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Understanding Patterns Of Endemic Dung Beetle (Coleoptera: Scarabaeidae: Scarabaeinae) Biodiversity In The Australian Wet Tropics Rainforest: Implications Of Climate Change

Thesis submitted by Marios Aristophanous (B.Sc) (GcertResMeth) 1st October 2014



Temnoplectron involucre Matthews, flightless subregional endemic species. Spec Uplands, Paluma, 900 m a.s.l., 25 / I / 2011.

For the degree of Doctor of Philosophy In the School of Marine and Tropical Biology James Cook University Townsville, Queensland Australia

STATEMENT OF SOURCES

Declaration

I, the undersigned, author of this work, declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

DEDICATION

This thesis is dedicated to my parents Aristos Costa Aristophanous and Chrystalla Charalambous Aristophanous,

"thank you"

and to the memory of my great-grandfather Kostas Xenophontos,

"grandad, I know now what you meant, and yes, I have built many homes"

Η παρούσα διατριβή είναι αφιερωμένη στους γονείς μου Άριστο Κώστα Αριστοφάνους και Χρυστάλλα Χαραλάμπους Αριστοφάνους,

«σας ευχαριστώ»

Και στη μνήμη του προπάππου μου Κώστα Ξενοφόντος,

«άπαππου, τωρά εκατάλαβα, και ναι, έχτισα πολλά σπίτια»

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Chapter 6

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THESIS ABSTRACT

Anthropogenic climate change is a major threat to global biodiversity, threatening many ecosystems and taxa with extinction. An understanding of the factors influencing species distribution and diversity is vital for assessing their vulnerability to climate change. This is particularly the case for tropical rainforest insects that constitute the bulk of all known biodiversity, provide many ecosystem services, and yet, remain poorly studied. Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are a keystone insect taxon of great ecological and economical importance. Their feeding and nesting behaviour contributes towards many ecological functions, such as the removal and recycling of animal waste. Thus, climate change induced alterations in dung beetle biodiversity have the potential to disrupt such ecosystem services, negatively impacting proper ecosystem functioning.

This thesis investigates the drivers of, and predicts the impacts of future climate change on, endemic dung beetle biodiversity in the Australian Wet Tropics (AWT) rainforest. Specifically, the aims of the thesis were to: (1) derive accurate estimations of dung beetle "realised" distributions and species richness within the AWT, (2) identify and understand patterns and drivers of dung beetle biodiversity in the AWT bioregion and (3) along elevational gradients, and (4) predict the impacts of climate change on the endemic dung beetles of the AWT.

Dung beetle distributions and patterns of biodiversity throughout the AWT were determined from standardised surveys and external databases. Targeted dung beetle surveys included dung-baited pitfall-traps across 20 sampling sites along four elevational gradients, between 2007 - 2009. The locality records from these surveys were supplemented with a large dung beetle database developed by Dr Geoff Monteith at the Queensland Museum.

As patterns of biodiversity arise due to the overlap of species distributions, an accurate estimation of the distributional extent of each species was required. The potential distribution of a species generated by a species distribution model (SDM) is often larger than that of its realised distribution; this is widely acknowledged in the literature but is rarely accounted for. In Chapter 3 (Aim 1) I quantified SDM over-prediction and derived accurate representations of species "realised" distributions and overall AWT dung beetle species richness, by using expert knowledge to clip "potential" species distributions to well known biogeographic limits. Potential distributions were, on average, 10 times larger than the realised distributions for flightless species and 1.2 times larger for winged species. A realised species richness model was generated by summing individual realised SDMs, which attained a higher correlation between observed and predicted, subregional and local species richness and composition, compared to the potential species richness model.

Using the realised species richness maps, I subsequently investigated patterns of dung beetle species richness and composition within well-known biogeographic subregions of the AWT (Chapter 4; Aim 2). Dung beetle subregional community structure has been influenced by historical rainforest refugia formed from climatic fluctuations of the Pleistocene. Subregions that maintained refugia during rainforest contraction events harboured distinct, species rich dung beetle assemblages, with subregionally endemic flightless species. Patterns of AWT β -diversity were due to species turnover, rather than nestedness, indicating species replacement between subregions. Patterns in AWT dung beetle species richness were mostly driven by a positive relationship with mammal species richness, indicating the importance of a functional trophic relationship. However, both dung beetle and mammal species richness were driven by similar responses to historical habitat stability (refugia) and climate variables associated with refugia, such as cooler temperatures and decreased seasonality.

As rainforest refugia occurred at higher elevations I then investigated patterns of dung beetle biodiversity along elevational gradients using standardised sampling techniques (Chapter 5; Aim 3). Isolation, persistence, and speciation within upland refugia resulted in distinct, cool-adapted, upland species assemblages that are generally more species rich, more abundant, have greater biomass, and have narrower elevational ranges compared to lowland assemblages. Greater mammal species richness and biomass at higher elevations, also associated with rainforest refugia, contributed towards the persistence and increased abundance and biomass of upland dung beetle species by providing greater dung resources. On some mountaintops these resources were dominated by high elevation, subregionally endemic, small bodied, flightless species that competitively excluded other species, thus decreasing species richness and diversity at higher elevations. Upland species have narrow elevational ranges indicating adaptation to the cool upland conditions with intolerance to high temperatures making them particularly vulnerable to future climate change.

To investigate the effects of climate change on the endemic dung beetles of the AWT (n = 70) I used SDMs to project their future distribution and population size at 10year time steps up to 2085, using the future climate projections of the latest four Representative Concentration Pathways (Chapter 6; Aim 4). By 2085, 57 (81%) of the dung beetle species modelled are predicted to become threatened by losing \geq 50% of their current distribution area. Additionally, 62 (88%) species are projected to lose \geq 50% of their current population size, based on worst-case concentration pathway RCP8.5. Dung beetle species richness within the AWT is predicted to drastically decrease with current species hotspots losing up to 33 species by 2085 based on RCP8.5. These results are expected to be exacerbated by taking into consideration climate change induced mammal (dung beetle food resource providers) defaunation, as predicted by other studies.

Decreases in dung beetle abundance and species richness are predicted to alter the many ecosystem services provided by dung beetles, thus negatively influencing the overall ecosystem health of the AWT rainforest. However, the results of this study also suggest that the negative impacts of climate change on dung beetle diversity can be reduced by increasing worldwide use of green technology and applying climate policies, as predicted by emission pathway RCP3-PD.

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LIST OF ABBREVIATIONS

AMT	Annual Mean Temperature
AP	Annual Precipitation
AU	Atherton Uplands
AUC	Area Under the receiver-operating characteristic Curve
AWT	Australian Wet Tropics
bc	bioclim
BIC	Bayesian Information Criterion
cm	centimetre
CRC	Cooperative Research Centre
CSIRO	Commonwealth Scientific and Industrial Research Organisation
CTBCC	Centre for Tropical Biodiversity and Climate Change
CU	Carbine Uplands
GAMM	Generalised Additive Mixed Models
GARP	Genetic Algorithm for Rule-set Production
GBM	Dr Geoff B. Monteith
GCM	Global Climate Model
hs	habitat stability
IndVal	species Indicator Value
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
JCU	James Cook University
km	kilometre
m a.s.l.	metres above sea level
Maxent	Maximum Entropy (modelling software)
maxTWP	maximum Temperature of the Warmest Period
minTCP	minimum Temperature of the Coldest Period
ml	millilitre
mm	millimetre

NMDS	Non Metric Multi Dimensional Scaling
NQ	North Queensland
NS	Not Significant
NT	Northern Territory
NVIS	National Vegetation Information System
PgC yr-1	petagrams of carbon per year
PHT	Pleistocene/Holocene Transition
popn.	population
ppm	parts per million
PS	Precipitation Seasonality
PWQ	Precipitation of the Wettest Quarter
QLD	Queensland
RCP	Representative Concentration Pathway
SAR	Species-Area Relationship
SDM	Species Distribution Model
SE	Standard Error
SEM	Structural Equation Model
spp.	species (plural)
SRES	Special Report on Emissions Scenarios - IPCC
S-SDM	Stacked-Species Distribution Model
SU	Spec Uplands
TS	Temperature Seasonality
ULR	Unique Locality Record
W m-2	Watts per metre squared
WU	Windsor Uplands
ybp	years before present

1.1 Patterns of biodiversity

Living organisms are not evenly distributed across the Earth's surface, nor can they be found in equal abundances and similar species assemblages (Ricklefs and Schluter 1993a, Gaston 2000). Thus, different geographical areas vary in regards to the total number of species (species richness), the variety of coexisting species (species composition) and the relative abundance of each species (assemblage structure). Such measurable attributes in the spatial variation of communities are herein referred to as patterns of biodiversity.

Attempts to understand the complexity of patterns of biodiversity and their drivers have focused on some of the more general spatial patterns of species richness along environmental gradients (Gaston 2000). Variation of species richness along latitudinal and elevational gradients have by far received the most attention (Pianka 1966, Stevens 1989, Rohde 1992, Stevens 1992, Gaston 1996, Koleff and Gaston 2001, Lomolino 2001, Willig et al. 2003, Kraft et al. 2011). The understanding of the processes and mechanisms that give rise to the patterns associated with these gradients, are expected to increase our understanding about the distribution of biodiversity on a global scale (Lomolino 2001, Willig et al. 2003). Latitudinal and elevational gradients in species richness are also important for climate change research. As local climatic conditions differ along latitude and elevation, organisms will experience and respond to different climatic regimes (Hodkinson 2005). Thus, the study of species biology, ecology, distribution, and diversity along these gradients offers insights as to the likely responses of species and communities to climate change (Hodkinson 2005). Understanding patterns of biodiversity also has important implications for conservation planning and management. By identifying and understanding why different areas possess more, rare, endemic, or threatened species,

scarce conservation effort and resources can be allocated accordingly (Srivastava and Vellend 2005).

1.2 What drives patterns of biodiversity?

"This exceeding productiveness [of Cerambycidae beetles] was due in part no doubt to some favourable conditions in the soil, climate, and vegetation, and to the season being very bright and sunny, with sufficient showers to keep everything fresh" (Wallace 1869).

Alfred Russel Wallace, while travelling in the Malay Archipelago attributed the high species richness of cerambycid beetles he caught within a square mile of "jungle" to a combination of favourable abiotic and biotic factors. Since then, more than 30 hypotheses have been proposed to account for patterns of species richness, especially along latitudinal gradients, and include, among others: area, evolutionary speed, environmental stability, productivity, biological interactions, and niche conservatism. These hypotheses have been reviewed elsewhere (Pianka 1966, Rhode 1992, Willig et al. 2003, Wiens and Donoghue 2004) and it is not within the scope of this section to review them again.

Ultimately, in order to understand current patterns of biodiversity it is necessary to understand the processes by which species and individuals are added to, or removed from a given locality. These are dispersal, recruitment, speciation, mortality, and extinction (Ricklefs 1987, Ricklefs and Schluter 1993b, Wiens and Donoghue 2004). The distribution of species is of fundamental importance as it is the overlap in distributional range that gives rise to species richness. Dispersal influences species distribution, speciation and extinction (e.g. immigration, emigration, post-dispersal isolation resulting in allopatric speciation or extirpation). Furthermore, in order for a species to be present at any given location and sustain an adequate population size it must be able to tolerate the abiotic (e.g. temperature) and biotic (e.g. competition, predation, parasitism) conditions of that location and the necessary resources for its survival must be present. Thus elements of the niche and population dynamics need to be taken into consideration (Hutchinson 1957).

1.3 Climate change and its threats to biodiversity

Anthropogenic climate change is a major threat to global biodiversity (Miles et al. 2004, Thomas et al. 2004, Maclean and Wilson 2011, Cahill et al. 2013, IPCC 2014, Jaeschke et al. 2014). Atmospheric concentrations of greenhouse gases, including CO₂, methane, and nitrous oxide have increased to unprecedented levels (IPCC 2013). Burning of fossil fuels and land use change are primarily responsible for a 40% increase in atmospheric CO₂ concentrations since pre-industrial times (IPCC 2013). This is disturbing the Earth's climate system and resulting in, among other things, increases in temperature, altered rainfall regimes, sea level rise, and ocean acidification (IPCC 2013). For example, global average temperature has increased by 0.85 °C since 1850 (IPCC 2013), with a notable increase in extreme temperature and rainfall events in recent years (Min et al. 2011, Coumou and Rahmstorf 2012, Coumou and Robinson 2013, Coumou et al. 2013, Zhang et al. 2013).

Physiological intolerance to altered climatic regimes and extreme weather events will alter species distributions, phenology, and biotic interactions thus increasing extinction riskfor some species in some localities, and favouring others(Walther et al. 2002, Somero 2010, Walther 2010). Poleward and upslope shifts in distribution have been predicted to take place as species attempt to track changes in climate to remain within climatically suitable environments (La Sorte and Thompson 2007, Raxworthy et al. 2008, Zuckerberg et al. 2009, Buermann et al. 2011, VanDerWal et al. 2013), and evidence of this has already been documented (Chen et al. 2009, Walther 2010, Chen et al. 2011, Menéndez et al. 2014). A reduction in climatically suitable space leads to contractions in distribution resulting in decreases in population size and ultimately decreases in species richness, as species become locally extirpated or extinct (Walther 2010, Maclean and Wilson 2011, Fordham et al. 2012, Ihlow et al. 2012, Urban et al. 2012). Alterations in biotic interactions may induce cascade effects resulting from negative impacts on, or the spatial/temporal-mismatch between, trophically interacting species, thus altering food web dynamics (Koh et al. 2004, Dyer and Letourneau 2013, Albouy et al. 2014, Moir et al. 2014), e.g. between dung beetles and mammals (Nichols et al. 2009, Coggan 2012), butterflies and their host plants (Schweiger et al. 2008, Schweiger et al. 2012), predators and their prey (Pearce-Higgins et al. 2010).

Although greater increases in temperature are anticipated in temperate regions, tropical species are regarded to be at a greater risk from climate change as they already inhabit warm environments close to their upper thermal tolerance, compared to species inhabiting cooler higher latitudes (Colwell et al. 2008, Deutsch et al. 2008, Diamond et al. 2012). Tropical montane fauna are further at risk due to narrower physiological tolerances and steeper elevational temperature gradients that effectively "compress" species ranges (Janzen 1967, Colwell et al. 2008, Raxworthy et al. 2008).

Species distribution models (SDMs) are increasingly being used to investigate the impacts of climate change on species distributions and diversity (Hijmans and Graham 2006, Araújo and New 2007, Thuiller et al. 2008, Anderson 2013). SDMs predict the distribution of species within a region by establishing a relationship between the occurrences of a particular species and the environmental variables from those occurrences (Elith et al. 2006, Franklin 2009). As SDMs are commonly generated using climatic variables, the predicted distributions are also known as the species' bioclimatic envelope or climatic niche (Nix 1986, Pearson and Dawson 2003). The future distribution of species can thus be projected based on future climate change scenarios and studies have shown that this approach is likely to reflect realistic changes (Parmesan and Yohe 2003, La Sorte and Thompson 2007, Maclean and Wilson 2011).

1.4 The Australian Wet Tropics and threats from climate change

The Australian Wet Tropics (AWT) comprises the largest extent of rainforest within Australia (\sim 7,200 km²) and is a narrow strip of land (\sim 470 km long × \sim 80 km wide) situated in north-eastern coastal Queensland between Townsville and Cooktown (Figure 2.1). The landscape of the AWT is characterised by a series of disjunct mountains with approximately one-third of the bioregion being higher than 600 m

a.s.l., with the highest peak, Mt Bartle Frere, reaching 1622 m a.s.l. (Rainforest Conservation Society of Queensland 1986, Stork et al. 2008). Mean annual temperatures range between 18 - 26 °C and annual rainfall is generally high (2,000 - 8,000 mm year⁻¹) with approximately 75–90% of precipitation falling during the austral summer (wet-season) between December and March (Rainforest Conservation Society of Queensland 1986, Stork et al. 2008).

The AWT rainforest is of Gondwanan origin and became isolated after Australia broke away from Antarctica and drifted into the tropics, and thus contains relictual flora and fauna with high levels of endemism (Rainforest Conservation Society of Queensland 1986). Although the AWT represents only a fraction (0.1%) of Australia's total land area, it is regarded as the most biologically diverse region within the continent harbouring large proportions of its species. For example, 25% of the plant genera of Australia, 30% of marsupial species, 60% of bat species, and 62% of butterfly species (Rainforest Conservation Society of Queensland 1986, Stork et al. 2008). The evolutionary uniqueness and global importance of the flora and fauna of the AWT ensured its world heritage listing in December 1988 (Valentine and Hill 2008).

Several lines of evidence ranging from charcoal deposits (Hopkins et al. 1993), fossilised pollen (Kershaw and Nix 1988), and marine cores (Kershaw 1994) demonstrate that the rainforests of the AWT have contracted and expanded during climatic changes associated with the glacial cycles of the Quaternary. Recently, paleoclimatic fluctuations have been modelled giving rise to more accurate reconstructions of paleovegetation dynamics and possible refugial areas and dispersal corridors within the AWT (Graham et al. 2006, Hilbert et al. 2007, VanDerWal et al. 2009a). The biogeographic and refugial history of the regions rainforest, along with species distributions and patterns of endemism have been used as a basis to compartmentalise the AWT into biogeographically distinct subregional units (Winter et al. 1984, McDonald 1992, Williams et al. 1996, Williams et al. 2008a, Yeates and Monteith 2008). Currently a total of 46 subregions are recognised within the AWT, with 33 of these containing significant portions of rainforest (Figure 2.1).

Although the AWT rainforests are protected from logging and development under the World Heritage Act, they are currently threatened from climate change (Hilbert et al. 2001, Hilbert 2008, Williams et al. 2008b). For example, AWT high elevation simple-notophyll and simple-microphyll vine fern forests are predicted to decrease by 60% with a temperature rise of 1 °C combined with a 10% decrease in precipitation (Hilbert et al. 2001). These forests may also be further threatened by rising cloud layers that are responsible for up to 60% of the monthly water input of highland rainforests (>1000 m a.s.l.) in the AWT (McJannet et al. 2007). Similarly, Williams et al. (2003) demonstrate that a 1 °C increase in temperature will lead to significant decreases in the core distributional area of almost all 65 regionally endemic vertebrates in the AWT, with 30 species predicted to completely lose their core environment with an increase of 3.5 °C. With a similar increase in temperature, 74% of rainforest birds of north-eastern Australia are predicted to become threatened due to decreases in their population size (Shoo et al. 2005).

The insects of the AWT are also predicted to become threatened by climate change with a large proportion (40%) of schizophoran flies projected to become extinct with a 3.5 °C increase in temperature (Wilson 2010). Likewise, 88% of flightless Carabidae ground beetle species are projected to lose 80% of their current population size under scenario SRES A2 (Staunton 2014, Staunton et al. 2014). Insects constitute the bulk of all known biodiversity and provide many ecosystem services (Wilson 1987). Thus, alterations in their distributions, abundance and species richness arising from climate change will have negative impacts on the proper functioning of the AWTs rainforests. An insect taxon of great ecological importance is the dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae; see below). As dung beetles depend on mammalian excrement, climate change may not only affect them through physiological constraints, but also by negatively influencing their resource providers, i.e. mammals (see Williams et al. 2003), instigating trophically-linked extinction cascades (Nichols et al. 2009). An investigation into the impacts of climate change on the dung beetles of the AWT is thus warranted.

1.5 Dung beetles

The term "dung beetle" is used to refer to dung feeding beetles of the families Scarabaeidae (subfamilies Aphodiinae and Scarabaeinae) and Geotrupidae (subfamily Geotrupinae) (Scholtz et al 2009). The Geotrupinae and Aphodiinae show greater species richness in cooler temperate regions, while the Scarabaeinae reach their greatest diversity in the tropics (Hanski and Cambefort 1991a, Scholtz et al 2009). Although Geotrupinae, Aphodiinae, and Scarabaeinae feed on dung, they have distinct breeding behaviours. Aphodiinae beetles, also referred to as dwellers or endocoprids, lay their eggs within the dung where the emerging larvae feed, mature, and pupate (Hanski and Cambefort 1991a). Geotrupinae may create burrows and provision their larvae with dung, but they do not provide parental care (Scholtz et al 2009). The Scarabaeinae have evolved more complex breeding and nesting behaviours along with a high level of parental care (Halffter and Edmonds 1982). Scarabaeinae tunnellers or paracoprids dig a tunnel below the dung and transport dung into the bottom of the burrow, sometimes forming a chamber (Halffter and Matthews 1966, Halffter and Edmonds 1982, Hanski and Cambefort 1991a). Within the burrow, beetles may either feed on the dung as part of their maturation-feeding period, compact the dung into a brood-mass where an egg is laid, or "mould" the dung into a brood-ball where an egg is laid (Halffter and Edmonds 1982). Scarabaeinae rollers or telocoprids form a ball of dung and roll it some distance away from the initial source where it is buried, and similar to tunnellers, may be used for adult feeding or oviposition (Halffter and Edmonds 1982). This thesis focuses solely on the Scarabaeinae, thus, any hereafter mention of dung beetles will refer to beetles belonging to the subfamily Scarabaeinae unless otherwise stated.

The feeding and nesting behaviour of dung beetles contributes to many key ecological functions that provide valuable ecosystem services such as the removal and recycling of animal waste, soil conditioning and aeration, reduction of micro– and macro– invertebrate dung–breeding parasites, and secondary seed dispersal (Spector 2006, Nichols et al. 2008). If these services are not performed ecosystems and human populations will be negatively affected. For example, in Australia, the native dung beetle fauna are not attracted to the dung of introduced ruminants such as cattle, as
they co-evolved with smaller and drier marsupial droppings (Waterhouse 1974). When cattle were first introduced in Australia, this resulted in the retention and accumulation of millions of tons of cattle dung on the soil surface that led to the fouling of valuable pasture land, population explosions of dung breeding flies (mainly the blood-feeding buffalo fly *Haematobia irritans exigua* and the bush fly *Musca vetustissima*), and an increase in livestock enteric parasites such as strongylene worms, all of which use dung as part of their incubation period (Waterhouse 1974, Bornemissza 1976). This resulted in decreased pasture and cattle productivity (Waterhouse 1974, Bornemissza 1976). Due to this, a total of 43 dung beetle species from Africa, Europe, and Hawaii were introduced into Australia between 1968 and 1984 for the biological control of cattle dung, dung-breeding flies, and cattle parasites by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) under the Australian Dung Beetle Program (Bornemissza 1976, Edwards 2007). A total of 23 species have now established on the continent where they successfully perform their ecosystem services (Edwards 2007).

The above not only illustrates the negative effects resulting from the absence of dung beetles in an ecosystem but also contributed towards the apparent neglect of native Australian dung beetles, that were deemed "economically less important", and have thus remained biologically and ecologically less studied (Doube et al. 1991). Despite this, Australian native dung beetles are taxonomically well known comprising a total of ~ 438 species in four tribes and 20 genera (Matthews 1972, 1974, 1976, Scholtz 2009a, Monteith pers. comm.). Also, dung beetles of the AWT have been taxonomically studied as a result of arthropod surveys initiated by the Queensland Museum, Brisbane (Monteith 1982, 1985a, b, 1989, Monteith and Davies 1991, Monteith 1995, Yeates et al. 2002, Yeates and Monteith 2008). A total of 176 dung beetle species are known from within the AWT bioregion that encompasses both dryopen forests and wet-closed rainforests (Matthews 1972, 1974, 1976, Monteith pers. comm.). A total of 92 species occur within the rainforests of the AWT, and as rainforests are restricted to the AWT, a high proportion (80%) of species are endemic to this habitat type. In addition, 35 rainforest dung beetle species are flightless and are restricted to one or a few subregional units within the AWT. As the majority of the above mentioned studies were taxonomic in nature, there have been no attempts in investigating the environmental factors influencing the distribution, diversity, and abundance of the AWT rainforest endemic dung beetles.

1.6 Thesis aims and structure

Understanding the drivers of patterns of biodiversity is basal to ecology and conservation science (Gaston 2000). Insects, and in particular beetles, constitute the bulk of all known biodiversity and carry out many ecosystem services (Wilson 1987). Dung beetles are especially important as they recycle animal waste and contribute to soil fertility and conditioning. The loss or restructuring of dung beetle assemblages arising from climate change and/or altered resource (dung) availability has the potential to disrupt the ecosystem services provided by dung beetles, threatening the proper ecosystem functioning of the AWT. Thus, this thesis investigates the effects of climate change on the native dung beetles endemic to the AWT rainforests. However, before attempting to predict how patterns of dung beetle diversity may change, identification and understanding of the current patterns and drivers of dung beetle distributions and patterns of biodiversity is required.

The overall aims of this thesis are to (1) produce accurate estimations of "realised" species distributions and richness for the AWT endemic rainforest dung beetles; (2) identify and understand the patterns and drivers of dung beetle biodiversity within the AWT and (3) along elevational gradients; and (4) predict the impacts of climate change on dung beetles within the AWT. Each aim forms the basis of the four data chapters (Chapters 2 - 5) that are brought together by the general thesis introduction (Chapter 1) and discussion (Chapter 6).

1.6.1 Aim **1.** Derive accurate estimations of "realised" species distributions and richness for the AWT endemic rainforest dung beetles (Chapter 3).

As patterns of biodiversity arise due to the overlap of species distributions, an estimation of the distributional extent of each species is required. To achieve this, I

generate Species Distribution Models (SDMs) for AWT endemic dung beetles based on relationships between species locality data and spatial layers of climatic variables using Maxent species distribution modelling software.

The potential distribution of a species generated by an SDM is often larger than that of its realised distribution. Although this over-prediction is widely acknowledged in the literature it is rarely accounted for. I quantify species distributional overprediction of "potential" SDMs and compare over-prediction between species with varying dispersal abilities and range sizes. I demonstrate the significance of distributional over-prediction of individual species models and the cumulative effect of summing potential distributions to estimate species richness.

Several studies have argued that more accurate "realised" distributions can be obtained by clipping potential distributions to e.g., biogeographic subregions or by expert polygons to manually remove the over-prediction – areas where the species is known to be absent based on expert knowledge and extensive sampling. I demonstrate the value of expert scrutiny and evaluation of SDM studies in deriving an accurate estimate of species "realised" distributions. By overlaying (i.e. summing) individual realised distributions a spatial estimate of AWT dung beetle realised species richness is generated, thus actualising Aim 1.

1.6.2 Aim **2.** Identify and understand patterns and drivers of dung beetle biodiversity within the AWT (Chapter 4).

Identifying where species are located and understanding why they are there is basal to the study of ecology and conservation science. I identify dung beetle patterns of species richness and composition and their drivers within the AWT bioregion.

The realised species richness map generated in Chapter 3 is used to identify patterns of dung beetle species richness and composition at a broad continuous spatial scale and within well-known biogeographic subregions of the AWT. I then investigate the direct and indirect effects of historical and contemporary drivers on patterns of species richness and the environmental correlates of species composition.

1.6.3 Aim **3.** Identify and understand patterns and drivers of dung beetle biodiversity along elevational gradients within the AWT (Chapter 5).

I use baited pitfall traps to collect standardised data along four elevational gradients within the AWT to identify patterns of species richness, abundance, biomass, composition, and elevational range limits. These patterns are then linked to environmental variables and along with the findings of Chapter 4, a holistic understanding of patterns of AWT dung beetle biodiversity is reached.

1.6.4 Aim **4.** Predict the impacts of climate change on the dung beetles of the AWT (Chapter 6)

Anthropogenic climate change is a major threat to global biodiversity, threatening many ecosystems and taxa with extinction. The impact of climate change on AWT dung beetles is predicted by projecting current species distributions to the year 2085 based on four Representative Concentration Pathways (RCPs). I quantify changes in distribution and population size for each species and for the assemblage as a whole.

CHAPTER 2. GENERAL METHODS

This thesis uses dung beetle data that I collected from 20 sampling sites within the AWT over a period of two years (2007 - 2009), and from a dung beetle database maintained by Dr Geoff Monteith of the QLD Museum, Brisbane. Chapters 3, 4 and 6 employ Species Distribution Modelling (SDM). SDMs rely on unique locality records of species presence. Therefore, these chapters combine locality records from my sampling and from the dung beetle database. Chapter 5 uses only data from my sampling. Thus, to avoid repetition, this section describes my sampling sites and design, outlines the dung beetle database, and explains SDM procedures. The following sections will be referred to in the *Methods* of subsequent chapters. However, methods specific to each chapter will be described only in the chapter in question.

2.1 Study sites

This thesis focuses on the rainforest of the AWT (Figure 2.1; see section 1.3). Four elevational gradients were sampled with sites (n = 20) located at approximately every 200 m increment in elevation, where possible (Figure 2.1; Table 2.1). The Carbine gradient spanned the entire mountain range from 100 m a.s.l. to its summit, 1200 m a.s.l.. The Atherton range is a complex series of mountains, and although 1000 m a.s.l. represented the peak within the sampled subregion, other subregions in the Atherton complex with mountains higher than 1000 m could not be sampled due to logistical reasons. The Spec and Windsor gradients were sampled from 350 to 1000 m a.s.l. and from 900 to 1300 m a.s.l. respectively, due to the absence of rainforest below these elevations. These sites were strategically selected so that approximately 95% of "climatic space" within rainforest habitat of the AWT bioregion was sampled as sampling took place along elevational gradients that spanned the latitudinal range of the AWT (Figure 2.1). The size of predicted refugia varied between these subregions

with Atherton having the largest refugium followed by Carbine and Spec, and with Windsor having the smallest predicted refugium (VanDerWal et al. 2009a).



Figure 2.1. The Australian Wet Tropics (AWT) bioregion showing the location of biogeographic subregions (dark grey outline). The current extent of rainforest is shaded in green. Filled black circles indicate location of sampling sites. Well-sampled subregions are circled (see section 3.3.1). The inset shows the location of the AWT within Australia.

Subregion	Site code	Elevation (digital)	Elevation (category)	Latitude (decimal)	Longitude (decimal)	Vegetation type
		(m a.s.l.)	(m a.s.l.)			
Spec	SU35	334	350	-19.0148	146.2654	Notophyll Vine Forest
Spec	SU6	671	600	-19.0026	146.2415	Medium Open Forest with regenerating rainforest understory
Spec	SU8	834	800	-19.0113	146.2214	Notophyll Vine Forest
Spec	SU10	950	1000	-19.0038	146.2093	Notophyll Vine Forest
Atherton	AU1	80	100	-17.7170	145.8594	Complex Mesophyll Vine Forest
Atherton	AU2	180	200	-17.6605	145.8737	Complex Mesophyll Vine Forest
Atherton	AU4	428	400	-17.6093	145.7664	Complex Mesophyll Vine Forest
Atherton	AU6	630	600	-17.6707	145.7167	Notophyll Vine Forest
Atherton	AU8	840	800	-17.6002	145.6346	Notophyll Vine Forest
Atherton	AU10	930	1000	-17.7007	145.5245	Notophyll Vine Forest
Carbine	CU1	115	100	-16.4688	145.3264	Mesophyll Vine Forest
Carbine	CU2	234	200	-16.4711	145.3210	Mesophyll Vine Forest
Carbine	CU4	440	400	-16.5329	145.3727	Mesophyll Vine Forest
Carbine	CU6	656	600	-16.5776	145.3057	Notophyll Vine Forest
Carbine	CU8	820	800	-16.5864	145.2976	Notophyll Vine Forest
Carbine	CU10	1016	1000	-16.5558	145.2784	Notophyll Vine Forest
Carbine	CU12	1210	1200	-16.5126	145.2705	Microphyll Fern Forest
Windsor	WU9	940	900	-16.2848	145.0841	Notophyll Vine Forest
Windsor	WU11	1071	1100	-16.2591	145.0438	Notophyll Vine Forest
Windsor	WU13	1280	1300	-16.2353	145.0088	Microphyll Fern Forest

Table 2.1. Characteristics of sampling sites. Vegetation types follow Webb (1978)and Specht (1970). GPS setting – WGS84, decimal degrees.

2.2 Sampling design

At each site (n = 20) a total of six pitfall traps (hereafter referred to as traps) were placed 15 m apart (Davis et al. 1999) under shady understorey conditions. Traps consisted of two round plastic food containers (11 cm diameter, 800 ml capacity) placed half way into the soil with one container inside the other so as to avoid soil disturbance upon servicing. Soil was mounded up to the top lip of the trap so beetles could walk freely up into the trap. This also protected against flooding by rain and so over-spilling of the preservative and subsequent loss of specimens. Phosphate buffered formaldehyde (4%) was used as a killing agent and preservative as it has a slower evaporation rate than other preservatives (Aristophanous 2010).

At each site, four traps were baited with ~ 60 ml (~ 50 mm diameter) of fresh Agile Wallaby (Macropus agilis Gould) dung and two traps were not baited as controls. Dung was wrapped in porous Chux [®] cleaning cloth and hung on top of the trap with a barbeque skewer. In order to protect the traps from mammal interference and in particular Giant White-tailed Rats (Uromys caudimaculatus Krefft), a ring of aviary mesh (mesh gap 25×25 mm; the largest dung beetle species in the AWT rainforests has a body length range of 15 - 18 mm) was placed around the trap. A thin metal (ZincAL) lid protected the trap from rainfall (Figure 2.2; Aristophanous 2010). Traps at all sites were serviced (i.e. cleared and re-baited) on an approximately monthly basis for a period of two years (May 2007 – May 2009; see Appendix 1 – 4 for dates). All traps remained "open" until the next sampling-trip. Sampling was conducted under permit WITK05468508 granted from the Environmental Protection Agency, Queensland Parks and Wildlife Service, Australia. I identified all dung beetle specimens to species level using taxonomic keys (Matthews 1972, 1974, 1976, Matthews and Stebnicka 1986, Storey and Weir 1990, Reid 2000, Reid and Storey 2000, Storey and Monteith 2000), with initial help and tutoring from Dr Geoff B. Monteith (GBM) of the Queensland Museum, Brisbane, and an AWT dung beetle reference collection (loan number: LEN-2214) provided by the museum. Subsets of specimens of which I identified were later taxonomically confirmed by GBM. However, I take full responsibility for all taxonomic identifications. Dung beetle voucher specimens (pinned and labelled) and all dung beetle specimens (preserved in vials with ethanol) from this study are deposited at the Centre for Tropical Biodiversity and Climate Change, James Cook University, Townsville.

2.3 Dung beetle database

The dung beetle database included results from targeted dung beetle collecting throughout the AWT using baited pitfall traps, flight intercept traps and litter extractions over twenty five years (1985-2000) under funding to GBM from the Wet Tropics Management Authority, the Australian Biological Resources Study, and the Rainforest CRC. To this database were added the AWT dung beetle holdings of the

Australian Museum (Sydney), CSIRO Australian National Insect Collection (Canberra), Museum of Victoria (Melbourne), Tasmanian Museum (Hobart), NT Department of Primary Industry, Fisheries and Mines (Darwin) and the Queensland Department of Agriculture, Fisheries and Forestry (Brisbane). These external museum datasets were validated by GBM under funding from the Commonwealth Department of Environment and Heritage. All literature records for AWT dung beetles were compiled and added to the database by GBM. Only records after the year 1970 were retained for this study to ensure record reliability. I examined all remaining records to detect geo-referencing errors.

Only native dung beetle species that are endemic to the AWT and known to occur within rainforest habitat were used in this study. Due to single locality records, reliable distribution models (see below) could not be fitted for three species (*Pseudignambia NQ15, P. NQ13, P. NQ16*) and these were removed from further analyses. The final version of the database totalled 3088 unique presence-only records for 70 species, of which 41 are winged and 29 are flightless. The code numbers used for undescribed species (e.g. NQ15, etc) are taken from a provisional system devised by GBM and Dr Tom A. Weir that is used for uniformity by most Australian museums. A recent revision of *Onthophagus millamilla* Matthews by Monteith & Storey (2013) narrows its status to that of an AWT rainforest endemic but this was too late for its inclusion in the analysis.



Figure 2.2. Pitfall trap with protective caging and cover placed on-top of a manually

constructed soil mound to prevent interference from mammals and dilution and/or overspilling from precipitation and surface runoff.

2.4 Species distribution modelling (SDM)

2.4.1 Potential species distributions

Models predicting the environmental suitability of each species across the AWT were generated using a maximum entropy approach (Maxent; Phillips et al. 2006) with default settings (Phillipsand Dudík 2008). This approach was preferred since it has been found to consistently outperform other distribution modelling methods (Elith et al. 2006). Maxent utilises presence-only data and statistically relates species records to a set of environmental variables in order to predict the suitability for the species (Elith et al. 2011). Presence only modelling methods can be subject to sampling bias (Yakulic et al. 2013). Thus, to account for any potential bias in the data-set a targetgroup background was used that consisted of the locations of all dung beetle species occurrence records, as recommended by Philips et al. (2009). By using this background, it is assumed that any sampling bias in occurrence records for a single species can also be observed in the background points, thus, in effect cancelling out the impact of any spatial sampling bias in the modelling exercise (Phillips and Dudik 2008, Elith and Leathwick 2009, Phillips et al. 2009). While it is undesirable to generate species distribution models for species with only a few (~5) ULR's (Hernandez et al. 2006, 2008), this was unavoidable in the present study as some flightless species have a restricted geographical distribution, and hence low ULR's. However, these localities, even though they are few, are representative of their entire range.Furthermore, Hernandez et al. (2006, 2008) have tested four different modelling methods (Bioclim, Domain, GARP, and Maxent) on their ability to predict the distribution of species with different sample sizes (ULR's), and found that Maxent produced the most consistently successful results for species with sample sizes as low as 5 ULR's, and thus their inclusion here is warranted. The climate variables used in this study were: (i) bc01 – annual mean temperature (AMT); (ii) bc04 – temperature seasonality (TS); (iii) bc05 - maximum temperature of the warmest period (maxTWP); (iv) bc06 – minimum temperature of the coldest period (minTCP); (v)

bc12 – annual precipitation (AP); (vi) bc15 – precipitation seasonality (PS); (vii) bc16 – precipitation of the wettest quarter (PWQ); and (viii) bc17 – precipitation of the driest quarter (PDQ). These variables were generated using the Climates package in R (VanDerWal et al. 2011) using monthly temperature and precipitation averages from Anuclim 5.1 software (McMahon et al. 1995). All surfaces were generated using, and aligned with, the ~ 250 m resolution digital elevation model (GEODATA 9-Second DEM, ver. 2; Geoscience Australia, www.ga.gov.au). Model performance was evaluated using the area under the receiver-operating characteristic curve (AUC) (Elith et al. 2006, Phillips et al. 2006, Franklin 2009). AUC ranges from 0 to 1, with values of 0.5 indicating that model fit is no better than random, values \geq 0.7 indicate "useful" models and values \geq 0.9 indicate models of "high" performance (Elith et al. 2006, Phillips et al. 2006, Franklin 2009).

The distribution model was converted from a continuous environmental suitability surface to a binary "suitable/unsuitable" or presumed "presence/absence" where the predicted environmental suitability values were above the species-specific "Balance training omission, predicted area and threshold value logistic threshold" obtained from the Maxent results output file. This threshold was used as it has produced realistic distributions for a variety of taxa within the AWT (VanDerWal et al. 2009b, Williams et al. 2010). The dung beetles of the AWT are highly habitat specific with changes between rainforest and open-forest assemblages occurring within tens of meters (Hill 1996). Since this study focuses on rainforest specialist species the probability of occurring outside rainforest boundaries was minimal. For this reason, the current extent of rainforest based on the National Vegetation Information System (NVIS) broad vegetation subgroups (Australian Government Department of the Environment and Water Resources, 2004) was used for masking the predicted species distributions. These distributions were treated as the "potential species distributions". Model post-processing was performed using the package SDM Tools (VanDerWal et al. 2012) in the R statistical program (R Development Core Team 2011).

2.4.2 Realised species distributions

The potential species distributions were examined by GBM, a dung beetle taxonomist, ecologist and authority on the AWT Scarabaeinae dung beetles whose expertise is based on many years of experience acquired from extensive sampling of the target taxon within the AWT region. For each species, subregions that the SDMs predicted to include suitable environment but where GBM was highly confident that the species was not present were removed. Predicted distributions were retained if there was any doubt that the species could occur there (Williams 2006, Williams et al. 2010). These distributions were treated as the "realised species distributions" (see Chapter 3). Distribution clipping was performed using the package SDMTools (VanDerWal et al. 2012) in the R statistical program (R Development Core Team 2011).

2.4.3 Species richness models

The individual potential and realised species distributions, based on environmental suitability values above the threshold, were converted to binary (0 = absence, 1 = presence) and summed to produce the potential and realised species richness models respectively. That is, the value of each cell of the species richness models equals the sum of all species that have a predicted distributional presence within that cell.

CHAPTER 3. ADVANCING REALISM IN SPECIES DISTRIBUTION MODELS THROUGH USE OF "REALISED", NOT "POTENTIAL" DISTRIBUTIONS

3.1 Introduction

Living organisms are not evenly distributed across the Earth's surface and consequently species richness and composition patterns result from the overlap of differing individual species distributions (Gaston 2000). Measures of species richness and species composition are commonly used to investigate the ecological determinants of biodiversity and to aid conservation planning (Rosenzweig 1995, Ricklefs 2004). Actual data of the extent of species distribution can be difficult to obtain, and quantifying species distribution limits a challenging task. Species distribution modelling (SDM) techniques allow the prediction of species' distributions using species locality data and a set of environmental layers (Elith et al. 2006). Binary (predicted presence/absence) distributions from a set of species can be summed to derive estimates of species richness and composition (Ferrier and Guisan 2006). This technique has been referred to as "predict first, ensemble later" (Ferrier and Guisan 2006) or "stacked species distribution models (S-SDMs)" (Guisan and Rahbek 2011).

Most SDMs are based solely on abiotic environmental variables, thus predicted distributions correspond to the fundamental or potential distribution, i.e. all the locations where a species could theoretically be present according to the set of environmental variables used in model creation (Hutchinson 1957, Pulliam 2000, Soberón and Peterson 2005). Because climatic variables are most commonly used in distribution modelling, the predicted distribution has also been referred to as the species' bioclimatic envelope or climatic niche (Pearson and Dawson 2003). SDMs tend to over-predict a species distribution because the potential distribution is inherently larger than the realised distribution (Anderson et al. 2003, Guisan and Thuiller 2005). Distribution over-prediction may be more likely for species with a

naturally restricted distribution and low dispersal abilities, such as small flightless species. Consequently, when potential distributions are summed the resulting potential species richness is an over-prediction of the number of sympatric species (Pineda and Lobo 2009).

In order to achieve realised species distributions, SDMs should ideally incorporate species-specific traits such as life-history characteristics, biotic interactions (e.g. resources, competition), and reliable absence data from environmentally favourable locations so as to account for biological, ecological, evolutionary and geographically dependent factors (Araújo and Luoto 2007, Heikkinen et al. 2007, Lobo 2008, Hanspach et al. 2010, Bateman et al. 2012, Bateman et al. 2013); however, such information is often unknown. In the absence of such data, several studies have argued that more accurate "realised" distributions can be obtained be clipping potential distributions to e.g., biogeographic subregions or by expert polygons to manually remove the over-prediction – areas where the species is known to be absent based on expert knowledge and extensive sampling (Williams et al. 2010, Staunton et al. 2014). Consequently, summing realised distributions, rather than potential distributions, should produce a more accurate representation of species richness, i.e. realised species richness.

Expert knowledge is regarded as "substantive information on a particular topic that is not widely known by others" and an expert as "someone who holds this knowledge and who is often deferred to in its interpretation" (Martin et al. 2012). However, experts may not necessarily exist for all taxa in any given region, and if they are available, incorporating their knowledge on a species-by-species basis is a time-consuming task (Seoane et al. 2005). Furthermore, this approach is often used without full quantification of the outcome (Williams et al. 2003, VanDerWal et al. 2009b, Williams et al. 2010, Reside et al. 2012, Reside et al. 2013, Staunton et al. 2014). Thus, the benefits of incorporating expert knowledge with SDMs should be evaluated in order to deem it a useful practice. Evaluation should be based on a well-sampled taxon within a well-sampled region if results are to be reliable. This study evaluates the benefit of expert knowledge in adjusting potential species distributions to realised distributions of 70 rainforest endemic dung beetle species (Coleoptera: Scarabaeidae: Scarabaeinae) with varying dispersal abilities and range sizes in a region with strong biogeographic barriers. By quantifying the overprediction of single species distributions and the accuracy of the resulting predicted assemblage structure, I demonstrate the value of expert scrutiny and evaluation of SDM studies.

3.2 Methods

3.2.1 Study region

This study focuses on the rainforests of the Australian Wet Tropics (AWT; Figure 2.1; see section 1.4).

3.2.2 Species data

Species locality records were obtained from surveys and external databases. Targeted dung beetle surveys included sampling at 20 sites along elevational gradients of four mountain ranges (Figure 2.1; see section 2.1 & 2.2). The locality records from these surveys were supplemented with a large dung beetle database developed by Dr Geoff B. Monteith at the Queensland Museum (see section 2.3). Only native dung beetle species that are endemic to the AWT and known to occur within rainforest habitat were used in this study. The final version of the database totalled 3088 presence-only records for 70 species, of which 41 are winged and 29 are flightless (see section 2.3).

3.2.3 Species distribution modelling

3.2.3.1 Potential species distributions

Models predicting the environmental suitability of each species across the AWT were generated using a maximum entropy (Maxent) approach (see section 2.4.1). These distributions were treated as the "potential species distributions".

3.2.3.2 Realised species distributions

The potential species distributions were examined by GBM., a dung beetle taxonomist, ecologist and authority on the AWT Scarabaeinae dung. For each species, subregions that the SDMs predicted to include suitable environment but where GBM. was highly confident that the species was not present were removed. Predicted distributions were retained if there was any doubt that the species could occur there (Williams 2006, Williams et al. 2010). These distributions were treated as the "realised species distributions" (see section 2.4.2).

3.2.3.3 Species richness models

The individual potential and realised species distributions, based on environmental suitability values above the threshold, were converted to binary (0 = absence, 1 = presence) and summed to produce the potential and realised species richness models respectively. That is, the value of each cell of the species richness models equals the sum of all species that have a distributional presence within that cell.

3.2.4 Identification of well-sampled subregions and local sites

I evaluated the impact of clipping distributions by expert knowledge by comparing the potential species richness and realised species richness to observed species occurrences. This comparison was done for alpha diversity (fine local spatial-scale) and gamma diversity (broad subregional spatial-scale). The most accurate observed values are expected to occur within well-sampled areas. For this reason, comparisons of observed vs. predicted richness and composition were made only between well-sampled subregional units and well-sampled local sites.

Well-sampled subregions were identified by applying the Chao2 incidence-based nonparametric species richness estimator (Colwell and Coddington 1994, Chao et al. 2005, Hortal et al. 2006, Trotta-Moreu and Lobo 2010). Observed subregional species richness (S_{obs}) was calculated as the total number of species having at least one Unique Locality Record (ULR) within the boundaries of that subregion. The number

of ULRs within the boundaries of each subregion was used as a measure of sampling effort and the following formula was applied to each subregion:

 $S_{Chao2} = S_{obs} + (O_{ULR}^2 / 2T_{ULR})$

Where S_{Chao2} is the estimated species richness of a subregion; S_{obs} is the observed species richness of a subregion; O_{ULR} is the number of species having only one ULR within that subregion; and T_{ULR} is the number of species having two ULRs within that subregion. Sampling completeness of each subregion was calculated by (S_{obs}/S_{Chao2}) · 100. Subregions with a sampling completeness value $\geq 75\%$ were regarded as well-sampled (see Pineda and Lobo 2009, Trotta-Moreu and Lobo 2010).

Sampling completeness of each local sampling site was assessed by coverage-based rarefaction using iNEXT online (Chao and Jost 2012, Hsieh et al. 2013). Coverage-based rarefaction and extrapolation methodology allowed for the comparison of species richness based on sample completeness (Chao and Jost 2012, Colwell et al. 2012, Chao et al. 2013) rather than number of individuals (Colwell and Coddington 1994, Colwell et al. 2004). The values of sample-coverage reported by this method indicate the percentage of species detected by the sampling regime (Chao and Jost 2012).

The boundaries of the well-sampled subregions represented the regions in which the gamma diversity richness measures were compared for potential and realised species richness and composition. The site coordinates of the well-sampled sites represented the 250 x 250 m pixel used for the species richness and composition comparisons for alpha diversity.

3.2.5 Evaluation of species distributions and species richness models

I assessed over-prediction of any single species distribution as the percentage of the potential distribution that differed from the expert-derived realised distribution. That is, the area of the realised distribution was subtracted from the potential distribution and the result expressed as a percentage of the total potential distribution. Differences

between the mean over-predictions of winged and flightless species were compared using unpaired Student's t-test.

Accuracy of the predicted diversity (richness and composition) for subregional and local assemblages was assessed. Pearson's correlations were used to compare observed and predicted species richness. As species richness values do not give an indication of which particular species are present or absent, the compositional similarity between observed and predicted species compositions of well-sampled subregions and well-sampled sites were investigated using Mantel tests. Mantel tests are similar to correlations but for a similarity-matrix (Legendre and Legendre 1998). Since compositional matrices were based on presence-absence data, as opposed to abundance data, the Jaccard distance-metric was used. Significance testing was based on the Monte Carlo method using 999 permutations (McCune et al. 2002). Student's t-tests and correlations were performed using R and Mantel tests using the "vegan" package (Oksanen et al. 2012) in the R statistical program (R Development Core Team 2011).

3.3 Results

3.3.1 Well-sampled subregions and sites

A total of 17 subregions (out of 46) were found to be well-sampled for dung beetles (see Appendix 5). These subregions capture the majority and full latitudinal extent of rainforest habitat within the AWT (Figure 2.1). All local sampling sites attained values of sample-coverage >99% indicating that they were well-sampled (see Appendix 6).

3.3.2 Evaluation of individual species distributions

There was high statistical performance of the modelled distributions, the AUC scores ranged from 0.8 to 1 with 91% of species having an AUC \geq 0.9. The over-prediction representing the difference of the area of the realised and potential distributions as a percentage of the potential was significant for all species (exemplar species shown in

Figure 3.1). The greatest over-prediction (>70%) occurred only for flightless species (Figure 3.2). There were significant differences in over-prediction (unpaired Student's t-test, t = 12.012, d.f. = 68, P < 0.001) based on dispersal abilities with over-predictions for flightless species averaging 75.9% (± 4.11% SE) and 20.5% (± 2.58% SE) for winged species. Further, small ranged species (defined by their realised distribution) had greater over-predictions (Pearson's R = -0.87, P < 0.001; Figure 3.3).

3.3.3 Evaluation of species richness models

There are substantial differences in the spatial patterns of potential and realised species richness (Figure 3.4). As expected, the potential richness model predicted higher overall species richness compared to the realised model (Figure 3.5; Table 3.1), particularly in the subregions of Atherton Uplands Bellenden Ker, Carbine Uplands, Windsor Uplands, Thornton Uplands, Finnigan Uplands, Malbon Thompson and Seymour Range (Figure 3.4).

The realised species richness model attained the highest correlation between observed and predicted subregional and local species richness and composition (Figure 3.5; Table 3.1). That is, not only did summing realised distributions produce an accurate estimate of the total number of species present but also an accurate representation of the particular set of species occurring in that area (i.e. the species pool). The realised model attained higher correlations for subregional diversity than for local diversity when compared to the potential model (Table 3.1).

This study has generated the most accurate individual species distribution (see Appendix 7) and species richness (Figure 3.4. b) models for the AWT endemic dung beetle fauna to date. The most species rich areas are located in the central Atherton subregions followed by the northern Carbine, Windsor and Thornton subregions. Subregions at the northern (Finnigan) and southern (Spec, Elliot) limits of the AWT have the lowest species richness (Figure 3.4. b).



Figure 3.1. Potential and realised distributions of (**a** & **b**) the winged *Temnoplectron politulum* Macleay and (**c** & **d**) the flightless *Temnoplectron monteithi* Reid & Storey dung beetles, demonstrating interspecies differences in the amount of potential distribution removed to achieve a representation of the realised distribution based on expert knowledge. Environmental suitability is indicated in a gradient from blue (less suitable) to red (most suitable). Grey areas are considered unsuitable for the species. Subregional outlines as in Figure 2.1.



Figure 3.2. Percentage distributional over-prediction of individual species potential distribution models for (**a**) all dung beetle species (n = 70), (**b**) winged species (n = 41) and (**c**) flightless species (n = 29). Over-prediction was calculated by subtracting the realised from the potential distribution and expressed as a percentage of the potential distribution.



Figure 3.3. Correlation between the percentage distributional over-prediction and the total realised distribution of each species. Over-prediction was calculated by subtracting the realised from the potential distribution and expressed as a percentage of the potential distribution. Open triangles = flightless species (n = 29), filled circles = winged species (n = 41).



Figure 3.4. AWT endemic dung beetle species richness maps derived by summing Maxent (**a**) individual potential species distribution models and (**b**) individual species distributions after they were clipped to expert knowledge, i.e. realised distributions. Species modelled are rainforest specialists thus only species richness values within the current extent of rainforest habitat are shown. Subregional outlines as in Figure 2.1.



Figure 3.5. Predicted species richness against observed species richness at the (a) subregional and (b) local scale. Filled circles and solid line = potential species richness, open squares and dashed line = realised species richness. Note the different x-axis limits. See Table 3.1 for correlation results.

Table 3.1. Correlations between observed and predicted species richness (Pearson's r) and composition (Mantel R) of the potential and realised species richness maps at the subregional scale (within well-sampled subregions, n = 17) and local scale (within well-sampled sites, n = 20).

	Subregio Gamma (nal scale diversity	Local scale Alpha diversity		
Richness map	Pearson's r	Mantel R	Pearson's r	Mantel R	
Potential	0.432^{NS}	0.403 *	0.688***	0.810**	
Realised	0.946***	0.915***	0.825***	0.875**	
			1		

NS - Not Significant, * P< 0.05, **P< 0.01, ***P< 0.001

3.4 Discussion

This study has shown that expert knowledge can be instrumental in providing better estimates of species distribution, richness and composition when modelling species distributions and species richness. I have demonstrated that, despite the sophistication of computational techniques, the idiosyncratic nature of species distributions requires expert intelligence to ensure meaningful outputs are produced. By incorporating knowledge on species, this method was able to accurately exclude areas that were predicted to be environmentally suitable yet where species were absent, probably due to factors associated with the historical biogeography of the region such as in-situ speciation and extinction filtering (Williams et al. 2008a, Yeates and Monteith 2008). The subsequent summing of individual species potential distributions transfers their associated error to the species richness model. Thus, potential species richness models drastically over-predict species richness at both the subregional- and local-scale producing inadequate representations of gamma and alpha diversity respectively. Maxent distributional overestimation into uninhabited biogeographic zones was also identified by Kohlmann et al. (2010) for Costa Rican dung beetles. While many studies have used the approach of post-hoc clipping of species distribution based on expert knowledge (Williams et al. 2003, VanDerWal et al. 2009b, Williams et al. 2010, Reside et al. 2012, Reside et al. 2013, Staunton et al. 2014), this study is the first to quantify the outcome and show the errors that are likely to occur if expert evaluation and adjustment is not performed.

Distributions of flightless species were most likely to be over-predicted. These species are restricted to high elevations of a single or a few mountaintops or subregions due to biogeographical and evolutionary constraints such as historical habitat isolation and dispersal limitation (Yeates et al. 2002, Yeates and Monteith 2008). Thus, climatically suitable areas at high elevations within uninhabited subregions contributed to increased values of over-prediction. The AWTs biogeographical history has also influenced the distributions of winged species, with historical rainforest contractions creating dispersal barriers (Graham et al. 2006, Yeates and Monteith 2008). For example, the Black Mountain Corridor (subregion number 15 in Figure 2.1) constitutes the northern or southern distributional limit for some species' distributions within the AWT (Graham et al. 2006, Moritz et al. 2009) including, among others, the dung beetle *Temnoplectron politulum* Macleay (cf. Figures. 3.1. a & 3.1. b; also see Bell et al. 2004, Bell et al. 2007).

This study has demonstrated that although modelled representations of species richness may be easily derived, they are not necessarily accurate. As such, these results have far-reaching consequences for all studies utilising SDMs, especially for conservation planning, biodiversity research, and climate change predictions. Conservation planning relies on the accurate identification of biodiversity hotspots for optimal reserve selection (Kohlmann et al. 2007, Guisan et al. 2013). Thus, the false presence or false absence of species can result in redundant reserves and ineffective allocation of both effort and resources (Rondinini et al. 2006). For example, if the potential species richness model generated in this study was used to guide conservation efforts based on species richness of AWT endemic dung beetles, then ineffective reserves would have been proposed with the possible neglect of genuinely rich areas. Furthermore, the geographic rarity of some species, e.g. flightless species, would have been underestimated due to model over-prediction leading to, for example, misallocation in IUCN protective status (IUCN 2012). In addition, this study highlights the importance of long term sampling campaigns coupled with taxonomic expertise, in order to have a correct number of species, and thus good analyses and extrapolations.

SDMs are increasingly being used to investigate the impacts of future climate change on the distribution of species (Pearson and Dawson 2003, Hijmans and Graham 2006). Species richness models are also used to quantify changes in species richness resulting from future climate scenarios (Williams et al. 2003, Hughes et al. 2012, Reside et al. 2012, Staunton et al. 2014). If species are predicted to lose distribution area under future climate change scenarios, then predictions of future proportional changes in distribution and species richness patterns will be inaccurate and the impacts of global warming underestimated. Furthermore, climate change will not only influence species directly, e.g. heat stress, but will also influence species indirectly by creating novel or enforcing pre-established biological interactions with other species. Therefore accurate understanding of species composition is important for understanding impacts of climate change.

Understanding the drivers of patterns of biodiversity is central to the study of ecology (Gaston 2000, Ricklefs 2004).Since species richness is the basic measure of biodiversity an accurate representation of its spatial distribution is required (Kohlmann et al. 2007). Inaccurate representations of species richness derived from potential species richness models, as generated in this study, will inevitably result in erroneous predictions regarding the factors responsible for driving and maintaining those species richness patterns.

Thus, it is recommended that studies utilising SDMs to derive a spatial representation of species distribution and associated measures of richness and composition should understand and acknowledge the potential biases including the over-prediction demonstrated here. Expert knowledge should be utilised wherever possible in order to increase the accuracy of species distributions and resulting species richness models.

CHAPTER 4. HISTORICAL AND CONTEMPORARY DRIVERS OF DUNG BEETLE BIODIVERSITY IN THE AUSTRALIAN WET TROPICS

4.1 Introduction

Patterns of biodiversity have gained much attention by ecologists with many hypotheses proposed to explain the causes or drivers of patterns (Pianka 1966, Rhode 1992, Ricklefs and Schluter 1993a, Rosenzweig 1995, Hubbell 2001, Willig et al. 2003, Wiens and Graham 2005). Contemporary patterns of biodiversity, such as species richness and similarity or dissimilarity in species composition across geographic space (β -diversity), are ultimately controlled by processes that effect speciation, extinction and dispersal (Ricklefs 1987, Ricklefs and Schluter 1993a, Gaston 2000). That is, the processes responsible for adding or removing species from any given locality.

Patterns of biodiversity are not static but shift through space and time (Rosenzweig 1995). Thus, in order to achieve a more comprehensive understanding of the determinants of biodiversity, both historical and contemporary influences need to be addressed (Ricklefs and Schluter 1993b, Brown 2001, Hawkins and Porter 2003b, Willig 2003). However, the complexity and interconnectedness between the abiotic and biotic environment results in no single hypothesis being able to explain all patterns of diversity of all taxa at all spatial scales throughout all points in time (Gaston 2000). And since "*nature cannot be understood by pretending that it is simple*" (Elton 1966), a more accurate representation of reality would be the simultaneous influence and relative balance (or imbalance) between multiple factors and processes that effect biodiversity directly and/or indirectly (Gaston 2000, Whittaker et al. 2001). Three factors that are commonly reported to influence patterns of biodiversity include historical habitat stability, contemporary climate, and resources (Rhode 1992, Willig et al. 2003, Graham et al. 2006).

Climatic oscillations during the Quaternary glacial cycles induced widespread fluctuations in forest extent worldwide, including the tropics (Haffer 1969). During rainforest contraction events, species became extinct or extirpated over large portions of their distributional range (Davis and Shaw 2001). However, some localities remained relatively stable in regards to climate and vegetation and thus acted as refugia, allowing the persistence of species and populations during full glacial conditions (Willis and Whittaker 2000, Graham et al. 2006). Fluctuations in rainforest extent along with the presence of refugia have played an important role in shaping contemporary patterns of biodiversity (Haffer 1969, Mayr and O'Hara 1986, Williams 1997, Graham et al. 2006).

Habitats that have remained stable throughout evolutionary and ecological time harbour more species as they provide a greater effective speciation time, allowing more species to arise and fill niches, i.e. evolutionary and ecological time hypothesis (Klopfer 1959, Pianka 1966, Taberlet and Cheddadi 2002, Graham et al. 2006). A more stable and hence predictable environment (e.g. climate) offers a greater probability of survival, thus increasing species persistence and inflating species richness, i.e. the environmental predictability hypothesis (Klopfer 1959, Pianka 1966, Rohde 1992, Willig et al. 2003). Isolation within refugia restricts gene flow between isolated populations and thus results in allopatric speciation via genetic drift, increasing species richness and endemism (Moritz et al. 2000, Smith et al. 2001). Furthermore, refugia can be regarded as islands of suitable habitat surrounded by a sea of unfavourable environmental conditions (Nix 1991). Such "islands" are thus influenced by the effects of area (size of refugium) and isolation (distance to closest refugium), i.e. are compatible with the theory of island biogeography (MacArthur and Wilson 1967, Haffer 1969). Thus, smaller more isolated refugia possess fewer species due to increased rates of extinction and decreased rates of immigration (MacArthur and Wilson 1967). Within a small refugium, isolation of small populations coupled with reduced resources leads to species loss, especially of extinction-prone species resulting in non-random extinctions (Haffer 1969, Williams 1997, Williams and Pearson 1997, Graham et al. 2006).

An interaction between dispersal ability and habitat stability also influences speciation and extinction rates. Dispersal-limited taxa are more prone to reproductive, and hence genetic isolation during rainforest contraction events increasing the probability of speciation (Graham et al. 2006). Additionally, a reduced likelihood of recolonisation following local extirpation increases extinction risk (Graham et al. 2006). Therefore, refugia may act as species filters and/or species pumps to varying degrees, dependent on the size of refugia and taxon in question (Williams 1997, Hewitt 2000), thus influencing both regional species richness and species composition between biogeographic subregions i.e. β -diversity. Variation in β -diversity can be attributed to nestedness and/or species turnover, which indicate the processes responsible for species loss or species replacement respectively (Baselga 2010). Nested species assemblages imply that species-poor assemblages are subsets of species-rich assemblages and are regarded as an indication of an orderly loss of species due to processes that have led to non-random extinctions (Patterson 1987, Ulrich 2007). On the other hand, assemblages characterised by species turnover imply the spatial replacement of certain species by others due to environmental sorting or spatial and historical constraints e.g. refugia (Vellend 2001, Baselga 2010).

Climate can influence species diversity directly due to species physiological requirements/tolerances. Fewer species are physiologically adapted to tolerate harsh, variable, and unpredictable climatic conditions that fall outside species specific organismal optima, i.e. the ambient energy hypothesis (Rhode 1992, Willig et al. 2003). Climate may also indirectly influence species diversity via its relationship with productivity and hence food resources. All else being equal, increased productivity results in increased species richness (Pianka 1966). An area with higher levels of productivity is more likely to contain a greater quantity and diversity of resource types, which in turn will favour a higher diversity of species in order to utilise those resources (Rosenzweig 1992). Such functional relationships should be most apparent for producer-consumer interactions and especially between trophically dependent taxa. For example, Kissling et al. (2007) show that in Africa, species richness of the fruit tree genus *Ficus* had the greatest direct effect on frugivorous bird species richness may not be causative, but rather result from both groups responding to similar

environmental variables. For example, Hawkins and Porter (2003a) found that butterfly and larval host-plant species richness were only weakly associated once environmental and topographic variables were incorporated into models, even though butterfly and host-plant richness showed a strong positive correlation.

Habitat stability, climate, and resources interact to influence patterns of biodiversity (Ricklefs and Schluter 1993b). Niche conservatism aims to explain how habitat stability and climate may interact to influence speciation, dispersal, and extinction (Ackerly 2003, Wiens and Donoghue 2004, Wiens and Graham 2005). Niche conservatism is a process by which species retain certain ancestral ecological traits, such as climatic tolerances (Wiens and Graham 2005). Although niche conservatism operates over long evolutionary time scales, aspects of the niche can be conserved across shorter evolutionary time, for instance, speciation events during the Pleistocene climatic fluctuations (Peterson and Nyari 2007). For example, speciation within a climatically stable refugium results in retention of narrow climatic tolerances that would later inhibit a species from dispersing/colonising areas with differing climatic conditions to those of the refugium (Ackerly 2003, Wiens and Donoghue 2004, Wiens and Graham 2005).

The Australian Wet Tropics (AWT; Figure 2.1) provides an opportunity to investigate the influence of historical and contemporary factors on biodiversity. The AWT, a World Heritage Area, is the most biodiverse region in Australia harbouring large proportions of the continent's taxa including many endemics (Rainforest Conservation Society of Queensland 1986). Several lines of evidence demonstrate that the rainforests of the AWT have contracted and expanded during the climatic fluctuations of the Quaternary (Kershaw and Nix 1988, Hopkins et al. 1993, Kershaw 1994). Persistence of rainforest at mostly high elevations gave rise to rainforest refugia (Hilbert et al. 2007, VanDerWal et al. 2009a) with refugial dynamics identified as playing an important role in shaping the patterns of biodiversity within the AWT (Williams 1997, Graham et al. 2006, Hilbert 2008, Williams et al. 2008a). However, the majority of studies in the AWT have focused on vertebrates with the regions invertebrates being much neglected (but see: Wilson et al. 2007a, Yeates and Monteith 2008, Staunton 2014). Invertebrates constitute the bulk of all known biodiversity (Erwin 1982, Wilson 1987) and are vital in maintaining proper ecosystem functioning (Wilson 1987, Hooper et al. 2005, Prather et al. 2012). Thus, determining the current status of invertebrate biodiversity and its drivers is crucial for its conservation and management and to predict how it will respond to global environmental change (Prather et al. 2012).

A taxon of particular ecological importance includes the dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). By feeding on animal excrement at both the adult and larval stage, dung beetles play a vital role in ecosystem processes and services including the removal and recycling of waste, micro- and macro-invertebrate parasite control, soil aeration and secondary seed dispersal (Spector 2006, Nichols et al. 2008). Although the taxonomy of this group within the AWT is relatively well known (Matthews 1972, 1974, 1976), there have been no attempts to determine the environmental variables explaining the diversity of this important functional group in the AWT.

Therefore, this study investigates the current patterns of dung beetle diversity to understand their drivers within the AWT bioregion. Specifically, spatial patterns of dung beetle species richness and composition are derived using species distribution models and the effects of historical habitat stability, contemporary climate, and food resources (i.e. mammal variables) on dung beetle diversity are investigated. Furthermore, relative effects of environmental variables on winged and flightless dung beetle species are examined separately to assess if species with differing dispersal ability are driven by different environmental variables.

4.2 Methods

4.2.1 Study region

This study focuses on the rainforests of the AWT (Figure 2.1; see section 1.4).

4.2.2 Dung beetle, mammal and environmental data

4.2.2.1 Dung beetle species richness

Continuous spatial layers of dung beetle realised species richness were generated by summing individual realised dung beetle SDMs (see section 2.4.3 & 3.2.3.2). A separate species richness map was created for winged (n = 42) and flightless (n = 29) species (Figures 4.1. a & b).

4.2.2.2 Mammal species richness and biomass

To examine the correlation between measures of dung beetle biodiversity and mammal species richness and biomass, spatial layers of mammal species richness and biomass were constructed. A mammal species richness layer (Figure 4.1. c) was generated with distribution maps of rainforest mammals produced using the same approach mentioned above and previously published in Williams et al. (2010). Biomass layers for each mammal species were generated by incorporating species specific measures of abundance and average body mass (see Williams et al. 2010) to the species distribution maps (see below). Individual mammal biomass layers were subsequently overlayed to produce a single surface layer of total mammalian biomass (Figure 4.1. d). This mammal biomass layer is regarded here as adequately representing dung beetle resource biomass as a direct relationship exists between mammal biomass and dung biomass (Hashim and Dafalla 1996).

Specifically the following formula was applied to each cell of the individual mammal species distribution maps; $\beta = K C_s A_{max} m_{mean}$ where: β = biomass index, constant K = 6.25 ha (i.e. area per cell, 250*250 m), C_s =environmental suitability predicted by MaxEnt, A_{max} = maximum abundance ha⁻¹ (data derived from the AWT vertebrate database maintained by the Centre for Tropical Biodiversity and Climate Change at James Cook University, Townsville, Australia by S. E. Williams), m_{mean}=mean mass (kg; Williams et al. 2010).

4.2.2.3 Historical habitat stability

The paleohabitat stability surface of VanDerWal et al. (2009a) and Graham et al. (2010) was used (Figure 4.1. e). These authors used Maxent methods to reconstruct the late Quaternary vegetation of the AWT using paleoclimate scenarios, and created a spatial stability layer that indexed the continuity in each place of predicted rainforest occurrence across multiple time periods over the last 20 k years.

4.2.2.4 Climate

Climate data included the spatial layers of the eight climate variables used in SDM construction: (i) bc01 - annual mean temperature (AMT); (ii) bc04 - temperature seasonality (TS; Figure 4.1. f); (iii) bc05 - maximum temperature of the warmest period (maxTWP; Figure 4.1. g); (iv) <math>bc06 - minimum temperature of the coldest period (minTCP); (v) <math>bc12 - annual precipitation (AP); (vi) bc15 - precipitation seasonality (PS; ; Figure 4.1. h); (vii) <math>bc16 - precipitation of the wettest quarter (PWQ; Figure 4.1. i); and (viii) <math>bc17 - precipitation of the driest quarter (PDQ). All surfaces were generated using and aligned with the ~ 250 m resolution digital elevation model (Figure 4.1. j; see section 2.4.1).

4.2.2.5 Data extraction

Values from the dung beetle species richness, mammal species richness, mammal biomass, habitat stability, eight climate layers, along with their latitude and elevation, were determined from a 1 km grid over the rainforest region of the AWT using the R package SDMTools (VanDerWal et al. 2012). This resulted in a total of 6085 data points (i.e. 250 m \times 250 m cells) for each variable. To investigate relationships between the size of refugia and dung beetle species richness, the amount of stable area within each subregion was calculated as the total area corresponding to habitat stability values greater than the 95th percentile of values from the stability ASCII using the R package SDMTools (VanDerWal et al. 2012).

Figure 4.1. Spatial patterns in species richness and environmental variables used in this study.(**a**) winged dung beetle species richness (42 species), (**b**) flightless dung beetle species richness (29 species), (**c**) mammal species richness, (**d**) mammal biomass index (kg/ha), (**e**) historical habitat stability index, (**f**) bc04: temperature seasonality, (**g**) bc05: maximum temperature of the warmest period (°C), (**h**) bc15: precipitation seasonality, (**i**) bc16: precipitation of wettest quarter (mm), (**j**) elevation (m a.s.l.). Hotter colours indicate higher values, except for habitat stability were they indicate lower values that correspond to greater stability.



4.2.3 Statistical analyses

4.2.3.1 Collinearity

Examination of a correlation matrix between all variables in the data set revealed collinearity between some climate variable pairs. If variables were collinear then only the variable showing the strongest correlation with dung beetle richness was kept for inclusion in subsequent analyses. This resulted in the retention of four, out of the eight climate variables: temperature seasonality, maximum temperature of the warmest period, precipitation seasonality, and precipitation of the wettest quarter (Figures 2. f– i). For subsequent analyses, variables were transformed accordingly in order to increase normality (Appendix 8).

4.2.3.2 Drivers of dung beetle species richness

Drivers of dung beetle species richness were investigated by determining the direct and indirect effects of predictor variables using structural equation modelling (SEM). SEM was preferred over more common multiple regression techniques because in multiple regression all predictor variables are treated as equal, and thus, any interrelations between variables are not analysed leading to the loss of potentially important information (Mitchell 1992, Grace and Bollen 2005). SEMs allow the specification and evaluation of hypothesised multivariate relationships and permit the partitioning of total effects of predictor variables into direct and indirect effects (Grace 2006). In SEM path diagrams, direct effects are shown by single headed arrows directly connecting two variables. If variables only receive a single headed arrow then the arrow value corresponds to a simple regression coefficient (Grace and Bollen 2005, Grace 2006). If variables receive two or more directed arrows then values correspond to partial regression coefficients that account for the simultaneous influence of the other variables (Grace and Bollen 2005, Grace 2006). Indirect effects are attained by calculating the sum of the products of all partial regression coefficients over all paths linking a predictor and a response variable, including indirect links between other predictor variables (Grace and Bollen 2005, Grace 2006). Total effects of a predictor variable on a response variable equal to the sum of its direct and total indirect effects (Grace and Bollen 2005, Grace 2006).

An a priori SEM for the current study was specified based on theoretically established relationships between topography, climate, habitat stability, mammal and dung beetle richness (Figure 4.2). A direct link between topographic variables (latitude and elevation) and species richness variables was not included, as the relationship between topography and species richness was regarded as non-causal, but rather reflected the influence of climate or other factors (see Hawkins and Diniz-Filho 2004). Separate SEMs were generated for winged and flightless dung beetle species to assess if species with differing dispersal ability are influenced by different environmental variables. To differentiate between the relative effects of mammal richness and mammal biomass (that were highly collinear, Pearson's r = 0.941), individual SEMs were generated using mammal richness then mammal biomass. Finally, to investigate the influence of historical habitat stability on dung beetle richness without the influence of environmental variables, SEMs were generated that excluded climate and topographic variables.

Due to a large sample size (n = 6085) the more commonly used χ^2 goodness-of-fit test could not be applied to the SEMs, and so overall model-fit was measured using the comparative fit index (CFI) which ranges from 0 to 1, with values closer to 1 indicating a better fit (Iacobucci 2010). Model comparisons were also made using the Bayesian information criterion (BIC) with models acquiring lower BIC values regarded as better at describing the data (Raykov and Marcoulides 2006). All SEM analyses were performed with the R statistical software (R Development Core Team 2014) using the package "lavaan" (Roseel et al. 2013).



Figure 4.2. Structural equation model (SEM) based on a priori relationships between the variables used in the current study. Variables enclosed by ellipses are latent (conceptual) variables that are indicated by *measured* variables enclosed in boxes. bc04 TS: temperature seasonality; bc05 maxTWP: maximum temperature of the warmest period; bc15 PS: precipitation seasonality; bc16 PWQ: precipitation of wettest quarter; Hs: habitat stability.

4.2.3.3 Drivers of dung beetle species composition

Dung beetle species presence within each subregion was derived from the SDMs of each species. Dung beetle assemblage structure and β -diversity between rainforested subregions of the AWT (*n*=33; Figure 2.1) was investigated by a combination of non-metric multidimensional scaling (NMDS), hierarchical clustering, indicator species analysis, and species turnover and nestedness analysis. SEMs could not be applied to the composition data as a sample size of at least 50 was required, *cf.* 33 subregions (Iacobucci 2010).

The variation in community composition between subregions was visualised using Kruskal's NMDS based on the Jaccard distance metric. NMDS was chosen over other ordination techniques due to its effectiveness in identifying the strongest structure with ecological community data (Clarke 1993, McCune et al. 2002) and the Jaccard distance metric was preferred due to its suitability for presence/absence data, as opposed to abundance data (McCune et al. 2002). NMDS places subregions in ordination space in such a way that ordination distances correspond to differences in
the similarity (subregions placed closer together) or dissimilarity (subregions placed further apart) in species composition (McCune et al. 2002). Relationships between subregional species composition and environmental variables were investigated by vector fitting that examines correlations between species composition and environmental vectors in ordination space, with significance based on 1,000 random permutations of the data (McCune et al. 2002). The direction of vectors indicate the direction of environmental gradients, and the vector length is proportional to the correlation strength between the ordination and the environmental variable (Oksanen 2011).

In addition, the Jaccard dissimilarity matrix was used to perform hierarchic clustering classification analysis. Hierarchical clustering simplifies compositional distance data by placing similar sites (subregions) into the same class and displaying the classes in the form of a nested dendrogram (Borcard et al. 2011). The cophenetic correlation (the correlation between the original dissimilarities and the dissimilarities estimated from the dendrogram) was used to identify which linkage method (simple, complete, or group average) most accurately reproduced the distance matrix (Borcard et al. 2011, Oksanen 2012). Initial NMDS trials separated only the Elliot Uplands from a tight group comprised of all other remaining subregions (Appendix 9).Therefore, the Elliot Uplands subregion was removed from further analyses so as to determine compositional structure between the remaining subregions.

Once subregional groupings were identified, an indicator species analysis was performed to identify which species were significantly concentrated within each group. Species indicator values (IndVal) were calculated as the product of the relative presence frequency of species within a subregional class or group of classes (see Dufrêne and Legendre 1997, Roberts 2012).

Finally, the AWT β -diversity was partitioned into its turnover and nestedness components by computing multi-site dissimilarities of the species presence-absence matrices (Baselga et al. 2013). This allowed the identification of the processes mostly contributing to the patterns in species composition, i.e. nestedness resulting from non-random extinctions, or turnover resulting from speciation due to historical and environmental constraints (Baselga 2010).

Ordination and hierarchical cluster analyses were performed using the "vegan" package (Oksanen et al. 2012), indicator species analysis using the "labdsv" package (Roberts 2012) and β -diversity partitioning using the "betapart" package (Baselga et al. 2013) in R (R Development Core Team 2014).

4.3 Results

4.3.1 Spatial patterns of dung beetle species richness and predictor variables

Winged dung beetle species richness across the AWT is predicted to be highest in the central Atherton Upland subregions and the Lamb Uplands (Figure 4.1. a). High numbers of winged dung beetle species also occur in the Carbine and Kirrama Uplands and generally at higher elevations with the lowlands having distinctly fewer species (Figures 4.1. a & j). Winged species also decrease in richness within subregions south of Atherton with the isolated rainforest of the Elliot Uplands having no AWT endemic species of winged dung beetles (Figure 4.1. a). The greatest numbers of flightless dung beetle species are predicted to occur in the Atherton Upland East Escarpment, Lamb Uplands, Atherton Uplands Central, and Carbine Uplands (Figure 4.1. b). The majority of flightless species are endemic to a single or few mountain-tops (i.e. subregionally endemic). This has resulted in lowland fragmentary spatial patterns in flightless dung beetle species richness as species distributions do not overlap (Figure 4.1. b). Flightless species do not occur on the Windsor Uplands even though this subregion has relatively high numbers of winged species. There is a distinct absence of flightless species in lowland subregions (Figure 4.1. b).

Patterns of mammalian species richness and biomass are similar to patterns of winged dung beetle richness although higher mammal species richness did not necessarily result in high mammal biomass values (Figures 4.1. c & d). This was due to differences in mammalian body mass, where a few larger species would result in higher values of biomass compared to smaller species. Higher elevations have been the most stable in terms of paleoclimate and rainforest habitat, and currently experience the lowest maximum temperatures of the warmest period (bc05; Figures 4.1. g & j). Temperature seasonality (bc04) increases gradually from north to south of the AWT (i.e. away from the equator), with coastal locations experiencing lower seasonality values compared to inland locations of the same latitude (Figure 4.1. f). The central Atherton subregions and coastal Cairns Cardwell Lowlands experience low precipitation seasonality (bc15), with the least seasonal and highest precipitation values reached at the highest elevations of the Atherton, Bellenden Ker, Bartle Frere, Carbine, and Thornton Uplands (Figures 4.1. h & i).

4.3.2 Drivers of dung beetle species richness

Winged and flightless dung beetle species richness is greatest in locations that were historically more stable, have greater mammal species richness and biomass, and experience cooler temperatures and lower precipitation seasonality (see Appendix 8 for bivariate Pearson correlations).

A comparison of SEMs that included environmental variables with mammal species richness and SEMs that included environmental variables with mammal biomass indicated that SEMs with mammal richness explained slightly more variance in dung beetle richness, attained slightly higher values of model fit, and had lower BIC values for both winged ($r^2 = 0.883$, CFI = 0.978, BIC = 11707; Figure 4.3. a) and flightless ($r^2 = 0.715$, CFI = 0.976, BIC = 10323; Figure 4.3. b) species richness, than did SEMs with mammal biomass: winged species ($r^2 = 0.870$, CFI = 0.974, BIC = 17909), flightless species ($r^2 = 0.698$, CFI = 0.971, BIC = 16221). Also, due to collinearity between mammal species richness and mammal biomass ($r^2 = 0.941$; see Appendix 8) only SEMs that included mammal richness are shown. However, as overall model variance explained and model fit differed only slightly between the two variables, any inferences based on mammal species richness also apply to mammal biomass.





(b) Flightless dung beetle species richness, model fit: CFI = 0.976



Figure 4.3. Structural equation models (SEMs) examining the influence of mammal species richness, habitat stability, and environmental variables, on (**a**) winged and (**b**) flightless dung beetle species richness. Estimated standardised partial regression coefficients are shown on each path (arrow) with the thickness of an arrow corresponding to the strength of its coefficient. bc04 TS: temperature seasonality; bc05 maxTWP: maximum temperature of the warmest period; bc15 PS: precipitation seasonality; bc16 PWQ: precipitation of wettest quarter.

SEM path diagrams revealed that mammal species richness had the greatest positive direct effect on winged dung beetle species richness, even when the effects of environmental variables were accounted for (standardised partial regression coefficient = 0.718; Figures 4.3. a & 4.4. a). Climate variables were the next most important variables showing strong total negative effects on winged dung beetle species richness, although most of their total effects were indirect via mammal species richness and habitat stability (Figures 4.3. a & 4.4. a). Habitat stability showed the lowest total positive effect on winged dung beetles species richness (Figure 4.4. a).

Mammal species richness decreased in importance in the SEM for flightless species richness, with the maximum temperature of the warmest period becoming the most important variable with the strongest negative direct and total effect (Figures 4.3. b & 4.4. b). The remaining climate variables showed lower total negative effects (Figures 4.3. b & 4.4. b). Similar to the SEM with winged species richness, habitat stability showed the lowest total positive effect on flightless dung beetle species richness (Figures 4.3. b & 4.5. b).

Elevation was the most important topographic variable for both winged and flightless dung beetle species richness, resulting in the greatest positive indirect effect via its strong negative effect on maximum temperature of the warmest period (Figure 4.3). Maximum temperature of the warmest period was also the climate variable that mostly negatively influenced both mammal species richness and habitat stability, followed by precipitation seasonality and temperature seasonality (Figures 4.3, 4.4. c & d).

The direct and total effects of habitat stability on winged and flightless dung beetle species richness were much lower than the bivariate correlation of habitat stability with winged and flightless dung beetle species richness (Figures 4.3 & 4.4; Appendix 8). This indicates that the effects of habitat stability were *suppressed* by other variables (see Grace 2006). In other words, the majority of spatial variation in habitat stability within the AWT was also represented by the climate and mammal species richness layers. To demonstrate this, SEMs were created that excluded environmental variables (Figure 4.5). These SEMs show that habitat stability has a

strong total positive effect on winged and flightless dung beetle species richness. However, most of the total effect of habitat stability on dung beetle richness is indirect via mammal species richness, as habitat stability has a strong positive direct effect on mammal species richness (Figure 4.5). The direct positive effect of habitat stability on dung beetle species richness is greater for flightless than winged species richness (Figure 4.5).



Figure 4.4. Stacked bars showing the estimated total effects compartmentalised into direct (black), and total indirect effects (grey) of predictor variables for (a) winged dung beetle species richness, (b) flightless dung beetle species richness, (c) mammal species richness and (d) habitat stability. Direct and indirect effects are standardised partial regression coefficients from structural equation models (see Figure 4.3). mam: mammal species richness; hs: habitat stability; bc04: temperature seasonality; bc05: maximum temperature of the warmest period; bc15: precipitation seasonality; bc16: precipitation of wettest quarter; elev: elevation; lat: latitude.



(a)Winged dung beetle species richness, model fit: CFI = 1.00

(c) Flightless dung beetle species richness, model fit: CFI = 1.00



Figure 4.5. Structural equation models (SEMs) examining the influence of mammal species richness and habitat stability, without environmental variables, on species richness of (**a**) winged and (**c**) flightless dung beetles. Estimated standardised partial regression coefficients are shown on each path arrow, with arrow thickness corresponding to the strength of its coefficient. Next to each SEM, stacked bars show the estimated total effects compartmentalised into direct (black) and total indirect (grey) effects for (**b**) winged and (**d**) flightless species richness.

The total area of stable habitat was also important in explaining subregional dung beetle species richness. Refugia persisted in cooler and less seasonal environments that corresponded to high elevations (VanDerWal et al. 2009a). Thus, subregions that had greater expanses of area above 800 m a.s.l. gave rise to larger refugia (Figure 4.6. a) that in turn harboured more dung beetle species, with size of refugium explaining more variance in flightless species richness ($r^2 = 0.471$; Figure 4.6. c) than winged species richness ($r^2 = 0.273$; Figure 4.6. b).

(b)

mam

hs



Figure 4.6. Relationships between subregional size of a refugium with (**a**) the area above 800 m a.s.l., (**b**) winged species richness and (**c**) flightless species richness.

4.3.3 Patterns and drivers of dung beetle species composition

Dung beetle compositional dissimilarity increased with increasing distance between subregions (Figures 4.7. a & c). Distinct southern, central and northern dung beetle assemblages were identified by NMDS ordination and hierarchical cluster analyses (Figures 4.7. a & c), that correspond to the presence, extent, and connectedness of historical rainforest refugia in the AWT (Figure 4.1. e). However, some discrepancies occurred between certain subregional groupings. For example, the northern central subregions of Windsor, Carbine, and the Black Mountain Corridor (group 2b), were grouped with the central Atherton subregions (group 2a) rather than their neighbouring northern Finnigan and Thornton subregions (group 3b; Figures 4.7. a & c). Also, the central isolated peaks of Bellenden Ker, Malbon Thompson, Seymour range, and Mt Annie (group 3a) were grouped with the northern group 3b, rather than their neighbouring Atherton subregions (group 2a; Figures 4.7. a & c). Lowland subregions were grouped with their adjacent upland subregions, indicating that they were more similar to their adjacent uplands than to other lowland subregions. For example, the Cairns Cardwell Lowlands (group 2ai) were more similar to the adjacent Atherton subregions (group 2aii), rather than the Ingham Lowlands (group 1b) or Mossman Lowlands (group 3bi).

Subregional groupings based on dung beetle compositional similarity/dissimilarity correlated with certain environmental variables (Figure 4.7. b). Dung beetle

assemblages of the central Atherton and Carbine subregions (group 2) were positively related to increased habitat stability, mammal species richness, and mammal biomass (Figures 4.7. a & b). The isolated peaks of group 3a were characterised by high values of precipitation in the wettest quarter (bc16; Figures 4.7. a & b). The southern subregions comprising group 1 had the greatest compositional dissimilarity between all other subregions (Figure 4.7. a) due to low precipitation in the wettest quarter, and increased precipitation and temperature seasonality (Figure 4.7. b).

Indicator species analysis revealed that the species indicative of each ordination/cluster group were mostly flightless (66%), and winged indicator species were only identified for clusters containing a lowland subregion (Table 4.1). Partitioning the overall AWT β -diversity into its nestedness and turnover components indicated that the assemblage patterns of winged dung beetles were mostly attributed to species turnover/replacement and to a much lesser degree nestedness/species loss (Table 4.2). β -diversity patterns of flightless species were almost entirely due to species turnover/replacement (Table 4.2).





Figure 4.7. (a) Non-metric multidimensional scaling ordination (stress = 0.14) of the AWT endemic dung beetle assemblage using Jaccard similarity index. Ellipses indicate subregional groups as identified by hierarchical clustering. Ellipse colours and labels match the coloured subregional cluster groups illustrated in Figure 4.7. c. (b) Environmental vectors showing the direction and magnitude of significant correlations (P < 0.001) within the ordination space of Figure 4.7. a. mam_rich: total mammal species richness; mam_bio: mean mammal biomass; hs: mean habitat stability; bc04: mean temperature seasonality; bc05: mean maximum temperature of the warmest period; bc15: mean precipitation seasonality; bc16: mean precipitation of wettest quarter. (c) Hierarchical cluster dendrogram using average linkage methods (sliced at a height of 0.4; see Appendix 10) of the AWT endemic dung beetle assemblage overlaid on a map of the AWT. Subregions with similar species assemblage structure belonging to the same cluster group are filled with the same colour. For the name of subregions belonging to each cluster see Figure 6a. For precise location of each subregion see Figure 2.1. Note that branch lengths do not indicate degree of similarity/dissimilarity between subregional groups.

Cluster Group	Indicator species	indVal	Flightless Y = Yes
1.	Temnoplectron involucre	1.00	Y
1a	Amphistomus pectoralis	0.67	Y
11	Lepanus NQ2	0.44	
10	Lepanus palumensis	0.35	
2.:	Onthophagus wilgi	0.50	
281	Onthophagus pillara	0.33	
o	Onthophagus NQ8	1.00	
2 a 11	Aptenocanthon winyar	0.88	Y
2 h	Temnoplectron lewisense	0.67	Y
20	Pseudignambia NQ8	0.67	Y
2:	Pseudignambia NQ4	1.00	Y
581	Pseudignambia NQ2	1.00	Y
2	Pseudignambia NQ16	0.25	Y
5811	Pseudignambia NQ15	0.25	Y
21.:	Temnoplectron monteithi	1.00	Y
301	Pseudignambia NQ5	1.00	Y
21.::	Temnoplectron finnigani	0.40	Y
3011	Temnoplectron reyi	0.23	

Table 4.1. Species with the highest indicator species value (IndVal) for eachordination/cluster group. Ordination/cluster groups as in Figures 4.7. a & b.

Table 4.2. Total β -diversity (β_{SOR}) of the AWT dung beetle assemblage partitioned into its species turnover (β_{SIM}) and nestedness (β_{NES}) components.

Species group	Total β–diversity (β _{SOR})	Species Turnover component (β _{SIM})	Nestedness component (β _{NES})
All species	0.86	0.73	0.13
Winged species	0.84	0.68	0.16
Flightless species	0.95	0.91	0.04

4.4 Discussion

A positive relationship between dung beetle and mammal species richness exists, while both are driven by similar responses to historical habitat stability and contemporary climate. The covariation between historical habitat stability, contemporary mammal species richness/biomass, and climate, makes their relative effects on dung beetle diversity difficult to disentangle. A similar problem was encountered by Hawkins and Porter (2003b) when trying to tease apart historical and contemporary effects on mammal and bird diversity in North America. Historical habitat refugia have left a strong signal on dung beetle species compositions in the AWT, with distinct assemblages occurring between disconnected and distant refugia, and similar assemblages between re-connected refugia. Subregionally endemic flightless species occur only in subregions that maintained refugia. Greater dung beetle species richness of both winged and flightless species occurs in locations with cooler temperatures, and lower temperature and precipitation seasonality values, i.e. climatic conditions associated with stable habitats such as refugia. These results indicate that historical habitat refugial dynamics have determined the subregional dung beetle species pools within the AWT. Within subregions, species are responding to current variations in climate and mammal richness/biomass (i.e. resource heterogeneity/quantity). These results are congruent with the findings of other studies investigating patterns of biodiversity in the AWT, especially in regards to mammal diversity (Williams 1997, Williams and Pearson 1997, Winter 1997, Williams et al. 2008a). A holistic understanding of the drivers of dung beetle species richness and composition can be achieved by considering the relationships between habitat stability, climate, and mammal diversity, and how they influenced processes responsible for the addition (i.e. persistence, recolonisation, speciation) or removal (extirpation, dispersal, extinction) of species within the AWT landscape.

During periods of rainforest contractions, refugia remained within cool wet environments, such as those associated with high elevations (Nix 1991, VanDerWal et al. 2009a). Lowland rainforests were mostly extirpated during this phase, and consequently, so were the majority of the lowland hot adapted dung beetle species. Populations of cool adapted species contracted with the rainforest and became isolated within refugia and were thus subjected to island like effects. Islands in this case referring to suitable habitat isolates surrounded by a sea of unfavourable environmental conditions (Nix 1991). A reduction in available habitat and resources (due to reduced mammal populations) is likely to have decreased dung beetle population sizes and resulted in extinction/extirpation. However, increased dung beetle species richness at higher and hence cooler elevations, indicates that many species persisted and/or speciated within refugia. This was especially the case within larger refugia that showed increased richness of both winged and flightless species, especially in the Atherton Uplands. Larger refugia also sustained greater species richness and abundance of mammals (Williams 1997, Winter 1997, Hocknull et al. 2007, Williams et al. 2008a). These provided a greater variety and quantity of dung resources that could in turn sustain a greater diversity and larger populations of dung beetles, increasing their probability of survival and hence persistence. The dependence of dung beetles on mammals via a functional trophic relationship, and the influence of rainforest refugia on both dung beetle and mammal diversity, have resulted in the spatial congruence of the richness patterns of both groups. The importance of a trophic relationship in determining spatial patterns of diversity between consumers and their resources has also been noted between frugivorous birds and fig trees (Ficus spp.) in sub-Saharan Africa (Kissling et al. 2007).

Greater mammalian species richness and biomass increases dung beetle species richness. For example, more mammal species invariably increases resource (dung) heterogeneity (i.e. dung size, shape, structure, and quality), that in turn increases the number of niches allowing more dung beetle species to specialise and co-exist, i.e. niche assembly hypothesis (Hutchinson 1959, Hanski and Cambefort 1991b, Kissling et al. 2007). Cambefort and Walter (1991) also report a greater dung beetle species richness in African tropical forests with a rich mammalian fauna compared to tropical forests with a poor mammalian fauna.

Refugia increase species richness and endemicity by creating conditions that favour allopatric speciation, i.e. restricting gene flow between isolated populations (Moritz et al. 2000, Smith et al. 2001). For example, within the AWT, the dung beetle sister species *T. monteithi*, *T. finnigani*, *T. lewisense* and *T. involucre* are restricted to single

and isolated mountain tops of the Thornton (TU), Finnigan (FU), Carbine (CU) and Spec (SU) subregions respectively, all of which sustained rainforest refugia during the Pleistocene climatic fluctuations (Hilbert et al. 2007, VanDerWal et al. 2009a). Molecular (mtDNA) analysis suggests that speciation of these four species occurred almost simultaneously from a common ancestor, confirming allopatric speciation of a single, once widespread species (Bell et al. 2004). Such speciation events also created unique species assemblages within refugia, as indicated by higher values of turnover (species replacement) rather than nestedness (orderly loss of species) in the AWT subregional β -diversity. However, for winged species, a small percentage of the AWT β -diversity was attributed to nestedness, suggesting non-random extinction and/or recolonisation. Nestedness results in compositional patterns where the poorest assemblage is a subset of the richest assemblage (Baselga 2010, Baselga and Orme 2012). This was the case between the richer upland subregions and their adjacent lowlands, providing evidence for extinctions in the lowlands followed by recolonisation from the species rich uplands, albeit by winged species. Furthermore, recolonisation also occurred between upland refugia during periods of rainforest expansion of the cool-wet Pleistocene/Holocene transition (PHT; c. 8 k ybp), and again under current climates (Graham et al. 2006). This was indicated by the similarity between the Atherton and Carbine assemblages, with dispersal between these two refugia taking place via the Black Mountain Corridor, a well established dispersal and recolonisation route (Williams et al. 2008a, Moritz et al. 2009). Furthermore, similarities in species composition between Carbine and Windsor coupled with the absence of flightless subregional endemics from Windsor suggests that the dung beetle assemblage of Windsor represents a recent colonisation from Carbine.

High values of dung beetle species turnover coupled with increased species richness in upland refugia indicate that refugia acted mostly as "species pumps", contrary to mostly "species filters" for the AWT mammalian fauna (Williams 1997). This difference can be attributed to the small body size and generalist feeding behaviour of the AWT dung beetles that would have allowed them to persist and speciate in smaller refugia (Yeates et al. 2002). That is, smaller organisms require less effective habitat and resources for survival (Blackburn and Gaston 1999). Also, the majority of AWT dung beetles are not specialised on the dung of a single mammal species [but see Wright (1997) for a study on an AWT non-rainforest dung beetle restricted to a single mammal species]. Some adults also feed on decomposing fruit and fungi (Hill 1996, Vernes et al. 2005, Aristophanous unpublished data) and can thus survive within a dung depauperate environment, such as a small refugium. Indeed, there are no subregionally endemic mammals present in the smaller refugia of the Spec, Malbon Thompson and Finnigan Upland subregions, whereas these subregions have subregionally endemic dung beetle species and other subregionally endemic insect species (Yeates et al. 2002).

The high incidence of flightlessness in dung beetles and other insects (Yeates et al. 2002, Bouchard et al. 2005, Yeates and Monteith 2008) within stable high elevations of the AWT is consistent with the hypothesis that habitat stability favours the loss of flight (Darlington 1943, Roff 1990). That is, dispersal in order to track or locate resources and favourable environments (i.e. climate) becomes redundant within isolated climatically stable refugia (Darlington 1943, Roff 1990, Roff 1994a, b). Furthermore, lower temperatures associated with high elevation refugia inhibit insect flight and any energy invested in wings and wing muscle development is wasted, thus providing a positive selection pressure towards flightlessness (Roff 1990, Scholtz 2009b).

Climate influenced dung beetle diversity both indirectly and directly. Indirect effects arose via the historical and current extent of rainforest habitat, and via effects on mammal species richness and biomass (see above). Direct effects of climate on dung beetle diversity arise due to species physiological requirements/tolerances. Species persisting and speciating in upland refugia are in general, those adapted to, or selected for, a cooler and more stable climate. According to the "ambient energy" hypothesis (Rhode 1992, Willig et al. 2003) increased species richness arises because fewer species are physiologically adapted to tolerate harsh and variable environments. In the case of the AWT, harsh (i.e. hotter) and variable (i.e. increased seasonality) environments are located in the lowland and southern subregions, with higher temperatures and dry–season severity possibly setting a physiological limit to the distribution of many species, resulting in decreased species richness within these

subregions. Although the thermal tolerances of AWT dung beetles are currently not known, intolerance to high temperatures has been identified as limiting the distribution of an AWT endemic possum (Krockenberger et al. 2012) and certain endemic Mycrohylid frogs (Andrés Merino-Viteri, pers. comm.). The retention of physiological intolerances to high temperatures may have been retained by niche conservatism within refugia (Wiens and Donoghue 2004, Wiens and Graham 2005), with high temperatures acting as physiological barriers to dispersal and thus restricting dung beetle species to the climatic conditions of refugia.

In conclusion, although the present study suggests that patterns of dung beetle species richness and composition are driven by contemporary variations in mammal species richness and climate, historical habitat stability has undoubtedly left a strong signal. Historical habitat stability has influenced dung beetles both directly via processes such as population isolation, speciation, extinction and dispersal, and indirectly via the effects of these processes on their habitat and mammalian resource providers, with the climatic conditions associated with rainforest refugia influencing both dung beetle and mammal diversity. Various combinations of these processes and the regions topography have resulted in a landscape characterised by complex patterns of dung beetle biodiversity of which certain subregions possess species assemblages that are refugial, others correspond to a mixture between refugial and recolonised species, and others have been more recently acquired (Williams et al. 2008a). Rainforest refugia have also been identified as determining the patterns of diversity of a variety of vertebrate and invertebrate taxa within the AWT and elsewhere, thus confirming the need to incorporate historical elements when investigating spatial patterns of biodiversity (Ricklefs and Schluter 1993b, Hawkins and Porter 2003b).

CHAPTER 5. DRIVERS OF DUNG BEETLE BIODIVERSITY ALONG ELEVATIONAL GRADIENTS IN THE AUSTRALIAN WET TROPICS

5.1 Introduction

In the previous chapter, I demonstrated that a combination of historical habitat stability, contemporary climate, mammal species richness, and mammal biomass played an important role in shaping dung beetle species richness and composition within the Australian Wet Tropics (AWT). However, all of these variables are themselves associated with the elevational gradient. Consequently, this chapter investigates elevational patterns of dung beetle biodiversity (i.e. species richness, abundance, biomass, and composition)in greater detail and at finer spatial scales in order to describe and understand how dung beetles respond to elevational gradients. Additionally, data used in this chapter are empirically obtained using standardised sampling techniques, as opposed to being derived from regional species distribution models as used in Chapter 4.

The investigation of patterns of biodiversity along elevational gradients can contribute towards our understanding of the drivers and maintenance of species diversity (Lomolino 2001). Furthermore, elevational gradients provide a natural experiment for investigating species responses along gradually changing environmental conditions (Rahbek 1995, Willig et al. 2011) and can be regarded as proxies for studying the effects of climate change on species diversity (Hodkinson 2005). Many hypotheses have been put forth to explain elevational gradients in species richness, and most of these have been borrowed from those explaining latitudinal patterns in species richness (Pianka 1966, Rohde 1992, Gaston 2000, Lomolino 2001).

The three most common relationships between species richness and elevation are a monotonic decrease, monotonic increase, and a peak at mid-elevations (i.e. unimodal

or humped relationship) (Rahbek 1995, Lomolino 2001, Rahbek 2005, Graham and Duda 2011). Identifying the causes of these relationships is a complicated, yet crucial, requirement towards any attempt to understand how species are distributed in space and time (Rosenzweig 1995). Variations in biodiversity along elevation inherently reflect abiotic and/or biotic gradients, such as gradients in area, climate, habitat stability, and resource availability (Lomolino 2001).

The species-area relationship (SAR) refers to the tendency of larger areas having more species than smaller areas, and is generally regarded as the closest thing to a rule in ecology (Preston 1962, MacArthur and Wilson 1967, Rosenzweig 1995, Lomolino 2000, Whittaker and Triantis 2012). The main ecological explanations for the SAR are based on increasing habitat heterogeneity and lower risk of extinction with increasing area (Rosenzweig 1995, Willig et al. 2003). A larger area is more likely to contain a variety of biomes, habitats, and niches, i.e. is more heterogeneous. Increased habitat heterogeneity leads to species adaptation, specialisation and ultimately speciation (Rosenzweig 1995, Willig et al. 2003). Heterogeneous environments are also more likely to contain geographical and/or ecological barriers that may prevent gene flow between populations, increasing speciation rates (e.g. allopatric speciation) and thus inflating species richness (Willig et al. 2003). Larger areas are also able to support greater amounts of resources that in turn, are able to support larger populations of a given species. Larger populations are less prone to extinction as they may possess multiple interconnected subpopulations which decrease the probability of extinction, i.e. metapopulation dynamics (Hanski et al. 1995).

Due to the (often) conical shape of mountains, area decreases with increasing elevation which "should" result in a monotonic decrease in species richness (Brown 2001). However, some mountains may plateau at certain elevations so that area exhibits a non-linear trend with elevation, and thus, elevations with the greatest spatial extent should possess more species owing to the mechanisms that give rise to the SAR (Lomolino 2001, Willig et al. 2003, Grytnes and McCain 2007).

Climatic variables such as temperature and precipitation vary along elevation. For example, as elevation increases temperature decreases at a generally predictable rate, while precipitation may be controlled by less "linear" functions (Hodkinson 2005). This is especially the case in some tropical regions such as the AWT where cloudstripping may account for large proportions (> 50%) of water input at high elevations (McJannet et al. 2007). Climatic gradients may influence species richness either directly, i.e. physiologically, or indirectly by dictating productivity or the amount of energy available to the system, i.e. the species-energy hypothesis (Wright 1983). The species-energy hypothesis suggests that partitioning of energy among species limits richness with more productive areas having greater species richness (Pianka 1966, Wright 1983, Currie 1991). However, it is not just the amount of energy that is important but rather energy availability for the trophic level of the taxonomic group in question (Whittaker et al. 2001). For example, the available energy that can be utilised by dung beetles refers to the amount of dung, which is related to mammal biomass (Hanski and Cambefort 1991a).

Higher elevations often experience a greater range of climatic conditions (Stevens 1992). Species at high elevations have adapted to this variability by possessing broader climatic tolerances, and are thus able to occupy a broader range of elevations (Stevens 1992). An increase in distributional range with increasing elevation has been likened to the increase in distributional range with increasing latitude, i.e. Rapoport's rule (Stevens 1992). Rapoport's rule implies that species at lower elevations, that have more predictable and thus less variable climate, will possess narrow elevational ranges. Therefore, narrow ranges at low elevations and broad ranges at high elevations will give rise to greater overlap of species ranges at lower and midelevations resulting in either a monotonic decrease or a humped relationship with elevation (Stevens 1992).

Mountain peaks are often small (in area) and isolated, i.e. by physiological barriers effectively creating "islands" (Nix and Switzer 1991). Thus, smaller and more isolated islands (e.g. mountaintops) may possess lower species richness due to lower immigration rates and higher probabilities of extinction, keeping with the theory of island biogeography (MacArthur and Wilson 1967). Furthermore, isolation may result in allopatric speciation leading to higher levels of endemism, and may account for a

pattern of reduced species richness and increased endemicity at higher elevations (Grytnes and McCain 2007).

Haffer (1969) postulated a historical explanation to account for greater species richness in lowland Amazonian birds. He proposed that during Pleistocene climatic fluctuations the rainforest contracted to patches of lowland refugia isolating much of the dependent fauna. Allopatric speciation led to differentiation of species assemblages with localised centres of distribution within refugial areas even after rainforest expansion led to re-connection between refugia (Haffer 1969). The inability of species to disperse into apparently favourable habitat has been explained by a hypothesis regarding species niche conservatism (Wiens and Donoghue 2004). That is, certain aspects of the niche, such as climatic tolerances, are conserved over time so that species lack the ability to disperse into novel climatic conditions (Peterson et al. 1999, Wiens and Donoghue 2004). Thus, refugia along with niche conservatism are able to explain pockets of increased species richness and endemism (Wiens and Graham 2005). Rainforest refugia, albeit at higher elevations, are important in shaping the patterns of diversity of dung beetles (Chapter 4) and of other taxa in the AWT (Williams et al. 2008a, Yeates and Monteith 2008).

Biological interactions also influence species richness (Pianka 1966). For example, competition for resources leads to finer niche compartmentalisation allowing the coexistence of many competitors and thus increasing species richness (Pianka 1966). However, fierce competition by a dominant species may decrease diversity and species richness by competitively decreasing abundance and competitively excluding other species (Horgan and Fuentes 2005).

Soil type is known to influence dung beetle species richness due to its effects on burying behaviour (Hanski and Cambefort 1991b). Certain species have preference to different types of soils depending on their texture, i.e. relative content of sand, silt, and clay (Doube 1991). Soil texture determines soil properties such as compactness and drainage that in turn influence dung beetles' ability to dig and burrow into the soil or survive during a rainfall event (Lumaret and Kirk 1991).

The hypotheses and processes stated above aim to explain patterns in species richness. However, more information can also be gained from communities by incorporating the number of individuals (i.e. abundance) of each species (Stuart-Smith et al. 2013). Just as species are not evenly distributed in geographical space they are also not equally abundant within their entire distributional range (Brown 1984). This variation in abundance can be viewed as a reflection of the suitability of their physical and biological environment, i.e. niche parameters (Hutchinson 1957, Brown 1984). Species will tend to be more abundant in places where most of their niche requirements are met and less abundant where these requirements are not met (Brown 1984). Similarly, the boundaries of the distributional range of a species can in turn be regarded as regions where one or more niche parameters become unfavourable thus creating a dispersal barrier (Brown 1984).

Variation in the abundance of species within a community can also give insights into division of resources with more abundant species using a greater portion of the available energy/resource (Pagel et al. 1991). However, in such cases it is important to consider body size as large bodied species require larger amounts of resources to satisfy their higher metabolic requirements (Pagel et al. 1991). Thus, the investigation of biomass provides an indication of the total resource utilised by particular species as it incorporates both abundance and body mass (Pagel et al. 1991).

The AWT is characterised by a series of disjunct mountains and thus provides an exceptional opportunity for the study of patterns of biodiversity along elevational gradients. Upland rainforest refugia have been identified as shaping the patterns of biodiversity of the regions flora and fauna (Hilbert 2008, Williams et al. 2008a, Yeates and Monteith 2008). Distribution modelling has also identified the importance of habitat stability and elevation in regards to dung beetle biodiversity (Chapter 4). However, as many factors vary along elevation, it is unlikely that the effects of rainforest refugia are independent from other factors. A more ecologically likely scenario should invoke combinations and complementarities of multiple hypotheses (Whittaker et al. 2001).

A series of AWT elevational transect studies relating to insect diversity have been previously undertaken by several Queensland museum expeditions in the 1980's (see Monteith 1982, 1985a, 1989, Monteith and Davies 1991, Monteith 1995). However, due to the broad taxonomic focus of these expeditions, standardised data (e.g. relating to species abundances) is currently lacking thus making ecological inferences difficult.

This study aims to provide an understanding on how abiotic and biotic factors along elevational gradients influence the species richness, abundance, biomass, and composition of Scarabaeinae dung beetle communities.

5.2 Methods

5.2.1 Study area

This study was conducted in the rainforest of the AWT (Figure 2.1; see section 1.4).

5.2.2 Study sites and sampling design

Four elevational gradients were sampled with sites (n = 20) located at approximately every 200 m increments in elevation (Figure 2.1; Table 2.1; see section 2.1). At each site a total of six pitfall traps (four baited, two non-baited/controls) were placed 15 m apart, and serviced on a monthly basis for a period of two years (see section 2.2).

5.2.3 Dung beetle data

5.2.3.1 Species Richness

To examine the efficiency of the sampling methodology, species richness of each site was assessed by coverage-based rarefaction using iNEXT (Chao and Jost 2012, Hsieh et al. 2013). Coverage-based rarefaction and extrapolation methodology allowed for the standardisation of species richness of elevational sites based on sample completeness (Chao and Jost 2012, Colwell et al. 2012, Chao et al. 2013) rather than sampling effort or number of individuals (Colwell and Coddington 1994, Colwell et al. 2004). Species richness was rarefied and extrapolated using a sample size equal to double the reference sample size (see Chao and Jost 2012, Hsieh et al. 2013) and also estimated using the commonly used Chao1 species richness estimator (Chao 1984).

5.2.3.2 Abundance

Pitfall traps were left "open" in the field for 20 to 58 days, depending on site and sampling trip (see Appendix 1 - 4). As traps were baited with dung, attractiveness and hence number of individuals caught, decreased with time as the dung bait dehydrated (Figure 5.1. a). Once the bait dehydrates and is no longer attractive to the dung beetles the capture rate of baited traps decreases, but does not reach a plateau as individuals still randomly fall into the trap. This random capture rate can be represented by the capture rate of the control traps (Figure 5.1. b). Thus, to account for the random (i.e. not–attracted) capture rate, the mean number of individuals caught in non baited traps was subtracted from the total number of individuals of each baited trap (abundance correction). This can be regarded as being equivalent to the baited trap catch-rate plateauing after bait dehydration (Figure 5.1. c) regardless of the total number of days the traps were left "open".

The "abundance correction" was applied individually to each species for every sampling-trip to account for any species–, site–, and season–specific differences in "random" catch rate. For example, flightless species may have a higher probability of randomly falling into a baited trap with dehydrated dung or a non baited trap than winged species as flightless species are more active on the forest floor in search of dung, as opposed to winged species that fly above the forest floor.





Figure 5.1. Graphical representation of the capture rates associated with **a**) baited pitfall traps, **b**) non baited pitfall traps, and **c**) the "adjusted" capture rate after subtracting the non baited capture rate from the baited capture rate demonstrating the standardisation of abundance used in this study.

5.2.3.3 Biomass

Mean dry-weight (mg) was calculated for the 21 most abundant species from every elevational site where >20 individuals were sampled on one particular sampling trip. From these species × site pairs, a total of 20 individuals were dried in a dehydrating oven at 70 °C for 48 hours, then weighed using an electronic balance (Mettler AE200) to the nearest 0.1 mg (Sample et al. 1993). A linear regression formula was derived using species log dry weight and log median length [log dry weight = $(2.757 \cdot \log median \ length) - 9.664$]. This formula was then used to predict the dry weight of the species that were not weighed by including their known length (sourced from Matthews 1972, 1974, 1976). Species specific biomass at each site was calculated as the product of the mean dry weight of each species with the total standardised abundance of that species at each site. Finally, total site biomass was the sum of all species' biomass found at that site.

5.2.3.4 Diversity and dominance

The dung beetle diversity of each site was calculated using the exponential of Shannon entropy or the "effective number of species" (Jost 2006). Converting the Shannon entropy into effective number of species allows for a more intuitive comparison of site diversity. For example, a site with 10 effective species can be regarded as having the same diversity as a community with 10 equally abundant species and would be twice as diverse as a community with five effective species (Jost 2006). Species dominance was calculated for each site using the Berger–Parker dominance index that expresses the proportional abundance of the most abundant species (Berger and Parker 1970). The Berger–Parker index was chosen as it is an intuitively simple index and is regarded as one of the most satisfactory diversity measures (May 1975, Magurran 2004).

While it is common practice to calculate diversity indices using abundance (as above) this does not take body mass into consideration. In the current data set, body mass (i.e. dry weight) ranged from 0.43 mg (*Lepanus pisoniae* Lea) to 62.36 mg (*Onthophagus mundill* Matthews). Dung beetle body mass is directly related to resource requirement and so plays an important role in the dung beetle community, as larger beetles are able to remove larger portions of the dung resource (Doube 1990, Hanski and Cambefort 1991a). To account for this functional characteristic on the impact of the dung beetle community, diversity and dominance indices were also calculated using values of species specific biomass (Saint-Germain et al. 2007).

The Spec 1000 m site was only sampled for one year, instead of two (Appendix 1). Thus, diversity and dominance indices for the Spec gradient were calculated using only one year's data to not affect diversity measures that are sensitive to species abundance.

5.2.3.5 Elevational range

The elevational range of each species was calculated as the difference between its maximum and minimum elevational presence from all four gradients. A mean elevational range for each site was calculated by averaging the range size of all species sampled at that site. Species with a total abundance (from all sites) of fewer than 10 individuals (n = 9) were removed for this analysis.

5.2.4 Environmental data

The environmental explanatory variables relating to climate, historical habitat stability and resources, i.e. mammal species richness and biomass, were extracted for each sampling site coordinate from corresponding AWT ASCII surface layers using the R package SDMTools (VanDerWal et al. 2012). The climate variables used in analyses were: bc01 – annual mean temperature (AMT), bc04 – temperature seasonality (TS), bc05 – maximum temperature of the warmest period (maxTWP),bc06 – minimum temperature of the coldest period (minTCW),bc12 – annual precipitation (AP), bc15 – precipitation seasonality (PS), bc16 – precipitation of the wettest quarter (PWQ) and bc17 – precipitation of the driest quarter (PDQ).

To investigate how the amount of available area varies along the elevational gradients and how it relates to dung beetle richness, the elevational band area of each site was calculated as the total area of rainforest within \pm 100 m of the digital elevation of each site (Table 2.1) from a digital elevation model of the AWT (DEM; Geoscience Australia, http://www.ga.gov.au/) using the R package SDMTools (VanDerWal et al. 2012).

Habitat heterogeneity values of each site were sourced from Parsons (2010). Habitat heterogeneity at each site was determined by visually estimating the percentage cover of the lower, middle, and upper shrub layers, and sub-canopy and canopy layers using the Braun-Blanquet scale with values assigned to each percentage class; 1: 1 - 5% cover, 2: 6 - 25%, 3: 26 - 50%, 4: 51 - 75%, 5: 76 - 100% (Sutherland 2006). Habitat heterogeneity values of each site were then calculated as the sum of all layer values.

Lastly, to investigate the influence of soil type on dung beetles along the elevational gradients, values of soil sand (%), silt (%), clay (%) and pH for each site were sourced from Parsons (2010) that were determined using the methods of Rhoades (1982).

5.2.5 Statistical analyses

5.2.5.1 Species richness, abundance and biomass

Generalised Additive Mixed Models (GAMMs) were used to determine the effect of all independent variables on total dung beetle species richness, abundance and biomass. The categorical subregion variable (i.e. Spec, Atherton, Carbine, Windsor) 70 was included as a random effect to reduce the number of estimated parameters and to develop a general model for the study region (Zuur et al. 2009). GAMM is a form of non-parametric regression able to identify non-linear relationships without any *a priori* assumptions by using smoothing curves (Zuur et al. 2009). A cubic regression spline smoother was applied and the amount of smoothing was estimated automatically using cross-validation (Zuur et al. 2009). A Poisson distribution with a log link function was used for species richness and abundance as they represented count data, while a Gaussian distribution and an identity link was used for biomass (Zuur et al. 2009). GAMM models were implemented using the mgvc package (Wood 2013) in R (R Development Core Team 2014).

5.2.5.2 Species composition and assemblage structure

Species compositional similarity/dissimilarity between elevational sites was investigated using non-metric multidimensional scaling (NMDS), hierarchical clustering, and species turnover and nestedness analysis. NMDS based on the Bray-Curtis distance metric was chosen over other ordination techniques due to its effectiveness with ecological community data based on abundances (McCune et al. 2002). Species abundances were square root transformed prior to ordination. To assess similarities in species composition between the two sampling years, ordinations based on each years' species–abundance matrix were compared using Procrustes rotation and the associated PROTEST permutation test (Jackson 1995, Peres-Neto and Jackson 2001). Procrustes analysis scales and rotates ordinations to find an optimal superposition that maximises their fit (Peres-Neto and Jackson 2001). The statistical significance of the Procrustean fit is then assessed by a permutation procedure (PROTEST) that derives a correlation-like statistic and an associated *P* value based on the Procrustes sum of squares, referred to as m_{12} (Jackson 1995, Peres-Neto and Jackson 2001).

Relationships between site species composition and environmental variables were investigated by vector fitting that examines correlations between species composition and environmental vectors in ordination space, with significance based on 1000 random permutations of the data (McCune et al. 2002, Oksanen 2011). The directions of vectors indicate the direction of the environmental gradients, and the vector length

is proportional to the correlation strength between the ordination and the environmental variable (Oksanen 2011).

In addition, the Bray-Curtis dissimilarity matrix was used to perform hierarchic clustering classification analysis. Hierarchical clustering simplifies compositional distance data by placing similar sites into the same class and displaying the classes in the form of a nested dendrogram (Borcard et al. 2011). The cophenetic correlation, the correlation between the original dissimilarities and the dissimilarities estimated from the dendrogram, was used to identify which linkage method (simple, complete or group average) most accurately reproduced the distance matrix (Borcard et al. 2011, Oksanen 2012).

Finally, to identify the processes mostly responsible for patterns in species composition and assemblage structure, the β -diversities between sites derived from incidence-based and abundance-based species matrices were partitioned into their two components: species turnover and nestedness for incidence patterns (Baselga 2010, 2012) and "balanced variation in species abundance" and "abundance gradients" for abundance-based patterns (Baselga 2013). Incidence-based species turnover and nestedness responsible for species loss and species replacement respectively (Baselga 2010, 2012), while balanced-variation-in-species-abundance and abundance-gradients are their abundance-based equivalents (Baselga 2013).

Ordination, vector fitting, hierarchical cluster, Procrustes and PROTEST analyses were performed using the package "vegan" (Oksanen et al. 2012), and partitioning of incidence-based and abundance-based β -diversity using the package "betapart" (Baselga et al. 2013) in R (R Development Core Team 2014).

5.3 Results

5.3.1 Taxonomic summary

A total of 61,550 individuals belonging to 49 species in 7 genera were collected in this study (Table 5.1). The Atherton gradient yielded the most species with a total of 33, Carbine and Windsor had a total of 29 and 26 species respectively, and the Spec gradient had the least, with 16 species. Thirty-eight species (77.5%) were endemic to the AWT and four species were flightless and restricted to the higher elevations of a single gradient (i.e. subregional mountaintop endemics). These were *Temnoplectron involucre* and *Amphistomus pectoralis* in Spec and *Temnoplectron lewisense* and *Amphistomus NQ1* in Carbine.

Rank–abundance patterns were typical of an ecological field study (Figure 5.2. a) and comprised a few abundant species and many rare species (Preston 1948) with the five most abundant species collectively accounting for 53% of all individuals. Three out of the four flightless subregional endemics were within the eight most abundant species and collectively accounted for 27% of all individuals in the study (Figure 5.2. a).

The abundant large bodied species, *Coptodactyla depressa* (body length range 11–16 mm; mean dry weight 59.6 mg), *Temnoplectron politulum* (5.5–7.5 mm, 14.97 mg) and *T. reyi* (5.5–7.5 mm, 13.51 mg) contributed 53% of the total biomass with *Coptodactyla depressa* singly accounting for 31.6% of total biomass (Figure 5.2. b). In terms of biomass, the small *T. lewisense* (3.5–5.0 mm, mean dry weight 5.72 mg) and *A. NQ1* (4–6 mm, 4.79 mg) ranked fourth and fifth respectively, despite their small body size and weight, due to their very high abundance (Figure 5.2. a & b).

Table 5.1. Species abundance matrix of the four elevational gradients sampled in this study. Canth. = Canthonini; Copri. = Coprini; Ontho. = Onthophagini; * = flightless species; NE = species not endemic to the AWT.

	Subregional gradient		S	pec		Atherton				Carbine						Windsor			TOTAL			
Tribe	Assumed elevation (m a.s.l.)	350	600	800	1000	100	200	400	600	800	1000	100	200	400	600	800	1000	1200	900	1100	1300	
	Amphistomus complanatus					7	93	112	97	65	318	60	77	6	660	275	16		160	351	172	2469
	Amphistomus NQ1 *															60	3563	538				4161
	Amphistomus NQ3	3						4	16	654	937											1614
	Amphistomus NQ4/NQ5									498	121					474	5293	1839				8225
	Amphistomus pectoralis *			15	8																	23
	Amphistomus pygmaeus					22	1		1						654	346			114	2619	1022	4779
	Boletoscapter cornutus	12	10	1		1	1		1	1												27
	Lepanus arator						22					1		8	11	35				6		83
	Lepanus furcifer		6	1										1	4	1					1	14
	Lepanus globulus ^{NE}					11	26	22	34	64	169	12	28	17	47	3	11		3			447
	Lepanus latheticus	40					9	1	15			1			7	1				11	2	87
	Lepanus monteithi									7	6	2				1			1			17
	Lepanus nitidus/dichrous					1	38	23	29	58	164	6		16	46	8	144		24			557
	Lepanus NQ2	2	1	1																		4
Canth	Lepanus palumensis	44	609	779	265																	1697
	Lepanus parapisoniae ^{NE}	2	2					1			6	4	2	13	3				1			34
	Lepanus pisoniae ^{NE}	1							2		6	24	1	14	37	2		2	39	3	26	157
	Lepanus ustulatus ^{NE}					1				1												2
	Lepanus villosus						100	19	5	1	14						8					147
	Monoplistes curvipes											1										1
	Monoplistes sp1					1	1															2
	Temnoplectron aeneopiceum	2	619	503	21			111	843		943											3042
	Temnoplectron bornemisszai								35	78	312			1	1		2		23	53	1	506
	Temnoplectron involucre *		1	1132	2506																	3639
	Temnoplectron laeve ^{NE}	130	53	3																		186
	Temnoplectron lewisense *															133	7414	1292				8839
	Temnoplectron politulum					173	576	3359	102	2116	549											6875
	Temnoplectron reyi											90	44	123	2230	579	1	1	149	703	79	3999
	Temnoplectron subvolitans									703					2	2	1994	138				2839
	Coptodactyla depressa	41	180	66	7	151	37	381	138	147	223	18	66	5	17	2	91	6	1357	722	1	3656
Copri	Coptodactyla nitida	202	5																			207
	Coptodactyla onitoides 🔤																		154	6		160
	Onthophagus bornemisszanus	3																				3
	Onthophagus bundara									4	1				1		24	19				49
	Onthophagus capella 🗠						2				2											4
	Onthophagus capelliformis					2	6				1											9
	Onthophagus darlingtoni							1	2	11	17				6	1	10	7		2		57
	Onthophagus dicranocerus						2	27	30	40	18				23	20	58	185		8	5	416
	Onthophagus gulmarri								-										4	6		10
	Onthophagus millamilla									1	24				7	130	133	172	1			468
Ontho	Onthophagus mulgravei					71	14	44	6			7	17	234	44	2			85			524
	Onthophagus mundill								-	1				60	26	9	8	34	3	65	38	244
	Onthophagus paluma				1				-			1						-	6			8
	Onthophagus pillara								3	6	3						15	2	4	1		34
	Unthophagus rubicundulus ""							45	4.6	100	43									<u> </u>		43
	Unthophagus wagamen						0-	15	16	186	37			1				79		1		335
	Unthophagus waminda						85	14	15	9	4				94	50	144	158	2	206	23	804
	Onthophagus yiryoront					4	1													20		5
	Untnophagus yungaburra																		14	28		42
I	TOTAL	482	1486	2501	2808	445	1014	4134	1390	4651	3918	227	235	499	3920	2134	18929	4472	2144	4791	1370	61550



Figure 5.2. a) Rank-abundance and **b)** rank-biomass plots of all species based on standardised abundance and biomass data. The highest ranking species are shown and an asterisk (*) denotes flightlessness.

5.3.2 Sampling completeness

Coverage-based rarefaction using iNEXT showed that sampling was complete at all sites (Table 5.2). Thus, extrapolated species richness was similar to sampled species richness, attaining highly significant correlations (Sm: Pearson's R = 0.90, P < 0.0001; Chao1: Pearson's R = 0.85, P < 0.0001). Total sampled species richness, total standardised abundance, and total standardised biomass were highly correlated to their respective means (Pearson's R > 0.97, P < 0.0001) and so total values, rather than means, were used in all further analyses.

5.3.3 Patterns of biodiversity along individual elevational gradients

5.3.3.1 Spec

The Spec gradient showed a slight decrease in species richness and an increase in abundance with increasing elevation (Figures 5.3. a & e). Biomass initially decreased with elevation but then increased sharply above 800 m a.s.l. (Figure 5.3. i). Diversity (as effective number of species) calculated using abundance and biomass, decreased

with elevation with a sharp decrease above 800 m (Figures 5.3. m & q). Dominance calculated using abundance and biomass was symmetrical to diversity with a sharp increase in dominance above 800 m (Figure 4. m & q). This increase in dominance and subsequent decrease in diversity was primarily due to the presence and very high abundance and biomass of the flightless species *T. involucre*, that is endemic to Spec and restricted to elevations above 800 m (Figure 5.4. a & b; Table 5.1). Furthermore, the abundance and biomass of *T. involucre* at 1000 m was greater than the combined total abundance and biomass of all other species found at that site (Figures 5.5. a & d). Elevational band area increased slightly with elevation, followed by a decrease after 800 m, with habitat heterogeneity being greatest at 800 m (Figure 5.3. u).

Table 5.2. Sampling sites showing total sampled species richness, abundance, and biomass. \hat{c} = the estimator of sample coverage suggested by Chao and Jost (2012). Sm = the estimated prediction function based on double sampling size (Chao and Jost 2012). Chao 1 = the commonly used estimator of species richness (Chao 1984). Note that values for SU10 are based on one year of monthly sampling whereas all other sites are based on two years of monthly sampling.

Site code	Elevation m a.s.l. (digital)	Elevation m a.s.l. (assumed)	Richness Total	Abundance Standardised total	Biomass (g) Standardised total	ĉ	Sm - double sample size	Chao1
SU35	334	350	12	482	16.85	0.9980	12.17	12.17
SU6	671	600	10	1486	21.06	0.9987	11.88	12.00
SU8	834	800	9	2501	14.79	0.9988	11.14	12.00
SU10	950	1000	6	2808	9.96	0.9996	6.00	6.00
AU1	80	100	12	445	12.25	0.9910	19.98	19.98
AU2	180	200	17	1014	12.56	0.9961	20.99	21.00
AU4	428	400	16	4135	73.46	0.9990	18.40	21.00
AU6	630	600	19	1390	23.33	0.9986	20.00	20.00
AU8	840	800	21	4651	66.22	0.9987	26.93	37.00
AU10	930	1000	23	3918	71.04	0.9995	24.49	25.00
CU1	115	100	13	227	3.24	0.9824	20.96	20.96
CU2	234	200	7	235	5.78	0.9958	7.50	7.50
CU4	440	400	13	499	7.01	0.9940	15.99	15.99
CU6	656	600	20	3920	44.67	0.9997	20.50	20.50
CU8	820	800	21	2134	17.39	0.9977	25.12	25.12
CU10	1016	1000	18	18929	79.03	1.0000	19.43	19.50
CU12	1210	1200	15	4472	27.13	0.9998	15.25	15.25
WU9	940	900	19	2144	92.33	0.9986	23.05	23.50
WU11	1071	1100	17	4791	74.9	0.9998	17.43	17.50
WU13	1280	1300	11	1370	10.06	0.9978	14.25	14.25



Figure 5.3. The four elevational gradients showing patterns of species richness (observed: solid line, predicted: dashed line), abundance, biomass, diversity (as Jost's effective number of species or exponent of Shannon entropy; x–axis), and dominance (Berger–Parker index; y–axis) based on species abundance and biomass (diversity: solid line, dominance: dashed line), total area (km²) per elevational band (solid line) and habitat heterogeneity (dashed line).



Figure 5.4. Elevational patterns of abundance and biomass of the most common species at each elevational gradient. The percentage next to the name of each gradient indicates the accumulative frequency of the plotted species. Note that the same coloured line in a different gradient does not correspond to the same species.



Figure 5.5. (**a**–**c**) Elevational abundance and (**d**–**f**) biomass of the dominant species at high elevations (closed circles, solid line) in relation to the abundance and biomass of all other species combined (open circles, dotted line). Windsor did not have any dominant upland species so it is not shown. Upland species, Spec: *Temnoplectron involucre**; Atherton: *Amphistomus NQ4/5, T. bornemisszai, T. subvolitans*; Carbine: *T. lewisense*, A. NQ1*, A. NQ4/5, T. subvolitans*. An asterisk (*) denotes subregional flightless endemics.

5.3.3.2 Atherton

Within the Atherton gradient, species richness increased with elevation with the 1000 m site having the greatest species richness of all sites in this study (Figure 5.3. b). Abundance and biomass also increased with elevation but showed a distinct trough at 600 m with peaks at 400 m and 800 m (Figures 5.3. f & j). Diversity calculated using abundance showed a sharp drop at 400 m, with 1000 m being the most diverse (Figure 5.3. n), whereas dominance based on abundance was greatest at 400 m and least at 1000 m (Figure 5.3. x). This was due to the high abundance of *T. politulum* dominating at 400 m, and the relatively similar abundance of many species at 1000 m (Figure 5.4. c). However, dominance regarding biomass at 400 m was not as pronounced (Figure 5.3. r), as it was shared with the less abundant but larger *C. depressa* (Figure 5.4. d). The trough in abundance and biomass at 600 m with a steady increase up to 1000 m was accompanied by an increase in diversity and
decrease in dominance indicating that both individuals and biomass were evenly distributed between more species (Figures 5.4. c & d). The high elevations of Atherton were not dominated by a few species, unlike Spec and Carbine (Figure 5.5. b & e). Elevational band area decreased slightly with elevation and habitat heterogeneity showed a distinct trough at 600 m and peaked at 800 m (Figure 5.3. v).

5.3.3.3 Carbine

The Carbine gradient demonstrated a hump-shape relationship with elevation with a peak at 800 m (Figure 5.3. c). Abundance and biomass increased with elevation but with two peaks at 600 m and 1000 m, and a drop at 800 m (Figures 5.3. g & k). The 1000 m site had the most number of individuals of any other site in this study (Figure 5.3. g). An examination of individual species abundances and biomass values indicated that 600 m was dominated by three species and 1000 m by a different set of four species, two of which are flightless subregional endemics, *Temnoplectron lewisense* and *Amphistomus NQ1*, and both restricted to elevations above 800 m (Figure 5.4. e & f; Table 5.1). The total abundance and biomass of the four high elevation species was greater than the combined total of all other remaining species (Figure 5.5. c & f). Elevational band area slightly decreased up to 800 m where it then increased up to 1000 m and 1200 m (Figure 5.3. w). Habitat heterogeneity peaked at 200 m then decreased up to 800 m where it increased again above this elevation (Figure 5.3. w).

5.3.3.4 Windsor

Species richness and biomass decreased with elevation although abundance peaked at 1100 m (Figures 5.3. d, h, i). Dominance in terms of abundance increased with elevation but decreased in terms of biomass (Figure 5.3. p & t). This was mostly due to a high abundance of the large and heavy *Coptodactyla depressa* at 900 m that dominated in terms of biomass and also led to the 900 m site having the greatest biomass of any other site in this study (Figures 5.3. i, 5.4. g & h). Elevational band area decreased with elevation while habitat heterogeneity was greatest at 1100 m (Figure 5.3. x).

5.3.4 Patterns of biodiversity resulting from the combination of elevational gradients

All elevational sites were combined to reach a clearer representation of the elevational patterns throughout the AWT. The Atherton, Carbine and Windsor gradients collectively produced a clear hump-shaped pattern with elevation whereas the Spec gradient displayed a monotonic decrease in richness (Appendix 11). Thus, the Spec gradient was removed from the combined species richness analysis, although reasons for its differing richness patterns are explored in the discussion. However, the Spec sites (excluding the 1000 m site that was sampled for one year instead of two) were retained in the abundance and biomass analyses. Due to low sample size (species richness: n = 16 sites; abundance and biomass: n = 19 sites), interactions between predictor variables could not be investigated and thus only bivariate GAMM regressions were performed.

5.3.5 Dung beetle elevational patterns of biodiversity and their environmental correlates

5.3.5.1 Species richness

Dung beetle species richness showed a hump-shaped relationship with elevation, peaking around 800 m (Figure 5.6. a). This significant, non-linear relationship with elevation, accounted for 63% of the variance in species richness (Table 5.3).

Species richness also showed significant unimodal relationships with mean annual temperature, maximum temperature of the warmest period, and habitat stability (Table 5.3). That is, species richness was highest at elevations where mean annual temperature ranges between 20–22 °C (Figure 5.6. b), the maximum temperature of the warmest period ranges between 28.5–29.5 °C (Figure 5.6. c), and the habitat stability index ranges between -60 – -100 (Figure 5.6. f).

Dung beetle species richness was greatest in cooler environments and with greater mammal biomass, as indicated by significant near-linear relationships between dung beetle species richness and the minimum temperature of the coldest period, and mammal biomass (Figures 5.6. d & e; Table 5.3).

The most variance in dung beetle species richness was explained by the maximum temperature of the warmest period (53%), annual mean temperature (47%) and habitat stability (37%; Table 5.3).



Figure 5.6. Significant relationships between dung beetle species richness and environmental variables based on Generalised Additive Mixed Models (GAMM). Dashed lines are ± 2 standard errors. Statistical details of models are presented in Table5.3. Green: Atherton; blue: Carbine; orange: Windsor.

5.3.5.2 Abundance

Dung beetle abundance was greatest at higher elevations that have cooler temperatures, greater mammal species richness and biomass, and that have been more stable (Figure 5.7). This was demonstrated by dung beetle (log) abundance showing significant near-linear positive relationships with elevation, mammal species richness, mammal biomass, and habitat stability, and negative relationships with annual mean temperature, maximum temperature of the warmest period, and minimum temperature of the coldest period (Figure 5.7; Table 5.3).

The most variance in dung beetle abundance was explained by mammal biomass (65%), annual mean temperature (63%), and maximum temperature of the warmest period (60%; Table 5.3).



Figure 5.7. Significant relationships between dung beetle log abundance and environmental variables based on Generalised Additive Mixed Models (GAMM). Dashed lines are ± 2 standard errors. Statistical details of models are presented in Table 5.3. Red: Spec (excluding SU10); green: Atherton; blue: Carbine; orange: Windsor.

5.3.5.3 Biomass

Dung beetle (log) biomass exhibited a unimodal relationship with elevation, peaking at 1000 m (Figure 5.8. a). Near-unimodal significant relationships were also identified with mean annual temperature (peak at 20.5 °C; Figure 5.8. b), maximum temperature of the warmest period (peak at 28.5 °C; Figure 5.8. c), minimum temperature of the

coldest period (peak at 12 °C; Figure 5.8. d) and habitat stability (peak at -60; Figure 5.8. g). Near-linear relationships were identified with mammal species richness and mammal biomass, with dung beetle biomass increasing with an increase in mammal species richness (Figure 5.8. e) and mammal biomass (Figure 5.8. f).

The most variance in dung beetle biomass was explained by annual mean temperature (52%), maximum temperature of the warmest period (48%), and mammal biomass (48%; Table 5.3).



Figure 5.8. Significant relationships between dung beetle log biomass and environmental variables based on Generalised Additive Mixed Models (GAMM). Dashed lines are ± 2 standard errors. Statistical details of models are presented in Table 5.3. Red: Spec (excluding SU10); green: Atherton; blue: Carbine; orange: Windsor.

Table 5.3. Results of Generalised Additive Mixed Models (GAMM) used to model the response of dung beetle species richness, abundance, and biomass to various environmental variables, with subregion included as a random variable. Only statistically significant relationships are shown. edf = estimated degrees of freedom for smooth term (1= linear); F = F-statistic; $r^2 =$ proportion of variance explained; **** p<0.0001, *** p<0.001, ** p<0.01, * p<0.05

	Specie	es richne	ss (n=16)	Log	abundar	nce (<i>n</i> =19)	Log biomass (n=19)			
Predictor variable	edf	F	r^2	edf	F	r^2	edf	F	\mathbf{r}^2	
Elevation	3.307	7.076	0.632 **	2.204	13.024	0.590 ***	2.962	6.172	0.440 **	
Latitude Annual mean temperature (bc01) Temperature concorrelity (bc04)	2.594	4.959	0.477 *	2.360	16.949	0.631 ****	2.446	8.530	0.524 **	
Max. temp. of warmest quarter (bc05) Min. temp. of coldest	2.707	7.045	0.532 **	2.250	12.845	0.589 ***	2.587	7.820	0.484 **	
quarter (bc06) Total annual precipitation (bc12) Precipitation	1	10.527	0.374 **	1.871	17.393	0.382 ****	2.079	7.484	0.431 **	
seasonality (bc15) Prec. of wettest quarter (bc16)										
Prec. of driest quarter (bc17)										
Mammal richness				1.443	14.614	0.501 ***	1.527	7.101	0.301 **	
Mammal biomass (log)	1.143	8.244	0.347 *	1	37.263	0.654 ****	1	18.921	0.484 ***	
Habitat stability	2.304	4.546	0.376 *	2.168	16.482	0.553 ****	1.935	8.191	0.469 **	
Log elevational band area (km ²)										
Habitat heterogeneity										
Soil pH										
Soil sand content										
Soil silt content										
Soil clay content										

5.3.5.4 Elevational band area and habitat heterogeneity

Rainforest elevational band area (log) and habitat heterogeneity, two variables corresponding to well-established hypotheses explaining patterns of species richness, were not significantly related to dung beetle species richness, abundance, or biomass. Also, precipitation and soil variables were not significantly related to dung beetle species richness, abundance or biomass (Table 5.3).

5.3.5.5 Species elevational range size

Species at higher elevations of the Spec, Atherton, and Carbine gradients have a narrow range size (i.e. contradicted Rapoport's rule; Figures 5.9. a; 5.10. a–c). Species on Windsor increase in elevational range size with increasing elevation (i.e. in line with Rapoport's Rule; Figures 5.9. a & 5.10. d). Additionally, species with a narrow range size have greater total abundance (Figure 5.9. b).



Figure 5.9. Relationships between **a**) elevation and mean elevational range and **b**) mean elevational range and log abundance within the four AWT subregional elevational gradients. Species with a total abundance of less than 10 individuals (n = 9) were excluded. Red: Spec; green: Atherton; blue: Carbine; orange: Windsor.



Figure 5.10. Species ranges along the four elevational gradients. Species range was assumed to be continuous between sampled minimum and maximum elevational presence. Circles denote species that were only sampled at one elevation within that subregion, although the same species may have a broader range within other subregions. Open circles and dashed lines denote species that were only sampled within a single gradient. Red colour denotes true subregional endemics (i.e. restricted to that gradient).

5.3.5.6 Species composition and assemblage structure

Species assemblages appeared to be structured by subregional biogeography and elevation, and did not differ between the two sampling years ($m_{12} = 0.022$, Procrustes correlation r = 0.988, P < 0.001). This was demonstrated by the NMDS (Figure 5.11. a) and hierarchical cluster analyses (Figure 5.11. b). The first NMDS dimension separated the sites according to latitude/subregion (Figures 5.11. a & 5.12. a) and temperature seasonality (bc04; Figures 5.11. c & 5.12. b) with the entire Spec gradient being very dissimilar to the rest of the sites due to greater temperature seasonality (Figure 5.12. b). The second NMDS dimension separated sites according to elevation (Figures 5.11. a & 5.13. a) and assemblage structure was correlated with the maximum temperature of the warmest period, mammal species richness, mammal biomass, and habitat stability (Figures 5.11. c & 5.13).

The greatest dissimilarity in dung beetle assemblage structure occurred between the entire Spec gradient and all other sites (Figure 5.11. b). The assemblage structure of the two highest elevation sites (1000 m and 1200 m) of Carbine was dissimilar to the remaining Carbine, Windsor and Atherton sites (Figures 5.11. a & b). Assemblage structure of the Windsor sites was most similar to the Carbine 600 m and 800 m sites (Figures 5.11. a & b). All Atherton sites were grouped together but separated according to elevation with the assemblage structure of the lowest elevation (100 m) being most dissimilar to the mid-elevational, 200 m – 600 m, and high-elevational, 800 m and 1000 m, groups (Figures 5.11. a & b).

Dissimilarity between high and low elevation assemblages resulting from restricted species distributions was also demonstrated by the indicator species analysis. Species occurring in assemblage cluster groups containing high elevation sites had more of their total abundance concentrated within those sites, thus resulting in high indicator values (IndVal; Table 5.4). Alternatively, the indicator species of low/mid elevation site clusters, particularly of Atherton and Carbine, had low indicator values, implying that species abundance was more spread among other sites, i.e. they were not site-specific (Table 5.4). Furthermore, the species most indicative of the high elevation sites of Carbine (1000 m & 1200 m) and Spec (800 m & 1000 m) were flightless subregional endemics (Table 5.4).



Figure 5.11. (a) Non-metric multidimensional scaling (NMDS) ordination (stress = 0.10) of the dung beetle assemblage along the four AWT elevational gradients using the Bray-Curtis distance metric. Labels correspond to the assumed elevation of each site (see Table 5.1). Coloured ellipses correspond to cluster groups identified in the hierarchical cluster analysis with the dendrogram sliced at a height of 0.42. (b) Hierarchical cluster dendrogram using average linkage methods for all elevational sites. Labels correspond to the assumed elevation of each site. (c) Environmental vectors showing the direction and magnitude of significant correlations (P< 0.001) within the ordination space of Figure 5.11. a., mam_rich: mammal species richness, mam_bio: mammal biomass, hs: habitat stability, bc04: temperature seasonality, bc05: maximum temperature of the warmest period.



Figure 5.12. Linear regression relationships between the first NMDS Dimension with (a) latitude ($F_{1,18} = 121.9$, Adj. R² = 0.86, P < 0.001) and (b) temperature seasonality (bc04; $F_{1,18} = 68.55$, Adj. R² = 0.78, P < 0.001).



Figure 5.13. Linear regression relationships of the second NMDS Dimension with (**a**) elevation ($F_{1,18} = 10.61$, Adj. $R^2 = 0.34$, P = 0.004), (**b**) maximum temperature of the warmest period (bc05; $F_{1,18} = 12.53$, Adj. $R^2 = 0.38$, P = 0.002), (**c**) mammal species richness ($F_{1,18} = 25.71$, Adj. $R^2 = 0.57$, P < 0.001), (**d**) mammal biomass ($F_{1,18} = 26.66$, Adj. $R^2 = 0.58$, P < 0.001) and (**e**) habitat stability ($F_{1,18} = 21.91$, Adj. $R^2 = 0.52$, P < 0.001).

Cluster group	Sites	Indicator species	IndVal	Flightless Y = Yes
8	SU35,	Coptodactyla nitida	1.000	
	SU6	Temnoplectron laeve	0.915	
7	SU8,	Amphistomus pectoralis	1.000	Y
1	SU10	Temnoplectron involucre	0.988	Y
1	A T T 1	Onthophagus yiryoront	0.857	
1	AUI	Lepanus ustulatus	0.667	
3	AU2, AU4,	Lepanus villosus	0.594	
	AU6	Temnoplectron politulum	0.391	
2	AU8,	Amphistomus NQ3	0.907	
2	AU10	Lepanus monteithi	0.597	
4	CU1, CU2,	Lepanus parapisoniae	0.347	
4	CU4	Onthophagus mulgravei	0.333	
6	CU6, CU8,	Amphistomus pygmaeus	0.665	
0	WU11, WU13	Temnoplectron reyi	0.545	
0	WIIO	Coptodactyla onitoides	0.953	
9	W U9	Onthophagus gulmarri	0.766	
5	CU10,	Amphistomus NQ1	0.955	Y
5	CU12	Temnoplectron lewisense	0.955	Y

Table 5.4. The top two indicator species with the highest Indicator-species-Value (IndVal) for each ordination/cluster group.

5.3.5.7 β-diversity partition

Partitioning the incidence-based dissimilarity between sites revealed that patterns in species composition were mostly attributed to species turnover i.e. replacement, and to a much lesser degree, nestedness (Table 5.5; note higher values of turnover indicated by hotter colours above the diagonal). However, the species found at lower elevational sites (\leq 400 m) of Carbine are nested subsets of the species richer 600 m and 800 m sites of the same gradient and of the entire Windsor gradient, as indicated by moderate values of nestedness and lower values of turnover between these sites (Table 5.5).

Incorporating species abundances and partitioning the abundance-based dissimilarity between sites revealed that the patterns in assemblage structure were mostly due to balanced-variation in species abundances. That is, individuals of some species in one site were substituted by a similar number of individuals of different species in another site, rather than the loss of individuals of the same species between sites, i.e. abundance–gradients (Table 5.6; note higher values of balanced–variation indicated by hotter colours above the diagonal). However, higher abundance–gradient values and lower balanced–variation values of the low elevations of Carbine with the mid elevations of Carbine and the entire Windsor gradient indicate that these sites share similar species with differences in their abundance (Table 5.6).

5.4 Discussion

Dung beetle patterns of biodiversity along elevational gradients in the AWT are driven by the regions' refugial history in combination with climate and mammal diversity. Historically stable habitats in the form of upland rainforest refugia have given rise to differing dung beetle assemblages between and among mountains, i.e. subregions, with evidence of recolonisation during rainforest expansion events. Isolation, persistence, and speciation within upland refugia resulted in distinct, cooladapted, upland species assemblages that are generally more species rich, abundant, have greater biomass, and have narrower elevational ranges compared to lowland assemblages. In the lowlands, species poor and nested assemblages indicate extinction and extirpation events with subsequent recolonisation from the species rich high elevations, albeit by climate generalists capable of recolonising the hotter lowlands. The results of this Chapter further support the findings of Chapter 4.

Isolation and persistence of dung beetle populations in upland refugia gave rise to allopatric speciation. This contributed towards the observed assemblage dissimilarity between, and along, elevational gradients that was characterised by a high degree of species turnover in β -diversity. Allopatric speciation is indicated by the presence of species restricted to the highest elevations of a single mountain (i.e. subregional endemics), for example, the flightless *Temnoplectron involucre* and *Amphistomus pectoralis* from the Spec gradient, and *T. lewisense* and *A. NQ1* from the Carbine gradient.

Table 5.5. Partitioned β -diversity of species presence-absence matrix of all elevational sampling sites into turnover (β_{SIM} , cells above the diagonal) and nestedness (β_{NES} , cells below the diagonal). The addition of β_{SIM} with β_{NES} yields the Sørenson dissimilarity (β_{SOR}) (see Baselga 2010). To aid interpretation cells are colour coded with hotter colours indicating higher values.

Sites	SU35	SU6	SU8	SU10B	AU1	AU2	AU4	AU6	AU8	AU10	CU1	CU2	CU4	CU6	CU8	CU10	CU12	WU9	WU11	WU13
SU35		0.286	0.429	0.500	0.833	0.750	0.583	0.500	0.750	0.583	0.667	0.571	0.750	0.667	0.750	0.917	0.833	0.750	0.750	0.750
SU6	0.188		0.143	0.333	0.714	0.714	0.714	0.571	0.714	0.714	0.857	0.857	0.714	0.714	0.714	0.857	0.857	0.857	0.857	0.714
SU8	0.150	0.000		0.167	0.714	0.714	0.714	0.571	0.714	0.714	0.857	0.857	0.714	0.714	0.714	0.857	0.857	0.857	0.857	0.714
SU10B	0.167	0.051	0.064		0.833	0.833	0.667	0.667	0.833	0.667	0.667	0.833	0.833	0.833	0.833	0.833	0.833	0.667	0.833	0.833
AU1	0.000	0.075	0.075	0.056		0.083	0.500	0.333	0.417	0.500	0.583	0.429	0.583	0.500	0.500	0.667	0.917	0.500	0.750	0.750
AU2	0.043	0.119	0.119	0.080	0.158		0.333	0.294	0.471	0.412	0.462	0.429	0.538	0.412	0.412	0.588	0.800	0.588	0.588	0.500
AU4	0.046	0.104	0.104	0.143	0.056	0.042		0.067	0.267	0.133	0.462	0.286	0.462	0.333	0.400	0.467	0.667	0.533	0.533	0.583
AU6	0.113	0.198	0.198	0.173	0.151	0.039	0.110		0.263	0.211	0.462	0.286	0.385	0.368	0.421	0.444	0.533	0.474	0.353	0.333
AU8	0.074	0.148	0.148	0.095	0.172	0.068	0.139	0.054		0.227	0.615	0.571	0.462	0.400	0.409	0.167	0.267	0.474	0.471	0.417
AU10	0.131	0.152	0.152	0.195	0.157	0.088	0.182	0.075	0.017		0.462	0.286	0.385	0.400	0.500	0.278	0.333	0.421	0.471	0.500
CU1	0.013	0.043	0.043	0.123	0.017	0.072	0.038	0.101	0.099	0.150		0.000	0.308	0.231	0.231	0.615	0.769	0.231	0.538	0.583
CU2	0.113	0.000	0.000	0.013	0.150	0.238	0.260	0.330	0.222	0.381	0.300		0.000	0.000	0.143	0.429	0.571	0.000	0.429	0.429
CU4	0.010	0.086	0.086	0.061	0.017	0.062	0.038	0.115	0.138	0.171	0.000	0.300		0.077	0.231	0.462	0.615	0.231	0.385	0.417
CU6	0.083	0.138	0.138	0.090	0.125	0.048	0.095	0.016	0.029	0.042	0.163	0.481	0.196		0.150	0.278	0.333	0.316	0.294	0.083
CU8	0.074	0.148	0.148	0.095	0.147	0.075	0.114	0.042	0.000	0.011	0.198	0.443	0.198	0.040		0.222	0.200	0.368	0.353	0.083
CU10	0.017	0.063	0.063	0.083	0.067	0.012	0.048	0.015	0.083	0.088	0.062	0.251	0.087	0.038	0.078		0.133	0.444	0.471	0.417
CU12	0.019	0.052	0.052	0.071	0.009	0.013	0.000	0.055	0.139	0.140	0.016	0.156	0.027	0.095	0.151	0.079		0.533	0.400	0.500
WU9	0.056	0.066	0.066	0.173	0.113	0.023	0.055	0.000	0.039	0.055	0.144	0.462	0.144	0.018	0.046	0.015	0.055		0.294	0.333
WU11	0.043	0.060	0.060	0.080	0.043	0.000	0.029	0.036	0.068	0.079	0.062	0.238	0.082	0.057	0.083	0.015	0.038	0.039		0.167
WU13	0.000	0.075	0.075	0.056	0.000	0.086	0.046	0.151	0.172	0.157	0.017	0.150	0.023	0.229	0.270	0.117	0.056	0.151	0.144	

Table 5.6. Partitioned Bray–Curtis dissimilarity of species-abundance matrix into balanced–variation in species abundances (Bray_{bal}; i.e. individuals of some species in one site are substituted by the same number of individuals of different species n another site; cells above the diagonal) and abundance–gradients (Bray_{gra}; i.e. some individuals are lost from one site to another; Bray_{GRA}, cells below the diagonal). The addition of Bray_{BAL} and Bray_{GRA} yields the Bray-Curtis dissimilarity index(see Baselga 2013). To aid interpretation cells are colour coded with hotter colours indicating higher values.

Sites	SU35	SU6	SU8	SU10B	AU1	AU2	AU4	AU6	AU8	AU10	CU1	CU2	CU4	CU6	CU8	CU10	CU12	WU9	WU11	WU13
SU35		0.716	0.800	0.817	0.919	0.889	0.903	0.853	0.913	0.903	0.907	0.891	0.977	0.914	0.987	0.922	0.977	0.916	0.883	0.987
SU6	0.066		0.419	0.623	0.861	0.922	0.648	0.348	0.873	0.350	0.921	0.740	0.988	0.961	0.994	0.875	0.988	0.875	0.875	0.996
SU8	0.078	0.102		0.143	0.973	0.983	0.824	0.817	0.983	0.818	0.952	0.953	0.988	0.983	0.996	0.984	0.991	0.984	0.984	0.997
SU10B	0.139	0.240	0.445		0.984	0.993	0.987	0.979	0.997	0.987	0.965	0.970	0.990	0.997	0.999	0.997	0.997	0.996	0.997	0.999
AU1	0.015	0.006	0.006	0.010		0.440	0.130	0.400	0.234	0.227	0.806	0.570	0.789	0.771	0.917	0.753	0.987	0.427	0.596	0.933
AU2	0.060	0.027	0.003	0.003	0.218		0.210	0.679	0.255	0.245	0.537	0.345	0.868	0.710	0.819	0.806	0.908	0.828	0.770	0.880
AU4	0.084	0.278	0.125	0.004	0.701	0.479		0.593	0.412	0.720	0.537	0.221	0.820	0.934	0.924	0.954	0.985	0.736	0.875	0.903
AU6	0.094	0.313	0.061	0.005	0.309	0.050	0.202		0.654	0.033	0.537	0.243	0.892	0.832	0.891	0.853	0.947	0.785	0.776	0.910
AU8	0.077	0.103	0.013	0.001	0.632	0.478	0.035	0.187		0.536	0.568	0.323	0.906	0.944	0.725	0.688	0.824	0.874	0.938	0.940
AU10	0.083	0.506	0.127	0.004	0.615	0.445	0.008	0.461	0.040		0.524	0.260	0.884	0.879	0.785	0.884	0.943	0.792	0.844	0.862
CU1	0.013	0.029	0.025	0.029	0.063	0.293	0.414	0.333	0.392	0.424		0.366	0.361	0.026	0.260	0.771	0.960	0.070	0.238	0.273
CU2	0.014	0.091	0.023	0.024	0.133	0.409	0.695	0.538	0.612	0.657	0.011		0.609	0.209	0.451	0.600	0.966	0.111	0.200	0.477
CU4	0.006	0.000	0.002	0.006	0.012	0.045	0.142	0.051	0.076	0.090	0.239	0.141		0.471	0.671	0.904	0.914	0.485	0.589	0.719
CU6	0.073	0.030	0.012	0.001	0.182	0.171	0.002	0.080	0.005	0.000	0.867	0.702	0.410		0.382	0.941	0.957	0.741	0.522	0.278
CU8	0.010	0.004	0.002	0.000	0.054	0.065	0.024	0.023	0.102	0.063	0.598	0.440	0.204	0.182		0.575	0.586	0.791	0.401	0.534
CU10	0.075	0.119	0.015	0.003	0.236	0.175	0.030	0.127	0.189	0.076	0.224	0.390	0.091	0.039	0.339		0.064	0.931	0.943	0.960
CU12	0.020	0.010	0.006	0.001	0.011	0.058	0.001	0.028	0.003	0.004	0.036	0.031	0.069	0.003	0.146	0.578		0.992	0.952	0.952
WU9	0.063	0.079	0.008	0.000	0.376	0.061	0.084	0.046	0.047	0.061	0.752	0.714	0.321	0.076	0.000	0.055	0.003		0.440	0.719
WU11	0.103	0.102	0.012	0.001	0.336	0.150	0.009	0.123	0.001	0.016	0.693	0.725	0.333	0.048	0.230	0.034	0.002	0.214		0.019
WU13	0.008	0.002	0.001	0.000	0.034	0.018	0.049	0.001	0.033	0.066	0.520	0.370	0.131	0.347	0.101	0.035	0.026	0.062	0.544	

Both Spec and Carbine have sustained isolated rainforest refugia (Hilbert et al. 2007, VanDerWal et al. 2009a). Molecular (mtDNA) analysis suggests that speciation of *T. involucre* and *T. lewisense* (along with another two subregionally endemic *Temnoplectron* species found in subregions not sampled in this study) occurred almost simultaneously from a common ancestor, confirming allopatric speciation of a single, once widespread species (Bell et al. 2004). Vicariance has also been proposed as the most likely mode of speciation for other high elevation endemic insects (Yeates et al. 2002, Bouchard et al. 2005) and vertebrates (Williams et al. 2008a) in the AWT.

The loss of flight and a reduction in body size is expected for species isolated within spatially restricted refugia (Darlington 1943, Roff 1990, Scholtz 2009b). Dispersal in order to track or locate resources and favourable environments (i.e. climate) becomes redundant within isolated, and climatically stable refugia (Darlington 1943, Roff 1990, Roff 1994a, b). Lower temperatures associated with high elevation refugia inhibit insect flight and energy invested in wings and wing muscle development is wasted (Roff 1990). Thus, a positive selection pressure towards flightlessness arises as the loss of wings and associated flight muscles allows energy to be re-diverted, ensuring faster developmental times and increased reproductive output (Roff 1990, Scholtz 2009b). The four flightless species mentioned above have a small body size, 3.5-6 mm (for comparison, the largest dung beetle species sampled in this study, Onthophagus capella Kirby, has a maximum body size of 17 mm). As refugia were in effect islands of suitable habitat surrounded by a sea of unfavourable environmental conditions (Nix 1991), species isolated within them underwent a decrease in body size, in line with the island rule (Lomolino 2005). A reduction in body size facilitates survival in resource-poor environments, such as isolated refugia, as fewer resources are required to attain a large population size (McNab 2002, 2010). Although the majority of studies investigating the island rule have focussed on vertebrates, and in particular mammals (see Lomolino 1985, 2005 and references therein), a reduction in body size on smaller islands has been documented for a tenebrionid beetle (Asida planipennis Schaufuss) in the western Mediterranean (Palmer 2002).

Many species became restricted to higher elevations as they adapted to the cooler and more stable temperatures of upland refugia. The confinement of upland species within their climatically suitable space resulted in narrower elevational range sizes. The hotter and more seasonal lowlands, inhabited by climate generalists, are in turn, characterised by broader elevational ranges. A pattern of decreasing elevational range size with increasing elevation contradicts Rapoport's rule (Stevens 1992). Rapoport's rule states that the elevational range of species increases with increasing elevation (Stevens 1992). This has been attributed to the generally broader climatic conditions that species have to tolerate at higher elevations. Broader climatic tolerances, in turn, allow species to occupy a wider elevational range. Clearly, this is not the case in the AWT, where species have adapted to the cooler and less seasonal climatic conditions of upland refugia. Restriction of many species to higher elevations implies a low tolerance to high temperatures and to greater temperature seasonality. Although thermal limits of the AWT dung beetles have not been investigated, a low tolerance to high temperatures has been identified in an AWT endemic upland vertebrate, Pseudocheirus archeri Collett - green ringtail possum (Krockenberger et al. 2012), Microhylid frogs (Andrés M. Viteri, pers. comm.), and Carabidae ground beetles (Kyran M. Staunton, pers. comm.). The above is supported by the fact that an inverse Rapoport's rule was identified for the Spec, Atherton, and Carbine gradients, that harboured refugia, while the Windsor gradient, that did not have a considerable refugium (and so did not support high elevation species), was in line with Rapoport's rule.

Narrow ranged species, inhabiting higher elevations were characterised by greater abundance and biomass. This is contrary to what is expected from narrow ranged species (Brown 1984). High local abundance of narrow ranged species has also been identified in some vertebrates of the AWT, and has been recognised as a means of compensating for geographic rarity and decreasing extinction risk (Williams et al. 2009). That is, geographically isolated, and hence, extinction prone species, are more likely to persist by attaining high local abundance (Williams et al. 2009). Furthermore, high local abundance allows the persistence of small bodied flightless species by increasing their probability of locating dung resources. That is, as stated by Matthews (1974) "...*the population density* [of flightless dung beetles] *must be exceptionally high...and food* [dung] *has to be sufficiently abundant for the beetles to, in effect, stumble across it with the necessary frequency*". Greater mammalian

species richness, abundance and biomass, also associated with rainforest refugia (Williams 1997, Williams et al. 2008a, Williams et al. 2009), result in greater dung resources at higher elevations, further contributing towards the increased abundance and biomass of high elevation dung beetle species.

The few hyper-abundant, upland species, dominated high elevation assemblages. For example, at the 1000 m site on the Spec gradient the abundance and biomass of T. involucre was greater than the combined abundance and biomass of all remaining species at that site. The same findings were identified for the combined abundance and biomass of the four most common species of the 1000 m and 1200 m sites of the Carbine gradient. However, this was not the case for the Atherton gradient, as total abundance and biomass at high elevations was shared between many species, and thus, resulted in low values of dominance and more effective number of species, i.e. more diverse (see Jost 2006). Interestingly, the highest elevations of the Spec and Carbine gradients are characterised by a decrease in dung beetle species richness, whereas species richness on the Atherton gradient steadily increases with elevation, peaking at the highest site. These differences can be attributed to the presence of hyper-abundant upland species that dominate resources and thus competitively exclude other species (Hanski 1991). Alternatively, the absence of hyper-abundant, subregionally endemic, upland species from Atherton, favours the coexistence of many equally abundant species, with the Atherton 1000 m site attaining the highest species richness and diversity values within this study.

Lowland dung beetle species underwent extinction or extirpation during rainforest contraction events. Many hot-adapted species were thus filtered from the AWT dung beetle assemblage, resulting in decreased species richness in the lowlands. During subsequent rainforest expansions, species that persisted in upland refugia, but could also tolerate higher temperatures, dispersed and recolonised the lowlands. This is indicated by moderate values of assemblage nestedness between the lowland and upland sites. Nestedness indicates non-random extinction events, with the species poor assemblages being subsets of the species rich assemblages (Baselga 2010, 2012). In turn, broader climatic tolerances of lowland species resulted in wider elevational ranges at lower elevations, as discussed above.

Dispersal and recolonisation also occurred between subregions, leading to assemblage nestedness between gradients (i.e. subregions). For example, Windsor, that did not harbour a refugium, was colonised from Carbine. This was indicated by assemblage nestedness between the lower elevations of Carbine with the Windsor gradient, coupled with the inclusion of the Windsor gradient with the Carbine gradient in the NMDS ordination and cluster analyses. As mentioned previously, dispersal would have taken place by species with broader climatic tolerances able to traverse the hotter lowlands. Thus, recolonisation occurred by the dung beetle species occurring in the Carbine lowlands, that also account for the increase in elevational range size with elevation, i.e. Rapoport's rule, found only on the Windsor gradient. However, the full elevational gradient of Windsor was not sampled due to the absence of rainforest, and so these findings should be viewed with caution.

Species richness on the Carbine gradient exhibited a hump shaped relationship with elevation. It has been postulated above that this may have arisen due to a decrease in species richness above 800 m resulting from the dominance, and thus, competitive exclusion of species by the hyper-abundant, small-bodied, flightless upland endemics. However, a peak at intermediate elevations could also arise due to the overlap of lowland and upland dung beetle assemblages. That is, on Carbine, many lowland species reach an upper elevational limit at the 800 m and 1000 m sites, and many upland species reach a lower elevational limit at the 600 m and 800 m sites. Consequently, the 800 m site corresponds to a transition zone between these two sets of species, and the greater overlap in elevational species ranges results in increased species richness. Furthermore, the 800 m site was characterised by a decrease in total abundance, biomass, and dominance, while diversity peaked. Inspection of individual species abundance and biomass along elevation identified two clear peaks in abundance, and especially biomass, between the lowland and upland assemblages. Abundance may be regarded as a sign of environment suitability, with species being more abundant where most of their niche requirements are met and less abundant where these requirements are not met (Brown 1984). At the 800 m Carbine site, this may indicate that both sets of species are found at the edges of their physiological or competitive optima, with no species being able to dominate, and thus resulting in a more diverse, species rich, mid-elevation community.

Patterns of elevational dung beetle species richness were not attributed to elevational band area and habitat heterogeneity, as significant relationships were not established between species richness and these variables. In fact, on some gradients, e.g. Carbine, both elevational band area and habitat heterogeneity were lowest at 800 m, and according to predictions, this site should have been characterised by low species richness values. However, the opposite was found with species richness peaking at this elevation (see above). Variation in soil type is also known to influence dung beetle species richness due to its effects on burying ability (Hanski and Cambefort 1991b). However, as with elevational band area and habitat heterogeneity, no relationship was found between dung beetles species richness and soil type, indicating the dominance of the other variables studied (see below) in structuring dung beetle biodiversity. Furthermore, it should be kept in mind that the full elevational range of the AWT was not sampled and the results of this study can benefit from sampling the upper elevational extent of other higher mountains/subregions.

In conclusion, dung beetle patterns of biodiversity along elevational gradients in the AWT are driven by the regions refugial history in combination with climate and mammal diversity. Isolation, persistence, and allopatric speciation on mountaintop refugia gave rise to distinct, species rich, high elevation assemblages. Speciation within geographically restricted refugia favoured the loss of flight and reduction in body size, as predicted by the island rule. Along with greater dung resources due to increased mammal species richness, abundance, and biomass at higher elevations, also attributed to rainforest refugia, these species achieved a high population size and dominated their assemblage by competitively excluding other species.

A decrease in species elevational range size with increasing elevation (inverse Rapoport's rule) suggests that adaptation to the cool and less seasonal upland environments gave rise to narrower climatic tolerances with intolerance to high temperatures. Species with broader climatic tolerances were able to disperse and recolonise the lowlands and other subregions following rainforest expansion events. A hump shaped relationship between species richness and elevation on the Carbine gradient can be explained by the overlap of lowland and upland assemblages.

Due to associations with upland refugia the dung beetles of the AWT are particularly threatened by climate change. This threat is exacerbated by the predicted impacts of climate change on their trophically dependent mammalian fauna (Williams et al. 2003, Williams et al. 2008b). Due to high levels of regional (AWT) and subregional (mountain) endemism within this landscape, any extinctions will result in the substantial loss of genetic diversity and thus evolutionary potential acquired during the region's biogeographic legacy.

CHAPTER 6. PROJECTED EFFECTS OF CLIMATE CHANGE ON THE DISTRIBUTION, POPULATION SIZE AND SPECIES RICHNESS OF THE AUSTRALIAN WET TROPICS ENDEMIC DUNG BEETLES

6.1 Introduction

Anthropogenic climate change is a major threat to global biodiversity, threatening many ecosystems and taxa with extinction (Miles et al. 2004, Thomas et al. 2004, Maclean and Wilson 2011, Bellard et al. 2012, Cahill et al. 2013, IPCC 2014, Jaeschke et al. 2014). Increases in temperature and alterations in precipitation regimes are predicted to alter species distributions and negatively impact species population dynamics (van de Pol et al. 2010, Verboom et al. 2010, Coulson et al. 2011, Hart and Gotelli 2011). Poleward and upslope shifts in distribution have been predicted to occur as species attempt to track changes in climate and remain within climatically suitable environments (La Sorte and Thompson 2007, Raxworthy et al. 2008, Zuckerberg et al. 2009, Buermann et al. 2011). Evidence of this is being documented (Chen et al. 2009, Walther 2010, Chen et al. 2011, Menéndez et al. 2014). Species tracking precipitation or a combination of temperature and precipitation are more likely to show multi-directional shifts (VanDerWal et al 2013). Reductions in climatically suitable habitats lead to contractions in distribution and population size, ultimately decreasing species richness as species become locally extirpated or extinct (Walther 2010, Maclean and Wilson 2011, Fordham et al. 2012, Ihlow et al. 2012, Urban et al. 2012). This is especially the case in locally adapted species with a narrow geographical range size e.g. mountain-top species (Parmesan 2006, Raxworthy et al. 2008, Schiffers et al. 2013). Alternatively, species with a broad geographic distribution will be less vulnerable to climate change as large heterogeneous areas are less likely to become climatically unsuitable as a whole, and larger populations are commonly associated with broader distributions and may contain greater genetic variability related to environmental tolerances (Isaac et al. 2009, Dawson et al. 2011, Kelly et al. 2011).

Climate change induced extinctions may not only arise due to species physiological intolerance to novel or "extreme" climatic conditions, but also due to altered biotic interactions (Walther 2010, Urban et al. 2012, Cahill et al. 2013). Alterations in biotic interactions may induce cascade effects resulting in negative impacts on, or the spatial/temporal mismatch between trophically interacting species. These changes can alter food web dynamics (Koh et al. 2004, Dyer and Letourneau 2013, Albouy et al. 2014, Moir et al. 2014) e.g. dung beetles and mammals (Coggan 2012), butterflies and their host–plants (Schweiger et al. 2008, Schweiger et al. 2012), predators and their prey (Pearce-Higgins et al. 2010). Furthermore, climate change may favour some competitors, predators, or pathogens leading to negative effects on focal species (Urban et al. 2012, Cahill et al. 2013, Pickles et al. 2013).

Tropical ecosystems contain the majority of the Earth's biodiversity and are severely threatened by climate change (Myers et al. 2000, Colwell et al. 2008, Zelazowski et al. 2011). Although greater increases in temperature are anticipated in temperate regions, tropical species are regarded to be at greater risk from climate change as they inhabit warmer environments, closer to their upper thermal tolerances (Colwell et al. 2008, Diamond et al. 2012). The Australian Wet Tropics (AWT) is no exception as it contains a large proportion of Australia's biodiversity (Rainforest Conservation Society of Queensland 1986), with many species predicted to be threatened by climate change (Williams et al. 2003, Williams et al. 2008b).

The evolutionary history of the AWT fauna has made them particularly sensitive to climate change, especially as increases in temperature are predicted to fall outside the range experienced by species during historical events (Williams et al. 2003, Williams et al. 2008b). Patterns of biodiversity of many taxa within the AWT have been moulded by rainforest contraction and expansion events resulting from Pleistocene climatic fluctuations (Graham et al. 2006, Hilbert 2008, Williams et al. 2008a, VanDerWal et al. 2009a, Chapters 4 & 5 this thesis). Contraction of rainforest in upland refugia resulted in lowland extinctions with species isolation and speciation

occurring in the climatically stable uplands (Williams 1997, Williams and Pearson 1997). This created cool-adapted and species rich high-elevation assemblages with the abundance of many species peaking at elevations > 600 m a.s.l. (Williams 1997, Williams and Pearson 1997). Additionally, refugial species inhabiting high elevation habitats are further threatened as they occur close to, or at, their distributional limit with little, or no room for upslope dispersal. For these species, only slight increases in temperature are projected to have deleterious effects (Williams et al. 2003).

Studies in the AWT have investigated the impacts of climate change on folivorous, frugivorous, and predatory vertebrates (Williams et al. 2003, Shoo et al. 2005, Anderson et al. 2013), predatory ground beetles (Staunton et al. 2014), and schizophoran flies (variety of functional guilds; Wilson 2010). However, little is known for ecologically important invertebrate nutrient recyclers. This study aims to fill this knowledge gap by investigating the likely impacts of climate change on the endemic AWT dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae), a keystone invertebrate taxon of great ecological and economical importance (Halffter and Matthews 1966, Hanski and Cambefort 1991a, Halffter and Favila 1993, Spector 2006). Dung beetles play a crucial role in many key ecological processes including the removal and recycling of waste, soil aeration and conditioning, seed dispersal, and reduction and control of micro- and macro-invertebrate parasites (Hanski and Cambefort 1991a, Spector 2006, Nichols et al. 2008). Thus, the disruption of such ecosystem services by alterations in dung beetle diversity has the potential to negatively influence overall ecosystem health (Hanski and Cambefort 1991a, Nichols et al. 2008, Prather et al. 2012).

Specifically, this study employs Maximum entropy (Maxent) methods (Phillips et al. 2006) to model the current, and project the future distribution and population size of 70 species of dung beetles endemic to the AWT rainforest, at 10-year time steps up to 2085, using the future climate projections of the latest four Representative Concentration Pathways (RCPs; Rogelj et al. 2012). For each species, an IUCN threatened category (IUCN 2012) is suggested based on the percentage distribution and population size projected to remain by 2085. The impacts of climate change on the overall dung beetle community are investigated by employing a "predict first,

ensemble later" approach (Ferrier and Guisan 2006) to project AWT dung beetle species richness based on the future RCPs. Moreover, to investigate if projections differed between broad and narrow distributed species, results were compared between winged and flightless dung beetle species groups.

6.2 Methods

6.2.1 Study region

This study focuses on the rainforest of the AWT (Figure 2.1; see section 1.4).

6.2.2 Species data

Species locality records were obtained from surveys and external databases. Targeted dung beetle surveys included sampling at 20 sites along elevational gradients of four mountain ranges (Figure 2.1; see section 2.1 & 2.2). The locality records from these surveys were supplemented with a large dung beetle database developed by Dr Geoff B. Monteith at the Queensland Museum (see section 2.3). Only native dung beetle species that are endemic to the AWT and known to occur within rainforest habitat were used in this study. The final version of the database totalled 3088 presence-only records for 70 species, of which 41 are winged and 29 are flightless (see section 2.3).

6.2.3 Present climate data

The climate data used for modelling species distributions under current climatic conditions included gridded spatial layers of the eight bioclimatic variables: (i) bc01 - annual mean temperature; (ii) bc04 - temperature seasonality; (iii) bc05 - maximum temperature of the warmest period; (iv) bc06 - minimum temperature of the coldest period; (v) bc12 - annual precipitation; (vi) bc15 - precipitation seasonality; (vii) bc16 - precipitation of the wettest quarter; and (viii) <math>bc17 - precipitation of the driest quarter (see section 2.4.1).

6.2.4 Future climate-change scenarios

Future climate projection surface layers of the eight bioclimatic variables mentioned above were based on four RCPs: RCP3–PD, RCP4.5, RCP6, and RCP8.5 (Table 6.1). RCPs are a set of greenhouse gas concentration and emission pathways that explore the impact of different climate policies (Moss et al. 2010, van Vuuren et al. 2011, Rogelj et al. 2012, IPCC 2013) as opposed to the no-climate-policy IPCC AR4 Special Report on Emission Scenarios (Nakicenovic et al. 2000). RCPs are based on the change in radiative forcing at the tropopause by the year 2100, due to increased CO_2 and other greenhouse gas concentrations arising from differing climate change policies (IPCC 2013). Radiative forcing, expressed in W m⁻² for each pathway is indicated by the number following the initials "RCP" (e.g. RCP6 indicates a pathway with radiative forcing of 6 W m⁻² by 2100). Thus, RCPs increase in severity, or decrease in climate policy, from RCP3–PD to RCP8.5 (Table 6.1).

Each RCP was calculated for each of 18 Global Climate Models (GCMs) including: cccma-cgcm31, ccsr-miroc32hi, ccsr-miroc32med, cnrm-cm3, csiro-mk30, gfdl-cm20, gfdl-cm21, giss-modeleh, giss-modeler, iap-fgoals10g, inm-cm30, ipsl-cm4, mpi-echam5, mri-cgcm232a, ncar-ccsm30, ncar-pcm1, ukmo-hadcm3, and ukmo-hadgem for 10-year time steps between 2015-2085 (for detailed information on each GCM see Table A1–3 *in* Reside et al. (2013)). Each 10–year time step was the 30–year average centred on that year, e.g. the climate representing the year 2020 was climate averaged from 2005 to 2035.

6.2.5 Species distribution modelling

Baseline models predicting the environmental suitability of each species across the AWT using present climatic conditions were generated using a maximum entropy (Maxent) approach (see section 2.4.1). As SDMs provide spatial predictions of a species' *potential* distribution they were converted to *realised* distributions by clipping over–predicted distribution to biogeographic boundaries based on expert knowledge (see section 2.4.2 & Chapter 3).

Pathway	Pathway description	^a Radiative forcing	Percentage renewable + nuclear energy use by 2100	^b Total CO ₂ emissions (PgC yr ⁻¹)	^c CO ₂ concentration (ppm)	^d Δ (°C) Mean (range)	°SRES equivalent
^f RCP3-PD	Low; Peak and decline	$3 \text{ W m}^{-2} \text{ before 2100,}$ declining to 2.6 W m ⁻² by 2100	87.5	-0.42	421	1 (0.3 - 1.7)	None
RCP4.5	Medium-Low	4.5 W m ⁻² post 2100	75	4.13	539	1.8 (1.1 - 2.6)	SRES B1
RCP6	Medium-High	6 W m ⁻² post 2100	43.7	13.82	670	2.2 (1.4 - 3.1)	SRES B2
RCP8.5	High and rising	8.5 W m ⁻² post 2100	31.2	28.77	936	3.7 (2.6 - 4.8)	SRES A1F1

Table 6.1. Details of the four Representation Concentration Pathways (RCPs) used in this study.

a - "Radiative forcing is the change in the net, downward minus upward, radiative flux (expressed in $W m^{-2}$) at the tropopause or top of atmosphere due to a change in an external driver of climate change, such as, for example, a change in the concentration of carbon dioxide or the output of the Sun" (see IPCC 2013).

b - Projected total anthropogenic CO₂ emissions (petagrams of carbon per year) by 2100 from fossil fuels, industry, agriculture, forestry, and land use sources. A negative value for RCP3-PD is achieved due to the use of carbon capture and storage technologies (see IPCC 2013).

c - Projected CO₂ concentrations (ppm) by the year 2100. (see IPCC 2013).

d - Projected change in global mean surface temperature (°C) for the period 2081-2100 relative to the reference period of 1986 - 2005.

e - Special Reports on Emission Scenarios equivalent (see Nakicenovic et al. 2000).

f - Also referred to as RCP2.6; PD = Peak and Decline.

Future species distributions were generated by projecting each species model onto future climates of the four RCPs for each of 18 GCMs for ten-year time steps between 2015-2085 (i.e. 576 future climate surfaces per species). Similar to baseline models, the future projections represented potential future distributions and thus an overestimate of the future realised distribution. Moreover, an appropriate dispersal scenario should also be considered when projecting species future distributions (Bateman et al. 2013). In the current study the most realistic dispersal scenario was to allow dispersal to occur within rainforest habitat and within subregional boundaries for both winged and flightless species. That is, species were allowed to disperse as long as environmental conditions (e.g. climate) were favourable within the preferred habitat type (rainforest), but would be stopped by subregional biogeographic barriers e.g. mountains. For the aforementioned reasons, potential future distributions were converted to realised distributions by clipping to both the present extent of rainforest and specific biogeographic subregional boundaries unique to each species (see Chapter 3). The current extent of rainforest was used because accurate projections of future rainforest extent are difficult to model due to uncertainties associated with future variations in precipitation (Hilbert et al. 2001, Hilbert 2008). However, under future climate scenarios the extent of rainforest as a whole is likely to remain the same while rainforest structural types are predicted to change (Hilbert et al. 2001, Hilbert 2008), and thus, clipping to current rainforest extent can be justified. Model post-processing was performed using the package SDMTools (VanDerWal et al. 2012) in the R statistical program (R Development Core Team 2014).

6.2.6 Projected distribution area and population size

Total distribution area in km² and an index of total population size were estimated for present and all future (RCP and GCM) scenarios. Realised species distribution area was calculated using the "ClassStat" function in the R package SDMTools (VanDerWal et al. 2012). Estimation of population size followed the approach of VanDerWal (2009b) that assumes a positive relationship between a species' predicted environmental suitability and local abundance. Thus, an index of a species' projected population size was calculated by summing the environmental suitability values of all cells of the realised species distribution models. Subsequently, the percent distribution

area and population size projected to remain by the year 2085 was calculated for each species per RCP per 10-year time-step.

Community-wide changes in distribution area and population size were also calculated by averaging across all species, and compared between winged and flightless species using unpaired Student's t-test, to assess the impacts of climate change between narrow (flightless) and broadly (winged) distributed species. For assemblage wide summaries, mean RCP projections were derived by averaging across individual species mean GCM projections.

Furthermore, an appropriate threatened category modified from the IUCN Red List Criteria (IUCN 2012) is suggested for each species. These categories were based on percent reduction in distribution area and population size for each RCP and 10-year time-step. Exact IUCN categories were not used as actual generation times, required for criterion A (IUCN 2012), are not known for each species. Also, percent loss in distribution area was preferred, rather than total area remaining required for criterion B (IUCN 2012), as this can be more intuitively compared among all species. Thus, the categories used in this study were: least concern (increase in distribution area or population size), near threatened (< 50% loss in distribution area or population size), vulnerable (\geq 50% & <70% loss), endangered (\geq 70% & <90% loss), critically endangered (\geq 90% & <100% loss), and extinct (100% loss; IUCN 2012). All analyses were performed using the package SDMTools (VanDerWal et al. 2012) in the R statistical program (R Development Core Team 2014).

6.2.7 Projected species richness

Future dung beetle species richness maps were generated for each RCP per 10-year time step by summing individual species future distributions. For each species, future realised distribution maps were generated by averaging across GCM projections for each RCP per 10-year time-step. Subsequently, the individual "mean" realised species distributions, based on environmental suitability values above the species-specific threshold, were converted to binary (0 = absence, 1 = presence) and summed to

produce a map of species richness, where the value of each cell equalled the sum of all species that have a distributional presence within that cell. Species richness maps were created using the package SDMTools (VanDerWal et al. 2012) in the R statistical program (R Development Core Team 2014).

6.3 Results

There was high statistical performance of the modelled distributions, with AUC scores ranging from 0.8 to 1 with 91% of species having an AUC \geq 0.9 (Table 6.2). The majority of species (88%) are projected to experience substantial loss in distribution area and population size by 2085 with only a few species (n = 3) showing an increase in distribution and population size (Table 6.2; exemplar species distribution maps shown in Figure 6.1). Percentage distribution and population size remaining by 2085 for all species based on all RCPs can be found in Appendix 12. Community-wide decreases in population size were consistently greater than decreases in distribution area with greater losses occurring with increasing RCP severity (Figures 6.2. a & d). The average distribution remaining for species is 31% (±11% SE) of present distribution area(Figure 6.2. a) and 25% (±10% SE) of present population size(Figure 6.2. d) projected for 2085 under worst-case pathway RCP8.5. Alternatively, increased use of renewable energy, carbon storage technologies, and climate policy, as outlined in the least-severe RCP3-PD, resulted in the retention of 80% (±7% SE) of present distribution area(Figure 6.2. a) and 63% (±11% SE) of present population size (Figure 6.2. b). Both mid-range RCP4.5 and RCP6 retained intermediate values of distribution area and population size (Figures 6.2. a & d).

Winged and flightless species retained an average of 33% ($\pm 10\%$ SE; Figure 6.2. b) and 29% ($\pm 6\%$ SE; Figure 6.2. c) of their present distributions, and 29% ($\pm 8\%$ SE; Figure 6.2. e) and 18% ($\pm 11\%$ SE; Figure 6.2. f) of their present population size respectively by 2085 under pathway RCP8.5. Although flightless species retained less distribution area and population size compared to winged species, these differences were not statistically significant (percent distribution area: unpaired Student's t-test,

t = 0.540, d.f. = 68, P = 0.591; population size: unpaired Student's t-test, t = 0.923, d.f. = 68, P = 0.359).

Greater numbers of species would become eligible for threatened IUCN categories in the future as RCP severity increased, reflecting greater loss in distribution area (Figure 6.3) and population size (Figure 6.4). More species become threatened based on decreases in population size than decreases in distribution area (Figures 6.3 – 6.5). By 2085, and based on worst-case pathway RCP8.5, 31 (44%) species are predicted to lose \geq 90% of their current population size and will thus become critically endangered (Figures 6.4. d & 6.5; Table 6.2). Overall, a total of 62(88%) dung beetle species (37 winged and 25 flightless) are projected to be threatened by losing \geq 50% of their current distribution area (Figure 6.5; Table 6.2). Two flightless species (*Pseudignambia NQ12* and *Aptenocanthon winyar*) are predicted to become extinct by 2085, losing 100% of their population size (Table 6.2).

Declines in distribution area also led to decreases in dung beetle species richness throughout the AWT by 2085 (Figure 6.6), with greater species loss occurring with increasing RCP severity (Appendix 13). Considering RCP8.5, greatest decrease in species richness occurred in the subregions of Kirrama, Atherton Koombooloomba, Atherton Walter Hill Range, Atherton East escarpment, and eastern Lamb Uplands with losses of up to 33 species (Figure 6.6. a - f). However, subregions of Atherton Herberton Range, southern Lamb, and Carbine Uplands maintained relatively high species richness by 2085, even under this most severe pathway (Figure 6.6. a - f).

Decreases in flightless species richness were greatest in the Atherton East Escarpment with nearly all flightless species being lost, followed by Atherton Herberton Range, Atherton Koombooloomba, Atherton Walter Hill Range, Lamb, and eastern Carbine Uplands. The Finnigan Uplands and Black Mountain Corridor are also projected to lose most/all of their flightless species (Figure 6.6. g - i). Thornton, Spec and parts of the Carbine Uplands were projected to retain all their flightless species (Figure 7. g – i).

Table 6.2. Data associated with individual species (n = 70) projection models for the year 2085 under worst-case Representative Concentration Pathway RCP8.5.

Species	ULR	AUC	Present area km2	2085 mean area km2 (±SE)	2085 % mean area (±SE)	2085 % mean popn size (±SE)	IUCN categorv
Pseudignambia NQ12 *	12	0.996	904	0 (±0)	0 (±0)	0 (±0)	Extinct
Aptenocanthon winyar *	9	0.995	1659	14 (±8)	1 (±0)	0 (±0)	Extinct
Onthophagus yungaburra	46	0.942	2259	62 (±34)	3 (±1)	1 (±1)	Critically Endangered
Aptenocanthon kabura *	2	1.000	145	5 (±3)	4 (±2)	2 (±1)	Critically Endangered
Aptenocanthon monteithi *	12	0.995	1979	76 (±28)	4 (±1)	2 (±1)	Critically Endangered
Amphistomus NQ4/NQ5	91	0.959	3226	204 (±88)	6 (±3)	2 (±1)	Critically Endangered
Temnoplectron finnigani *	12	0.999	280	22 (±9)	8 (±3)	2 (±1)	Critically Endangered
Aptenocanthon wollumbin *	4	0.989	23	3 (±1)	13 (±3)	2 (±1)	Critically Endangered
Onthophagus NQ3	5	0.903	2601	145 (±45)	6 (±2)	3 (±1)	Critically Endangered
Amphistomus NQ3	43	0.958	2315	185 (±96)	8 (±4)	3 (±2)	Critically Endangered
Onthophagus bundara	41	0.957	2483	225 (±105)	9 (±4)	3 (±2)	Critically Endangered
Onthophagus bornemisszanus	24	0.930	3103	284 (±70)	9 (±2)	3 (±1)	Critically
Temnoplectron lewisense *	40	0.987	612	95 (±22)	16 (±4)	3 (±1)	Critically
Amphistomus NQ1 *	26	0.992	327	58 (±19)	18 (±6)	3 (±1)	Critically
Pseudignambia squamata *	6	0.991	345	60 (±19)	18 (±5)	3 (±1)	Critically
Pseudignambia NQ10 *	8	0.985	603	47 (±23)	8 (±4)	4 (±2)	Critically
Pseudignambia NQ8 *	6	0.983	629	105 (±36)	17 (±6)	4 (±1)	Critically
Onthophagus pillara	69	0.944	3157	310 (±139)	10 (±4)	5 (±2)	Critically
Onthophagus wagamen	56	0.957	4330	603 (±253)	14 (±6)	5 (±3)	Critically
Onthophagus darlingtoni	95	0.934	4582	881 (±195)	19 (±4)	6 (±1)	Critically
Lepanus NQ1 *	3	0.941	24	5 (±1)	21 (±4)	6 (±1)	Critically
Pseudignambia mimerops *	7	0.968	1046	150 (±57)	14 (±5)	7 (±3)	Critically
Onthophagus dicranocerus	171	0.921	5771	902 (±314)	16 (±5)	7 (±3)	Critically
Temnoplectron bornemisszai	133	0.919	5653	942 (±338)	17 (±6)	7 (±3)	Critically
Pseudignambia NQ1 *	8	0.981	1696	297 (±134)	18 (±8)	7 (±4)	Critically
Onthophagus NQ8	11	0.968	2353	340 (±153)	14 (±6)	9 (±5)	Critically
Amphistomus complanatus	170	0.926	5443	932 (±337)	17 (±6)	9 (±4)	Critically
Lepanus NQ3	44	0.937	4209	757 (±217)	18 (±5)	9 (±3)	Critically
Onthophagus waminda	119	0.906	6182	1119 (±292)	18 (±5)	9 (±3)	Critically
Temnoplectron aeneopiceum	67	0.935	3349	732 (±143)	22 (±4)	9 (±2)	Critically
Temnoplectron subvolitans	83	0.952	3866	673 (±202)	17 (±5)	10 (±4)	Endangered Critically
Lepanus latheticus	56	0.925	6466	1123 (±256)	17 (±4)	10 (±2)	Endangered Critically
Lepanus palumensis	36	0.966	2837	719 (+129)	25 (+5)	10 (+2)	Endangered Critically
Boletoscapter cornutus	81	0.893	6365	1062 (±212)	17 (±3)	11 (±2)	Endangered Endangered

Onthophagus mundill	60	0.969	2745	559 (±122)	20 (±4)	11 (±3)	Endangered
Lepanus arator	45	0.949	4814	1109 (±239)	23 (±5)	11 (±3)	Endangered
Amphistomus pygmaeus	71	0.934	4855	1641 (±252)	34 (±5)	11 (±3)	Endangered
Onthophagus wilgi	35	0.962	2112	391 (±172)	19 (±8)	12 (±7)	Endangered
Coptodactyla depressa	245	0.875	6702	1457 (±260)	22 (±4)	12 (±2)	Endangered
Onthophagus binyana	65	0.934	6066	1092 (±179)	18 (±3)	13 (±2)	Endangered
Lepanus villosus	62	0.932	4535	931 (±317)	21 (±7)	13 (±6)	Endangered
Onthophagus NQ9	14	0.909	1557	495 (±130)	32 (±8)	13 (±4)	Endangered
Pseudignambia NQ3 *	8	0.998	477	90 (±37)	19 (±8)	14 (±10)	Endangered
Pseudignambia NQ7 *	7	0.892	503	165 (±32)	33 (±6)	14 (±3)	Endangered
Temnoplectron politulum	177	0.904	4721	1512 (±261)	32 (±6)	15 (±4)	Endangered
Pseudignambia NQ9 *	2	0.985	446	114 (±40)	25 (±9)	16 (±8)	Endangered
Aptenocanthon speewah *	3	0.970	278	80 (±19)	29 (±7)	16 (±4)	Endangered
Lepanus nitidus/dichrous	148	0.913	6029	1986 (±426)	33 (±7)	17 (±5)	Endangered
Lepanus furcifer	16	0.924	2996	784 (±102)	26 (±3)	18 (±3)	Endangered
Pseudignambia NQ17 *	3	0.955	278	95 (±20)	34 (±7)	18 (±5)	Endangered
Onthophagus gulmarri	30	0.929	2872	1158 (±185)	40 (±6)	21 (±4)	Endangered
Pseudignambia NQ11 *	2	0.999	165	46 (±15)	28 (±9)	23 (±12)	Endangered
Onthophagus capelliformis	66	0.893	5526	2092 (±409)	38 (±7)	23 (±6)	Endangered
Temnoplectron monteithi *	11	0.999	566	83 (±46)	15 (±8)	24 (±20)	Endangered
Pseudignambia NQ5 *	3	0.993	745	337 (±70)	45 (±9)	25 (±8)	Endangered
Aulacopris matthewsi *	4	0.998	476	116 (±46)	24 (±10)	26 (±15)	Endangered
Coptodactyla storeyi	59	0.991	2362	845 (±89)	36 (±4)	29 (±4)	Endangered
Lepanus NQ2	18	0.992	1227	464 (±101)	38 (±8)	32 (±9)	Vulnerable
Temnoplectron reyi	115	0.956	2457	1303 (±213)	53 (±9)	32 (±7)	Vulnerable
Pseudignambia NQ2 *	2	0.988	171	87 (±18)	51 (±10)	33 (±10)	Vulnerable
Temnoplectron involucre *	25	0.995	300	166 (±21)	55 (±7)	40 (±12)	Vulnerable
Pseudignambia NQ14 *	2	0.976	43	32 (±4)	73 (±9)	41 (±9)	Vulnerable
Amphistomus pectoralis *	13	0.992	408	230 (±30)	56 (±7)	48 (±11)	Vulnerable
Monoplistes curvipes	44	0.892	4832	3602 (±278)	75 (±6)	48 (±4)	Vulnerable
Coptodactyla nitida	92	0.924	2438	2376 (±265)	97 (±11)	60 (±9)	Near Threatened
Pseudignambia NQ6 *	1	1.000	119	110 (±6)	92 (±5)	65 (±8)	Near Threatened
Pseudignambia NQ4 *	1	1.000	171	164 (±6)	95 (±3)	72 (±6)	Near Threatened
Monoplistes tropicus	8	0.803	3067	3137 (±0)	102 (±0)	133 (±2)	Least Concern
Onthophagus yiryoront	13	0.925	3507	3847 (±132)	110 (±4)	166 (±14)	Least Concern
Coptodactyla ducalis	8	0.995	1312	2654 (±28)	202 (±2)	375 (±18)	Least Concern

ULR = unique locality records; AUC = area under the receiver-operating characteristic curve; present area = the distribution area (climatic niche) in km^2 predicted using present (1990-2010) climatic conditions; 2085 mean area km^2 = the mean distribution area in km^2 projected to remain in 2085; 2085 % mean area = the mean distribution area projected to remain in 2085 expressed as a percentage of the present distribution area; 2085 % mean popn size = the percentage of present population size (summed environmental suitability) projected to remain in 2085. IUCN category = suggested based on projected 2085 % mean popn size. Flightless species are noted by an asterisk (*). 2085 predictions based on exposure to Representative Concentration Pathway RCP8.5 and means were calculated from the individual predictions of 18 GCMs. Species are ranked from the greatest to smallest loss in projected 2085 % mean popn size to order species from the most to least vulnerable. For individual species projections of all years based on all RCPs see Appendix 12.



Figure 6.1. Dung beetle interspecies variation in projected change of environmental suitability from present to the year 2085 following exposure to worst-case Representative Concentration Pathway RCP8.5 (mean of 18 GCMs). Species are ordered from (**a**) increase in environmental suitability to (**d**) greatest decrease in environmental suitability. Note that *Amphistomus NQ1* is a flightless subregional endemic restricted to the Carbine Uplands. Subregional outlines as in Figure 2.1.



Figure 6.2. Mean (\pm SE) percent (**a-c**) distribution (climatic niche) area and (**d-f**) population size (summed environmental suitability) projected to remain by the year 2085 for different dung beetle species groups (columns) following exposure to the four Representative Concentration Pathways (RCP3-PD, RCP4.5, RCP6, RCP8.5) averaged across 18 GCM's and species (all species: n = 70, winged species: n = 41, flightless species: n = 29).



Figure 6.3. Predicted number of species that would become eligible for each IUCN category based on loss of **distribution area** (climatic–niche) by 2085, for different dung beetle species groups (rows) following exposure to the four Representative Concentration Pathways (columns). Blue = Least Concern (increase in distribution area): green = Near Threatened (<50% loss); yellow = Vulnerable (\geq 50% &<70% loss), orange = Endangered (\geq 70 & <90% loss), red = Critically Endangered (\geq 90% & <100% loss), black = Extinct (100% loss).


Figure 6.4. Predicted number of species that would become eligible for each IUCN category based on loss of **population size** (summed environmental suitability) by 2085, for different dung beetle species groups (rows) following exposure to the four Representative Concentration Pathways (columns). Blue = Least Concern (increase in population size): green = Near Threatened (<50% loss); yellow = Vulnerable (\geq 50% & <70% loss), orange = Endangered (\geq 70 & <90% loss), red = Critically Endangered (\geq 90% & <100% loss), black = Extinct (100% loss).



Figure 6.5. Projected number of winged (n = 41) and flightless (n = 29) threatened species (i.e. sum of species in IUCN categories Vulnerable, Endangered, and Critically Endangered) for each Representative Concentration Pathway (RCP). For each scenario the left–bar corresponds to projections based on distribution area and the right–bar to projections based on population size. Numbers correspond to bar values (i.e. no. species) with the number of extinct species (i.e. projected to lose 100% of distribution area or population size) denoted in brackets.



Figure 6.6. Projected species richness patterns and total number of species lost within the Australian Wet Tropics (AWT), for different dung beetle species groups (rows) for present and the year 2085 following exposure to worst-case Representative Concentration Pathway RCP8.5 (mean of 18 GCMs).

6.4 Discussion

6.4.1 Effects of climate change on AWT dung beetle biodiversity

This study suggests dramatic reductions in future distribution and population size of the AWT endemic dung beetles, with the majority of species (88%) becoming threatened by 2085, based on worst-case pathway RCP8.5. Contractions in distribution are in turn accompanied by extensive losses in overall species richness throughout the AWT bioregion. These results are congruent with the findings of similar studies investigating the effects of climate change on other AWT fauna including mammals and birds (Williams et al. 2003, Shoo et al. 2005, Anderson et al. 2013), frogs (Shoo 2005), Carabidae ground beetles (Staunton 2014) and schizophoran flies (Wilson 2010). This indicates that climate change presents a significant threat to the regions biodiversity despite formal World Heritage protection (Williams et al. 2003, Williams et al. 2008b). However, the results of this study also suggest that the negative impacts of climate change on dung beetle biodiversity can be considerably reduced by increasing worldwide use of green technology and applying/adhering to climate policy, as indicated by pathway RCP3-PD. While intermediate and worst-case RCPs may be more realistic, best-case mitigation pathway RCP3-PD is technically possible if the right socio-economic and political conditions are created (van Vuuren et al. 2007, Sanford et al. 2014) leading to more effective Earth system governance and planetary stewardship (Biermann et al. 2012).

Decreases in population size are predicted to be more severe than decreases in distribution, although not significantly. This indicates that even though certain areas may still be climatically habitable, overall climatic suitability will be low. Similar decreases in population size have been identified for the regions birds and microhylid frogs (Shoo et al. 2005, Shoo 2005). Thus, studies investigating only declines in distribution area without considering decreases in population size may be underestimating the overall threat or extinction risk of many species to climate change (Shoo et al. 2005, Williams et al. 2008b).

Negative effects of climate change were similar between winged and flightless species, although flightless species showed a greater (non-significant) decrease in remaining distribution and population size. This indicates that both narrow and broad ranged species are equally threatened, a result highlighting the shared evolutionary history of both groups, their dependency on climatically stable high elevations, and thus, their susceptibility to alterations in climate. However, decreases in species richness were less in the northern and southern regions of the AWT, suggesting that species inhabiting more seasonal environments may be more resilient to climate change. This finding is congruent with hypotheses predicting higher resilience in species inhabiting more variable high latitude environments (Parmesan 2006). Areas predicted to retain most of their current species warrant further investigation into their potential utilisation as future refugia (Reside et al. 2013, Reside et al. 2014).

6.4.2 Elevational shifts in distribution and thermal tolerance

To compensate for a warming climate, dung beetles are predicted to undergo shifts in distribution resulting in range contractions, decreases in population size, subsequent reductions in species richness, and thus, altered assemblage compositions. Shifts in the elevational distribution of species are expected for a variety of taxa worldwide (Wilson et al. 2005, Colwell et al. 2008, Lenoir et al. 2008, Raxworthy et al. 2008, Chen et al. 2011) including the AWT (Williams et al. 2003, Shoo et al. 2005, Anderson et al. 2013, Staunton et al. 2014).

Elevational shifts in insect distributions, as a response to recent climate warming, have already been detected (Konvicka et al. 2003, Wilson et al. 2007b, Menéndez et al. 2014). For example, in the south-western Alps (France) and Sierra Nevada (Spain), up to 63% and 90% of sampled dung beetle species experienced upslope range shifts over a 14-year and 24-year period respectively (Menéndez et al. 2014). Menéndez et al. (2014) also identified that range shifts in the south-western Alps resulted from expansion of upper range limits, a finding of particular relevance to the AWT dung beetles as some species, especially flightless species, already occur at the maximum elevational limit of their distribution with little or no available space for upward range

expansion, e.g. *Temnoplectron involucre*, *T. lewisense*, *Amphistomus NQ1* (see Chapter 5).

Thermal tolerances of AWT dung beetles are currently unknown. However, studies investigating temperature tolerances of some AWT endemic vertebrates have identified low thermal maxima in limiting species distributions to higher elevations (Krockenberger et al. 2012; Merino-Viteri, unpublished data). For example, Pseudocheirus archeri Collett (green ringtail possum) has been found to be intolerant of temperatures above 30 °C, a finding responsible for limiting its distribution to elevations above 300 m a.s.l. (Krockenberger et al. 2012). Furthermore, the abundance of *P. archeri* in the field declined significantly at sites where the average maximum temperature of the warmest week of the year was above 30 °C (Krockenberger et al. 2012). Microhylid frogs, endemic to high elevations within the AWT, also have low thermal maxima (Andrés Merino-Viteri, unpublished data) and experience a narrow range of temperature variability within their current distribution. Within the entire distribution of *Cophixalus concinnus* Tyler (beautiful nursery-frog, endemic to the Thornton Uplands), annual mean temperature varies by only 1.1 °C (Williams et al. 2008b), and consequently, modelling predicts that this species will become extinct with an increase in temperature of as little as 1 °C (Williams et al. 2003).

6.4.3 Effects of climate change on dung beetle food resource availability, quantity, and nutritional quality

Climate change may not only influence species directly due to species physiological requirements/tolerances, but also indirectly via effects on their food supply and habitat (Cahill et al. 2013). By feeding on mammal excrement at both the adult and larval stage, dung beetles are inherently dependent on mammals through a functional trophic relationship (Halffter and Matthews 1966, Halffter and Edmonds 1982). Dung beetle diversity, is thus, strongly linked to mammal diversity (Hanski and Cambefort 1991a). The AWT is no exception, with mammal species richness and biomass explaining a large percentage of the variation of dung beetle species richness, composition, abundance, and biomass (Chapter 4). Therefore, any changes in the

mammalian fauna will have cascade effects on the trophically dependent dung beetles (Nichols et al. 2009, Coggan 2012). The mammals of the AWT have been identified to be especially threatened by climate change, with significant declines in core environmental area of the majority of species (Williams et al. 2003). Such declines in distribution and abundance of mammals will result in dramatic declines in food quantity and availability that will, in turn, negatively impact dung beetle diversity.

Evidence of changes in dung beetle diversity owing to changes in mammal diversity have already been noted in tropical ecosystems. For example, Andresen and Laurance (2007) studied changes in dung beetle diversity along a mammal hunting intensity gradient in Panama. They found that heavily hunted areas underwent alterations in dung beetle community composition, with decreases in both species richness and abundance. Likewise, altered dung beetle assemblages were noted following mammal defaunation from selective hunting in Brazilian Atlantic rain forest (Culot et al. 2013). Thus, similar changes in dung beetle diversity may be expected from alterations in mammalian diversity resulting from climate change.

Further indirect effects of climate change on dung beetles may arise due to alterations in dung nutritional quality resulting from changes in foliar chemistry. Under laboratory conditions of increased atmospheric CO_2 levels, the leaves of two AWT rainforest trees, that are important in the diets of folivorous marsupials, showed lower concentrations of nitrogen and sodium, increased levels of condensed tannins, and increases in leaf thickness and toughness (Kanowski 2001). Similar findings, along with decreases in leaf carbohydrates were also documented for tropical trees in Panama under elevated CO_2 concentrations (Coley et al. 2002). Such changes in foliage chemistry, reduce leaf nutritional quality and digestibility, not only influencing folivorous mammal abundance and distribution (Lawler et al. 2000, Kanowski 2001, Coley et al. 2002) but also the nutrient content of their dung (Hume 1977, 1982, Putman 1984, Cork 1996).

Decreases in dung nitrogen and carbohydrate content will negatively impact dung beetle reproductive success. Nitrogen is required by both male and female dung beetles for maturation after hatching, e.g. muscle development, with females also requiring nitrogen for egg maturation, whereas the larvae require carbohydrate rich dung (Cambefort and Hanski 1991). As such, the reproductive rate and success of dung beetles is influenced by variations in dung quality (Tyndale-Biscoe et al. 1981, Macqueen et al. 1986, Ridsdill-Smith 1986, Edwards 1991). In south eastern Australia, the native *Onthophagus granulatus* Boheman produced five times more brood balls with nutrient-rich than with nutrient-poor dung (Tyndale-Biscoe et al. 1981). Additionally, altered dung moisture content resulting from increasing temperatures and altered rainfall regimes will negatively influence dung beetle reproductive success. Dung beetles prefer dung with intermediate moisture content as very wet dung is unsuitable for larval development and dung that is too dry may become completely desiccated, and thus unsuitable by the time larvae complete their development (Gittings and Giller 1998).

6.4.4 Effects of climate change on dung beetle rainforest habitat

Dung beetles and mammals of the AWT ultimately depend on rainforest habitat. Thus, any alterations in rainforest extent will influence dung beetle distributions and ultimately diversity. In general, the distribution of rainforest is determined by interactions between rainfall, seasonality of rainfall, and fire (Hilbert et al. 2001, Little et al. 2012). Variations in rainfall and fire regimes with climate change are uncertain and difficult to model (Hilbert et al. 2001). Alternatively, future modelling projections have concentrated on possible changes in rainforest structural types (e.g. mesophyll vine forests, notophyll vine forests, etc.) rather than distribution of rainforest as a whole (Hilbert et al. 2001). Using artificial neural networks and ten future climate scenarios, Hilbert et al. (2001) predict that most forest types in the AWT will experience climatic conditions favourable for other forest types, resulting in structural shifts in forest distributions. The most threatened forest type was predicted to be highland simple notophyll and simple microphyll vine fern forests and thickets, that decrease by 60% with a temperature rise of 1 °C combined with a 10% decrease in precipitation (Hilbert et al. 2001). High elevation forest types may also be further threatened by rising cloud layers that are responsible for up to 60% of the monthly water input of highland forests (>1000 m a.s.l.) in the AWT (McJannet et al. 2007) and elsewhere (Foster 2001, Bruijnzeel 2002, Holder 2004). Changes in

rainforest structural types and especially the loss of high elevation forest types will further exacerbate the predicted negative impacts of climate change on dung beetle diversity noted in this study.

6.4.5 Disruption of dung beetle mediated ecosystem services

Due to the removal and burial of animal waste, dung beetles play a key role in the maintenance of proper ecosystem function. Ecosystem services provided by dung beetles include nutrient cycling, soil aeration, secondary seed dispersal, reduction of fly populations, and reduction of dung-mediated parasites (Spector 2006, Nichols et al. 2008). Alterations in dung beetle diversity, as predicted in this study, will disrupt such services and along with climate change induced alterations in leaf decomposability (Parsons et al. 2012, Parsons et al. 2014) pose a major threat to AWT nutrient recycling, and thus, overall ecosystem health (see Nichols et al. 2008, Beynon et al. 2012, Prather et al. 2012).

Certain dung beetle species may have disproportionate influence on ecosystem functions (Slade et al. 2007, Slade et al. 2011). For example, exclusion experiments demonstrated that the elimination of large bodied dung beetles from a naturally occurring assemblage reduced dung removal by ~75% (Slade et al. 2007). Within the AWT, certain subregionally endemic flightless montane species are hyper-abundant comprising a large proportion of total dung beetle biomass (see Chapter 5). Decreases in the population size of these species, as predicted in this study, will thus have disproportionate negative effects on ecosystem processes. Moreover, even seemingly "redundant" species may be critical as species rich dung beetle assemblages have been found to achieve greater dung decomposition rates compared to species poor assemblages (Beynon et al. 2012). Similarly, dung removal rates have been found to be significantly positively correlated with dung beetle species richness but not with dung beetle abundance or biomass (Slade et al. 2011). The maintenance of species rich assemblages is thus vital for overall ecosystem stability and health (McCann 2000).

6.4.6 Conclusion

This study identified that the majority of AWT native dung beetles are particularly vulnerable to climate change, through modelled future changes in distribution, population size, and species richness. These results should be regarded as conservative as interactions between dung beetles and mammal food resources and rainforest habitat were not incorporated into the models. Inclusion of these factors would have further increased model uncertainty associated with projecting distributions into the future. Although, studies investigating the impacts of climate change on the AWT rainforest and mammals predict drastic changes in rainforest structural types and mammal defaunation, both of which would further exacerbate the negative impacts of climate change on dung beetles. Decreases in dung beetle abundance and species richness are predicted to alter the many ecosystem processes provided by dung beetles, thus negatively influencing the ecosystem health of the AWT rainforest. However, the results of this study also suggest that the negative impacts of climate change on dung beetles diversity can be reduced by increasing worldwide use of green technology and applying climate policies. Adherence to climate policies is required if we are to minimise atmospheric greenhouse gasses, limit temperature increases, and reduce the loss of biodiversity.

7.1 Overview

Understanding the drivers of patterns of biodiversity is basal to ecology and conservation science (Ricklefs and Schluter 1993a, Gaston 2000). This thesis aimed to identify spatial patterns of dung beetle biodiversity within the Australian Wet Tropics (AWT), understand their drivers, and predict the likely impacts of climate change on dung beetle distribution and population size.

As patterns of biodiversity arise due to the overlap of species distributions, an estimation of the distributional extent of each species was required. This was achieved in Chapter 3 with the production of accurate "realised" species distribution maps of the AWT dung beetles. Chapter 4 followed by summing the realised species distribution maps to generate and investigate patterns of dung beetle species richness and composition within the AWT region, and within well known biogeographic subregions. These diversity patterns were linked to historical and contemporary factors including habitat stability, climate, mammal richness, and mammal biomass (food resources). Chapter 5 investigated patterns of dung beetle biodiversity along elevational gradients by using a two-year standardised pitfall-trap sampling program. Finally, Chapter 6 utilised SDMs to project dung beetle distributions and population size into the future using climate change scenarios based on Representative Concentration Pathways (RCPs). The major findings of this thesis are summarised and discussed below.

7.2 Summary of major findings

7.2.1 Aim 1. Derive accurate estimations of "realised" species distributions and richness for the AWT endemic rainforest dung beetles (Chapter 3).

Chapter 3 derived accurate representations of species "realised" distributions and overall AWT dung beetle species richness by using expert knowledge to clip "potential" species distributions to well known biogeographic limits.

The potential distributions were, on average, 10 times larger than the realised distributions for flightless species and 1.2 times larger for winged species. Thus, overprediction is greatest for species with limited dispersal ability and an inherently smaller distributional range size. The realised species richness model attained the highest correlation between observed and predicted subregional and local species richness and composition. That is, not only did summing realised distributions produce an accurate estimate of the total number of species present but also an accurate representation of the particular set of species occurring in that area (i.e. the species pool).

Expert knowledge can be instrumental in providing better estimates of species distribution, richness, and composition when modelling species distributions and species richness. The consequences to conservation science and biodiversity management are therefore apparent and severe. Beyond the policy and management implications, the findings of Chapter 3 will be beneficial to many researchers and provide a much needed and straightforward first–step towards more accurate spatial representations of species distribution and richness derived from SDMs.

This study also highlights the important work and contribution of taxonomists and museum collections. Accurate identification of species is vital and data associated with museum specimens invaluable for the creation of SDMs. Intensive sampling regimes and taxonomists are responsible for the production of regional and local species lists with which SDMs can be compared.

7.2.2 Aim 2. Identify and understand patterns and drivers of dung beetle biodiversity within the AWT (Chapter 4).

I investigated patterns of dung beetle species richness and composition within the AWT region and within well-known biogeographic subregions using the realised species richness maps generated in Chapter 3. I demonstrated that AWT dung beetle assemblage structure has been influenced by historical habitat stability and the presence of rainforest refugia. Subregions that maintained refugia during rainforest contraction events throughout the climatic fluctuations of the Pleistocene harboured distinct, species rich dung beetle assemblages with the presence of subregionally endemic flightless species. These results indicate that rainforest refugia favoured the persistence and speciation of dung beetles and thus acted as species pumps. However, outside of refugia species and populations became extirpated or extinct, with rainforest refugia now acting as species filters. Rainforest expansion events reconnected refugia and allowed the dispersal and recolonisation of some species, as evidenced by similarities between species assemblages of currently isolated, but historically reconnected subregions (e.g. between the Atherton and Carbine subregions via the Black Mountain Corridor). These results are congruent with the findings of previous studies that report similar influences of refugia on the fauna of the AWT (Yeates et al. 2002, Graham et al. 2006, Williams et al. 2008a, Yeates and Monteith 2008) and elsewhere (Haffer 1969, Taberlet and Cheddadi 2002, Dubey and Cosson 2007, Byrne 2008, Hortal et al. 2011).

The functional trophic relationship between dung beetles and mammals was identified as the most important determinant of dung beetle species richness. Dung beetle species richness was also determined by the climatic variables associated with the presence of historical habitat stability, i.e. refugia. That is, greater dung beetle species richness is found in areas with lower maximum temperatures and lower temperature seasonality. The size of refugia was also important as greater species richness in both winged and flightless species is found in areas that harboured larger refugia. However, the presence of subregionally endemic dung beetles in subregions with small refugia, along with the absence of subregionally endemic vertebrates, indicates that dung beetles were able to persist and speciate in smaller refugia owing to their small body size and hence lower area requirements. Similar conclusions were reached by other studies investigating patterns of insect endemism within the AWT (Moritz et al. 2001, Yeates et al. 2002, Yeates and Monteith 2008).

7.2.3 Aim 3. Identify and understand patterns and drivers of dung beetle biodiversity along elevational gradients within the AWT (Chapter 5).

Dung beetle patterns of biodiversity along elevational gradients are driven by the AWT's refugial history in combination with climate and mammal diversity. Refugia have given rise to differing dung beetle assemblages between and among mountains with evidence of post rainforest expansion and recolonisation events. Increasing species richness, abundance, biomass, species turnover, and narrow elevational ranges with increasing elevation indicated persistence and speciation of a distinct, species rich and cool adapted upland assemblage. Lower dung beetle species richness in the lowlands along with an indication of nestedness in β -diversity suggests extinction in the lowlands and subsequent recolonisation from the species rich uplands (albeit by climate generalists and winged species capable of recolonising the hotter lowlands). Greater mammalian species richness and biomass at higher elevations, also associated with rainforest refugia, contributed towards the persistence and increased abundance and biomass of upland dung beetle species by providing greater dung resources. On mountains that harboured upland endemic dung beetles the greater resources were dominated by these small bodied flightless species, which competitively excluded other species, and in turn, resulted in decreased species richness and diversity at higher elevations.

For the preparation of Chapter 5, I conducted extensive systematic sampling of dung beetles over a two year period (2007–2009). Not only did this data give valuable insights into the diversity of AWT dung beetles and their determinants (see above);

but also produced the first large scale standardised survey of this group. This baseline data–set can be used to monitor changes in distribution and abundance of species in the future (see section 7.3.1 below). Such large scale standardised surveys are needed if we are to document, monitor, and ultimately protect biodiversity.

7.2.4 Conclusion based on findings of Chapters 4 & 5

Variations in patterns of dung beetle biodiversity have arisen due to the orographic heterogeneity of the AWT, that influenced environmental conditions and hence the presence of refugia. Variability in size and extent of refugia influenced speciation and extinction events resulting in a landscape characterised by complex patterns of biodiversity in which certain subregions possess species assemblages that are refugial, others are comprised of a mixture between refugial and recolonised species, and others have been more recently acquired. Specific subregional species pools resulted in distinct species interactions (e.g. dominance of small flightless subregionally endemic species), that subsequently influenced species diversity (e.g. competitively excluded other species thus decreasing overall species richness), ultimately giving rise to present day patterns of biodiversity.

7.2.5 Aim 4. Predict the impacts of climate change on the dung beetles of the AWT (Chapter 6)

Chapter 6 utilised SDMs to predict the impacts of climate change on the dung beetles of the AWT, using future climate projections based on the four Representative Concentration Pathways (RCPs).

Climate change is predicted to have a pronounced negative effect on the dung beetles of the AWT. By 2085, a total of 57 (81%) dung beetle species are predicted to become threatened by losing \geq 50% of their current distribution area and 62 (88%) species are projected to lose \geq 50% of their current population size, based on worst-case concentration pathway RCP8.5. Dung beetle species richness within the AWT is predicted to drastically decrease with current species hotspots losing up to 33 species by 2085 based on RCP8.5. Decreases in dung beetle abundance and species richness

will alter the many ecosystem processes provided by dung beetles, thus negatively influencing the overall ecosystem health of the AWT rainforest. However, the results of Chapter 6 also suggest that the negative impacts of climate change on dung beetle diversity can be reduced by increasing worldwide use of green technology and applying climate policies. Adherence to climate policies is required if we are to minimise atmospheric greenhouse gasses, limit temperature increases, and reduce the loss of biodiversity.

7.3 Future research directions

This thesis has increased the accuracy of modelled dung beetle species distributions, gained a holistic understanding of the drivers of dung beetle patterns of biodiversity within the AWT, and predicted the likely impacts of climate change on dung beetle distributions, population size and species richness. However, there is still much to learn about dung beetle ecology and biology in the AWT. I make the following suggestions for future research based on some of the findings of this thesis.

7.3.1 AWT dung beetle monitoring program

An important future research direction stemming from this thesis will be the establishment of an AWT dung beetle monitoring program. I have collected standardised data along elevational gradients of several mountains (subregions) spanning the latitudinal extent of the AWT. I have identified the current elevational limits and abundance of dung beetle species based on two years of extensive sampling. This has created a much needed baseline data–set to which future sampling can be compared. Future changes in the elevational extent and abundance of dung beetles can now be easily identified and linked to changes in future climate. Several target species can be selected for monitoring. Target species should have definite elevational limits on a single mountain range, with distinct elevational peaks in abundance, so as to allow the detection of shifts in elevational extent and abundance. Furthermore, species exhibiting a peak in abundance at the maximum available elevation of their respective mountain range should be especially monitored. I have

selected six target species based on the above criteria (Table 7.1). Due the relative ease by which dung beetles can be adequately sampled (i.e. baited pitfall traps), a dung beetle monitoring program will be cost and time effective, maximising the use of scarce conservational resources.

Table 7.1. Dung beetle target species proposed for future monitoring showing their elevational limits and elevational peak in abundance. Note that the peak in abundance of *Temnoplectron involucre* and *Amphistomus NQ3* already occurs at the maximum available elevation of their respective mountain range. Flightless species indicated with an asterisk (*).

Subregion	Species	Elevation min (m. a.s.l.)	Elevation max (m. a.s.l.)	Elevational peak in abundance (m. a.s.l.)
Spec	Temnoplectron involucre *	600	1000	1000
	Temnoplectron aeneopiceum	350	1000	600
Atherton	Amphistomus NQ3	400	1000	1000
Carbine	Temnoplectron lewisense *	800	1200	1000
	Amphistomus NQ1 *	800	1200	1000
	Temnoplectron reyi	100	1200	600

7.3.2 Improve dung beetle SDM predictions

SDM predictions can be improved by incorporating biotic interactions such as food resources, i.e. mammalian dung. As I demonstrated in Chapter 3, SDMs tend to overpredict a species realised niche. One reason for this is that SDMs include only abiotic climate variables without considering biotic interactions. Dung beetles depend on mammalian dung during both the adult and larval life history stages. Therefore, the spatial layers representing mammal species richness (dung variety) and mammal biomass (dung quantity) that I produced in Chapter 4 should be evaluated for their potential use in predicting dung beetle distributions along with climate. Furthermore, future changes in mammal species richness and biomass with climate change will also influence dung beetle diversity (see Chapter 6). Thus, spatial layers of future mammalian species richness and biomass should also be incorporated in dung beetle future projections. Including biotic interactions in SDMs has been shown to improve model predictions (Bateman et al. 2012, Wisz et al. 2013). However most results are based on interacting pairs of species, and care should be taken when introducing a spatial layer of an entire species assemblage (e.g. mammal species richness), as this will introduce the accumulated error associated with the individual species projections into the models.

7.3.3 Identify dung beetle thermal maxima and minima

In Chapter 5 I hypothesise that the lower elevational limits of some dung beetle species may correspond to high temperature intolerance. Intolerance to high temperatures is a prediction based on the narrow elevational range size that is characteristic of upland species. Narrow range sizes would have arisen due to isolation, persistence, and/or speciation in cool stable climates of refugia. Experiments aimed in identifying the thermal maxima and minima of AWT dung beetles will be fruitful. Comparisons should be made between species restricted to high elevations (i.e. flightless subregional endemics) and broadly distributed species. I expect flightless subregional endemics that speciated in upland refugia to have lower thermal maxima. It would also be interesting to compare the thermal tolerance of flightless subregional endemics from different subregions spanning the latitudinal range of the AWT. I would expect species from the more seasonal and hotter southern subregions (i.e. Elliot and Spec Uplands) to have a higher temperature tolerance than species from the northern subregions (i.e. Carbine Uplands). Information on temperature tolerance would also be of great benefit when predicting species responses to climate change.

7.3.4 Assess the role of competition in influencing dung beetle diversity.

In Chapter 5 I postulate that very abundant, small-bodied, flightless species at higher elevations, may decrease overall species richness by out-competing other species, through dominating resource patches and thus preventing access to dung (i.e. reproduction) for other species. This should be investigated by experimentation. A good location and species assemblage to test these assumptions would be the 1000 m and 1200 m sites of the Carbine Uplands. At these sites, the flightless subregional

endemics *Temnoplectron lewisense* and *Amphistomus NQ1* are the most abundant species, and species richness along this mountain decreases above 800 m coinciding with the lowest elevational presence of these two flightless species (see chapter 5). Experiments should aim to answer the following questions: (1) Do individuals of flightless species arrive first at a dung patch? (2) How long does it take for a pair of beetles of each species (and also varying densities of individuals) to relocate and burry a standardised quantity of dung? (3) What is the average brood-ball (egg) production of each species? (4) What is the effect of intra- and interspecies competition at varying densities and varying species pairs on brood mass production? (5) What is the development time (egg to adult) of each species?

If dung beetle individuals belonging to flightless species are consistently the first to arrive at a dung patch and are able to relocate/bury dung at a faster rate than other species then they will be at a competitive advantage. By being smaller bodied, flightless species will most likely produce more brood-balls, and thus more offspring, per volume of dung. By quantifying the effect of interspecies competition at varying densities and species combinations, the influence of competition can be identified. Lastly, determining the developmental time of each species will identify the number of possible generations per year/season. If smaller species are able to complete multiple generations per year, and other species e.g. only one, then this will also contribute to the high density of flightless species. Such experiments need to be carried out in the field and lab, and should follow the methods of Giller and Doube (1989). Live trapping of dung beetles can be achieved using baited pitfall traps filled with sandy soil instead of a preservative. Beetles will fall inside the pitfall trap and instinctively burry themselves in the soil. The soil can then be carefully emptied into a sorting tray to select live specimens to be used in experiments.

7.3.5 Identify the utilisation and preference of non-dung food resources

Dung beetles feed on mammalian dung, but some species may feed on other food types such as carrion and/or decomposing fruit and/or fungi (Hill 1996, Halffter and Halffter 2009). Utilising food types other than dung would be advantageous,

especially in a dung depauperate environment such as the lowlands or in locations were rainforest refugia would have been too small to maintain many mammals. Also, a generalist feeding habit may account for the greater abundance of high elevation flightless species (see above, and Chapter 5). Therefore, it is important to determine which species utilise food types other than dung and also if certain species have a preference for a particular food type. I have already collected such data from both low and high elevations in the Spec, Atherton and Carbine Subregions. I placed pitfall traps baited with dung, carrion, decomposing fruit, and decomposing fungi (four replicates per food type) 50 m apart, to identify which species were attracted to certain food types. Furthermore, to identify if there was a preference for a particular food type I conducted a choice experiment in the field. I placed a cluster of four traps (one meter from each other) with each trap containing one of the four food types mentioned above. There was a total of four replicate clusters. The close proximity of each food type "forced" dung beetles to make a choice and I assumed that beetles would have chosen the food type that was most attractive, i.e. preferred. The results of these experiments will be published elsewhere.

Although adults may feed on food sources other than dung, this does not automatically imply that the larvae can also utilise these alternate resources (Halffter and Halffter 2009). If nidification (larval feeding) using non dung resources does not occur then a high local abundance, or survival in dung depauperate environments cannot be explained by a generalist diet. Thus, laboratory breeding experiments should be carried out so as to identify (1) if adults produce brood-balls and lay eggs using non-dung resources, and (2) if larva can survive on non-dung food resources.

7.3.6 Investigate seasonal patterns of dung beetle diversity

Understanding the temporal dynamics (i.e. seasonality) of species is important for monitoring species responses to climate change (Grimbacher and Stork 2009). Furthermore, minimising temporal overlap and thus relieving competition has been hypothesised as facilitating the co-existence of many ecologically similar dung beetle species (Giller and Doube 1989, Vernes et al. 2005). Also, by identifying if peaks in seasonal abundance correspond to freshly emerged or diapausing individuals, the number of generations per year can be elucidated gaining crucial ecological knowledge on AWT dung beetles. I have collected such data by sampling dung beetles on a monthly basis and noting if individuals were freshly hatched. Freshly hatched individuals were identified by an unsclerotised and hence lighter coloured exoskeleton, along with minimal tibial wear on the forelegs (Tyndale-Biscoe 1978). These results will be published elsewhere.

7.4 Concluding statement

This thesis has generated the most accurate AWT dung beetle distribution models and species richness models to date. Using these models and from extensive ground based sampling data I investigated and gained an understanding of the drivers of dung beetle spatial patterns of biodiversity. Finally, I projected species distribution models into the future and assessed the potential impacts of climate change on the dung beetles of the AWT. The findings of this thesis have made significant contributions to the fields of species distribution modelling and biodiversity theory. Baseline data resulting from this work can be used to monitor dung beetle populations to inform conservation and management actions.

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APPENDICES

SU35	SU6	SU8	SU10
11 / V / 07	11 / V / 07	11 / V / 07	
05 / VI / 07	05 / VI / 07	05 / VI / 07	
10 / VII / 07	10 / VII / 07	10 / VII / 07	
21 / VIII / 07	21 / VIII / 07	21 / VIII / 07	
25 / IX / 07	25 / IX / 07	25 / IX / 07	
12 / XI / 07	12 / XI / 07	12 / XI / 07	
13 / XII / 07	13 / XII / 07	13 / XII / 07	
31 / I / 07	31 / I / 07	31 / I / 07	
20 / II / 08	20 / II / 08	20 / II / 08	
10 / III / 08	10 / III / 08	10 / III / 08	
16 / IV / 08	15 / IV / 08	15 / IV / 08	
15 / V / 08			
30 / VI / 08			
13 / VIII / 08			
24 / IX / 08			
10 / XI / 08			
16 / XII / 08			
16 / I / 09			
13 / I I / 09			
10 / III / 09			
15 / IV / 09			
13 / V / 09			

Appendix 1. Dates pitfall-traps were serviced for the Spec gradient

AU1	AU2	AU4	AU6	AU8	AU10
08 / V / 07	08 / V / 07	06 / V / 07	07 / V / 07	07 / V / 07	07 / V / 07
14 / VI / 07	15 / VI / 07	13 / VI / 07	13 / VI / 07	18 / VI / 07	17 / VI / 07
31 / VII / 07	31 / VII / 07	01 / VIII / 07	01 / VIII / 07	01 / VIII / 07	01 / VIII / 07
28 / VIII / 07	28 / VIII / 07	29 / VIII / 07			
30 / IX / 07	30 / IX / 07	01 / X / 07	01 / X / 07	01 / X / 07	01 / X / 07
25 / X / 07	26 / X / 07	25 / X / 07			
03 / XII / 07	03 / XII / 07	04 / XII / 07			
17 / I / 08	19 / I / 08	17 / I / 08	18 / I / 08	18 / I / 08	18 / I / 08
10 / II / 08	10 / II / 08	10 / II / 08	11 / II / 08	11 / II / 08	11 / II / 08
11 / III / 08	11 / III / 08	11 / III / 08	12 / III / 08	12 / III / 08	12 / III / 08
07 / V / 08	07 / V / 08	06 / V / 08			
12 / VI / 08					
28 / VII / 08	28 / VII / 08	28 / VII / 08	29 / VII / 08	29 / VII / 08	29 / VII / 08
01 / IX / 08	01 / IX / 08	01 / IX / 08	02 / IX / 08	02 / IX / 08	02 / IX / 08
16 / X / 08					
27 / XI / 08	27 / XI / 08	28 / XI / 08	28 / XI / 08	27 / XI / 08	26 / XI / 08
28 / XII / 08	28 / XII / 08	29 / XII / 08	29 / XII / 08	29 / XII / 08	30 / XII / 08
27 / I / 09	27 / I / 09	29 / I / 09	28 / I / 09	28 / I / 09	28 / I / 09
23 / II / 09	23 / II / 09	24 / II / 09	Road closed	24 / II / 09	24 / II / 09
26 / III / 09	26 / III / 09	26 / III / 09	27 / III / 09	25 / III / 09	25 / III / 09
04 / V / 09	04 / V / 09	04 / V / 09	05 / V / 09	05 / V / 09	05 / V / 09
21 / VI / 09	21 / VI / 09	18 / VI / 09	18 / VI / 09	18 / VI / 09	20 / VI / 09

Appendix 2. Dates pitfall-traps were serviced for the Atherton gradient

CU1	CU2	CU4	CU6	CU8	CU10	CU12
06 / V / 07	06 / V / 07	03 / V / 07	04 / V / 07			
26 / VI / 07	26 / VI / 07	25 / VI / 07	25 / VI / 07	25 / VI / 07	21 / VI / 07	21 / VI / 07
05 / VIII / 07	05 / VIII / 07	04 / VIII / 07				
31 / VIII / 07	31 / VIII / 07	02 / IX / 07	02 / IX / 07	02 / IX / 07	31 / VIII / 07	31 / VIII / 07
04 / X / 07	04 / X / 07	03 / X / 07				
18 / X / 07	18 / X / 07	17 / X / 07	17 / X / 07	18 / X / 07	18 / X / 07	18 / X / 07
07 / XII / 07	07 / XII / 07	06 / XII / 07	05 / XII / 07			
20 / I / 08	20 / I / 08	19 / I / 08	20 / I / 08	20 / I / 08	22 / I / 08	22 / I / 08
15 / II / 08	15 / II / 08	12 / II / 08	14 / II / 08			
20 / III / 08	20 / III / 08		16 / III / 08	18 / III / 08	17 / III / 08	17 / III / 08
05 / V / 08	05 / V / 08	05 / V / 08	03 / V / 08			
19 / VI / 08	24 / VI / 08	19 / VI / 08				
01 / VIII / 08	01 / VIII / 08	31 / VII / 08	30 / VII / 08			
05 / IX / 08	05 / IX / 08	03 / IX / 08				
23 / X / 08	23 / X / 08	24 / X / 08	23 / X / 08			
01 / XII / 08	01 / XII / 08	28 / XI / 08	30 / XI / 08			
04 / I / 09	04 / I / 09	04 / I / 09	03 / I / 09			
01 / II / 09	01 / II / 09	29 / I / 09	30 / I / 09			
27 / II / 09	27 / II / 09	25 / II / 09				
04 / IV / 09	04 / IV / 09	04 / IV / 09	01 / IV / 09	01 / IV / 09	31 / III / 09	31 / III / 09
06 / V / 09	06 / V / 09	08 / V / 09	07 / V / 09			
26 / VI / 09	26 / VI / 09	25 / VI / 09	27 / VI / 09	27 / VI / 09	27 / VI / 09	26 / VI / 09

Appendix 3. Dates pitfall-traps were serviced for the Carbine gradient

WU9	WU11	WU13
05 / V / 07	05 / V / 07	05 / V / 07
23 / VI / 07	23 / VI / 07	22 / VI / 07
03 / VIII / 07	03 / VIII / 07	03 / VIII / 07
01 / IX / 07	01 / IX / 07	01 / IX / 07
21 / X / 07	21 / X / 07	21 / X / 07
06 / XII / 07	06 / XII / 07	06 / XII / 07
21 / I / 08	21 / I / 08	21 / I / 08
13 / II / 08	13 / II / 08	
15 / III / 08	14 / III / 08	15 / III / 08
04 / V / 08	04 / V / 08	04 / V / 08
22 / VI / 08	21 / VI / 08	21 / VI / 08
31 / VII / 08	31 / VII / 08	31 / VII / 08
04 / IX / 08	04 / IX / 08	04 / IX / 08
26 / X / 08	26 / X / 08	26 / X / 08
29 / XI / 08	29 / XI / 08	29 / XI / 08
02 / I / 09	02 / I / 09	02 / I / 09
31 / I / 09	31 / I / 09	31 / I / 09
26 / II / 09	26 / II / 09	26 / II / 09
03 / IV / 09	03 / IV / 09	03 / IV / 09
08 / V / 09	08 / V / 09	08 / V / 09
29 / VI / 09	28 / VI / 09	28 / VI / 09

Appendix 4. Dates pitfall-traps were serviced for the Windsor gradient

Appendix 5. List of subregions identified to be well-sampled (sampling completeness \geq 75%) showing the total area of rainforest and the number of dung beetle species observed from database locality records. The subregion code corresponds to the numbers in Figure 2.1.

Subregion code	Subregion abbreviation	Subregion name	Rainforest area (km ²)	Richness observed	Sampling completeness (%)
3	FUN	Finnigan Uplands North	75	11	97.78
6	FUS	Finnigan Uplands South	181	14	100
7	TU	Thornton Uplands	241	15	98.36
8	WU	Windsor Uplands	216	23	78.63
11	ML	Mossman Lowlands	267	15	78.26
12	CU	Carbine Uplands	440	32	80.00
15	BM	Black Mountain Corridor	275	23	88.04
18	LU	Lamb Uplands	278	38	93.66
20	AU_BK	Atherton Uplands BK	171	13	78.31
21	SR	Seymour Range	7	9	84.91
22	AU_CE	Atherton Uplands Central	38	31	92.54
27	AU_HR	Atherton Uplands Herberton Range	127	33	89.19
29	AU_WR	Atherton Uplands Walter Hill Range	664	28	96.14
30	AU_KO	Atherton Uplands Koombooloomba	567	34	89.08
32	KU	Kirrama Uplands	503	24	79.34
35	LE	Seaview Range Lee Uplands	211	15	85.71
39	SU	Spec Uplands	181	15	98.36

Appendix 6. List of sampling sites showing their total observed (i.e. sampled) species richness and sampling-completeness (i.e. sample-coverage). Sample-coverage was estimated using iNEXT online (see Chao and Jost 2012, Hsieh et al. 2013).

Site	Latitude	Longitude	Elevation	Richness	Sampling
ID	(decimal)	(decimal)	(m a.s.l.)	observed	completeness (%)
SU35	-19.0148	146.2654	334	12	99.80
SU6	-19.0026	146.2415	671	10	99.87
SU8	-19.0113	146.2214	834	9	99.88
SU10	-19.0038	146.2093	950	6	99.96
AU1	-17.7170	145.8594	80	12	99.10
AU2	-17.6605	145.8737	180	17	99.61
AU4	-17.6093	145.7664	428	16	99.90
AU6	-17.6707	145.7167	630	19	99.86
AU8	-17.6002	145.6346	840	21	99.87
AU10	-17.7007	145.5245	930	23	99.95
CU1	-16.4688	145.3264	115	13	98.24
CU2	-16.4711	145.3210	234	7	99.58
CU4	-16.5329	145.3727	440	13	99.40
CU6	-16.5776	145.3057	656	20	99.97
CU8	-16.5864	145.2976	820	21	99.77
CU10	-16.5558	145.2784	1016	18	100
CU12	-16.5126	145.2705	1210	15	99.98
WU9	-16.2848	145.0841	940	19	99.86
WU11	-16.2591	145.0438	1071	17	99.98
WU13	-16.2353	145.0088	1280	11	99.78

Appendix 7. Realised species distribution models of 70 dung beetle species endemic to the AWT used in this study. Environmental suitability is indicated in a gradient from blue (less suitable) to red (most suitable). Grey areas are considered unsuitable for the species. ULR = Unique Locality Records, AUC = area under the receiver–operating characteristic curve.

















Appendix 8. Correlations, covariances, means, and standard deviations (SD) for the variables used in the structural equation models (SEM). Values in bold and shaded above the diagonal are Pearson correlations and unshaded values on and below the diagonal are covariances. Transformations performed in order to improve normality are noted within brackets below each variable. **winged rich:** winged dung beetle richness; **flightless rich:** flightless dung beetle richness; **mam** rich: mammal species richness; **mam bio**: mammal biomass; **hs:** habitat stability; **bc04:** temperature seasonality; **bc05:** maximum temperature of the warmest period; **bc15:** precipitation seasonality; **bc16:** precipitation of wettest quarter; **elev:** elevation; **lat:** latitude.

	winged rich (sqrt)	flightless rich (sqrt)	mam rich (sqrt)	mam bio (sqrt)	hs (log x+1)	bc04 (sqrt)	bc05 (log x+1)	bc15 (log x+1)	bc16 (sqrt)	elevation (sqrt)	lat
winged rich (sqrt)	0.884	0.766	0.910	0.824	0.771	-0.135	-0.720	-0.416	0.093	0.692	0.294
flightless rich (sqrt)	0.387	0.288	0.770	0.692	0.699	-0.091	-0.754	-0.211	-0.029	0.725	0.214
mam rich (sqrt)	0.577	0.279	0.455	0.941	0.811	0.076	-0.787	-0.489	0.025	0.737	0.097
mam bio (sqrt)	0.788	0.378	0.646	1.036	0.760	0.287	-0.796	-0.431	-0.184	0.797	-0.090
hs (log x+1)	0.174	0.090	0.131	0.185	0.058	0.069	-0.800	-0.448	0.052	0.758	0.085
bc04 (sqrt)	-0.117	-0.045	0.047	0.270	0.015	0.858	-0.270	-0.266	-0.419	0.223	-0.956
bc05 (log x+1)	-0.013	-0.008	-0.010	-0.016	-0.004	-0.005	0.000	0.287	0.180	-0.905	0.135
bc15 (log x+1)	-0.018	-0.005	-0.015	-0.020	-0.005	-0.011	0.000	0.002	-0.535	-0.085	0.214
bc16 (sqrt)	0.375	-0.066	0.073	-0.809	0.054	-1.673	0.015	-0.106	18.581	-0.434	0.313
elevation (sqrt)	4.908	2.937	3.752	6.123	1.373	1.561	-0.135	-0.029	-14.116	57.009	-0.027
lat	0.249	0.103	0.059	-0.082	0.018	-0.797	0.002	0.009	1.214	-0.180	0.810
Mean	0.639	2.543	2.142	2.722	-1.919	16.713	2.477	1.910	34.427	20.966	-17.369
SD	0.537	0.940	0.674	1.018	0.240	0.926	0.020	0.046	4.311	7.550	0.900

Appendix 9. Non-metric multidimensional scaling ordination of the AWT endemic dung beetle assemblages within all subregions. Note that by including the subregion Elliot Uplands (EU), compositional structure could not be determined between remaining subregions. See Figure 4.7. a for NMDS that excluded the Elliot Uplands.



Appendix 10. Hierarchical cluster dendrogram using average linkage methods of the AWT endemic dung beetle species compositions within subregions. This cluster dendrogram was sliced at a height of 0.4 and displayed in Figure 8. c.



nmds hclust (*, "average")

Appendix 11. Relationship between dung beetle species richness and elevation. The Black line indicates a smoothed fit produced by a Generalised Additive Mixed Model (GAMM) based on data from Atherton (green), Carbine (blue) and Windsor (orange). The red line indicates a linear regression based on only Spec data.



Appendix 12. Mean (±SE) percent distribution area (climatic niche; left column) and population size (summed environmental suitability; right column) projected to remain for each species (n=70) following exposure to the four Representative Concentration Pathways (RCP3-PD, RCP4.5, RCP6, RCP8.5) averaged across 18 GCM's. Flightless species are noted by an asterisk (*).




























All species (n=70) a) Present b) RCP3-PD c) RCP4.5 d) RCP6 e) RCP8.5 42 42 42 42 42 Winged species (n=41) f) Present g) RCP3-PD h) RCP4.5 i) RCP6 j) RCP8.5 36 Flightless species (n=29) k) Present I) RCP3-PD m) RCP4.5 n) RCP6 o) RCP8.5

Appendix 13. Projected species richness patterns (mean of 18 GCMs) within the Australian Wet Tropics (AWT) for different dung beetle species groups (rows) from present and the year 2085 following exposure to the four Representative Concentration Pathways (RCPs).