological studies have analysed seasonal variability of flightless insects in the Wet Tropics (C. Frith & Frith, 1985; D. Frith & Frith, 1990; Holt, 1985), and none have considered flightless ground beetles. Investigations into the seasonal changes of this major flightless group are vital for monitoring and interpreting responses of this highly vulnerable taxa to climate change impacts.

Here, we analyse changes in richness and abundance of adult flightless ground beetles in the Wet Tropics, in relation to temporal seasonal variability and spatial differences in the seasonality of a location. To do this, we use pitfall trapping techniques across multiple altitudes and latitudes. First, we determine if flightless ground beetle abundance and richness change with time across a two year period. Second, we investigate the extent to which abundance changes can be linked to climatic variables. Third, we test if different levels of precipitation and temperature seasonality, across a landscape, relate to changes in abundance and richness of flightless ground beetles.

4.3 Methods

4.3.1 Study area

This study was conducted in north-eastern Australia (between 20°S, 147°E and 15°s, 145°E) within the Wet Tropics bioregion which is approximately 10,000 km² in area and has been listed as a World Heritage Area since 1988 due to the high biodiversity and endemism of the regions rainforests. This study was confined to elevational gradients within rainforest and covered a range of structural rainforest types from the complex mesophyll vine forest in fertile lowlands to upland simple notophyll vine forest and, in the case of Bellenden Ker Uplands, simple microphyll vine-fern thickets above 1500m a.s.l. (Adam, 1992).

Generally, high annual rainfall occurs throughout the Wet Tropics (2,000-8,000 mm per year) (Bonell & Callaghan, 2008) with approximately 75-90 % of precipitation occurring between November and April (McDonald & Lane, 2000). Additionally, rainforests located at elevations above 1,000 m a.s.l. receive up to 66% of their monthly water input from cloud stripping (McJannet et al., 2007) making the rainfall estimates an under-estimate of total water input. Temperatures vary throughout the region and on average decrease at a rate of 1°C with every 200 m of increased elevation (L. Shoo et al., 2005). Approximately one-third of the Wet Tropics bioregion is higher than 600 m a.s.l., where annual mean temperatures are below 22°C (N. E. Stork et al., 2009).

The five subregions sampled were Spec Uplands, Atherton Uplands, Bellenden Ker Uplands, Carbine Uplands, and Windsor Uplands. The sites sampled within these subregions expressed a variety of precipitation and temperature values within the environmental space of the Wet Topics (Figure 4.1.) Bellenden Ker Uplands is noticeably the wettest and coolest of these subregions and has the lowest precipitational seasonality. Alternatively, Spec Uplands contained some of the driest sites recorded. This subregion was also characterised by the highest precipitation and temperature seasonality values of the five subregions.

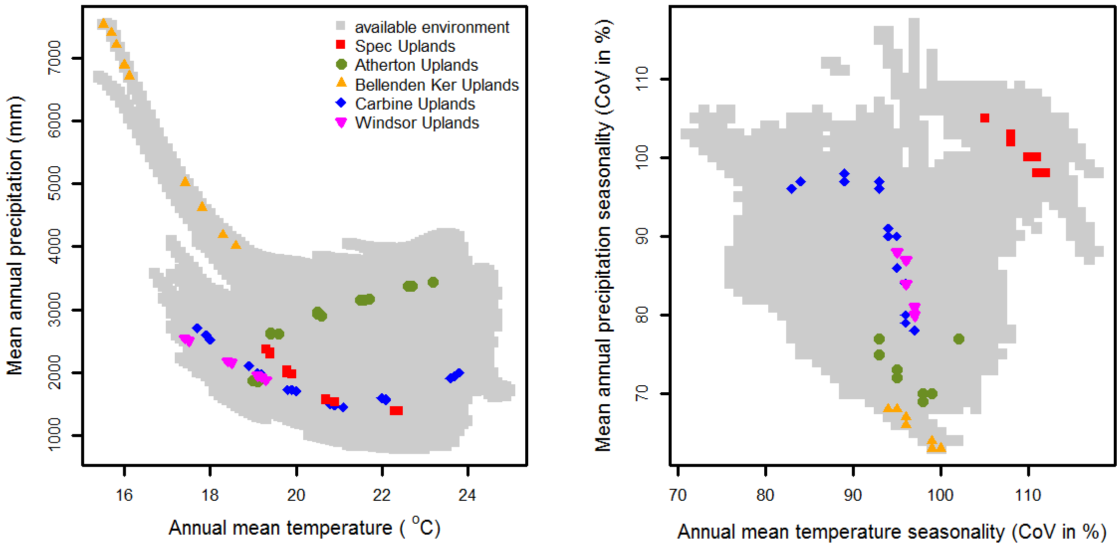

Figure 4.1. Plots of study sites within the environmental space of habitats containing rainforest in the Wet Tropics.

4.3.2 Experimental design and sampling methods

Two different sets of experimental designs and sampling methods have been analysed in this study, data set A and B. Data set A is the main data set from which most analyses derive. Data set B comprises of flightless ground beetle data extracted from a previous project, using similar methodology, simply for comparisons of seasonal trends in activity across two years. Direct comparisons between the two data sets could not be made due to differences in experimental designs and sampling methodologies nonetheless, data set B provided valuable insight into seasonal trends over multiple years. In order to produce directly comparable data sets based on equal sampling efforts within each data set, only 12 months of sampling was analysed from each subregion. In order to avoid digging-in bias, whereby high abundances are recorded simply due to a newly placed trap disturbing the normal environment (Digweed et al., 1995), the first month of sampling was not included in any data set. Data set A was analysed at the subregions Spec Uplands, Atherton Uplands, Carbine Uplands & Windsor Uplands from June 2008 until June 2009, whereas data set B was analysed from May 2007 until May 2008. Bellenden Ker Uplands was unable to be accessed until December 2008 and was therefore analysed from January 2009 until January 2010.

This study was designed to sample flightless ground beetles at approximately 200 m a.s.l. elevational intervals within each subregion. Elevations sampled within each subregion were: Spec Uplands - 350, 600, 800 & 1,000 m a.s.l.; Atherton Uplands - 100, 200, 400, 600, 800 & 1,000 m a.s.l.; Bellenden Ker Uplands – 1,000, 1,200, 1,400 & 1,600 m a.s.l.; Carbine Uplands - 100, 400, 600, 800, 1,000 & 1,200 m a.s.l.; Windsor Uplands - 900, 1,100 & 1,300 m a.s.l. (Chapter 4.3 - Appendix 3.1). At each elevation, we established three sites separated by ca. 400 m (with the exception of Spec Uplands 350 m where the sites were separated by 200 m due to there being only a small patch of rainforest). At Carbine Uplands, we were unable to find suitable sites at 200 m a.s.l. due to topographical constraints. At each replicate site, three pitfall traps were set, each 15 m apart. These traps were serviced monthly and the catches were pooled together for each replicate. The above methodological specifications fulfil pitfall trapping guidelines considered to reduce general problems associated with capturing ground beetles (Kotze et al., 2011).

Aristophanous (2010) outlined pitfall trap designs, however, a more detailed account is as follows. Each trap consists of two overlayed circular plastic containers (diameter 11.5 cm, depth 10 cm) which are set flush with a soil mound created to redirect water flow. The traps are protected from rain by a square metal lid (26cm x 26cm) fixed with wire to a ring of aviary mesh (height 7.8 cm) consisting of square gaps (2.5cm x 2.5cm). The same mesh covered container openings to prevent frogs and skinks from falling in and all mesh was fixed to the ground using wire pegs. Propylene Glycol (100%) was poured into the containers (depth 2.5 cm) as a preservative. With this design, the internal plastic containers were entirely protected by metal against rats. Propylene Glycol was used due to its resistance to evaporation, non-toxic properties and odourless nature (Aristophanous, 2010; Kotze et al., 2011). Pigs overturned traps in some drier locations (e.g. Carbine Uplands 600 m a.s.l. & Windsor Uplands 900 m a.s.l.) and these were reinforced using star pickets and wire.

Data set B differed from data set A in that Bellenden Ker Uplands was unable to be accessed and therefore not sampled. Also in data set B a different 1,000 m site at Spec Uplands (SU10A2) was used and the elevation Carbine Uplands 200 m a.s.l. was included in this sampling regime. Within each elevational band, six pitfall traps were set at only one site instead of three traps at three sites. Of these six traps, four were baited with dung to attract dung beetles and two were considered controls and left unbaited. Each trap was set 15 m apart. All six trap samples were pooled together to provide one catch for each elevational gradient per month. Whilst this design lacked replication within elevations, it still provided valuable species abundance data.

The pitfall traps used in data set B were structurally identically to those in data set A, except without wire mesh covering the container opening. Agile Wallaby (*Macropus agilis*) dung formed into ping pong ball sizes and wrapped with cloth (CHUX®) were used as bait and suspended directly above the container with a wooden kebab skewer. Phosphate Buffered Formaldehyde (4%) was used as a preservative (depth 4.5cm) as it evaporates at a slower rate than ethanol and preserves internal organs unlike Propylene Glycol (Aristophanous, 2010).

4.3.3 Environmental description

Temperature was recorded using the DS1923 temperature/relative humidity logger iButton® system which recorded values 1.5 m above ground every 15 minutes at site 1 of each elevation. Rainfall values for the entire trapping duration for each site were taken from Bureau of Meteorology's (BOM's) Australian Water Availability Project (AWAP) site http://www.bom.gov.au/jsp/awap/rain/index.jsp. Bioclimatic variables used to model carabid distributions were annual mean temperature (BC01), temperature seasonality (BC04), maximum temperature of warmest period (BC05), minimum temperature of coldest period (BC06), annual precipitation (BC12), precipitation seasonality (BC15), precipitation of wettest quarter (BC16) and precipitation of driest quarter (BC17). These variables have been strongly linked to vertebrate and dipteran distributions throughout the Wet Tropics (J. Vanderwal et al., 2009; Jeremy VanDerWal, Luke P Shoo, et al., 2009; R. D. Wilson, 2010).

In particular interest in this chapter are the above bioclimatic variables temperature seasonality and precipitation seasonality. Temperature seasonality is defined as "Temperature Coefficient of Variation (C of V) - the standard deviation of the weekly mean temperatures expressed as a percentage of the mean of those temperatures (i.e. the annual mean); for this calculation, the mean in degrees Kelvin is used avoiding the possibility of having to divide by zero, but does mean that the values are usually quite small". Precipitation seasonality is defined as "Precipitation Seasonality (C of V) - the standard deviation of the weekly precipitation estimates expressed as a percentage of the mean of those estimates (i.e. the annual mean)". The bioclimatic variables were derived using the Anuclim 5.1 software (McMahon et al., 1995) and a 80-m-resolution digital elevation model (DEM; resampled from GEODATA 9-second DEM, ver.2; Geoscience Australia, http://www.ga.gov.au/).

4.3.4 Data analysis

As pitfall traps are *in situ* passive sampling devices they only capture animals actively moving across the ground. These means that the number of animals sampled is a measure of activity density and does not necessarily estimate abundance (Greenslade, 1964; Thiele, 1977). Despite this, the term abundance is still generally used instead of activity density (Kotze et al., 2011) and this project adheres to such protocol. However, it is important to note, in this study, the abundance values analysed temporally are fundamentally different to the abundance values analysed spatially. With temporal data, a zero value does not mean that the beetles are not present, but simply that they are not active at that time. Whereas, with spatial data, zero values imply that to the beetles sampled in this study are not present in that locality.

Observed species richness and relative abundance (the proportion of the total abundance sampled) values were compared against two-monthly sampling units to describe seasonal patterns in abundance for data sets A and B. This sampling unit was chosen as it was the shortest time period by which equal sampling efforts could be represented. Chao 1 species richness values were also plotted in order to account for any enhancing effect abundance may have on relative species richness values. By using this rarefaction estimator of species richness we reduce the bias caused by uneven numbers of individuals across samples and better include the influence of rare species, thereby reducing negative bias with incomplete sampling of sites (Chao et al., 2005).

Total abundance data from each sampling unit was overlayed onto simultaneous rainfall and temperature data for each subregion in order to determine relationships between seasonal data. The rainfall data was summed and temperature data was averaged for each sampling unit. Rainfall and temperature data from lowland transects such as Atherton Uplands 100 m a.s.l. and Carbine Uplands 100 m a.s.l., where ground beetles were not sampled during the entire study, were not used in these analyses. The effect of the overturned traps on trends and patterns analysed was deemed negligible as these events occurred during the dry season in drier locations where ground beetles were not sampled in the serviceable traps.

Abundance data was transformed using square-root transformations to increase normality, as is suggested for ground beetles (Kotze et al., 2011) and count data (Crawley, 2003). Linear models were then created, using the adehabitat package from the R statistical program v2.12.1 (R Development Core Team, 2010), of monthly abundance data against total monthly precipitation and mean monthly temperature, for each subregion. Square-root transformed abundance data were further correlated using linear regressions against precipitation and temperature seasonality values (BC15 & BC04 respectively) of each site using the adehabitat and visreg packages from the R statistical program v2.12.1 (R Development Core Team, 2010). Cubic relationships were fit due to an increased R value. This analysis was only performed on data set A samples so that BK could be included and equal sampling of each site represented.

Changes in species richness and abundances, as precipitation seasonality increased, were investigated by creating generalised linear mixed models fit by Laplace approximation, with elevation as the single explanatory variable, using the lme4 package in the R statistical program v2.12.1 (R Development Core Team, 2010). The entire community data was used and subregion was included as a random factor to control for the effects of these areas on the data. This random effects model was appropriate as the observed clusters (subregional assemblages) were regarded as random samples from a large, possibly infinite, pool (entire Wet Tropics) of possible clusters (Broström & Holmberg, 2011). Poisson distributions were utilised as count data was analysed and overdispersion was accounted for by adding the number of observations as a second random factor for both the richness and abundance models (Broström & Holmberg, 2011; Zuur et al., 2009).

4.4 Results

4.4.1 Seasonality and temporal changes in richness and abundance

Relative abundance of ground beetles increased during sampling from November to February at all subregions (Figure 4.2A&B). These results are reinforced with species richness data collected from data set B. When the effect of abundance on richness is removed, by using the Chao 1 predictor of abundance, peaks in richness still occur at all subregions during the November to February collections for both years (Figure 4.2C). The exception to this is in Bellenden Ker Uplands where a peak also occurs in the May-June collection.

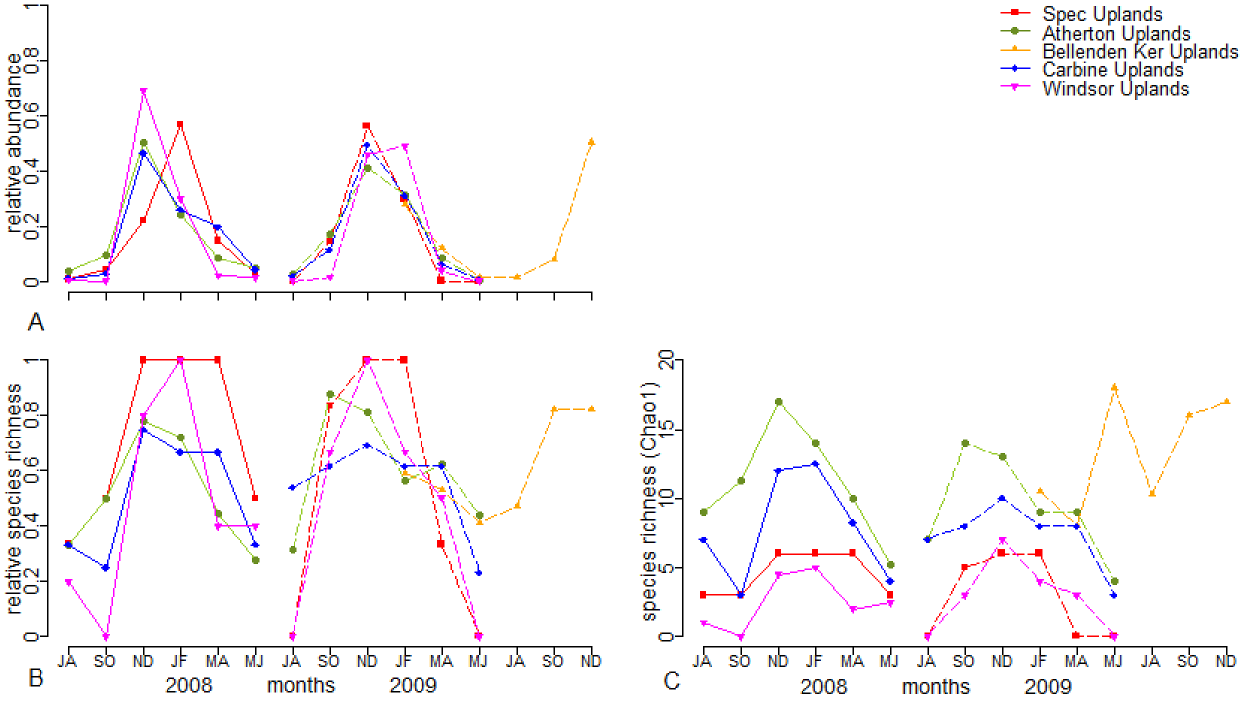

Figure 4.2. Seasonal trends of beetle abundance and richness. Plots of (A) relative abundance (B) relative species richness and (C) species richness (Chao1) of ground beetles sampled during each two month period from July-August (JA). Solid line = data set B, dashed line = data set A.

Total abundance is lowest during the driest period of the year (approximately May - August) and then increases with the first wet season rains (Figure 4.3A-D). Total abundance then peaks either simultaneously or one to two months prior to the highest rainfall values for all subregions (Figure 4.3A-D).

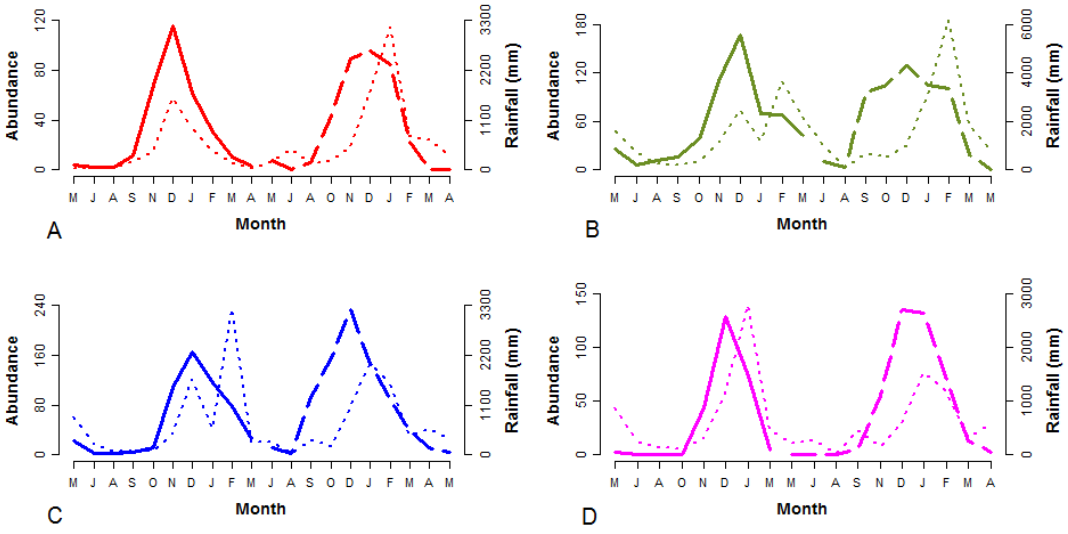

Figure 4.3A-D. Seasonal relationships between beetle abundance and rainfall trends. Total abundance of ground beetles sampled from data set B, 2007-08 (solid line) and data set A 2008-09 (dashed line) collections for each subregion and total rainfall (dotted line). (A)=Spec Uplands, (B)=Atherton Uplands, (C)=Carbine Uplands, (D)=Windsor Uplands.

Peaks in total abundance occurred simultaneously with peaks in mean temperature for both data sets at all subregions (Figure 4.4A-D). The coolest time of year, around June - August, also coincided with lowest abundance records.

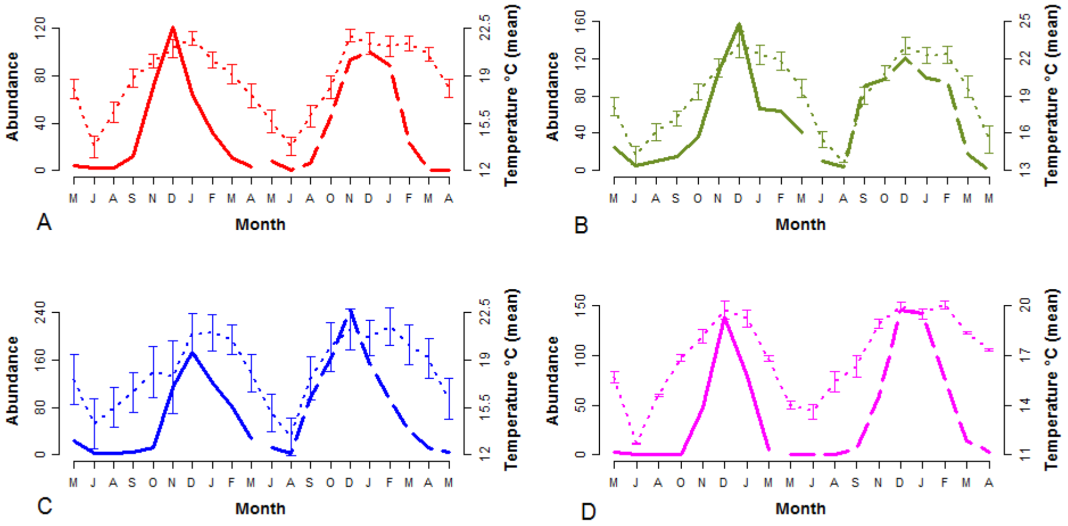

Figure 4.4A-D. Seasonal relationships between beetle abundance and temperature trends. Total abundance of ground beetles sampled from data set B 2007-08 (solid line) and data set A 2008-09 (dashed line) collections for each subregion and mean temperature (±SE, dotted line). (A)=Spec Uplands, (B)=Atherton Uplands, (C)=Carbine Uplands, (D)=Windsor Uplands.

Peaks in abundance coincided with peaks in both rainfall and temperature from data collected at Bellenden Ker Uplands from November 2009- December 2010 (Figure 4.5A & B). Lowest abundance records also occurred during the driest, coldest times of the year.

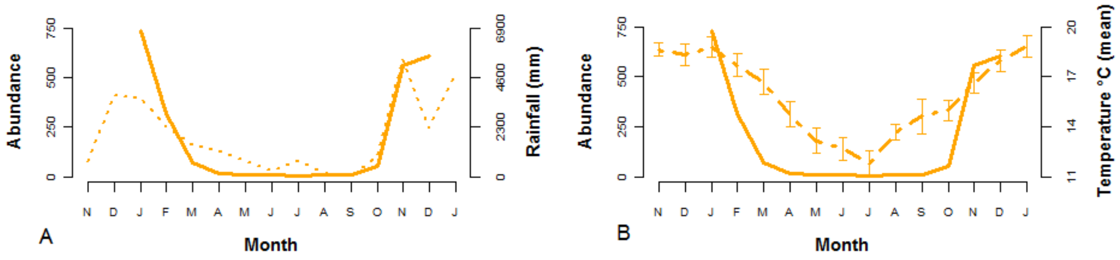

Figure 4.5A&B. Seasonal relationships between beetle abundance and rainfall and temperature trends for Bellenden Ker Uplands. Total abundance of ground beetles sampled from Bellenden Ker Uplands from data set A, January 2009-December 2010. (A) Background measurements of total rainfall (dotted line), (B) background measurement of mean temperature (±SE, dotted line).

Monthly abundance data of ground beetles correlated significantly with total monthly rainfall values for most subregions, with results from the Atherton Uplands assemblage being marginally significant (Table 4.1). The same abundances correlated significantly with mean monthly temperature values for all subregions (Table 4.1).

Table 4.1. Seasonal relationships between beetle abundance and rainfall and temperature trends. Abundance (square-root transformed) of ground beetles sampled within each subregion correlated with total monthly precipitation and mean monthly temperature for each subregion sampled. *P* values represented by * are significant $P < 0.05$.

Subregion	Total abundance	Rainfall		Temperature	
		Adj. R^2	*P* value	Adj. R^2	*P* value
Mt. Spec	651	0.38	*	0.51	*
Atherton Uplands	1095	0.15	0.059	0.81	*
Mt. Bellenden Ker	2428	0.73	*	0.76	*
Carbine Uplands	1336	0.23	*	0.62	*
Mt. Windsor	671	0.33	*	0.68	*

4.4.2 Seasonality and spatial changes in richness and abundance

Total abundance (square-root transformed) of ground beetles sampled from dataset A was modelled using precipitation and temperature seasonality indices for each site. Only precipitation seasonality was found to significantly correlate with regional abundance ($F_{3,65} = 21.37$, Adj. $R^2 = 0.47$, $P < 0.001$; Figure 4.6A & B). Similarly, precipitation seasonality and not temperature seasonality significantly correlated with flightless ground beetle richness in the Wet Tropics ($F_{3,65} = 19.7$, Adj. $R^2 = 0.45$, $P < 0.001$; Figure 4.6C & D)

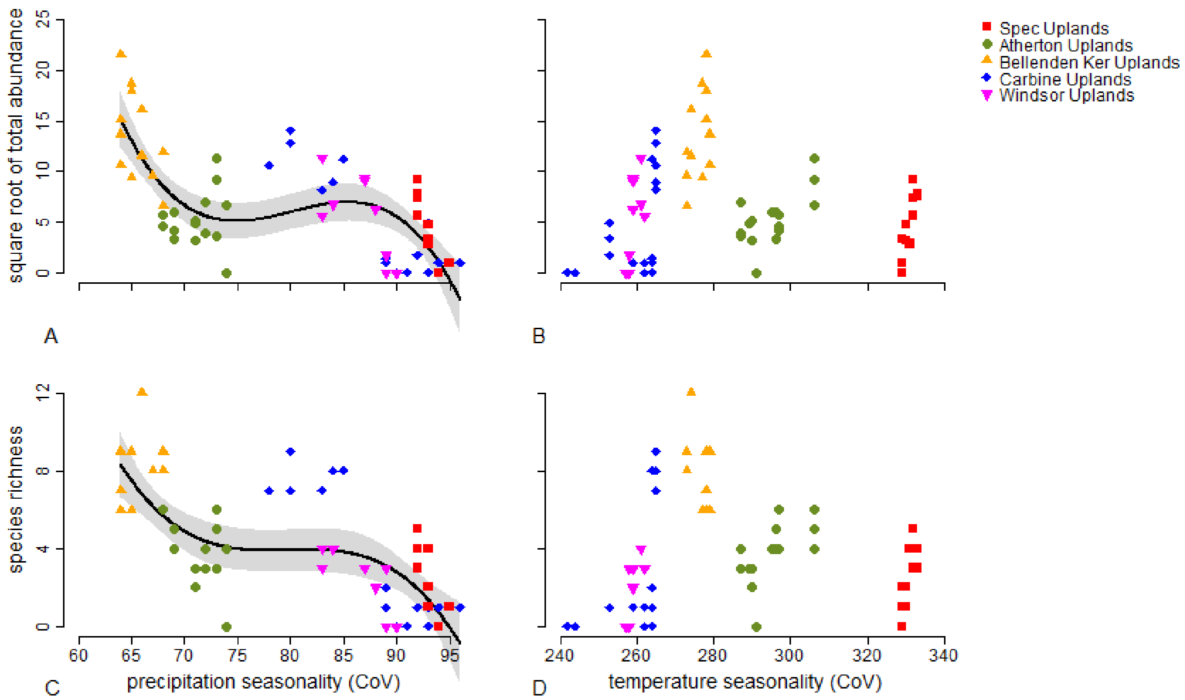

Figure 4.6A-D. Relationship between beetle richness and abundance and precipitation seasonality. Linear regression of cubic relationships between: (A) total abundance (square-root transformed) of ground beetles sampled from data set A and precipitation seasonality ($F_{3,65}$ = 21.37, Adj. R²= 0.47, $P < 0.001$), (B) total abundance and temperature seasonality (not significant $P < 0.05$), (C) observed species richness and precipitation seasonality ($F_{3,65}$ = 19.7, Adj. R²= 0.45, $P < 0.001$), and (D) observed species richness and temperature seasonality. Grey areas indicate the 95% confidence interval.

Both species richness and abundance of flightless ground beetles correlate negatively with precipitation seasonality in the Wet Tropics (Pr(>|z|) <0.05; Table 4.2).

Table 4.2. Relationship between beetle richness and abundance and precipitation seasonality. Generalised linear mixed model of species richness and abundance, of the entire flightless ground beetles community sampled, correlated positively with precipitation seasonality as the only explanatory variable (Pr(>|z|)<0.05). Subregion was included as a random factor to control for its effect on the richness model (variance = 0.94, standard deviation = 0.97) and abundance model (variance = 7.34, standard deviation = 2.71). Pr(>|z|) values represented by * are significant Pr(>|z|)<0.05.

dependent variable	independent variable	estimate	standard error	z	n	Pr(>|z|)
richness	precipitation seasonality	-0.13	0.02	-6.8	69	*
abundance	precipitation seasonality	-0.33	0.05	-6.5	69	*

4.5 Discussion

4.5.1 Spatial changes in richness and abundance relating to seasonality

Richness and abundance values of flightless ground beetles correlated negatively with precipitation seasonality throughout the Wet Tropics. Subregional sites such as those in Bellenden Ker Uplands, characterised by low precipitation seasonality, contained a high richness and abundance of flightless ground beetles. On the other hand, sites in Spec Uplands and the lower elevations of Carbine Uplands and Windsor Uplands, where precipitation seasonality values were higher, displayed decreased values of richness and abundance of flightless ground beetles. These results were further reinforced by the generalised linear mixed models which determined significant negative correlations between both richness and abundance of flightless ground beetles and precipitational seasonality in the Wet Tropics.

The implications of these findings are that flightless ground beetles are more species-rich and abundant in areas characterised by more consistent levels of rainfall. Few studies have linked spatial variations of invertebrate richness and abundance to variances in precipitation seasonality. However, this finding is similar to that of schizophoran flies in upland habitats throughout the Wet Tropics for which abundance values are also negatively correlated with precipitation seasonality (R. D. Wilson, 2010). Likewise, in Costa Rica, abundances of montane insects were lower in areas characterised by severe dry seasons (Janzen, 1973). For vertebrates, spatial patterns of bird abundance throughout the Wet Tropics were attributed primarily to precipitation seasonality (Williams & Middleton, 2008). This study suggested that birds experienced a bottleneck of resources (including insect availability) during the dry season which limits population sizes to degrees dependent on the severity of the dry season (Williams & Middleton, 2008). Species richness of microhylids frogs throughout the Wet Tropics correlated negatively with precipitation seasonality (Williams & Hero, 2001). Given the similarity of habitats occupied by both taxa in the Wet Tropics, often under logs and in moist conditions, similar correlations with climatic factors between species are logical.

Our findings that both richness and abundance increase in areas characterised by greater precipitational seasonality supports the time-stability hypothesis (Klopfer, 1959). This hypothesis was formulated to help explain variations of species richness across latitudinal gradients (Klopfer, 1959) and climatic stability is considered to have greatly influenced current community patterns of vertebrates throughout the Wet Tropics (Graham et al., 2006; Williams, 1997). For flightless invertebrates in the Wet Tropics, endemic taxa were suggested to have evolved *in situ* in subregions containing refugial rainforest habitat that were protected during historical climatic fluctuations (Yeates et al., 2002). The results in our study support this supposition by displaying the sensitivity of flightless ground beetles to habitats characterised by high precipitation seasonality, a measure of climatic variability.

Reductions in both the richness and abundance of flightless ground beetles in the Wet Tropics are expected to occur due to climate change projections. These projections state an increasing severity of dry seasons throughout the Wet Tropics (Suppiah et al., 2007). Therefore as the seasonality throughout the Wet Tropics increases, flightless ground beetle populations are likely to decrease even further, with currently small populations perhaps becoming untenable. The beetles' low vagility means that migration to suitable habitats is greatly restricted. Therefore, flightless ground beetles will be one of the most sensitive taxa to climate change impacts in the Wet Tropics.

4.5.2 Temporal changes in richness and abundance between seasons

Flightless ground beetles display seasonal abundance and richness trends reflecting heightened activity during the wet season and inactivity during the dry season. This pattern was consistently expressed for abundance and richness values of assemblages from all subregions over two years. The exception to this trend was noted for the species in Bellenden Ker Uplands where a peak in estimated richness also occurred in the May-June collection. As higher proportions of singletons positively affect the Chao 1 rarefaction estimator, this peak is suspected to have occurred due to a high number of singletons captured at this time. It is important to note however, that any seasonal decreases in species richness values recorded are considered to be due to inactivity rather than an actual absence of species. Therefore, the results clearly show high wet season and low dry season activity of flightless ground beetles in all subregions sampled.

This result is common to studies of other tropical invertebrates which display peaks in activity during the wet season and troughs in the dry season (Buskirk & Buskirk, 1976; Erwin & Scott, 1980; Hammond, 1990; Lowman, 1982). Dipteran abundance over a variety of elevations in the Wet Tropics has also been noted to decrease during the dry season (R. D.

Wilson, 2010; Rohan D. Wilson et al., 2007). Similarly, highly seasonal patterns in abundance and richness, with peaks during the wet season were noted for dung beetles, adult Trichoptera and other litter invertebrates in the Wet Tropics (Benson & Pearson, 1988; C. Frith & Frith, 1985; D. Frith & Frith, 1990; Hill, 1993; Holt, 1985). Within the northern Wet Tropics, a recent study by Grimbacher & Stork (2009), who comprehensively sampled lowland Coleoptera, found little evidence for seasonality when the beetle assemblage was considered as a whole. However they did note that larger, predatory beetles displayed more seasonal trends in abundance (Grimbacher & Stork, 2009).

Despite the relative stability of the upland habitats in the Wet Tropics, flightless ground beetles are clearly sensitive to seasonal variations in environmental conditions. It is vital to know when adults of this group are active so that effective monitoring can occur. Future monitoring is best performed both during the wet season and using a long-term sampling design, so that values are not negativity biased by periods of inactivity.

4.5.3 Linking seasonal abundance changes to environmental factors

Abundance of flightless ground beetles was intimately linked to seasonal variability of both rainfall and temperature. Beetle abundance, a measure of activity, was extremely low during the dry season (May to August). Between these months, lowest temperatures were also recorded. As the rain began to fall during August and September, the abundance of flightless ground beetles began to increase. Abundance then peaked either simultaneously, or one to three month prior to (December to January) the wettest periods. Peaks in abundance also coincided with the hottest temperature records. The presence of positive relationships between abundance and rainfall and temperature were supported by multiple correlations.

Changes in abundance of flightless ground beetles are correlated with seasonal environmental trends. Our results confirm many tropical forest studies where fluctuations in rainfall are considered the drivers of seasonal variations in arthropod abundance, including ground beetles (Boinski & Fowler, 1989; D. Frith & Frith, 1990; Holt, 1985; Janzen, 1983; Paarman 1986 in Lovei & Sunderland, 1996; V. Novotny et al., 2002; H. Wolda, 1988; Henk Wolda & Denlinger, 1984). It has been suggested that the most demanding lifecycle activities such as reproduction and growth need to occur during the most environmentally optimal time of year (Visser & Both, 2005). Subsequently, seasonal changes in abundance of adult beetles may largely result from environmental pressures on larval stages (Grimbacher & Stork, 2009). Perhaps the wettest period of the year buffers flightless ground beetle eggs and larvae from negative environmental pressures such as desiccation. Nests of *Trichosternus fax* with 1st instar larvae and eggs were found in January of 2009 and 2010 in Bellenden Ker Uplands. Insect eggs are permeable to water and therefore prone to desiccation (Wigglesworth, 1953). Each egg was cased in wet soil assumed to be fashioned by the adult found guarding them. Furthermore, first instar larvae of *Pamborus tropics* and, almost certainly, *Trichosternus montorum* were also found during January of 2010 in the same location. Ground beetle larvae are weakly sclerotised and considered sensitive to dry conditions (Lovei & Sunderland, 1996). Precipitation levels were some of the highest recorded for this area during these times and, due to these beetles' low tolerances to desiccation (Lovei & Sunderland, 1996), the wet season is strongly suspected to drive the optimal environmental conditions for reproduction and growth of these beetles.

Food availability has also been implicated in driving seasonal changes in abundance for other tropical invertebrates (Henk Wolda, 1978). Ground beetles generally prey on smaller leaf litter invertebrates (Lovei & Sunderland, 1996) which, within the Wet Tropics, are more abundant during the wet season (C. Frith & Frith, 1985; D. Frith & Frith, 1990; Holt, 1985). Therefore, prey availability may positively affect the variability of flightless ground beetle abundance throughout the year. Interestingly, while ground beetles are sensitive to maximum temperatures (Chapter 2), counter-intuitively they are active during the hottest time of year. Behavioural modifications such as nocturnal foraging and restricted high altitude ranges may be compromises this group endure in order to access greater food availability in hotter conditions.

The strength of the links between beetle abundance and seasonal changes in rainfall and temperature implies that this group may be highly sensitive to seasonal changes driven by climate change. If dry seasons increase in severity, as predicted (Suppiah et al., 2007), then the time in which flightless ground beetles are active will be reduced. They will subsequently have less time to reproduce, hatch and develop as well as access food. Therefore an increase in dry season severity is certain to be an additional stress to this, already vulnerable, group.

4.6 Conclusion

The precipitational seasonality of a habitat is strongly negatively correlated with the richness and abundance of flightless ground beetles throughout the Wet Tropics. This supports the time-stability hypothesis whereby more climatically stable habitats contain greater diversity. Furthermore, these beetles display highly seasonal patterns of richness and abundance with peaks in abundance, or activity, occurring in the wet season when it is wetter and hotter. As dry seasons are projected to increase in severity with climate change (Suppiah et al., 2007), flightless ground beetles are expected to decline in both richness and abundance in the future. It is worthwhile noting that there are many more species of flightless insects in the Wet Topics than just ground beetles (Yeates & Monteith, 2008). To date, very little research has been performed linking flightless insects to climate change concerns in the Wet Tropics. If the other flightless taxa display seasonal trends as strongly as flightless ground beetles, further research is imperative for determining and monitoring negative effects of climate change on such a highly species rich group.

Chapter 5. Ant compositional changes and climatic correlates: could they both affect flightless ground beetle richness and abundance?

Staunton, K., Burwell, C., Robson, S. K. A. & Williams, S. E.

5.1 Abstract

Understanding how species' interactions affect current distributions is vital to accurately projecting climate change impacts on communities. Competition is a fundamental species' interaction within communities whereby the stronger competitor may limit the distribution of the weaker party. Tropical flightless ground beetles are taxa which expresses highly restricted mountain-top ranges, suggested to result from either intolerance of lowland climates or overwhelming competition from lowland ants. This study simultaneously investigates the role of biotic (ant) and abiotic (climatic) factors on the richness and abundance of flightless ground beetles. The Wet Tropics World Heritage Area (herein after 'the Wet Tropics') in Northern Australia is a tropical region known to express highly diverse flightless insect taxa with extremely restricted mountain top ranges, including flightless ground beetles. We used pitfall sampling across elevational gradients within the rainforest habitats of five mountain ranges in the Wet Tropics to capture ant community patterns. Ant species richness is negatively correlated with elevation throughout this region. Compositional changes of the ant community were intimately linked to current climatic conditions with similar assemblages occurring throughout the lowland habitats sampled. In relation to sympatric flightless ground beetles, ant species richness negatively correlated with both beetle abundance and richness. However, compared to climatic correlates, ant richness did not best explain variance in flightless ground beetle abundance or richness values. These results suggest that current distributions of flightless ground beetles are predominantly linked to environmental correlates rather than competition with ants. Therefore, climate change is predicted to have greater impacts on flightless ground beetle populations in the Wet Tropics via environmental correlates rather than interactions with ants.

5.2 Introduction

Understanding factors associated with species' distribution boundaries is vital to projecting species range shifts due to climate change impacts. Climate change is expected to not only affect species' ranges directly, via changes in environmental factors, but also indirectly through species interactions (Parmesan, 2006; Walther et al., 2002). Future, climate change impacts such as species migrations, are suggested to negatively affect the species richness of many biodiversity hotspots (Thuiller, 2007). Tropical forests comprise the predominant habitat type of biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000) among which habitats across elevational gradients are extremely species-rich (Bruhl et al., 1999). Within tropical mountain ranges, as future climates continue to warm, lowland species are shifting their distributions upwards and invading highland habitats (Chen et al., 2011; J. Alan Pounds et al., 1999; Raxworthy et al., 2008). Such migrations are projected to not only result in a significant paucity of lowland species (Colwell et al., 2008), but as species invade new habitats, competitive interactions can result in significant biodiversity loss (Mainka & Howard, 2010). Clearly comprehensive understanding of the threats that lowland species pose to upland habitat specialists is urgently required. However, to date, little research has occurred investigating such risks in a climate change context.

As tropical ants shift their distributions upwards in elevation, new species interactions are likely to occur. Ants have already been suggested to significantly impact assemblage structures of other arthropods within lowland rainforest habitats (Bruhl et al., 1999; Floren, Biun, & Linsenmair, 2002; Laakso, 1999). While certain ants obtain food resources through activities such as tending to honey dew and consuming extrafloral nectaries, generally ants are predators and scavengers of other arthropods (Hölldobler & Wilson, 1990). Subsequently, ants affect the presence of other arthropods either directly through predation or indirectly through competition (Floren et al., 2002; Hawes et al., 2002; Savolainen & Vepsäläinen, 1988). Within tropical mountain ranges, as elevation increases, ants generally decline in diversity (Fisher, 1999; D. M. Olson, 1994). This paucity of upland representatives is linked to environmental conditions becoming increasingly cool, clouded and moist at high elevations (Bruhl et al., 1999; Brian L. Fisher, 1998; C. Rahbek, 1995). As climate change continues to warm tropical environments (Suppiah et al., 2007), ants are expected to shift their distributions into highland environments (Staunton et al., 2011).

Flightless ground beetles (Carabidae) are known to display highly restricted mountain top distributions within tropical rainforest habitats (Chapter 2, 3). High richness and abundance of this group have been significantly correlated with climatic factors such as maximum temperature values across elevational gradients (Chapter 2, 3). Flightless ground beetles, throughout Wet Tropics World Heritage Area (herein after “the Wet Tropics”), are determined to be most plentiful in cool, wet, highland habitats (Chapter 2). However, restricted highland distributions of ground beetles have also been suggested to result from pressure through competition with lowland ants (Darlington, 1971; D. M. Olson, 1994). Ants are considered to be the stronger competitor and actively exclude ground beetles through either predation or competition (Darlington, 1943; Hawes et al., 2002; Reznikova & Dorosheva, 2004). Furthermore, studies suggest that to disregard the influence of ants on ground beetle communities results in misleading conclusions (Hawes et al., 2002; Lovei & Sunderland, 1996). If ants do out-compete flightless ground beetles, and climate change enables ants to establish greater populations in highland habitats, impacts on beetle assemblages may be dramatic.

The Wet Tropics is an ideal location to investigate the potential risks lowland ants pose to upland flightless ground beetle populations. This area is located in northern Australia and is internationally recognised for the high levels of biodiversity and endemism it contains. This region consists of a multitude of subregions containing geographically distinct upland blocks separated by lowland gullies and drier habitats (Nix, 1991; Williams et al., 2003). Within the separated mountain top habitats is a highly biodiverse community of flightless insect taxa among which flightless ground beetles represent a significant predatory component (Yeates et al., 2002). However, ants within this region remain largely unstudied with only preliminary work having been performed (Majer et al., 2001; Yek et al., 2009).

This project aims to examine the relative roles of sympatric ant richness patterns or climatic factors in influencing the richness and abundance patterns of flightless ground beetles in the Wet Tropics. First, the ant community in the Wet Tropics is revealed and links to environmental correlates determined. Second, changes in ant species richness are assessed across elevational gradients. Third, links are determined between ant richness patterns and co-located flightless ground beetle richness and abundance. Finally, changes in ant richness are compared with climatic variables to determine which of these factors best explain patterns of beetle richness and abundance.

5.3 Methods

5.3.1 Study area

This study was conducted in north-eastern Australia (20° to 15°S and 147° to 145°E) within the Wet Tropics bioregion which is approximately 10,000 km² in area (Figure 5.1). The Wet Tropics has been listed as a World Heritage Area since 1988 due to the high biodiversity and endemism of the region's rainforests. This study was confined to rainforest and covered a range of structural rainforest types across elevational gradients from complex mesophyll vine forest in the fertile lowlands to upland simple notophyll vine forest and, in the case of Bellenden Ker Uplands, simple microphyll vine-fern thickets above 1,500 m a.s.l. (Adam, 1992).

Generally, annual rainfall throughout the Wet Tropics is high (2,000 – 8,000 mm per year) (Bonell & Callaghan, 2008) with approximately 75 - 90 % of precipitation falling between November and April (McDonald & Lane, 2000). Additionally, rainforests located at elevations above 1,000 m a.s.l. receive up to 66% of their monthly water input from cloud stripping (McJannet et al., 2007). Rainfall estimates, therefore, under-estimate total water input. Approximately one-third of the Wet Tropics bioregion is higher than 600 m a.s.l., where annual mean temperatures are below 22°C (N. E. Stork et al., 2009).

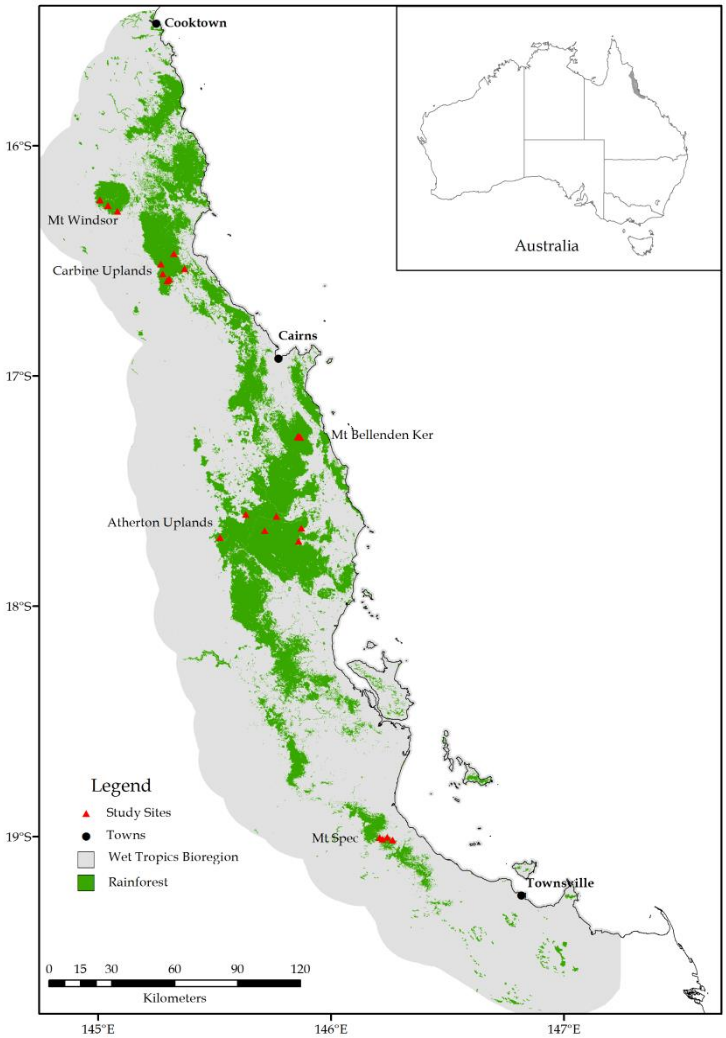

Figure 5.1. Map of Wet Tropics bioregion showing the current extent of rainforest and study sites.

5.3.2 Experimental design and sampling methods

The five study areas were located within the Spec Uplands, Atherton Uplands, Bellenden Ker Uplands, Carbine Uplands and Windsor Uplands subregions (Figure 5.1). The southern-most subregion is Spec Uplands with Atherton Uplands and Bellenden Ker Uplands situated in the middle of the Wet Tropics and Carbine Uplands and Windsor Uplands both located in the north. Within each subregion, the available elevational gradients within contiguous rainforest were utilised. The extent of the elevational gradient sampled varied between subregions due to differences in the availability and accessibility of rainforest habitats.

This study was designed to sample ants at approximately 200 m a.s.l. elevational intervals within each subregion. Elevations sampled within each subregion were: Spec Uplands - 350, 600, 800 & 1,000 m a.s.l.; Atherton Uplands - 100, 200, 400, 600, 800 & 1,000 m a.s.l.; Bellenden Ker Uplands – 1,000, 1,200, 1,400 & 1,600 m a.s.l.; Carbine Uplands - 100, 400, 600, 800, 1,000 & 1,200 m a.s.l.; Windsor Uplands - 900, 1,100 & 1,300 m a.s.l. (Chapter 3 - Appendix 5.1). At each elevation, we established three sites separated by ca. 400 m (with the exception of Spec Uplands 350 m where the sites were separated by 200 m due to there being only a small patch of rainforest). At Carbine Uplands, we were unable to find suitable sites at 200 m a.s.l. due to topographical constraints. At each replicate site, three pitfall traps were set, each 15 m apart. These traps were serviced monthly and the catches were pooled together for each replicate.

Ants were sorted to species and morphospecies in the Queensland Museum, relative to samples already stored in that facility. Identifications were finalised by Chris Burwell and a reference collection of species identified in this chapter are located in the Queensland Museum.

Each pitfall trap consisted of two circular plastic containers (one set within the other) of diameter 11.5 cm, depth 10 cm. These were set flush with the surface of a soil mound created to prevent flooding of the trap. Traps were protected from rain by a square metal lid (length 26 cm) fixed with wire to a ring of aviary mesh (height 7.8 cm) consisting of square gaps (length 2.5 cm). Container openings were covered with the same mesh and all mesh was fixed to the trap using wire pegs. Mesh covered container openings in order to prevent frogs and skinks from falling in. All external components of the traps were metal for protection from rats, *Rattus spp.*. Propylene glycol (100%, depth 2.5 cm) was used as the preservative in traps due to its resistance to evaporation and low mammalian toxicity (Aristophanous, 2010). Some traps in drier locations (e.g. Carbine Uplands 600 m a.s.l. & Windsor Uplands 900 m a.s.l.) had to be reinforced using star pickets and wire to prevent disturbance by feral pigs, *Sus scrofa*.

5.3.3 Environmental variables

Temperature and precipitation data used in this study bioclimatic variables, derived using the Anuclim 5.1 software (McMahon et al., 1995) and a 80-m-resolution digital elevation model (DEM; resampled from GEODATA 9-second DEM, ver.2; Geoscience Australia, http://www.ga.gov.au/). Bioclimatic variables used were annual mean temperature (BC01), temperature seasonality (BC04), maximum temperature of warmest period (BC05), minimum temperature of coldest period (BC06), annual precipitation (BC12), precipitation seasonality (BC15), precipitation of wettest quarter (BC16) and precipitation of driest quarter (BC17). These variables have been strongly linked to vertebrate and dipteran distributions throughout the Wet Tropics (J. Vanderwal et al., 2009; Jeremy VanDerWal, Luke P Shoo, et al., 2009; R. D. Wilson, 2010). At each elevational site 10 m × 50 m transects were set to determine the heterogeneity of structures on the forest floor. The proportion of forest floor within this transect covered by rocks, logs and buttress roots was estimated and recorded using a scale from 0 to 4, where 0 = absent, 1 = 1-24%, 2 = 25-49%, 3 = 50-74% and 4 = 75-100%. Litter standing crop was also recorded using volume measurements from two sites per elevational transect during the wet season (Parsons et al., 2009).

5.3.4 Data analysis

5.3.4.1 *Sampling Effort*

As pitfall traps are *in situ* passive sampling devices, they only capture animals actively moving across the ground. These means that the number of animals sampled is a measure of activity density and does not necessarily estimate abundance (Greenslade, 1964; Thiele, 1977). Despite this, the term abundance is still generally used instead of activity density (Kotze et al., 2011) and this project adheres to such protocol.

In order to produce directly comparable data sets based on equal sampling effort, only 2 months of samples were analysed from each subregion. The first month of sampling was not included in any data set in an effort to remove digging-in bias, whereby insects are attracted to new structures in their environment and unusually high values are recorded (Digweed et al., 1995). Ants used in this project derived from two, monthly samples taken during November and December 2008 for all subregions except Bellenden Ker Uplands which derived from the same months, but a year later due to site accessibility restrictions.

Sampling efficiency was assessed by creating species accumulation curves derived from Chao 1 species richness estimator data per trap for every two month sampling unit, per site using the *adehabitat* package of the R statistical program v2.12.1(R Development Core Team, 2010). By using this rarefaction estimator of species richness, we reduce the bias caused by uneven numbers of individuals across samples and better includes the influence of rare species thereby reducing negative bias with incomplete sampling of sites (Chao et al., 2005). The resulting samples therefore derived from 1 (two-month sample) x 9 traps per elevation within each subregion. Therefore, 36 samples derived from the four different elevations sampled at Spec Uplands and Bellenden Ker Uplands, 54 samples from the six different elevations sampled at Atherton Uplands and Carbine Uplands and 27 samples from the three different elevations sampled at Windsor Uplands.

5.3.4.2 *Species richness across elevation*

Species richness variance across the elevational gradient was analysed using the *fossil* package from the R statistical program v2.12.1 (R Development Core Team, 2010). Chao1 estimates of species richness were calculated based on data derived from the same two-month sample units as above, per elevational site (points 2, 4, and 6). Furthermore, observed species richness values were also averaged from these three elevational sites per elevation of every subregion.

Changes in species richness, as elevation increased, was investigated by creating a generalised linear mixed model fit by Laplace approximation, with elevation as the single explanatory variable, using the *lme4* package in the R statistical program v2.12.1 (R Development Core Team, 2010). The entire community data was used and subregion was included as a random factor to control the effects of these areas on the data. This random effects model was appropriate as the observed clusters (subregional assemblages) were regarded as random samples from a large, possibly infinite, pool (entire Wet Tropics) of possible clusters (Broström & Holmberg, 2011). Poisson distributions were utilised as count data was analysed and overdispersion was accounted for by adding the number of observations as a second random factor for both the richness and abundance models (Broström & Holmberg, 2011; Zuur et al., 2009).

Combinations of the eight bioclimatic variables were analysed to determine which best explained changes in observed ant species richness between sites in the wet tropics. This was performed using best sub-set multiple linear regressions between total observed species richness values and co-located environmental data using the *leaps* package from the R statistical program v2.12.1 (R Development Core Team, 2010). The best model, derived from one of or any combination of the explanatory variables, was determined using Bayesian Information Coefficients (BICs). Whilst, this statistical modelling technique is slightly different from the more standard variable selection methods of stepwise regression as it better accounts for co-linearity problems between explanatory variables (Mac Nally, 2000), some removal of significantly cross-correlated variables was still required.

5.3.4.3 *Compositional patterns of community data*

Compositional variations between subregion assemblages were investigated with non-metric multi-dimensional scaling ordination (NMDS). All multivariate analyses were performed using the *vegan* package from the R statistical program v2.12.1 (Clarke, 1993; R Development Core Team, 2010). Abundance data were square-root transformed prior to analyses to increase normality as is suggested for count data (Crawley, 2003) and reduce the effect of high abundance counts simply due to traps being placed close to ant nests. The ordination was constructed from a matrix of Bray-Curtis dissimilarity values between all pairs of sites for each elevation. In order to determine any correlations between environmental data and assemblage patterns, bioclimatic data and habitat heterogeneity variables were correlated with the ordination pattern of ant assemblages. Relevant levels of significance were based on 1000 permutations of variable data.

The relationships between the community composition and significantly correlated environmental factors were determined also using the *vegan* package. The environmental factors analysed included: bioclimatic data, forest floor heterogeneity (all three structures assessed individually and combined), leaf litter depth and elevation. These relationships were investigated through analysis by permutational multivariate analysis of variance using distance matrices (1000 permutations). This analysis calculated *F* statistics (pseudo-*F*) using a semi-metric distance measure (Bray-Curtis) to relate variation in a matrix, in this case species abundance data at each site, to predictor variables, thereby obtaining *P* values using permutation techniques (1000 unrestricted permutations of raw data; Zapala & Schork, 2006). The patterns displayed within the NMDS were further analysed. This was performed using best sub-set multiple linear regressions between the values where sites were positioned, across both dimension 1 and 2 axes, and co-located environmental data. Similar to above (when analysing species richness), the *leaps* package from the R statistical program was used and the best model, derived from any combination of the explanatory variables, was determined using Bayesian Information Coefficients (BICs).

For the model determined by best sub-set regression, the influence of each environmental factor on the variance of each axis (dimension 1 and 2) were plotted as partial-regression plots using the *car* package from the R statistical program v2.12.1 (R Development Core Team, 2010). When multiple independent variables (X1, X2) predict one dependant variable (Y), the effect of X1 on Y can be seen after removing the (linear) effect of X2 on Y. This was achieved by using the ‘avplots’ function in the *car* package which regresses Y against X2, X1 against X2 and creates partial-regression plots of the residuals of the former against those of the latter (Weisberg, 2005). For ease of interpretation, the independent variable (X1) reported on in each partial-regression plot is referred to as “Residuals of X1” and dependent variable (Y) referred to as “Residuals of Y”.

Levels of similarity between subregional assemblages were investigated through pairwise comparisons using Analysis of Similarities (ANOSIM). This program executes multivariate ANOVA, using 999 permutations, to calculate *P* values derived from pseudo *F* statistics of the distance measures (M. J. Anderson, 2005). ANOSIM produces an R statistic, ranging from -1 to +1, based on the difference of mean ranks between subregional assemblages where +1 equals a complete dissimilarity of assemblages. Zero represents completely random assemblage structures, whereas any departure from zero indicates that dissimilarities among different subregions are greater than dissimilarities within each subregion (M. J. Anderson, 2005).

5.3.4.4 *Ant and flightless ground beetle comparisons*

Relationships between ant richness and abundance and flightless ground beetle richness and abundance were presented using linear regressions determined using the *adehabitat* package from the R statistical program v2.12.1 (R Development Core Team, 2010). The relationship between ant richness and beetle abundance was also captured with both a linear regression. However, in order to determine if there was any conditional relationship of ant richness on beetle abundance, quantile regression was performed (Koenker, 2005) of the 90th percentile using *quantreg* package, also with the R statistical program. The relationships between beetle and ant abundance and richness values were further explored using generalised linear mixed models fit by Laplace approximation. Subregion was included as a random factor to control for the effects of these areas on the data and Poisson distributions were utilised and overdispersion accounted for by adding the number of observations as a second random factor for both the richness and abundance models (Broström & Holmberg, 2011; Zuur et al., 2009).

To determine how well the variance of flightless ground beetle richness and abundance throughout the Wet Tropics was explained by ant richness, as an explanatory variable compared to the eight BIOCLIM variables, best sub-set multiple linear regressions were performed again using the *leaps* package. Similar to above, the best models, derived from all possible combinations of explanatory variables, were determined using the BICs.

5.4 Results

5.4.1 Taxonomic summary

A total of 7,987 worker ants were identified, belonging to 52 genera and 183 species/morphospecies (Table 5.1). The most species-rich genera included *Pheidole* (22 spp.), *Rhytidoponera* (12 spp.) and *Strumigenys* (12 spp.). Similar abundances of workers were sampled from Spec Uplands, Atherton Uplands and Carbine Uplands, despite there being only four sites at Spec Uplands compared to six for each of the other two subregions. Fewer individuals were recorded from the higher positioned transects in Bellenden Ker Uplands and Windsor Uplands. The proportion of species endemic to a single subregion was 49% per cent (89 of 183 species) and only four per cent of species (8 of 183) were sampled in all five subregions.

Table 5.1. Table of ant species sampled. Total abundance of the two-month sampling period (Abund.) and elevational range (Range; ’00 m a.s.l.) of species sampled are indicated for each subregion. Species listed alphabetically.

	Spec Uplands		Atherton Uplands		Bellenden Ker Uplands		Carbine Uplands		Windsor Uplands	
Species	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range
Acropyga sp. A					4	10-12				
Aenictus sp. A			5	1-2			42	1-4		
Aenictus sp. B			3	2						
Amblyopone australis							1	8		
Anochetus graeffei			1	2						
Anonychomyrma WT.A	148	1-10	141	1-4			222	1-12	64	9
Anonychomyrma WT.B	369	3.5-6	29	1-10	72	10-12	60	1-10	2	9
Anonychomyrma WT.C					30	12-16	31	8-12	97	11-13
Anonychomyrma WT.D							66	10-12	51	11-13
Anonychomyrma WT.E	1	8	8	2-10	26	12-16	4	10	10	11-13
Anonychomyrma WT.F			1	4			2	1-4		
Anonychomyrma WT.G									5	9
Aphaenogaster pythia	1	3.5								
Calyptomyrmex WT.A	3	3.5-10								
Camponotus 'mackayensis'							4	1-10	1	11
Camponotus sp. A							6	1-4		
Camponotus sp. B	10	3.5-8	1	10	28	10-12	34	1-12	40	9-13
Camponotus sp. C	5	6	6	1						
Camponotus sp. D	1	3.5								

	Spec Uplands		Atherton Uplands		Bellenden Ker Uplands		Carbine Uplands		Windsor Uplands	
Species	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range
Camponotus vitreus			1	2			1	1		
Carebara sp. A	19	6-8	2	8-10			4	1-6		
Carebara sp. B	13	6-8	2	2			8	1-10		
Carebara sp. C	1	8	1	4			1	12		
Cerapachys sp. A	1	8	1	4						
Cerapachys sp. B			1	4						
Crematogaster sp. A					1	10	5	1-6		
Crematogaster sp. B			2	2-10			1	4	4	11
Crematogaster sp. C	1	3.5	2	1-6	3	10				
Cryptopone sp. A					2	12	1	10	1	11
Cryptopone sp. B			1	6						
Discothyrea sp. A	1	3.5								
Eurhopalothrix WT.A							2	1		
Heteroponera sp. B	9	3.5-10								
Heteroponera sp. C							1	12		
Heteroponera sp. D			6	2-6						
Heteroponera sp. E							40	1-10	6	9-11
Heteroponera sp. F			3	1	1	12	1	10	1	13
Hypoponera sp. A			2	2			4	12		
Hypoponera sp. B	3	6-8	3	2-10			1	1	1	11
Hypoponera sp. C			1	8	1	14	1	4	1	9
Iridomyrmex sp. A			1	2						

	Spec Uplands		Atherton Uplands		Bellenden Ker Uplands		Carbine Uplands		Windsor Uplands	
Species	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range
Leptogenys bidentata			2	2						
Leptogenys diminuta			8	1						
Leptogenys ebina			1	4			5	10		
Leptogenys podenzanai							2	12		
Leptogenys sjostedti	5	6	35	2-10						
Leptogenys sp. A	28	3.5-10								
Leptogenys sp. B			18	1-10	4	12	17	10-12	2	11
Leptogenys sp. C			2	2-8			2	8-10		
Leptogenys sp. E							1	8		
Leptogenys turneri	1	3.5								
Leptomyrmex rufipes	12	3.5-8	2	1-4						
Leptomyrmex sp. A			1	1			48	10-12		
Leptomyrmex unicolor							39	1-6	4	9
Leptomyrmex varians ruficeps			23	1-8	9	10	42	1-12	4	11-13
Mayriella abstinens			1	4	1	12			1	11
Mayriella spinosior			2	1						
Meranoplus sp. A	2	3.5	11	2-6			32	6-12	10	9
Meranoplus sp. B							1	6		
Monomorium floricola							6	1		
Monomorium nigriceps					1	16				
Monomorium petiolatum			1	4	1	10				
Monomorium ravenshoense			3	2-8	1	16				

	Spec Uplands		Atherton Uplands		Bellenden Ker Uplands		Carbine Uplands		Windsor Uplands	
Species	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range
Monomorium sp. A			1	8	4	10-16				
Monomorium sp. B					1	10				
Monomorium sp. C					2	14-16				
Monomorium sp. D					11	14-16				
Monomorium sp. E					1	12				
Monomorium sp. F							1	1		
Monomorium WT.A	1	3.5	4	4-10			1	1	2	11
Myrmecia miniscula					7	10-12	8	10-12		
Myrmecia mjobergi			1	8	37	10-12	3	10-12		
Myrmecia nigrocincta	2	3.5	10	2-4						
Myrmecia rowlandi			1	1						
Myrmecina sp. A					3	16				
Myrmecina sp. B					1	16				
Myrmecina sp. C			1	8						
Myrmecorhynchus sp. A									1	13
Notostigma carazzii	41	6	81	1-10			10	6-8	6	9
Odontomachus cephalotes			21	2-4			33	1-6		
Onychomyrmex hedleyi					4	12-14	3	6-12		
Onychomyrmex WT.A			1	10						
Orectognathus sp. A			1	6						
Orectognathus sp. B			1	6						
Orectognathus sp. C			2	2-6						

	Spec Uplands		Atherton Uplands		Bellenden Ker Uplands		Carbine Uplands		Windsor Uplands	
Species	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range
Pachycondyla australis	3	6-10	1	10						
Pachycondyla obscurans			28	1-4			33	6		
Pachycondyla sp. A					5	14				
Pachycondyla sp. B					23	10-12				
Pachycondyla sp. C	1	3.5	10	1-4						
Pachycondyla sp. D							4	10		
Pachycondyla sp. E	5	6-10	9	8						
Pachycondyla sp. F			6	6-10						
Pachycondyla sp. G			4	1			4	6	2	9
Pachycondyla sp. H							1	1-6		
Paratrechina sp. A	16	3.5-6	36	1-8	3	10	31	4-6	5	9-11
Paratrechina sp. B			2	10					1	9
Paratrechina sp. C									2	9
Paratrechina sp. D	5	6-10	3	10			1	8	1	13
Paratrechina sp. E	4	3.5-8	2	6-8			1	1	4	11
Pheidole M			10	1						
Pheidole sp. AA	298	3.5-8	111	1-8			78	1-4	2	9-13
Pheidole sp. AB	477	3.5-10	3	8			82	1-12	15	9-11
Pheidole sp. AC	102	3.5-10	303	1-10	102	10-12	267	1-12	16	9-11
Pheidole sp. AD	2	3.5	2	8						
Pheidole sp. AF	15	6-10	218	8-10	109	10	247	8-12		
Pheidole sp. AG	168	10	200	6-8			11	1		

	Spec Uplands		Atherton Uplands		Bellenden Ker Uplands		Carbine Uplands		Windsor Uplands	
Species	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range
Pheidole sp. AH	6	6	4	1-6			4	6-8	5	9
Pheidole sp. AI	1	10	7	4-8						
Pheidole sp. AJ	1	8	4	1			1	1	7	11
Pheidole sp. AK	24	3.5-10					12	1-8	1	9
Pheidole sp. AL			9	2						
Pheidole sp. AM			3	4						
Pheidole sp. AN			2	4						
Pheidole sp. AO									238	9-13
Pheidole sp. AP					50	12-16				
Pheidole sp. AQ					565	10-16				
Pheidole sp. B			1	1			116	1-2		
Pheidole sp. F			4	1			2	1		
Pheidole sp. G			3	2-4						
Pheidole sp. M			90	1-4			39	1-6		
Pheidole sp. N	1	10					27	1-4		
Pheidole sp. O							3	1-4		
Pheidolegeton affinis			6	1-4			5	1-4		
Plagiolepis sp. A	2	3.5								
Platythyrea parallela	1	6								
Podomyrma sp. A			1	4			1	4		
Podomyrma sp. B	1	3.5							1	11
Polyrhachis (Cyrtomyrma) sp. A	1	3.5								

	Spec Uplands		Atherton Uplands		Bellenden Ker Uplands		Carbine Uplands		Windsor Uplands	
Species	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range
Polyrhachis (Cyrtomyrma) sp. B							4	4-8		
Polyrhachis (Cyrtomyrma) sp. C							1	6		
Polyrhachis (Hedomyrma) sp. A	1	3.5								
Polyrhachis(Myrmathrinax) delicata							1	1		
Polyrhachis clio	1	3.5								
Ponera sp. A									3	11
Ponera sp. B	2	6-8								
Ponera sp. C			2	1			1	1		
Pristomyrmex wilsoni							1	8		
Prolasius WT.A	16	3.5-6	7	1-8	1	14	7	8-12	5	9-13
Prolasius WT.B	1	10							16	11-13
Rhytidoponera kurandensis			1	10			58	1	33	9-13
Rhytidoponera chnoopyx			52	1-10	1	10				
Rhytidoponera impressa	45	3.5-10								
Rhytidoponera metallica	4	3.5								
Rhytidoponera purpurea			65	1-10	2	10	22	1-10	55	9
Rhytidoponera scabrior A					31	10-12				
Rhytidoponera scabrior B			9	8						
Rhytidoponera scabrior C							29	10-12		
Rhytidoponera spoliata							6	1-4		
Rhytidoponera victoriae	148	3.5-10	116	2-10			69	8-12	19	9-11

	Spec Uplands		Atherton Uplands		Bellenden Ker Uplands		Carbine Uplands		Windsor Uplands	
Species	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range
Rhytidoponera WT.A	12	3.5-6	55	1-6						
Rhytidoponera WT.B	11	3.5-8	12	2-4						
Solenopsis sp. A	1	3.5	8	1-10	1	10	5	1-12	14	11-13
Sphinctomyrmex sp. A							2	6		
Sphinctomyrmex sp. B							1	4		
Stigmacros sp. A	1	6								
Stigmacros sp. B							1	6	1	9
Strumigenys juxta			1	4						
Strumigenys anetes							2	10-12		
Strumigenys cingatrix			1	2					1	11
Strumigenys emdeni									4	11
Strumigenys guttulata	1	3.5								
Strumigenys orthanetes			1	10			2	10-12	2	13
Strumigenys paranetes	3	6-10	3	2-6			1	10		
Strumigenys philiporum							1	10		
Strumigenys sp. A	1	6								
Strumigenys sp. B	1	10								
Strumigenys sp. C	2	3.5								
Strumigenys szalayi			1	4						
Tapinoma sp. A	2	3.5-8							1	11
Tapinoma sp. B	1	3.5								
Technomyrmex shattucki			7	2-4					1	9

	Spec Uplands		Atherton Uplands		Bellenden Ker Uplands		Carbine Uplands		Windsor Uplands	
Species	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range	Abund.	Range
Technomyrmex sp. A			7	2-4			2	1-4	1	11
Technomyrmex sp. B	1	10	10	2-10	13	10	28	4-12	23	9-13
Technomyrmex sp. C							2	6		
Tetramorium turneri	11	3.5-6	1	2	3	10			1	9
Tetramorium validiuscutum	7	3.5	10	1-4			2	1		
Tetramorium sp. A					8	10-14				
Turneria bidentata			1	6					1	11
Vollenhovia sp. A	1	8	1	4			1	1		
Vombisidris australis							1	1	2	9
Vombisidris renatae							2	1-2		
Total	2086		1912		1173		2019		797	

5.4.2 Sampling effort

Accumulation curves for assemblages at Spec Uplands, Bellenden Ker Uplands and Windsor Uplands were reaching asymptote (Figure 5.2). However, curves assessing the sampling efficacy at Atherton Uplands and Carbine Uplands indicate that further sampling would result in more comprehensive representations of those assemblages.

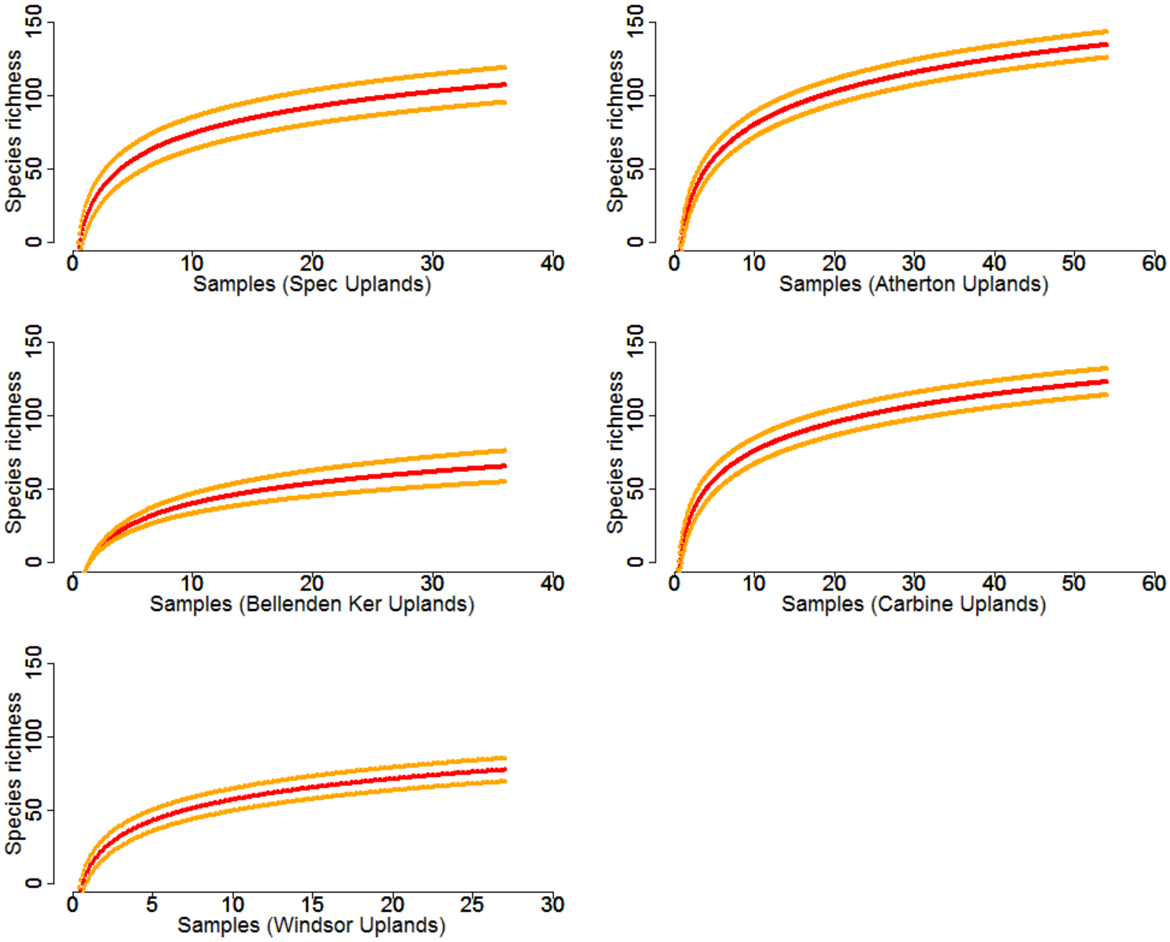

Figure 5.2. Efficacy of sampling efforts for each subregion presented using accumulation curves of species richness and number of samples. Chao1 species richness estimations are displayed from the two months of sampling analysed with 95% confidence intervals.

5.4.3 Species richness and abundance across elevation

Species richness values, both observed and estimated, decreased as the elevation of sites sampled increased throughout the Wet Tropics (Figure 5.3). Lower elevations among the Carbine Upland and Atherton upland subregions had the highest richness values, whereas higher elevations in the Windsor Upland and Bellenden Ker Uplands subregions displayed the lowest richness values.

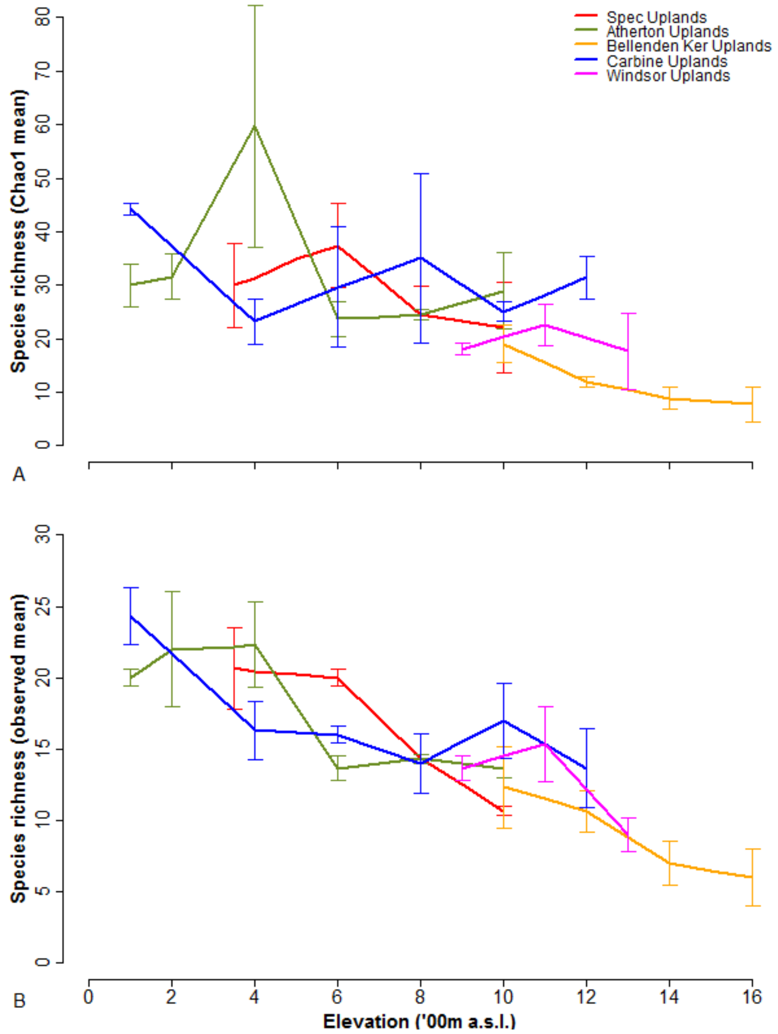

Figure 5.3 A&B. Ant species richness across the entire elevation gradient. **(A)** Estimated species richness (Chao1 mean (±SE, n=3)), **(B)** observed species richness (±SE, n=3) of ant communities across elevational gradients for each subregion.

Ant species richness decreases with elevation in the Wet Tropics (Pr(>|z|) <0.05; Table 5.2).

Table 5.2. Relationship between ant species richness and elevation using generalised linear mixed model of species richness and abundance, of the entire ant community sampled, correlated positively with elevation as the only explanatory variable (Pr(>|z|)<0.05). Subregion was included as a random factor to control for its effect on the richness model (variance = 0.1032, standard deviation = 0.3212). Pr(>|z|) values represented by * are significant Pr(>|z|)<0.05.

dependent variable	independent variable	estimate	standard error	z	n	Pr(>|z|)
ant species richness	elevation	0.0014	0.0001	10.1	69	*

Annual mean temperature (BCO1) was the climatic correlate, among all possible combinations of the eight bioclimatic explanatory variables, which best explaining the variance in observed ant species richness within the Wet Tropics (model Adj. $R^2 = 0.573$, s.e. = 0.362, n =69, $P < 0.001$; Table 5.3, Figure 5.4 & Appendix 5.3).

Table 5.3. Environmental correlate best describing variance in observed ant species richness throughout the Wet Tropics determined using best sub-set regression models. Model chosen displayed the highest baysian information criterion (BIC). Adj. R^2 = Adjusted R^2. Std err. = standard error, n=69.

Predicted variable	Variable	T value	*P* (variables)	Model Adj. R^2	Model *P*	Std. err.	BIC
ant richness	(Intercept)	-6.44	<0.0001	0.573	<0.0001	3.62	-51.2
	BC01	9.59	<0.0001				

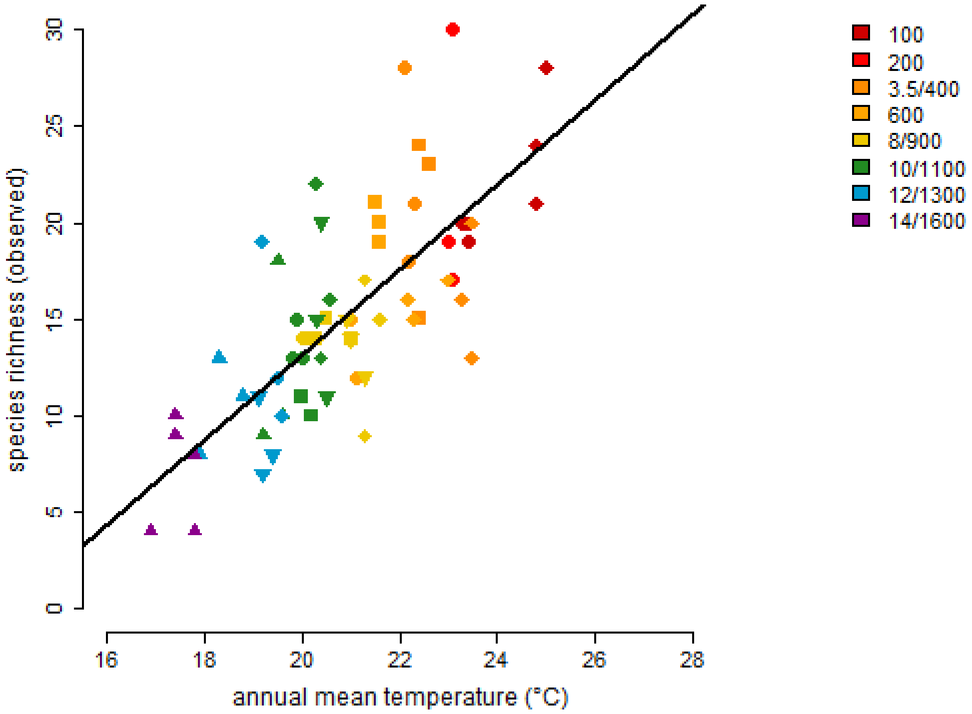

Figure 5.4. The change in observed species richness relating to annual mean temperature. The environmental factor best explaining variation of ant species richness within the Wet Tropics. Legend indicates the elevations of the different sites at meters above sea level. Model Adj. $R^2 = 0.573$, s.e. = 0.362, n =69, $P < 0.001$. Colours represent different groups of elevations of sites at meters above sea level. Shapes represent subregion sampled whereby □ = Spec Uplands, ○ = Atherton Uplands, △ = Bellenden Ker Uplands, ◇ = Carbine Uplands & ▽ = Windsor Uplands.

5.4.4 Compositional patterns of community data

Compositional turnover occurs across elevational gradients both within subregional assemblages and across subregions in the Wet Tropics (Figure 5.5). Each subregional ant assemblage is unique within the Wet Tropics. However, a large overlap is noted of the lowest subregional sites at Atherton Uplands and Carbine Uplands. Ant compositional changes only correlated with climatic factors recorded. Climatic factors, across elevational gradients, have stronger relationships with assemblage structures than geographic distances, as all lowland sites correlate with hotter and drier conditions and most highland sites are associated with cooler, wetter conditions (Figure 5.5; Table 5.4).

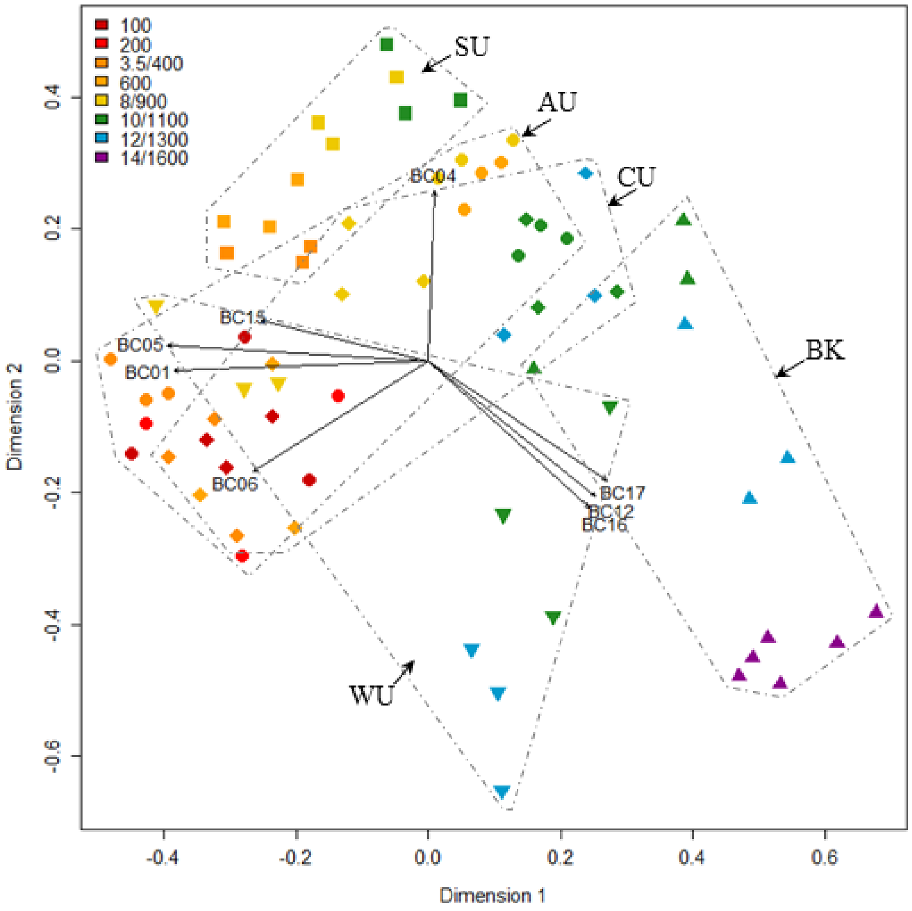

Figure 5.5. Similarity of ant assemblage structures for different subregions in the Wet Tropics shown using ordination plot of communities at all subregions (stress=0.22). Vectors of site environmental variables displaying significant correlations (P <0.001) with species data are overlayed. BC01= annual mean temperature, BC04= temperature seasonality, BC05= maximum temperature of warmest period, BC06= minimum temperature of coldest period, BC12= annual precipitation, BC15= precipitation seasonality, BC16= precipitation of wettest quarter, BC17= precipitation of driest quarter. Colours represent different groups of elevations of sites at meters above sea level. Shapes represent subregion sampled where □ = Spec Uplands (SU),○ = Atherton Uplands (AU), △ = Bellenden Ker Uplands (BK), ◇= Carbine Uplands (CU) & ▽ = Windsor Uplands (WU).

Community composition significantly changed in relation to variance of all eight climatic variables and elevation when analysed using permutational multivariate analysis (Table 5.4).

Table 5.4. Compositional change of the entire Wet Tropics ant community sampled in relation to climatic correlates. Permutational multivariate analyses of assemblage compositional change regarding the seven significant environmental variables displayed on the ordination as well as elevation. BC01= annual mean temperature, BC04= temperature seasonality, BC05= maximum temperature of warmest period, BC06= minimum temperature of coldest period, BC12= annual precipitation, BC15= precipitation seasonality, BC16= precipitation of wettest quarter, BC17= precipitation of driest quarter.

Independent variable	Pseudo-$F_{1,68}$	P value
BC01	10.5	< 0.001
BC04	5.2	< 0.001
BC05	10.9	< 0.001
BC06	7.7	< 0.001
BC12	8.8	< 0.001
BC15	6.7	< 0.001
BC16	8.9	< 0.001
BC17	8.9	< 0.001
Elevation	10	< 0.001

Maximum temperature of the warmest period and precipitation seasonality were the climatic correlates best explaining the variance in sites plotted across the NMDS dimension 1axis (model Adj. $R^2 = 0.822$, s.e. = 0.128, n =69, $P < 0.001$; Table 5.5, Figure 5.6, Appendix 5.4).

Table 5.5. Model determining which environmental correlates best describe variance in Dimension 1 axis of the above ordination (Figure 5.5). Model performed using best sub-set regression. Adj. R^2 = Adjusted R^2, Std err. = standard error, n =69. BC05 = maximum temperature of warmest period & BC15 = precipitation seasonality.

Predicted variable	Variable	T value	P (variables)	Model Adj. R^2	Model P	Std. err.	BIC
Dimension 1	(Intercept)	17.17	<0.001	0.822	<0.001	0.128	-106.5
	BC05	-13.44	<0.001				
	BC15	-2.73	<0.01				

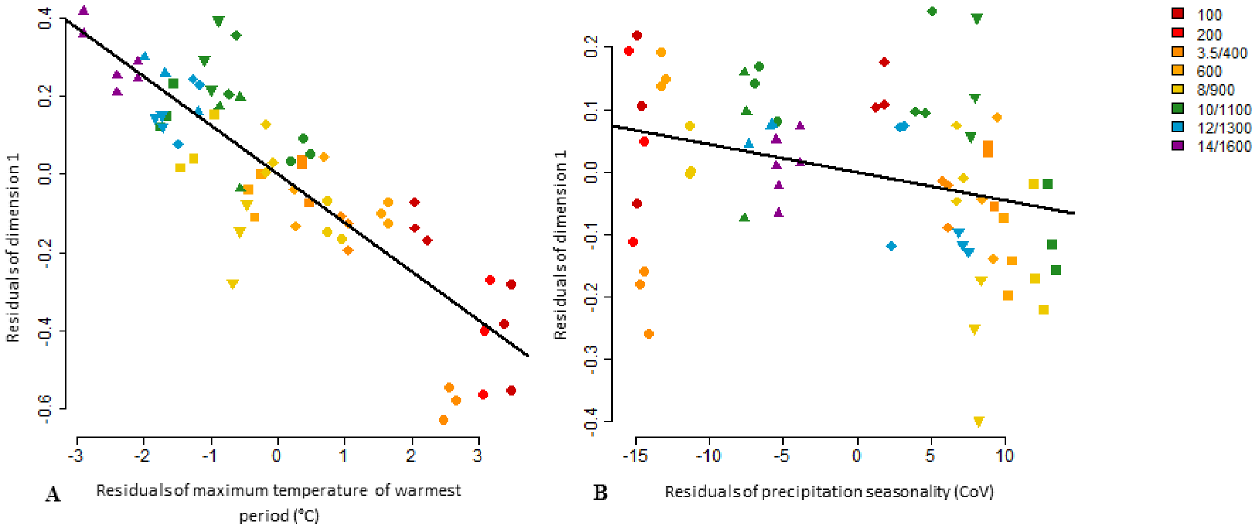

Figure 5.6A-B. The environmental factors best explaining variation of point across Dimension 1 of the NMDS of ants throughout the Wet Tropics. These partial-regression plots derive from the best model selected using best sub-set multiple linear regression analysis. Model Adj. $R^2 = 0.822$, s.e. = 0.128, n = 69, $P < 0.001$. (A) Residuals of maximum temperature of the warmest period (t value = -13.43, s.e. = 0.009, n =69, Pr(>|t|) < 0.001), (B) residuals of precipitation seasonality (t value = -2.7, s.e. = 0.002, n =69, Pr(>|t|) < 0.01). Colours represent different groups of elevations of sites at meters above sea level. Shapes represent subregion sampled where □= Spec Uplands,○ = Atherton Uplands, △= Bellenden Ker Uplands, ◇= Carbine Uplands &
▽= Windsor Uplands.

The combination of temperature seasonality, annual precipitation and precipitation seasonality composed the model best explaining the variance in sites plotted across the NMDS dimension 2 axis (model Adj. $R^2 = 0.576$, s.e. = 0.174, n =69, $P < 0.001$; Table 5.6 & Figure 5.7).

Table 5.6. Model determining which environmental correlates best describe variance in Dimension 2 axis of the NMDS. Model performed using best sub-set regression. Adj. R^2 = Adjusted R^2, Std err. = standard error, n =69. BC04 = temperature seasonality, BC12 = annual precipitation, BC15 = precipitation seasonality.

Predicted variable	Variable	T value	*P* (variables)	Model Adj. R^2	Model *P*	Std. err.	BIC
Dimension 2	(Intercept)	-0.57	0.57	0.576	<0.0001	1.74	-45.4
	BC04	6.31	<0.0001				
	BC12	-5.81	<0.0001				
	BC15	3.12	<0.01				

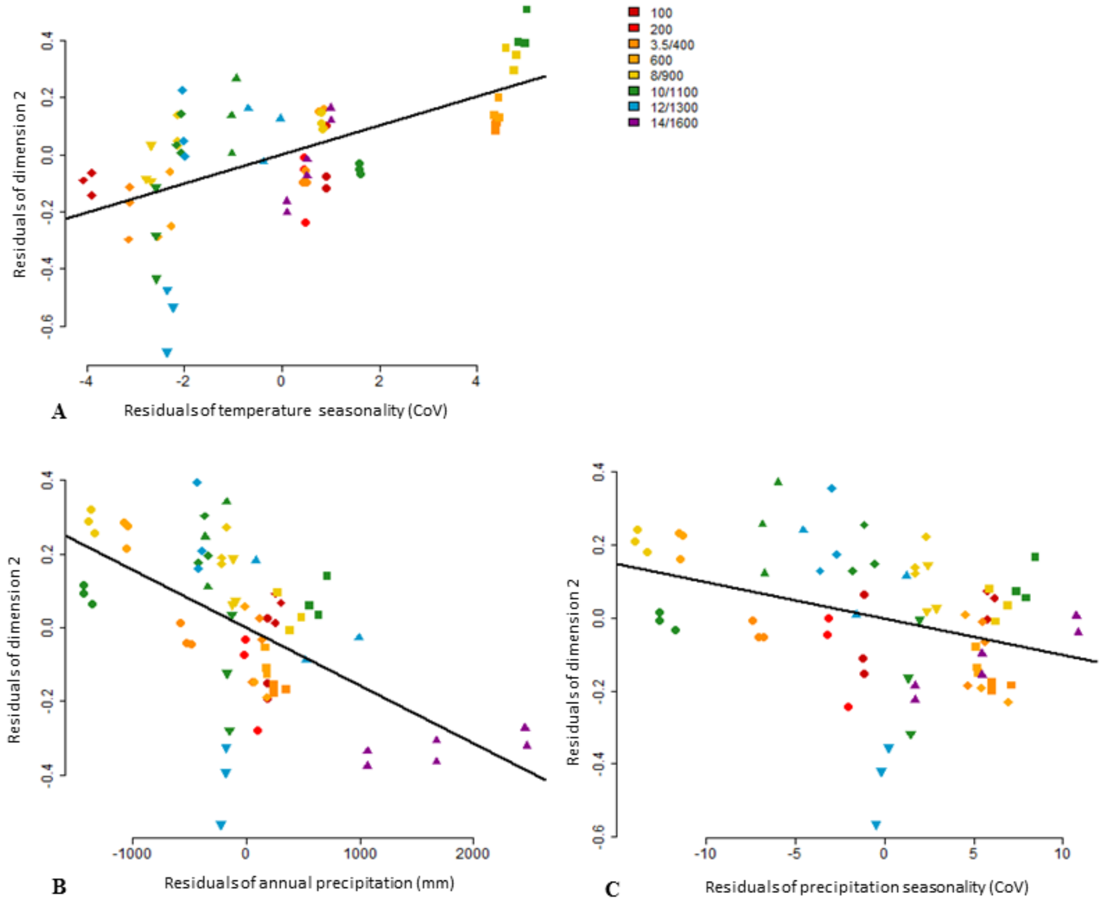

Figure 5.7A-C. The environmental factors best explaining variation of point across Dimension 2 of the NMDS of ants throughout the Wet Tropics. These are partial-regression plots from the best model selected using best sub-set multiple linear regression analysis. Model Adj. $R^2 = 0.576$, s.e. = 0.174, n = 69, $P < 0.001$. (A) Residuals of temperature seasonality (t value = 6.31, s.e. = 0.008, n =69, Pr(>|t|) < 0.001), (B) residuals of annual precipitation (t value = 1-5.81, s.e. = 0.00003, n =69, Pr(>|t|) < 0.001), (C) residuals of precipitation seasonality (t value = -3.1, s.e. = 0.003, n =69, Pr(>|t|) < 0.01). Colours represent different groups of elevations of sites at meters above sea level. Shapes represent subregion sampled where □ = Spec Uplands, ○ = Atherton Uplands, △ = Bellenden Ker Uplands, ◇ = Carbine Uplands & ▽ = Windsor Uplands.

Atherton Uplands contained the greatest number of species observed with Bellenden Ker Uplands being the least species-rich of the subregional assemblages sampled (Table 5.7). All subregional assemblages were statistically unique, however, Atherton Uplands and Carbine Uplands shared the greatest number of species. Spec Uplands and Atherton Uplands, and Carbine Upland and Windsor Uplands, also shared a large proportion of species. The greatest differences in assemblage structure existed between Spec Uplands and Bellenden Ker Uplands. The neighbouring Atherton Uplands and Bellenden Ker Uplands were even more dissimilar in assemblage structure than the most geographically distant pair of subregional assemblages (Spec Uplands and Windsor Uplands; Table 5.7).

Species contributing the most to dissimilarity between subregional assemblages derived from the genera *Pheidole*, *Anonychomyrma* or *Rhytidoponera* (Appendix 5.1). The vast majority of the top six species contributing the most to dissimilarities between subregions displayed broad elevational ranges throughout multiple subregions (Appendix 5.1). Therefore, variations between subregional assemblages are not due to high proportions of subregional endemics but rather due to differences in distributions of widespread species. A similar trend exists across the elevational gradient where differences between lowland and upland assemblages were predominantly due to a lack of species with large elevational ranges in highland sites, rather than a high proportion of species restricted to upland habitats (Appendix 5.2; Table 5.1). Only one species restricted to high elevational ranges contributed a noticeably to dissimilarity between elevational sites and this was *Pheidole sp. AQ*, an abundant species confined to the Bellenden Ker Uplands transect.

Table 5.7. Dissimilarity of ant assemblages structures for each subregions. Numbers of shared species between subregions (above the diagonal). Total numbers of species for each subregion with unique species (in parentheses) to each subregion (in the diagonal). Values below the diagonal are ANOSIM R statistics indicating the degree of difference between subregions. All pairwise comparisons of subregions using ANOSIM were significant at *P*<0.05. All values are based on observed sample data from: Spec Uplands (SU), Atherton Uplands (AU), Bellenden Ker Uplands (BK), Carbine Uplands (CU) & Windsor Uplands (WU) subregions.

	SU	AU	BK	CU	WU
SU	**68 (21)**	42	11	30	25
AU	0.28	**101 (24)**	22	53	36
BK	0.84	0.71	**41 (14)**	21	17
CU	0.28	0.16	0.64	**91 (24)**	40
WU	0.57	0.49	0.59	0.23	**54 (6)**

5.4.5 Relationship between ant and flightless ground beetle community trends

Ant species richness is negatively correlated with both flightless ground beetle abundance and species richness values (Figure 5.8). Furthermore, quantile regression indicates that the variance in ant richness may even act as a limiting threshold of beetle abundance. Additionally, this data does not support any relationship between ant abundance and either beetle richness or abundance.

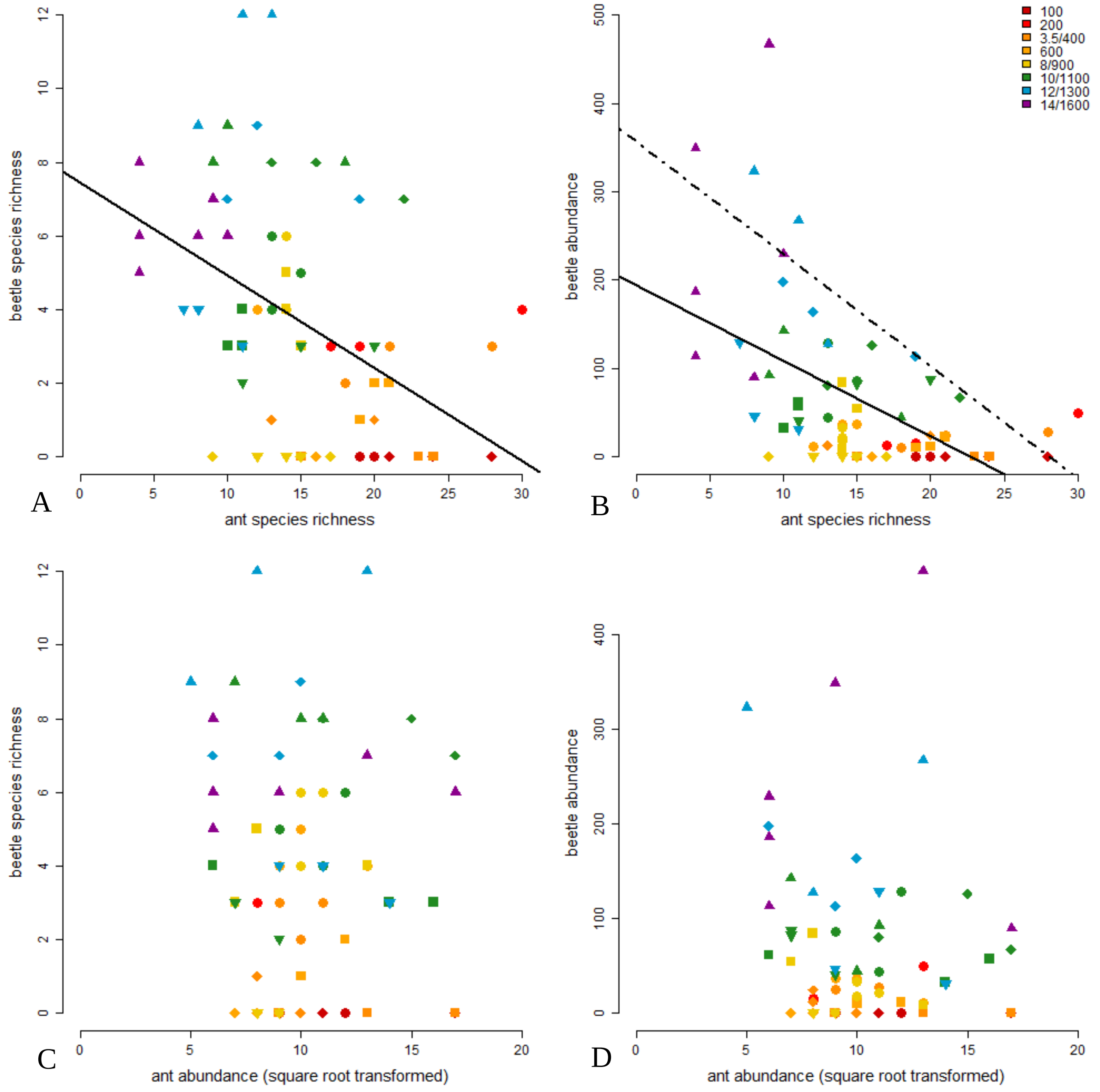

Figure 5.8A-D. Relationship between the presence of flightless ground beetles and ants throughout the five subregions. (A) Linear regression is presented for total flightless ground beetle species richness and ant species richness recorded from each site ($F_{1,67} = 15.8$, Adj. $R^2 = 0.18$, $P < 0.001$). (B) Linear regression (solid line) is presented for total flightless ground beetle abundance and ant species richness recorded from each site ($F_{1,67} = 24.71$, Adj. $R^2 = 0.26$, $P < 0.001$) and quantile regression (dot-dashed line) of the 90th percentile of the total flightless ground beetle abundance and ant species richness recorded from each site (t-value = -2.3, Std. err. = 0.012, Pr(>|t|)= 0.02). Further linear regressions are presented for (C) total flightless ground beetle richness and ant abundance (square root transformed) recorded from each site (P = not significant) and (D) total flightless ground beetle abundance and abundance (square root transformed) recorded from each site (P = not significant). Colours represent different groups of elevations of sites at meters above sea level. Shapes represent subregion sampled where □= Spec Uplands, ○= Atherton Uplands, △= Bellenden Ker Uplands, ◇ = Carbine Uplands & ▽ = Windsor Uplands.

Both species richness and abundance of flightless ground beetles decrease as ant species richness increases throughout the Wet Tropics (Pr(>|z|) <0.05; Table 5.8).

Table 5.8. Generalised linear mixed model of species richness and abundance, of the entire flightless ground beetles community sampled, correlated negatively with ant species richness as the only explanatory variable (Pr(>|z|)<0.05). Subregion was included as a random factor to control for its effect on the significant richness model (variance = 0.1231, standard deviation = 0.3509) and abundance model (variance = 0.3929, standard deviation = 0.6268). Pr(>|z|) values represented by * are significant (Pr(>|z|)<0.05) and by NS are not significant.

dependent variable	independent variable	estimate	standard error	z	n	Pr(>|z|)
beetle richness	ant richness	-0.0645	0.0219	-2.95	69	*
beetle abundance	ant richness	-0.1916	0.0555	-3.45	69	*
beetle richness	ant abundance	0.0002	0.0923	0.003	69	NS
beetle abundance	ant abundance	0.0179	0.0328	0.545	69	NS

The model which best-explained variance in the flightless ground beetle richness values included the climatic variables: maximum temperature of the warmest period, precipitation seasonality, precipitation of the driest quarter, temperature seasonality and maximum temperature of the coldest period (model Adj. $R^2 = 0.746$, s.e. = 1.61, $P < 0.001$; Table 5.9). It is important to note ant richness did not significantly contribute to the best model explaining flightless ground beetle richness despite being included as an explanatory variable.

Table 5.9. Model determined to best-explain flightless ground beetle richness. Model performed using best sub-set regression. Adj. R^2 = Adjusted R^2, Std. err. = standard error, BIC = Bayesian information criterion, n = 69. BC04= temperature seasonality, BC05= maximum temperature of warmest period, BC06= minimum temperature of coldest period, BC15= precipitation seasonality, BC17= precipitation of driest quarter.

Predicted variable	Variable	T value	*P* (variables)	Model Adj. R^2	Model *P*	Std. err.	BIC
beetle richness	(Intercept)	10.15	<0.0001	0.746	<0.0001	1.61	-74.3
	BC04	3.72	<0.001				
	BC05	-6.43	<0.0001				
	BC06	3.93	<0.001				
	BC15	-7.22	<0.0001				
	BC17	-5.35	<0.0001				

Beetle abundance was best explained using only two climatic factors, maximum temperature of warmest period and precipitation of wettest quarter (model Adj. $R^2 = 0.611$, s.e. = 57.1, $P < 0.001$; Table 5.10). Similar to above, ant richness did not contribute to the model best explaining flightless ground beetle abundance in the Wet Tropics, despite being included in the analysis as an explanatory variable.

Table 5.10. Model determined to best explain flightless ground beetle abundance. Model performed using best sub-set regression. Adj. R^2 = Adjusted R^2, Std. err. = standard error, BIC = Bayesian information criterion, n =69. BC05= maximum temperature of warmest period, BC16= precipitation of wettest quarter.

Predicted variable	Variable	T value	*P* (variables)	Model Adj. R^2	Model *P*	Std. err.	BIC
beetle abundance	(Intercept)	5.19	<0.0001	0.611	<0.0001	57.07	-54.5
	BC05	-5.74	<0.0001				
	BC16	3.16	<0.01				

5.5 Discussion

5.5.1 Relationships between ant and flightless ground beetle community trends

Variances of flightless ground beetle abundance and richness, throughout the Wet Tropics, were best explained by climatic factors and not relationships with ant richness. Despite significant negative correlations between ant richness and both beetle abundance and richness within the Wet Tropics, environmental factors best explained these patterns of the flightless ground beetles sampled. The climatic factors best explaining change in beetle richness, from highest contribution to least, included: maximum temperature of the warmest period, precipitation seasonality, precipitation of the driest quarter, temperature seasonality and maximum temperature of the coldest period. Furthermore, maximum temperature of the warmest period and minimum temperature of the coldest period best explained beetle abundances changes between sites sampled in the Wet Tropics. Neither of these models included ant richness as an explanatory factor. Therefore, when compared with climatic factors, ant richness does not contribute as strongly to models which best explain variances in flightless ground beetle richness and abundance throughout the Wet Tropics.

The restricted highland distributions of flightless ground beetles throughout the Wet Tropics are more strongly linked to intolerances of lowland climatic conditions rather than negative interactions with lowland ant assemblages. This finding contributes to the understanding of the importance of ant communities in driving flightless ground beetles to high elevational habitats. Lowland ants have been suggested to compete with flightless ground beetles and therefore restrict the beetles' distributions across tropical elevational gradients to upland habitats (Darlington, 1971; D. M. Olson, 1994). Negative interactions have been recorded between ants and ground beetles (Hawes et al., 2002; Reznikova & Dorosheva, 2004). However, no study, to date, has investigated the strength of the correlations between beetle diversity patterns and ant richness across elevational gradients relative to other explanatory variables. As ant richness does not contribute to a model which best explains variance in beetle richness and abundance, this data does not support a hypothesis that ants currently exert pressure on the range boundaries of flightless ground beetles in this region. Instead, current richness and abundance patterns of flightless ground beetles in the Wet Tropics are most strongly linked to variances in climate across the elevational gradient.

5.5.2 Compositional patterns of the ant community are strongly linked to climatic factors, not geographical barriers.

Site assemblages grouped in accordance to climatic factors rather than geographic differences. Sites at similar elevations express comparable assemblages. Similarity between subregional assemblages was also highlighted by the fact that high proportions of species were shared between subregions. Even the subregions furthest apart, Spec Uplands and Windsor Uplands, shared 25 species (36% of the total species sampled at Spec Uplands and 46% of the species recorded from Windsor Uplands). The assemblage noted at the Windsor Uplands 900 m a.s.l. was very similar to the lowland assemblages, in similar climatic conditions, sampled at both Atherton Uplands and Carbine Uplands.

Dissimilarities between subregional assemblages were most clearly displayed between highland sites (above 1,000 m a.s.l.) throughout the Wet Tropics. This indicates that different assemblages have been able to colonise upland habitats for each subregion. Compositional turnover occurred as elevation increases both within and between subregions. Generally, dissimilarities of assemblages both between subregions and elevations were mainly due to differences in the distributions of common, widespread species rather than due the presence of species with narrow geographical or elevational ranges.

Strong relationships were determined between compositional changes within the ant community and climatic correlates. The environmental factors which best-explain the community turnover across the ordination dimension 1, the dimension which largely captures elevational change associated with distance between sites, are primarily maximum temperature of warmest period and the precipitation seasonality. Furthermore, both temperature and precipitation seasonality, in conjunction with annual precipitation, best-explained assemblage turnover across the ordination's second dimension.

Ant assemblages were noted to be intimately linked to climatic variables, regardless of geographical distances. This pattern differs greatly to the highly restricted upland species, such as flightless ground beetles, which display notable separations between subregional assemblages (Chapter 3). The most notable geographic barrier to dispersal throughout the Wet Tropics is the Black Mountain Barrier (BMB). This area extends across the Barron Valley near Cairns and is suggested to have negatively affected migration of cool-adapted species between northern and central subregions (Nix, 1991) resulting in pre-Pleistocene isolation of these assemblages (Schneider et al., 1998). As well as flightless ground beetles, a multitude of rainforest species including non-volant mammals, skinks and even schizophoran flies display distributions which are thought to have been affected by this barrier (Bell et al., 2010; Joseph, Moritz, & Hugall, 1995; R. D. Wilson, 2010). In contrast, ant assemblages sampled in this study do not appear to be greatly influenced by the BMB. More than half the species found within Atherton Uplands and Carbine Uplands were common to both subregions. Indeed, at similar elevations, central and northern assemblages are very alike. With such strong links to climatic factors and the distributions unrestricted by geographical barriers, lowland ants are expected to be highly capable of migrating upwards in elevation, if future climatic conditions become favourable.

5.5.3 Ant species richness and abundance declines with increasing elevation throughout the Wet Tropics

Ant species richness significantly declined with increasing elevation throughout the Wet Tropics. This pattern was best explained by declining annual mean temperatures across the elevational gradient. These findings suggest that these ants are best suited to the lowland warm climates throughout this region. Compared to Yek *et al.* (2009), who also investigated ants within the Wet Tropics, this finding confirms their observed pattern of higher ant species richness at lower elevations in the Atherton region. However, our findings oppose their pattern of lower estimated ant species richness at higher elevations. Yek *et al.* (2009) stated that insufficient sampling resulted in high level of uncertainty regarding their high elevation data. The more extensive sampling in performed in this current study, across multiple elevational gradients, has more clearly shown a decrease in ant richness as elevation increases throughout the Wet Tropics. Research by van Ingen et al. (2008) assessed ant species richness across the elevational gradient (600 - 1,100 m a.s.l) on Mt Lewis in the Wet Tropics. This study also found declining ant richness as elevation increased, however it is worthwhile noting that other forest types (Savannah woodland and Tall open forest) were included in this analysis.

A decline in ant richness with increasing elevation is a finding that is common among other entomological studies both in Australia and internationally (Burwell & Nakamura, 2011; Fisher, 1999; D. M. Olson, 1994; Staunton et al., 2011). Such declines in richness have been attributed to intolerances to cool, wet conditions, at and above, cloud caps on mountain peaks (Bruhl et al., 1999; Brian L. Fisher, 1998; C. Rahbek, 1995). Cold conditions and low levels of radiation, found in cloud caps, have also been suggested to negatively affect the foraging ability of ants (Brian L. Fisher, 1998; C. Rahbek, 1995). Furthermore, wet soil and leaf litter are suggested to impair nest building and the mobility of small ants (Bruhl et al., 1999).

Throughout the Wet Tropics, climate projections primarily outline increased temperatures (Suppiah et al., 2007). Such climatic changes will result in more tolerable climatic conditions for ants at higher elevations. Therefore, there is great potential, in future, for ants to increase their presence in upland habitats.

5.6 Conclusion

The ant community within the Wet Tropics is strongly linked to climatic conditions and displays high similarity of assemblages within similar climates, regardless of geographical distance or barriers to dispersal. Consequently, the lowland ant community in the Wet Tropics is expected to be able to easily migrate up mountains when climatic conditions become favourable. As lowland ant assemblages are more species rich in the Wet Tropics than the highland assemblages, climate change is likely to have significant impacts of future ant assemblages in this region. However, despite negative correlations between flightless ground beetles and ants across elevational gradients, variances in both beetle abundance and richness are best-explained by climatic factors. Therefore, flightless ground beetles are considered to respond primarily to changes in climate rather than future ant invasions.

Chapter 6. General Discussion

Two fundamental, ecological questions have always been - where are species, and why? This thesis asked "where the current distributions of flightless ground beetles throughout the Wet Tropics are?", and "how are these beetle distributions influenced by environmental factors and a potential competing group, ants?" Distributions of beetles were determined using both spatial distribution modelling and standardised sampling across elevational gradients. Changes in community patterns were then linked to environmental factors across spatial and temporal frameworks. Additionally, relationships between flightless ground beetle and ant (a suggested competitor) richness or abundance changes were investigated across elevational transects. Finally, the vulnerability of future flightless ground beetles was assessed in a climate change context, under multiple emissions scenarios. This chapter presents the major findings of this thesis regarding the distributional patterns of flightless ground beetles linked to biotic and abiotic factors and projected under future climate change scenarios.

6.1 Summary of major findings

Flightless ground beetles were modelled in Chapter 2 to predominantly inhabit upland areas characterised by stable, cool and wet environmental conditions. These beetles generally displayed highly restricted distributions, and is therefore were most species-rich, in such habitats. Of the climatic variables modelled to best explain this taxa's species richness, maximum temperature of the warmest period contributed the most. These distribution and richness patterns supported the time-stability hypothesis (whereby, more climatically stable habitats contain greater diversity) as this group's primary habitat, upland rainforest, is considered to be the most stable habitat within the region.

Flightless ground beetle communities were noted in Chapter 3 to be highly distinct between subregions throughout the Wet Tropics. Such high levels of dissimilarity of flightless ground beetle assemblages between subregional blocks were attributed to factors including: low dispersal between subregions, a high level of *in situ* evolution, extinction filtering events and current climatic conditions. Regarding current climatic factors, differences between subregional assemblages were linked to changes of: temperature seasonality, maximum temperature, precipitation seasonality, wet season rainfall and minimum temperatures.

Furthermore, species richness and abundance of flightless ground beetles significantly increased with elevation throughout the Wet Tropics and therefore species generally inhabit cooler, wetter locations.

The patterns revealed in Chapter 3, using standardised baseline sampling, strongly support the patterns modelled in Chapter 2. Both chapters state that the flightless ground beetle community, within the Wet Tropics, is comprised of species displaying highly restricted distributions which are strongly linked to changes in environmental conditions. In both chapters, the beetles were noted to prefer upland habitats, known to be stable throughout time, and currently characterised by cool, wet conditions.

Richness and abundance changes of the flightless ground beetle community were not only strongly linked spatial variance in climatic factors, but also seasonal changes. Chapter 4 clearly showed that beetle activity increased between November and February (during the wet season) and correlated positively with changes in both temperature and precipitation. Across the Wet Tropics landscape, the precipitation seasonality of a site negatively correlated with both richness and abundance of flightless ground beetles. This pattern, like Chapter 2, supports the time-stability hypothesis. This chapter strongly linked seasonal changes in environmental factors to changes in activity, richness and abundance of flightless ground beetles.

The literature suggests that flightless ground beetles display restricted mountain-top ranges due to either intolerance of lowland climatic factors or overwhelming competition from lowland ant species. Chapter 5 addresses such suggestions by analysing co-located ant and flightless ground beetle data across multiple elevational transects. This thesis includes the first ever detailed description of the ant community within the Wet Tropics, across multiple subregions.

Like flightless ground beetles, the ant community is strongly linked to climatic conditions. However, unlike flightless ground beetles, ants display highly similar assemblages within similar climates throughout the Wet Tropics, regardless of geographical distance, elevation, or barriers to dispersal. Consequently, the lowland ant community, which is highly species-rich, is expected to be able to easily migrate up mountains, as climatic conditions become favourable due to climate change. Such migrations would result in much greater species richness in future highland ant assemblages.

Negative correlations were revealed between flightless ground beetles and ants across the elevational gradients. However, despite such correlations, variances in both beetle abundance and richness were best-explained by climatic factors. Subsequently, flightless ground beetles are considered to respond primarily to changes in climate, rather than ant richness or abundance, across the elevational gradients. Therefore, any future reductions in flightless ground beetles are expected to predominantly occur due to changes in climatic conditions.

Flightless ground beetles, throughout the Wet Tropics, are projected to substantially reduce their current range sizes, population sizes and species richness under all emission scenarios. These projections were determined using multiple emissions scenarios, derived from the Intergovernmental Panel on Climate Change's Special Report on Emissions Scenarios. Future ranges are projected to contract as distributions shift upwards and subsequently species richness is expected to decline. However, the greatest impact of climate change on flightless ground beetles was indicated to be extreme reductions in abundance, with 88% of species modelled predicted to decline in population size by over 80%, for the most severe emission scenario by the year 2080. Of this taxa, species currently restricted to more marginal mountain ranges (those characterised as drier and with lower summits) are projected to be the most vulnerable to climate change impacts. Seasonal investigations also indicate that, as flightless ground beetles are inactive during dry seasons, projected increases in dry season length will negatively affect this taxa. These results suggest that flightless ground beetles are among the most vulnerable taxa to climate change impacts so far investigated in the Wet Tropics. Such findings have dramatic implications for all other flightless insect taxa and, therefore, the future biodiversity of this region.

6.2 Future research directions

Flightless ground beetles are highly vulnerable to projected climate change impacts. This high sensitivity implies that similar flightless mountain-top taxa, the vast majority of which remain unstudied, may be similarly threatened by climate change. Future research must address this lack of understanding if climate change impacts on mountain-top ecosystems are to be comprehensively understood.

Much work is currently underway investigating the implementation of corridors between habitats which allow species to migrate as climatic conditions change (Sawyer, Epps, & Brashares, 2011). However, as flightless mountain-top taxa are inherently poor dispersers, often inhabiting the highest possible extent of their distributions and do not live in lowland habitats, corridors between forested habitats will not help them migrate to suitable refugia. One controversial solution suggested to help species with low vagility survive future climatic changes is assisted migration, whereby humans physically relocated concerned species (McLachlan, Hellmann, & Schwartz, 2007). Future research must investigate the efficacy of options such as assisted migration before climate change irreversibly denigrates populations of flightless mountain-top taxa.

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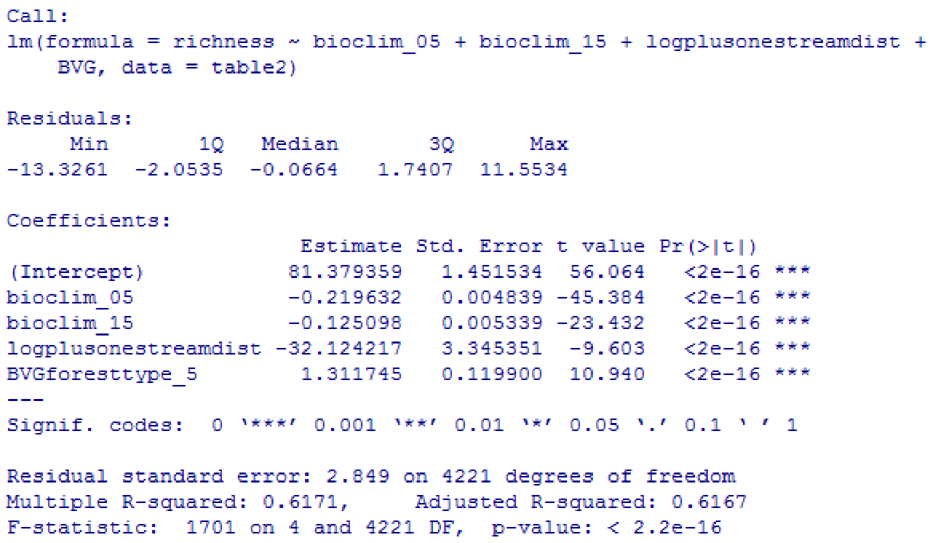
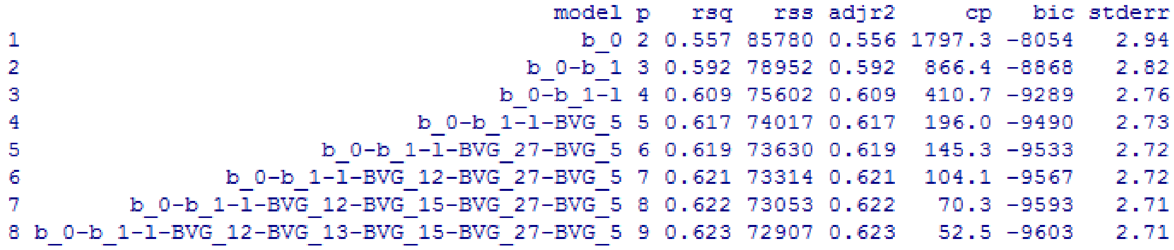
Appendix

Appendix 2.1. Raw data output for the computation of the richness versus environmental variable best sub-set regression model (Table 3.1). Note: additional vegetation types include: BVG27 = heathland and scrub, BVG12 = dry woodland, BVG15 = woodland, BVG13 = dry to moist woodland.

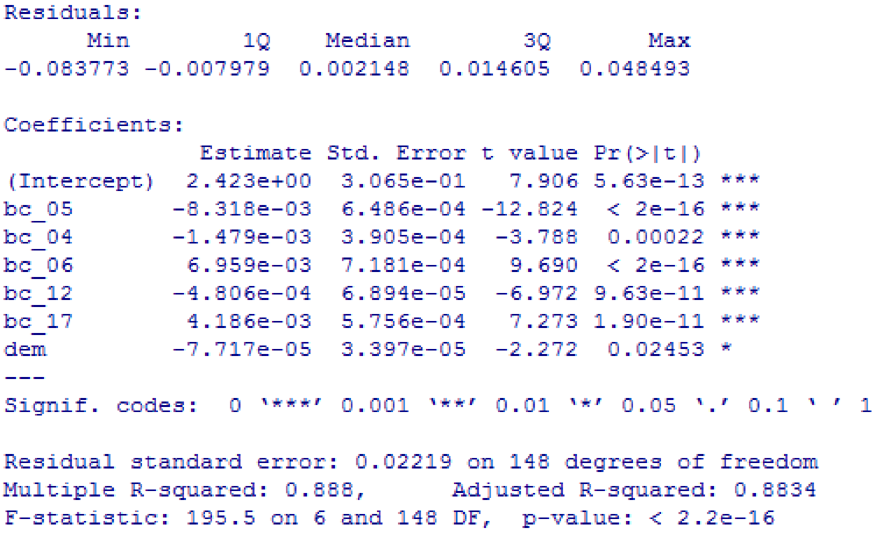


```
Call:
lm(formula = richness ~ bioclim_05 + bioclim_15 + logplusonestreamdist +
    BVG, data = table2)

Residuals:
     Min       1Q   Median       3Q      Max
-13.3261  -2.0535  -0.0664   1.7407  11.5534

Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)          81.379359   1.451534  56.064   <2e-16 ***
bioclim_05           -0.219632   0.004839 -45.384   <2e-16 ***
bioclim_15           -0.125098   0.005339 -23.432   <2e-16 ***
logplusonestreamdist -32.124217   3.345351  -9.603   <2e-16 ***
BVGforesttype_5        1.311745   0.119900  10.940   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 2.849 on 4221 degrees of freedom
Multiple R-squared: 0.6171,     Adjusted R-squared: 0.6167
F-statistic:  1701 on 4 and 4221 DF,  p-value: < 2.2e-16
```

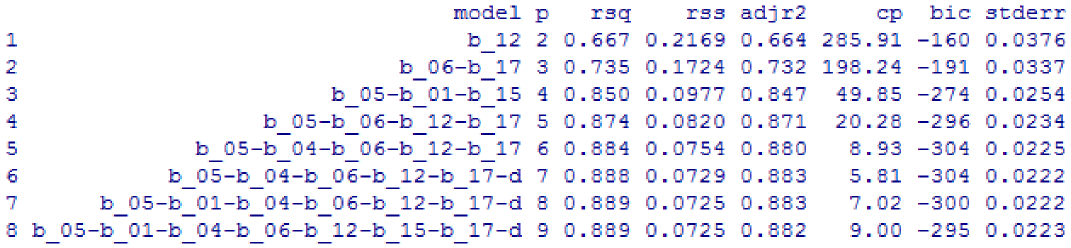


```
                                          model p   rsq   rss adjr2     cp   bic stderr
1                                           b_0 2 0.557 85780 0.556 1797.3 -8054   2.94
2                                       b_0-b_1 3 0.592 78952 0.592  866.4 -8868   2.82
3                                     b_0-b_1-1 4 0.609 75602 0.609  410.7 -9289   2.76
4                               b_0-b_1-1-BVG_5 5 0.617 74017 0.617  196.0 -9490   2.73
5                        b_0-b_1-1-BVG_27-BVG_5 6 0.619 73630 0.619  145.3 -9533   2.72
6                 b_0-b_1-1-BVG_12-BVG_27-BVG_5 7 0.621 73314 0.621  104.1 -9567   2.72
7          b_0-b_1-1-BVG_12-BVG_15-BVG_27-BVG_5 8 0.622 73053 0.622   70.3 -9593   2.71
8 b_0-b_1-1-BVG_12-BVG_13-BVG_15-BVG_27-BVG_5 9 0.623 72907 0.623   52.5 -9603   2.71
```

Appendix 2.2. Raw data output for the computation of the model which best explained variance in the projected loss of total abundance of the 14 endemic species (year 2080, SRES A2). bc_12 = precipitation seasonality, bc_05 = maximum temperature of warmest period, bc_04 = temperature seasonality, bc_06 = minimum temperature of coldest period, bc_17 = precipitation of driest quarter, dem = digital elevation model.

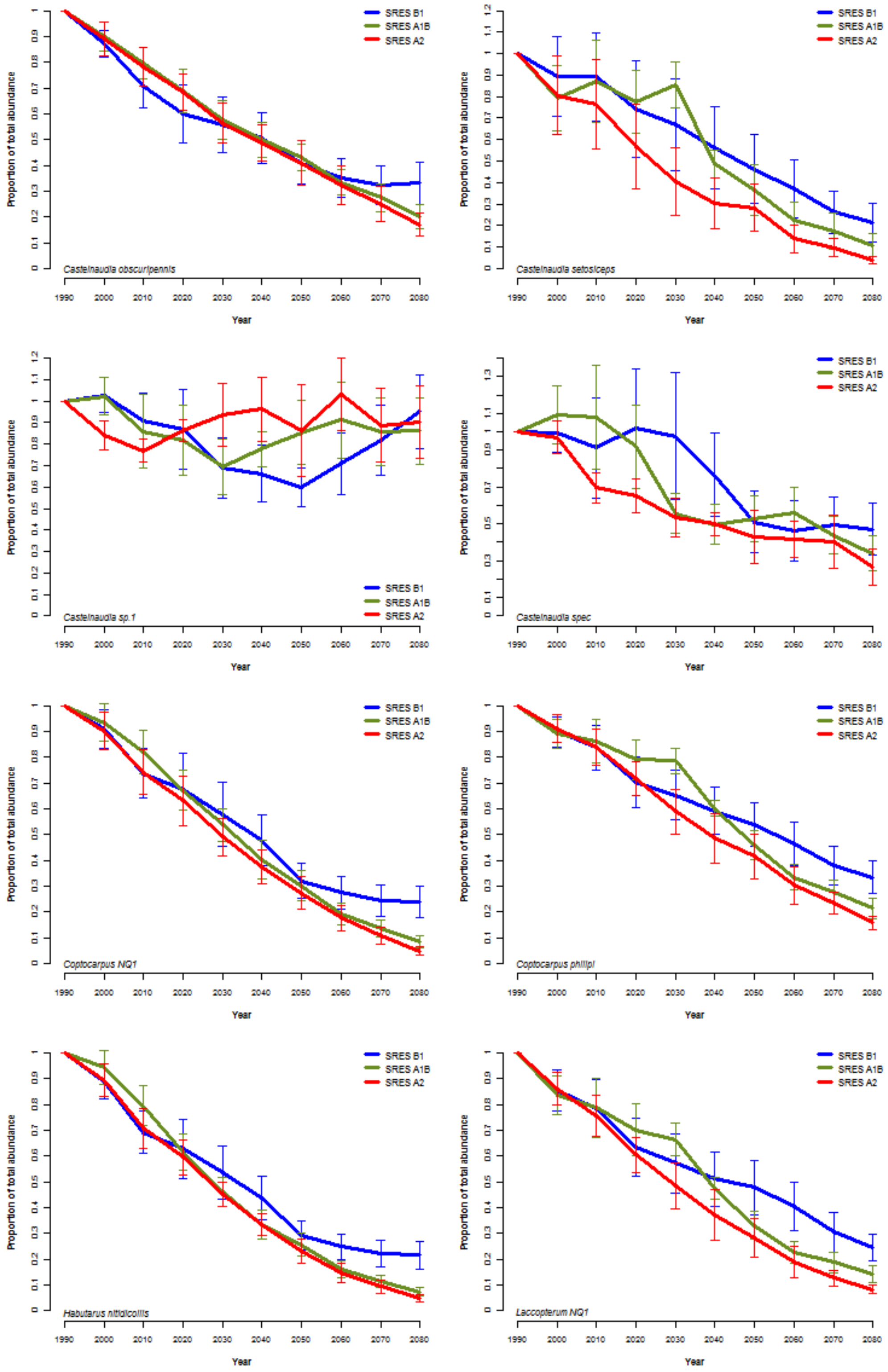


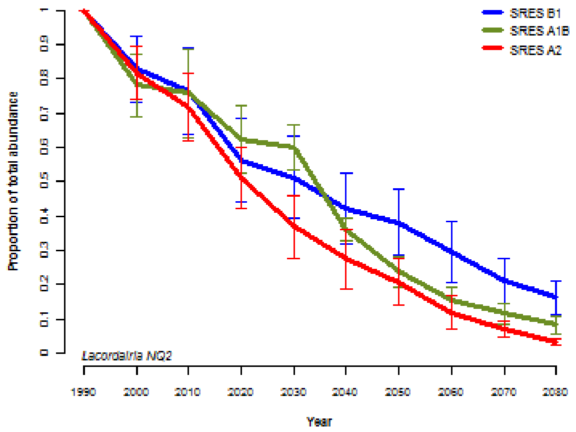
```
Residuals:
      Min        1Q    Median        3Q       Max 
-0.083773 -0.007979  0.002148  0.014605  0.048493 

Coefficients:
              Estimate Std. Error t value Pr(>|t|)    
(Intercept)  2.423e+00  3.065e-01   7.906 5.63e-13 ***
bc_05       -8.318e-03  6.486e-04 -12.824  < 2e-16 ***
bc_04       -1.479e-03  3.905e-04  -3.788  0.00022 ***
bc_06        6.959e-03  7.181e-04   9.690  < 2e-16 ***
bc_12       -4.806e-04  6.894e-05  -6.972 9.63e-11 ***
bc_17        4.186e-03  5.756e-04   7.273 1.90e-11 ***
dem         -7.717e-05  3.397e-05  -2.272  0.02453 *  
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 

Residual standard error: 0.02219 on 148 degrees of freedom
Multiple R-squared: 0.888,      Adjusted R-squared: 0.8834 
F-statistic: 195.5 on 6 and 148 DF,  p-value: < 2.2e-16 
```

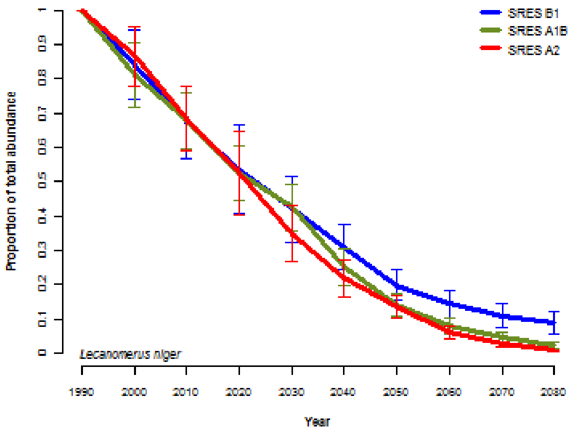


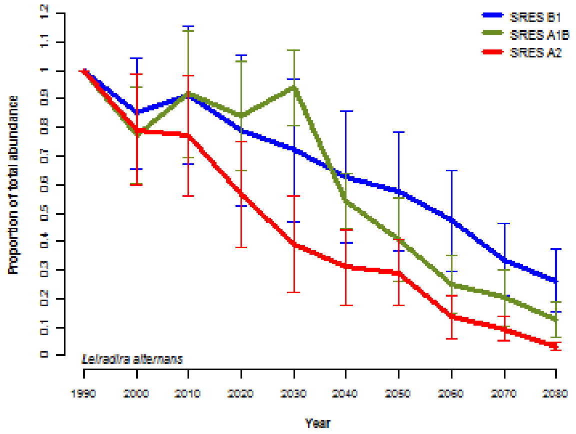
```
                                 model p   rsq    rss adjr2     cp  bic stderr
1                                 b_12 2 0.667 0.2169 0.664 285.91 -160 0.0376
2                            b_06-b_17 3 0.735 0.1724 0.732 198.24 -191 0.0337
3                       b_05-b_01-b_15 4 0.850 0.0977 0.847  49.85 -274 0.0254
4                  b_05-b_06-b_12-b_17 5 0.874 0.0820 0.871  20.28 -296 0.0234
5             b_05-b_04-b_06-b_12-b_17 6 0.884 0.0754 0.880   8.93 -304 0.0225
6           b_05-b_04-b_06-b_12-b_17-d 7 0.888 0.0729 0.883   5.81 -304 0.0222
7      b_05-b_01-b_04-b_06-b_12-b_17-d 8 0.889 0.0725 0.883   7.02 -300 0.0222
8 b_05-b_01-b_04-b_06-b_12-b_15-b_17-d 9 0.889 0.0725 0.882   9.00 -295 0.0223
```

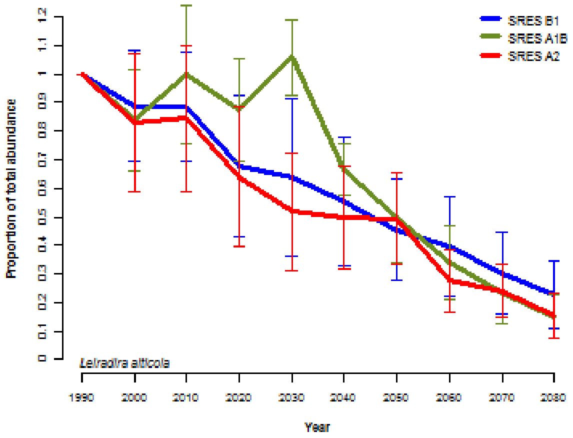
Appendix 2.3. Projected changes in the proportion of total population for each of 43 flightless ground beetle species in the Wet Tropics using three emission scenarios from the SRES and eight GCMs. Error bars represent variation between model outputs.

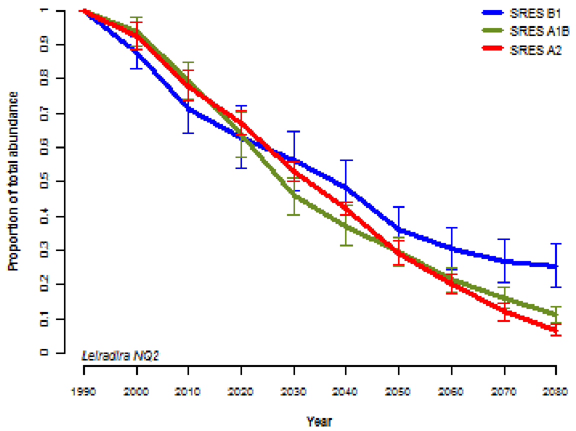


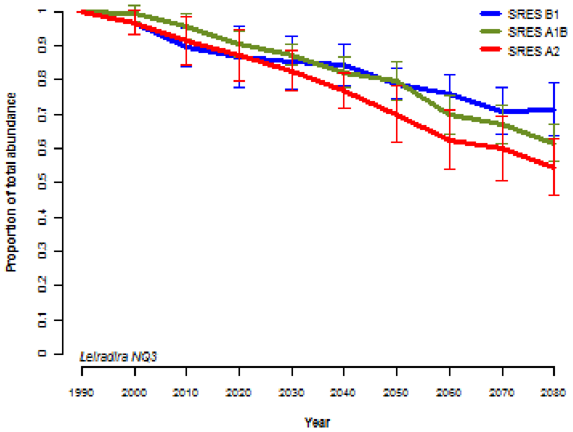

Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year
SRES B1
SRES A1B
SRES A2
Lacordairia NQ2

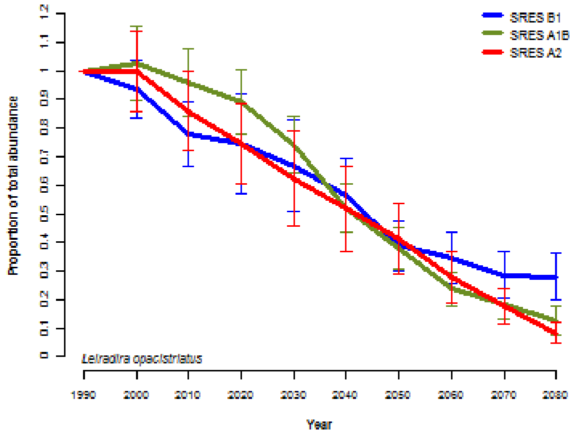

Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year
SRES B1
SRES A1B
SRES A2
Lecanomerus niger

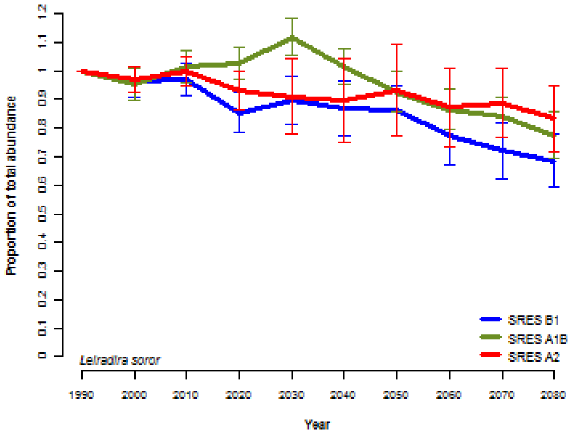

Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year
SRES B1
SRES A1B
SRES A2
Leiradira alternans

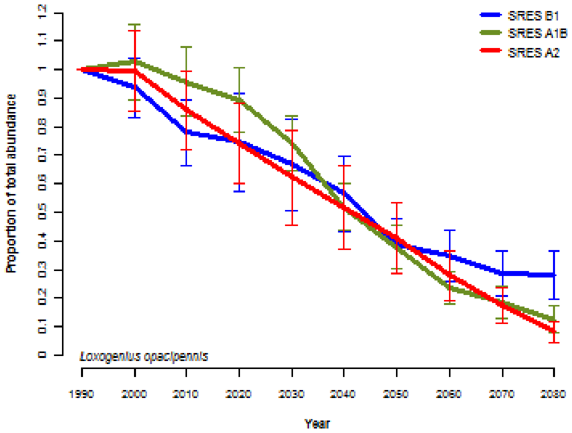

Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year
SRES B1
SRES A1B
SRES A2
Leiradira alticola

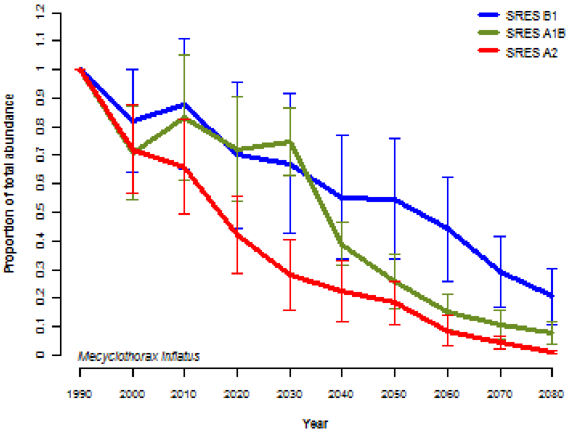

Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year
SRES B1
SRES A1B
SRES A2
Leiradira NQ2

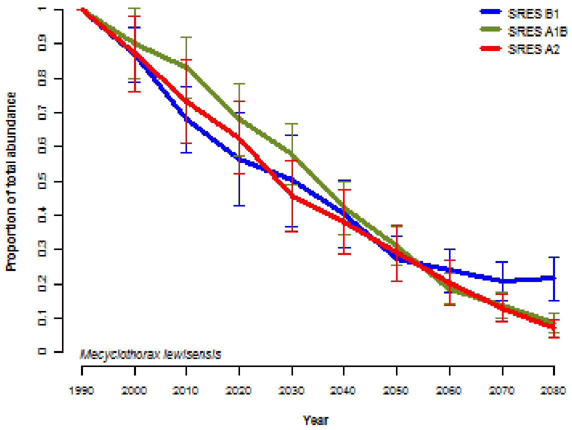

Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year
SRES B1
SRES A1B
SRES A2
Leiradira NQ3

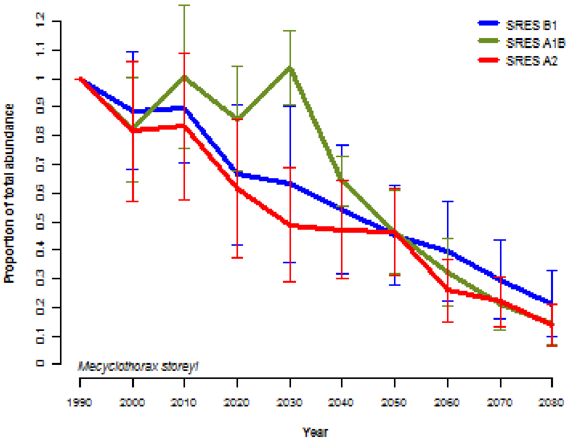

Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year
SRES B1
SRES A1B
SRES A2
Leiradira opacistriatus

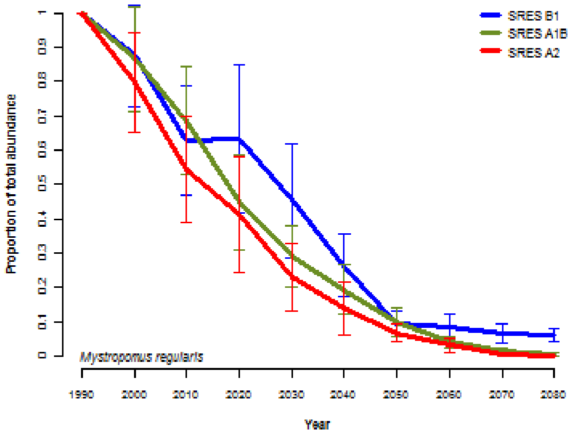

Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year
SRES B1
SRES A1B
SRES A2
Leiradira soror

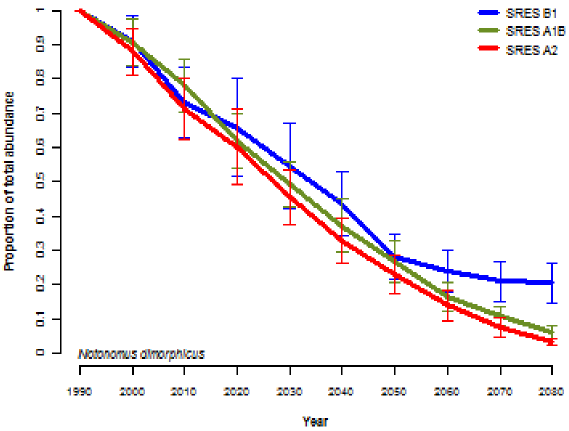

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1 1.1 1.2
Loxogenius opacipennis
1990 2000 2010 2020 2030 2040 2050 2060 2070 2080
Year

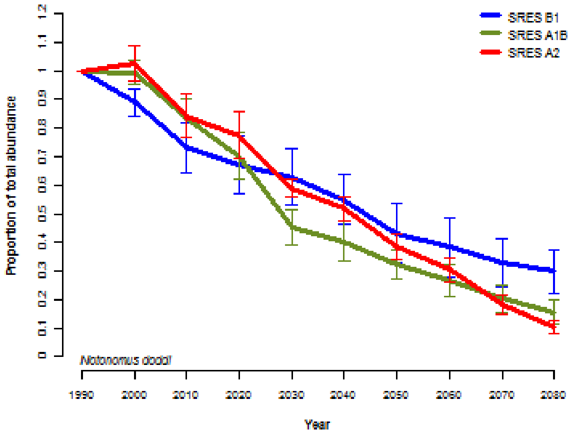

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1 1.1 1.2
Mecyclothorax inflatus
1990 2000 2010 2020 2030 2040 2050 2060 2070 2080
Year

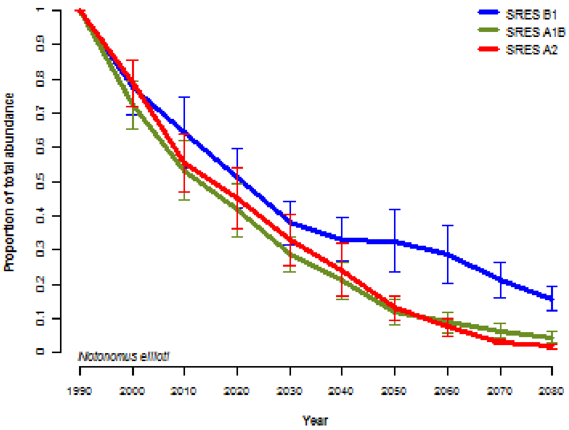

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Mecyclothorax lewisensis
1990 2000 2010 2020 2030 2040 2050 2060 2070 2080
Year

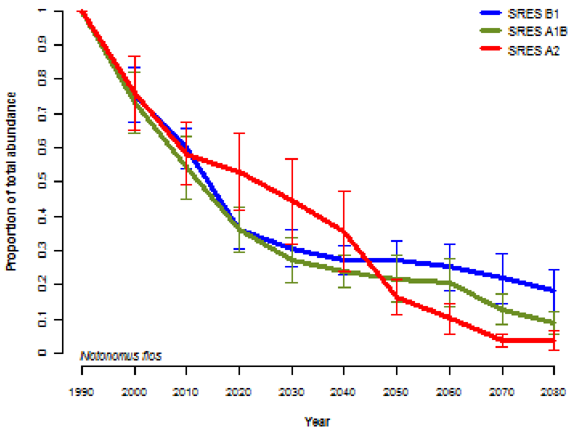

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1 1.1 1.2
Mecyclothorax storeyi
1990 2000 2010 2020 2030 2040 2050 2060 2070 2080
Year

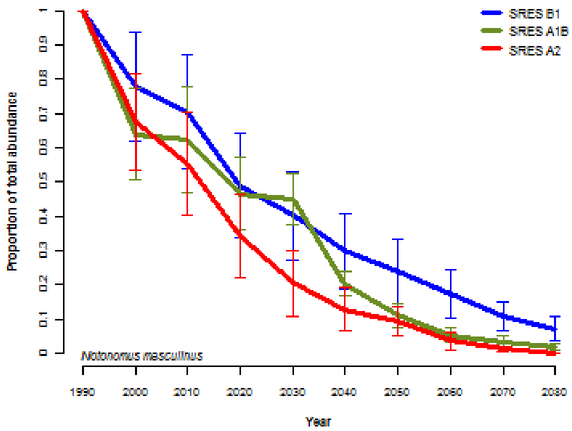

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Mystropomus regularis
1990 2000 2010 2020 2030 2040 2050 2060 2070 2080
Year

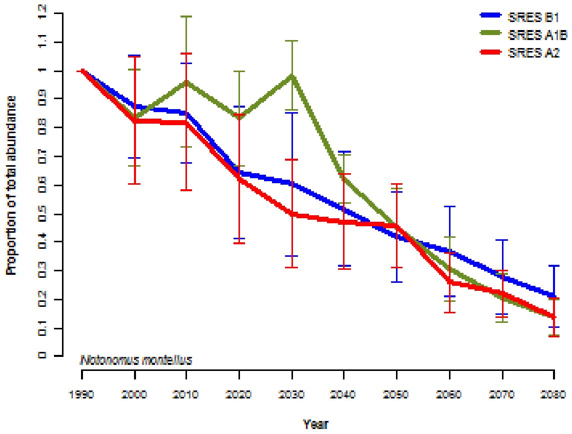

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Notonomus dimorphicus
1990 2000 2010 2020 2030 2040 2050 2060 2070 2080
Year

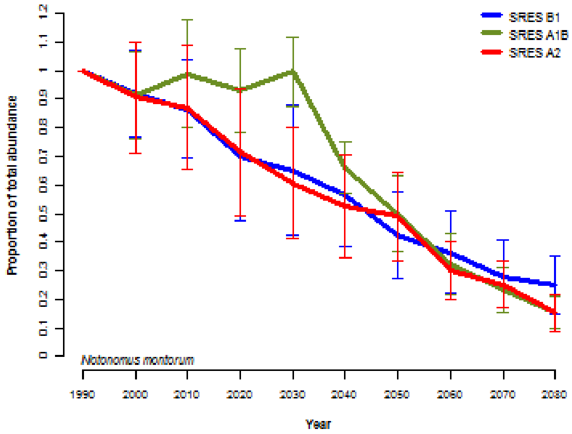

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1 1.1 1.2
Notonomus doddi
1990 2000 2010 2020 2030 2040 2050 2060 2070 2080
Year

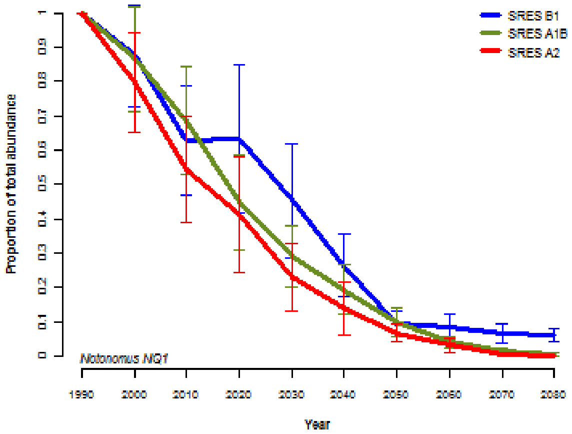

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Notonomus ellioti
1990 2000 2010 2020 2030 2040 2050 2060 2070 2080
Year

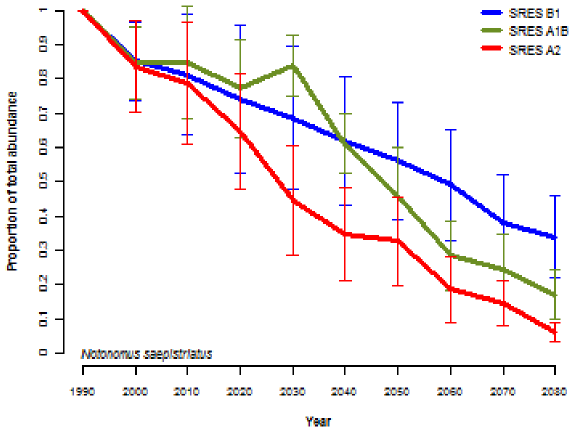

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Notonomus flos
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year

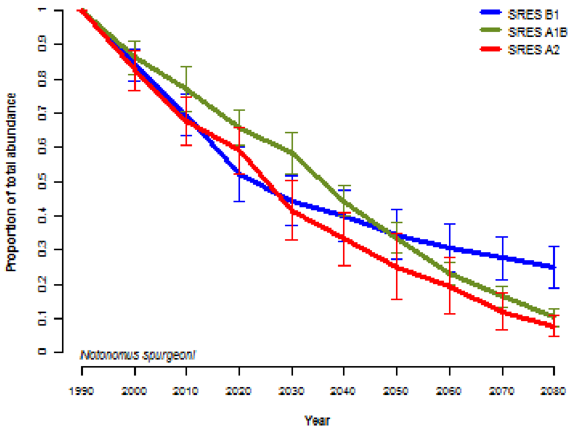

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Notonomus masculinus
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year

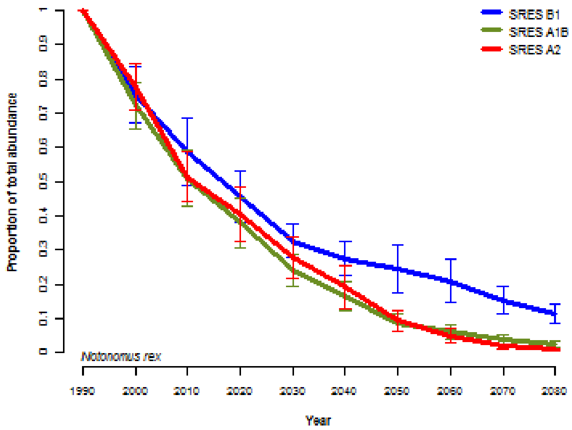

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
Notonomus montellus
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year

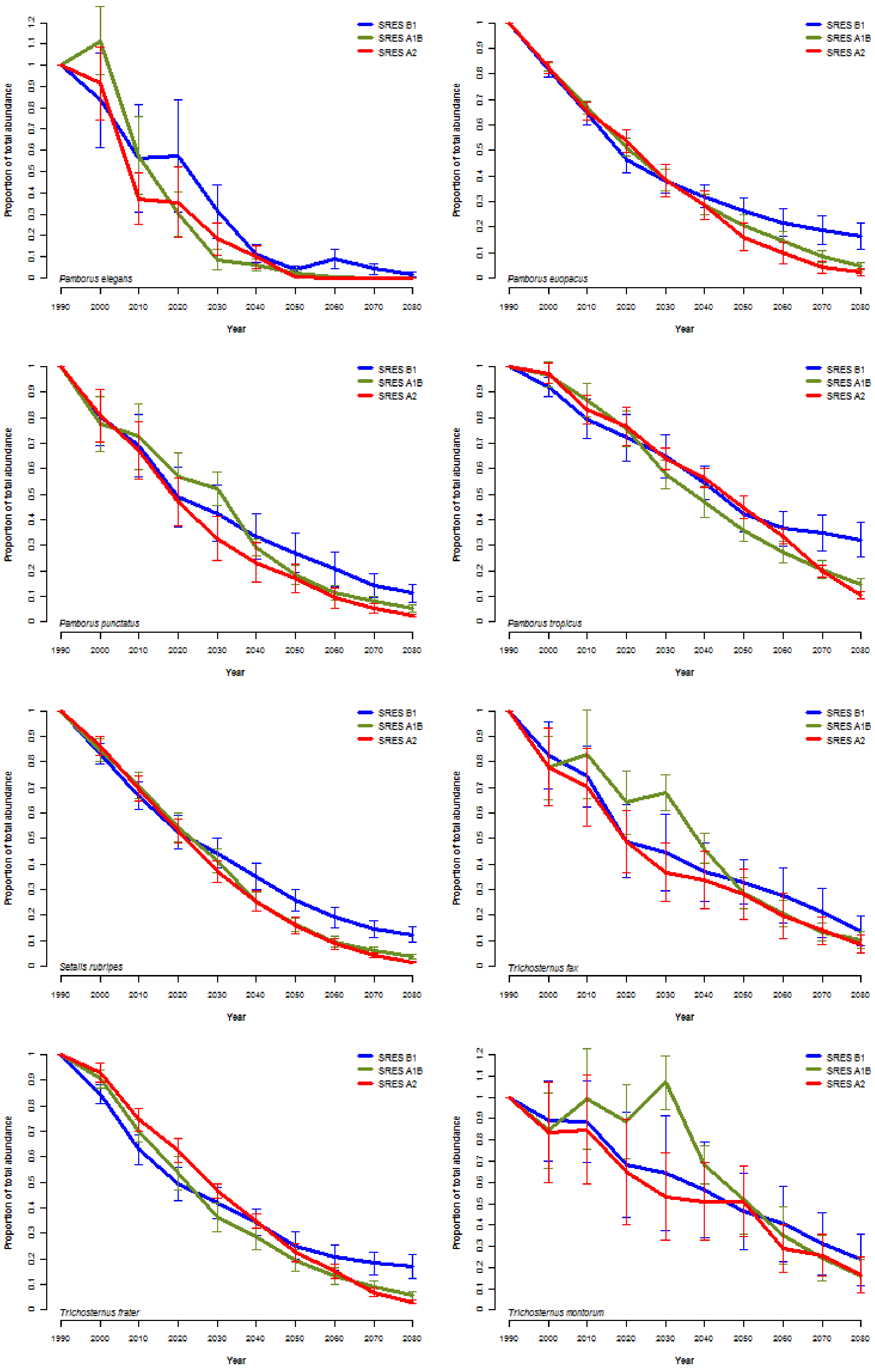

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
Notonomus montorum
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year

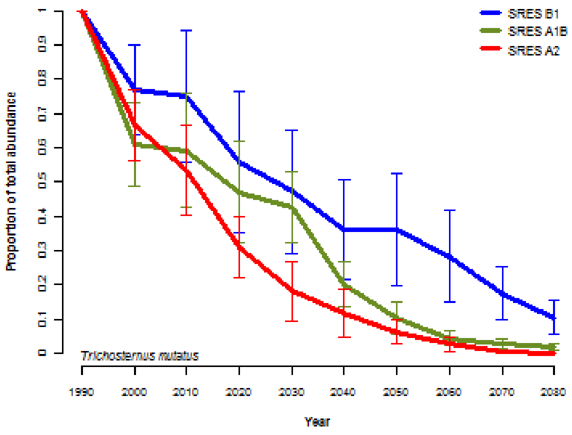

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Notonomus NQ1
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year

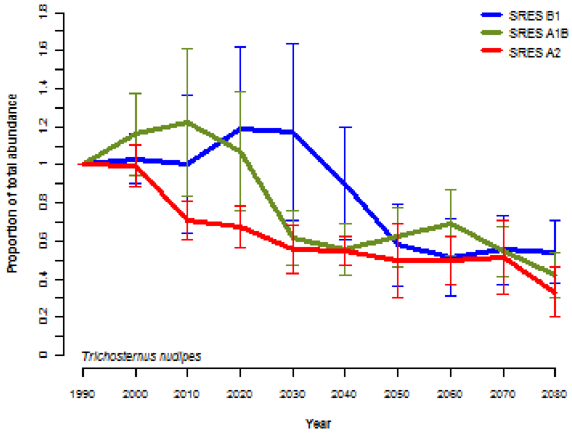

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Notonomus saepistriatus
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year

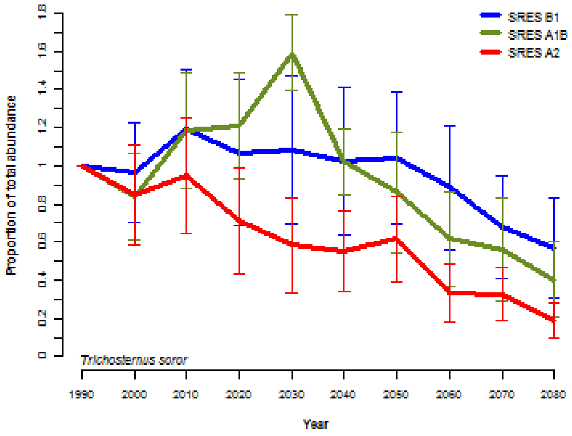

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Notonomus spurgeoni
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year


SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Notonomus rex
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year

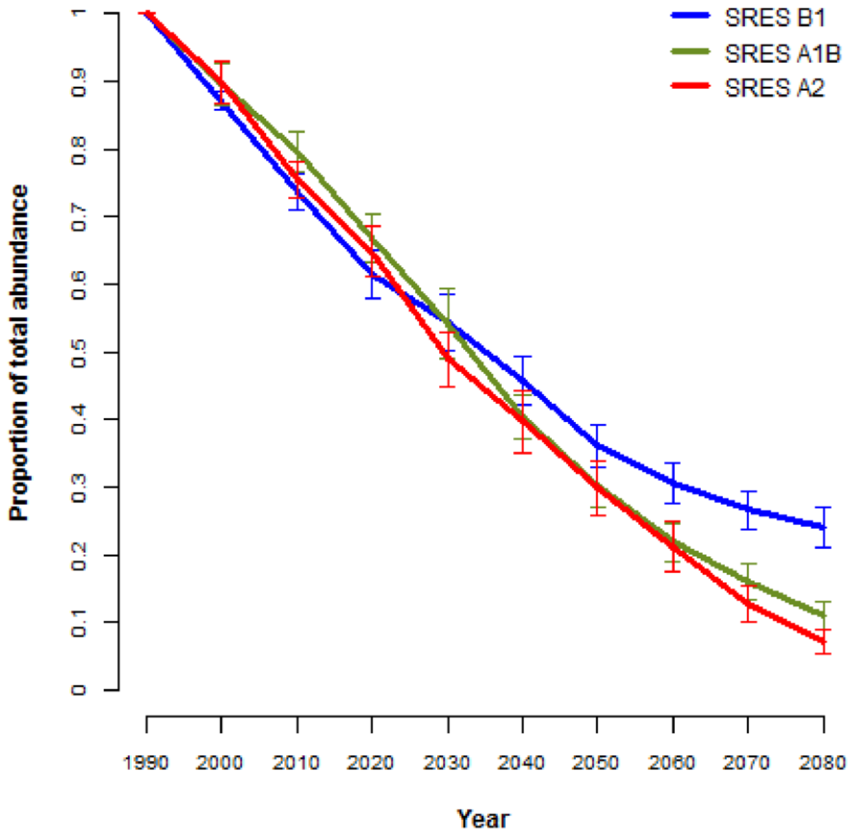

SRES B1
SRES A1B
SRES A2
Proportion of total abundance
Year
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Pamborus elegans
Pamborus euopacus
Pamborus punctatus
Pamborus tropicus
Setalis rubripes
Trichosternus fax
Trichosternus frater
Trichosternus montorum


SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Trichosternus mutatus
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year


SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
Trichosternus nudipes
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year


SRES B1
SRES A1B
SRES A2
Proportion of total abundance
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
Trichosternus soror
1990
2000
2010
2020
2030
2040
2050
2060
2070
2080
Year

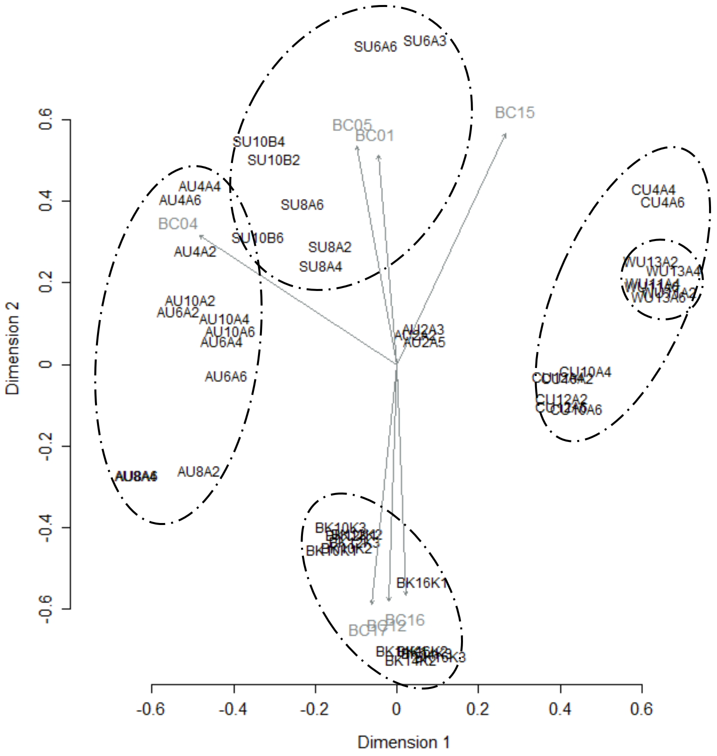
Appendix 2.4. Projected changes in the proportion of total current population for the eight flightless ground beetle species in the Wet Tropics for which more than 30 point locality records were obtained. Species included are: Lecanomerus niger, Pamborus euopacus, Castelnaudia setosiceps, Mystropomus regularis, Notonomus spurgeoni, Notonomus doddi, Pamborus tropicus and Castelnaudia obscuripennis. Projections use three emission scenarios from the SRES (B1, A1B and A2) and eight GCMs. Error bars represent variation between model outputs.



Appendix 3.1. Replicate codes Spec Uplands (SU), Atherton Uplands (AU), Bellenden Ker Uplands (BK), Carbine Uplands (CU), Windsor Uplands (WU) and locations (GPS setting - WGS84, decimal degrees)

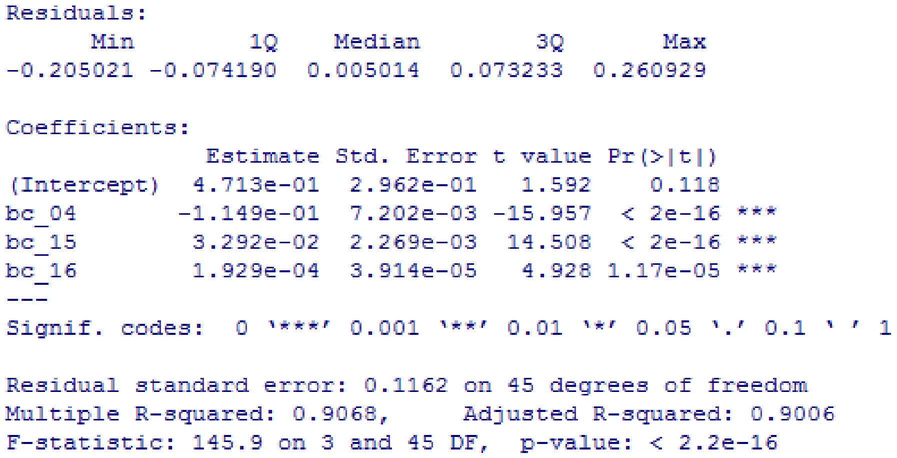
Replicate	Latitude	Longitude	Height (m a.s.l.)	Location name
SU350A1	-19.0139787	146.2668612	324	Paluma Range Road
SU350A2	-19.01484047	146.2654037	334	Paluma Range Road
SU350A3	-19.01543334	146.2667789	340	Paluma Range Road
SU6A2	-19.00261633	146.2415251	671	Paluma Range Road
SU6A3	-19.00261368	146.2430833	661	Paluma Range Road
SU6A6	-19.00085923	146.247205	609	Paluma Range Road
SU8A2	-19.01134381	146.2214001	834	Paluma Range Road
SU8A4	-19.01118481	146.2244222	846	Paluma Range Road
SU8A6	-19.00876483	146.2270462	795	Paluma Range Road
SU10B2	-19.00378261	146.2092744	899	Paluma Range Road
SU10B4	-19.00141961	146.2082595	881	Paluma Range Road
SU10B6	-19.00221106	146.2052631	880	Paluma Range Road
AU1A1	-17.71670041	145.86284	80	Japonvale
AU1A2	-17.7169538	145.8613391	80	Japonvale
AU1A3	-17.71700607	145.8594433	80	Japonvale
AU2A2	-17.66048632	145.8736668	180	Mena Creek
AU2A3	-17.65999818	145.8720673	180	Mena Creek
AU2A5	-17.65803935	145.8693175	190	Mena Creek
AU4A2	-17.60929842	145.7664095	428	K-Tree Road
AU4A4	-17.60822594	145.7697811	411	K-Tree Road
AU4A6	-17.60782846	145.7741659	400	K-Tree Road
AU6A2	-17.67066916	145.7167358	630	South Johnstone Foresty Camp
AU6A4	-17.67300424	145.7145039	627	South Johnstone Foresty Camp
AU6A6	-17.67597315	145.7124654	611	South Johnstone Foresty Camp
AU8A2	-17.60019808	145.634556	840	Maalan Road
AU8A4	-17.6029758	145.6324338	840	Maalan Road
AU8A6	-17.60369044	145.6299312	809	Maalan Road
AU10A2	-17.70066965	145.5244897	930	Charmillan Creek
AU10A4	-17.7026933	145.5268302	932	Charmillan Creek
AU10A6	-17.70615356	145.5267359	920	Charmillan Creek
BK10K1	-17.26642578	145.8722112	948	Mt. Bellenden Ker Eastern Slope
BK10K2	-17.2659517	145.8698719	990	Mt. Bellenden Ker Eastern Slope
BK10K3	-17.26422021	145.8673333	1003	Mt. Bellenden Ker Eastern Slope
BK12K1	-17.26286444	145.8657143	1166	Mt. Bellenden Ker Eastern Slope
BK12K2	-17.26280287	145.8660156	1192	Mt. Bellenden Ker Eastern Slope
BK12K3	-17.25938353	145.8606844	1216	Mt. Bellenden Ker Eastern Slope
BK14K1	-17.2647206	145.8583377	1459	Mt. Bellenden Ker Eastern Slope

BK14K2	-17.26436835	145.8583775	1479	Mt. Bellenden Ker Eastern Slope
BK14K3	-17.26400707	145.8584173	1509	Mt. Bellenden Ker Eastern Slope
BK16K1	-17.26357484	145.8539331	1535	Mt. Bellenden Ker Ridge
BK16K2	-17.2616295	145.8591702	1537	Mt. Bellenden Ker Ridge
BK16K3	-17.25935686	145.8591702	1575	Mt. Bellenden Ker Ridge
CU1A1	-16.46883266	145.3264474	115	Mossman Gorge
CU1A3	-16.4704621	145.3245416	133	Mossman Gorge
CU1A5	-16.47013084	145.3226714	162	Mossman Gorge
CU4A2	-16.53288906	145.3726638	440	Rex Range
CU4A4	-16.53464361	145.3693701	415	Rex Range
CU4A6	-16.53911001	145.3661846	420	Rex Range
CU6A2	-16.57764758	145.3057005	656	Mt. Lewis Road
CU6A4	-16.57739771	145.3094228	624	Mt. Lewis Road
CU6A6	-16.57840977	145.3127592	601	Mt. Lewis Road
CU8A2	-16.58640134	145.2976211	820	Mt. Lewis Road
CU8A4	-16.58419506	145.2996646	813	Mt. Lewis Road
CU8A6	-16.58453862	145.303007	800	Mt. Lewis Road
CU10A2	-16.55578091	145.2783645	1016	Mt. Lewis Road
CU10A4	-16.55292244	145.2801982	978	Mt. Lewis Road
CU10A6	-16.55102963	145.2807865	940	Mt. Lewis Road
CU12A2	-16.51257598	145.270542	1210	Mt. Lewis Road
CU12A4	-16.51507882	145.2726929	1181	Mt. Lewis Road
CU12A6	-16.51648475	145.2755187	1160	Mt. Lewis Road
WU9A2	-16.28476505	145.0840876	940	Mt. Windsor Road
WU9A4	-16.28513625	145.087162	928	Mt. Windsor Road
WU9A6	-16.28658435	145.0904224	886	Mt. Windsor Road
WU11A2	-16.25913233	145.0437955	1071	Mt. Windsor Road
WU11A4	-16.25920351	145.0475925	1080	Mt. Windsor Road
WU11A6	-16.26044685	145.0511255	1080	Mt. Windsor Road
WU13A2	-16.23531394	145.008827	1280	Mt. Windsor Road
WU13A4	-16.23247429	145.006639	1283	Mt. Windsor Road
WU13A6	-16.22966978	145.009155	1260	Mt. Windsor Road

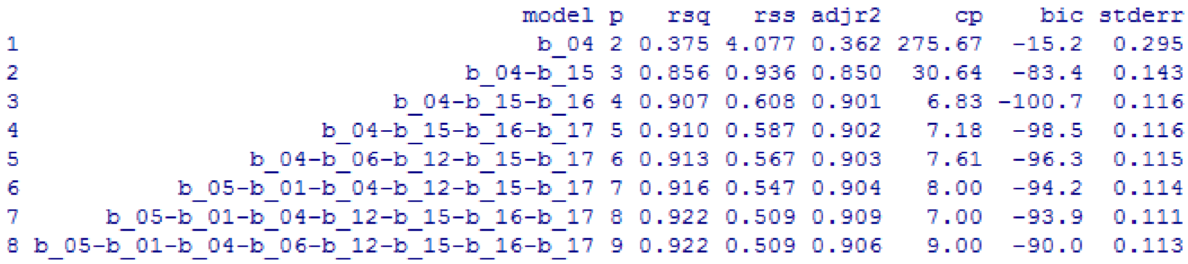


Appendix 3.2. Ordination plot of communities at all subregions (stress=0.21). Specific sites are displayed through using text rather than symbols. Vectors of site environmental variables displaying significant correlations (*P*<0.001) with species data overlayed. Spec Uplands (SU), Atherton Uplands (AU), Bellenden Ker Uplands (BK), Carbine Uplands (CU), Windsor Uplands (WU).

Appendix 3.3. Raw data output for the computation of the dimension 1 versus environmental variable best sub-set regression model (Table 3.5).

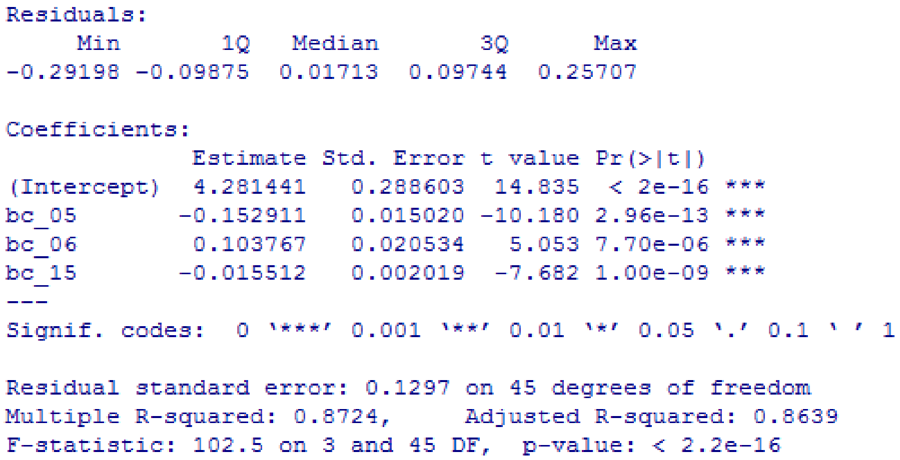


```
Residuals:
      Min        1Q    Median        3Q       Max
-0.205021 -0.074190  0.005014  0.073233  0.260929

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  4.713e-01  2.962e-01   1.592    0.118
bc_04       -1.149e-01  7.202e-03 -15.957  < 2e-16 ***
bc_15        3.292e-02  2.269e-03  14.508  < 2e-16 ***
bc_16        1.929e-04  3.914e-05   4.928 1.17e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.1162 on 45 degrees of freedom
Multiple R-squared: 0.9068,     Adjusted R-squared: 0.9006
F-statistic: 145.9 on 3 and 45 DF,  p-value: < 2.2e-16
```

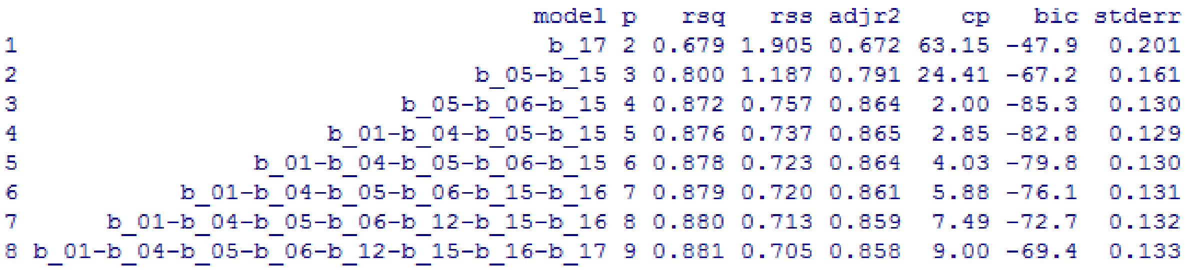


```
                                     model p   rsq   rss adjr2     cp    bic stderr
1                                     b_04 2 0.375 4.077 0.362 275.67  -15.2  0.295
2                                b_04-b_15 3 0.856 0.936 0.850  30.64  -83.4  0.143
3                           b_04-b_15-b_16 4 0.907 0.608 0.901   6.83 -100.7  0.116
4                      b_04-b_15-b_16-b_17 5 0.910 0.587 0.902   7.18  -98.5  0.116
5                 b_04-b_06-b_12-b_15-b_17 6 0.913 0.567 0.903   7.61  -96.3  0.115
6            b_05-b_01-b_04-b_12-b_15-b_17 7 0.916 0.547 0.904   8.00  -94.2  0.114
7       b_05-b_01-b_04-b_12-b_15-b_16-b_17 8 0.922 0.509 0.909   7.00  -93.9  0.111
8 b_05-b_01-b_04-b_06-b_12-b_15-b_16-b_17 9 0.922 0.509 0.906   9.00  -90.0  0.113
```

Appendix 3.4. Raw data output for the computation of the dimension 2 versus environmental variable best sub-set regression model (Table 3.6).



```
Residuals:
     Min       1Q   Median       3Q      Max
-0.29198 -0.09875  0.01713  0.09744  0.25707

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  4.281441   0.288603  14.835  < 2e-16 ***
bc_05       -0.152911   0.015020 -10.180 2.96e-13 ***
bc_06        0.103767   0.020534   5.053 7.70e-06 ***
bc_15       -0.015512   0.002019  -7.682 1.00e-09 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.1297 on 45 degrees of freedom
Multiple R-squared: 0.8724,     Adjusted R-squared: 0.8639
F-statistic: 102.5 on 3 and 45 DF,  p-value: < 2.2e-16
```



```
                                     model p   rsq   rss adjr2    cp   bic stderr
1                                     b_17 2 0.679 1.905 0.672 63.15 -47.9  0.201
2                                b_05-b_15 3 0.800 1.187 0.791 24.41 -67.2  0.161
3                           b_05-b_06-b_15 4 0.872 0.757 0.864  2.00 -85.3  0.130
4                      b_01-b_04-b_05-b_15 5 0.876 0.737 0.865  2.85 -82.8  0.129
5                 b_01-b_04-b_05-b_06-b_15 6 0.878 0.723 0.864  4.03 -79.8  0.130
6            b_01-b_04-b_05-b_06-b_15-b_16 7 0.879 0.720 0.861  5.88 -76.1  0.131
7       b_01-b_04-b_05-b_06-b_12-b_15-b_16 8 0.880 0.713 0.859  7.49 -72.7  0.132
8 b_01-b_04-b_05-b_06-b_12-b_15-b_16-b_17 9 0.881 0.705 0.858  9.00 -69.4  0.133
```

Appendix 4.1. Replicate codes Spec Uplands (SU), Atherton Uplands (AU), Bellenden Ker Uplands (BK), Carbine Uplands (CU), Windsor Uplands (WU) and locations (GPS setting - WGS84, decimal degrees).

Replicate	Latitude	Longitude	Height (m.a.s.l.)	Location name
SU350A1	-19.0139787	146.2668612	324	Paluma Range Road
SU350A2	-19.01484047	146.2654037	334	Paluma Range Road
SU350A3	-19.01543334	146.2667789	340	Paluma Range Road
SU6A2	-19.00261633	146.2415251	671	Paluma Range Road
SU6A3	-19.00261368	146.2430833	661	Paluma Range Road

SU6A6	-19.00085923	146.247205	609	Paluma Range Road
SU8A2	-19.01134381	146.2214001	834	Paluma Range Road
SU8A4	-19.01118481	146.2244222	846	Paluma Range Road
SU8A6	-19.00876483	146.2270462	795	Paluma Range Road
SU10B2	-19.00378261	146.2092744	899	Paluma Range Road
SU10B4	-19.00141961	146.2082595	881	Paluma Range Road
SU10B6	-19.00221106	146.2052631	880	Paluma Range Road
AU1A1	-17.71670041	145.86284	80	Japonvale
AU1A2	-17.7169538	145.8613391	80	Japonvale
AU1A3	-17.71700607	145.8594433	80	Japonvale
AU2A2	-17.66048632	145.8736668	180	Mena Creek
AU2A3	-17.65999818	145.8720673	180	Mena Creek
AU2A5	-17.65803935	145.8693175	190	Mena Creek
AU4A2	-17.60929842	145.7664095	428	K-Tree Road
AU4A4	-17.60822594	145.7697811	411	K-Tree Road
AU4A6	-17.60782846	145.7741659	400	K-Tree Road
AU6A2	-17.67066916	145.7167358	630	Sth Johnstone Foresty Camp
AU6A4	-17.67300424	145.7145039	627	Sth Johnstone Foresty Camp
AU6A6	-17.67597315	145.7124654	611	Sth Johnstone Foresty Camp
AU8A2	-17.60019808	145.634556	840	Maalan Road
AU8A4	-17.6029758	145.6324338	840	Maalan Road
AU8A6	-17.60369044	145.6299312	809	Maalan Road
AU10A2	-17.70066965	145.5244897	930	Charmillan Creek
AU10A4	-17.7026933	145.5268302	932	Charmillan Creek
AU10A6	-17.70615356	145.5267359	920	Charmillan Creek
BK10K1	-17.26642578	145.8722112	948	Mt. Bellenden Ker Eastern Slope
BK10K2	-17.2659517	145.8698719	990	Mt. Bellenden Ker Eastern Slope
BK10K3	-17.26422021	145.8673333	1003	Mt. Bellenden Ker Eastern Slope
BK12K1	-17.26286444	145.8657143	1166	Mt. Bellenden Ker Eastern Slope
BK12K2	-17.26280287	145.8660156	1192	Mt. Bellenden Ker Eastern Slope
BK12K3	-17.25938353	145.8606844	1216	Mt. Bellenden Ker Eastern Slope
BK14K1	-17.2647206	145.8583377	1459	Mt. Bellenden Ker Eastern Slope
BK14K2	-17.26436835	145.8583775	1479	Mt. Bellenden Ker Eastern Slope

BK14K3	-17.26400707	145.8584173	1509	Mt. Bellenden Ker Eastern Slope
BK16K1	-17.26357484	145.8539331	1535	Mt. Bellenden Ker Ridge
BK16K2	-17.2616295	145.8591702	1537	Mt. Bellenden Ker Ridge
BK16K3	-17.25935686	145.8591702	1575	Mt. Bellenden Ker Ridge
CU1A1	-16.46883266	145.3264474	115	Mossman Gorge
CU1A3	-16.4704621	145.3245416	133	Mossman Gorge
CU1A5	-16.47013084	145.3226714	162	Mossman Gorge
CU4A2	-16.53288906	145.3726638	440	Rex Range
CU4A4	-16.53464361	145.3693701	415	Rex Range
CU4A6	-16.53911001	145.3661846	420	Rex Range
CU6A2	-16.57764758	145.3057005	656	Mount Lewis Road
CU6A4	-16.57739771	145.3094228	624	Mount Lewis Road
CU6A6	-16.57840977	145.3127592	601	Mount Lewis Road
CU8A2	-16.58640134	145.2976211	820	Mount Lewis Road
CU8A4	-16.58419506	145.2996646	813	Mount Lewis Road
CU8A6	-16.58453862	145.303007	800	Mount Lewis Road
CU10A2	-16.55578091	145.2783645	1016	Mount Lewis Road
CU10A4	-16.55292244	145.2801982	978	Mount Lewis Road
CU10A6	-16.55102963	145.2807865	940	Mount Lewis Road
CU12A2	-16.51257598	145.270542	1210	Mount Lewis Road
CU12A4	-16.51507882	145.2726929	1181	Mount Lewis Road
CU12A6	-16.51648475	145.2755187	1160	Mount Lewis Road
WU9A2	-16.28476505	145.0840876	940	Mount Windsor Road
WU9A4	-16.28513625	145.087162	928	Mount Windsor Road
WU9A6	-16.28658435	145.0904224	886	Mount Windsor Road
WU11A2	-16.25913233	145.0437955	1071	Mount Windsor Road
WU11A4	-16.25920351	145.0475925	1080	Mount Windsor Road
WU11A6	-16.26044685	145.0511255	1080	Mount Windsor Road
WU13A2	-16.23531394	145.008827	1280	Mount Windsor Road
WU13A4	-16.23247429	145.006639	1283	Mount Windsor Road
WU13A6	-16.22966978	145.009155	1260	Mount Windsor Road

Appendix 4.2. Table of species sampled from data sets A & B. Indication of subregion endemics Y=Yes, N=No. Abundance (A,B= data set A, data set B) and elevational range (‘00m a.s.l.) of species sampled within each subregion. Spec Uplands (SU), Atherton Uplands (AU), Bellenden Ker Uplands (BK), Carbine Uplands (CU), Windsor Uplands (WU).

Species	Mt. Spec (A,B)	Range	Atherton Uplands (A,B)	Range	Mt. Bellenden Ker (A)	Range	Carbine Uplands (A,B)	Range	Mt. Windsor (A,B)	Range
Castelnaudia obscuripennis							45,6	4-12	165,46	9-13
Castelnaudia setosiceps			7,12	4-10	63	10-12				
Castelnaudia sp.1	16,9	3.5-6								
Castelnaudia spec	46,39	6-10								
Coptocarpus NQ1							1,0	12.		
Coptocarpus philipi					1	12.				
Craspedophorus sp.1			6,1	2-4						
Feronista sp.1					4	12-16				
Feronista sp.2							6,0	10-12		
Feronista sp.3					3	12.				
Laccopterum sp.1			19,21	8.						
Laccopterum sp.2			3,0	4.						
Lecanomerus limbatus			2,0	8.						
Lecanomerus niger			1,2	8.	7	10-14				
Lecanomerus sp.1							1,1	12.		
Lecanomerus sp.2			0,1							
Leiradira alternans			8,47	6-10						
Leiradira alticola					217	10-16				
Leiradira NQ2							6,8	10-12		
Leiradira opacistiatus			5,1	6.						
Leiradira soror					8	12.				
Loxogenius opacipennis			0,1	4.			0,5	2-12		
Mecyclothorax storeyi					2	14.				
Mystropomus regularis	73,132	8-10	20,19	6-10	507	10-16	140,56	8-12		

Species	Mt. Spec (A,B)	Range	Atherton Uplands (A,B)	Range	Mt. Bellenden Ker (A)	Range	Carbine Uplands (A,B)	Range	Mt. Windsor (A,B)	Range
Notonomus dimorphicus							46,11	10-12		
Notonomus doddi	5,13	8-10					1,0	8.	13,6	11-13
Notonomus flos							77,241	10-12		
Notonomus masculinus			71,17	6-10						
Notonomus montellus					28	10-16				
Notonomus montorum					811	10-16				
Notonomus NQ1									17,4	9-13
Notonomus spurgeoni							26,4	10-12		
Oodes sp.1			14,2	2-4			1,0	6.		
Pamborus euopacus							418,196	10-12	221,21	11-13
Pamborus punctatus			1,4	10.	64	10-16				
Pamborus tropicus	150,4	8-10	258,182	4-10					1,2	9.
Pheropsophus verticalis			59,88	2.						
Prosopogmus sp. 2									1,0	9.
Scaratini NQ1			0,1	4.						
Setalis rubripes			0,3	8.	1	12.				
Trichosternus fax					297	14-16				
Trichosternus frater							24,15	10-12		
Trichosternus montorum					337	10-16				
Trichosternus mutatus			56,18	10.						
Trichosternus nudipes	50,78	6-10								
Trichosternus soror			21,18	6-8	78	10-12				
Total		340, 311		551, 544		2428		792, 544		418, 253

Appendix 5.1. Species contributing the most the dissimilarities between subregional assemblages according to simper analysis. Pairwise comparisons of subregional assemblages displayed with percentage of cumulative contribution of the six foremost species and their total elevational ranges for all subregions sampled.

Sites	Species	Cumulative contribution (%)	Elevational range ('00 m a.s.l.)
SU & AU	*Pheidole sp. AB*	8	1 to 12
	Pheidole sp. AA	14	1 to 13
	Pheidole sp. AG	18	1 to 10
	Pheidole sp. AC	23	1 to 12
	Anonychomyrma WT. A	28	1 to 12
	Rhytidoponera victoriae	**32**	2 to 12
SU & BK	*Pheidole sp. AQ*	10	10 to 16
	Pheidole sp. AB	19	1 to 12
	Rhytidoponera victoriae	25	2 to 12
	Pheidole sp. AA	29	1 to 13
	Anonychomyrma WT. B	34	1 to 12
	Pheidole sp. AC	**38**	1 to 12
SU & CU	*Pheidole sp. AB*	8	1 to 12
	Pheidole sp. AA	13	1 to 13
	Rhytidoponera victoriae	18	2 to 12
	Pheidole sp. AC	22	1 to 12
	Anonychomyrma WT. A	27	1 to 12
	Anonychomyrma WT. B	**31**	1 to 12
SU & WU	*Pheidole sp. AB*	8	1 to 12
	Rhytidoponera victoriae	14	2 to 12
	Pheidole sp. AA	18	1 to 13
	Anonychomyrma WT. A	23	1 to 12

Sites	Species	Cumulative contribution (%)	Elevational range ('00 m a.s.l.)
	Pheidole sp. AO	28	9 to 13
	Anonychomyrma WT. C	**32**	8 to 16
AU & BK	*Pheidole sp. AQ*	10	10 to 16
	Pheidole sp. AC	16	1 to 12
	Pheidole sp. AF	22	6 to 12
	Pheidole sp. AG	25	1 to 10
	Rhytidoponera victoriae	29	2 to 12
	Anonychomyrma WT. B	**32**	1 to 12
AU & CU	*Pheidole sp. AC*	6	1 to 12
	Pheidole sp. AF	11	6 to 12
	Anonychomyrma WT. A	16	1 to 12
	Pheidole sp. AG	19	1 to 10
	Rhytidoponera victoriae	23	2 to 12
	Pheidole sp. AA	**26**	1 to 13
AU & WU	*Pheidole sp. AC*	5	1 to 12
	Pheidole sp. AO	10	9 to 13
	Anonychomyrma WT. C	15	8 to 16
	Anonychomyrma WT. A	19	1 to 12
	Pheidole sp. AF	22	6 to 12
	Rhytidoponera purpurea	**26**	1 to 10
BK & CU	*Pheidole sp. AQ*	10	10 to 16
	Pheidole sp. AC	17	1 to 12
	Anonychomyrma WT. A	22	1 to 12

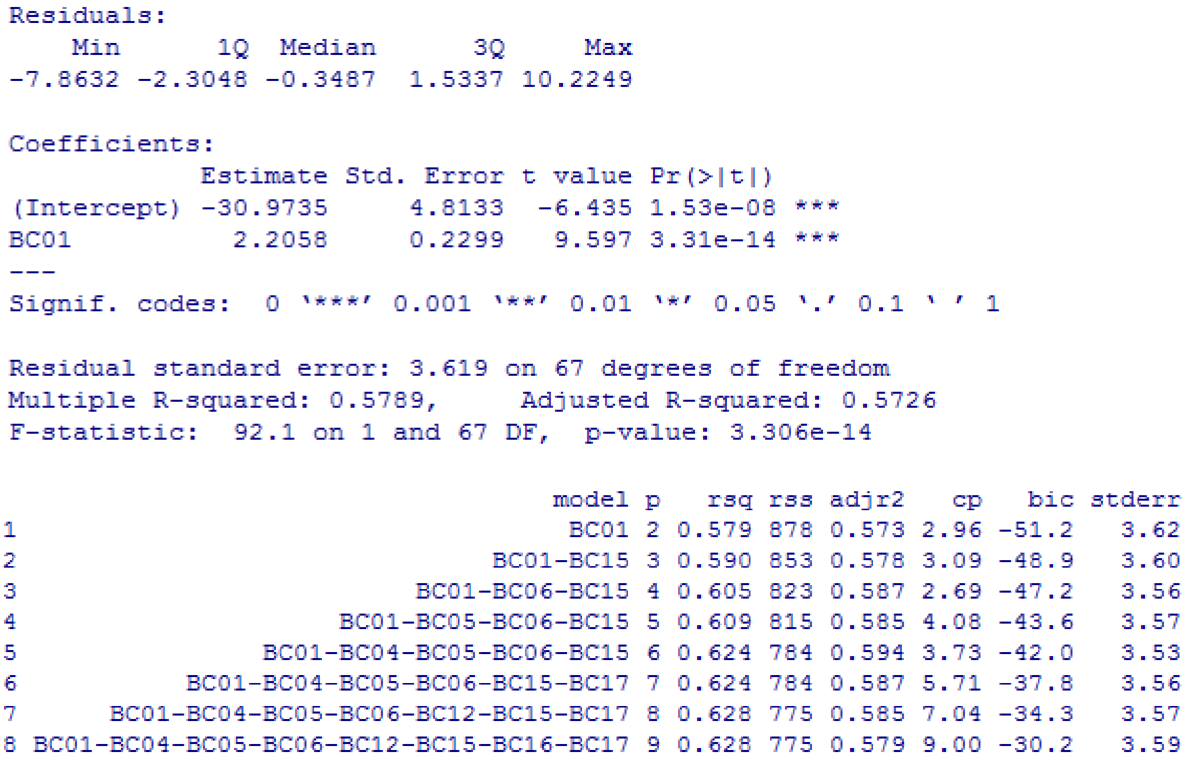
Sites	Species	Cumulative contribution (%)	Elevational range ('00 m a.s.l.)
	Pheidole sp. AF	27	6 to 12
	Anonychomyrma WT. B	30	1 to 12
	Pheidole sp. AP	**33**	12 to 16
BK & WU	*Pheidole sp. AQ*	12	10 to 16
	Pheidole sp. AO	18	9 to 13
	Anonychomyrma WT. C	23	8 to 16
	Pheidole sp. AP	27	12 to 16
	Anonychomyrma WT. A	30	1 to 12
	Rhytidoponera. kurandensis	**33**	1 to 13
CU & WU	*Pheidole sp. AC*	6	1 to 12
	Anonychomyrma WT. A	11	1 to 12
	Pheidole sp. AO	16	9 to 13
	Anonychomyrma WT. C	21	8 to 16
	Rhytidoponera purpurea	24	1 to 10
	Anonychomyrma WT. D	**28**	10 to 13

Appendix 5.2. Species contributing the most the dissimilarities between elevational groups according to simper analysis. Pairwise comparisons of subregional assemblages displayed with percentage of cumulative contribution of the six foremost species and their total elevational ranges for all subregions sampled.

Elevational groups (‘00m a.s.l.)	Species	Cumulative contribution (%)	Elevational range ('00 m a.s.l.)
1-2 & 3.5-6	*Pheidole sp. AA*	6	1 to 13
	Anonychomyrma WT. A	11	1 to 12
	Pheidole sp. AC	14	1 to 12
	Rhytidoponera purpurea	18	1 to 10
	Anonychomyrma WT. B	21	1 to 12
	Pheidole sp. M	**24**	1 to 6
1-2 & 8-11	*Pheidole sp. AA*	6	1 to 13
	Pheidole sp. AF	10	6 to 12
	Anonychomyrma WT. A	15	1 to 12
	Pheidole sp. AC	19	1 to 12
	Rhytidoponera victoriae	23	2 to 12
	Pheidole sp. AB	**26**	1 to 12
1-2 & 12-16	*Pheidole sp. AQ*	7	10 to 16
	Pheidole sp. AA	13	1 to 13
	Anonychomyrma WT. A	18	1 to 12
	Anonychomyrma WT. C	21	8 to 16
	Pheidole sp. AC	25	1 to 12
	Rhytidoponera purpurea	**28**	1 to 10
3.5-6 & 8-11	*Anonychomyrma WT. A*	6	1 to 12
	Pheidole sp. AC	11	1 to 12

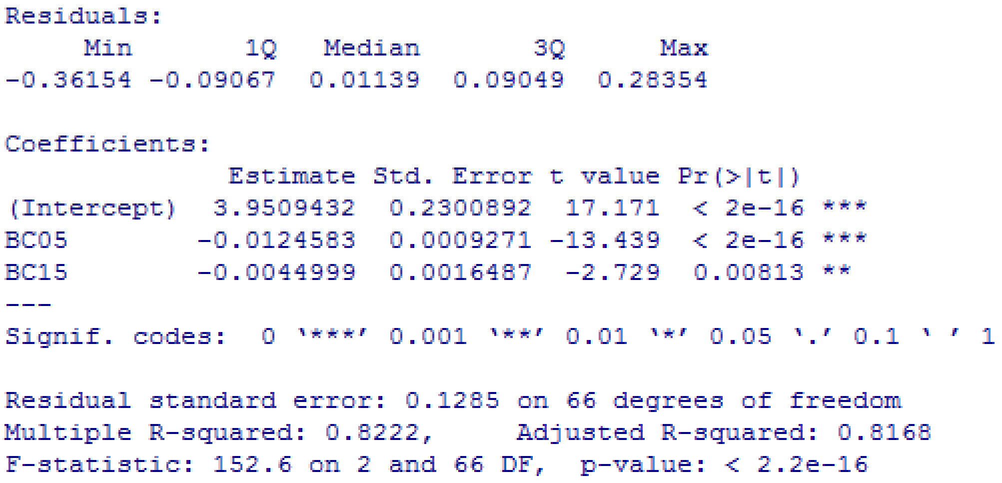
Elevational groups (‘00m a.s.l.)	Species	Cumulative contribution (%)	Elevational range ('00 m a.s.l.)
	Pheidole sp. AF	16	6 to 12
	Pheidole sp. AB	21	1 to 12
	Pheidole sp. AA	25	1 to 13
	Rhytidoponera victoriae	**29**	2 to 12
3.5-6 & 12-16	*Pheidole sp. AQ*	8	10 to 16
	Anonychomyrma WT. A	14	1 to 12
	Pheidole sp. AC	19	1 to 12
	Pheidole sp. AA	23	1 to 13
	Anonychomyrma WT.C	27	8 to 16
	Anonychomyrma WT. B	**31**	1 to 12
8-11 & 12-16	*Pheidole sp. AQ*	9	10 to 16
	Pheidole sp. AC	16	1 to 12
	Pheidole sp. AF	22	6 to 12
	Pheidole sp. AB	27	1 to 12
	Rhytidoponera victoriae	31	2 to 12
	Anonychomyrma WT. C	**36**	8 to 16

Appendix 5.3. Raw data output for the computation of the Dimension 1 versus environmental variable best sub-set regression model (Table 5.5).

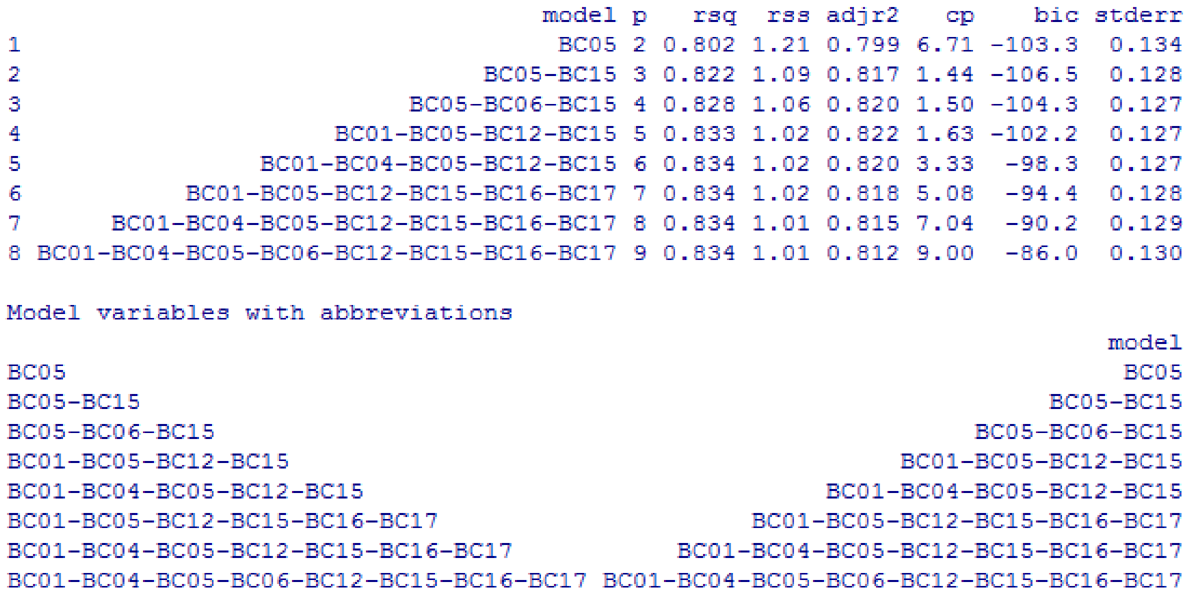


```
Residuals:
    Min      1Q  Median      3Q     Max 
-7.8632 -2.3048 -0.3487  1.5337 10.2249 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept) -30.9735     4.8133  -6.435 1.53e-08 ***
BC01          2.2058     0.2299   9.597 3.31e-14 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

Residual standard error: 3.619 on 67 degrees of freedom
Multiple R-squared: 0.5789,	Adjusted R-squared: 0.5726 
F-statistic:  92.1 on 1 and 67 DF,  p-value: 3.306e-14 

                                   model p   rsq rss adjr2   cp   bic stderr
1                                   BC01 2 0.579 878 0.573 2.96 -51.2   3.62
2                              BC01-BC15 3 0.590 853 0.578 3.09 -48.9   3.60
3                         BC01-BC06-BC15 4 0.605 823 0.587 2.69 -47.2   3.56
4                    BC01-BC05-BC06-BC15 5 0.609 815 0.585 4.08 -43.6   3.57
5               BC01-BC04-BC05-BC06-BC15 6 0.624 784 0.594 3.73 -42.0   3.53
6          BC01-BC04-BC05-BC06-BC15-BC17 7 0.624 784 0.587 5.71 -37.8   3.56
7     BC01-BC04-BC05-BC06-BC12-BC15-BC17 8 0.628 775 0.585 7.04 -34.3   3.57
8 BC01-BC04-BC05-BC06-BC12-BC15-BC16-BC17 9 0.628 775 0.579 9.00 -30.2   3.59
```

Appendix 5.4. Raw data output for the computation of the Dimension 2 versus environmental variable best sub-set regression model (Table 5.6).



```
Residuals:
     Min       1Q   Median       3Q      Max 
-0.36154 -0.09067  0.01139  0.09049  0.28354 

Coefficients:
              Estimate Std. Error t value Pr(>|t|)    
(Intercept)  3.9509432  0.2300892  17.171  < 2e-16 ***
BC05        -0.0124583  0.0009271 -13.439  < 2e-16 ***
BC15        -0.0044999  0.0016487  -2.729  0.00813 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

Residual standard error: 0.1285 on 66 degrees of freedom
Multiple R-squared: 0.8222,	Adjusted R-squared: 0.8168 
F-statistic: 152.6 on 2 and 66 DF,  p-value: < 2.2e-16 
```



```
                                             model p   rsq  rss adjr2   cp    bic stderr
1                                             BC05 2 0.802 1.21 0.799 6.71 -103.3  0.134
2                                        BC05-BC15 3 0.822 1.09 0.817 1.44 -106.5  0.128
3                                   BC05-BC06-BC15 4 0.828 1.06 0.820 1.50 -104.3  0.127
4                              BC01-BC05-BC12-BC15 5 0.833 1.02 0.822 1.63 -102.2  0.127
5                         BC01-BC04-BC05-BC12-BC15 6 0.834 1.02 0.820 3.33  -98.3  0.127
6                    BC01-BC05-BC12-BC15-BC16-BC17 7 0.834 1.02 0.818 5.08  -94.4  0.128
7               BC01-BC04-BC05-BC12-BC15-BC16-BC17 8 0.834 1.01 0.815 7.04  -90.2  0.129
8 BC01-BC04-BC05-BC06-BC12-BC15-BC16-BC17 9 0.834 1.01 0.812 9.00  -86.0  0.130

Model variables with abbreviations
                                                                                   model
BC05                                                                                BC05
BC05-BC15                                                                      BC05-BC15
BC05-BC06-BC15                                                            BC05-BC06-BC15
BC01-BC05-BC12-BC15                                                  BC01-BC05-BC12-BC15
BC01-BC04-BC05-BC12-BC15                                        BC01-BC04-BC05-BC12-BC15
BC01-BC05-BC12-BC15-BC16-BC17                              BC01-BC05-BC12-BC15-BC16-BC17
BC01-BC04-BC05-BC12-BC15-BC16-BC17                    BC01-BC04-BC05-BC12-BC15-BC16-BC17
BC01-BC04-BC05-BC06-BC12-BC15-BC16-BC17 BC01-BC04-BC05-BC06-BC12-BC15-BC16-BC17
```