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Beyond simple means: Integrating extreme events and biotic interactions in species distribution models

Conservation implications for the northern bettong (*Bettongia tropica*) under climate change

PhD thesis submitted by
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(BSc, GDipResMethods)
July 2010

For the degree of Doctor of Philosophy
In Zoology and Tropical Ecology
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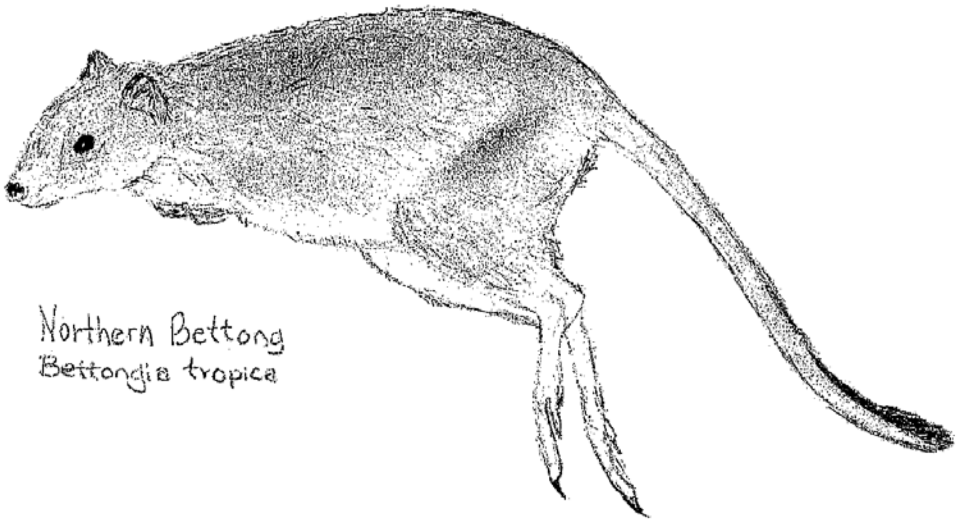

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Publications associated with this thesis

Peer-reviewed publications

- **Bateman BL**, Kutt AS, Vanderduys EP, and Kemp JE (2010) Small-mammal species richness and abundance along a tropical altitudinal gradient: an Australian example *Journal of Tropical Ecology* 26, 139-149 (Appendix E)
- **Bateman BL**, Johnson CN (2011). The influences of climate, habitat and fire on the distribution of cockatoo grass (*Alloteropsis semialata*) (Poaceae) in the Wet Tropics of northern Australia. *Australian Journal of Botany* 59 (4), 315-323 (Chapter 3)

Manuscripts in press

- **Bateman BL**, VanDerWal J, and Johnson CN (in press) Nice weather for bettongs: improving species distribution modelling using temporal variation in weather and extreme weather events. *Ecography* (Chapter 5)

Manuscripts in review

- **Bateman BL**, VanDerWal J, Williams SE, Johnson CN (in review) How much influence do biotic interactions have on predictions of shifts in species distributions under climate change? *Diversity and Distributions* (Chapter 4)
- **Bateman BL**, Johnson CN, Abell SE (in review) The influence of habitat and climate on the availability of truffles as a resource for the endangered northern bettong (*Bettongia tropica*). *Australian Journal of Zoology* (Chapter 2)

Manuscripts in preparation

- **Bateman BL**, VanDerWal J, and Johnson CN (in prep) A review of Species Distribution Modelling (SDMs): where to from here? To be submitted to *Diversity and Distributions* (Chapter 1 and Chapter 6)
- **Bateman BL**, Johnson CN, Baker A, Parsons M (in prep) Proactive conservation in the face of climate change; climate refugia for the northern bettong. To be submitted to *Conservation Biology* (Chapter 6)
- **Bateman BL**, Johnson CN (in prep) Distribution, current and future predictions, of the rufous bettong (*Aepyprymnus rufescens*). To be submitted to *Australian Mammalogy* (Chapter 4,6)
- **Bateman BL**, Johnson CN (in prep) Using probability of detection to determine survey effort and population decline of the northern bettong. To be submitted to *Wildlife Research* (Appendix B)

Reports

- **Bateman BL** Status of the northern bettong on the Coane Range (in prep) Report to the Australian Wildlife Conservancy
- **Bateman BL** Status of the northern bettong ; future management options (in prep) Report to Queensland Parks and Wildlife Service

Conference presentations

- Ecological Society of Australia (2010) Canberra, Australia (Oral Presentation)
  - **Bateman BL**, VanDerWal J, and Johnson CN (2009). Nice weather for bettongs: using weather events, not climate means, to model the distribution and competitive outcomes of marsupials
- Society for Conservation Biology: 24th international congress for conservation biology (2010) Edmonton, Canada (Poster Presentation)
  - **Bateman BL**, VanDerWal J, and Johnson CN (2010) Using events in species distribution modelling: implications of extreme events on current distributions and competitive outcomes
- Marine and Tropical Sciences Research facility Annual Conference (2010) Cairns, Australia (Oral Presentation)
  - **Bateman BL**, VanDerWal J, and Johnson CN (2010) Using events in species distribution modelling: implications of extreme events on current distributions and competitive outcomes
- The 10th International Congress of Ecology: Ecology in a Changing Climate (2009) Brisbane, Australia (Oral Presentation)
  - **Bateman BL**, VanDerWal J, and Johnson CN (2009) Modelling Biotic Interactions Under Climate Change Scenarios: Predicting northern bettong (*Bettongia tropica*) Distribution
- Australian Mammal Society (2009) Perth, Australia (Oral Presentation)
  - **Bateman BL**, VanDerWal J, and Johnson CN (2009) Modelling Biotic Interactions Under Climate Change Scenarios: Predicting northern bettong (*Bettongia tropica*) Distribution
    - Commendation, Adolph Bolliger Award, best spoken presentation by a student
- Marine and Tropical Sciences Research facility Annual Conference (2009) Townsville, Australia (Poster Presentation)
  - **Bateman BL**, VanDerWal J, Johnson CN, and Williams (2009) Distribution modelling of the northern bettong
- Ecological Society of Australia (2009) Sydney, Australia (Oral Presentation)
  - **Bateman BL,** VanDerWal J, and Johnson CN (2009). Predicting northern bettong distribution

Other publications

The following publications were also generated during my candidature:

Manuscripts in press

- Fuentes MMPB, **Bateman BL**, Hamann M (in press) Exposure of sea turtle nesting sites to tropical cyclone activity: an important factor in sea turtle nesting distribution. *Journal of Biogeography*

Manuscripts in review

- Kutt AS, **Bateman BL**, and Vanderduys EP (in prep) Reptile species richness and abundance along a rainforest-savanna altitude gradient in north-eastern Australia. *Australian Journal of Zoology*

Manuscripts in preparation

- VanDerWal J, Kutt A, Perkins G, **Bateman BL**, Perry J, Murphy HT (in prep) 60 years of climate change: identifying the species-specific rates of change in Australian birds To be submitted to *Nature*
- VanDerWal J*, **Bateman BL***, Murphy HT, and Reside A (* equal contribution) (in prep) Dispersal Appropriateness of full-, partial- and no-dispersal scenarios in climate change impact modelling To be submitted to *Journal of Biogeography*
- **Bateman BL**, VanDerWal J, Pauza M, and Johnson CN (in prep) Modeling the distribution of the Tasmanian bettong (*Bettongia gaimardi*): climate, weather and fox impact. To be submitted to *Austral Ecology*

Thesis abstract

In order to adopt pertinent management strategies for a species, it is imperative to have an understanding of its distribution and requirements. Species distribution models (SDMs) are broadly applied in ecological studies to generate hypotheses on both current and future distributions of a species. These models utilise statistical approaches to link where a species occurs with environmental data from those locations to infer hypotheses about factors limiting the species' distribution. SDMs have many applications in conservation biology, including being one of the few tools capable of predicting the impacts of climate change on a species. However, applications of SDMs are often limited to using long-term climate means and some measure of variability to represent 'environment'. Although climate is an important factor determining a species distribution, it is not the sole driver. These models exclude important influences such as biotic interactions, physiological limitations, and extreme weather events. Models based only on long-term climate overlook these factors. As these models are used for assessing conservation goals, it is critical to assess their limitations and usefulness.

I address the limitations of current SDM applications in my thesis, with the goal of improving their theoretical underpinning. I used the endangered northern bettong (*Bettongia tropica*), a tropical rat-kangaroo, as a study species for my research. The northern bettong is an ideal SDM candidate: it is a small, narrowly endemic species, restricted in habitat and diet. The ecology of the species is well understood, with knowledge on key process, interactions, and dietary requirements. I examined the links between climate, limiting resources, biotic interactions (competition with the more generalist rufous bettong (*Aepyprymnus rufescens*)) and

extreme weather events to enhance the ecological theory of SDMs. Additionally, I developed suggestions for the proactive management of the northern bettong. In order to do this, this thesis had several components: 1) examination of the distribution and limits of northern bettong key resources for inclusion into SDMs; 2) assessment of the role of biotic interactions in SDMs; and 3) investigation of the impact of extreme weather events on current distributions.

Two crucial food resources for the northern bettong are ‘truffles’ and cockatoo grass (*Alloteropsis semialata*); I assessed site- and regional-scale effects of short-term weather, long-term climate and habitat on the distribution of these resources. Habitat type did have an influence on truffles, as did key soil nutrients, although these factors could only explain a small percentage of the variation in truffle availability. The availability of truffles was directly influenced by weather and climate, with temperature and precipitation driving productivity at both the site and regional scale. The long-term reliability of truffles as a resource may be linked to weather and could be detrimentally affected by increasing seasonality and dry season severity, particularly within the range edges of northern bettong distribution. Key ‘extreme’ weather events were identified to limit truffle abundance, which in turn would limit the distribution of the northern bettong; thus this resource provided a good modelling candidate for use in biotic interaction assessment. Cockatoo grass has a broad tolerance to temperature and precipitation values although appears to be limited by drought conditions in the dry season. Habitat features have a strong role in determining cockatoo grass density, with a positive response to a late dry season burn indicating this species may benefit from fire. Cockatoo grass distribution was also affected by climate, making it an appropriate variable for inclusion into biotic interaction models, although more research on the affect of fire and climate change on its distribution is warranted.

In order to assess the influence of biotic interactions on SDM predictions under climate change, the spatial distribution of the northern bettong was modelled with and without biotic interactions (two resources and the potential competitor) and their predictions compared under varying degrees of global warming. Climate-only models increasingly diverged from those including biotic interactions with increasing global warming. I showed that SDM exercises that explicitly include known biological interactions provide better, ecologically realistic predictions under climate change. As interactions are currently not included in the vast majority of SDMs, this has ramifications for the usefulness of current climate change impact assessments that employ SDM.

Long-term climate data masks short-term weather events; these weather events may be ‘extreme’ relative to a species and as such, have huge implications on local population densities. To explore this, I defined extreme weather events in terms of the ecology of the northern bettong. These extreme weather events (e.g. droughts and heat waves) were used to model the temporal variability in the short-term suitability of habitat for both the northern bettong and its potential competitor, the rufous bettong. Severe drought and temperature variability limited local population densities of the northern bettong at the edge of this species’ range, and induced contractions in its distribution and niche tracking. Such contractions coincided with beneficial outcomes for the rufous bettong. Populations close to the edge of the range of this species occur in low densities as a result of frequent changes in the suitability of weather and increased pressure from their competitor. Traditional SDMs utilise data limited to spatial scale and do not detect dynamic processes such as temporal shifts in suitable weather and competitive outcomes between species. Failure to include extreme events can lead to overestimation of suitable habitat, which has implications for use in management decisions.

I integrated all of the results from my data chapters to improve our ecological understanding of the northern bettong. Northern bettongs may be vulnerable to climate change, particularly within populations at the edge of its range. Proactive conservation planning to mitigate the impacts of climate change can begin with the knowledge of predicted distributions, identified refugial areas (areas likely to maintain resources under climate change), and the impacts of extreme weather events, variable weather, and competitive pressure from the rufous bettong.

I demonstrate that although the use of SDM in climate change impact assessments is beneficial as a first pass for conservation and adaptation efforts, they can be improved with species-specific, ecologically relevant knowledge. The importance of my study was to highlight how climate-only models are limited in detecting important influences on a species distribution in time, as well as space. Improving on models by addressing these limitations provides for more realistic model outputs that can be utilized with greater confidence in proactive conservation efforts. The models developed here will be used in management decisions for the endangered northern bettong, to help ensure its continued persistence in a changing climate.

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Chapter 1 : General introduction[1]

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[1] **Bateman BL**, VanDerWal J, and Johnson CN (in prep) A review of species distribution modelling (SDMs): where to from here? To be submitted to *Diversity and Distributions* (with Chapter 6)

1.1 Ecological context

1.1.1 The concept of the niche

Ecologists seek to understand why species occur where they do. The concept of the niche, a theoretical representation of where a species could occur in the environment, is at the ecological foundation of our understanding of this (Begon *et al.* 2006). As a theoretical concept, the niche does not indicate an actual place in the habitat, but rather an idea of where a species could occur. The niche of a species occupies many dimensions, given by species-specific requirements and physiological thresholds relative to available conditions. A species' fundamental niche, as described by Hutchinson (1957), is an 'n-dimensional hypervolume' describing an environmental space in which a species is able to persist in the absence of effects of other species. Taking into account the existence of sink habitats, this persistence must be maintained (that is, net population growth is positive) independent of immigration from source populations (Chase & Leibold 2003; Martinez-Meyer 2005). In reality, a species' fundamental niche is constrained by interactions with other species through competition, predation and so on. These interactions limit species, and the portion of the fundamental niche that is occupied a when these interactions operate on the species is termed its realized niche (Hutchinson 1957). When the theoretical concepts of the fundamental and realized niche are projected onto geographical space they give the potential and realized (actual) distribution of a species respectively (Pearson 2007). Few species occupy all areas of habitat that are suitable (their potential distribution) for their physiological needs (Anderson *et al.* 2002). This is due to other factors that occur in geographical space such as biotic interactions, anthropogenic impacts, local historical events, barriers, or dispersal limitations (Martinez-Meyer 2005; Jimenez-Valverde *et al.* 2008). Where a species does occur, its actual (or realized) distribution, is dynamic both in environmental and geographical space (Jimenez-Valverde *et al.* 2008; Sinclair *et al.* 2010). For instance, competition for resources could occur in the same space but at different times (Araújo & Guisan 2006).

1.1.2 Species distribution modelling

1.1.2.1 What is a SDM?

To project the concept of the niche into geographical space, species distribution models (SDMs) are often used. These models often derive statistical relationships between where a species occurs and the “environment” at these locations; these statistical relationships can infer hypotheses about factors limiting species distributions (Elith & Leathwick 2009). SDMs aim to identify the potential distribution of a species, but often the predictions lie somewhere between the potential and realized distribution because the statistical relationships are based on occurrences from within the realized distribution (Araújo & Guisan 2006; Jimenez-Valverde *et al.* 2008). As not all possible combinations of variables along the axes defining the fundamental niche are likely to exist in the landscape, this potential distribution is only a subset of the fundamental niche that is environmentally feasible (Guisan & Thuiller 2005). Therefore SDMs do not describe the niche, but rather make simulations of the projected distribution of a species which can be used to formulate hypotheses about a species niche (Jimenez-Valverde *et al.* 2008) and to predict the potential distribution, or areas in geographical space that have suitable abiotic conditions for a species (Araújo & Guisan 2006).

While most SDMs are correlative (phenomenological) models, a few process-based (mechanistic) models based on physiology exist. Mechanistic models are suited to identification of the fundamental niche as they identify the physiological limits of a species, whereas correlative pattern-based models have access only to observed locality records and may not identify the full potential distribution of a species. However, mechanistic models currently do not account for non-climatic influences on species occurrences, and thus provide only a ‘broad envelope’ of suitable environmental conditions of a species (Pearson & Dawson 2003). This means that models will never be fully realized and do not predict where a species actually will be able to persist, as they do not take into account factors such as dispersal limitations or biotic interactions. Mechanistic models are often based on physiological studies on a limited number of individuals and thus neglect intra-species variation and metapopulation differences (Pearson & Dawson 2003). Correlative models have been shown to perform as well or better than some mechanistic models in predicting suitable habitat of a species (Robertson *et al.* 2003; Kearney *et al.* 2010). This thesis will focus on phenomenological modelling: for a review of mechanistic modelling approaches to species distribution modelling, see Kearney and Porter (2009). Several papers have reviewed in depth the history, ecological principles, various modelling algorithms and methodologies, and assumptions of correlative SDMs (see Guisan & Zimmermann 2000; Elith & Burgman 2002, 2003; Munoz & Felicisimo 2004; Guisan & Thuiller 2005; Elith *et al.* 2006; Pearson *et al.* 2006; Guisan *et al.* 2007; Graham *et al.* 2008; Elith & Graham 2009) and will not be discussed in detail here. A good synthesis of the general concepts and background of SDM’s is provided in Pearson (2007) and Elith and Leathwick (2009). This thesis relies on the use of Maxent (v. 3.3.1) (Phillips *et* *al.* 2006) for species distribution modelling, with each data chapter using outputs from this program in some capacity. This program has been shown to outperform other species distribution modelling algorithms (Elith *et al.* 2006; Hernandez *et al.* 2006; Hijmans & Graham 2006; Guisan *et al.* 2007; Pearson *et al.* 2007; Elith & Graham 2009) and therefore has been selected for this thesis. A detailed review of Maxent, including the technical underpinnings of this program, has been provided in Appendix A for quick reference to each relevant portion of the data chapters.

1.1.2.2 How to know it's working: Model evaluation

Evaluating the performance of a model is necessary to assess its predictive performance and suitability for the intended application (Araújo & Guisan 2006). Validation of a model consists of assessing how well the model represents the natural situation it set out to describe. To assess this, utilization of an independent data set is ideal, preferably from sites other than the locations used for model development and representative of the region for which the model was designed (Pearce & Ferrier 2000; Araújo & Guisan 2006). If independent data are lacking, existing data can be statistically split or re-sampled using cross-validation, bootstrapping or jack-knifing (Pearce & Ferrier 2000). These data partitioning techniques all assume that samples randomly selected from the original data are independent observations. This assumption is likely to inflate results (that is, to be over-optimistic) where true accuracy can only be observed using independent field observations (Araújo *et al.* 2005).

Models should be adequate, reliable and discriminatory in their predictive ability. Discrimination is the ability to assess the difference between occupied and unoccupied sites in an evaluation dataset (Pearce & Ferrier 2000). Model adequacy is the ability of a model to accurately predict relevant biological patterns or provide working hypotheses relative to the purpose and within the appropriate setting identified for the study (Guisan & Zimmermann 2000; Pearce & Ferrier 2000). Reliability is the probability of predicting occurrences accurately at a given site and within ecological reason. Model evaluation is often accomplished using the area under the receiver operating characteristic (ROC) curve, or the AUC, an index of performance (Hanley & McNeil 1982). Where model sensitivity is true positives and specificity is true negative, the ROC is a plot of sensitivity versus ‘1-specificity’ across a range of possible thresholds. The AUC indicates the proportion of correctly predicted presences (sensitivity) in direct relation to the proportion of observed absences that are incorrectly predicted (1-specificity) (Pearson 2007). In other words, the AUC provides a measure of predictive performance across a full range of possible thresholds, and is equal to the probability that a classifier will rank a randomly chosen positive instance higher than a randomly chosen negative one. Values of the AUC range from 0 to 1, with 0.5 being complete randomness (no discrimination), values between 0.7 and 0.9 representing useful discrimination, and above 0.9 high discrimination (Elith *et al.* 2006; Guisan *et al.* 2007). This value provides an index of the ability of a model to correctly predict occupied and unoccupied space (Elith *et al.* 2006).

Recent work has criticized the sole use of AUC for model discrimination, on the grounds that it is strongly affected by how restricted a species distribution is (Lobo *et al.* 2008). Species that are restricted in distribution can be modelled with greater accuracy than common and generalist species (Elith *et al.* 2006; Lobo *et al.* 2008). It is evident that new model evaluation techniques are needed (Elith & Graham 2009). Lobo *et al.* (2010) suggest observing omission and commission errors in combination for evaluating the reliability of models. Model validation of SDMs predicting onto novel environments, such as changes in climate, is relatively neglected (Araújo *et al.* 2005). Because these events take place in the future, or are not documented such as recent range shifts, there are no data that can be used for evaluation**.**

1.1.2.3 Improving SDMs for prediction

SDMs have a variety of applications in conservation biology. Habitat suitability predicted from such models can be used to assess the impact of invading species, and climate or land use change (Guisan & Thuiller 2005). Such predictions can be used to guide field surveys aiming to find new populations in un-surveyed sites of high potential (Bourg *et al.* 2005; Guisan *et al.* 2006a), direct field work and reduce costs of surveys (Stockwell & Peterson 2002), identify suitable sites for reintroductions (Pearce & Lindenmayer 1998), and support conservation planning and reserve selection (Loiselle *et al.* 2003).

Mitigating the impacts of climate change on species is critical, and proactive planning will be necessary to accomplish this (Thuiller *et al.* 2008) but depends on forecasting tools (Thuiller *et al.* 2008). Recent advances in modelling techniques, improvements in model output evaluation, and an increase in data availability and quality (i.e. finer scale resolution) have led to an expansion in the application of SDMs to many aspects of ecological research including conservation and management of species under climate change (Guisan & Thuiller 2005). As species are already shifting their distributions in response to global warming (Parmesan & Yohe 2003; Root *et al.* 2003; Root *et al.* 2005; Parmesan 2006) there is a need to adopt a proactive approach to conservation (Thuiller *et al.* 2008). To accomplish this, some prediction of a species response to climate change is necessary, and

SDMs make such forecasts (Thuiller *et al.* 2008). SDMs are one of the best tools for predicting the impacts of climate change on a species and its distribution, and are more often being relied upon for this (Pearson & Dawson 2003; Araújo *et al.* 2005; Martinez-Meyer 2005; Jimenez-Valverde *et al.* 2008; Thuiller *et al.* 2008; Elith & Leathwick 2009; Fitzpatrick & Hargrove 2009; Sinclair *et al.* 2010). However, this field of research is still in its youth, and many limitations have been identified in the recent literature (see Guisan & Thuiller 2005; Martinez-Meyer 2005; Araújo & Guisan 2006; Beaumont *et al.* 2008; Elith & Graham 2009; Elith & Leathwick 2009).

One of the most significant limitations of the application to conservation planning, although rarely examined, is the impact of biotic interactions on species distributions. Biotic interactions are likely to alter under climate change, as species respond idiosyncratically to changes in climate (Davis *et al.* 1998a; Davis *et al.* 1998b; Davis & Shaw 2001; Pearson & Dawson 2003; Martinez-Meyer 2005). Incorporating biotic interactions into SDMs will be important to determine the impacts on species distributions, particularly at the margins of a species' shifting range (Thuiller *et al.* 2008), where it is likely that populations will respond differently to those in the core (Anderson *et al.* 2009; Brook *et al.* 2009).

The impacts of extreme weather events are also not addressed in current SDMs, despite our knowledge that these events can alter survival and growth rates of species (Brook *et al.* 2009). This might also be particularly so for populations at the range margins (Parmesan *et al.* 2000). SDMs also do not account for the dynamic nature of a species potential distribution, which can shift, expand and contract temporally (Pearman *et al.* 2008; Sinclair *et al.* 2010).

Future studies utilizing SDMs need to address the shortcomings of current applications in order to provide more robust and reliable outputs. This includes making more ecologically realistic models by addressing the many factors that determine relative vulnerability of a species to global climate change (Williams *et al.* 2008). This is a critical step for bridging the gap between research outputs and conservation goals (Thuiller *et al.* 2008). Model reliability is necessary for conservation planning, management decisions, the formulation of policy and a proactive approach to the potential impacts of climate change on species, and their distributions.

1.1.3 An ideal candidate: the northern bettong (*Bettongia tropica*)

The reliability of SDM outputs is dependent on several factors, including type of modelling algorithm (Elith *et al.* 2006), use and choice of data (Araújo & Guisan 2006; Lozier *et al.* 2009; VanDerWal *et al.* 2009a), and model evaluation (Araújo & Guisan 2006; Lobo *et al.* 2008). Reliability can also depend on the choice of species being modelled, as ecological characteristics of a species determine how well its distribution can be modelled (Pearce *et al.* 2001; McPherson & Jetz 2007). For instance, differences in niche breadth can yield different accuracies: wide ranging generalist species are often modelled at lower accuracy than restricted species (Brotons *et al.* 2004; Tsoar *et al.* 2007; Jimenez-Valverde *et al.* 2008). A restricted range gives the ability to capture comprehensive data on environmental tolerances within a small scale, allowing for better discrimination of suitable habitat (Brotons *et al.* 2004). It also alleviates concerns of overestimation of habitat due to population-specific local adaptations that are more likely with widespread species (McPherson & Jetz 2007). A study by McPherson and Jetz (2007) revealed that species with small geographic range and high habitat specificity are ideal subjects for SDM on the basis of their prediction reliability. Other characteristics favourable to distribution modelling are: occurrence in areas of well mapped habitat, non-migratory or nomadic habit, small body size, and endemicity (narrowly defined). Additionally, ecological knowledge of a species, where available, can be used to improve the predictive power of a model (Austin 2002; Araújo & Luoto 2007).

The northern bettong (*Bettongia tropica*) was selected as an ideal candidate for SDMs and was chosen as the study species for this thesis. There is good knowledge of the ecology of the northern bettong (Winter 1992; Johnson & McIlwee 1997; Laurance 1997; Winter 1997a; Pope *et al.* 2000; Vernes 2000; Vernes *et al.* 2001; Vernes & Pope 2001; Vernes & Haydon 2001; Vernes 2003; Vernes *et al.* 2004; Vernes & Pope 2006; Abell-Davis 2008; Mathams 2008).

The northern bettong (Figure 1.1a) is a small (1.2 kg) endangered rat-kangaroo (Potoroidae) endemic to tropical northeast Queensland (Baillie & Groombridge 1996; Johnson & McIlwee 1997; Laurance 1997; Burnett & Winter 2008). It is a member of the Potoroidae family (Bettongs, Potoroos and Rat-kangaroos within the superfamily Macropodoidae (Kangaroos and their relatives) (Claridge *et al.* 2007). Bettongs are typically small (most species are less than 2 kg), nocturnal species with short rounded ears, semi-prehensile tails, short muscular forearms with small clawed paws used in foraging, and well developed hind legs with elongated hind feet (Claridge *et al.* 2007).

This species is restricted to a narrow strip (< 10 km wide) of *Eucalyptus* and *Allocasuarina* woodland on the western edge of the Great Dividing Range within the Wet Tropics, NE Queensland, Australia. The entire range of the northern bettong extends 275 km from south to north, with populations fragmented across the Wet

Tropics (Baillie & Groombridge 1996; Vernes & Pope 2001). This restriction is due to the specialized mycophagous diet of the northern bettong (Johnson & McIlwee 1997; McIlwee & Johnson 1998). Mycophagy, or fungus consumption, is common among Australian mammals (Claridge & May 1994) and is especially significant among the Potoroidae. The digestive system of Potoroids includes a fermentation chamber in the foregut, and this confers a greater efficiency in assimilating nutrients and extracting energy from fungus (McIlwee & Johnson 1998). Members of the Potoroidae family have therefore been able to specialize on fungal diets whereas other mycophagous mammals must supplement fungus with other food types.

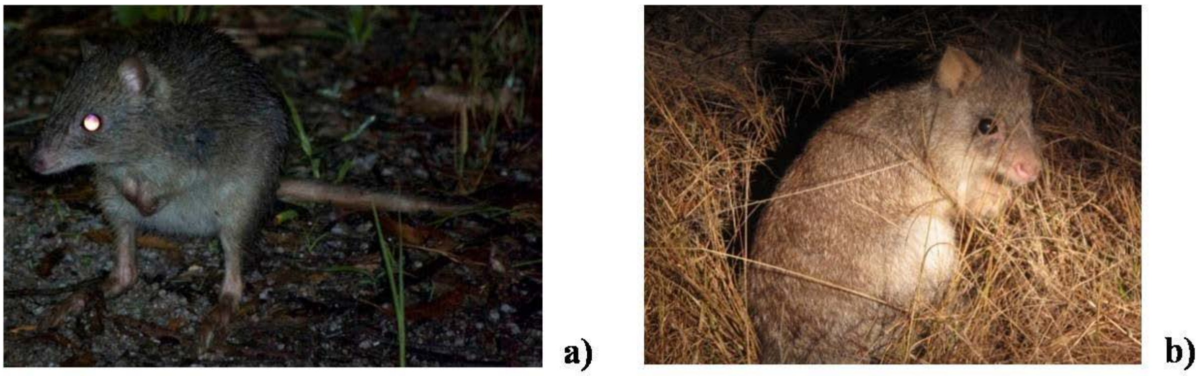

Figure 1.1 Photographs of a) the northern bettong (courtesy of Jeremy Little) and b) the rufous bettong (courtesy of Brad Bateman).

The northern bettong depends on ‘truffles’ (sporocarps of subterranean ectomycorrhizal fungi) as its main food resource and its body condition declines when truffle availability is low (Johnson & McIlwee 1997). However, truffle fruiting is seasonal and linked to rainfall, and thus suitable habitats for the northern bettong are close to the sclerophyll-rainforest ecotone where rainfall is high (though seasonal); rainforest vegetation is unsuitable because it does not support appropriate truffle species (Vernes 1999). Northern bettong distribution is thus limited to the narrow band of sclerophyll habitat where truffle productivity is highest. The northern bettong also depends on cockatoo grass (*Alloteropsis semialata*) during periods of low truffle production, especially the late dry season (Abell *et al.* 2006). Habitat for the northern bettong must therefore contain both truffles and cockatoo grass to maintain populations throughout the year, further limiting their distribution.

Fitting with the requirements for a good SDM candidate, the northern bettong is also not a migratory species and has a relatively small body size (~ 1.2 kg). There is also sufficient knowledge on key interactions with other species, including competition with the closely related rufous bettong (*Aepyprymnus rufescens*) (Figure 1.1b) (Winter 1997a; McIlwee & Johnson 1998). The mapping coverage for Australia is well established, with data sources for vegetation and geology (WTMA), climate (ANUCLIM), topography (ANUDEM), weather (AWAP), and fire frequency (NAFI), to name a few, readily available for use in modelling.

In addition to being an ideal candidate for SDM, the northern bettong is a keystone species. Bettong foraging behaviour promotes soil turnover, water infiltration, and facilitates the dispersal of truffles spores, all of which contribute to maintaining forest health (Claridge & May 1994; Garkaklis *et al.* 1998; Bougher & Lebel 2001; Garkaklis *et al.* 2004). The northern bettong has undergone a large range contraction since European settlement that has fragmented suitable habitat and isolated the remaining populations (Winter 1997b). Because of its restricted distribution, decline in quality and extent of habitat, and occurrence at less than five localities the northern bettong is listed as endangered by the IUCN (Baillie & Groombridge 1996; Burnett & Winter 2008). Historic records south of the Wet Tropics, near Rockhampton, as well as from the western edge of the Wet Tropics suggest this species once had a larger range (Winter 1997a). Past contractions have occurred towards higher rainfall areas, with drought and past climate change and their interactions with anthropogenic factors, such as changes in fire regime, habitat alteration or clearing, logging and cattle-grazing suspected to be the cause (Winter 1992; Winter 1997a; Winter 1997b; Abell-Davis 2008). The northern bettong is one of five bettong species that occurs in Australia, all of which have declined since European settlement (Johnson 2006). Once widespread across much of southern and eastern Australia, bettong species such as the brush-tailed bettong (*Bettongia penicillata*), the burrowing bettong (*Bettongia lesueur*), and the eastern bettong (*Bettongia gaimardi*), have experienced large range contractions with the latter two species extinct on the mainland (Short & Turner 1993; Johnson 2006). The closely related rufous bettong, although more widespread and common than the other bettong species, has also suffered range contractions such that it now occurs only in tropical and subtropical north-eastern Australia (Short 1998; Johnson 2006). Drought, anthropogenic factors and predation by the introduced red fox (*Vulpes vulpes*) have been implicated in these range contractions (Short 1998).

It is speculated that the northern bettong may have reached the Wet Tropics as recently as 6500-7000 years ago (Winter 1997b) during a cooler wetter period when the expansion of wet sclerophyll forest (Nix & Switzer 1991) allowed southern species (such as the closely related *Bettongia gaimardi* or *Bettongia penicillata ogilbi*) to expand north, before the northern bettong became isolated in its current range (Winter 1997b). More recent genetic analyses suggest the species may have been present in the Wet Tropics prior to this time (Pope *et al.* 2000). Regardless of the time of first occurrence in the Wet Tropics, it appears that historic climate change induced expansions and contractions of rainforests and associated wet sclerophyll forests in this region have played a major role in shaping the distribution of the northern bettong (Winter 1997b; Pope *et al.* 2000). The current range of this species will probably be sensitive to future climate change as well, with a predicted increase in rainfall variability and increases in length and severity of the dry season (Walsh & Ryan 2000; Hughes 2003). The northern bettong is an ideal candidate to test enhancements of SDMs through the incorporation of links between climate, limiting resources, biotic interactions, extreme events and distribution. Such modelling exercises will also allow us to make future predictions of the effects of climate change on the northern bettong, and to formulate a proactive conservation plan for its management.

1.2 Goals, aims and objectives of the research

Given the limitations of current SDM approaches described above, and the importance of distribution modelling in generating predictions of the effects of climate change on species distributions, the goal of this research was to contribute to the theory of species distribution modelling by addressing these limitations. In addition, the northern bettong is an ideal candidate for such studies, and, as an endangered species, would benefit from such exercises. Thus, the aims of this study were to:

1) To enhance the theory of species distribution modelling, by going beyond simple climate means to assess the implications that biotic interactions and extreme weather events have on model outcomes.
2) To improve our ecological understanding and conservation strategies of the northern bettong, using enhanced SDM techniques to give a better understanding of suitable habitat for the species, now and in the future.

To achieve these aims, my study has four specific objectives:

1.2.1 Aim 1. To enhance the theory of species distribution modelling:

Objective 1. Examine the distribution and limits of northern bettong key resources for inclusion into SDMs (Chapters 2-3). Understanding the ecology of the northern bettong includes gathering knowledge on the species that it interacts with. By examining the present day distribution and environmental influencers of these resources, one can identify if they will be good candidates for SDMs as interacting species. I investigate site and regional scale environmental features to assess what factors influence truffle (Chapter 2) and cockatoo grass (Chapter 3) distributions in the Australian Wet Tropics.

Objective 2. Assess the role of biotic interactions in SDMs (Chapter 4). Current applications of SDMs do not take into account biotic interactions. There is a need to assess what impact the inclusion of biotic interactions in distribution models might have on predictions of the distributions of species in altered climates. I assess the impact that inclusion of interactions has on model outputs, and if this gives more realistic predictions under future climate scenarios

Objective 3. Investigate the impact of extreme weather events on current distributions (Chapter 5). Extreme weather events affect species on many levels, yet they are not currently included in distribution models. As SDM outputs are based on a static niche and defined by long-term climate means, the dynamic effects of extreme weather impacts are not revealed. I examine if temporal variation in suitable habitat for a species occurs, and if extreme weather events have implications in what determines short-term habitat suitability and/or the competitive outcomes of species.

1.2.2 Aim 2. To improve our ecological understanding and conservation strategies of the northern bettong:

Objective 4. Develop proactive management strategies to mitigate the impact of climate change on the northern bettong (Chapter 6). Creating management plans for the conservation of endangered species requires detailed information on many ecological aspects of that species. Uncertainty over the impacts of climate change make conservation planning for a species a difficult task, and SDM are one of the few tools available to tackle this issue. From the results of my data chapters (Chapters 2-5) I provide suggestions for proactive management options for the northern bettong in the face of climate change.

1.3 Thesis framework and outline

This thesis consists of six chapters, structured so that results from earlier objectives/chapters could be utilized as a foundation for subsequent chapters (as outlined below and illustrated in Figure 1.2).

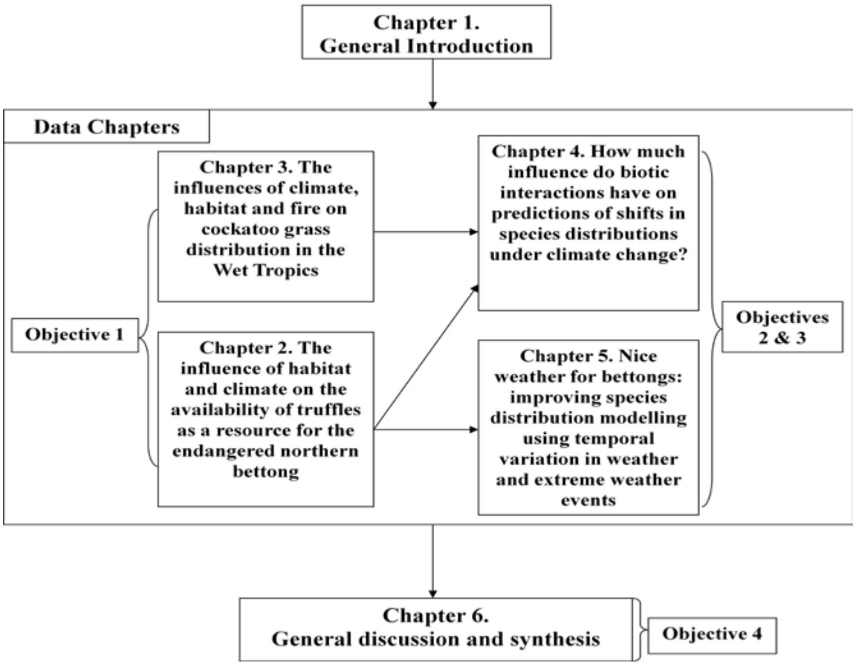

Figure 1.2. Thesis structure and outline.

The thesis introduction (Chapter 1) presents relevant material to this study and develops the overall thesis rationale. Chapters 2-3 (Objective 1) assess the influences on the distribution of key resources of the northern bettong, and tests whether these resources are suitable candidates for SDMs. Chapter 4 (Objective 2) uses results from Chapters 2-3 to examine the influence of biotic interactions in SDMs. Chapter 5 (Objective 3) uses data from Chapter 2 and Chapter 4 to assess how extreme weather events can be used in SDM research. The last section (Chapter 6) provides a general discussion and synthesis of the preceding chapters, highlighting the importance of this study in both SDM research and in conservation planning for an endangered marsupial species (Objective 4). The thesis has been set out to facilitate the publication of individual data chapters (Chapters 2-5) in peer-reviewed journals. Therefore, some overlap between the content of some chapters is inevitable. Structuring the thesis this way allows each chapter to be formulated as a discrete entity. Each of these data chapters, as well as components of the introduction and discussion will be submitted to international scientific journals (see following outline of chapters).

Chapter 1. General introduction. In this chapter I provide a background of the theory of species distribution modelling and highlight the limitations to current applications. I also discuss why the northern bettong is an ideal candidate for SDM research and provide relevant information on this species ecology.

Publication:

- **Bateman BL**, VanDerWal J, and Johnson CN (in prep) A review of species distribution modelling (SDMs): where to from here? To be submitted to *Diversity and Distributions* (with Chapter 6)

Chapter 2. The influence of habitat and climate on the availability of truffles as a resource for the endangered northern bettong (*Bettongia tropica*). In this chapter, I use data collected on truffle abundance and biomass to determine the factors that influence distribution at both the site and regional scale. In addition, comparisons are made on truffle availability between sites within the core and edge of northern bettong distribution. Conclusions will be used to assess if truffles are a good candidate in SDM studies.

Publication:

- **Bateman BL**, Johnson CN, Abell SE (in review) The influence of habitat and climate on the availability of truffles as a resource for the endangered northern bettong (*Bettongia tropica*). *Australian Journal of Zoology*

Chapter 3. The influences of climate, habitat and fire on cockatoo grass distribution in the Wet Tropics. In this chapter, I investigate the site-specific and regional environmental influences on cockatoo grass. An experimental burn was also conducted, and data were collected over one-year to assess the impacts of fire on this species. Conclusions will be used to assess if cockatoo grass is a good candidate in SDM studies.

Publication:

- **Bateman BL**, Johnson CN (2011). The influences of climate, habitat and fire on the distribution of cockatoo grass (*Alloteropsis semialata*) (Poaceae) in the Wet Tropics of northern Australia. *Australian Journal of Botany* 59 (4), 315-323

Chapter 4. How much influence do biotic interactions have on predictions of shifts in species distributions under climate change? In this chapter, I address a limitation that has been identified in the current approach to SDMs; failure to take into account biotic interactions. I assessed the impact of including biotic interactions as predictor variables in SDMs under climate change scenarios. I compared the performance of models with and without interactions in varying future climates to determine if interactions impact model output and if they make for more realistic predictions.

Publications:

- **Bateman BL**, VanDerWal J, Williams SE, Johnson CN (in review) How much influence do biotic interactions have on predictions of shifts in species distributions under climate change? *Diversity and Distributions*

Chapter 5. Nice weather for bettongs: improving species distribution modelling using temporal variation in weather and extreme weather events. In this chapter, I provide the first SDM study to include extreme weather events in model building and address another identified limitation of current SDM applications; failure to take into account extreme weather events and temporal variability. Here I include more dynamic information in SDMs using weather and extreme weather events to account for temporal variation to better define short term habitat suitability, provide more precise information on the location of range boundaries and predict the outcome of competition between species. Results were used to assess whether the current SDM application adequately captures overall habitat suitability for a species, and if extreme weather events are affecting population dynamics.

Publication:

- **Bateman BL**, VanDerWal J, Johnson CN (in press) Nice weather for bettongs: improving species distribution modelling using temporal variation in weather and extreme weather events. *Ecography*

Chapter 6. General Discussion and Synthesis. In this chapter I provide a summary of the major results of this study and develop a synthesis to address their implications in:

1) The enhancement of SDM theory. A discussion on how the results of my study have improved our understanding of both modelling theory and its application.

Conclusions from this study have possible implications for advancement of this field.

2) Implications in northern bettong conservation and ecological understanding. I discuss how my results have contributed towards the understanding of northern bettong ecology. Drawing from all chapters I outline a plan for proactive management of the northern bettong in the face of climate change.

Publication:

- **Bateman BL**, Johnson CN, Baker A, Parsons M (in prep) Proactive conservation in the face of climate change; climate refugia for the northern bettong. To be submitted to *Conservation Biology*

Additional Publications and Reports (from various Chapters and Appendices):

- **Bateman BL**, Johnson CN (in prep) Distribution, current and future predictions, of the rufous bettong (*Aepyprymnus rufescens*). To be submitted to *Australian Mammalogy* (with Chapter 4)
- **Bateman BL**, Johnson CN (in prep) Using probability of detection to determine survey effort and population decline of the northern bettong. To be submitted to *Wildlife Research* (Appendix B)
- **Bateman BL** Status of the northern bettong on the Coane Range (in prep) Report to the Australian Wildlife Conservancy
- **Bateman BL** Status of the northern bettong ; future management options (in prep) Report to Queensland Parks and Wildlife Service

Chapter 2 . The influence of habitat and climate on the availability of truffles as a resource for the endangered northern bettong (*Bettongia tropica*)[1]

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[1] **Bateman BL**, Johnson CN, Abell SE (in review) The influence of habitat and climate on the availability of truffles as a resource for the endangered northern bettong (*Bettongia tropica*). *Australian Journal of Zoology*

2.1 Abstract

The endangered northern bettong (*Bettongia tropica*) occurs in four discrete populations in far north Queensland Australia, at a high density only in the core of its range (Lamb Range). It is not known why *B. tropica* populations are low in density at the northern and southern parts (Coane Range) of its range. This specialist mycophagous marsupial is known to depend on a consistent availability of ‘truffles’, the below-ground fruit-bodies of ectomycorrhizal fungi. Truffle distribution in the Australian tropics has been shown to be influenced by aspects of climate, in particular seasonality of precipitation. Therefore, it is possible that in regions where bettongs occur in lower densities, climate may not adequately support the truffle resource.

This hypothesis was tested at both the site scale (Coane range) and with a regional analysis of the factors influencing truffle availability in the sclerophyll woodlands of the Wet Tropics where *B. tropica* occurs. Although truffle availability on the Coane Range was shown to respond to habitat features, these could explain only a small percent of the variance in truffle availability. Climate and weather variables did strongly influence the availability of truffles. Precipitation in the preceding month was positively related to truffle availability within both the Lamb and Coane Range, although there was less rainfall and truffle abundance at the latter. The regional modelling also predicted that the climate of the Coane Range was marginal in terms of truffle availability. Lower truffle abundance and more variable biomass recorded on the Coane Range was due to sub-optimal climate conditions and more variable weather and could explain why *B. tropica* populations occur in lower densities there. These results infer that increasing temperatures, more seasonal precipitation and harsher dry seasons, predicted for this region to occur as a result of

climate change, will have dramatic detrimental impacts on truffle productivity and thus population densities of *B. tropica* and other Australian mammals that also depend on them.

2.2 Introduction

Australia has a high diversity of hypogeous ectomycorrhizal fungi (ECM), and in particular, of sequestrate (truffle-like fungi) species (Bougher & Lebel 2001). There are currently 87 known genera and 294 species (Bougher & Lebel 2001) in Australia, with representatives of four of the five fungal divisions (including Zygomycota, Glomeromycota, Ascomycota, and Basidiomycota) (Abell-Davis 2008). It is estimated that up to 2450 species of sequestrate fungi occur in Australia, as it is thought that only 12-23% of the species have been identified (Bougher & Lebel 2001). ECM play a key role in Australian ecosystems, participating in an important association with the roots of trees and shrubs. Mycorrhiza fungi colonise the roots of plants via mycelium (vegetative thread-like hyphae), facilitating the uptake of soil nutrients and water as well as providing protection from pathogens. In return, the fungus receives photosynthetic carbohydrates from their plant hosts (Claridge 2002; Nehls *et al.* 2010). ECM are especially important in Australia's nutrient-poor and dry soils, and are common in sclerophyll forest and woodlands (Abell-Davis 2008).

'Truffles' are the fruiting bodies of hypogeous (below-ground) ECM fungi. Mammals detect truffles by smell and dig them up, leading to spore dispersal either through the air, attachment to or, more importantly, via the digestive tract of the mammal (Claridge & May 1994; Johnson 1996). In Australia, the probability of finding mycophagous species, such as rat-kangaroos and bandicoots, is highest in habitats with high truffle productivity (Claridge & May 1994; Claridge 2002).

The endangered northern bettong (*Bettongia tropica*) is a truffle specialist (Johnson 1996; Abell et al. 2006). The majority of its diet consists of ECM fungi (McIlwee & Johnson 1998) and body condition of bettongs in the wild declines when truffle availability is seasonally low (Johnson & McIlwee 1997). *B. tropica* distribution is both seasonally and spatially linked with truffle availability (Abell et al. 2006; Abell-Davis 2008). Due to this specialisation, *B. tropica* is limited to areas that have high truffle abundance within the Wet Tropics region (Johnson 1996; Abell et al. 2006). Both climate and local habitat-specific features affect where truffles occur (Claridge 2002). Precipitation is an important driver of truffle reproduction (Johnson 1994; Claridge et al. 2000a; Jumpponen et al. 2004; Abell et al. 2006; Claridge et al. 2009), and in the Wet Tropics strong seasonal variation in truffle availability is linked to precipitation (Abell *et al.* 2006). Truffle productivity is highest in a narrow band of sclerophyll habitat where precipitation is high (though seasonal) (Vernes 1999). Although rainforest habitats experience higher precipitation they are not used by *B. tropica* because most fungi that form mycorrhiza with rainforest plants are non-ECM types and produce small or no sporocarps (Johnson & McIlwee 1997).

B. tropica is restricted to four known areas: the Lamb Range, Coane Range, Carbine Uplands, and Windsor Uplands. Of these locations only the Lamb Range populations, which occur at the centre of the species range, have high densities (Winter 1997a; Vernes & Pope 2006). The outlying populations, which occur north (Carbine and Windsor Uplands) and south (Coane Range) occur in lower densities. Local declines have been recorded from both north (Windsor Uplands) (Winter

1997a) and south (Coane Range) of *B. tropica's* distribution. On the Coane Range a recent survey failed to detect a single individual over several years of intense, significant survey effort (Appendix B). It is currently unknown why populations outside the Lamb Range, including the Coane Range, have lower densities and are thus prone to local extinctions. An examination of the critical food source of *B. tropica* could help us to understand this.

Little is known about the distribution of ECM fungi in relation to biotic and abiotic features in tropical Australia. Most work on the distributional ecology of these organisms has been conducted in southern Australian temperate systems, and extrapolation of patterns found there to tropical systems may be unreliable (Abell-Davis 2008). As the Lamb Range is more stable climatically than northern and southern portions of the Wet Tropics, experiencing lower seasonality in both temperature and precipitation seasonality (Williams & Middleton 2008), it is possible that the marginal regions experience less suitable climate and weather conditions for truffles. As truffles are strongly affected by climate and weather, more seasonal weather patterns could lead to inconsistent truffle availability, which could make areas experiencing those weather patterns less suitable for *B. tropica*.

The aim of this study was to identify the factors that influence total truffle availability (by combining all taxa into a single category) as a *B. tropica* food resource in the sclerophyll woodlands of the Australian Wet Tropics. Combining taxa is logical given that bettongs have been shown to feed on the full range of species found within this region (Vernes *et al.* 2001). Truffle availability will be examined in relation to climate variables and local habitat-specific features to determine the factors that influence availability to bettongs. This will help us to understand if the highly seasonal climate experienced by the northern and southern populations of *B. tropica* affects truffle availability, making them less reliable as a resource in the long-term, and thus reducing the density of bettong populations. The distribution and habitat factors influencing truffle availability at the southern limit of *B. tropica*, on the Coane Range was examined in this study. Results from this region were then compared with the Lamb Range, where bettong populations occur in higher densities and where truffle distribution and abundance have been studied by both Abell-Davis (2008) and Mathams (2008).

2.3 Methods

2.3.1 Study area

For local scale analysis, the study site was located within sclerophyll woodlands on the Australian Wildlife Conservancy (AWC) managed Mt Zero-Taravale wildlife sanctuary on the Coane range, in the Wet Tropics of north-eastern Queensland Australia (146°11’E, 19°07’S) (Figure 2.1). A total of eight survey sites were selected in two vegetation types along a gradient from wet to dry sclerophyll forest types, and sampling two geological substrates (Figure 2.1). Precipitation varies along this gradient from 2,000 mm/annum in the north east to less than 800 mm/annum on the western border of the property (Stanton 2007), creating a steep transition in vegetation community from rainforest to dry sclerophyll forests. Forest types selected for this survey were the higher precipitation *Allocasuarina* very tall open forests, (type 10 and 11, Stanton 2007) and *Eucalyptus* woodlands, (type 40 and 64, Stanton 2007) and were situated at different altitudes due to the nature of the vegetation gradient. Wet sclerophyll sites were excluded from this survey, as Abell *et al.* (2006) found that fungal availability was low throughout the year in this habitat type.

Allocasuarina very tall to extremely tall open forest sites were dominated by *Corymbia intermedia*, *Allocasuarina torulosa*, *Syncarpia glomulifera* and *Eucalyptus resinifera*. *Eucalyptus* woodlands were dominated by either *Eucalyptus portuensis* (type 40) with *Syncarpia glomulifera*, *Corymbia intermedia*, *Corymbia leptoloma*, and *Corymbia abergiana*, or *Corymbia citriodora* (type 64) with *Eucalyptus portuensis*, *Eucalyptus tereticornis*, and *Lophostemen suaveolans* (Stanton 2007). The understorey in all sites was predominately grass, with kangaroo grass (*Themeda triandra*) dominant. Four sites were surveyed in each vegetation type (*Allocasuarina* or *Eucalyptus*). The four *Allocasuarina* or *Eucalyptus* sites were further divided so that two of the sites were assigned to rhyolite and two to granite substrates (Figure 2.1). Sites were spaced at least 500 m apart.

Truffle records from across the Wet Tropics region of Australia were utilised to evaluate the regional scale influences of climate on truffles. Truffle occurrence data were obtained from this survey and other field surveys (using the same field methods) for truffles in the region (Abell-Davis 2008; Mathams 2008) (Figure 2.1).

All truffle species were combined to yield one grouping representing truffles as a food resource with a total of 307 presence records. The modelling algorithm used in regional scale modelling, Maxent (see description below), is a viable modelling technique with as few as five occurrence records (Pearson *et al.* 2007) and the output can provide a measure of potential abundance for a species (VanDerWal *et al.* 2009b) making it a suitable surrogate for productivity. Due to limited sampling in the region, truffle records are restricted to the wet to dry sclerophyll woodlands gradient, occurring adjacent to rainforest. Williams *et al.* (2010) have shown that for targeted analysis on species or taxa that are restricted to certain habitat types, good data coverage within the appropriate habitat gradient is sufficient to identify what is unique about that niche with respect to the full background.

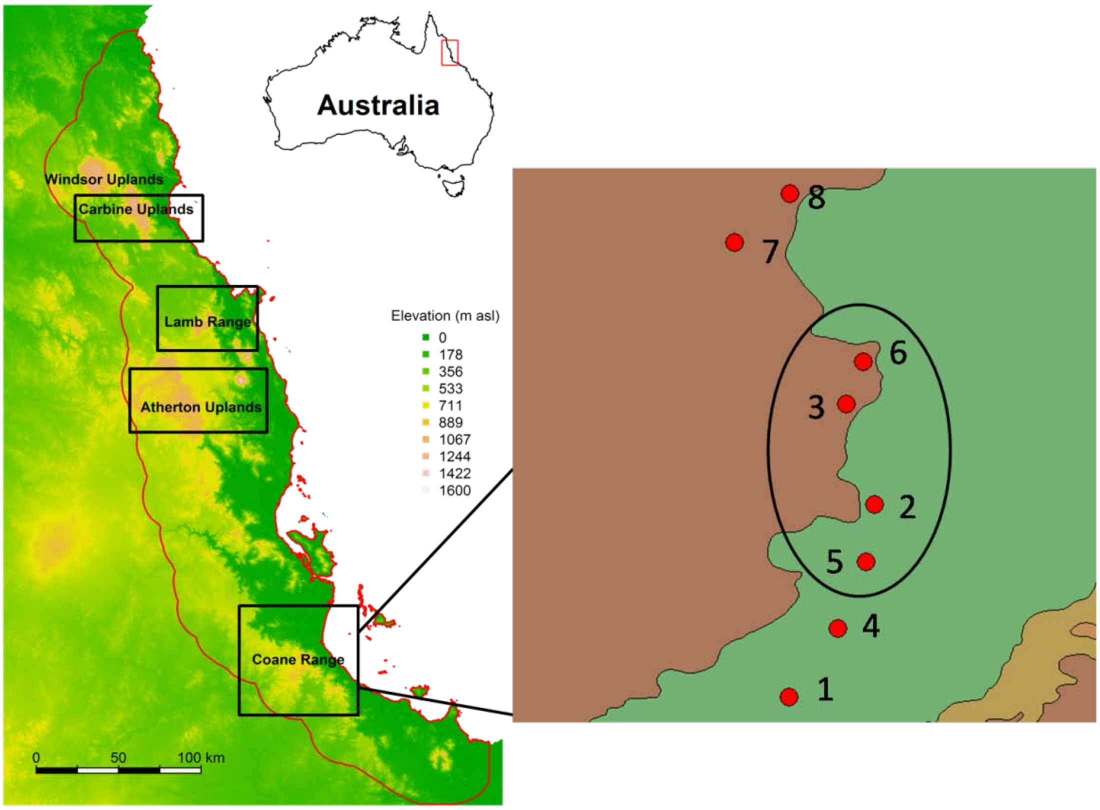

Figure 2.1. Location of study region in the Wet Tropics, north-eastern Australia; inset is a map of sites within the Coane Range where site scale surveys were conducted; brown colour represent granite and green represents rhyolite; sites occurring within the circle are *Allocasuarina* forest and sites outside are *Eucalyptus* woodlands. Larger areas indicated on the map (in boxes) are the regions where all truffle occurrence records were collected from, for use in regional scale modelling.

2.3.2 Field methods

2.3.2.1 Truffle sampling

Truffle sampling was adapted from the methodology of Abell *et al.* (2006). In each site, four replicate 50 m by 20 m (1,000 m^2) quadrats were established adjacent to each other. Quadrats were sampled once only to minimize habitat disturbance typical of this destructive sampling method and to allow fungal recovery after surveys. All quadrats were set up along the same contour of their long axes to maintain topographical position and minimise heterogeneity within sites. Sites were surveyed four times giving a total of 32 surveys, in December 2006 (transition period from dry to wet season), April 2007 (late in the wet season), July 2007 (early in the dry season), and December 2007 (transition period from dry to wet season), with one quadrat per sites sampled at each seasonal survey. In order to account for the limitations inherent with the sampling design, several analyses were conducted in an attempt to address all spatial and temporal variation and issues of independence. Hence, climate and weather data were derived for each of the sites, rather than for each quadrat within sites (as these are too close together to have distinct climate or weather attributes), while habitat based analyses were compared using all quadrat data.

A 160 person-minute timed survey of each quadrat was conducted by raking leaf litter and digging soil throughout the entire quadrat using truffle forks. Abell *et al.* (2006) and Claridge *et al.* (2000b) used this time-standardized survey method because it allows repeated surveys of large areas in a relatively short time and minimizes damage to the site. Truffles were found by closely examining all leaf litter and soil for evidence of fungal activity (i.e. hyphae), with effort subsequently concentrated when such evidence was noted. All truffles found were collected and micro-habitat details at each collection site were noted (distance to nearest tree and tree species, distance and angle from centre point of quadrat). The number of individual sporocarps in each fruiting patch found within the quadrat was recorded. A patch was defined as sporocarps of the same species occurring together within a 1 m radius. Truffles were identified to morpho-group by sporocarp appearance, then dried, weighed for biomass (g), and processed for spore examination. Photographs of truffle spores and sporocarps were used to identify specimens to genus.

Although it is known that different taxa of truffles may respond differently to environmental cues (Johnson 1994; Jumpponen et al. 2004; Abell-Davis 2008), in the Australian Wet Tropics the availability of truffles in the landscape has been shown to respond to similar cues such as precipitation (Abell *et al.* 2006). Here, all truffle records were combined across species to represent truffles as a single taxonomic group; this was done because the aim was to assess availability of truffles as a resource for *B. tropica*. Abundance and biomass of truffles collected within a total of 32,000 m^2 were converted to a per hectare measure to estimate the availability of truffles as a resource (as per Abell *et al.* 2006). To provide a measure of habitat quality and truffle availability throughout the landscape, a measure of truffle availability per home range was also calculated. The home range of *B. tropica* has been estimated at 59 ha (Vernes & Pope 2001), and this is the value used here for truffle availability per home range. Truffle abundance and biomass per hectare values from the Coane Range were compared to abundance and biomass measures on the Lamb Range (from Abell *et al.* 2006; SE Abell-Davis unpublished data) using a one-way analysis of variance (ANOVA, F). Surveys conducted on the Lamb Range during the late dry season, where truffle availability is low (Abell *et al.* 2006), were excluded from this comparison, as no late dry season survey was conducted on the Coane Range.

2.3.2.2 Environmental sampling

Measurement of local habitat features was adapted from Abell *et al.* (2006) and all data were collected for each quadrat (n = 32) over each of the four sampling surveys. Variables were recorded along the long axis of each quadrat on a transect bisecting the centre of the plot. Data consisted of counts within 1 m of either side of the transect, as well as estimations of percentage cover taken from midway along the transect. Microhabitat variables were characterised following the method of Abell-Davis (2008), which was adapted from Claridge *et al.* (2000a), as briefly described below.

Biotic variables included the number of stems of potential host species (*Allocasuarina* and *Eucalyptus*) along the centre transect. Variables recorded by estimated percentage cover were: canopy, understorey, and litter layer. Thirteen random measures of litter layer depth (cm) were obtained throughout the quadrat.

Abiotic factors recorded were slope (measured with a clinometer), and altitude (m above sea level) obtained from handheld GPS. Three soil samples were collected from each quadrat, from the top middle and bottom of the slope along the centre transect following the method of Abell-Davis (2008). Data were collected for each quadrat (n = 32) and then averaged for each site (n= 8) over each of the four sampling surveys. Soil samples were analysed for soil Nitrogen in weight percentage (N), mean total Phosphorus (P), Carbon in weight percentage (C), Sulphur in weight percentage (S), the CN ratio, and average soil moisture (averaged across all three samples). A total of 96 soil samples were collected from eight sites and four sampling periods. Mean soil moisture was determined for each site (mL/g) for each survey from wet and dry weights averaged over each sample (top, middle, bottom of slope). Soil samples were sieved to 2mm to separate earth material from gravel. To determine total P (µg/g), each sample was processed using a single digestion method followed by an adaptation of Murphy and Riley’s (1967) single solution method (Anderson & Ingram 1989). Soil N, C, and S were determined with an Elementar

Vario Max CNS Analyser (Elementar, Hanau Germany) by the Sediment lab, School of Earth and Environmental Sciences, James Cook University, Townsville.

The climate data were long-term climate means and were derived from ANUCLIM 5.1 (McMahon *et al.* 1995) software using monthly averages and an 80 m DEM re-sampled from ~250m (GEODATA 9 Second DEM Version 2; Geoscience Australia, http://www.ga.gov.au/). Eight climate variables were selected with the aims of maximizing climate information and minimizing the number of highly inter-correlated variables. Variables were: annual mean temperature (°C), temperature seasonality (coefficient of variation (C of V)), maximum temperature of warmest period (°C), minimum temperature of coldest period (°C), annual precipitation (mm), precipitation seasonality (C of V), precipitation of wettest quarter (mm), and precipitation of driest quarter (mm). Climate data were extracted from GIS layers (ANUCLIM) for each of the eight fungal survey sites as well as all truffle records from within the Wet Tropics.

In addition, precipitation data was extracted from the Bureau of Meteorology (BOM) (http://www.bom.gov.au/climate/data/) for precipitation data one month prior to each of the surveys. Data was extracted from two weather stations, Paluma, Ivy Cottage QLD (12.2 km east of the study site; Wet BOM hereafter) and Horse Shoe Bend, QLD (12.7 km west of the study site; Dry BOM hereafter), and averaged to provide one measure (Average BOM hereafter). Rain gauge data was also provided by the AWC for one month prior to each of the surveys for two locations, Mt Zero (northern portion of study site) and Taravale (southern portion of study site) and the values were averaged to provide one measure for each survey period (Rain Gauge hereafter).

2.3.3 Analysis

2.3.3.1 Site scale

The Shapiro-Wilk (SW-W) test for normality revealed that Mean P (SW-W = 0.95, p = 0.22) and CN ratio (SW-W = 0.98, p = 0.84) were normally distributed. The data for N, C, S, soil moisture, abundance of sporocarps, and dry weight (biomass) departed from normality (N: SW-W = 0.87, $p \leq 0.01$, C: SW-W = 0.88, $p \leq 0.005$, S: SW-W = 0.65, $p \leq 0.00001$, soil Moisture: SW-W = 0.92, $p \leq 0.05$, average abundance of sporocarps: SW-W = 0.84, $p \leq 0.001$, and average biomass: SW-W = 0.66, $p \leq 0.00001$). These variables could not be normalised by transformation, so a Kruskal-Wallis one-way non-parametric analysis of variance (H) was used to test variation in the median of all data against vegetation and geology type. This was undertaken as an exploratory approach to determine how best to group data for further analysis. Truffle biomass (g) and abundance (number of sporocarps) were tested using a Kruskal-Wallis one way non-parametric analysis of variance (H) to test variation in the median of all data against season (represented by each survey).

In order to further examine the relationship between truffle availability and environmental features, another analysis was conducted. A Spearman rank correlation matrix was used to reduce the number of correlated variables (10 environmental variables were recorded). Pairs of variables with high Spearman pair-wise correlation coefficients ($r \geq 0.6$) were reduced to a single variable to represent the pair. All variables were standardised for further analysis.

A Poisson Generalised Linear Model (GLM) with a log link function was used to examine the relationship between the selected variables and truffle abundance. A Kullback-Leibler (K-L) information-theoretic approach was used to construct all possible model configurations (best subsets), using the Akaike Information Criterion (AIC) as an objective means of model selection (Burnham & Anderson 2002). This uses Akaike model weights (w_i), or relative strengths of evidence, to determine the most parsimonious models rather than classic hypothesis testing methods (Burnham & Anderson 2002). All analyses were conducted in R (v2.10.0, http://www.r-project.org), using the MuMIn R package (http://cran.r-project.org/web/packages /MuMIn/index.html). The second-order information criterion (the AIC_c) was used to correct for sample bias ($n/K < 40$) (Burnham & Anderson 2002). The model with the lowest AIC_c value ($AIC_{c\ min}$) was selected as the best-supported model and plausible models were presented if they fell within 2 AIC_c units (Δ_i) of the $AIC_{c,min}$, although models within 4-7 AIC_c units (Δ_i) were retained as they still contain support (Burnham & Anderson 2002). Akaike model weights (w_i) were used to calculate the relative likelihood, or weight of evidence as being the most parsimonious model, for each model in the set. Model weights vary from 0 (no support) to 1 (complete support). Model weights were used to calculate evidence ratios to determine if one model was convincingly better than the others or if a 95% confidence set of models was needed (Burnham & Anderson 2002). Percent deviance explained is provided as a measure of model fit.

Model averaging was conducted to determine the relative importance of each variable contributing to model building. A measure of variable importance was calculated by summing all of the weight scores (w_i) for any model of which the variable was a component, with values closer to 1 being relatively more important and values above 0.5 considered good (Ritchie *et al.* 2009). Parameter estimates, standard errors, and upper and lower confidence intervals were calculated for each variable. The parameter estimates are reported with confidence intervals, to show whether or not the estimate of effect size overlapped zero. The magnitude (impact on model building) and direction of the effect (positive or negative) are indicated by the direction and magnitude of the parameter estimate.

To examine if climate factors influence truffle availability at a site scale, climate variables (extracted per site) were examined against truffle biomass and abundance using linear regression analysis. Truffle availability was also tested in relation to precipitation data using linear regression analysis, with abundance and biomass values per truffle survey examined in relation to precipitation data one month prior to each survey period (using both BOM data and collected rain gauge data). This was then compared with the linear regression analysis of truffle abundance and biomass and precipitation events two months prior to surveys for the Lamb Range from Abell-Davis (2008), and precipitation events one months prior to surveys for the Lamb Range (SE Abell-Davis, unpublished data) to determine if truffles respond to precipitation in the same way on the Coane Range and Lamb Range. To determine if there is an effect of site on truffle production independent of prior precipitation events, an analysis of covariance (ANCOVA; F) was undertaken with site as a random factor, precipitation as the covariate, and truffle abundance (log transformed) as the dependent variable. The one month preceding precipitation values for each survey were then compared with long-term means to determine if the survey had above or below average precipitation values. Truffle availability in above average precipitation surveys was compared with below average precipitation surveys using a Kruskal-Wallis one way non-parametric analysis of variance (H).

2.3.3.2 Regional scale modelling

Maxent (v. 3.3.1) (Phillips *et al.* 2006) was used to correlate occurrence of truffles with the eight selected climate variables to estimate probabilities of presence across the landscape. Probability of presence was used as a measure of productivity, as truffles are presumably ubiquitous throughout this region given appropriate conditions but some areas are more likely to be consistently productive and thus are more likely to provide occurrence records. Maxent is a presence-only modelling algorithm that has been shown to outperform other presence-only modelling techniques (Elith *et al.* 2006; Hernandez *et al.* 2006; Hijmans & Graham 2006; Guisan *et al.* 2007); see Appendix A for a more detailed review of Maxent and the technical underpinnings of this program. Maxent was parameterized with default settings (Phillips & Dudik 2008) with the exception of the removal of threshold and hinge features, because this produces more ecologically realistic response curves (Austin 2007). I have addressed any spatial bias in the data set accordance to the literature in using a spatial buffer and drawing the 10,000 background points from near locations where records are known (VanDerWal *et al.* 2009a). This approach provides better model discrimination and addresses spatial biases that are often inherent in data sets on species distributions. Maxent models were evaluated using the area under the receiver operating characteristic (ROC) curve, the AUC (Area Under Curve), with values above 0.5 are better than random predictions, with those above 0.7 being considered useful (Elith *et al.* 2006) and those above 0.9 highly accurate (Guisan *et al.* 2007).

For comparison purposes only, individual Maxent models were also created for both the Lamb Range truffle records only and the Coane Range truffle records only in order to determine how they compare to the full Wet Tropics model. Limited results are presented in relation to where the Coane Range represents as a climatic outlier. In addition, to determine the climatic seasonality of each region where truffle occurrences were recorded in the Wet Tropics, the values for the ANUCLIM variables of temperature seasonality and precipitation seasonality were extracted for each location and compared using a scatter plot.

Once the top three climate variables that contributed to model building of truffles across the Wet Tropics were determined, the values for each of those climate variables were extracted from all of the Coane Range truffle occurrences. The values experienced at the Coane Range sites can be compared to the response curves developed by Maxent (see Appendix A for more details on response curves) to see where they lie along the gradient of probability of occurrence. This was done to determine if the Coane Range is indeed an outlier in terms of climate conditions for the region. In addition, the extracted climate values were used to observe the differences between top four sites in terms of truffle availability (highest values of truffle abundance and biomass) with the bottom four sites in relation to top three variables.

2.4 Results

2.4.1 Site scale

A total of 44 patches (including individual sporocarps) of truffles were found, containing 162 total sporocarps with a total weight of 137.85 g biomass from all sites and sampling sessions. This was an average of 13.75 patches per hectare, with patches tending to contain few truffle sporocarps (3.68 per patch) that were large (3.13 g per sporocarp). Truffle abundance per hectare on the Coane Range (52.18 ha^{-1} ± 31.51 SD) was significantly less than the Lamb Range (174.44 ha^{-1} ±

56.92 SD) (from Abell *et al.* 2006) when surveys from the same time of year were compared (F= 13.54, p ≤ 0.05). This translates to 3078.62 sporocarps per *B. tropica* home range on the Coane Range, and 10,291.96 sporocarps per *B. tropica* home range on the Lamb Range. Truffle biomass on the Coane Range (44.61 g/ ha^{-1} ± 26.96 SD) was higher than biomass measures from the Lamb Range (27.96 g/ ha^{-1} ± 9.63 SD; SE Abell-Davis, unpublished data) although not significantly (F = 1.00, p = 0.36). In terms of *B. tropica* home range, the Coane Range had an average of 2.63 kg per home range whilst the Lamb Range had only 1.65 kg per home range, but biomass was more variable on the Coane Range (± 1.59 kg SD) than the Lamb Range (± 0.56 kg SD). Ten genera were identified: *Castoreum*, *Mesophellia*, *Scleroderma*, *Gummiglobus*, *Labyrinthomyces*/*Dingleya*, *Stephanospora*, *Hysterangium*, *Malajczukia*, *Sclerogaster*, and *Pogiesperma*. *Mesophellia* represented 47% of the overall biomass and 23.5% of the total abundance of all truffles found, followed by *Castoreum* with 24% of the total biomass and 14% of the overall biomass.

Exploration of the data revealed that average truffle abundance and biomass, as well as soil Nitrogen, Carbon, Sulphur, CN ratio and soil moisture were different between *Allocasuarina* forest and *Eucalyptus* woodlands, with all values higher in *Allocasuarina* forest (Table 2.1). Phosphorus concentration did not differ between vegetation types. There was no difference between granite and rhyolite substrates for any variables (Table 2.2).

The ten environmental variables were reduced to five variables due to colinearity. The variables retained included litter cover, soil moisture, *Allocasuarina* density, Phosphorous, and slope. Litter cover was positively correlated with percentage canopy cover (r = 0.72), Carbon (r =0.68), and Nitrogen (r = 0.67). Soil moisture was also positively correlated with Nitrogen (r = 0.77), Carbon (r =0.76), and percentage canopy cover (r = 0.73). *Allocasuarina* density was positively correlated with altitude (r = 0.82), understorey cover (r = 0.80), litter layer depth (r = 0.68), Nitrogen (r = 0.66), and Carbon (r = 0.60). Phosphorus and Slope were not correlated with any other variables.

The best-supported model predicting truffle abundance included Phosphorus, *Allocasuarina* density, and litter cover (Table 2.3). Eight models had support, with model 1 being 21 times more likely than model eight, 14 times more likely than models 6 and 7, 4.67 times more likely than models 4 and 5, 3.23 times more likely than model 3, and 2.33 times more likely than model 2 (Table 2.3). This indicated that model 1 had considerable support, models 2 and 3 had some support, while models 4-8 had considerably less support. The percent deviance explained was 36.29 for model 1, 37.10 for model 2, and 35.06 for model 3, indicating that the environmental variables collected could not account for a large proportion of variation in truffle abundance.

The most important variables ($w_i \geq 0.5$, confidence intervals do not intersect zero) were litter cover ($w_i = 1.0$), and Phosphorous ($w_i = 0.99$), followed by *Allocasuarina* density ($w_i = 0.75$), and soil moisture ($w_i = 0.44$) (Table 2.4). The coefficient estimates indicated that litter cover had the largest relative (positive) effect on truffle abundance, closely followed by phosphorous (negative) (Table 2.4). Truffle abundance was positively related to *Allocasuarina* density, with a smaller effect (Table 2.4). Slope was not considered a reliable parameter estimate because confidence intervals overlap with zero and variable weighting was low (Table 2.4).

Table 2.1. Analysis of variance on truffles (abundance (number of sporocarps) and biomass) and soil nutrients and moisture between *Allocasuarina* forest and *Eucalyptus* woodlands. Shown are mean, median, standard error (SE), Kruskal-Wallis (H), and significance (p) value for comparisons. * indicates significant variation.

	Eucalyptus			***Allocasuarina***				
Variable	**Median**	**Mean**	**SE**	**Median**	**Mean**	**SE**	**H**	**p**
Truffle abundance	0.00	3.14	1.45	6.50	8.43	1.60	6.62	0.01*
Truffle biomass (g)	0.00	3.09	2.28	2.70	6.75	2.01	4.52	0.05*
Nitrogen (%)	0.14	0.15	0.01	0.40	0.42	0.04	19.05	0.00001*
Carbon (%)	2.32	2.60	0.29	8.92	8.90	0.87	19.46	0.00001*
Sulphur (%)	0.01	0.01	0.01	0.02	0.02	0.00	11.88	0.001*
CN Ratio (%)	16.86	16.87	0.69	21.04	21.48	0.70	13.18	0.0005*
Soil moisture (mL/g)	0.09	0.08	0.01	0.14	0.16	0.02	10.05	0.01*
Phosphorus (µg/g)	0.15	0.16	0.02	0.19	0.19	0.01	1.54	0.22

Table 2.2. Analysis of variance on truffles (abundance (number of sporocarps) and biomass) and soil nutrients and moisture between granite and rhyolite geology; Shown are mean, median, standard error (SE), Kruskal-Wallis (H), and significance (p) value for comparisons. * indicates significant variation.

	Rhyolite			**Granite**				
Variable	**Median**	**Mean**	**SE**	**Median**	**Mean**	**SE**	**H**	**p**
Truffle abundance	3.00	4.80	1.24	4.00	6.92	2.10	0.06	0.82
Truffle biomass (g)	1.60	2.49	1.21	3.10	7.73	2.87	1.61	0.21
Nitrogen (%)	0.20	0.24	0.03	0.37	0.34	0.06	0.06	0.80
Carbon (%)	3.63	4.99	0.77	7.64	6.63	1.35	0.15	0.70
Sulphur (%)	0.01	0.02	0.00	0.01	0.01	0.00	0.0005	0.98
CN Ratio (%)	19.12	19.82	0.98	19.36	18.43	0.83	0.28	0.60
Soil moisture (mL/g)	0.12	0.11	0.01	0.13	0.13	0.03	0.09	0.77
Phosphorus (µg/g)	0.16	0.17	0.01	0.19	0.18	0.02	0.51	0.48

Table 2.3. The results of Poisson Generalized linear modelling (GLM) using Akaike's information criterion (AICc) for truffle abundance (number of sporocarps). Values represent the number of parameters (K), maximised log-likelihood (Log(L)), Akaike's information criterion corrected for small sample sizes (AICc), AICc model differences (Δ), Akaike model weights (wi), and the percent deviance explained (% Dev). Models are ranked relative to the AICc min, or model with the smallest AICc, in descending order. The eight highest ranked models are shown (between Δ 0-7 of AICc min). †Variable codes refer to: P, Phosphorous (µg/g); A, *Allocasuarina* density, LC, Litter Cover (%); SM, soil moisture (mL/g); S, Slope.

Model	**Variable**†	**Variable**†	**Variable**†	**Variable**†	**Variable**†	**K**	**Log(L)**	**AIC$_c$**	**Δ**	w_i	**% Dev**
1	P	A	LC			5	-97.79	208.30	0	0.42	36.29
2	P	SM	A	LC		6	-97.00	209.99	1.69	0.18	37.10
3	P	SM	LC			5	-98.99	210.71	2.40	0.13	35.06
4	P	LC				4	-100.84	211.42	3.12	0.09	33.16
5	P	A	LC	S		6	-97.75	211.50	3.20	0.09	36.33
6	P	SM	A	LC	S	7	-96.98	213.57	5.27	0.03	37.12
7	P	SM	LC	S		6	-98.87	213.75	5.45	0.03	35.17
8	P	LC	S			5	-100.73	214.20	5.90	0.02	33.26

Table 2.4. Model averaging results for relative importance of contributing variables to Poisson generalized linear models (GLM) using Akaike's information criterion (AIC$_c$) for truffle abundance (number of sporocarps). Values represent the relative importance of each variable (w_i), average estimates (estimate), standard errors (SE), and upper and lower confidence intervals (CI).

Variable	w_i	**Estimate**	**SE**	**Lower CI**	**Upper CI**
(Intercept)		1.49	0.10	1.27	1.70
Litter Cover (%)	1.0	0.76	0.16	0.42	1.09
Phosphorus (µg/g)	0.99	-0.36	0.11	-0.57	-0.14
Allocasuarina density	0.75	0.16	0.12	-0.08	0.39
Soil Moisture (mL/g)	0.44	0.07	0.10	-0.14	0.28
Slope (°)	0.19	0.0008	0.02	-0.05	0.05

Truffle biomass had a significant relationship with several climate variables. A positive relationship between truffle biomass and annual precipitation ($r = 0.71$, $p \leq 0.05$, $R^2 = 0.50$) and precipitation of the driest quarter ($r = 0.72$, $p \leq 0.05$, $R^2 = 0.51$) was found. Negative relationships were found with annual mean temperature ($r = - 0.73$, $p \leq 0.05$, $R^2 = 0.53$), maximum temperature of the warmest period ($r = - 0.72$, $p \leq 0.05$, $R^2 = 0.54$), minimum temperature of the coldest period ($r = - 0.74$, $p \leq 0.05$, $R^2 = 0.55$), and precipitation seasonality ($r = - 0.72$, $p \leq 0.05$, $R^2 = 0.52$). Truffle abundance only had a significant relationship with minimum temperature of the coldest period ($r = - 0.72$, $p \leq 0.05$, $R^2 = 0.51$).

There was no difference detected in truffle availability between survey periods (abundance $H = 4.97$, $p = 0.17$; biomass $H = 2.69$, $p = 0.44$) and thus no patterns of seasonality could be discerned. This may be a product of a failure to survey during the late dry season (September) when truffles have been shown to be less abundant in this region (Abell *et al.* 2006). Truffle abundance was also positively influenced by precipitation in the preceding one month (Rain Gauge data, $r = 0.90$, $p = 0.10$, $R^2= 0.81$; Average BOM data $r = 0.86$, $p = 0.12$, $R^2= 0.78$) although more surveys are needed to determine if the relationship is significant (Figure 2.2). This is comparable with the relationship found by Abell-Davis (2008), where truffle abundance had a significant positive relationship with precipitation two months prior to surveys on the Lamb Range, as well as a positive relationship with precipitation one month prior to surveys (Figure 2.2). It appears that truffle abundance is responding to prior precipitation events in the same way on both the Lamb Range and Coane Range, but there tends to be less truffles as well as less total precipitation in the prior precipitation events on the Coane Range (Figure 2.2). ANCOVA analysis revealed that for both one and two month precipitation time lags, there was no site effect on truffle abundance between the Coane Range and Lamb Range (precipitation two months prior F = 1.31, p = 0.31; precipitation one month prior F = 0.43, p = 0.66), but there was an effect of precipitation prior to the surveys (precipitation two months prior F = 44.71, $p \leq 0.0001$; precipitation one month prior F = 16.20, $p \leq 0.01$).

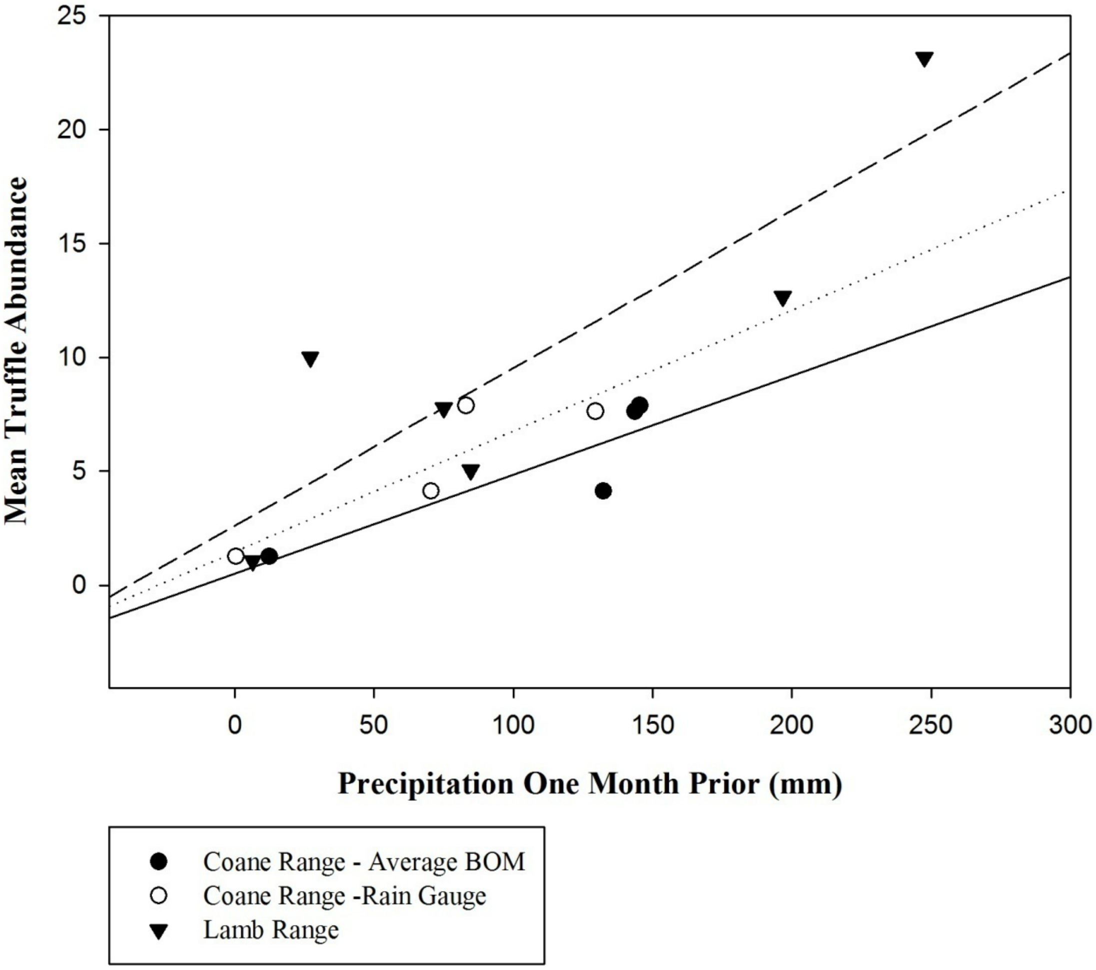

Figure 2.2. The relationship between mean truffle abundance and precipitation one month prior to the survey. The Coane Range Average BOM is represented by a solid line, Coane Range Rain Gauge by a is dotted line, and the Lamb Range by the dashed line.

A positive relationship was found with biomass and precipitation one month prior to truffle surveys (Rain Gauge data, r = 0.97, $p \leq 0.05$, $R^2 = 0.93$; Average BOM data r = 0.84, p = 0.16, $R^2 = 0.71$) (Figure 2.3). However, truffle biomass had a stronger relationship with precipitation in the preceding one month on the Coane range than on the Lamb Range (Figure 2.3). There was a site effect (F=4.89, p≤ 0.5), but no precipitation effect (F=4.11, p = 0.07) on biomass.

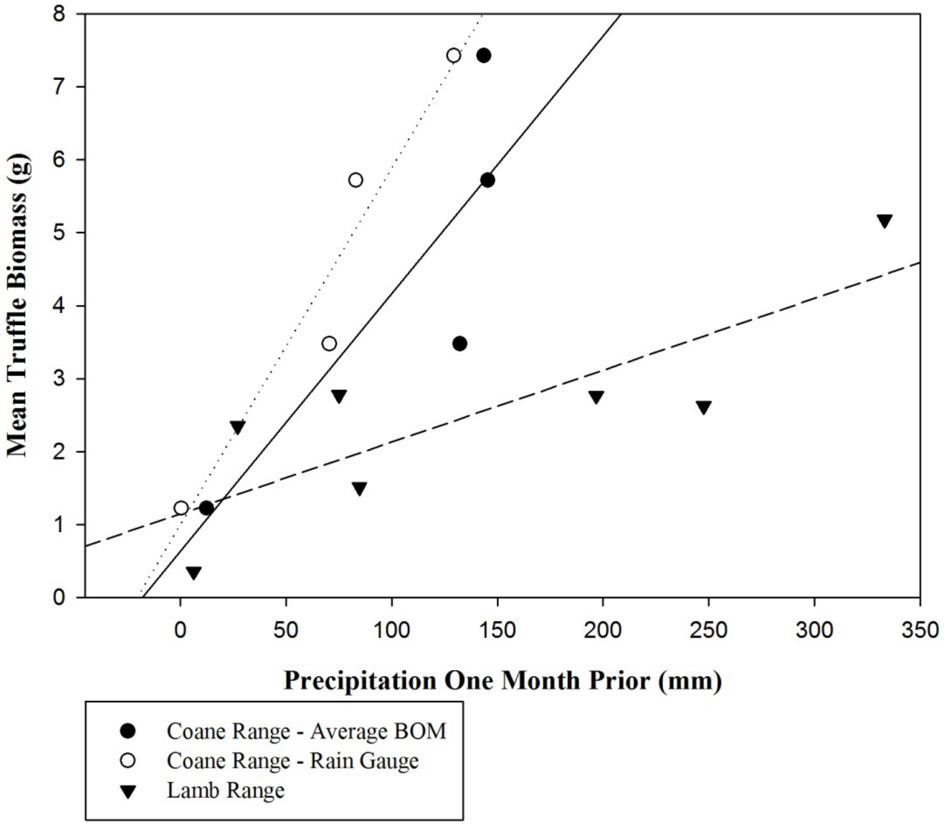

Figure 2.3. The relationship between mean truffle biomass and precipitation one month prior to the survey. The Coane Range Average BOM is represented by a solid line, Coane Range Rain Gauge by a is dotted line, and the Lamb Range by the dashed line.

On the Coane Range, the first two surveys periods (December 2006 and April 2007) had below average precipitation in the month preceding the surveys while the second two survey periods (July 2007 and December 2007) had above average precipitation in the month preceding the surveys (Table 2.5). If truffle availability is examined in terms of this variation in precipitation through the study period, then significantly higher abundance (7.75 sporocarps ± 6.6 SD) was found during surveys with above average precipitation the preceding month to the survey (H = 4.43, $p \leq 0.05$) than the other surveys (3.17 sporocarps ± 4.71 SD). Biomass followed a similar pattern with higher values in surveys with above average precipitation the preceding month to the survey (6.57 g ± 9.47 SD) than the other surveys (2.73 g ± 5.50 SD), although the relationship was not significant (H = 2.31 p = 0.13).

Table 2.5. Precipitation data for the preceding one month to each truffle survey on the Coane Range. Presented are the rainfall data for the survey (Survey Rainfall) and the long-term mean for each preceding month. Data for each are provided by rain gauge measurements (Rain Gauge), Horse Shoe Bend weather station to the west (Dry BOM), Paluma weather station to the east (Wet BOM) and the average of all rainfall data together. Surveys represent: Survey 1, December 2006; Survey 2, April 2007; Survey 3, July 2007; Survey 4, December 2007. All rainfall data are in mm.

	Survey Rainfall				**Long-term Mean**			
Survey	Rain Gauge	Dry BOM	Wet BOM	**Average**	Rain Gauge	Dry BOM	Wet BOM	**Average**
1	0.5	0.0	24.9	**8.47**	62.41	55.2	170.6	**96.07**
2	70.5	51.4	213.3	**111.73**	120.95	124.1	349	**198.02**
3	129.5	99.8	187.6	**138.97**	50.75	12.1	59.6	**40.82**
4	83	19	271.8	**124.60**	67.41	55.2	170.6	**97.74**

In the surveys with above average precipitation, *Mesophellia* (32.58 %), *Gummiglobus* (28.30 %), and *Castoreum* (22.64 %) make up the highest percentage of biomass, whilst *Gummiglobus* (30.39 %), *Hysterangium* (19.61), *Pogiesperma* (14.71 %) make up the highest percentage of abundance. In the surveys with below average precipitation, *Castoreum* (50.73 %), *Mesophellia* (30.03 %), and *Scleroderma* (18.34 %) make up the highest percentage of biomass, whilst *Castoreum* (38.46 %), *Scleroderma* (28.21 %), and *Mesophellia* (20.51 %) make up the highest percentage of abundance.

2.4.2 Regional scale modelling

Comparing sites where truffle occurrence records were obtained, truffles on the Coane Range experience both high temperature and precipitation seasonality in comparison with the Lamb Range and the Atherton Tablelands (Figure 2.4).

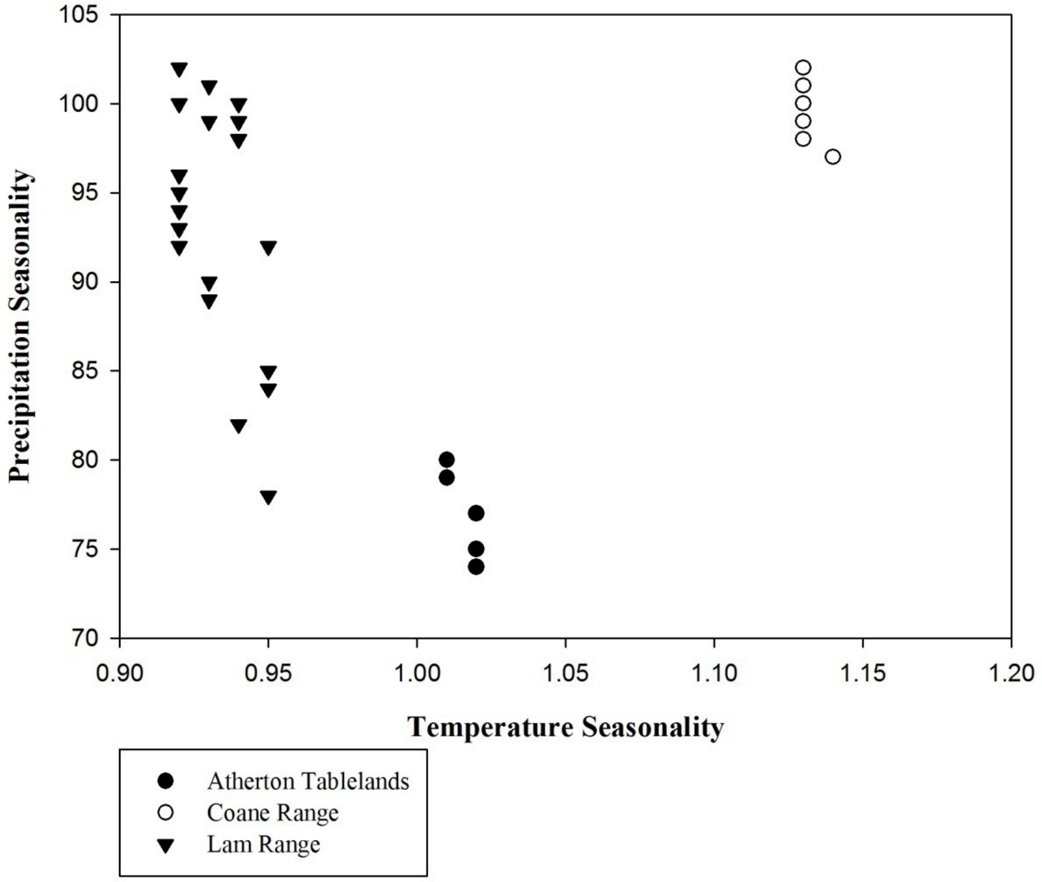

Figure 2.4 Plot of ANUCLIM variables, precipitation seasonality versus temperature seasonality for all sites surveyed for truffles within the Australian Wet Tropics. The Coane Range, Lamb Range, and Atherton Tablelands are shown. Seasonality is measured as the Coefficient of Variation.

This was further corroborated by the individual Maxent models developed for the Lamb Range (temperature seasonality range 0.65-1.15) and Coane Range (temperature seasonality range 1.05 – 1.20), indicating the Coane Range is at the upper limits of temperature seasonality in comparison to the truffles across the Wet Tropics (temperature seasonality range 0.70 – 1.40).

The Maxent model training AUC value was 0.98, indicating that model discrimination was high and this model can be considered highly accurate (Guisan *et al.* 2007). Maxent modelling revealed that maximum temperature of the warmest period (51.4%) had the strongest influence on the distribution of truffles over the Wet Tropics, followed by precipitation of the driest quarter (18%) and annual mean temperature (12.5%) (Table 2.6). The probability of presence peaks when the maximum temperature of the warmest period was 24.5 °C (Figure 2.5), precipitation during the driest quarter was 125 mm (Figure 2.6), and mean annual temperature was 16° C (Figure 2.7). Truffle occurrence declined as temperatures increased, with probability of presence low where temperatures were above 30°C in the warmest period.

Table 2.6. Percent contribution of each climate variable used in maxent model building for truffles in the Wet Tropics. Percent contribution is the estimated relative contribution each variable has in model building.

Variable	**Percent Contribution**
Maximum Temperature Warmest Period (°C)	51.4
Precipitation of Driest Quarter (mm)	18.0
Annual Mean Temperature (°C)	12.5
Precipitation of Wettest quarter (mm)	9.6
Temperature Seasonality (C of V)	5.9
Annual Precipitation (mm)	1.1
Minimum Temperature Coldest Period (°C)	1.0
Precipitation Seasonality (C of V)	0.5

In this study on the Coane Range, only a portion of the climatic niche modelled for the Wet Tropics was represented at the survey sites. Sites with truffle occurrences ranged from 28.5 – 29.7°C for maximum temperature of the warmest period ranges, which is at the higher end of the range for the entire Wet Tropics model and within the decreasing slope of probability of occurrence for the resource (Figure 2.5). Truffle sites on the Coane Range also experienced conditions in the decreasing slope of probability of occurrence for precipitation of the driest quarter with a range of 61 – 121 mm of precipitation (Figure 2.6). The range for annual mean temperature was 19.1-20.50°C, towards the hotter portion of the gradient in the decreasing slope of probability of occurrence for this resource (Figure 2.7).

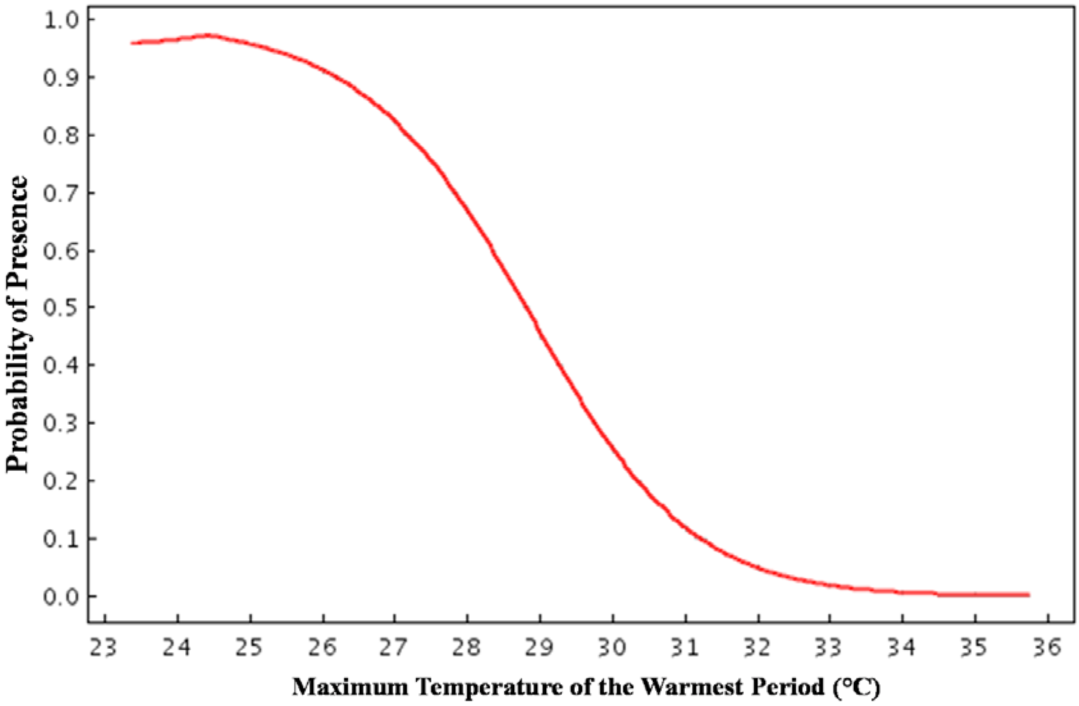

Figure 2.5. Response curve of truffles (probability of presence) to maximum temperature of the warmest period (°C) in the Australian Wet Tropics. This Figure is adapted from the maxent model output response curve plots. Response curves represent how the predicted suitability (probability of presence) is dependent on the variable selected.

On the Coane Range, sites that had higher truffle availability (the top four sites (2, 3, 6 and 7) average abundance (7.5 sporocarps ± 4.51 SD) and biomass (10.12 g ± 3.61 SD)) experienced lower maximum temperatures in the warmest period (28.72 °C ± 0.22 SD versus 29.33 °C ± 0.30 SD), lower annual mean temperatures (19.38 °C ± 0.28 SD versus 20.07 ± 0.31 SD), and more precipitation in the driest quarter (109.5 mm ± 12.18 SD versus 78. 0 mm ± 14.47 SD) than the sites with lower truffle availability (the bottom four sites (1, 4, 5 and 8) average abundance (3.5 sporocarps ± 2.89 SD) and biomass (1.86 g ± 0.56 SD)). This is consistent with higher probabilities of occurrences on the regional scale throughout the Wet Tropics, including the stable Lamb Range region, although still on the lower end for probability of occurrence.

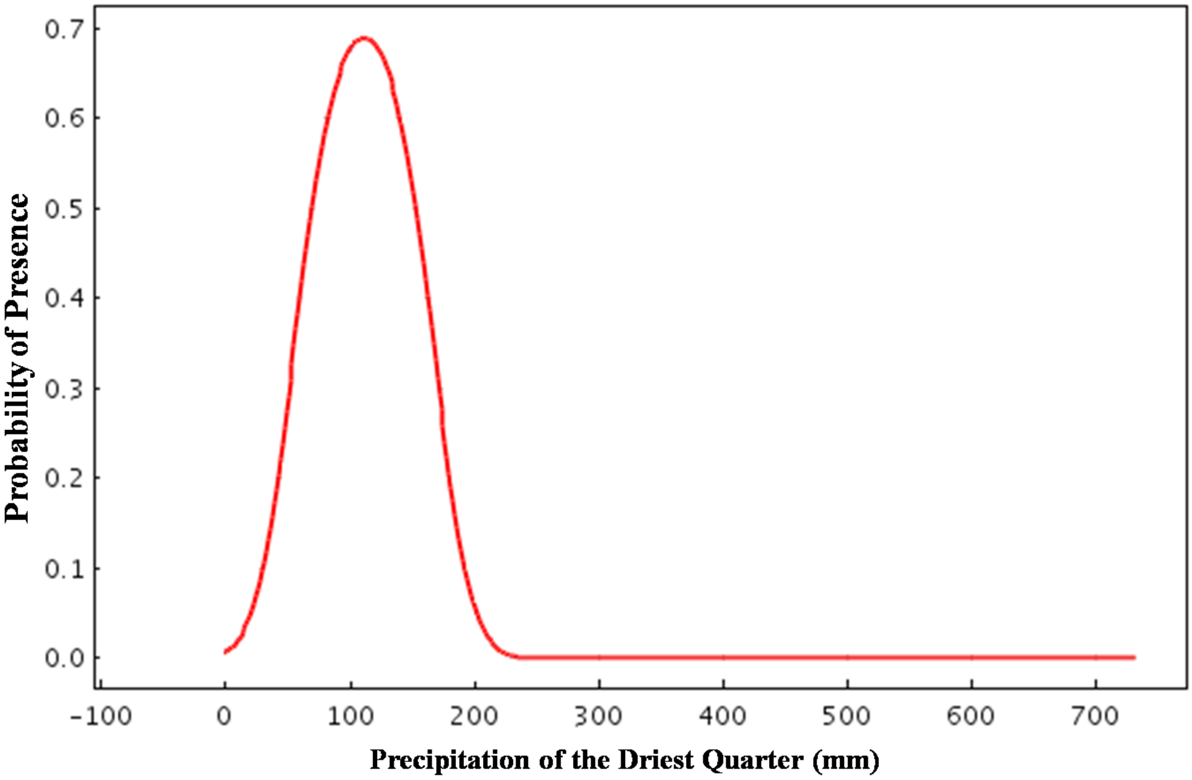

Figure 2.6. Response of truffles (probability of presence) to precipitation of the driest quarter (mm) in the Australian Wet Tropics. This Figure is adapted from the maxent model output response curve plots. Response curves represent how the predicted suitability (probability of presence) is dependent on the variable selected.

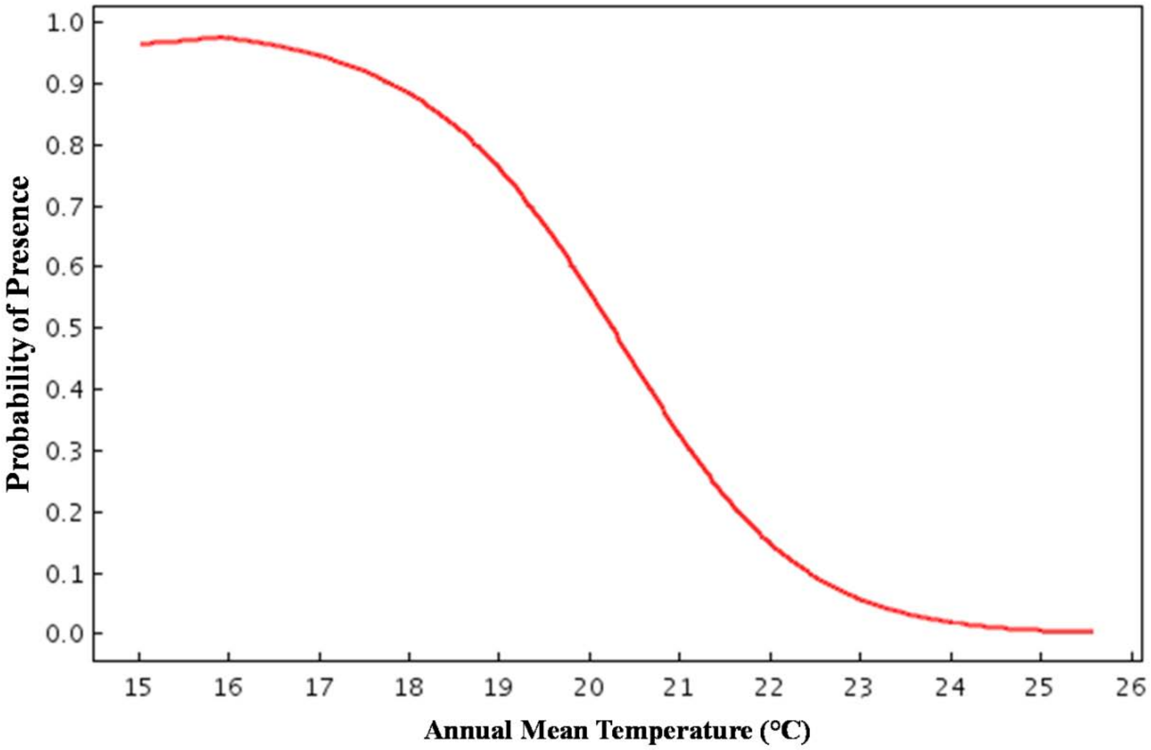

Figure 2.7. Response of truffles (probability of presence) to annual mean temperature (°C) in the Australian Wet Tropics. This Figure is adapted from the maxent model output response curve plots. Response curves represent how the predicted suitability (probability of presence) is dependent on the variable selected.

2.5 Discussion

Truffle availability was higher in *Allocasuarina* forest than *Eucalyptus* woodlands within the southern Wet Tropics study site on the Coane Range. Previous work has also shown *Allocasuarina* forests to have higher densities of hypogeous fungal sporocarps than *Eucalyptus* woodlands in this region (Vernes et al. 2004; Abell-Davis 2008; Mathams 2008). Both tree types form symbiotic relationships with ectomychorrhizal fungi (Bougher & Lebel 2001) and share many common fungal symbionts, although an inoculation study showed that *Allocasuarina* species formed associations with ectomychorrhizal fungi more readily (Theodorou & Reddell 1991). This could be related to higher nutrient demands of the *Allocasuarina* species. *Allocasuarina* forest has higher soil Nitrogen levels than

Eucalyptus woodlands as *Allocasuarina* species form a symbiosis with Nitrogen fixing Actinomycetes (*Frankia*) (Dawson *et al.* 1989; Duponnois *et al.* 2003). Nitrogen fixation is dependent on the uptake of limiting nutrients such as Phosphorus, and ectomychorrhizal fungi facilitate this and can promote actinorhizal nodule formation and function (Duponnois *et al.* 2003). In low nutrient soils, *Allocasuarina* species are dependent on their fungal symbionts, particularly in Phosphorus limited environments such as this (Duponnois *et al.* 2003). The synergistic effect of both symbionts could confer an advantage on *Allocasuarina* species.

Interestingly, high Nitrogen levels are known to limit ectomychorrhizal root formation, but low levels of soil Phosphorus, such as in Australian soils, counter this effect (Wallander & Nylund 1992; Wallander 1995; Nilsson & Wallander 2003; Abell-Davis 2008). This appears to be true in this study, where truffle abundance was positively related to Nitrogen and negatively with Phosphorous. When Phosphorous is limiting, host plants have reduced shoot growth, reducing their nitrogen demand and allowing their fungal symbionts to partition their carbon supply from nitrogen assimilation to reproduction and growth (Wallander & Nylund 1992; Wallander 1995; Abell-Davis 2008). Thus, increasing levels of soil P are detrimental to truffle productivity and ectomychorrhizal formation (Bougher *et al.* 1990). Abell-Davis (2008) also found a negative relationship between truffle productivity and Phosphorous, with higher Phosphorus levels associated with wetter habitat types closer to the rainforest boundary than mesic *Allocasuarina* and dry *Eucalyptus* habitat types (Harrington & Sanderson 1994). Higher soil moisture levels in the wetter habitats can increase the mineralisation of both Nitrogen and Phosphorous (Trudell & Edmonds. 2004; Abell-Davis 2008). The soil moisture content of the *Allocasuarina* forest appears to maintain soil moisture levels above a dry threshold that may limit truffle productivity but below that of wetter forest types, where high moisture content impedes ectomychorrhizal formation (Claridge *et al.* 1993; Bougher & Lebel 2001; Abell *et al.* 2006; Abell-Davis 2008).

Local scale habitat factors could only explain a small percentage of the variability in truffle availability, and it is likely that weather and climate are also acting here. The ecotonal forest in the Wet Tropics lies on a vegetation gradient that is linked to altitude, with cooler high precipitation closed forests at higher altitudes transitioning to lower altitude dry savanna woodlands on the lower western margin of the region (Webb 1968; Harrington & Sanderson 1994). The sites in this survey were spread along this gradient, with *Allocasuarina* forests on the wetter/higher altitude and *Eucalyptus* woodlands on the drier/lower altitude (Mathams 2008). Truffle distribution and diversity may be greatly influenced by such changes in vegetation along climatic gradients through direct impacts of temperature, precipitation or to changes in host plant species (O'Dell *et al.* 1999; Bougher & Lebel 2001; Claridge *et al.* 2009). Regardless, climate variables such as precipitation have been found to influence truffle productivity within species of host plants (O'Dell *et al.* 1999). This may reveal that truffles at this study site are responding to climatic changes along this ecotonal gradient, with a positive relationship with climatic factors associated with *Allocasuarina* forest types.

Within the Coane Range, several climate variables had strong relationships with truffle availability indicating that climate can control truffle productivity at local scales. In particular, biomass was linked to higher annual and dry season precipitation, and lower annual and summer temperatures and precipitation seasonality. Previous studies in Australia have found that climate influences truffle production, with either precipitation or temperature indicated as important (Johnson 1994; Claridge et al. 2000a; Jumpponen et al. 2004; Abell et al. 2006; Claridge et al. 2009). In tropical Australia, truffle production has been linked most strongly with precipitation, which is reduced in the late dry season or times of drought (Abell *et al.* 2006). No fungal survey was conducted in this study during the late dry season (September), however surveys that experience lower than average precipitation events in the month prior to sampling had significantly less truffle abundance. In addition, precipitation events one month prior to the surveys were positively related to truffle abundance and biomass which is consistent with previous studies that have also found truffle availability was positively correlated with 1- 2 months precipitation lag (North 2002; Abell-Davis 2008). Therefore, years with below average precipitation may limit truffle availability (Meyer & North 2005). This effect could be confounded by hotter temperatures, as truffle productivity declines with high temperatures (above 30°C) (Fogel 1976) and is governed by an interaction between moisture and ambient temperatures (Fogel 1976; Claridge et al. 1993; Jumpponen et al. 2004).

Abell *et al.* (2006) found on average significantly higher truffle abundance (174.44 ha^{-1}, or 10,291.96 sporocarps per home range) on the Lamb Range than was found in this study on the Coane Range (52.18 ha^{-1}, or 3078.62 sporocarps per home range). Truffle abundance has the same response to precipitation on the Coane Range and Lamb Range, but there were less truffle abundance and less precipitation experienced on the Coane Range. In addition, there was no site effect on truffles, indicating that the main difference between truffle availability between these two regions is due to weather, and in particular precipitation events. This reveals that *B. tropica* habitat quality on the Coane Range, in terms of the reliability of truffle availability, is poor compared to the Lamb Range where *B. tropica* populations occur in higher densities. Lower abundances of truffles on the Coane Range could explain why *B. tropica* populations are less abundant there.

Although truffles were less abundant on the Coane Range in comparison with the Lamb Range, truffle biomass was relatively high within a single bettong home range on the Coane Range (44.61 g/ ha^{-1} or 2.63 kg per home range). This was due to patches having few but large truffles. This is because the most common truffles found were from the family Mesophelliaceae, including *Mesophellia* and *Castoreum* spp. *Mesophellia* and *Castoreum* truffles tend to be large, have a thick shell-like peridium (skin) and are considered fire adapted and tolerant to desiccation (Claridge *et al.* 2009). This could indicate that the truffles that are persisting on the Coane Range are those that are adapted to drought conditions. Regardless of their occurrence, there was still a high variability in truffle biomass on the Coane Range throughout the survey. This indicates that despite their drought tolerance, those species still require a certain level of precipitation to stimulate fruiting. In addition, the higher biomass on the Coane Range (although not significantly higher than found on the Lamb Range) can be explained by differences in the taxonomic assemblage between these two regions. This dominance by larger drought tolerant species from the Mesophelliaceae family is in contrast to the Lamb Range, which had many small, highly abundant thin peridium species that exhibited a negative relationship between biomass and high levels of precipitation (Abell-Davis 2008).

It is apparent that truffles on the Coane Range experience sub-optimal climate conditions, occurring where summer temperatures are hotter and precipitation during the dry season is lower than in areas that are predicted as high suitability for this resource across the Wet Tropics. The Coane Range occurs in a more climatically seasonal region of the Wet Tropics than the Lamb Range, with higher temperature and precipitation seasonality experienced at the truffle sites, as well as greater dry season severity (Williams & Middleton 2008). As truffles at this site are already at their upper summer temperature limits and lower dry season precipitation limits, any further pressure from drought could significantly impede truffle productivity. This could indicate a vulnerability of animal species that use truffles as a resource, including *B. tropica*, to drought events (Abell-Davis 2008). *Bettongia tropica* abundance is already limited within drier sites that have reduced dry season fungal availability, as fungi are consumed less and body condition deteriorates (Johnson & McIlwee 1997). This restricts the species to habitat types closer to the rainforest edge, with higher or more regular precipitation (Johnson & McIlwee 1997; Abell-Davis 2008). The recent failure to detect *B. tropica* on the climatically seasonal Coane Range (Appendix B) may be linked to declines in truffle availability in association with several years of below average precipitation (2001 – 2005, BOM) that was experienced in this region. This indicates that *B. tropica* population stability is dependent on stable climates suitable for truffle availability for the majority of the year (Abell-Davis 2008).

B. tropica has also declined elsewhere, with contraction of populations occurring from south to north and west to east towards higher precipitation areas (Winter 1992; Winter 1997a; Winter 1997b; Abell-Davis 2008). Drought has already been implicated in local extinctions of several bettong species, which as a genus are highly mycophagist (Short 1998). Bettong species such as the brush-tailed bettong (*Bettongia penicillata*), the rufous bettong (*Aepyprymnus rufescens*) the burrowing bettong (*Bettongia lesueur*), and the eastern bettong (*Bettongia gaimardi*), have experienced large range contractions towards higher precipitation regions, with the latter two species now extinct on the mainland (Short & Turner 1993; Johnson 2006).

Truffle productivity in the Wet Tropics appears to be influenced by a diverse array of factors acting together, such as weather events, climate and local scale factors. As truffles appear to be strongly linked with precipitation and other weather events, climate averages may not be entirely appropriate for distribution modelling and a more dynamic approach looking at weather and weather events may be necessary.

Truffle productivity can also be affected by soil type (Bougher & Lebel 2001), but no differences in relation to geology were observed here. This may be a result of the choice of soil type, although this was limited by the habitat types of the study site. Soil derived from granite and rhyolite substrata are both nutrient poor as both parent materials are low mineral, acid igneous rock (Webb 1969; Miller & Woodrow 2008). Future studies on the impact of nutrient rich soil types in the Wet Tropics on truffle productivity are needed. Nutrient rich basaltic soil types may be the best choice due to their location near granite soil types within appropriate habitat types of the region (Laurance 1997). Future studies should also address the poor availability of truffle data and occurrence records that limited this study and attempt to understand the individualistic distribution of truffles at the species or genus level.

Increasing temperatures, more seasonal precipitation and increases in length and severity of the dry season predicted for the region as a result of climate-change (Walsh & Ryan 2000; Hughes 2003) could have dramatic detrimental impacts on truffle productivity. It is likely that climate-change will marginalise entire portions of *B. tropica's range* through reduced truffle availability, placing pressure on a species already endangered and restricted in its distribution. Improved knowledge on the factors that limit truffles in the landscape, and in turn the species that depend on them for survival such as *B. tropica*, is imperative.

Chapter 3 . The influences of habitat, fire and climate on cockatoo grass (*Alloteropsis semialata*) distribution in the Wet Tropics.[1]

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[1] **Bateman BL**, Johnson CN (2011). The influences of climate, habitat and fire on the distribution of cockatoo grass (*Alloteropsis semialata*) (Poaceae) in the Wet Tropics of northern Australia. *Australian Journal of Botany* 59 (4), 315-323

3.1 Abstract

Cockatoo grass (*Alloteropsis semialata* (R. Br.) A. Hitchc) is considered a keystone species in northern Australian ecosystems as it provides a food resource for many species, including several endangered vertebrates. This study examined both local and regional environmental factors influencing cockatoo grass distribution and abundance in the Wet Tropics of north Queensland, Australia. Local distribution and abundance were investigated in the sclerophyll ecotone between open woodland and tall open forest, because little is known about cockatoo grass distribution within this habitat; also, the endangered northern bettong (*Bettongia tropica*) is restricted to this habitat and depends on cockatoo grass for its survival. Regional scale modelling of distribution was undertaken to examine the climatic tolerances of cockatoo grass in Queensland.

Density of cockatoo grass was negatively related to litter cover, soil moisture, and the presence of two dominant grass species, *Themeda triandra* (Forssk.,(R.Br.) Stapf) and *Cleistochloa subjuncea* (C.E.Hubb.). Soil nutrients (Nitrogen, Carbon, Sulphur, and CN ratio) were positively related to density of cockatoo grass. A late dry season experimental burn demonstrated that cockatoo grass had high survival to fire, with increased density and flowering in response to fire. Regional scale modelling using climate variables indicated that temperature of the warmest period, temperature seasonality and dry season rainfall had the greatest effects on distribution of cockatoo grass: there was a negative association of occurrence with warm period temperature (above 30° C) and a positive association with moderate levels of dry season rainfall.

Cockatoo grass in the woodland-forest ecotone in the Wet Tropics appears to be influenced by several environmental features associated with the ground layer.

The species benefits from the reduction in litter cover and competing grass species that result from management actions such as prescribed burning. Understanding of the factors limiting this species, both at a local and regional scale, can be used to guide management of this ecotone habitat for both cockatoo grass and the survival of other species that depend on it.

3.2 Introduction

Cockatoo grass (*Alloteropsis semialata* (R. Br.) A. Hitchc.) is a widespread species native to northern Australia, New Guinea and Melanasia (Bostock & Holland 2007), and also occurs throughout parts of Africa and Asia (Crowley & Garnett 2001). In Australia, its seeds and culms provide food resources for many animal species, such that it is considered to be a keystone species sustaining biodiversity in savanna ecosystems of northern Australia (Crowley 2008). Several bird species, such as the golden-shouldered parrot (*Psephotus chrysopterygius*), and the Gouldian finch (*Erythrura gouldiae*) (Crowley & Garnett 2001; Dostine *et al.* 2001; Abell *et al.* 2006; Crowley 2008) depend on cockatoo grass. The endangered marsupial, the northern bettong (*Bettongia tropica*), depends on the culms of cockatoo grass when availability of its main food source, truffles, is low during the late dry season (Johnson & McIlwee 1997; Abell *et al.* 2006). Northern bettongs live close to the wet sclerophyll-rainforest ecotone, where cockatoo grass is generally less abundant than in dry *Eucalyptus* woodland, probably due to shading by wet sclerophyll vegetation (Vernes 1999; Vernes 2003; Abell *et al.* 2006; Mathams 2008). Information on the ecological factors limiting the distribution and abundance of cockatoo grass is therefore crucial for an understanding of limits to the distribution of the northern bettong.

Although it is rarely the dominant grass species, cockatoo grass is thought to indicate a healthy ecosystem with an appropriate fire management and minimal grazing impacts (Crowley 2008; Mathams 2008). Fire has been shown to benefit cockatoo grass in savanna environments (Woinarski *et al.* 2004; Crowley *et al.* 2009; Scott *et al.* 2009; Russell-Smith *et al.* preprint), but little is known about this species in closed forest systems such as wet sclerophyll forest. A reduction of frequency and intensity of fires since European settlement has facilitated a transition of wet sclerophyll habitats towards a denser mid canopy structure due to encroachment of pioneer rainforest vegetation and increase of *Allocasuarina* spp. (Withers & Ashton 1977; Withers 1978; Kellman 1986; Harrington & Sanderson 1994; Lunt 1998; Abell *et al.* 2006). Where fire has been absent for long periods, vegetation thickening in the ground layer is also observed, with an increase in shade-tolerant sedge species and rainforest vines (Everson *et al.* 1988). This may suppress cockatoo grass.

It is unclear to what extent altered fire regimes may have suppressed cockatoo grass within this ecotonal habitat. Although individual plants are relatively resistant to fire due to the ability of tillers to survive long periods in dormancy, cockatoo grass relies on vegetative persistence, flowers early in the wet season, and lacks a persistent seed bank, making it sensitive to heavy grazing and wet season fires (Crowley & Garnett 2001). The combination of changes in fire regime, grazing pressure, and shading could prevent the regeneration of cockatoo grass, and declines have already been noted within *Allocasuarina* forest in some areas (B. Bateman, pers. obs.).

The aim of this study was to investigate the distribution and abundance of cockatoo grass in the ecotone between wet sclerophyll forest and dry woodland on the margins of the Wet Tropics region in north Queensland. I explored how the current distribution of this species is influenced by environmental features within the ecotone habitat, and what role a single fire may play in structuring this community. Specifically, I asked the following questions: where does cockatoo grass grow in relation to habitat features such as soil, light, habitat structure, and vegetation communities within this habitat? What is the relationship between cockatoo grass and other grass species in the wet sclerophyll ecotone? How is this affected by a single late dry season fire? To answer these questions, I first conducted a site scale survey of cockatoo grass in *Allocasuarina*/sclerophyll woodlands of the Coane Range situated in the Wet Tropics of north Queensland. In addition, I explore the regional-scale climatic factors that influence the distribution of this species within the region.

3.3 Methods

3.3.1 Study sites

The study was conducted at the Mt Zero –Taravale wildlife sanctuary (Australian Wildlife Conservancy) on the Coane Range, northeast Queensland (146°11’E, 19°07’S). Five treatment sites (Site 1: 146°09’E, 19°03’S, altitude 855m; Site 2: 146°10’E, 19°02’S, altitude 801m; Site 3: 146°11’E, 19°08’S, altitude 796 m; Site 4: 146°11’E, 19°07’S, altitude 850m; Site 5: 146°10’E, 19°04’S, altitude 900m) were selected to examine the relationship between cockatoo grass density and habitat features within the wet sclerophyll ecotone and to conduct an experimental burn.

Each treatment site contained three 50 m x 20 m replicate plots, and was isolated from the surrounding habitat by fire-breaks created by a road grader. Sites were chosen in similar habitat types located 500 m apart to maintain independence, and situated in areas suitable for performing containable experimental burns. For direct comparison to treatment sites to detect effects of an experimental burn on cockatoo grass, five control sites (also with 3 plots per site) were established adjacent to them.

The sites fell along a gradient from tall open forest to medium woodlands situated on granite derived soils (Stanton 2007). All sites were located in wet/mesic sclerophyll *Allocasuarina* habitat types, which occur on the transition between tall open forest and open woodland. Dominant tree species in the canopy were *Eucalyptus resinifera*, *Syncarpia glomulifera*, *Corymbia intermdia*, *E. reducta*, *E. portuensis,* and *C. leptoloma*, *C. reducta*, *C. abergiana* (Stanton 2007). All sites have *Allocasuarina torulosa* trees and saplings in the sub-canopy and understorey. Each site was selected for known or suspected presence of cockatoo grass. The dominant grass species at most sites was *Themeda triandra* (Forssk.,(R.Br.) Stapf) and/or *Cleistochloa subjuncea* (C.E.Hubb.). Other common grass species occurring throughout the sites included *Imperata cylindrica* and *Panicum* spp.

3.3.2 Sampling methods

3.3.2.1 Environmental data

Environmental data (11 variables) were collected for each treatment site in a pre-burn survey (November 2007, Survey 1). All data were collected for each plot (n = 12; Site 3 excluded) before an experimental burn was conducted. Site 3 did not contain cockatoo grass before or after the experimental burns, and was removed from further analysis. Variables were recorded along a permanent 20m transect established within each plot. Data consisted of measurements taken from the centre of each transect as well as estimations of percentage cover over the whole transect.

Soil was collected from each plot at the centre of the 20-m transect for each survey period. Soil samples were analysed for the soil nutrients (mg/g) Nitrogen (N), Carbon (C), Sulphur (S), and the CN ratio, important determinants of soil fertility and pH levels. Mean soil moisture was determined for each plot (mL/g) for each survey from wet and dry weights. Soil samples were sieved to 2mm to separate earth material from gravel. Soil N, C, and S were those available to be tested with an Elementar Vario Max CNS Analyser (Elementar, Hanau Germany) by the Sediment lab, School of Earth and Environmental Sciences, James Cook University, Townsville. Soil variables were collected at the pre-burn survey and all subsequent surveys.

Twenty 1m^2 quadrats, placed every 1 m on either side of a permanent 20 m transect, were assessed for percentage of total grass cover, total grass density, *Themeda triandra* cover, and *Cleistochloa subjuncea* cover. Density was measured as the number of individual plant stems or shoots within the quadrat. Percentage cover, the amount of total vegetative growth covering a quadrat, was visually estimated as a percentage, giving an estimate of the projected foliage cover, and an indication of ecological dominance for each species. Dominant species (*T. triandra* and *C. subjuncea*) for each plot were then combined and averaged to represent the total cover and density measure per plot. In addition percentage litter cover and litter layer depth (cm) were measured, as an average of thirteen random samples, per plot

3.3.2.2 Experimental burn

In order to examine both the relationship of cockatoo grass with habitat features and to observe the effect of a single late dry season fire on cockatoo grass and its relationship with other grass species, additional surveys were conducted after an experimental burn (November 2007). After the pre-burn survey, two surveys were conducted; in the first wet season after the experimental burn (post-burn/wet surveys: April 2008, Survey 2) and a survey conducted one year after burning (November 2008, Survey 3). Due to unforseen problems, the control plots could not be surveyed until the post-burn/wet surveys (Survey 2, after the experimental burn occurred) and thus were assessed only in the post-burn/wet and one-year post-burn surveys to detect effects of the burn. Burns were of low to moderate intensity across plots, with flame height varying from 0.3 to 6 m (*Allocasuarina* flare-ups accounted for larger flames). Site 5 was not burned during this period due to a change in fire weather, and thus was removed from all post-burn analysis. Thus sites 1, 2, and 4 were the remaining sites available for full analysis of the effects of fire on cockatoo grass. A prescribed burn in the vicinity of site 4 was not contained and as a consequence, control site 4 (plots 1, 2, and 3) were burnt just before the one-year post-burn surveys. No analyses were conducted on the data collected from control site 4 for the one-year post-burn survey.

Each of three plots in all of the five treatment sites were assessed for the presence and density of cockatoo grass pre-burning within the twenty 1m^2 quadrats along the permanent 20-m transect. All individual cockatoo grass plants in the plots were tagged to assess post-fire survivorship. Cockatoo grass plants develop subterranean tillers (Crowley & Garnett 2001), which are shoots that sprout from the base of the plant. Any vegetative growth of cockatoo grass observed within a permanent 10 cm diameter plot around each plant was regarded as being from the same individual plant. Each plant was marked within a sub-quadrat using an individually numbered tag attached to a 10 cm ring encircled around the base of the plant and secured using a metal peg. Survivorship was measured as presence or absence of a living individual plant in each marked sub-quadrat throughout the survey, and calculated as the number of cockatoo grass plants in each survey over the initial population density of each plot. All individual cockatoo grass plants flowering along transects were recorded. Control sites were assessed for flowering at the post-burn/wet survey and the one-year post-burn survey. Cockatoo grass survival in the unburnt control plots was assessed at the one-year post-burn survey for direct comparison with the treatment sites.

3.3.3 Analysis

Environmental variables collected during the pre-burn habitat surveys (treatment sites only) were examined to test for site-specific features associated with cockatoo grass density. Because many environmental variables were recorded (total = 11), a Spearman rank correlation matrix was used to reduce the number of correlated variables. Pairs of variables with high Spearman pair-wise correlation coefficients ($r \geq 0.5$) were reduced to a single variable to represent the pair. All variables were standardised for further analysis.

These selected variables were then used as independent variables in a Generalised Linear Model (GLM) for cockatoo grass density. As cockatoo grass density was count data, the Poisson distribution was used with a log link function. A Kullback-Leibler (K-L) information-theoretic method to model relationships was undertaken to construct all possible model configurations (best subsets), using the Akaike Information Criterion (AIC) as an objective means of model selection (Burnham & Anderson 2002). This is not a hypothesis testing method, but rather a model selection method that uses Akaike model weights (w_i), or relative strengths of evidence, to determine the most parsimonious models (Burnham & Anderson 2002). All analyses were conducted in R (v2.10.0, http://www.r-project.org), with use of the MuMIn R package (http://cran.r-project.org/web/packages/MuMIn/index.html). To correct for bias ($n/K < 40$), the second-order information criterion (the AIC_c) was used for each model (Burnham & Anderson 2002). The best-supported model was selected as the $AIC_{c\ min}$ (the model with the lowest AIC_c value). Plausible models were presented if they fell within 2 AIC_c units (Δ_i) of the $AIC_{c\ min}$ (the model with the lowest AIC_c value), although models within 4-7 AIC_c units (Δ_i) were retained as they still contain support (Burnham & Anderson 2002). The relative likelihood, or weight of evidence as being the most parsimonious model, was calculated for each model in the set using Akaike model weights (w_i). Model weights vary from 0 (no support) to 1 (complete support).

Evidence ratios were calculated from model weights to determine if one model was convincingly better than the others or if a 95% confidence set of models was needed (Burnham & Anderson 2002). A measure of model fit is provided as the percent deviance explained.

In addition, to determine the relative importance of each variable contributing to model building, model averaging was conducted. Variable importance was assessed as the sum of the weight scores (w_i) for each model of which the variable was a component, with values closer to 1 being relatively more important and values above 0.5 considered good (Ritchie *et al.* 2009). Akaike model weights were used to weight the parameter estimates and variance (standard error) associated with each model. The parameter estimates are reported with confidence intervals, to show whether or not the estimate of effect size overlapped zero. The magnitude (impact on model building) and direction of the effect (positive or negative) are indicated by the direction and magnitude of the parameter estimate.

For analysis of grass data post-burn, all data distributions were tested for normality by Shapiro-Wilk (SW-W). The distribution of cockatoo grass density was non-normal (SW-W = 0.76, p = 0.00005) and was transformed (log(x+1)) for nested ANOVA analysis (SW-W = 0.95, p = 0.18). Control sites were included in data analysis only for surveys 2 and 3 (with control site 4 removed for survey 3 due to fire; see methods). Data on cockatoo grass survival were not assessed for normality as values were uniformly high and approaching one. To determine how immediate survival was affected by the experimental burn, survival was assessed one week post-burn. Data were then compared between all surveys to determine if time from burn influenced survival, as well as between sites, and plots to determine if site-specific factors influenced survival. To determine if treatment sites differed from control sites, a comparison with control sites was undertaken for one year post-fire (sites 1 and 2 only as site 4 had been inadvertently burned by this time). To examine if cockatoo grass flowering differed between control and treatment sites, a chi-square test for homogeneity (χ^2) was used.

The distributions of total density and cover (*T. triandra* and *C. subjuncea* combined) were non-normal (total cover: SW-W = 0.70, $p \leq 0.00001$; and total density: SW-W = 0.91, $p \leq 0.05$), and could not be normalised by transformation. To test for variation in total density and cover among treatment sites, plots and surveys, a Kruskal-Wallis one way non-parametric analysis of variance (ANOVA, H) was used.

3.3.4 Regional scale modelling

To determine large-scale controls on cockatoo grass distribution a species distribution model was generated using location records from across Queensland. Location records (248 records) were obtained from the Queensland Herbarium and supplemented with opportunistic data collected by the author and records obtained in other studies from the Wet Tropics region (Abell *et al.* 2006; Mathams 2008). Cockatoo grass has a broad distribution and its climatic tolerances may not be completely captured by Queensland records, but I felt that a distribution model based on Queensland records would indicate what climatic factors might influence its occurrence in wet sclerophyll communities in Queensland.

Climate data were entered as long-term climate means, derived from ANUCLIM 5.1 (McMahon *et al.* 1995) software using monthly averages and an 80m DEM re-sampled from ~250m (GEODATA 9 Second DEM Version 2; Geoscience Australia, http://www.ga.gov.au/). They included the following variables: annual mean temperature (°C), temperature seasonality (coefficient of variation (C of V)), maximum temperature of warmest period (°C), minimum temperature of coldest period (°C), annual precipitation (mm), precipitation seasonality (C of V), precipitation of wettest quarter (mm), and precipitation of driest quarter (mm).

The program Maxent was used to correlate cockatoo grass records with climate. Maxent generates a distribution map of the probability of presence for a given species from occurrence records (Phillips *et al.* 2006). It consistently outperforms other algorithms in its predictive performance for building distribution models from presence-only data (Elith *et al.* 2006; Hernandez *et al.* 2006; Hijmans & Graham 2006; Guisan *et al.* 2007; Pearson *et al.* 2007; Elith & Graham 2009). Maxent was parameterized with default settings (Phillips & Dudik 2008) except that threshold and hinge features were removed, because this produces more ecologically realistic response curves (Austin 2007). Ten thousand background points were selected at random from regions represented by a 100 km species-specific buffer around the occurrence points (as per VanDerWal *et al.* 2009a). Models were evaluated using the area under the receiver operating characteristic (ROC) curve, the AUC (Area Under Curve). Values above 0.5 are better than random predictions, with those above 0.7 being considered useful (Elith *et al.* 2006) and those above 0.9 highly accurate (Guisan *et al.* 2007).

3.4 Results

3.4.1 Site scale

3.4.1.1 Environmental features

Environmental variables were reduced to five variables due to colinearity. The variables retained included litter cover, litter layer depth, total grass density, percentage cover of *C. subjuncea*, and Nitrogen. Litter cover was positively correlated with soil moisture (r = 0.84), as was litter layer depth (r =0.62). Nitrogen was positively correlated with C (r = 0.94), total grass cover (r = 0.63), *T. triandra* cover (r = 0.62), CN ratio (r = 0.60), and S (r = 0.59). Grass density was negatively correlated to total grass cover (r = - 0.67) and *T. triandra* cover (r = - 0.66). Percentage cover of *C. subjuncea* was not correlated with any other variables.

The best supported model predicting cockatoo grass density included litter cover, grass density, Nitrogen, and percentage cover of *C. subjuncea* (Table 3.1). Four models had support, with model 1 being 22.33 times more likely than model four, 7.44 times more likely than model 3, and 3.19 times more likely than model 2 (Table 3.1). This indicated that model 1 had considerable support, model 2 had some support while models 3 and 4 had considerably less support. The percent deviance explained was 95.93 for model 1 and 93.68 for model 2, indicating good model fits to the data.

Table 3.1. The results of Poisson Generalized linear modelling (GLM) using Akaike’s information criterion (AICc) for cockatoo grass density (per m^2). Values represent the number of parameters (K), maxamised log-likelihood (Log(L)), Akaike’s information criterion corrected for small sample sizes (AICc), AICc model differences (Δ), Akaike model weights (wi), and the percent deviance explained (% Dev). Models are ranked relative to the AICc min, or model with the smallest AICc, in descending order. The 4 highest ranked models are shown (between Δ 0-7 of AICc min). †Variable codes refer to: LC, Litter Cover (%); GD, Grass Density (per m^2); N, Nitrogen (mg/g); CC, *C. subjuncea* percentage cover (%); LL, Litter Layer Depth (mm).

Model	**Variable†**	**Variable†**	**Variable†**	**Variable†**	**K**	**Log(L)**	**AIC$_c$**	**Δ**	**w_i**	**% Dev**
1	LC	GD	CC	N	6	-30.04	88.88	0	0.67	95.93
2	LC	GD	N		5	-35.56	91.18	2.23	0.21	93.68
3	LC	LL	GD		5	-36.48	92.95	4.08	0.09	93.31
4	LC	LL	GD	N	6	-33.23	95.34	6.52	0.03	94.61

Table 3.2. Model averaging results for relative importance of contributing variables to Poisson generalized linear models (GLM) using Akaike’s information criterion (AIC$_c$) for cockatoo grass density (per m^2). Values represent the relative importance of each variable (w_i), average estimates (estimate), standard errors (SE), and upper and lower confidence intervals (CI).

Variable	**w_i**	**Estimate**	**SE**	**Lower CI**	**Upper CI**
	Intercept	1.71	0.23	1.17	2.24
Grass Density (%)	1.0	-1.77	0.17	-2.56	-0.99
Litter Cover (%)	1.0	-1.62	0.001	-2.01	-1.23
Nitrogen (mg/g)	0.88	0.32	0.07	0.17	0.48
C. subjuncea Cover (%)	0.67	-0.33	0.16	-0.67	0.02
Litter Layer (mm)	0.08	-0.03	0.06	-0.15	0.09

The most important variables ($w_i \geq 0.5$, confidence intervals do not intersect zero) were litter cover ($w_i = 1$), and grass density ($w_i = 1$), followed by Nitrogen ($w_i = 0.88$), and *C. subjuncea* cover ($w_i = 0.67$) (Table 3.2). The coefficient estimates indicated that grass density had the largest relative (negative) effect on cockatoo grass density, closely followed by litter cover (negative) (Table 3.2). Cockatoo grass density was positively related to Nitrogen, with a smaller effect (Table 3.2). *C. Subjuncea* cover was negatively related to cockatoo grass density, but was not considered a reliable parameter estimate because confidence intervals overlap with zero (Table 3.2).

These results indicate that cockatoo grass density was also negatively related to soil moisture, and positively to C, S and CN ratio as well as total grass cover and *T. triandra* cover.

3.4.1.1 Experimental burn

Density of cockatoo grass did not differ between control and treatment sites ($F = 0.02$, $p = 0.88$) over the survey (post-burn/wet and one-year post surveys only; pre-burn survey omitted as controls were not surveyed at this time) (Figure 3.1) although the treatment sites had higher average density measures over both surveys than did the control sites (Table 3.3; survey averages). Within burn treatment sites, cockatoo grass density varied among sites ($F = 83.34$, $p \leq 0.00001$) and surveys ($F = 16.54$, $p \leq 0.0001$) (Figure3.1) but not among plots within sites ($F = 2.47$, $p = 0.11$). Post-burn /wet surveys (Survey 2) had the highest density, followed by one-year post-burn (survey 3), with pre-burn surveys (survey 1) having the lowest density of cockatoo grass (Table 3.3). There was no site-survey interaction effect on cockatoo grass density ($F = 1.14$, $p = 0.37$)**.**

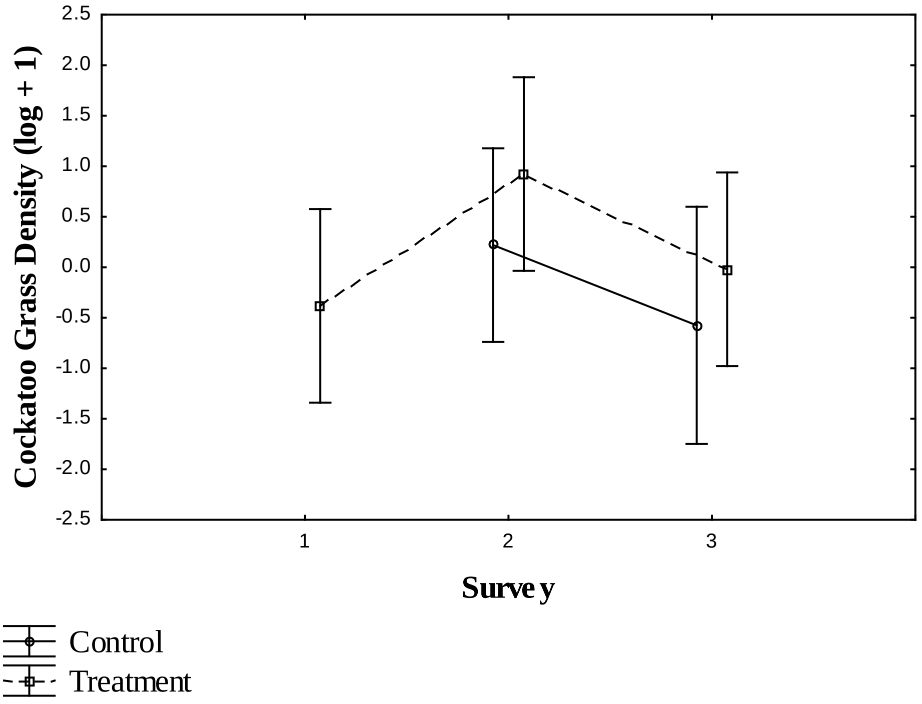

Figure 3.1. Cockatoo grass density (per m^2) for burn treatments versus control plots by survey. Survey 1: pre-burn; survey 2: post-burn/post wet; survey 3: one-year post-burn. (Survey 1 omitted for control sites). Error bars represent standard error.

Cover and density of *T. triandra* and *C. subjuncea* were combined to create a total cover and density measure of grasses other than cockatoo grass, as these two grasses form large clumping tussocks and were the dominant species across all sites. Across all surveys, density of cockatoo grass decreased with increasing total cover ($r = -0.43$, $p \leq 0.05$, $R^2 = 0.18$). However, when comparing sites pre-burn to post-burn, cockatoo grass was negatively correlated with *T. triandra* density ($r = -0.76$, $p \leq 0.05$, $R^2 = 0.58$) and positively correlated with *T. triandra* percentage cover ($r = 0.84$, $p \leq 0.01$, $R^2 = 0.71$) prior to the experimental burn and was negatively related to both *C. subjuncea* cover ($r = -0.49$, $p \leq 0.05$, $R^2 = 0.24$) and total cover ($r = -0.50$ $p \leq 0.05$, $R^2 = 0.25$) after the burn. The inverse relationship between *T. triandra* is a product of grass clumping; individuals became more readily identified when total cover was lower, as large grass clumps of *T. triandra* made individuals indistinguishable. Maximum total cover measured at all sites never exceeded 50%.

Table 3.3. Cockatoo grass density (per m^2) by site and survey period, including survey average grouped as treatment or control sites. Mean and standard error (SE) are presented. T represents treatment site and C represents control site. Surveys were not conducted for control sites Pre-burn or control site 4 at the one year post survey due to fire (—).

a) Treatment Site	**Pre Burn**		**Post Burn/Wet**		**1 Year Post**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
T1	0	0	0.53	0.09	0.17	0.17
T2	0.85	0.13	2.9	0.43	1.47	0.03
T4	3.75	1.37	9.25	2.21	3.4	0.79
Survey Average	1.53	0.69	4.23	1.45	1.68	0.52

b) Control Site	**Pre Burn**		**Post Burn/Wet**		**1 Year Post**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
C1	—	—	0.68	0.41	0.62	0.35
C2	—	—	0.57	0.30	0.85	0.45
C4	—	—	9.22	3.63	—	—
Survey Average	—	—	3.49	1.78	0.73	0.26

Survival of tagged cockatoo grass plants was highest immediately after the burns, 1 week post-fire (survival proportion: 0.99 ± 0.01 SE), followed by the post-burn wet season surveys (survival proportion: 0.97 ± 0.02 SE) and less survival one-year post-fire (survival proportion: 0.92 ± 0.03 SE) ($H = 7.12$, $p=0.03$). No variation between sites ($H = 1.28$, $p= 0.53$) or plots ($H = 2.79$, $p= 0.25$) was found. Control sites could only be compared at one-year post-fire, and including only sites 1 and 2, with site 4 omitted due to the inadvertent fire through this site. There was no significant difference between control and treatment sites ($H = 1.76$, $p = 0.18$) although control sites had a slightly higher survival (control 0.97 survival ± 0.02 SE, treatment 0.94 survival ± 0.02 SE).

In the post-burn/wet survey, only treatment (burnt) sites were observed with flowering cockatoo grass. In the treatment sites, 16 plants were observed flowering on the measured transects out of a total of 722 counted cockatoo grass plants. No flowering cockatoo grass plants were found in the surrounding un-burnt vegetation. Control sites had 628 cockatoo grass total plants over all of the measured transects, with zero flowering ($\chi^2 = 13.79$, $p \leq 0.05$). Observations on control site 4, which was accidentally burned just before the one-year post surveys, revealed many flowering cockatoo grass plants while no other sites (treatment or control) were noted to be flowering at this time. Previous observations have also noted cockatoo grass flowering in sites that had been burnt, but not within immediately adjacent un-burnt sites (separated by a road as a fire break) containing a thick grass sward dominated by *T. triandra* (B. Bateman, personal observation).

3.4.2 Regional scale modelling

Model evaluation (AUC = 0.81) indicated that the model had good discrimination and should be considered useful in its predictive performance (Elith *et al.* 2006; Guisan *et al.* 2007). The variable with highest contribution to the model was the maximum temperature of the warmest period (59.8%), followed by temperature seasonality (14.5%) and precipitation of the driest quarter (8.5%). From the records obtained within Queensland, it appears that cockatoo grass can persist over large maximum temperature ranges, from 22° C to 38° C (Figure 3.2). However, probability of occurrence begins to decline above 30°C, and the ideal temperature is close to 26°C. Temperature seasonality appears to limit cockatoo grass on either end of the extremes, from 20 (CV) to 220 (CV) being the full range this species experiences in Queensland. Probability of occurrence is highest at around 90 (CV) (Figure 3.3). Cockatoo grass occurs where precipitation of the driest quarter ranged from 0 mm to 400 mm, with probability of occurrence greatest between 200 and 250mm (Figure 3.4).

Despite cockatoo grass records being sourced only from within Queensland, it appears that the large-scale model presented here captures the near full range of tolerances for the climate variables most important to model development of this species (Figure 3.2 - 3.4).

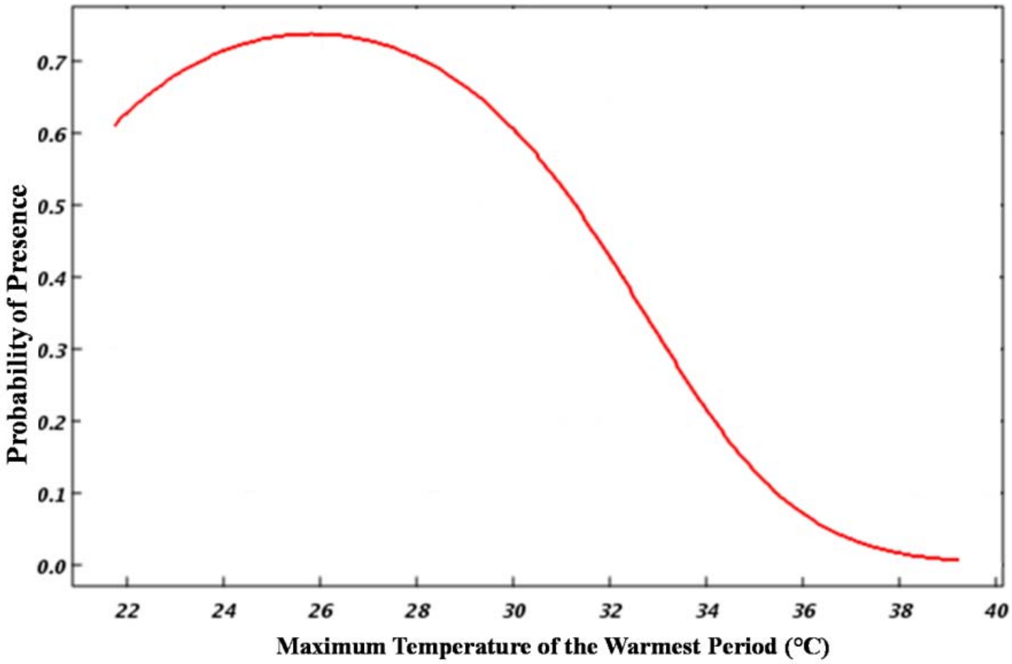

Figure 3.2. Response curve of cockatoo grass (probability of presence) to maximum temperature of the warmest period (°C) in Queensland, Australia. This Figure is adapted from the maxent model output response curve plots. Response curves represent how the predicted suitability (probability of presence) is dependent on the variable selected.

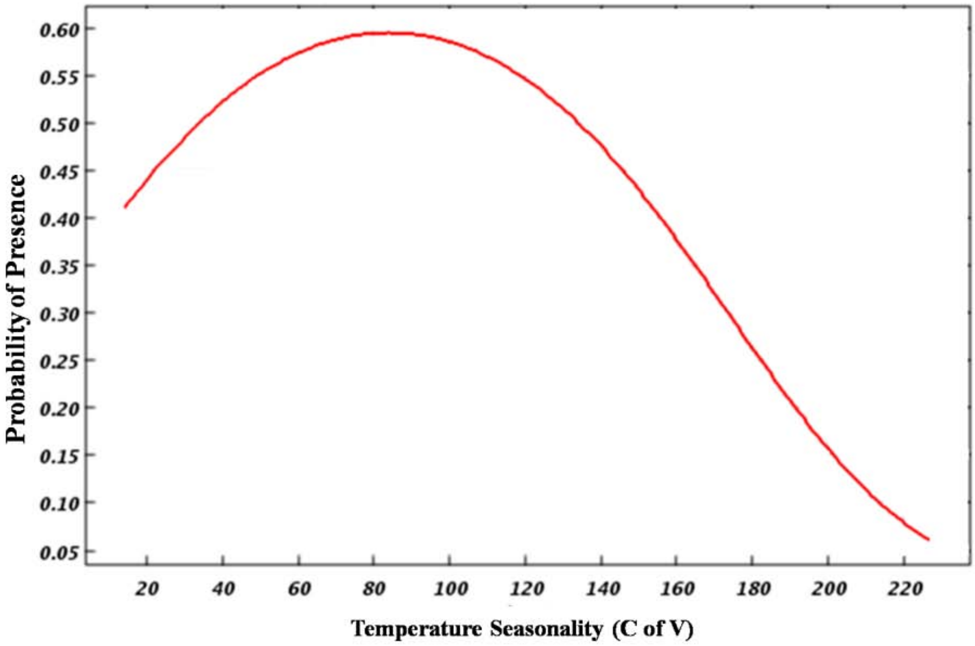

Figure 3.3. Response of cockatoo grass (probability of presence) to temperature seasonality (C of V) in Queensland, Australia. This Figure is adapted from the maxent model output response curve plots. Response curves represent how the predicted suitability (probability of presence) is dependent on the variable selected.

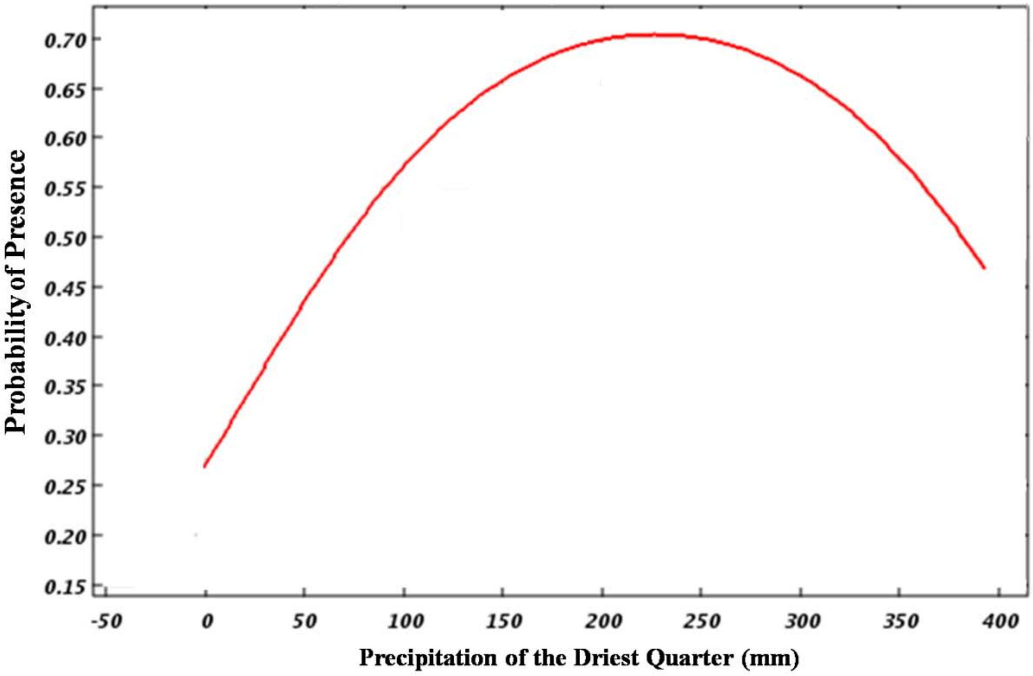

Figure 3.4. Response curve of cockatoo grass (probability of presence) to precipitation of the driest quarter (mm) in Queensland, Australia. This Figure is adapted from the maxent model output response curve plots. Response curves represent how the predicted suitability (probability of presence) is dependent on the variable selected.

3.5 Discussion

In this ecotone habitat, the density of cockatoo grass was negatively related to litter cover and soil moisture, as well as to the presence of two dominant grass species, *T. triandra* and *C. subjuncea*. Grass species have been shown to be suppressed by litter cover deposited by woody plants in such habitat types (Scott 2008). Shading and litter cover reduce light levels at the grass layer, influence temperature and soil moisture levels, have chemical and mechanical effects, and can suppress establishment, germination, growth, biomass, reproductive allocation and production for some grasses (Jensen & Gutekunst 2003; Scott 2008). Fire can influence the litter layer and shading, with less frequent fires leading to more shading and litter accumulation (Scott 2008). In a greenhouse experiment Scott (2008) found that growth of cockatoo grass was suppressed by the litter layer, with less seedling emergence in litter treatments than non-litter treatments, especially when sown under the litter layer. Early successional species such as cockatoo grass are out-competed by later successional species with larger seed size under litter layer and shade (Jensen & Gutekunst 2003). Cockatoo grass may be utilizing a ‘gap-detecting’ mechanism by which it takes advantage of favourable light levels created by disturbances such as fire, while failing to germinate under a dense litter layer or dense vegetation (Jensen & Gutekunst 2003).

In the absence of fire or other disturbances, *Allocasuarina* spp. can invade and dominate, causing the decline of eucalypts and increase in shading (Withers & Ashton 1977; Withers 1978; Kellman 1986; Lunt 1998; Abell *et al.* 2006; Crowley *et al.* 2009). An invasive climax species, *Allocasuarina* spp. can form dense stands when fire is absent for long periods, as saplings become less sensitive to fire after reaching 200 cm in height (Kellman 1986). *Allocasuarina* spp. drop high volumes of needles under their canopy (Withers & Ashton 1977), and this litter layer has an allelopathic effect and can physically restrict the germination and seedling establishment of other species (Withers 1978; Abell-Davis 2008). The direct impact of *Allocasuarina* needles on cockatoo grass was not studied during this experiment, but it was noted that there was generally fewer grass species under dense *Allocasuarina* needle litter. The thick needle bed associated with encroaching *Allocasuarina torulosa* pockets and related canopy cover had a lower diversity of grass species than adjoining woodlands. The absence of cockatoo grass in sites where it was previously recorded (McIlwee & Freeman 1998) in the study area, along with an increase in density of *Allocasuarina torulosa*, is of concern, (B. Bateman pers. obs., M. Parsons, pers. obs.).

The negative relationship between cockatoo grass density and soil moisture is consistent with previous studies. Mathams (2008) surveyed cockatoo grass across an environmental gradient from wet sclerophyll to dry sclerophyll habitat in the Wet Tropics, and found that it was less abundant in wetter habitat types with higher soil moisture, ground cover percentage, and higher densities of *Allocasuarina* species, while abundance increased with number of *Eucalyptus* species present, in more open grassy habitats. This was similar to the findings of Abell et al. (2006) and Vernes (2003) and suggests that cockatoo grass prefers soils under *Eucalyptus* trees, as leaf litter under eucalypts creates hydrophobic soils (Scott 2000; Doerr *et al.* 2006).

Nitrogen, along with C and S, were positively related to density of cockatoo grass. Nitrogen is a limiting factor of plant growth in tropical systems. Cockatoo grass produces more biomass at higher N levels, allowing for more storage in the corm and for sexual reproduction, which is an advantage post-fire in the absence of competition for light when the high assimilation and fast growth rates conferred by this corm facilitate re-sprouting and recruitment (Ripley *et al.* 2008). Nitrogen is often higher in the litter layer, where it may be mobilised due to low decomposition rates preventing replenishment of soil nutrients (Chen *et al.* 2001; Parsons & Congdon 2008; Prusty *et al.* 2009). As litter layer depth and litter cover were both negatively related to cockatoo grass density, litter nutrient mobilization could be negatively influencing soil nutrient levels. Fire may play a key role in releasing some of this N for availability, at least on the short-term (Wan *et al.* 2001). Indeed, higher N values were found in the post-burn surveys, although this was not a significant difference (not presented).

To my knowledge, this is the first study on the impact of fire on cockatoo grass at the wetter end of its environmental range. Cockatoo grass had high survival (≥ 92%) through the late dry season following an experimental burn, similar to un-burnt plots. High survival was probably due to dry season dormancy, as early senescence in combination with an underground carbohydrate storage base tends to make the species resistant to burning (Everson *et al.* 1988; Crowley & Garnett 2001). Cockatoo grass has been shown to not suffer detrimental effects due to fire, with quick recovery attributed to the reallocation of below ground biomass for regrowth (Ripley *et al.* 2010). Data from this study also indicate that fire promotes flowering in cockatoo grass. Crowley and Garnett (2001) suggest that fire synchronises flowering in this species and promotes seed production. Flowering and seed production are highest in the first wet season after burning, as biomass levels are low, and there is greater nutrient availability due to removal of larger and nutrient-demanding perennial grass species (Garnett & Crowley 2002; Lunt & Morgan 2002; Williams *et al.* 2005). Flower production may also be driven by light availability and release from competition as a dense, closed grass layer reduces flowering productivity (Lunt & Morgan 2002).

Fire had a positive impact on density of cockatoo grass, particularly in the first wet season after the burn, and this effect was still observable one year after. A reduction in cockatoo grass density was observed one year after the burn for both treatment and control sites, probably due to dry season senescence. However, density measures in treatment sites were still higher than pre-burn measures, in accord with other studies that have shown a positive relationship of cockatoo grass to fire frequency (Woinarski *et al.* 2004; Crowley *et al.* 2009; Scott *et al.* 2009; Russell-Smith *et al.* preprint). The benefit of fire for cockatoo grass may be due not only to the reduction in litter layer accumulation (Scott 2008), but also to reduction of larger more competitive grass species (Morgan & Lunt 1999). Density of cockatoo grass was negatively related to cover and density of two dominant grass species in this study, *C. subjuncea* and *T. triandra*. Tall perennial grasses, such as *T. triandra,* with long growing periods and high potential growth rate, expanded tussock structure, and which deposit a dense layer of ground litter, are likely to be strong competitors for water and nutrients (Grime 1973; Walker *et al.* 1997; Lunt 2003; Cole & Lunt 2005). In addition, as cockatoo grass is suppressed by shade, tall thick ground cover ($\geq$ 200mm in height) is likely to reduce the photosynthetic energy output required for growth (Everson *et al.* 1988). *T. triandra* quickly dominates the landscape in the absence of biomass reduction due to burning, grazing, or some other management, out-competing inter-tussock species such as cockatoo grass (Walker *et al.* 1997; Morgan & Lunt 1999; Lunt 2003). This is likely to occur in areas where fire has been absent for long periods.

As fire frequency influences biomass accumulation and structural dominance, short fire intervals may be needed to deal with competitive *Allocasuarina* species (Lunt 1998) and facilitate the coexistence of subordinate grass species such as cockatoo grass (Lunt & Morgan 2002). Fire intervals of five years are suggested to maintain *T. triandra* while allowing inter-tussock flora to co-exist (Morgan & Lunt 1999), and might benefit cockatoo grass as it experience a boom 2-4 years post disturbance (Walker *et al.* 1997). As this study examined only a single late dry season fire within this ecotone habitat, future studies will need to be conducted using a variety of fire regimes over a long time period to fully understand the relationship of cockatoo grass and fire, and to develop an appropriate fire frequency management regime.

At the larger scale, both temperature and precipitation appear to limit cockatoo grass, although it has broad tolerances. The climate model appears to identify a broad niche which encompasses the sclerophyll to savanna habitats within which this species occurs. Cockatoo grass distribution is limited at either end of this gradient by wetter conditions adjacent to rainforest habitats as well as by hotter and drier conditions of inland savannas.

The persistence of cockatoo grass is dependent on vegetative growth, which depends on moisture availability (Crowley & Garnett 2001). Cockatoo grass is therefore vulnerable to drought as growth stagnation will occur if minimum moisture levels, provided by 40 mm of rainfall or more, are not maintained (Crowley & Garnett 2001). Precipitation in the dry season is thus an important limiting factor. Abundance of the C4 form of cockatoo grass found in Australia (a C3 form of this species is found in South Africa) is limited by drought and arid conditions, as investment in below ground biomass storage hinders recovery during drought (Ripley *et al.* 2007; Ibrahim *et al.* 2008; Ripley *et al.* 2008). The probability of occurrence of cockatoo grass declined with hotter and more variable temperatures (higher summer temperatures and increased temperature seasonality), conditions which could also lead to reduced soil moisture. The probability of presence of cockatoo grass also declined in areas experiencing high rainfall. This indicates that high levels of rainfall can have a negative impact on this species, as was seen also at the site level with increase soil moisture levels. Higher dry season rainfall measurements in the regional scale model likely indicate habitats in the wetter end of the sclerophyll woodland gradient including rainforest habitats.

The influence of fire and grazing pressure, factors likely to influence the distribution of this species, were not included in the regional scale modelling of cockatoo grass distribution as data availability at this scale is at present too coarse for useful model inputs. To improve the climate-based predictions presented here, a more detailed model should be developed using fire data layers as they become available. Factors such as fire frequency, fire weather, grazing pressure, and their likely interactions could be integrated to develop a more useful model of cockatoo grass distribution which could help us understand the factors limiting this species on a larger scale.

Chapter 4 : How much influence do biotic interactions have on predictions of shifts in species distributions under climate change?[1]

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[1] **Bateman BL**, VanDerWal J, Williams SE, Johnson CN (in review) How much influence do biotic interactions have on predictions of shifts in species distributions under climate change? *Diversity and Distributions*

4.1 Abstract

Species distribution models (SDMs) are commonly used to predict how species distributions may shift in order to track climate. These predictions rarely incorporate biotic interactions despite our understanding that such interactions are likely to change in novel climate scenarios. The aim of this study was to measure the effects of including biotic interactions in species distribution models on predictions of distribution shifts under climate change. I evaluated performance of distribution models for an endangered marsupial, the northern bettong (*Bettongia tropica*), comparing models that used only climate variables with models that also took into account interactions with two crucial food resources and a competitor. I developed separate climate-based distribution models for the northern bettong, its two main food resources and the competitor species. I then constructed a series of models for the northern bettong, by adding interactions with other species to the climate-only model. I did this first by including estimates of climate suitability for the two food resources as additional predictor variables in the northern bettong climate model, to make a climate+resource model; then by adding suitability estimates for the competitor species to construct a climate+resource+competition model. I projected these models onto seven future climate scenarios which diverged progressively from the present climate. I compared predictions of northern bettong distribution made by these differently-structured models, using a ‘global’ metric, the *I*- similarity statistic, to measure overlap in distribution, and a ‘local’ metric to identify where predictions differed significantly. The inclusion of biotic interactions improved model performance (based on AUC scores). Over moderate climate changes, up to 3.0 °C of warming, the climate-only model for the northern bettong gave similar predictions of distribution to the more complex models, with differences only at the

margins of predicted distributions. For climate changes beyond 3.0 °C, model predictions diverged significantly. The interactive model predicted less contraction of distribution than the simpler climate-only model. Distribution models that account for interactions with other species are more ecologically realistic in principle, and in practice perform better than simplistic models based on climate alone when projecting onto future climates. Nonetheless, the predictions of climate-only models are similar to those of interactive models, and serve as useful approximations for them, under the present climate and for moderate departures from that climate. For larger climate changes, however, shifts in distribution of interacting species assume increasing importance and cause predictions of interactive models to diverge from climate-only models, meaning that climate-only models become less useful. I conclude that ecologically realistic models, that incorporate interactions with other species, are needed for long-term prediction of changes in distribution of species of concern under climate change.

4.2 Introduction

Global temperatures are expected to rise rapidly over the next century. Many species are unlikely to be able to adapt *in situ* to the novel environments produced by a warming climate, and will instead need to shift their distributions to track suitable climates if they are to persist (Hughes 2003; Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006). Species distribution models (SDMs) are commonly used to estimate the extent to which species distributions will need to shift in order to track climate, and to guide conservation and management under climate change (Hijmans & Graham 2006; Fitzpatrick & Hargrove 2009). Often, SDM techniques include only environmental variables, generally climatic variables alone, and explicitly disregard the influence of other species on the distribution of the species in question (Davis *et al.* 1998a; Austin 2002; Thuiller *et al.* 2008). There are many factors that determine the relative vulnerability of a species to global climate change which will need to be considered to have ecologically realistic models; this includes biotic interactions (Williams *et al.* 2008).

Biotic interactions shape the realized niche (*sensu* Hutchinson 1957) and consequently, the distributions of species. Biotic interactions are implicit in models that describe the current distributions of species, because those distributions reflect interactions with other species as well as the abiotic factors that define the fundamental niche. However, if biotic interactions are not explicit in SDMs, it is possible those models will not be useful in predicting shifts in distribution under climate change (Davis *et al.* 1998a; Pearson & Dawson 2003; Schweiger *et al.* 2008). This is because species tend to respond idiosyncratically to climate change (Davis & Shaw 2001; Parmesan 2006; Heikkinen *et al.* 2007; Preston *et al.* 2008; Schweiger *et al.* 2008; Fitzpatrick & Hargrove 2009). Individualistic responses to shifting climates could lead to the breakdown of current interactions between species and formation of new ones (Hughes 2000; Preston *et al.* 2008; Schweiger *et al.* 2008). Such changes could cause shifts in distribution that would not be predicted by a SDM constructed using only climate variables associated with the current distribution of the target species (Araújo & Luoto 2007; Preston *et al.* 2008; Schweiger *et al.* 2008). The more specialized a species is, and the more dependent on particular other species, the more likely that changes in interactions with other species will play a role in shaping future distributions (Araújo & Luoto 2007; Preston *et al.* 2008). Models that do not incorporate interactions may over-predict suitable habitat (Araújo & Luoto 2007; Heikkinen *et al.* 2007). Because climate-based single-species models are so widely used to predict the effects of climate change on species distributions, one needs to ask the question: to what extent do the predictions of climate-only models differ from predictions of models that include interactions with other species?

Previous work that has incorporated biotic interactions in SDMs has focused predominantly on interactions involving facilitation or competition (Davis *et al.* 1998a; Araújo & Luoto 2007; Heikkinen *et al.* 2007; Preston *et al.* 2008; Schweiger *et al.* 2008). Results from these studies indicated that the inclusion of biotic interactions affected predicted distributions. Other interactions such as pollination, herbivory, predation, parasitism might also be accounted for, as all may have some impact on species responses to a changing climate (Araújo & Guisan 2006; Araújo & Luoto 2007; Thuiller *et al.* 2008). In particular, the availability of resources that are directly consumed by the species are rarely included as explicit variables in SDMs. The inclusion of resource availability should give us more mechanistic and useful models (Guisan & Zimmermann 2000; Austin 2002; Austin 2007).

The predictive value of distribution models is often evaluated by use of the area under the receiver operating characteristic (ROC) curve, the AUC (Area Under Curve). AUC scores are generally regarded as estimates of a model's ability to fit to current distribution, but better reflect whether the modelled niche is broad or narrow (Lobo *et al.* 2008). Model evaluations are fit to current distributions, and are not assessed into future climate projections. I present an additional model comparison methodology which allowed me to make quantitative comparison of the extent to which models differ in their prediction of distributions. In order to discriminate between models, I have applied two techniques to assess model consistency and differences among model projections: a 'global' metric, the *I*-similarity statistic, to determine if predictions differed significantly, and a 'local' metric to identify where predictions differed. The *I*-similarity statistic used in this study has recently been applied to species distribution modelling by Lozier *et al.* (2009) as a measure of the degree of similarity between two distribution model outputs. I have used it in a new way by assessing at what temperature (of global warming) and to what extent models spatially diverge from current predictions and to what degree the inclusion of biotic interactions altered model output. The local metric allows the observation of where in geographical space models significantly differ.

Including biotic interactions in SDMs requires more knowledge of the biology of the organism than is available for many species (Baselga & Araújo 2009). But there is a need for realistic models, and it is therefore necessary to evaluate the effect of model predictions of including biotic interactions (Heikkinen *et al.* 2007). This is accomplished in this paper by comparing the predictions of models with and without biotic factors under global warming scenarios. I examined how the inclusion of both positive and negative biotic interactions affected the future distributions predicted for an endangered marsupial species, the northern bettong (*Bettongia tropica* Wakefield, 1967). Climate models were developed for each of the northern bettong, its two main food resources and a competitor species. Distributions of the northern bettong were first projected using models that included only climate variables, and then for models that also incorporated distributions of the two food resources, and a competing species. I compared the predictions of climate-only and climate-plus-interaction models over a range of scenarios representing increasing climate change, from zero to 6 degrees of warming. This allowed me to test whether climate-only models gave predicted distributions that approximate those of models that incorporated more ecological information, and to show how divergence of model projections depended on the magnitude of climate change.

4.3 Methods

4.3.1 Study Species

The northern bettong is a small (1.2 kg) marsupial ‘rat-kangaroo’ endemic to northeast Queensland, Australia (Figure 4.1), and is listed as endangered (Baillie & Groombridge 1996; Burnett & Winter 2008). It is an ideal organism for my purpose because it is a well-studied specialist (McPherson & Jetz 2007) with a restricted geographic range (Figure 4.1). It is mycophagous, a specialist consumer of ‘truffles’ (underground sporocarps of ectomychorrhizal fungi) (Johnson & McIlwee 1997; Claridge *et al.* 2007). Truffle production is linked to climate, with both rainfall and temperature influencing availability (Johnson 1994; Claridge *et al.* 2000a; Jumpponen *et al.* 2004; Abell *et al.* 2006; Claridge *et al.* 2009). Truffle fruiting in tropical Australia is influenced by weather and is seasonal, with a decline in abundance during the late dry season (Abell *et al.* 2006). Northern bettongs decline in body condition when truffle availability is low, and are unlikely to adapt to a changed climate by switching their diet (Johnson & McIlwee 1997). As climate has a strong influence on truffles, it is likely that the northern bettong will need to track climate-forced changes in the distribution of this key food resource.

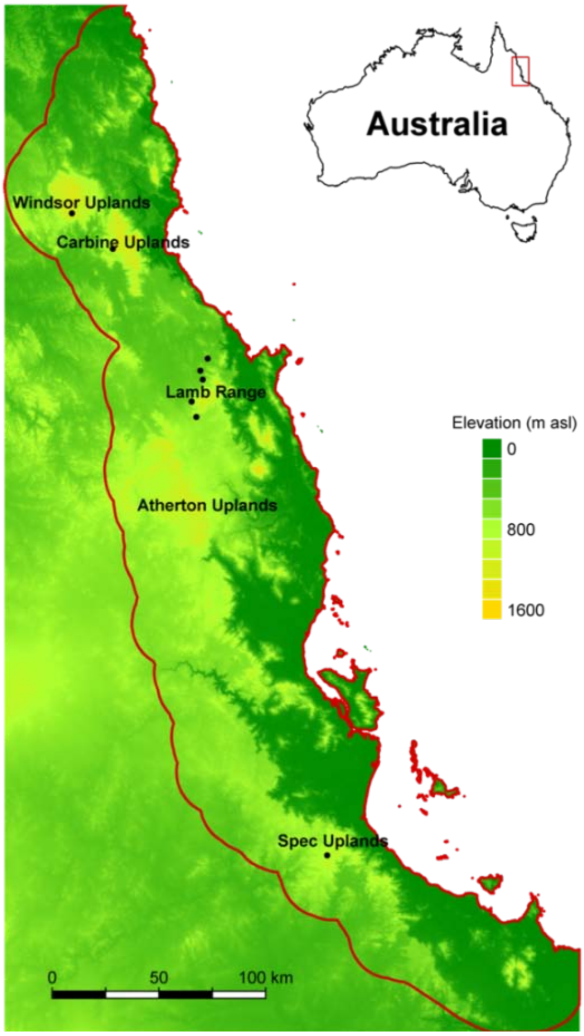

Figure 4.1. Location of study area within Australia with known present day locations of northern bettong populations (central location of known populations indicated by black dots).

When truffle abundance is seasonally low, the northern bettong feeds on the fleshy stem-bases of cockatoo grass (*Alloteropsis semialata*, (R. Br) Hitchcock.) (Johnson & McIlwee 1997; Abell *et al.* 2006). Both food resources are needed to sustain northern bettong populations throughout the year. The rufous bettong (*Aepyprymnus rufescens*, Gray, 1837) is a member of the same family but is larger

(3.0 kg) and is considered a competitor. It has a more general diet and feeds on a wider range of grasses while using truffles and cockatoo grass opportunistically, and it has a wider geographic distribution (McIlwee & Johnson 1998; Claridge *et al.* 2007). Although the two species generally do not occupy the same areas at the same time, their distributions abut and occasionally overlap. The rufous bettong has been observed to increase in areas from which northern bettongs have declined. Previous habitat mapping on both species suggests niche overlap and competition (Winter 1997a).

4.3.2 Modelling

Distributions of the northern bettong were modelled using Maxent (Maxent ver. 3.3.1) (Phillips *et al.* 2006). This modelling algorithm outperforms other algorithms for building SDMs from presence-only data (Elith *et al.* 2006; Hernandez *et al.* 2006; Guisan *et al.* 2007), and it performs well under current, past and future climate scenarios, matching closely the predictions of models produced by mechanistic approaches (Hijmans & Graham 2006; Kearney *et al.* 2010). See Appendix A for a more detailed review of Maxent.

Species occurrence data for the northern bettong (881 occurrence records, 326 unique location records), rufous bettong (1343 occurrence records, 179 unique location records) and cockatoo grass (248 occurrence records, 213 unique location records) were obtained from field surveys and institutional databases. Truffle records (307 occurrence records, 59 unique location records) were obtained solely from field surveys, as distributional data on these taxa are limited. Maxent has been shown to work well with as few as five records (Pearson *et al.* 2007). Truffle occurrences represent the combined records of all hypogeous macrofungal species likely to be eaten by northern bettongs and indicated the availability of truffles as a resource. All species records were collected within the state of Queensland, Australia, with northern bettong and truffle records restricted to the Wet Tropics region. The records used here are representative of the full range of the northern bettong distribution and truffles as a resource for northern bettongs within the Wet Tropics Sclerophyll woodland. I recognize that cockatoo grass occurs across northern Australia although only Queensland records were used, and that although this species is being modelled here as a resource of the northern bettong within the Wet Tropics, restricting these records may lead to an incomplete sampling of the niche in other contexts (Beaumont *et al.* 2009). However, results from Chapter 3 indicate that, at least for the top three variables contributing to cockatoo grass model building, that the niche has been adequately sampled.

Climate variables were based on long-term climate means, derived from ANUCLIM 5.1 (McMahon *et al.* 1995) software using monthly averages and an 80m DEM re-sampled from ~250m (GEODATA 9 Second DEM Version 2; Geoscience Australia, http://www.ga.gov.au/). Variables were: mean annual temperature, temperature seasonality, maximum temperature of warmest period, minimum temperature of coldest period, annual precipitation, precipitation of wettest quarter, precipitation of driest quarter and precipitation seasonality. Climate variables were selected to give the most climate information while avoiding strongly inter-correlated variables. All models were projected onto seven future climate scenarios as per Beaumont *et al.* (2008). These scenarios were Ozclim datasets (www.csiro.au/ozclim) that tracked monthly minimum and maximum temperature, and precipitation. They represent local changes in the eight selected temperature and precipitation variables per degree of global warming, applied at 0.5 degree intervals from current to 6.0°C global warming.

Maxent was parameterized with default settings (Phillips & Dudik 2008) with the exception of the removal of threshold and hinge features, because this produces more ecologically realistic response curves (Austin 2007). 10,000 background points were selected at random from regions represented by a 100 km species-specific buffer around the occurrence points. A buffer of this size is optimal for my study region (VanDerWal *et al.* 2009a) and was selected so that subtle changes in suitability could be detected at fine scales. Current distributions were projected onto the future climate scenarios using the 'fade by clamping' feature in Maxent which allows some extrapolation onto novel environments, but in a constrained manner so that extrapolation is faded as predictions stray from known conditions. See review of Maxent for more details (Appendix A).

Current distributions were modelled for each of the northern bettong, cockatoo grass, truffles and rufous bettong based solely on climate; these models were then projected onto the future scenarios. The Maxent output models of predicted suitability of the resources and competitor were then used as additional predictor variables, in addition to the climate variables, to recreate models for the northern bettong altering the environmental variables to represent climate + resources and climate + resources + competitor.

4.3.3 Analyses

Models were evaluated under present climate using area under the receiver operating curve (AUC of the ROC). In Maxent, AUC values are defined on the training data using background points (pseudo-absences) so that the maximum attainable value is less than one (Phillips *et al.* 2006). Values above 0.5 are better than random predictions, with those above 0.7 being considered useful (Elith *et al.* 2006) and those above 0.9 being highly accurate (Guisan *et al.* 2007). To define a cut-off point for the model in which absences can be inferred, I applied the 'balance threshold' that minimized 6 x training omission rate + 0.4 x cumulative threshold + 1.6 x fractional predicted area. Grid-cells with values below this threshold were rescaled to zero with all values above this threshold retaining their predicted environmental suitability value. This threshold was selected as it has previously ranked consistently as the best threshold value for species in this region (VanDerWal *et al.* 2009a; Willams *et al.* 2010). The likely impacts of climate change on each species were assessed by projecting the models onto the individual future scenarios, as well as averaging the predictions to produce a 'most-likely' outcome.

Projected distributions were compared using two metrics: a 'global' metric, the *I*-similarity statistic (Warren *et al.* 2008), to determine if and when predicted distributions significantly differed, and a 'local' metric to identify where predictions differed. This similarity statistic was proposed by Warren *et al.* (2008) to compare niche equivalency. The *I*-similarity statistic sums the pair-wise differences between two predictions to create a single value representing their similarity. The *I*-similarity statistic ranges from a value of 0, where two distributions have no overlap, to 1 where they are identical (Warren *et al.* 2008). Model comparison was undertaken examining the *I*-similarity statistic from current (0°C) through increasing global warming temperatures; comparisons included a within model comparison and a between model comparison. Within model comparisons indicate how each model diverges from current predictions (0°C) through each increasing temperature step. Between model comparisons indicate how much the compared models overlap at each temperature step. Model comparisons were undertaken using one way analysis of variance (ANOVA, F).

To identify locations where predictions of habitat suitability differed significantly between models, I applied the methodology of Januchowski *et al.* (2010). Significance of the location-specific (cell-specific) differences between predictions was calculated as the probability for any single difference relative to the mean and variance of all location-specific differences. The probability value represents the area under the curve of a Gaussian distribution defined by the mean and variance across all cells. The spatial surface representing the individual significance values was reclassified to indicate areas where the first distribution predicted significantly more suitable habitat (SD ≥ 0.975), where the second distribution did (SD ≤ 0.025), and where there was no significant difference between models.

4.4 Results

All models for current distributions performed well on AUC scores and gave predicted distributions that were better than random (Elith *et al.* 2006; Guisan *et al.* 2007). AUC values were high for all northern bettong climate-based models (>0.989) and the truffle model (0.984), and moderate for the more generalist species models, cockatoo grass and the rufous bettong (0.809 and 0.789, respectively) (Model outputs are depicted in Figure 4.2 as the current distributions maps). Inclusion of the biotic factors into the northern bettong models improved the AUC from 0.989, for the climate-only model, to 0.994 for both northern bettong models that included biotic interactions.

4.4.1 Comparison of current and projected distributions

The *I*-similarity statistic was used to compare current distributions of northern bettongs, rufous bettongs, cockatoo grass and truffles with projected distributions of those same taxa under climate change. It showed significant divergence between current and projected future distributions for all taxa (Table 4.1a). Most models showed significant (F statistics, presented in Table 4.1) divergence from around 0.5 degrees of global warming, although cockatoo grass and the rufous bettong did not show significant divergence until around 1.0 – 1.5 °C of warming (Figure 4.3). Model divergence showed a decline in overlap between current and future distributions for all models, with the most dramatic changes for the northern bettong climate-only model, and truffles (Table 4.1a, Figure 4.3). This can be interpreted as either a predicted loss in habitat, or a shifting of predicted habitat away from its current distribution. For truffles, cockatoo grass and the rufous bettong, the divergence was due to loss in habitat, while all northern bettong models registered both habitat loss and shifting of predicted habitat (Figure 4.2).

I also measured overlap in the projected distributions of different taxa, under current and future climates. This analysis revealed changes in the overlap of different taxa that were minor for small degrees of warming, but became significant beyond 2.5 to 3.0° C (Figure 4.4, Table 4.1b). Below this threshold, northern bettong models (climate-only, climate + resources, and climate + resources + competitor) had high model consensus ($I \geq 0.75$ at 0°C) and models seemed stable with only minor changes in the *I*-similarity statistic (Figure 4.4a, Table 4.1b). Above the threshold, climate-only models diverged significantly from the two models that included interactions, with *I*-similarity statistic values less than 0.37 at 6° C (Table 4.1b). Models with interactions also diverged significantly from each other although *I*-similarity statistic values remained high ($I \geq 0.66$ at 6° C) (Table 4.1b Figure 4.4a).

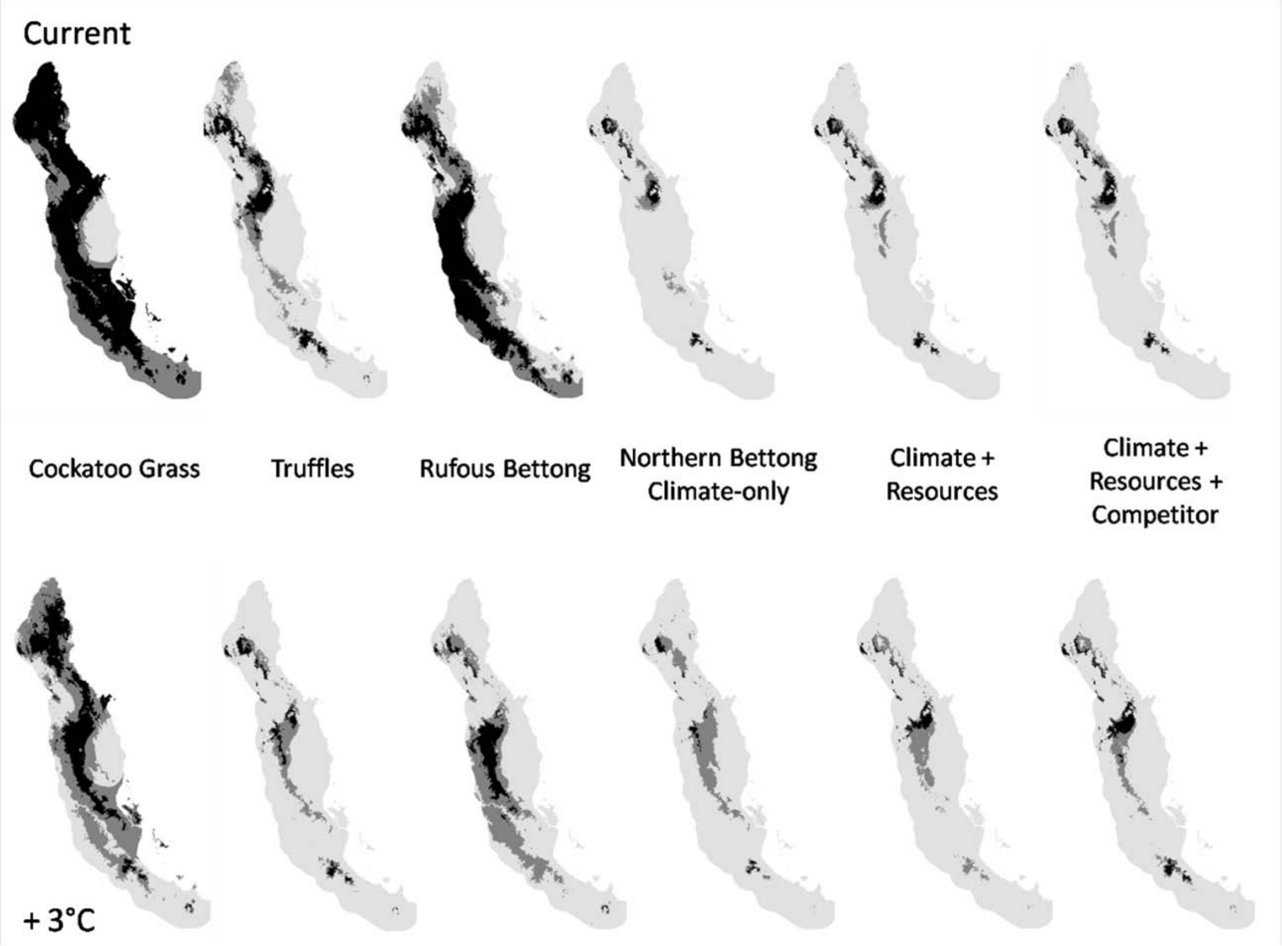

Figure 4.2. Predicted Species Distributions at both current (above) and + 3.0° C (below) global warming. Models represented are, from left to right , cockatoo grass- climate, truffles-climate, rufous bettong- climate, northern bettong climate-only, northern bettong climate + resources , and northern bettong climate + resources + competitor. Colour classifications are as follows: black as high suitability (upper 50% of presence threshold), dark grey as medium suitability (lower 50% of presence threshold), and light grey (below threshold for presence) defining all regions of the study area of low suitability.

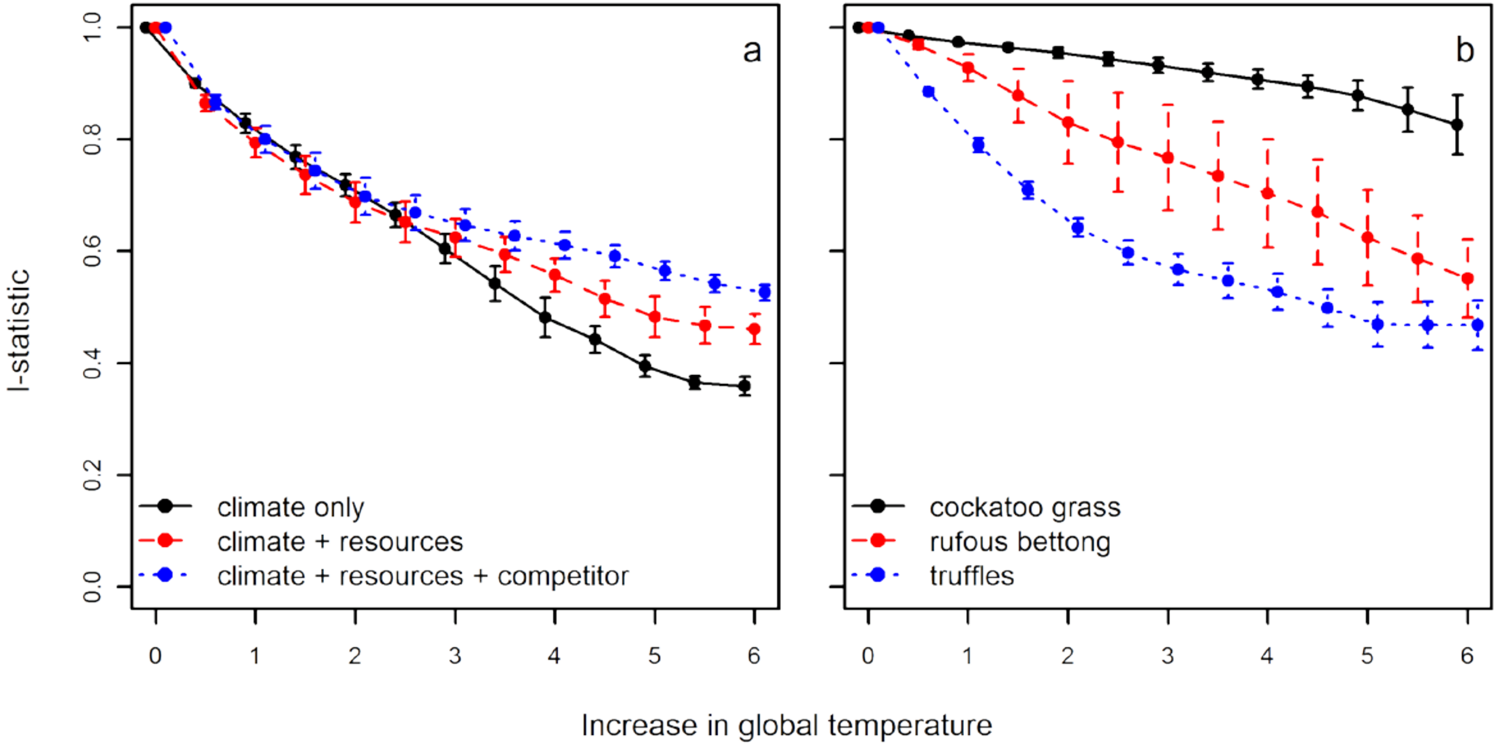

Figure 4.3. *I*- similarity statistic values versus increase in global temperature (°C) for within model comparisons. Within model comparisons represent how each model differs through each temperature step as compared to that same model from the previous temperature interval. Plots represent a) the comparison within each northern bettong modelling scenario (climate only, climate + resources, and climate + resources + competitor) and b) the comparison within resources (cockatoo grass and truffles) and competitor species (rufous bettong). For each scenario, mean and standard error bars of *I*- similarity statistic values (average of seven future climate scenarios) per temperature interval (from 0 – 6 °C global warming) are presented (average of seven future climate scenarios (GCMs).

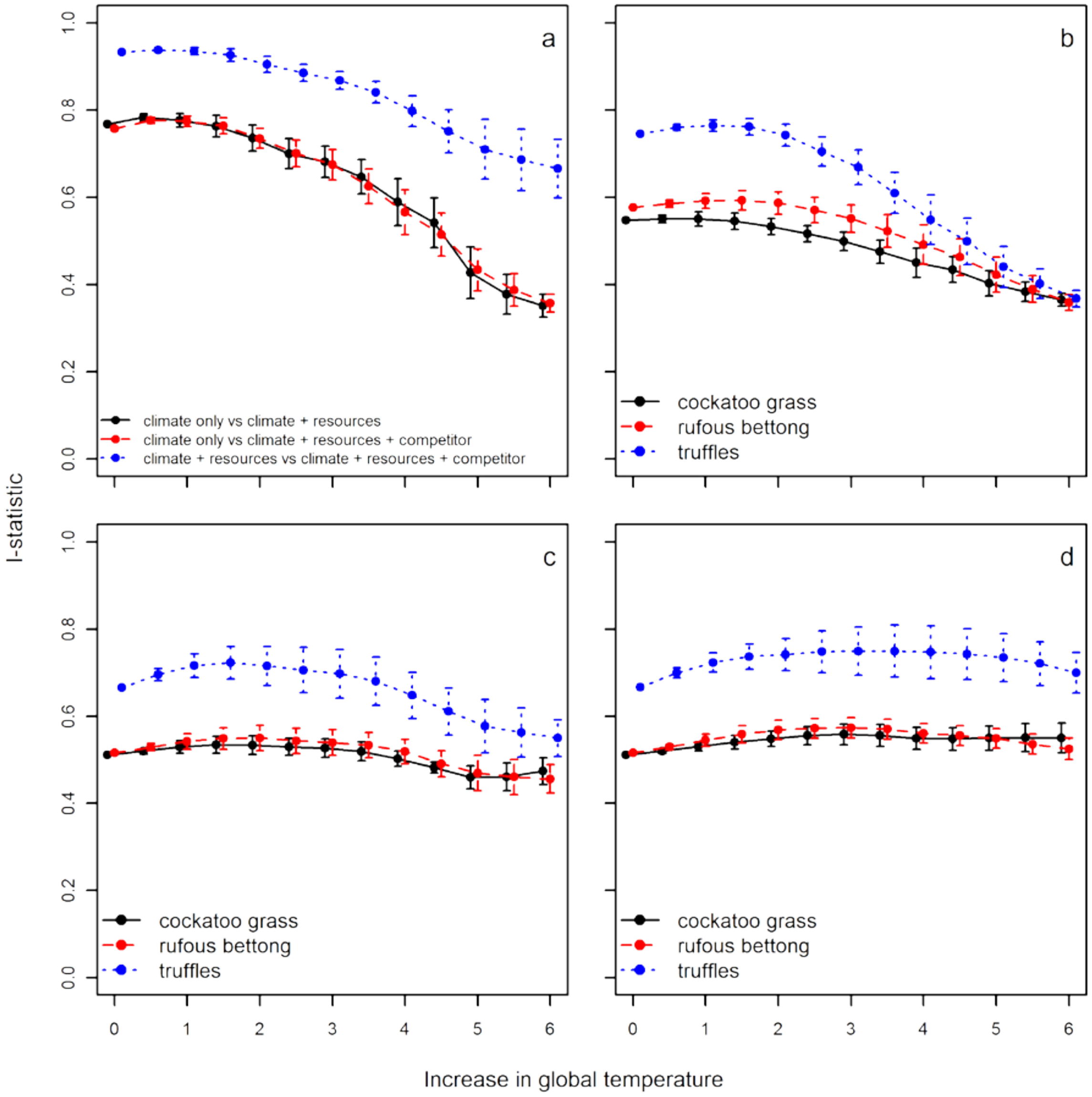

Figure 4.4. *I*- similarity statistic values versus increase in global temperature (°C) for between scenario comparisons. Between model comparisons represent how each northern bettong scenario modelled differs through each temperature step as compared to the other defined model. Plots represent a) between northern bettong scenarios; b) between northern bettong climate-only and the models for the resources and competitor species; c) between northern bettong climate + resource and the models for the resources and competitor species; and d) between northern bettong climate + resource + competitor and the models for the resources and competitor species. For each scenario, mean and standard error bars of *I*- similarity statistic values (average of seven future climate scenarios) per temperature interval (from 0 – 6 °C global warming) are presented (average of seven future climate scenarios).

Table 4.1. Model comparison results for a) within model divergence through increasing temperature steps and b) between models overlap through increasing temperature steps. Within model comparisons indicate how each model diverges from current predictions (0°C) through each increasing temperature step. Between model comparisons indicate how much the compared models overlap at each temperature step. Note that all temperature steps also indicate associated changes in the selected climate variables. All northern bettongs models are indicated by their scenario name (climate-only, climate + resources, or climate + resources + competitor). Shown are F statistics, p value for model comparison and mean values and standard deviations for each *I* value/temperature step indicated. * indicates significant results P ≤ 0.05; indicates significant results ** P ≤ 0.00; † indicates an increase in *I* value; ‡note that all models had *I* values of 1.00 at 0°C so temperature values of 0.5°C is used.

a) within

Base Model	**Comparison Model**	**F**	**p**	***I* (0.5°C)‡**	***I* (3°C)**	***I* (6°C)**
climate-only (0°C)	climate-only (> 0 °C)	116.31	0.0000**	0.90 ± 0.02	0.60 ± 0.06	0.36 ± 0.02
climate + resources (0°C)	climate + resources (> 0 °C)	27.23	0.0000**	0.86 ± 0.04	0.62 ± 0.08	0.46 ± 0.02
climate + resources + competitor (0°C)	climate + resources + competitor (> 0 °C)	278.7	0.0000**	0.87 ± 0.03	0.65 ± 0.07	0.53 ± 0.02
truffles (0°C)	truffles (> 0 °C)	43.33	0.0000**	0.89 ± 0.02	0.57 ± 0.04	0.47 ± 0.11
cockatoo grass (0°C)	cockatoo grass (> 0 °C)	6.43	0.00000**	0.98 ± 0.01	0.93 ± 0.07	0.83 ± 0.13
rufous bettong (0°C)	rufous bettong (> 0 °C)	4.50	0.00002**	0.97 ± 0.02	0.77 ± 0.04	0.55 ± 0.17

b) between

Base Model	**Comparison Model**	**F**	**p**	***I* (0°C)**	***I* (3°C)**	***I* (6°C)**
climate-only	climate + resources	20.18	0.0000**	0.77 ± 0.00	0.68 ± 0.09	0.35 ± 0.07
climate-only	climate + resources + competitor	25.47	0.0000**	0.76 ± 0.00	0.68 ± 0.09	0.36 ± 0.05
climate-only	Truffles	20.92	0.0000**	0.75 ± 0.00	0.67 ± 0.10	0.37 ± 0.05
climate-only	cockatoo grass	11.32	0.0000**	0.55 ± 0.00	0.50 ± 0.05	0.37 ± 0.03
climate-only	rufous bettong	9.01	0.0000**	0.58 ± 0.00	0.55 ± 0.08	0.36 ± 0.04
climate + resources	Truffles	2.11	0.03*	0.67 ± 0.00	0.70 ± 0.14†	0.55 ± 0.10
climate + resources	cockatoo grass	2.14	0.02*	0.51 ± 0.00	0.53 ± 0.05†	0.47 ± 0.08
climate + resources	rufous bettong	1.71	0.08	0.52 ± 0.00	0.54 ± 0.07†	0.46 ± 0.08
climate + resources + competitor	Truffles	0.36	0.97	0.67 ± 0.00	0.75 ± 0.14†	0.70 ± 0.11†
climate + resources + competitor	cockatoo grass	0.50	0.91	0.51 ± 0.00	0.56 ± 0.06†	0.55 ± 0.08†
climate + resources + competitor	rufous bettong	1.03	0.43	0.52 ± 0.00	0.57 ± 0.06†	0.53 ± 0.06†
climate + resources	climate + resources + competitor	7.77	0.00000**	0.93 ± 0.00	0.87 ± 0.05	0.67 ± 0.16
truffles	cockatoo grass	0.79	0.66	0.665 ± 0.00	0.64 ± 0.08	0.60 ± 0.05

Modelling using climate only suggested that with increasing change from the present climate, predicted distributions of northern bettong and its food resources become more disjunct (Figure 4.4b), with a significant decrease in overlap between the bettong (climate-only) and its food resources ($I \leq 0.37$ at 6° C for all; Table 4.1b). The climate + resources model significantly differed from both food resources, but *I*-similarity statistic remained fairly constant with an initial increase in overlap at 3° C, but declining at 6° C (Table 4.1b, Figure 4.4c). No significant difference was observed between the model and the competitor species predicted distribution (Table 4.1b).

The climate + resources + competitor model did not significantly differ from either resource model or the competitor species model (Table 4.1b, Figure 4.4d). An increase was noted in overlap with this model and all interacting species throughout the increasing temperature steps, indicating this northern bettong model best incorporates predicted shifts in all species, thus tracking their changes (Table 4.1b).

4.4.2 Refugia

Hereafter, I focus on results relating to the differences between current distributions and distributions at + 3.0° C global warming, this being a common threshold at which significant changes in distributions were predicted by all models. Significant differences between northern bettong models are depicted in geographical space to highlight where models predict more or less suitable habitat (Figure 4.5).

All models reveal three refugial areas to which suitable habitat for the northern bettong contracts in global warming scenarios, referred to hereafter as the northern (Windsor and Carbine uplands) central (Lamb Range), and southern (Spec uplands) refugia (Figure 4.1). Differences between scenarios are particularly evident in the central refugium, where climate-only model predicts more suitable habitat in the southern portion of the Atherton Uplands than either climate + resources (Figure 4.5a) or climate + resources + competitor (Figure 4.5b). This region coincides with areas that are predicted to be less suitable (at current and + 3.0° C) for the main food resource of northern bettong (truffles) (Figure 4.3). 'Truffles' was identified as the most important predictor variable when evaluated both in comparison with other predictors and alone in the Maxent jack-knifing analysis (see Appendix A) for both climate + resources or climate + resources + competitor models. This area is also predicted to be highly suitable for the competitor species (rufous bettong) but also for the seasonal resource (cockatoo grass) (Figure 4.3).

Figure 4.5. Distribution maps of significant difference at +3.0° C global warming between (a) northern bettong climate-only and climate + resources; and (b) northern bettong climate-only and climate + resources + competitor. Black areas represent where the northern bettong climate-only model predicts significantly more suitable habitat (SD >0.975), dark grey areas where the other modelled scenario predicts significantly more suitable habitat (SD <0.025), and light grey defining all regions of the study area.

Significantly more suitable habitat was predicted by the resource and competitor model in the southern refugium (Figure 4.5). With increasing temperatures, however, this region becomes less suitable for northern bettong resources, while in the northern and central regions their resources persist (data not shown). The northern refugium has significantly more suitable habitat predicted by the climate-only model, although all northern bettong models predict small amounts of suitable habitat there in future climate scenarios (Figure 4.5).

The model that included both resources and the competitor had the greatest overlap with the food resources of the northern bettong and appeared to be tracking resources, which are important variables in the models. This model predicted high suitability for the northern bettong in areas where both resources are predicted, and appears to buffer out areas that are predicted as highly suitable for the competitor species (particularly in the southern and central refugia) (Figure 4.3).

4.5 Discussion

My results show that for small changes in climate, models that were based only on climate variables made similar predictions of distribution change to models that also included biotic interactions. However, for climate changes involving 3° C or more of warming, model predictions were sensitive to model structure: climate-only models gave projected distributions that differed from models that included interactions with resources and a competing species. This suggests that single-species climate-only distribution models may usefully approximate more ecologically realistic models when projected over small or moderate increments of climate change, but to understand the impacts of larger changes it is necessary to model the effects of climate on interactions among species.

The climate-only model for the northern bettong predicted a greater extent of suitable habitat, suggesting broad environmental tolerances that were not relevant given the restricted distribution of essential food resources. It has been noted before that models that do not account for biotic interactions can overestimate the potential habitat for species (Guisan *et al.* 2006b; Preston *et al.* 2008). The southern part of the central refugium, where potential habitat is probably overestimated by the climate-only model, coincides with low suitability for the main food resource (truffles) but high suitability for the competitor species, the rufous bettong, and seasonal resource (cockatoo grass). Cockatoo grass is also eaten by the rufous bettong (McIlwee & Johnson 1998).

The climate + resources + competitor model incorporated more ecological information than the other models, and should therefore have provided the most realistic predictions of distributions. This model projected more suitable habitat for the northern bettong under a warming climate than was predicted by the climate-only model, due to increased distributional overlap of crucial food resources. This model allowed me to represent the effects on northern bettong distribution of tracking of resources, accounting for idiosyncratic responses of different resources to a changing climate. Species tracking of suitable climate and resources interactions is a more likely response to climate change than *in situ* adaptation to novel climates or shifts to new resources (Hughes 2003; Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006). This model's predictions were also sensitive to the competitor species, with similar distribution overlap as predicted under current conditions identifying areas where the two species have niche overlap. Although ecological understanding of the organisms being modelled is necessary for such techniques I believe such will be necessary to provide more robust models when extrapolating to new climate systems.

Previous studies have shown that including biotic interactions into SDM's improved predictions of species distributions (Araújo & Luoto 2007; Heikkinen *et al.* 2007; Schweiger *et al.* 2008) and are needed to confidently predict the impacts of climate change. Studies to date have integrated both facilitation and competition into models, but not essential food resources. Facilitative interactions were assessed by Schweiger *et al.* (2008), Preston *et al.* (2008) and Araújo and Luoto (2007) through the utilization of larval host plants for the modelled butterfly species, whereas Heikkinen *et al.* (2007) explored the interaction between cavity-creating woodpecker species and the owl species that depend on such cavities. These studies integrate biotic interactions that occur for only one part of the life cycle of the species being modelled, thus neglecting other interactions that may be integral throughout its lifetime. SDMs that included competitive interactions were developed by Davis *et al.* (1998a) and Leathwick and Austin (2001), for interactions between fruit-flies and parasitoid wasps, and competition between tree species respectively. As a negative interaction, competition reveals only where a species may fail, as competition prevents the full occupation of the fundamental niche (Martinez-Meyer 2005). It is important to incorporate both positive and negative interactions, as positive interactions may be just as important (Araújo & Guisan 2006) and help to reveal locations of high suitability. Inclusion of resource variables in this study dramatically affected model behaviour, and it has been suggested that such variables will improve the application of models on a broader scale (Guisan & Zimmermann 2000; Austin 2002; Austin 2007). Models that include both positive and negative biotic interactions will presumably make more accurate predictions of changes in distribution under climate change, and should be used where possible (Davis *et al.* 1998a; Preston *et al.* 2008).

Although the models for the interacting species are themselves climate-only models, my results suggest that if other levels of biotic interactions are incorporated into these models, then the divergences between these models would be presumably even larger than observed. Regardless, the food resources modelled in this study are more likely to be predominantly controlled by climate than either bettong species. In particular, truffles (as a taxa) are subject to strong climate and weather influences and thus are a good candidate for SDM modelling.

My results suggest that SDMs which do not include relevant biotic interactions may not give useful predictions under climate change (Araújo & Luoto 2007; Heikkinen *et al.* 2007; Schweiger *et al.* 2008; Fitzpatrick & Hargrove 2009). Use of the *I*-similarity statistic allowed me to determine if models were significantly different from each other in projected climate scenarios beyond the present climate that accounted for in the AUC scores. This allowed me to determine to what extent biotic interactions impact model predictions, and at what temperature model divergences occurred. The spatial maps of significant difference revealed where models differed, which was used in combination with ecological knowledge of the species to determine why such differences occur and which models are likely to be more realistic. Uncertainties in species range shifts and climate change predictions in general leave conservationists worried by the application of SDMs. For application in conservation settings, SDMs that lack information on ecological interaction may be unable to model responses to climate change (Fitzpatrick & Hargrove 2009). Inclusion of species interactions can improve predictions and can help bridge the gap between conservation goals and research outputs (Thuiller *et al.* 2008). By providing more realistic models based on an ecological understanding of a species needs and an inclusion of relevant interactions, SDMs will be able to aid proactive conservation efforts in the face of global climate change.

Chapter 5 : Nice weather for bettongs: improving species distribution modelling using temporal variation in weather and extreme weather events[1]

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[1] **Bateman BL**, VanDerWal J, Johnson CN (in press) Nice weather for bettongs: improving species distribution modelling using temporal variation in weather and extreme weather events. *Ecography*

5.1 Abstract

Current applications of species distribution models (SDM) are typically static, in that they are based on correlations between where a species has been observed (ignoring the date of the observation) and environmental features, such as long-term climate means, that are assumed to be constant for each site. Because of this SDMs do not account for temporal variation in the distribution of suitable habitat across the range of a species. Here, I demonstrate the temporal variability in the potential geographic distributions of an endangered marsupial, the northern bettong *Bettongia tropica* as a case study. Models of the species distribution using temporally matched observations of the species with weather data (including extreme weather events) at the time of species observations, were better able to define habitat suitability, identify range edges and uncover competitive interactions than models based on static long-term climate means. Droughts and variable temperature are implicated in low densities and local extinctions of northern bettong populations close to range edges. Further, I show how variable weather can influence the results of competition with the common rufous bettong (*Aepyprymnus rufescens*). Because traditional SDMs do not account for temporal variability of suitable habitat, static SDMs may underestimate the impacts of climate change particularly as the incidence of extreme weather events is likely to rise.

5.2 Introduction

Species distribution models (SDMs) are increasingly used to characterize the ecological niches of species and to project those niches onto geographical space in order to predict species occurrences now or in the future (Guisan & Thuiller 2005; Araújo & Guisan 2006; Hijmans & Graham 2006; Jimenez-Valverde *et al.* 2008; Thuiller *et al.* 2008; Elith & Leathwick 2009; Fitzpatrick & Hargrove 2009). Typically, SDMs are a static representation of suitable habitat for a species (Franklin 2010) and do not account for temporal variation in habitat suitability (but see Reside et al. 2010). SDMs are often based on simple correlations between species occurrences and environmental features (Elith *et al.* 2006), without reference to the date of occurrence, and environmental variables associated with a location are assumed to be constant.

This static approach may be valid for features such as substrate or topography which can reasonably be assumed constant, but problems arise when climate variables are entered into SDMs. Such variables are usually entered as long-term means (for example, 30 or 50 year averages of mean annual temperature and precipitation) that describe a climate regime (Elith *et al.* 2006), rather than as explicit measures that represent time-specific patterns of weather (but see Reside et al. 2010). This is a weakness, for two reasons. First, the long-term mean of a variable like temperature is an abstraction that tells us little about the temperatures that organisms actually experience through their lifetimes, or at stages of their lives that are crucial for fitness. Second, we know that occasional episodes of extremes of temperature, rainfall or other climate variables can have large impacts on the distribution and abundance of species (Parmesan *et al.* 2000; Brown *et al.* 2001; Korpimaki *et al.* 2004; Thibault & Brown 2008; Albright *et al.* 2010), but these extremes are not depicted by mean values (Zimmermann et al. 2009). In order to determine the main drivers of habitat suitability of a species, one may need to control for time scale so the importance of such extreme weather events in shaping a species distribution can be determined.

In addition, populations close to range boundaries are likely to be more sensitive to environmental change than those within the core (Anderson et al. 2009). Populations on the edge of the range are likely to be more vulnerable to extreme weather events, defined as episodes during which conditions move outside the range that an organism can endure (Gutschick & BassiriRad 2003). This is because they may be living close to the limits of their physiological tolerances (Parmesan *et al.* 2000; Thuiller *et al.* 2008; Brook *et al.* 2009). If a site becomes increasingly subject to episodes of unsuitable conditions for a species, such as when suitable climate conditions shift away from the present location within the trailing edge of a species range, traditional static SDMs will have low ability to represent this (Akçakaya *et al.* 2006; Anderson *et al.* 2009). In addition, competition from invading species is also likely to have a more pronounced negative impact within the trailing edge of a species range (Anderson et al. 2009) which could compound the problem of shifting suitable habitat in the short-term. As a result, traditional climate-based SDMs may have limited capacity to discriminate suitable from unsuitable sites now or in the future, such that species may be uncommon or absent in areas predicted to have high environmental suitability for them (Jentsch *et al.* 2007; Jentsch & Beierkuhnlein 2008). In other words, static SDMs represent a good depiction of where a species has occurred over an average of 30-50 years, but are of little use when determining the persistence of a species through time in all parts of that range.

For all of these reasons, I hypothesize that including more dynamic information in SDMs to account for temporal variation, such as that produced by weather and extreme weather events, will a) better define short term habitat suitability than models based on long-term climate values, b) provide more precise information on the location of range boundaries (range edge versus core), and c) potentially allow better prediction of the outcome of competition between species. Additionally, I seek to determine if extreme weather events are important drivers of temporal variation in suitable habitat, and if range edges are more responsive than the range core to such events.

5.3 Methods

5.3.1 Study species

I tested these ideas using two marsupial species, the endangered northern bettong (*Bettongia tropica*) and it potential competitor, the rufous bettong (*Aepyprymnus rufescens*).

The endangered species, the northern bettong, occurs only in a narrow band of habitat within the Australian Wet Tropics, where precipitation is high and the environment is suitable for its primary food source, ‘truffles’ (underground sporocarps of ectomychorrhizal fungi), while the generalist species, rufous bettong, occurs across a broad gradient of temperature and precipitation (Johnson & McIlwee 1997; Vernes 1999). Truffle availability is linked to short-term weather patterns (rainfall and temperature) that drive truffle fruiting events (see Chapter 2; Abell *et al.* 2006), and truffle availability in this region is highest in wetter habitat types (Vernes 1999). While both species feed on truffles and grasses, the persistence of the northern bettong may be linked to consistent availability of truffles (Johnson &

McIlwee 1997; McIlwee & Johnson 1998), because truffles are the major diet item for most of the year. These two species are known to occupy the same areas within the drier end of the northern bettongs range. However, they appear not to co-occur at the same sites at the same time (Winter 1997a), and there is one documented case of a shift from sole occupation of a site by the northern bettong to sole occupation by the rufous bettong. This happened between 2003 and 2006 at the southern edge of the northern bettong's range (on the Coane Range; Figure 5.1a, adapted from Chapter 4) (Appendix B) where the northern bettong occurs in much lower densities than in the core of its distribution (on the Lamb Range; Figure 5.1a) (Winter 1997a; Vernes & Pope 2006).

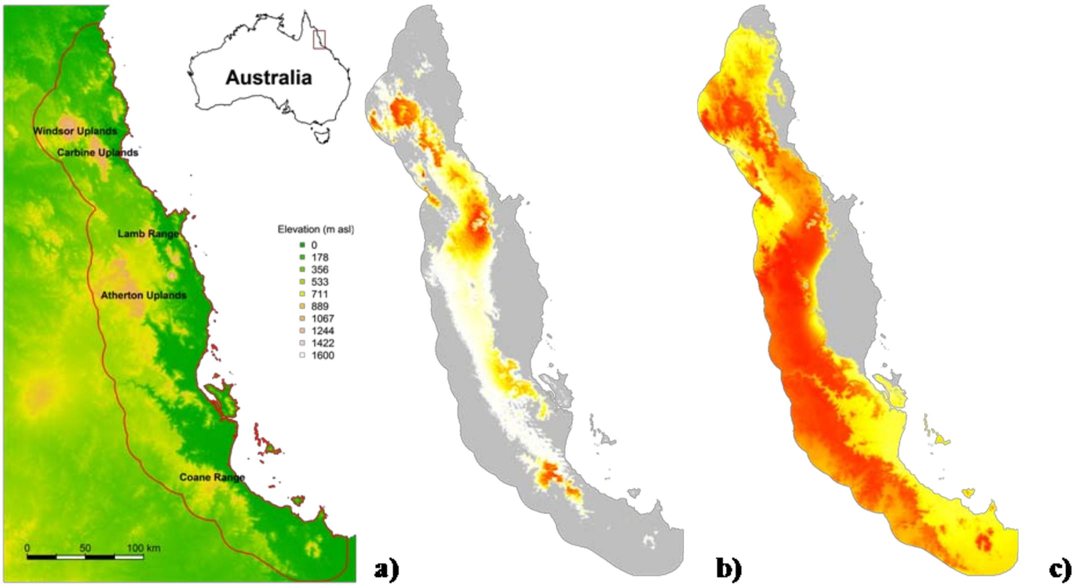

Figure 5.1. Location of a) study region within Australia with the names of regions of interest, and current predicted distribution based on long-term climate data of b) the northern bettong and c) the rufous bettong for the Wet Tropics, Australia (from Chapter 4). Orange is high suitability, yellow medium and white low with grey representing the background shape of the Wet Tropics and is not suitable habitat. Areas of high suitability (orange) are predicted to have high abundances of species while areas of white are predicted to have low abundances (VanDerWal *et al.* 2009b). This figure is adapted from Chapter 4.

Earlier surveys in this area, in the late 1980's and early 1990's, failed to detect the northern bettong but recorded rufous bettongs inhabiting the area (Laurance 1997;

Winter 1997a). Although occasional fluctuations between northern and rufous bettongs are noted within the core population, these occur only at the western, drier edge of the northern bettong's range in that area (Winter 1997a; Vernes & Pope 2006). It is unknown what factors cause such population contractions and expansions of the two species.

5.3.2 Analysis

First, I tested if weather could provide a more accurate discrimination of suitable habitat than long-term climate means (adapted from Chapter 4). Climate-only distribution models were developed for both the northern bettong and rufous bettong using Maxent (Maxent ver. 3.3.1) (Phillips et al. 2006) (Figure 5.1; adapted from Chapter 4). Data used were occurrence records for the northern bettong (881 occurrence records, 326 unique location records) and rufous bettong (1343 occurrence records, 179 unique location records). All records were collected from the state of Queensland, Australia. Maxent was parameterized with default settings with the exception of the removal of threshold and hinge features. Background points were selected at random from regions represented by a 100 km species-specific buffer around the occurrence points, as in VanDerWal et al. (2009a). The AUC (Area Under Curve; or the area under the receiver operating characteristic (ROC) curve) was used for model evaluation, with values above 0.5 are better than random predictions, and those above 0.7 considered useful (Elith *et al.* 2006) and those above 0.9 highly accurate (Guisan *et al.* 2007).

Climate variables, based on long-term climate means (1961-1990), were derived from ANUCLIM 5.1 software (McMahon et al. 1995) using monthly averages and an 80m DEM re-sampled from ~250m (GEODATA 9 Second DEM

Version 2; Geoscience Australia, http://www.ga.gov.au/). Variables were: mean annual temperature, temperature seasonality, maximum temperature of warmest period, minimum temperature of coldest period, annual precipitation, precipitation of wettest quarter, precipitation of driest quarter and precipitation seasonality.

Second, to examine the potential for weather to define range boundaries and the outcome of competition I defined extreme weather events in terms of the biological sensitivity of truffles within this ecosystem. Weather data were generated from the Australian Water Availability Project (AWAP) for the time period 1980-2008 (http://www.bom.gov.au/jsp/awap/). Data consisted of daily precipitation and temperature values at ~5 km (0.05 degree) resolution, and summarized into 18 variables. Variables were selected to represent two kinds of extreme events in particular: droughts and heat waves. The thresholds used to define these events as ‘extreme’ were based on the biological sensitivity of relevant organisms (Gutschick & BassiriRad 2003). Drought events were defined as 14-day periods with less than 50 mm rainfall. The 14-day criterion was used as it has been identified as the time period over which truffle production responds to weather, in particular rainfall (Claridge *et al.* 2000b), and a rainfall threshold of 50 mm was chosen based on expert opinion that rainfall events of 50 mm or more are needed to trigger truffle fruiting in this region. Consecutive days with temperatures above 28° C are considered heat waves based on the upper limits of both truffle tolerances in the Wet Tropics (Chapter 2) and temperature tolerances of bettongs (Seebeck & Rose 1988; Rose *et al.* 1990).

Summary weather variables included: maximum temperature (mean and standard deviation SD), minimum temperature (mean and SD), temperature range (mean and SD), and rainfall (mean and SD). The extreme events variables were: the number of heat waves (consecutive days above 28° C within the summarized period), the length of heat waves (mean and SD), total degree days above 28° C (measure of temperatures above 28° C), number of drought periods (consecutive 14 day periods with total rainfall below 50 mm), length of drought periods (mean and SD), and rainfall during drought periods (minimum, total, and daily). Variables were summarized for a period of five-years prior to the date of a presence/absence record to include any time lag that may occur between the event and its impact on a population.

Models were built for three cases to assess the impact of extreme weather events on short-term habitat suitability and competitive outcomes. These included the 1) northern bettong records from the core (Lamb Range) versus the southern range edge of its range (Coane Range), 2) northern bettong versus the rufous bettong, where both models were built using presence records as the binomial response and 3) northern bettong presence and absence at its southern range edge (Coane Range). The Coane Range was selected out of the sites from the range edges due to sufficient data availability (12 unique time/location presence records; from years 1997-1998, 2001, and 2003) and the accessibility of absence data (48 unique time/location absence records; from years 2006-2008) from comprehensive trapping surveys (Appendix B). Presence or absence records used in each model were associated with both location and date which was then used to identify the value for each weather variable prior to the presence/absence event (for each summarized time period). Species occurrence data, including spatial and temporal data, for the northern bettong (414 unique time/location presence records; from years 1981, 1983-1985, 1987-2005, and 2008) and rufous bettong (930 unique time/location presence records; from years 1980-2008) were obtained from field surveys and institutional databases. Records were obtained only for the period between 1980 to 2008, as this is when northern bettong records were consistently and reliably collected (Winter 1997a).

Distribution models using weather data were built using generalized linear modelling (GLM). A Kullback-Leibler (K-L) information-theoretic method was used to construct all possible model configurations (best subsets) (Burnham & Anderson 2002). A binomial distribution was used to represent the occurrence records for model comparisons. The Bayesian information criterion (BIC) was used in model selection to account for sample sizes and penalize over-parameterisation (Burnham & Anderson 2002). Models were filtered using the Variance Inflation Factor (VIF) set at a value of five, a more stringent value than the recommended value of 10, to remove models with highly correlated predictor variables (Zuur et al. 2010). After model filtering, models within seven BIC units (Δ_i) of the BIC_{min}, the model with the lowest BIC_c value, were retained (Burnham & Anderson 2002). A measure of accuracy was calculated to determine how well the models predicted the binomial response of the species records. This accuracy measure was the proportion of occurrence records predicted accurately by each model.

Model averaging was conducted to determine the relative importance of each variable contributing to model building. A measure of variable importance, or variable weight, was calculated by summing all of the weight scores (w_i) for any model of which the variable was a component. The top variables with the top three variable weight scores were plotted in a 3-dimensional scatter plot. Top variables were then projected onto geographical space from 1980 to 2008 using daily weather information, summarized to monthly layers, for the region. Predictions were clipped to fit within predictions of suitable habitat, as given by a climate-based distribution model created in Maxent to exclude areas below 400 m altitude. This was done as northern bettongs are known to only occur above this altitude (Winter & Johnson 1995) and to compensate for coarse resolution of the weather data. All analyses were conducted in R (v2.10.0, http://www.r-project.org).

5.4 Results

5.4.1 Long-term climate predictions

Habitats of high suitability for the northern bettong under current climate conditions are predicted, based on climate-only models, in several areas of the Wet Tropics bioregion (Figure 5.1b). Additionally, the climate-only SDMs indicated high suitability and niche overlap between northern and rufous bettongs (Figure 5.1b and 5.1c). Top variables for the northern bettong climate-only model (AUC = 0.989) were annual mean temperature (25.9%), maximum temperature of the warmest period (21.2%), and temperature seasonality (15.6%). Top variables for the rufous bettong climate-only model (AUC= 0.789) were temperature seasonality (22.3%), precipitation of the driest quarter (19.8%), and maximum temperature of the warmest period (19.5%).

5.4.2 Using weather to build distribution models

All models built using weather performed well (Table 5.1) indicating models were useful and highly accurate. AUC scores closely matched accuracy scores and are not reported here. Top variables from model averaging are presented here, while the entire set of candidate models are presented in Appendix C. For the northern bettong core versus edge, the top variables were temperature variability ($w_i = 0.83$), daily rainfall of drought periods (w_i = 0.11), and rainfall variability (w_i = 0.09). Top variables for the comparison of northern bettong to rufous bettongs were temperature variability (w_i = 0.1), rainfall variability (w_i = 0.99), and average maximum temperature (w_i = 0.98), although total degree-days above 28° C (w_i = 0.95) and maximum temperature variability (w_i = 0.94) were also important. For northern bettong presence and absence, the top variables were the number of drought periods (w_i = 0.34), average rainfall of drought periods (w_i = 0.31), and average rainfall (w_i = 0.29).

Table 5.1. Generalized linear modelling accuracy measures for the three model cases. NB indicates northern bettong. Average accuracy is the average of all accuracy values across the top models selected (Appendix C). Standard deviation (S.D) of model accuracy is presented.

Model Scenario	Average Accuracy	S.D.
NB Core vs. NB Southern Range edge	1.0	0.00
Northern Bettong vs. Rufous Bettong	0.97	0.001
NB Presence vs. NB Absence	0.996	0.02

There were distinct differences in the weather of the core of the northern bettong range (Lamb Range; high density northern bettong populations) and the southern range edge (Coane Range) (Figure 5.2). Top variables from generalized linear model outputs gave complete discrimination between populations (accuracy = 1.0). In the south, minimum temperature was more variable and drought periods had lower daily rainfall than in the core of the range; that is, weather was more variable and droughts more harsh. The core population on the Lamb Range had higher daily rainfall, and rainfall was also more consistent during low-rainfall periods. Minimum temperatures were less variable. This evidently represents ‘good northern bettong weather’ given the higher abundance achieved on the Lamb Range.

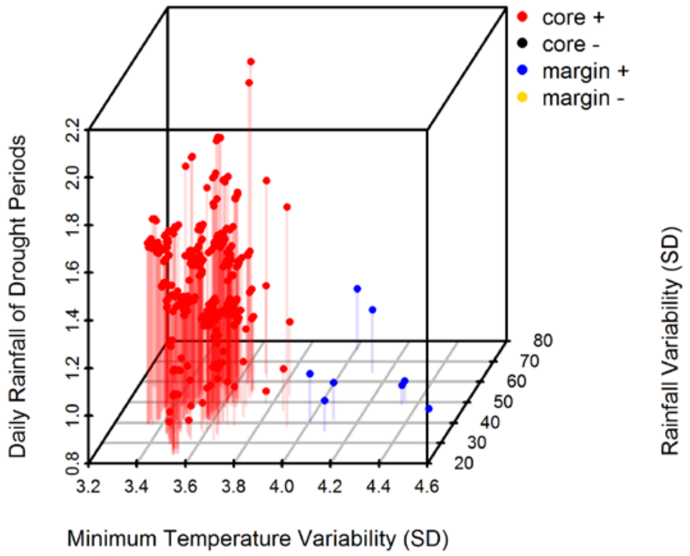

Figure 5.2. Top variables based on generalised linear model outputs for northern bettong Lamb Range versus northern bettong Coane Range records. Records are indicated as those accurately predicted (Lamb Range in red, Coane Range in blue) and those, if any, inaccurately predicted (Lamb Range in black, Coane Range in yellow).

Weather conditions did not discriminate conditions associated with occurrences of northern and rufous bettongs quite so clearly. Although the species occupy separate regions of the environmental space defined by weather variables, there was a narrow overlap zone between them (Figure 5.3). The rufous bettong occurred where minimum temperature was more variable and rainfall less variable, with higher maximum temperatures (accuracy = 0.97). The top model (Appendix C) for northern bettong versus rufous bettong included minimum temperature variability, rainfall variability, average length of heat waves, average length of drought, and daily rainfall of drought indicating that, although extreme weather events are not captured in the top variables, the most parsimonious model did contain them.

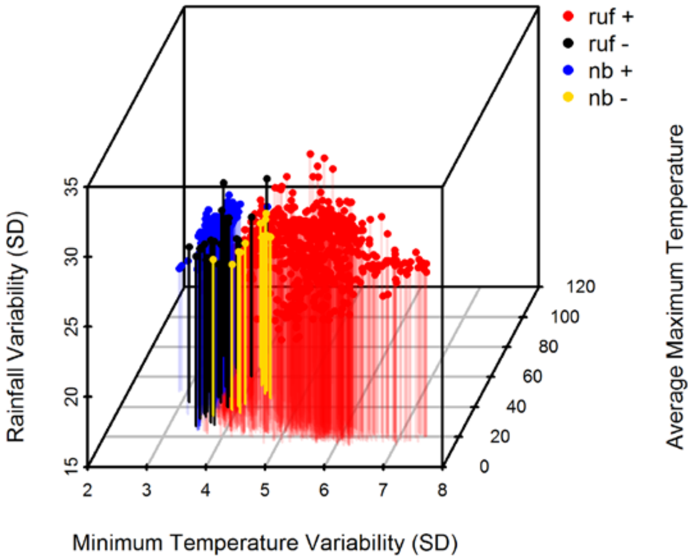

Figure 5.3. Top variables based on generalised linear model outputs for northern bettong versus rufous bettong records. Records are indicated as those accurately predicted (rufous bettong in red, northern bettong in blue) and those, if any, inaccurately predicted (rufous bettong in black, northern bettong in yellow).

Comparing presence and absence records of the northern bettong at the southern range edge (on the Coane Range) revealed a clear separation in weather (Figure 5.4; accuracy = 1.0). Absence records were associated with longer drought periods (less ‘dry clusters’ of longer duration) indicating prolonged periods with consecutive 14-day periods of less than 50 mm rainfall. Absences also had higher total rainfall within drought periods, but this is a product of having longer consecutive dry periods as the measure was of rainfall across the entire drought. Presence records were associated with shorter and more variable drought periods, often with intense drought periods (low rainfall within drought periods) but which were not prolonged. Average rainfall over each five-year period was higher when northern bettongs were present than when they were absent.

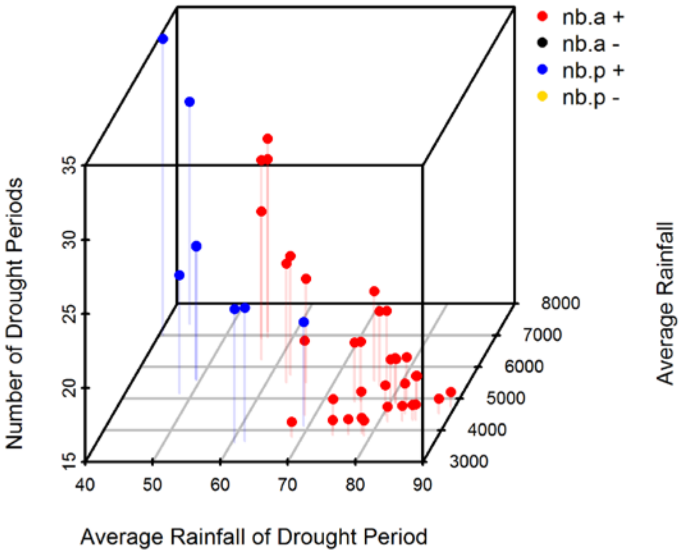

Figure 5.4. Top variables based on generalised linear model outputs for northern bettong presence and absence on the Coane Range. Records are indicated as those accurately predicted (absence red, presence in blue) and those, if any, inaccurately predicted (absence in black, presence in yellow).

5.4.3 Weather models in geographical space through time

Reconstruction of weather patterns through space and time suggest that the northern bettong and rufous bettong are in a dynamic relationship with each other (Appendix D; Animated Figure 5.1). Regions identified as highly suitable from climate only models (see Figure 5.1) at the range edge of the northern bettong distribution showed variation through time in weather suitable for that species. Fluctuations in weather in this environmental space lead to alternations between conditions suitable for northern and rufous bettongs. Suitable weather conditions for each species oscillate through time over the whole Wet Tropics region, with temporal expansions and contractions of suitable weather for each species observed. These expansions and contractions occur in proximate relation to each other, with a narrow overlap zone where competitive interactions are likely to take place. In geographic space, this overlap zone is more pronounced within the southern edge, where complete shifts between suitable weather for each species are observed. Within the core of this species range, the overlap zone between northern and rufous bettongs is minimal, and occurring at the western, drier portion of northern bettong range.

Suitability of weather for the northern bettong, as indicated by weather conditions in the core of the distribution, also fluctuated through time (Appendix D; Animated Figure 5.2). This oscillation of suitable weather varied across the distribution predicted for the species from the climate-only model. Sometimes the core area and range edges have similar weather conditions with connectivity established throughout the Wet Tropics. At other times the distribution of suitable weather contracted, especially due to increased drought and amplified temperature variability at range edges. This fragmented the potential distribution of the species.

Data from the southern range edge for particular time slices show how changes in weather have affected populations at the edges of the species range. Trapping surveys revealed that in October 1997 northern bettongs were present within the southern range edge, but by May 2006 they could not be detected despite considerable trapping effort, and had been replaced by the rufous bettong (Appendix B); evidently the local distribution of the northern bettong had contracted and the population decreased in abundance (Figure 5.5). Northern bettong presences in the southern range edge coincide with weather conditions matching that of the core population (Lamb range). This was also supported by geographical depiction of the interaction between northern and rufous bettongs and weather (Figure 5.6). In October 1997 much of the Wet Tropics is indicated as experiencing weather consistent the overlap zone between these two species. By May 2006, however, weather conditions are more suitable for rufous bettongs over much of the Wet Tropics including the southern range edge.

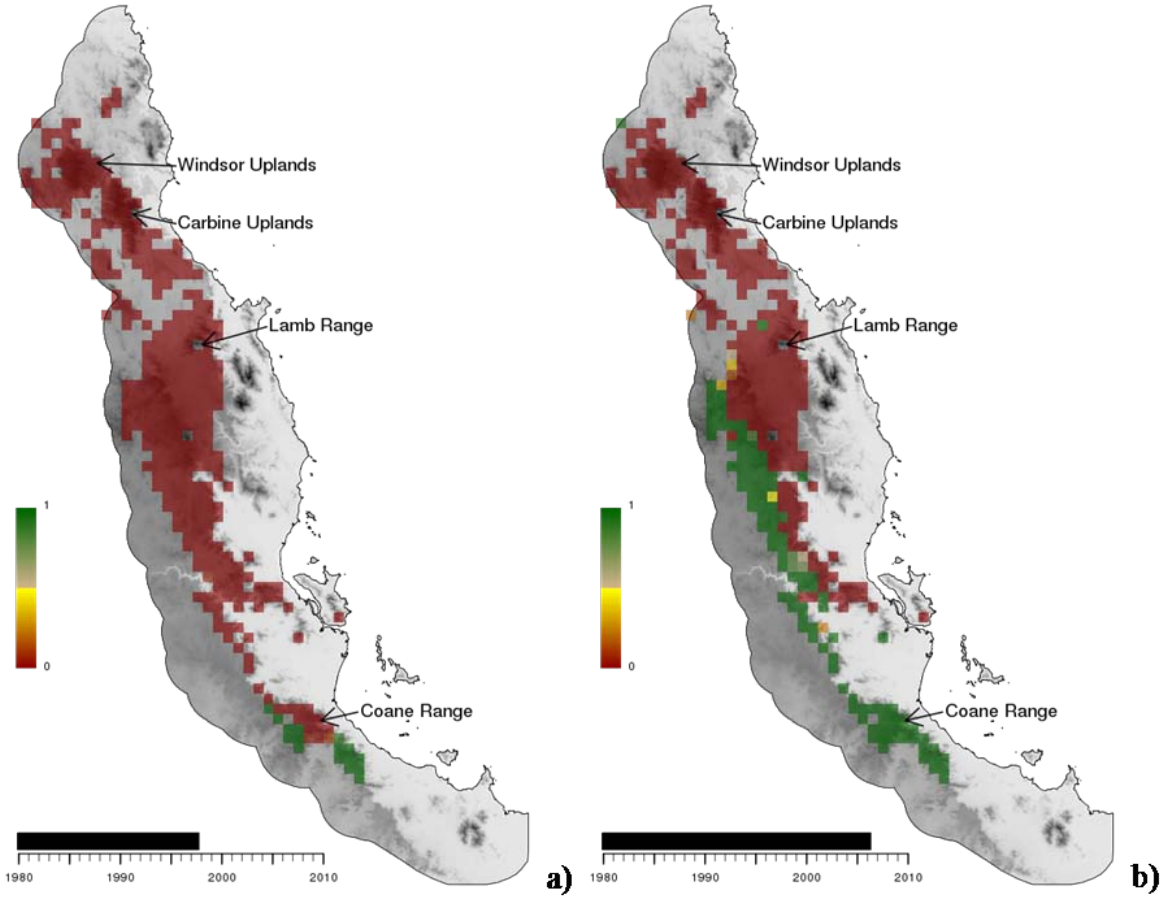

Figure 5.5. Generalised linear modelling top variable weather models in geographical space in different time slices for the core (Lamb Range) versus southern margin (Coane Range); the core represents ‘stable bettong weather’ represented by red here and the southern margin ‘weather’ is represented by green: a) October 1997 when bettongs were present in the southern margin; b) May 2006 when bettongs were absent in the southern margin. See full animation in Appendix D.

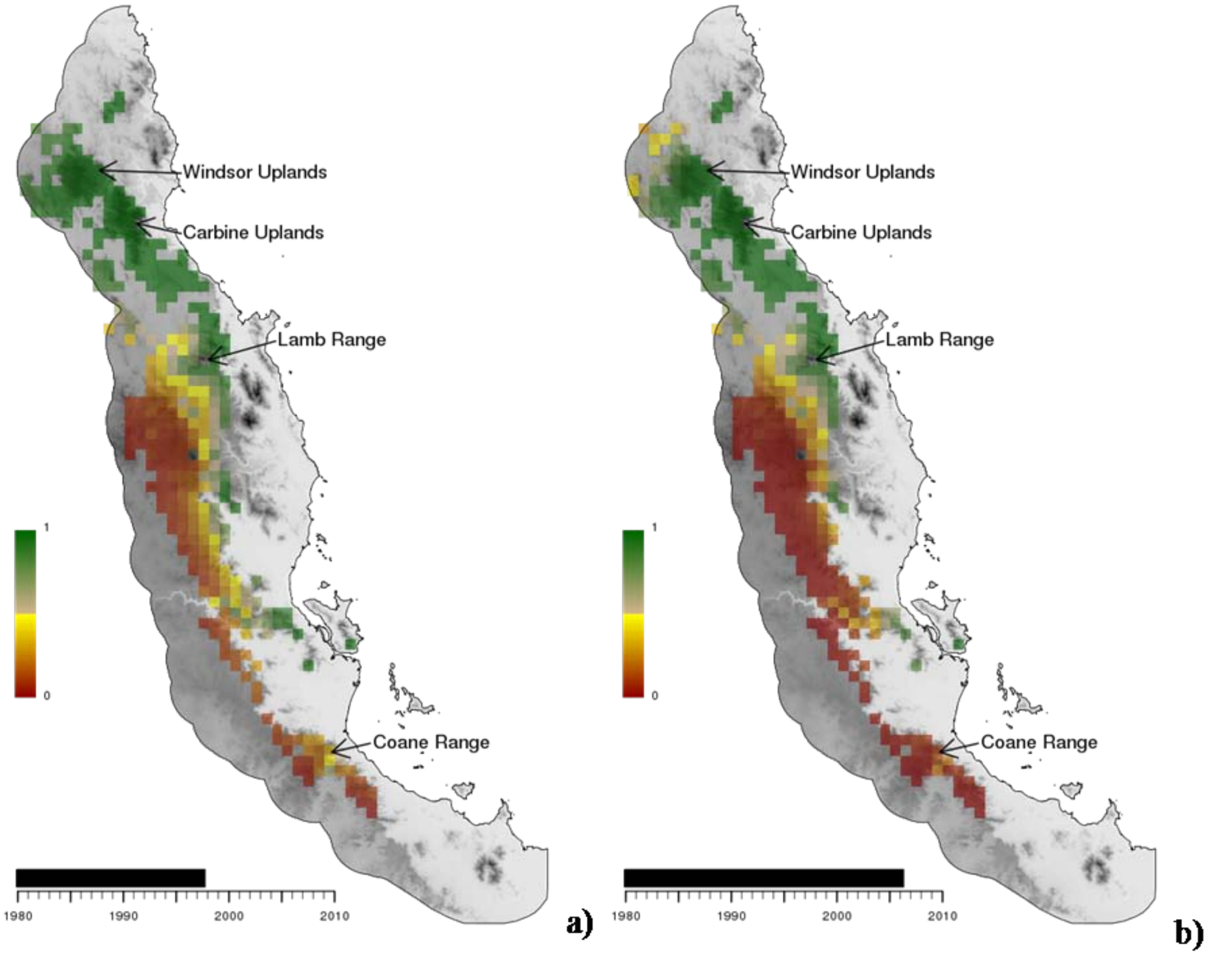

Figure 5.6. Generalised linear modelling top variable weather models in geographical space in different time slices for northern bettongs versus rufous bettongs; northern bettong 'weather' is represented by green, rufous bettong 'weather' represented by red, and the niche overlap zone between these species is identified by yellow-tan: a) October 1997 when northern bettongs were present in the southern margin; b) May 2006 when northern bettongs were absent in the southern margin. See full animation in Appendix D.

5.5 Discussion

Despite knowledge to the contrary, many exercises examining the distribution and abundance of species (including correlative SDMs as used here) make an assumption that species are in equilibrium with their environments (Pearson & Dawson 2003); I highlight the inappropriateness of this assumption here. I show a system of temporally variable weather, where short-term weather conditions appear to be driving spatial patterns of distribution and abundance for these two bettongs. Here, I show the approximate set of climate conditions, or in this case weather conditions, in which a species can occur (the Grinnellian niche; e.g., Soberón 2007) do change in geographical space and fluctuate across the landscape on the short-term. Particularly within the range edge for the northern bettong, these changes have induced niche tracking for these bettong species; that is when species, limited by physiological boundaries, follow their favourable environmental conditions (niche) through geographical space or face local extinction within their present range (Tingley et al. 2009). Although the climate-based distribution model of the northern bettong reasonably reproduced the 30-year range of the species, it did not account for the dynamics of suitable habitat within this range over time. Short-term weather events determined that range boundaries (core versus edge) experienced greater fluctuations in short-term weather suitability and provided insight into why some areas predicted from climate-based models to have high suitability for the northern bettong do not, in fact, support high density, stable populations.

Both weather and extreme weather events identified range boundaries as areas with high variability in weather and fluctuations in suitable weather conditions for the endangered northern bettong. In particular, extreme weather events which could be shown to better determine the range edge for the northern bettong, as well as its absence within this edge habitat. The importance of extreme weather events and their influence on temporal variation in suitable habitat of a species can be overlooked when climate models based on long-term means are used to characterize the distribution of a species, as the impacts of extremes are smoothed out and muted (Zimmermann et al. 2009). Organisms at their range limits are often most affected by extreme events like droughts, as they are likely to be already close to the limits of their physiological tolerances (Parmesan *et al.* 2000; Archaux & Wolters 2006). Range contractions due to extreme heat or drought have been noted in the trailing edge of species ranges, and the effects of competition can be amplified during such times (Gutschick & BassiriRad 2003; Anderson *et al.* 2009; Zimmermann *et al.* 2009). This is because the impacts of biotic interactions are likely to be greatest close to the range limits of a species, where expansions and contractions of distribution of interacting species occur in response to changes in weather (Davis 1986; Anderson *et al.* 2009). The core region of the northern bettong consistently had less severe droughts and less variable temperatures, and weather conditions tended to be unsuitable for the rufous bettong. The stability of favourable weather and the suitability of the long-term climate of this region (Williams & Middleton 2008), coupled with less pressure from competitive interactions, can explain why northern bettongs reach their highest abundance there.

Despite arguments that competitive interactions are implicit in SDM outputs (Davis *et al.* 1998b; Guisan *et al.* 2002; Kearney & Porter 2004; Sinclair *et al.* 2010) as records are taken from a species realized niche, I show here that unless temporal variation is included this is not the case. In my study, climate based SDM failed to recognize competitive interactions between two species, because the use of spatial data with no temporal component was not sufficient to identify that these species do not co-exist in time. Here, competitive outcomes between species evidently tracked short-term weather; therefore weather data are needed to make predictions on where and when species are likely to occur. Niche tracking was observed between the competing bettong species, with temporal changes in suitable weather conditions fluctuating across the landscape. Shifts in a species range are likely to occur where changes in the climate space have occurred (i.e. increasing weather variability and extreme weather events) and/or where pressure from competition varies through time (Nogués-Bravo 2009). Although none of the top variables in the comparison between northern and rufous bettong weather contained an extreme weather event, the top models and other important variables did include heat waves, droughts, and degree days above 28°C indicating that both weather and extreme weather events are important drivers of temporal variation in both species. Time lags of five years were used in this study, so that the necessary length of time was needed for the effect of an event to be noticeable in fluctuations between these populations.

Periods of severe drought and variable temperatures presumably affected northern bettong populations through the decrease of truffle productivity. Truffles are particularly sensitive to environmental changes and abiotic stress (Bougher & Lebel 2001; Brown *et al.* 2001) and are not consistent in the environment at all times (see Chapter 2; Abell *et al.* 2006). Truffle reproduction is strongly linked to both rainfall and temperature, and truffle availability is low during drought; that is truffles are a stochastic food resource that would not be well represented in SDMs by long-term climate means. More stable weather, with less severe droughts of shorter duration, would ensure continuous truffle availability as truffles in this region have a 1-2 month lag in response to rainfall events (see Chapter 2; Abell-Davis 2008). Weather conditions at the core of northern bettong habitat are sufficiently stable to provide a consistent supply of truffles as a food resource. In marginal habitats, truffle productivity is presumably more variable and northern bettongs would need to contract to wetter areas, tracking suitable conditions where truffles may persist (Johnson & McIlwee 1997). Species abundances are often dictated by the indirect impact of weather through the regulation on food resource availability (Lewellen & Vessey 1998; White 2008 and references therin). Specialization may confer a competitive edge where resources are abundant and particularly within the core of suitable climate (Rosenzweig & Lomolino 1997; Ritchie *et al.* 2009). If the abundance of this resource diminishes or its suitable habitat contracts, than this competitive edge may be lost. Extreme population contractions, range shifts or potential local extinctions could occur if unsuitable conditions persist (Parmesan et al. 2000) and are coupled with competition and resource limitations (Brown et al. 2001).

This study shows that models using long-term climate means may underestimate the impacts of climate change on species distribution due to over-prediction of high suitability in marginal areas that often have unfavourable weather (Reside et al. 2010). The synergistic effect of extreme weather and habitat fragmentation adds to this problem (Laurance & Williamson 2001; Piessens *et al.* 2009). With extreme weather events predicted to increase (Jentsch et al. 2007), information on how such events affect species now should help us prepare for changes in climate in the future. Failure to address temporal dynamics of weather (including extreme events) in SDMs may lead to underestimation of the impacts of climate change, and result in misinformed conservation planning. In order to make meaningful predictions in the face of climate change and facilitate pre-emptive conservation planning, extreme weather events will need to be assessed in research on species distribution modelling to identify the areas of highest conservation priority.

Chapter 6 : General discussion and synthesis[1]

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[1] **Bateman BL**, Johnson CN, Baker A, Parsons M (in prep) Proactive conservation in the face of climate change; climate refugia for the northern bettong. To be submitted to *Conservation Biology*

6.1 Species distribution models and climate change

For proactive planning in response to future climate change, the impacts of a changing climate on a species need to be assessed. SDMs offer us a useful tool for approximating climate impacts on species distributions and potential shifts from current habitats, but should be used cautiously when limited to climate-only approaches (Pearson & Dawson 2003; Araújo *et al.* 2005). In order for forecasts developed from SDMs to be useful in proactive conservation planning and management, uncertainties in model outputs need to be addressed (Thuiller *et al.* 2008). This study has highlighted how the inclusion of biotic interactions and extreme events are imperative to successful predictions of a species distribution. As there are many factors contributing to climate change vulnerability, addressing issues such as biotic interactions and extreme events bring us one step closer to developing more realistic model predictions (Williams *et al.* 2008).

6.2 Thesis summary and implications

The goal of this research was to contribute to the theory of species distribution models by addressing current limitations in their application. Additionally, the northern bettong was identified as an ideal candidate for such studies, and, as an endangered species, would benefit from such exercises. To achieve these goals, I addressed specific aims and objectives, which are summarised below.

6.2.1 Aim 1. To enhance the theory of species distribution modelling

The results from this study suggest that current applications of SDMs are limited as they do not take into account biotic interactions or extreme weather events.

Objective 1. Examine the distribution and limits of northern bettong key resources for inclusion into SDMs (Chapters 2-3).

Chapters 2 and 3 were focused on collecting data and providing key results needed for subsequent chapters. In Chapter 2, I assessed site and regional scale impacts on the limits and distribution of truffles as a resource for northern bettongs in the Australian Wet Tropics in order to; 1) gain knowledge about the limiting factors of this taxon and 2) to develop truffle distribution models for use as biotic interaction variables in SDM comparisons. Habitat type and soil nutrients were the best indicators of truffle availability at the site scale, although were only able to explain a small percentage of the variation in the data. The availability of truffles appears to be directly influenced by weather (e.g. precipitation events one month prior) and climate at both the site and regional scale, making them ideal SDM candidates. In the southern part of the Wet Tropics the taxa may be persisting at its upper thermal and lower precipitation limits as well is in high temperature seasonality. In addition, truffle availability here was lower and more variable than found in areas with high density northern bettong populations. These sub-optimal climate conditions and reduced truffle availability are likely linked to less reliable truffle availability in the long-term, and could indicate why northern bettong populations on the Coane Range occur in low densities. Information on the temperature tolerances of truffles was also identified for use in defining extreme weather events (Chapter 5).

In Chapter 3, cockatoo grass (*Alloteropsis semialata*) was studied at the site and regional scale. Models were built for cockatoo grass suggesting that this species has a wide tolerance for maximum temperature of the warmest period. The study at the site scale identified that cockatoo grass was negatively affected by the presence of dominant grass species and by litter cover and soil moisture. Cockatoo grass had high survival to a late dry season burn, and increased density as a result. Although the impacts of fire are not modelled on the regional scale or into future climate scenarios, the implications of this result are discussed under Objective 4. Cockatoo grass distribution was also influenced by climate making it a sufficient candidate for inclusion into biotic interaction models, although more research on the impacts of fire and climate change on its distribution is warranted.

Objective 2. Assess the role of biotic interactions in SDMs (Chapter 4).

In Chapter 4, I investigated the use of biotic interactions in SDMs on predictions of distribution shifts under climate change. Distribution models accounting for interactions are more ecologically realistic and are more useful in climate change scenarios. This is especially important for larger climatic changes, where climate-only models diverge from those including biotic interactions. I conclude that ecologically realistic models, that incorporate interactions with other species, are needed for long-term prediction of changes in distribution of species of concern under climate change. This has implications for the current applications of SDMs predicting climate change impacts, and that present model outputs that consistently ignore interaction may be erroneous.

Objective 3. Investigate the impact of extreme weather events on current distributions (Chapter 5).

In this chapter, I test for temporal variation in suitable habitat, and whether extreme weather events were drivers of this. In addition, I assessed whether accounting for temporal variation better defined range boundaries and competitive outcomes of species interactions than traditional climate-based models. I demonstrated that extreme weather events are integral in defining the distribution of the northern bettong; severe drought and temperature variability have been identified here as limiting the northern bettongs distribution and altering competitive outcomes particularly at the edge of this specie range. Population expansions and contractions (niche tracking) are linked to oscillating weather conditions. Populations within the range edges of this species likely fail to reach high densities as a result of frequent changes in the suitability of weather and increased pressure from their competitor. Current applications of SDMs fail to identify dynamic processes such as temporal shifts in suitable weather and competitive outcomes between species, as SDMs utilize data limited to spatial scale.

6.2.2 Aim 2. To improve our ecological understanding and conservation strategies of the northern bettong

The results of this study will be synthesized here to examine the implications they have in relation to the northern bettong and conservation efforts. Proactive management strategies for climate change impacts are suggested.

Objective 4. Develop proactive management strategies to mitigate the impact of climate change on the northern bettong (Chapter 6).

Recovery objectives for the northern bettong are outlined by the Environmental Protection Agency (2007a) in the National recovery plan for the northern bettong *Bettongia tropica.* Several key objectives were addressed by this study (Figure 6.1)

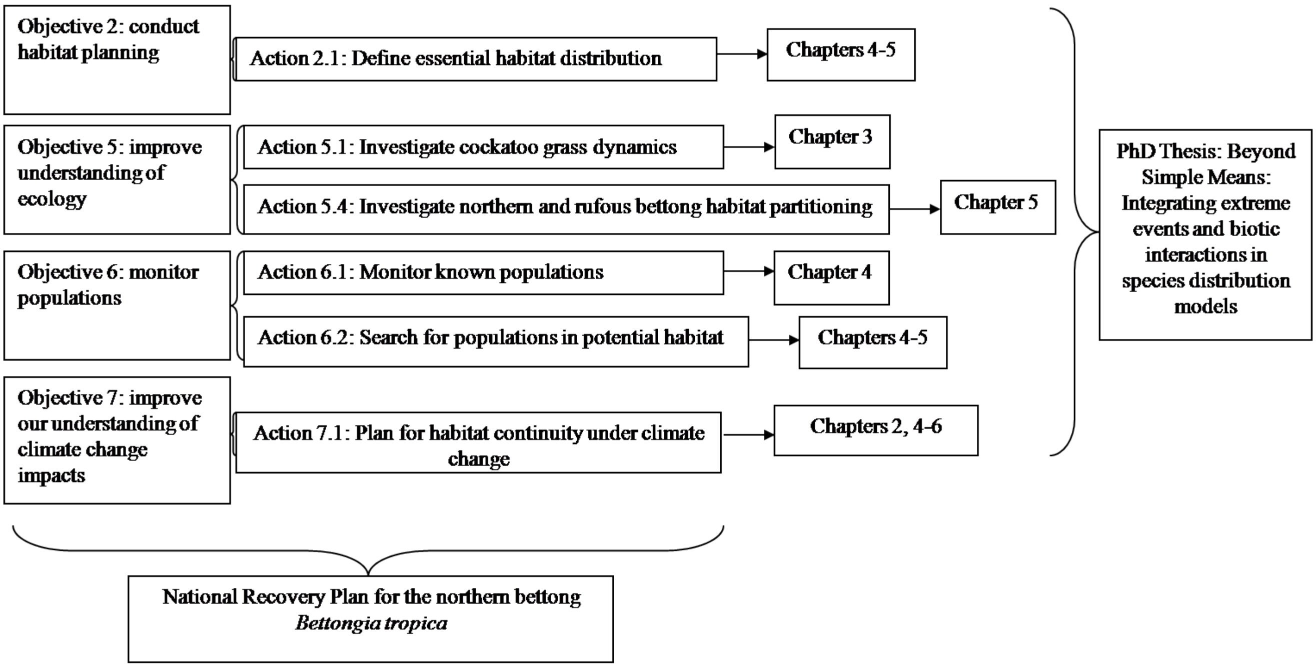

Figure 6.1. Key objectives and actions for the recovery of the northern bettong that are addressed in this thesis.

In order to create a sound management plan for any species, it is important to define what the essential habitat and distribution of that species is. Habitat models have been previously developed for the northern bettong (Laurance 1997; Winter 1997a; Hilbert *et al.* 2001), but were limited and refinement was needed. Newer and more robust modelling techniques and climate change data are available today, providing more accurate model outputs. Hilbert *et al.* (2001) suggested that their model was limited as it mapped vegetation type as a surrogate for bettong occurrence records, but in hindsight recognized their choice of vegetation was not the essential habitat for the species. In addition they anticipated modelling food resources such as truffles and including competition measure would be a better approach. Integrating both resources and competition, as well as adding a temporal component into the models presented here (Chapters 5- 6) provided for more realistic predictions for this species.

Model outputs for the current predicted distribution can be used to search for northern bettong populations within suitable habitat (Figure 6.2, from Chapter 4). As shown by the recent discovery of the Coane Range population (D. Storch personal communication; McIlwee & Freeman 1998), it is possible that low density populations can still be uncovered. Search effort can be directed utilising fine-scale weather data (Chapter 5) to determine which areas will have suitable weather conditions for the northern bettong in exclusion of the rufous bettong. This information can also be used to monitor known populations, as continued knowledge on population trends will be integral for successful management and mitigation of threats. This study suggests that recent declines of the northern bettong within its range margins may have been a result of severe and prolonged droughts and variable weather compounded by increased pressure of competition with the rufous bettong (Chapter 5). This is in agreement with previous work suggesting the possibility of active displacement of the northern bettong by the rufous bettong in some areas (Winter 1997a). Specialization by the northern bettong on truffles may confer a competitive edge when resources are abundant (Rosenzweig & Lomolino 1997; Ritchie *et al.* 2009), but this competitive edge is lost if this resource diminishes or its suitable habitat contracts/shifts. The more variable weather and climate conditions found within the southern range edge indicate truffles are already within sub-optimal conditions here, and the lower and more variable truffle availability found in this location suggest a system more vulnerable to environmental change and droughts (Chapter 2). Alternatively, the change from northern to rufous bettongs in this area may be caused by shifting suitable weather conditions in space for both species; that is northern bettongs track suitable habitat for truffles, contracting towards wetter habitat types during environmentally stressful times. The rufous bettong could then move into areas that are suitable for them as they become un-occupied by the northern bettong. Regardless of active displacement through competition or a change and replacement through niche tracking, it appears that habitat partitioning between these two species occurs on a temporal scale in accordance with weather conditions.

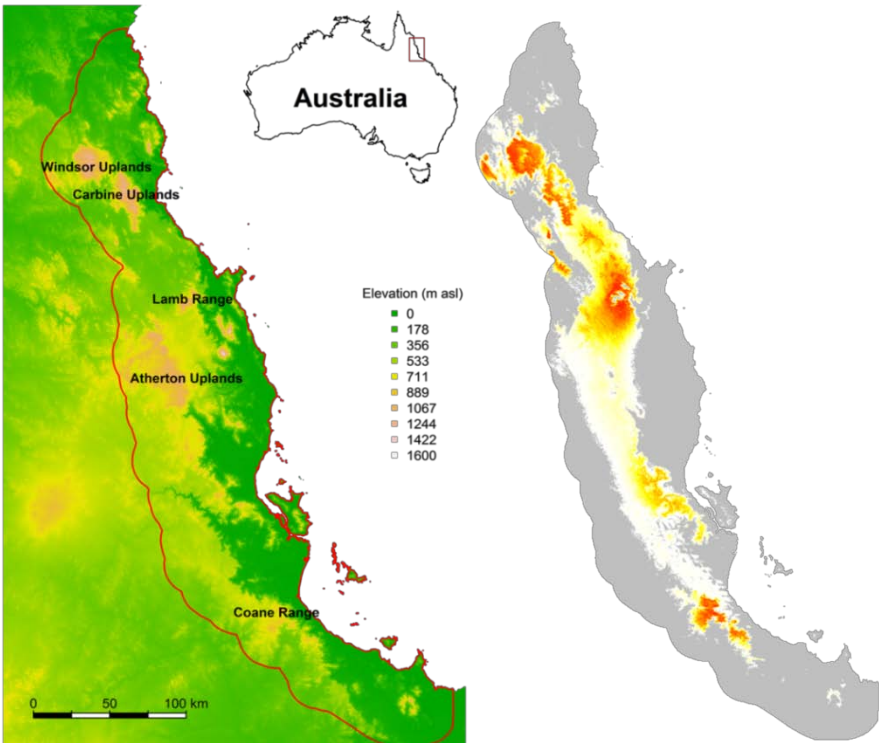

Figure 6.2. Current predicted distribution of the northern bettong in the Australian Wet Tropics (From Chapter 4).

In addition, an understanding of the influences that different land management regimes have on northern bettong populations is important. The role of fire on the key resource, truffles, has been investigated in this region, and outcomes suggest that the northern bettong is a fire-adapted species (Vernes 2000; Vernes *et al.* 2001; Vernes & Pope 2001; Vernes & Haydon 2001; Vernes *et al.* 2004). The impact of fire on cockatoo grass in northern bettong habitat was not assessed before this study (Chapter 3). The methodology I developed for the survey of cockatoo grass has since been replicated within the core distribution of the northern bettong on the Lamb Range, adding more detailed information on the cockatoo grass-fire interaction across the species range.

Based on this work and the previous studies on bettong-truffle-fire interactions, fire management strategies can be developed to ensure persistence of northern bettong food resources across the landscape. Declines in northern bettong populations have been noted in areas where fire regimes have become less frequent (low intensity fires) (Winter 1992; Laurance 1997; Vernes *et al.* 2001). The increase of *Allocasuarina torulosa* and other vegetation changes, as a result of infrequent fires, needs to be directly examined to determine if there is a causal relationship between this and bettong declines. The relationship between fire and climate change was not addressed here, although recent work suggests fire frequency will be dramatically altered and likely increase in north-eastern Australia (Krawchuk *et al.* 2009). The impacts of fire on both truffles and cockatoo grass in changing climates still needs to be addressed, as the synergistic impacts of altered climate and fire regimes may have significant effects. Populations within the range edges may be particularly vulnerable, as key resources are already within the physiological tolerances of climate (Chapter 2).

The results from this study (Chapters 4-5) suggest that the northern bettong may be vulnerable to climate change, particularly within populations at its range margins (range edge). SDMs have importance for conservation planning at regional level (Ferrier *et al.* 2002) and predicting climate refugia for this species and planning for habitat continuity between current and future habitat is essential. Identifying the refugia that will be resistant to the impacts of climate change is an increasingly recognized management strategy (Noss 2001; Botkin *et al.* 2007; Shoo *et al.* 2011). The predicted distribution of the northern bettong with global warming has been established by this study (Figure 6.3, from Chapter 4), and the inclusion of biotic interactions in the development of this model will make for more useful decisions of species management under climate change (Sinclair *et al.* 2010). Refugia predicted for the northern bettong on the Lamb Range and Atherton-Evelyn tablelands are identified by other studies as key refugial areas for this region and priority for protection (Shoo *et al.* 2011, SE Williams unpublished data). Large portions of these refugial areas have been degraded due to European land management practices (Shoo *et al.* 2011). As current northern bettong populations are not known to occur on the Atherton-Evelyn uplands, strategies will need to be developed to provide for habitat continuity between this region and the high density population on the Lamb Range. New approaches are available to assess habitat fragmentation, species movement ability and metapopulation dynamics that could be utilized in the selection of appropriate areas for restoration of habitat or establishment of continuity (Drielsma & Ferrier 2009; Shoo *et al.* 2011). Assisted colonization is also another option (Hoegh-Guldberg *et al.* 2008) although the impacts of such translocations need to be addressed (Ricciardi & Simberloff 2009). As there are historical records of northern bettongs from this region (Winter 1997a) it is likely the impacts within this ecosystem will be minimal, apart from the current occupation of this range by the competitor species (rufous bettong).

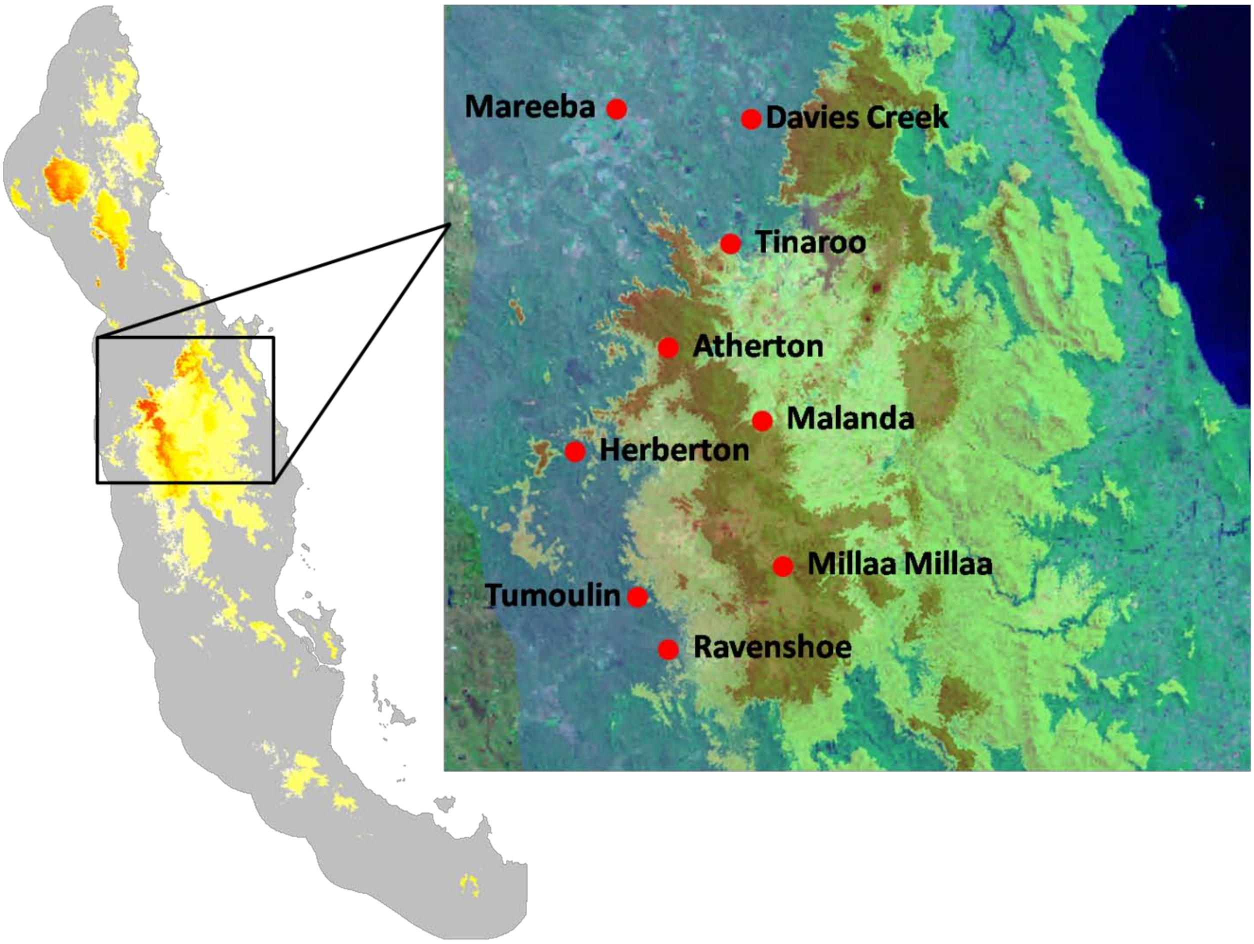

Figure 6.3. Future (+ 6° C global warming) predicted distribution of the northern bettong in the Australian Wet Tropics. Inset; close up of central refugia (From Chapter 4).

The populations within current day range edges are likely to be affected, as more variable weather and severity of droughts are already having an effect. In the southern range edge, it is likely that some degree of resource management will need to be implemented. Resource propagation (cockatoo grass re-vegetation, promotion of truffle fruiting) or supplemental feeding has been suggested for other endangered species and might be warranted with the northern bettong (Garnett & Crowley 2002; Treby 2007). The dynamic interaction between northern and rufous bettong needs to be monitored, and can be anticipated with fine-scale weather data. The northern range margins (Mt Windsor and Mt Carbine) appear to maintain suitable habitat in future climate scenarios, despite having low density populations currently. Changes in fire regimes may have some role in declines here (Winter 1997a), although similar oscillations (as compared to the Coane Range) of suitable weather and dynamic interactions with rufous bettongs were observed over shorter time periods (not presented here). There is limited data available from these regions, and more field studies are needed to determine what is influencing these populations.

Management strategies have been suggested here as ways of addressing several aspects of northern bettong ecology. It is clear that northern bettongs are limited by drought, which has been implicated in the decline of other bettong species (Short 1998). With droughts and seasonal weather patterns predicted to increase in this region, this is the most important factor to focus on for management, with an emphasis on proactive conservation planning to mitigate the impacts of climate change.

6.3 Future research directions

Although the modelling techniques detailed in this study represent advancements to the field of predictive modelling, there are many other limitations to current SDM applications. In order to continue making meaningful advancements in our ability to forecast species distributions, I suggest the following research direction.

(1) Downscaling of weather data

At present the available weather data is at a 5 km resolution. Downscaling of this data to a higher resolution will capture finer-scale information. This is required for species with a restricted range where lower resolution may lump occurrence sites into one value and overlook important ecological processes.

(2) Predictions using future weather scenarios over climate change scenarios

As extreme events are lost in long-term climate averages, forecasting onto future weather predictions might be ideal. Events are predicted to increase in both magnitude and frequency, and forecasts of species distributions utilising weather scenarios may identify areas of particular conservation concern.

(3) Identifying temporal dynamics overlooked by SDMs

Current SDM outputs are based on the assumption that spatial data will be enough to accurately define the distribution of a species. The use of temporal data in SDMs is limited and underestimated. This has already been identified as being important for highly mobile species (Reside *et al.* 2010). Future work should focus on identifying other important temporal influences on a species distribution.

(4) Integrating population models

Linking pattern-based distribution models with dynamic population viability models has been recognised previously as an important step in SDM research (Brook *et al.* 2009). Traditional SDMs can predict high suitability in areas of low population abundance (VanDerWal *et al.* 2009b), such as was shown in Chapter 5. Incorporating information from both may yield more robust results. Alternatively, the use of abundance data needs to be more thoroughly explored, and studies into body condition along specific gradients could be undertaken.

(5) Species dispersal and population establishment abilities

More detailed information on species' dispersal abilities and how long it will take to establish new populations in novel areas is needed. If a species distribution will shift under future climate scenarios, we need to know if it will be able to both reach these new areas and establish itself along with this shifting. This information can then be included into model building to improve our predictions (Anderson *et al.* 2009). Recent advances have been made so that metapopulation dynamics in relation to the landscape and habitat fragmentation offer promising avenues (Drielsma & Ferrier 2009).

(6) Model evaluation

Recent criticism has targeted the current use of AUC scores to evaluate model performance (Lobo *et al.* 2008). More reliable evaluation techniques need to be developed so that SDM researchers can be confident in their model outputs. New techniques are becoming available, although it is likely that several tools will be necessary for the task (Phillips & Elith 2010).

6.4 Concluding remarks

In order to create meaningful predictions of the impacts of climate change on a species, ecologically relevant knowledge, beyond just simple climate means, needs to be included. My study highlighted how the inclusion of biotic interactions and extreme weather events were important factors influencing a species distribution in time and as well as space. Model outputs yielded different results when climate-only models were compared to those including either interactions or events.

As the field of species distribution modelling is relatively new, advancements are occurring at a rapid pace. Predictions of species distributions need to be regularly updated in consensus with the current improvements of modelling techniques. The continuing growth of knowledge of SDM theory and research attending to model limitations forces those using SDMs to step out of the status quo of delivering climate-only based models. As models become more realistic, the gap between theory and management will be lessened so that conservationists are confident in SDM predictions, and proactive rather than reactive policies can be put in place.

References

Abell-Davis, S. E. 2008. Tropical Hypogeous Fungal Sporocarp Distribution in Time and Space: Implications for an Endangered Specialist Mycophagous Marsupial, *Bettongia tropica*. Page 127. School of Marine and Tropical Biology. James Cook University, Cairns.

Abell, S. E., P. A. Gadek, C. A. Pearce, and B. C. Congdon. 2006. Seasonal resource availability and use by an endangered tropical mycophagous marsupial. Biological Conservation **132**:533-540.

Accad, A., V. J. Neldner, B. A. Wilson, and R. E. Niehus 2008. Remnant vegetation in Queensland. Analysis of remnant vegetation 1997-1999-2000-2001-2003-2005, including regional ecosystem information. Queensland Herbarium, Environmental Protection Agency, Brisbane.

Akçakaya, H. R., S. H. M. Butchart, G. M. Mace, S. N. Stuart, and C. Hilton-Taylor. 2006. Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. Global Change Biology **12**:2037-2043.

Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, C. H. Flather, P. D. Culbert, B. D. Wardlow, and V. C. Radeloff. 2010. Effects of drought on avian community structure. Global Change Biology **16**:2158-2170.

Anderson, B. J., H. R. Akçakaya, M. B. Araújo, D. A. Fordham, E. Martinez-Meyer, W. Thuiller, and B. W. Brook. 2009. Dynamics of range margins for metapopulations under climate change. Proceedings of the Royal Society B: Biological Sciences **276**:1415-1420.

Anderson, R. P., A. T. Peterson, and M. Gomez-Laverde. 2002. Using niche-based modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos **98**:3-16.

Anderson, S. E., and J. S. I. Ingram 1989. Tropical soil biology and fertility: a handbook of methods. C.A.B. International, Aberystwyth.

Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography **33**:1677-1688.

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography **16**:743-753.

Araújo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. Validation of species-climate impact models under climate change. Global Change Biology **11**:1504-1513.

Archaux, F., and V. Wolters. 2006. Impact of summer drought on forest biodiversity: what do we know? Annals of Forest Science **63**:645-652.

Austin, M. P. 2002. Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. Ecological Modelling **157**:101-118.

Austin, M. P. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling **200**:1-19.

Baillie, J., and B. Groombridge. 1996. the I.U.C.N. Red List of Threatened Animals. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

Baselga, A., and M. B. Araújo. 2009. Individualistic vs community modelling of species distributions under climate change. Ecography **32**:55-65.

Beaumont, L. J., R. V. Gallagher, W. Thuiller, P. O. Downey, M. R. Leishman, and L. Hughes. 2009. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. Diversity and Distributions **15**:409-420.

Beaumont, L. J., L. Hughes, and A. J. Pitman. 2008. Why is the choice of future climate scenarios for species distribution modelling important? Ecology Letters **11**:1135-1146.

Begon, M., C. R. Townsend, and J. L. Harper 2006. Ecology: From individuals to ecosystems. Blackwell Publishing, Malden, USA, Oxford, UK, Carlton, Australia.

Belbin, L. 1991. Semi-strong hybrid scaling: a new ordination algorithm. Journal of Vegetation Science **2**:491-496.

Belbin, L. 1993. PATN: Pattern Analysis Package. CSIRO Division of Wildlife & Ecology, Canberra.

Bostock, P. D., and A. E. Holland, editors. 2007. Census of Queensland flora 2007. Queensland Herbarium and Environmental Protecion Agency, Brisbane.

Botkin, D. B., H. Saxe, M. B. Araújo, R. Betts, R. H. W. Bradshaw, T. Cedhagen, P. Chesson, T. P. Dawson, J. R. Etterson, D. P. Faith, S. Ferrier, A. Guisan, A. S. Hansen, D. W. Hilbert, C. Loehle, C. Margules, M. New, M. J. Sobel, and D. R. B. Stockwell. 2007. Forecasting the effects of global warming on biodiversity. BioScience **57**:227-236.

Bougher, N. L., T. S. Grove, and N. Malajczuk. 1990. Growth and Phosphorus Acquisition of Karri (*Eucalyptus diversicolor* F. Muell.) Seedlings Inoculated with Ectomycorrhizal Fungi in Relation to Phosphorus Supply. New Phytologist **114**:77-85.

Bougher, N. L., and T. Lebel. 2001. Sequestrate (Truffle-like) fungi of Australia and New Zealand. Australian Systematic Botany **14**:439-484.

Bourg, N. A., W. J. McShea, and D. E. Gill. 2005. Putting a cart before the search: successful habitat prediction for a rare forest herb. Ecology **86**:2793-2804.

Bowman, D. M. J. S. 2000. Australian rainforests: islands of green in the land of fire. Cambridge University Press, Cambridge.

Braithwaite, R. W., and P. Brady. 1993. The delicate mouse, *Pseudomys delicatulus*: a continuous breeder waiting for the good times. Australian Mammalogy **16**:93-96.

Braithwaite, R. W., and A. D. Griffiths. 1996. The paradox of *Rattus tunneyi*: endangerment of a native pest. Wildlife Research **23**:1-21.

Brook, B. W., H. R. Akçakaya, D. A. Keith, G. M. Mace, R. G. Pearson, and M. B. Araújo. 2009. Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. Biology Letters **5**:723-725.

Brotons, L., W. Thuiller, M. B. Araújo, and A. H. Hirzel. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography **27**:437-448.

Brown, J. H., T. G. Whitham, S. K. M. Ernest, and C. A. Gehring. 2001. Complex species interactions and the dynamics of ecological systems: Long-term experiments. Science **293**:643-650.

Bullock, S. H., H. A. Mooney, and E. Medina 1995. Seasonally dry tropical forests. Cambridge University Press, New York.

Burnett, S. 1997. Colonizing cane toads cause population declines in native predators: reliable anecdotal information and management implications. Pacific Conservation Biology **3**:65-72.

Burnett, S., and J. Winter. 2008. *Bettongia tropica*. IUCN 2009. IUCN Red List of Threatened Species.

Burnham, K. P., and D. R. Anderson 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Chase, J. M., and M. A. Leibold 2003. Ecological niches - linking classical and contemporary approaches. The University of Chicago press, Chicago.

Chen, C. R., L. M. Condron, M. R. Davis, and R. R. Sherlock. 2001. Effects of land-use change from grassland to forest on soil sulfur and arylsulfatase activity in New Zealand. Australian Journal of Soil Research **39**:749-757.

Claridge, A. W. 2002. Ecological role of hypogeous ectomycorrhizal fungi in Australian forests and woodlands. Plant and Soil **244**:291-305.

Claridge, A. W., S. C. Barry, S. J. Cork, and J. M. Trappe. 2000a. Diversity and habitat relationships of hypogeous fungi. II. Factors influencing the occurrence and number of taxa. Biodiversity and Conservation **9**:175-199.

Claridge, A. W., S. J. Cork, and J. M. Trappe. 2000b. Diversity and habitat relationships of hypogeous fungi. I. Study design, sampling techniques and general survey results. Biodiversity and Conservation **9**:151-173.

Claridge, A. W., and T. W. May. 1994. Mycophagy among Australian mammals. Australian Journal of Ecology **19**:251-275.

Claridge, A. W., A. P. Robinson, M. T. Tanton, and R. B. Cunningham. 1993. Seasonal production of hypogeal fungal sporocarps in a mixed-species eucalypt forest stand in South-eastern Australia. Australian Journal of Botany **41**:145-167.

Claridge, A. W., J. Seebeck, and R. Rose 2007. Bettongs, Potoroos, and the Musky Rat-Kangaroo. CSIRO Publishing, Collingwood.

Claridge, A. W., J. M. Trappe, D. J. Mills, and D. L. Claridge. 2009. Diversity and habitat relationships of hypogeous fungi. III. Factors influencing the occurrence of fire-adapted species. Mycological Research **113**:792-801.

Clayton, M. C., J. C. Wombey, I. J. Mason, R. T. Chesser, and A. Wells 2006. CSIRO list of Australian vertebrates: a reference with conservation status. CSIRO Publishing, Collingwood.

Cole, B. I., and I. D. Lunt. 2005. Restoring Kangaroo Grass (*Themeda triandra*) to grassland and woodland understoreys: a review of establishment requirements and restoration exercises in south-east Australia. Ecological Management & Restoration **6**:28-33.

Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: what have we learned so far? American Naturalist **163**:1-23.

Crawley, M. J. 1993. Glim for ecologists. Blackwell Scientific Publications, Oxford.

Crowley, G. M. 2008. Cockatoo grass *Alloteropsis semialata* as a keystone species in northern Australia. Northern Territory Naturalist **20**:58-63.

Crowley, G. M., and S. T. Garnett. 2001. Growth, seed production, and effect of defoliation in an early flowering perennial grass, *Alloteropsis semialata* (Poaceae), on Cape York Peninsula, Australia. Australian Journal of Botany **49**:735-743.

Crowley, G. M., S. T. Garnett, and S. Shephard. 2009. Impact of storm-burning on *Melaleuca viridiflora* invasion of grasslands and grassy woodlands on Cape York Peninsula, Australia. Austral Ecology **34**:196-209.

Currie, D. J., and J. T. Kerr. 2008. Tests of the mid-domain hypothesis: a review of the evidence. Ecological Monographs **78**:3-18.

Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998a. Making mistakes when predicting shifts in species range in response to global warming. Nature **391**:783-786.

Davis, A. J., J. H. Lawton, B. Shorrocks, and L. S. Jenkinson. 1998b. Individualistic Species Responses Invalidate Simple Physiological Models of Community Dynamics under Global Environmental Change. Journal of Animal Ecology **67**:600-612.

Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. Pages 269-284 in J. M. Diamond, and T. L. Case, editors. Community Ecology. Harper and Rowe, New York.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science **292**:673-679.

Dawson, J. O., D. G. Kowalski, and P. J. Dart. 1989. Variation with soil depth, topographic position and host species in the capacity of soils from an Australian locale to nodulate *Casuarina* and *Allocasuarina* seedlings. Plant and Soil **118**:1-11.

Dennis, R. L. H., and C. D. Thomas. 2000. Bias in Butterfly Distribution Maps: The Influence of Hot Spots and Recorder's Home Range. Journal of Insect Conservation **4**:73-77.

Doerr, S. H., R. A. Shakesby, W. H. Blake, C. J. Chafer, G. S. Humphreys, and P. J. Wallbrink. 2006. Effects of differing wildfire severities on soil wettability and implications for hydrological response. Journal of Hydrology **319**:295-311.

Dostine, P. L., G. C. Johnson, D. C. Franklin, Y. Zhang, and C. Hempel. 2001. Seasonal use of savanna landscapes by the Gouldian finch, *Erythrura gouldiae*, in the Yinberrie Hills area, Northern Territory. Wildlife Research **28**:445-458.

Drielsma, M., and S. Ferrier. 2009. Rapid evaluation of metapopulation persistence in highly variegated landscapes. Biological Conservation **142**:529-540.

Duponnois, R., S. Diedhiou, J. L. Chotte, and M. O. Sy. 2003. Relative importance of the endomycorrhizal and (or) ectomycorrhizal associations in *Allocasuarina* and *Casuarina* genera. Canadian Journal of Microbiology **49**:281-287.

Elith, J., and M. A. Burgman. 2002. Predictions and their validation: rare plants in the Central Highlands, Victoria, Australia. Pages 303 - 313 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurences: issues of accuracy and scale. Island Press, Washington D. C. .

Elith, J., and M. A. Burgman. 2003. Habitat models for PVA. Pages 203 - 235 in C. A. Brigham, and M. W. Schwartz, editors. Population Viability in

Plants. Conservation, Management and Modeling of Rare Plants. Springer-Verlag, New York.

Elith, J., and C. H. Graham. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. Ecography **32**:66-77.

Elith, J., C. H. Graham, Robert P. Anderson, S. F. Miroslav Dudík, Antoine Guisan, Robert J. Hijmans, Falk Huettmann, John R. Leathwick, Anthony Lehmann, Jin Li, Lucia G. Lohmann, Bette A. Loiselle, Glenn Manion, Craig Moritz, Miguel Nakamura, Yoshinori Nakazawa, Jacob McC. M. Overton, A. Townsend Peterson, Steven J. Phillips, Karen Richardson, Ricardo Scachetti-Pereira, Robert E. Schapire, Jorge Soberón, Stephen Williams, Mary S. Wisz, and Niklaus E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**:129-151.

Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction across Space and Time. Annual Review of Ecology, Evolution, and Systematics **40**.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions **17**:43-57.

Environmental Protection Agency. 2007a. National Recovery Plan for the northern bettong *Bettongia tropica*. Report to Department of the Environment and Water Resources, Canberra. Queensland Parks and Wildlife Service, Brisbane.

Environmental Protection Agency. 2007b. Regional Ecosystem Description Database (REDD). Environmental Protection Agency.

Everson, C. S., T. M. Everson, and N. M. Tainton. 1988. Effects of intensity and height of shading on the tiller initiation of six grass species from the Highland sourveld of Natal. South African Journal of Botany **54**:315-318.

Ferrier, S., G. Watson, J. Pearce, and M. Drielsma. 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. Biodiversity and Conservation **11**:2275-2307.

Fitzpatrick, M. C., and W. W. Hargrove. 2009. The projection of species distribution models and the problem of non-analog climate. Biodiversity and Conservation **18**:2255-2261.

Fogel, R. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas Fir stand. Canadian Journal of Botany **54**:1152-1161.

Franklin, J. 2010. Moving beyond static species distribution models in support of conservation biogeography. Diversity and Distributions **16**:321-330.

Freitag, S., C. Hobson, H. C. Biggs, and A. S. Van Jaarsveld. 1998. Testing for potential survey bias: the effect of roads, urban areas and nature reserves on a southern African mammal data set. Animal Conservation **1**:119-127.

Garkaklis, M. J., J. S. Bradley, and R. D. Wooller. 1998. The effects of Woylie (*Bettongia penicillata*) foraging on soil water repellency and water infiltration in heavy textured soils in southwestern Australia. Austral Ecology **23**:492-496.

Garkaklis, M. J., J. S. Bradley, and R. D. Wooller. 2004. Digging and soil turnover by a mycophagous marsupial. Journal of Arid Environments **56**:569-578.

Garnett, S. T., and G. M. Crowley. 2002. Recovery Plan for the golden-shouldered parrot *Psephotus chrysopterygius* 2003-2007. Report to Environment Australia, Canberra. Queensland Parks and Wildlife Service, Brisbane.

Goodman, S. M., and B. P. N. Rasolonandrasana. 2001. Elevational zonation of birds, insectivores, rodents and primates on the slopes of the Andringitra Massif, Madagascar. Journal of Natural History **35**:285-305.

Graham, C. H., J. Elith, R. J. Hijmans, A. Guisan, A. T. Peterson, and B. A. Loiselle. 2008. The influence of spatial errors in species occurrence data used in distribution models. Journal of Applied Ecology **45**:239-247.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature **242**:344-347.

Guisan, A., O. Broennimann, R. Engler, M. Vust, N. G. Yoccoz, A. Lehmann, and N. E. Zimmermann. 2006a. Using Niche-Based Models to Improve the Sampling of Rare Species. Conservation Biology **20**:501-511.

Guisan, A., T. C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling **157**:89-100.

Guisan, A., C. H. Graham, J. Elith, F. Huettmann, and N. S. Distri. 2007. Sensitivity of predictive species distribution models to change in grain size. Diversity and Distributions **13**:332-340.

Guisan, A., A. Lehmann, S. Ferrier, M. Austin, J. M. C. Overton, R. Aspinall, and T. Hastie. 2006b. Making better biogeographical predictions of species' distributions. Journal of Applied Ecology **43**:386-392.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**:993-1009.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**:147-186.

Gutschick, V. P., and H. BassiriRad. 2003. Extreme events as shaping physiology, ecology, and evolution of plants: Toward a unified definition and evaluation of their consequences. New Phytologist **160**:21-42.

H-Acevedo, D., and D. J. Currie. 2003. Does climate determine broad-scale patterns of species richness? a test of the causal link by natural experiment. Global Ecology & Biogeography **12**:461-473.

Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology **143**:29-36.

Harrington, G. N., and K. D. Sanderson. 1994. Recent contraction of wet sclerophyll forest in the wet tropics of Queensland due to invasion by rainforest. Pacific Conservation Biology **1**:319-327.

Hawkins, B. A., J. A. F. Diniz-Filho, and A. E. Weis. 2005. The mid-domain effect and diversity gradients: is there anything to learn? American Naturalist **166**:140-143.

Heaney, L. R. 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. Global Ecology and Biogeography **10**:15-39.

Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson, and J.-H. Körber. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. Global Ecology and Biogeography **16**:754-763.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography **29**:773-785.

Hijmans, R. J., and C. H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology **12**:2272-2281.

Hilbert, D. W., A. W. Graham, and T. A. Parker. 2001. Tall open forest and woodland habitats in the Wet Tropics: Responses to climate and implications for the northern bettong (*Bettongia tropica*). Page 45. Tropical Forest Research Series: Reports 1. Cooperative Research Centre for Tropical Rainforest Ecology and Management & CSIRO Tropical Forest Research Centre, Cairns, Atherton

Hirzel, A., and A. Guisan. 2002. Which is the optimal sampling strategy for habitat suitability modelling. Ecological Modelling **157**:331-341.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted Colonization and Rapid Climate Change. Science **321**:345-346.

Hortal, J., J. Rodriguez, M. N. Nieto-Díaz, and J. M. Lobo. 2008. Regional and environmental effects on the species richness of mammal assemblages. Journal of Biogeography **35**:1202-1214.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution **15**:56-61.

Hughes, L. 2003. Climate change and Australia: Trends, projections, and impacts. Austral Ecology **28**:423-443

Hutchinson, G. E. 1957. Concluding Remarks. Cold Spring Harbor Syposium Quantitiatve Biology **22**:415-427.

Hutchinson, G. R. 1959. Homage to Santa Rosalia, or why are there so many different kinds of animals ? The American Naturalist **93**:145 - 159.

Ibrahim, D. G., M. E. Gilbert, B. S. Ripley, and C. P. Osborne. 2008. Seasonal differences in photosynthesis between the C3 and C4 subspecies of *Alloteropsis semialata* are offset by frost and drought. Plant, Cell & Environment **31**:1038-1050.

Januchowski, S. R., R. L. Pressey, J. VanDerWal, and A. Edwards. 2010. Characterizing errors in digital elevation models and estimating the financial costs of accuracy. International Journal of Geographical Information Science **24**:1327-1347.

Jensen, K., and K. Gutekunst. 2003. Effects of litter on establishment of grassland plant species: the role of seed size and successional status. Basic and Applied Ecology **4**:579-587.

Jentsch, A., and C. Beierkuhnlein. 2008. Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. Comptes Rendus Geosciences **340**:621-628.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and the Environment **5**:365-374.

Jimenez-Valverde, A., J. M. Lobo, and J. Hortal. 2008. Not as good as they seem: the importance of concepts in species distribution modelling. Diversity and Distributions **14**:885-890.

Johnson, C. N. 1994. Fruiting of hypogeous fungi in dry sclerophyll forest in Tasmania, Australia: seasonal variation and annual production. Mycological research **98**:1173-1182.

Johnson, C. N. 1996. Interactions between mammals and ectomycorrhizal fungi. Trends in Ecology and Evolution **11**:503-507.

Johnson, C. N. 2006. Australia’s mammal extinctions: a 50 000 year history. Cambridge University Press, Melbourne.

Johnson, C. N., and A. P. McIlwee. 1997. Ecology of the northern bettong, *Bettongia tropica*, a tropical mycophagist. Wildlife Research **24**:549-559.

Jumpponen, A., A. W. Claridge, J. M. Trappe, T. Lebel, and D. L. Claridge. 2004. Ecological relationships among hypogeous fungi and trees: inferences from association analysis integrated with habitat modeling. Mycologia **96**:510-525.

Kanowski, J., J. Middleton, R. Jensen, and S. Legge. 2010a. Camera trap fauna survey of Mt Zero-Taravale Sanctuary; 2008-2009. A report to the Australian Wildlife Conservancy.

Kanowski, J., E. Mulder, and R. Jensen. 2010b. Mount Zero-Taravale Survey September 2010. A report to the Australian Wilidlife Conservancy.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters **12**:334-350.

Kearney, M., and W. P. Porter. 2004. Mapping the fundamental niche: Physiology, climate, and the distribution of a nocturnal lizard. Ecology **85**:3119-3131.

Kearney, M. R., B. A. Wintle, and W. P. Porter. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation Letters **3**:203-213.

Kellman, M. 1986. Fire sensitivity of *Casuarina torulosa* in North Queensland, Australia. Biotropica **18**:107-110.

Kelt, D. A. 1999. Assemblage structure and quantitative habitat relations of small mammals along an ecological gradient in the Colorado Desert of southern California. Ecography **22**:659-673.

Körner, C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. Trends in Ecology & Evolution **15**:513-514.

Körner, C. 2007. The use of 'altitude' in ecological research. Trends in Ecology & Evolution **22**:569-574.

Korpimaki, E., P. R. Brown, J. Jacob, and R. P. Pech. 2004. The Puzzles of Population Cycles and Outbreaks of Small Mammals Solved? BioScience **54**:1071-1079.

Krawchuk, M. A., M. A. Moritz, M.-A. Parisien, J. Van Dorn, and K. Hayhoe. 2009. Global Pyrogeography: the Current and Future Distribution of Wildfire. PLos One **4**:e5102.

Kutt, A. S., and J. C. Z. Woinarski. 2007. The effects of grazing and fire on vegetation and the vertebrate assemblage in a tropical savanna woodland in north-eastern Australia. Journal of Tropical Ecology **23**:95-106.

Lacher, T. E., and C. J. R. Alho. 2001. Terrestrial small mammal richness and habitat associations in an Amazon Forest-Cerrado contact zone. Biotropica **33**:171-181.

Laurance, W. F. 1997. A distributional survey and habitat model for the endangered northern Bettong *Bettongia tropica* in tropical Queensland. Biological Conservation **82**:47-60.

Laurance, W. F., and G. B. Williamson. 2001. Positive Feedbacks among Forest Fragmentation, Drought, and Climate Change in the Amazon. Conservation Biology **15**:1529-1535.

Leathwick, J. R., and M. P. Austin. 2001. Competitive Interactions between Tree Species in New Zealand's Old-Growth Indigenous Forests. Ecology **82**:2560-2573.

Lewellen, R. H., and S. H. Vessey. 1998. The effect of density dependence and weather on population size of a polyvoltine species. Ecological Monographs **68**:571-594.

Lobo, J. M., A. Jimenez-Valverde, and J. Hortal. 2010. The uncertain nature of absences and their importance in species distribution modelling. Ecography **33**:103-114.

Lobo, J. M., A. Jiménez-Valverde, and R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography **17**:145-151.

Loiselle, B. A., C. A. Howell, C. H. Graham, J. M. Goerck, T. Brooks, K. G. Smith, and P. H. Williams. 2003. Avoiding pitfalls of using species distribution models in conservation planning. Conservation Biology **17**:1591-1600.

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography **10**:3-13.

Lozier, J. D., P. Aniello, and M. J. Hickerson. 2009. Predicting the distribution of Sasquatch in western North America: anything goes with ecological niche modelling. Journal of Biogeography **36**:1623-1627.

Lunt, I. D. 1998. *Allocasuarina* (Casuarinaceae) invasion of an unburnt coastal woodland at Ocean Grove, Victoria: Structural changes 1971-1996. Australian Journal of Botany **46**:649-656.

Lunt, I. D. 2003. A Protocol for Integrated Management, Monitoring, and Enhancement of Degraded *Themeda triandra* Grasslands baseed on Plantings of Indicator Species. Restoration Ecology **11**:223-230.

Lunt, I. D., and J. W. Morgan. 2002. The role of fire regimes in temperate lowland grasslands of southeastern Australia in R. A. Bradstock, J. E. Williams, and M. A. Gill, editors. Flammable Australia: fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge.

Martin, T. G., and S. McIntye. 2007. Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. Conservation Biology **21**:504-514.

Martinez-Meyer, E. 2005. Climate Change and Biodiversity: Some Considerations in Forecasting Shifts in Species' Potential Distributions. Biodiversity Informatics **2**:42-55.

Mathams, S. G. 2008. A reassessment of a northern bettong (*Bettongia tropica*) reintroduction site quantifying fine-scale habitat and critical food resources and the development of a methodology for future assessment of potential habitat. Page 25. School of Natural and Rurual Systems Management. University of Queensland, Brisbane.

McCain, C. M. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. Journal of Biogeography **31**:19-31.

McCain, C. M. 2005. Elevational gradients in diversity of small mammals. Ecology **86**:366-372.

McCain, C. M. 2007a. Area and mammalian elevational diversity. Ecology **88**:76-86.

McCain, C. M. 2007b. Could temperature and water availability drive elevational species richness patterns? a global case study for bats. Global Ecology and Biogeography **16**:1-13.

McCain, C. M. 2009. Global analysis of bird elevational diversity. Global Ecology and Biogeography **18**:346-360.

McIlwee, A., and A. Freeman. 1998. The discovery of Northern Bettongs (*Bettongia tropica*) at Paluma, North Queensland. Report to the Department of Environment.

McIlwee, A. P., and C. N. Johnson. 1998. The contribution of fungus to the diets of three mycophagous marsupials in Eucalyptus forests, revealed by stable isotope analysis. Functional Ecology **12**:223-231.

McMahon, J. P., M. F. Hutchinson, H. A. Nix, and K. D. Ord 1995. ANUCLIM User's Guide, Version 1. Australian National University, Canberra.

McPherson, J. M., and W. Jetz. 2007. Effects of species' ecology on the accuracy of distribution models. Ecography **30**:135-151.

Mena, J. L., and E. Vázquez-Domínguez. 2005. Species turnover on elevational gradients in small rodents. Global Ecology & Biogeography **14**:539-547.

Meyer, M. D., and M. P. North. 2005. Truffle abundance in riparian and upland mixed-conifer forest of California's southern Sierra Nevada. Canadian Journal of Botany **83**:1015-1020.

Middleton, J., and S. Legge. 2007. Northern bettong discussion paper. A report to the Australian Wildlife Conservancy.

Miller, R. E., and I. E. Woodrow. 2008. Resource availability and the abundance of an N-based defense in Australian tropical rain forests. Ecology **89**:1503-1509.

Morgan, J. W., and I. D. Lunt. 1999. Effects of time-since-fire on the tussock dynamics of a dominant grass (*Themeda triandra*) in a temperate Australian grassland. Biological Conservation **88**:379-386.

Munoz, J., and A. M. Felicisimo. 2004. Comparison of statistical methods commonly used in predictive modelling. Journal of Vegetation Science **15**:285-292.

Murphy, J., and J. P. Riley. 1967. A modified single solution method for determination of phosphate in natural waters. Analytica Chimica Acta **27**:31-36.

Nehls, U., F. Göhringer, S. Wittulsky, and S. Dietz. 2010. Fungal carbohydrate support in the ectomycorrhizal symbiosis: a review. Plant Biology **12**:292-301.

Neldner, V. J., B. A. Wilson, E. J. Thompson, and H. A. Dillewaard 2004. Methodology for survey and mapping of regional ecosystems and vegetation communities in Queensland. Version 3.1. Queensland Herbarium, Environmental Protection Agency, Brisbane.

Nilsson, L. O., and H. Wallander. 2003. Production of External Mycelium by Ectomycorrhizal Fungi in a Norway Spruce Forest Was Reduced in Response to Nitrogen Fertilization. New Phytologist **158**:409-416.

Nix, H. A., and M. A. Switzer 1991. Rainforest Animals: Atlas of Vertebrates Endemic to Australia's Wet Tropics. Australian National Parks and Wildlife Service, Canberra.

Nogués-Bravo, D. 2009. Predicting the past distribution of species climatic niches. Global Ecology and Biogeography **18**:521-531.

Nogues-Bravo, D., M. B. Araujo, T. Romdal, and C. Rahbek. 2008. Scale effects and human impact on the elevational species richness gradients. Nature **453**:216-219.

Nor, S. M. 2001. Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. Global Ecology and Biogeography **10**:41-62.

North, M. 2002. Seasonality and abundance of truffles from oak woodlands to red fir forests. Pages 91-98 in J. Verner, editor. Proceedings of a Symposium on the Kings River Sustainable Forest Ecosystems Project: Progress and Current Status. USDA Forest Service, Pacific Southwest Research Station

Noss, R. F. 2001. Beyond Kyoto: Forest management in a time of rapid climate change. Conservation Biology **15**:578-590.

O'Brien, E. M. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. Journal of Biogeography **25**:379-398.

O'Dell, T. E., J. F. Ammirati, and E. G. Schreiner. 1999. Species richness and abundance of ectomycorrhizal basidiomycete sporocarps on a moisture gradient in the Tsuga heterophylla zone. Canadian Journal of Botany **77**:1699-1711.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics **37**:637-669.

Parmesan, C., T. L. Root, and M. R. Willig. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society **81**:443-450.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**:37-42.

Parsons, S. A., and R. A. Congdon. 2008. Plant litter decomposition and nutrient cycling in north Queensland tropical rain-forest communities of differing successional status. Journal of Tropical Ecology **24**:317-327.

Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling **133**:225-245.

Pearce, J., S. Ferrier, and D. Scotts. 2001. An evaluation of the predictive performance of distributional models for flora and fauna in north-east New South Wales. Journal of Environmental Management **62**:171-184.

Pearce, J., and D. Lindenmayer. 1998. Bioclimatic analysis to enhance reintroduction biology of the endangered helmeted honeyeater (*Lichenostomus melanops cassidix*) in Southeastern Australia. Restoration Ecology **6**:238-243.

Pearman, P. B., A. Guisan, O. Broennimann, and C. F. Randin. 2008. Niche dynamics in space and time. Trends in Ecology & Evolution **23**:149-158.

Pearson, R. G. 2007. Species' Distribution Modeling for Conservation Educators and Practitioners. Synthesis. American Museum of Natural History.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology & Biogeography **12**:361-371.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography **34**:102-117.

Pearson, R. G., W. Thuiller, M. B. Araújo, E. Martinez-Meyer, L. Brotons, C. McClean, L. Miles, P. Segurado, T. P. Dawson, and D. C. Lees. 2006. Model-based uncertainty in species range prediction. Journal of Biogeography **33**:1704-1711.

Peterson, A. T., M. Papeş, and M. Eaton. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography **30**:550-560.

Phillips, S., and J. Elith. 2010. POC-plots: calibrating species distribution models with presence-only data. Ecology **91**:2476-2484.

Phillips, S. J. 2008. Transferability, sample selection bias and background data in presence-only modelling: a response to Pearson et al. (2007). Ecography **31**:272-278.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modelling of species geographic distributions. Ecological Modelling **190**:231-259.

Phillips, S. J., and M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography **31**:161-175.

Phillips, S. J., and M. Dudík. 2004. A maximum entropy approach to species distribution modeling. International Conference on Machine Learning, Banff, Canada.

Phillips, S. J., M. Dudík, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications **19**:181-197.

Piessens, K., D. Adriaens, H. Jacquemyn, and O. Honnay. 2009. Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. Oecologia **159**:117-126.

Pope, L. C., A. Estoup, and C. Moritz. 2000. Phylogeography and population structure of an ecotonal marsupial, Bettongia tropica, determined using mtDNA and microsatellites. Molecular Ecology **9**:2041-2053.

Preston, K., J. T. Rotenberry, R. A. Redak, and M. F. Allen. 2008. Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. Global Change Biology **14**:2501-2515.

Prusty, B. A. K., R. Chandra, and P. A. Azeez. 2009. Distribution of carbon, nitrogen, phosphorus, and sulfur in the soil in a multiple habitat system in India. Australian Journal of Soil Research **47**:177-189.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography **18**:200-205.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. American Naturalist **149**:875-902.

Rahbek, C., N. J. Gotelli, R. K. Colwell, G. L. Entsminger, T. F. L. V. B. Rangel, and G. R. Graves. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. Proceedings of the Royal Society Biological Sciences Series B **274**:165-174.

Recher, H. F. 1969. On the relation of birds and habitat in Australia and North America. American Naturalist **103**:75-79.

Reddy, S., and L. M. Dávalos. 2003. Geographical sampling bias and its implications for conservation priorities in Africa. Journal of Biogeography **30**:1719-1727.

Reed, J. M. 1996. Using statistical probability to increase confidence of inferring species extinction. Conservation Biology **10**:1283-1285.

Reside, A. E., J. VanDerWal, A. S. Kutt, and G. C. Perkins. 2010. Weather, not climate, defines distributions of vagile species. PLos One **5**:e13569.

Ricciardi, A., and D. Simberloff. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology & Evolution **24**:248-253.

Rickart, E. A. 2001. Elevational diversity gradients, biogeography and the structure of montane mammal communities in the intermountain region of North America. Global Ecology and Biogeography **10**:77-100.

Ripley, B., G. Donald, C. P. Osborne, T. Abraham, and T. Martin. 2010. Experimental investigation of fire ecology in the C3 and C4 subspecies of *Alloteropsis semialata*. Journal of Ecology **98**:1196-1203.

Ripley, B. S., T. I. Abraham, and C. P. Osborne. 2008. Consequences of C4 photosynthesis for the partitioning of growth: a test using C3 and C4 subspecies of *Alloteropsis semialata* under nitrogen-limitation. Journal of Experimental Botany **59**:1705-1714.

Ripley, B. S., M. E. Gilbert, D. G. Ibrahim, and C. P. Osborne. 2007. Drought constraints on C4 photosynthesis: stomatal and metabolic limitations in C3 and C4 subspecies of *Alloteropsis semialata*. Journal of Experimental Botany **58**:1351-1363.

Ritchie, E. G., J. K. Martin, C. N. Johnson, and B. J. Fox. 2009. Separating the influences of environment and species interactions on patterns of distribution and abundance: competition between large herbivores. Journal of Animal Ecology **78**:724-731.

Robertson, M. P., C. I. Peter, M. H. Villet, and B. S. Ripley. 2003. Comparing models for predicting species' potential distributions: a case study using correlative and mechanistic predictive modelling techniques. Ecological Modelling **164**:153-167.

Root, T. L., D. P. MacMynowski, M. D. Mastrandrea, and S. H. Schneider. 2005. Human-modified temperatures induce species changes: Joint attribution. Proceedings of the National Academy of Sciences of the United States of America **102**:7465-7469.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature **421**:57-60.

Rose, R. W., R. Swain, and S. L. Bryant. 1990. Body Temperature Rhythm and Regulation in the Tasmanian Bettong *Bettongia gaimardi* Marsupialia Potoroidae. Comparative Biochemistry & Physiology A **97**:573-576.

Rosenzweig, M. L., and M. V. Lomolino. 1997. Who gets the short bits of the broken stick? in W. E. Kunin, and K. J. Gaston, editors. The Biology of

Rarity; causes and consequences of rare-common differences. Chapman & Hall, London.

Rowe, R. J. 2009. Environmental and geometric drivers of small mammal diversity along elevational gradients in Utah. Ecography **32**:411-422.

Russell-Smith, J., O. Price, and B. Murphy. preprint. Managing the matrix: decadal responses of eucalypt-dominated mesic savanna to ambient fire regimes in three north Australian conservation reserves. Ecological Applications.

Sanchez-Cordero, V. 2001. Elevataion gradients of diversity for rodents and bats in Oaxaca, Mexico. Global Ecology & Biogeography **10**:63-76.

Sattler, P. S., and R. D. Williams, editors. 1999. The conservation status of Queensland's bioregional ecosystems. The Environmental Protection Agency Brisbane.

Schmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography **12**:1-20.

Schulman, L., T. Toivonen, and K. Ruokolainen. 2007. Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. Journal of Biogeography **34**:1388-1399.

Schweiger, O., J. Settele, O. Kudrna, S. Klotz, and I. Kühn. 2008. Climate change can cause spatial mismatch of trophically interacting species. Ecology **89**:3472-3479.

Scott, D. F. 2000. Soil wettability in forested catchments in South Africa; as measured by different methods and as affected by vegetation cover and soil characteristics. Journal of Hydrology **231-232**:87-104.

Scott, K. A. 2008. Effect of fire regime on grass-layer plant dynamics in a tropical savanna. Page 195. Faculty of Education, Health, and Science. Charles Darwin University, Darwin.

Scott, K. A., S. A. Setterfield, A. N. Andersen, and M. M. Douglas. 2009. Correlates of grass-species composition in a savanna woodland in northern Australia. Australian Journal of Botany **57**:10-17.

Seebeck, J., and R. W. Rose. 1988. Potoroidae. Pages 202-224 in D. Dalton, editor. Mammals of Australia. Government Publishing, Canberra.

Shoo, L. P., C. Storlie, J. VanDerWal, J. Little, and S. E. William. 2011. Targeted protection and restoration to conserve tropical biodiversity in a warming world. Global Change Biology **17**:186-193.

Short, J. 1998. The extinction of rat-kangaroos (Marsupialia: Potoroidae) in New South Wales, Australia. Biological Conservation **86**:365-377.

Short, J., and B. Turner. 1993. The distribution and abundance of the burrowing bettong (Marsupialia: Macropodoidea). Wildlife Research **20**:525-534.

Sinclair, S. J., M. D. White, and G. R. Newell. 2010. How useful are species distribution models for managing biodiversity under future climates? Ecology and Society **15**:8. [online].

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters **10**:1115-1123.

Stanton, P. 2007. The vegetation and ecosystems of the Mount Zero-Taravale Sanctuary. Australian Wildlife Conservancy.

Stockwell, D. R. B., and A. T. Peterson. 2002. Effects of sample size on accuracy of species distribution models. Ecological Modelling **148**:1-13.

Theodorou, C., and P. Reddell. 1991. *In vitro* synthesis of ectomycorrhizas on Casuarinaceae with a range of mycorrhizal fungi. New Phytologist **118**:279-288.

Thibault, K. M., and J. H. Brown. 2008. Impact of an extreme climatic event on community assembly. Proceedings of the National Academy of Sciences **105**:3410-3415.

Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. 2008. Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology, Evolution and Systematics **9**:137-152.

Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz. 2009. Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences **106**:19637-19643.

Treby, D. L. 2007. Supplementary feeding and husbandry required for translocation of the northern hairy-nosed wombat (*Lasiorhinus krefftii*). School of Animal Studies. University of Queensland, Brisbane.

Trudell, S. A., and R. L. Edmonds. 2004. Macrofungus communities correlate with moisture and nitrogen abundance in two old-growth conifer forests, Olympic National Park, Washington, USA. Canadian Journal of Botany **82**:781-800.

Tsoar, A., O. Allouche, O. Steinitz, D. Rotem, and R. Kadmon. 2007. A comparative evaluation of presence-only methods for modelling species distribution. Diversity and Distributions **13**:397-405.

van Ingen, L. T., R. I. Campos, and A. N. Andersen. 2008. Ant community structure along an extended rain forest-savanna gradient in tropical Australia. Journal of Tropical Ecology **24**:445-455.

VanDerWal, J., L. P. Shoo, C. Graham, and S. E. William. 2009a. Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? Ecological Modelling **220**:589-594.

VanDerWal, J., L. P. Shoo, C. N. Johnson, and Stephen E. Williams. 2009b. Abundance and the Environmental Niche: Environmental Suitability Estimated from Niche Models Predicts the Upper Limit of Local Abundance. The American Naturalist **174**:282-291.

Vernes, K. 2000. Immediate effects of fire on survivorship of the northern bettong (*Bettongia tropica*): An endangered Australian marsupial. Biological Conservation **96**:305-309.

Vernes, K. 2003. Fine-scale habitat preferences and habitat partitioning by three mycophagous mammals in tropical wet sclerophyll forest, north-eastern Australia. Austral Ecology **28**:471-479.

Vernes, K., M. Castellano, and C. N. Johnson. 2001. Effects of season and fire on the diversity of hypogeous fungi consumed by a tropical mycophagous marsupial. Journal of Animal Ecology **70**:945-954.

Vernes, K., C. N. Johnson, and M. A. Castellano. 2004. Fire-related changes in biomass of hypogeous sporocarps at foraging points used by a tropical mycophagous marsupial. Mycological Research **108**:1438-1446.

Vernes, K., and L. C. Pope. 2001. Stability of nest range, home range and movement of the northern bettong (*Bettongia tropica*) following moderate-intensity fire in a tropical woodland, north-eastern Queensland. Wildlife Research **28**:141-150.

Vernes, K. A. 1999. Fire, Fungi and a tropical mycophagist: Ecology of the northern bettong (*Bettongia tropica*) in fire-prone sclerophyll forest. Department of Zoology and Tropical Ecology. James Cook University, Townsville.

Vernes, K. A., and D. T. Haydon. 2001. Effect of fire on northern bettong (*Bettongia tropica*) foraging behaviour. Austral Ecology **26**.

Vernes, K. A., and L. C. Pope. 2006. Population density of the northern bettong *Bettongia tropica* in northeastern Queensland. Australian Mammalogy **28**:87-92.

Walker, B. H., J. L. Langridge, and F. McFarlane. 1997. Resilience of an Australian savanna grassland to selective and non-selective perturbations. Australian Journal of Ecology **22**:125-135.

Wallander, H. 1995. A new hypothesis to explain allocation of dry matter between mycorrhizal fungi and pine seedlings in relation to nutrient supply. Plant and Soil **168-169**:243-248.

Wallander, H., and J. E. Nylund. 1992. Effects of excess nitrogen and phosphorus starvation on the extramatrical mycelium of ectomycorrhizas of *Pinus sylvestris* L. New Phytologist **120**:495-503.

Walsh, K. J. E., and B. F. Ryan. 2000. Tropical Cyclone Intensity Increase near Australia as a Result of Climate Change. Journal of Climate **13**:3029-3036.

Wan, S., D. Hui, and Y. Luo. 2001. Fire Effects on Nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecological Applications **11**:1349-1365.

Warren, D. L., R. E. Glor, M. Turelli, and D. Funk. 2008. Environmental Niche Equivalency versus Conservatism: Quantitative Approaches to Niche Evolution. Evolution **62**:2868-2883.

Webb, L. J. 1968. Environmental relationships of the structural types of Australian rainforest vegetation. Ecology **49**:296-311.

Webb, L. J. 1969. Edaphic differentiation of some forest types in eastern Australia Part 2: soil chemical factors. Journal of Ecology **57**:817-830.

White, T. C. R. 2008. The role of food, weather and climate in limiting the abundance of animals. Biological Reviews **83**:227-248.

Willams, S. E., J. VanDerWal, J. Isaac, L. P. Shoo, C. Storlie, S. Fox, E. E. Bolitho, C. Moritz, C. Hoskin, and Y. M. Williams. 2010. Distributions, life history characteristics, ecological specialisation and phylogeny of the rainforest vertebrates in the Australian Wet Tropics bioregion. Ecology **91**:2493-2493.

Williams, P. R., R. A. Congdon, A. C. Grice, and P. J. Clarke. 2005. Effect of season of burning and removal of herbaceous cover on seedling emergence in a eucalypt savanna of north-eastern Australia. Austral Ecology **30**:491-496.

Williams, S. E., and H. Marsh. 1998. Changes in small mammal assemblage structure across a rain forest / open forest ecotone. Journal of Tropical Ecology **14**:187-198.

Williams, S. E., H. Marsh, and J. Winter. 2002. Spatial scale, species diversity, and habitat structure: Small mammals in Australian tropical rain forest. Ecology **83**:1317-1329.

Williams, S. E., and J. Middleton. 2008. Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. Diversity and Distributions **14**:69-77.

Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann, and G. Langham. 2008. Towards an Integrated Framework for Assessing the Vulnerability of Species to Climate Change. PLoS Biol **6**:e325.

Williams, S. E., J. VanDerWal, J. Isaac, L. P. Shoo, C. Storlie, S. Fox, E. E. Bolitho, C. Moritz, C. Hoskin, and Y. M. Williams. 2010. Distributions, life history characteristics, ecological specialisation and phylogeny of the rainforest vertebrates in the Australian Wet Tropics bioregion. Ecology **91**:2493.

Winter, J. 1997a. Distribution of the northern bettong *Bettongia tropica* in north-eastern Australia. World Wildlife Fund for Nature, Australia.

Winter, J., and P. M. Johnson. 1995. Northern Bettong in R. Strahan, editor. The Mammals of Australia. Reed New Holland, Sydney.

Winter, J. W. 1992. Population assessment of the northern brush-tailed bettong on the Mt. Windsor tableland, north-eastern Queensland. The Department of Environment and Heritage.

Winter, J. W. 1997b. Responses of Non-volant Mammals to Late Quaternary Climatic Changes in the Wet Tropics Region of North-eastern Australia. Wildlife Research **24**:493-511.

Withers, J. 1978. Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. II. The differential seedling establishment of *Eucalyptus ovata Labill*. and *Casuarina littoralis Salisb*. Australian Journal of Botany **26**:465-483.

Withers, J., and D. Ashton. 1977. Studies of the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. I. The structure and regeneration. Australian Journal of Botany **25**:623-637.

Woinarski, J. C. Z., D. J. Milne, and G. Wanganeen. 2001. Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. Austral Ecology **26**:360-370.

Woinarski, J. C. Z., J. Risler, and L. Kean. 2004. Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical *Eucalyptus* open forest, Northern Territory, Australia. Austral Ecology **29**:156-176.

Woinarski, J. C. Z., R. J. Williams, O. Price, and B. Rankmore. 2005. Landscapes without boundaries: wildlife and their environments in northern Australia. Wildlife Research **32**:377-388.

Zimmermann, N. E., N. G. Yoccoz, T. C. Edwards, E. S. Meier, W. Thuiller, A. Guisan, D. R. Schmatz, and P. B. Pearman. 2009. Climatic extremes improve predictions of spatial patterns of tree species. Proceedings of the National Academy of Sciences **106**:19723-19728.

Zuur, A. F., E. N. Leno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution **1**:3-14.

Appendix A : A review of species distribution modelling with Maxent[1]

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[1] Please note references for Appendix A listed in main reference section

A review of Maxent: a commonly used species distribution modelling technique

Background information

Species distribution models (SDMs) are commonly used to characterize the ecological niches of species and to generate predictions about species current and future distributions (Guisan & Thuiller 2005; Hijmans & Graham 2006; Thuiller *et al.* 2008; Fitzpatrick & Hargrove 2009). SDMs are developed to help define the relationship between where a species occurs and the environmental features that are found at those locations (Elith *et al.* 2006; Elith & Leathwick 2009) in order to derive a measure of the suitability for that species in geographical space (VanDerWal *et al.* 2009b). These models are useful in estimating the relative likelihood that a given location will occupied by a species and can be used to generate hypothesis on the current distributions of species and to predict their future distributions under climate change (Araújo & Guisan 2006; Jimenez-Valverde *et al.* 2008; Elith & Leathwick 2009).

Throughout this thesis I have used SDMs to examine ecological questions, particularly in my first two data chapters (Chapter 2 and 3) and, in the final two data chapters (Chapter 4 and 5), examine how SDM techniques can be improved by adding more ecologically relevant mechanisms. A detailed review is provided in the introduction of this thesis (Chapter 1) on the general concepts of SDMs. Maxent, the modelling technique used throughout this thesis, is commonly used in the species distribution modelling literature (Phillips *et al.* 2006, which introduced Maxent, has been cited 795 times) and is commonly used in SDM research for a variety of applications and aims (as highlighted in Elith *et al.* 2011).

Here, I will provide a brief review of the technical aspects and general terms used in Maxent so that the background information necessary for understanding model development and the methods utilised in this thesis are covered. Several papers (Phillips & Dudík 2004; Phillips *et al.* 2006; Phillips 2008; Phillips & Dudik 2008; Phillips *et al.* 2009; Elith *et al.* 2011) offer a more detailed explanation of the mathematics and technical aspects behind Maxent which will not be covered is depth here; all material for this review has been sourced from these resources. A recent review of Maxent by Elith *et al.* (2011) provides a description of the algorithm and all of the technical underpinnings of the program in a description targeted at ecologists (Elith *et al.* 2011).

A tutorial of Maxent has been written by one of the developers of Maxent and is available online (www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc). This tutorial entitled ‘A Brief Tutorial of Maxent’ (based on Phillips *et al.* 2006; Phillips & Dudik 2008) covers the setup of the program and includes detailed explanation on how to use the program including an example dataset for a practice model run. This tutorial is updated as newer versions of Maxent become available.

Technical aspects of Maxent

The Maxent program

Maxent is a stand-alone presence-only modelling algorithm software package free to use and can be downloaded at http://www.cs.princeton.edu/~schapire/maxent/. This modelling algorithm consistently outperforms other algorithms for building SDMs from presence-only data in its predictive performance (Elith *et al.* 2006; Hernandez *et al.* 2006; Hijmans & Graham 2006; Guisan *et al.* 2007; Pearson *et al.* 2007; Elith & Graham 2009) during model evaluation (see Chapter 1 for details on model evaluation). The most comprehensive evaluation compared 16 common modelling methods, using data for 226 species across 6 regions, of which Maxent consistently achieved high predictive performance for three evaluation statistics, and outperformed other modelling methods (Elith *et al.* 2006). It has been shown to perform well under current, past and future climate scenarios, matching closely the predictions of models produced by mechanistic approaches (Hijmans & Graham 2006; Kearney *et al.* 2010). It therefore provides an excellent tool for predictive modelling of species distributions and indicates why it is so widely applied and commonly used (Elith *et al.* 2011).

Maxent is a maximum entropy approach algorithm that makes predictions from incomplete information and generates a probability distribution for a given species (Phillips *et al.* 2006). The model integrates all that is known whilst assuming nothing about what is unknown; that is it chooses a model consistent with all facts but otherwise stays close to uniform as possible (it achieves maximum entropy). This uniform distribution is however subject to constraints; otherwise all possible phrases would be given equal probability (Phillips *et al.* 2006). The information given to Maxent are: a study area in geographical space, a set of features for that given study area which are representative of ‘real-valued’ variables, and occurrence records which represent sample points from within that study area (Phillips *et al.* 2006). Maxent generates a probability distribution for a species that is defined on this geographical space made up by the study area (as pixels). The constraints represent expected values of the features, where each feature should match the average of the values for the given sample points within error bounds (Phillips *et al.* 2006). That is, the model constraints ensure that the average of a given feature is close to the values across all location with presences (Elith *et al.* 2011). As we are trying to establish a probability distribution, a ranking of sites in the environment of possible presence, these constraints allow the model to allocate a probability score evenly across the area of interest but with respect to the average values of the environmental data given at each of the species occurrence locations.

How the models are built

To predict the suitable habitat of a species Maxent requires both species occurrence data and environmental data relating to the study region where that species occurs. Environmental data can be either continuous or categorical variables. Common environmental variables include climate, topography, geology, soil class, and vegetation although most models rely on climate variables only (Elith *et al.* 2011). Maxent is presence-only modelling technique and does not require absence data. Presence-only modelling has its advantages when absence records are not available or are unreliable, which is often the case with species datasets. If the surveys conducted to obtain the species data are not sufficient to detect a species (i.e. the species was present at the time of survey but was not detected) or the environmental conditions present are suitable for the species but other factors prevent it from occurring there (i.e. to biotic interactions, disturbance events or dispersal barriers) then we obtain false absences. False absences such as these can bias the results of SDMs, and even though the environment is suitable for the species, the model will identify it as being unsuitable (Hirzel & Guisan 2002; Jimenez-Valverde *et al.* 2008).

Without reliable absence data, locations representative of the environmental conditions where a species does not occur, presence-only modelling must evaluate other data to understand what factors shape the distribution of presences. Maxent uses ‘background’ points, a representative of the range of environmental conditions present in the modelling region (Phillips *et al.* 2009). These background data do not represent ‘pseudo-absences’ but rather a comparison in which the model can discern what is unique about the presence locations with respect to the entire study area (Phillips *et al.* 2009). Species occurrence locations could by chance be included as part of this background as it is randomly sampled and does not take into account presence records (Pearson 2007; Elith *et al.* 2011). This is so the model can discriminate between locations where a species occurs and the overall environment (background) of the study area to define the potential niche of a species.

To address spatial biases in datasets, such as survey effort biases which are common in species occurrence record data sets (Freitag *et al.* 1998; Dennis & Thomas 2000; Reddy & Dávalos 2003; Schulman *et al.* 2007), the background data may be manipulated so that it reflects the same bias as the occurrence data (Ferrier *et al.* 2002; Phillips *et al.* 2009). This is done so that the model can discriminate between the sample locations and the background from within the sampled space only, so that appropriate habits for the species can be identified (Phillips *et al.* 2009). The use of a buffer (also known as a mask), a spatially defined distance at the appropriate scale to the study region around sample points, has been used to address spatial biases in SDMs (VanDerWal *et al.* 2009a). This is the methodology adapted in this thesis to account for any spatial biases that are present in my data sets.

Feature types

The environmental variables provided to Maxent are used to create ‘features’ so that complex relationships can be modelled (Elith *et al.* 2011). The output can be thought of as a combined product of all possible pair-wise comparisons of the original environmental variables. By transforming the original environmental variables (Elith *et al.* 2011), non-linear functions can be fit to generate more realistic models of complex relationships between species and their environment (Austin 2002). These features are used to constrain the probability distribution generated in Maxent model training (Phillips *et al.* 2006; Phillips & Dudik 2008).

There are six default features available in Maxent, although removing some of these may be ideal for creating simpler models that are easier to interpret (Elith *et al.* 2011). The estimated distribution from the model is a product of the constraints imposed by the selected features. The six feature types (linear, quadratic, product, threshold, hinge and discrete) and brief explanation of each are presented in Table Appendix A.1.

Running the model

During model training, maxent performs ‘runs’ in which it assesses the defined environmental layers in relation to the occurrence data (sample points) and background points. With each model, Maxent performs iterations where it uses the known information to adjust the uniform distribution by repeatedly improving the fit of the data and generating a probability distribution over the defined study area (Phillips *et al.* 2006; Phillips & Dudik 2008). This probability is measured in 'gain' which at the outset, is equal to zero (gain of uniform distribution), and with each subsequent iteration the gain is increased with increasing probabilities of sample locations (Phillips *et al.* 2006; Phillips & Dudik 2008). After the run has finished, the gain indicates the average likelihood that a sample point will be ranked higher than a random background point. This gain is similar to the deviance or goodness of fit measures, used in general additive models and generalized linear models (Phillips *et al.* 2006; Phillips & Dudik 2008).

To prevent overfitting and produce accurate models that have generality Maxent also uses regularization, or smoothing, with gain by introducing error bounds, a measure of deviation allowed around the means (Elith *et al.* 2011).

The probability distribution generated by Maxent is then presented as the logistic output where the data is rescaled, in a nonlinear way, so that each pixel within the study area is assigned a probability value from 0 to 1 (with 1 being the highest predictions of suitability and 0 being predictions of unsuitable habitat) (Phillips *et al.* 2006; Phillips & Dudik 2008). This is an attempt to estimate the probability of presence of a species given the environment at that location (Phillips *et al.* 2006; Phillips & Dudik 2008; Elith *et al.* 2011) and can be thought of as a relative ranking of the predicted suitability of sites based on the given data.

Table Appendix A.1. Description of each maxent feature type (Phillips et al. 2006; Phillips & Dudik 2008). Details are given on how the feature transforms the original variables as well as how it affects the predicted distribution (adapted from Online Appendix l, Elith *et al.* 2011).

Feature Type	**Variable Type**	**Transformation**	**Constraint**
Linear	Continuous	Variable alone	Distribution is constrained where the average of each variable is the same expectation of average over the sample locations.
Quadratic	Continuous	Square of variable	In combination with linear features, the distribution is constrained where the variance of the variables is the same expectation of the variance at each sample location. Introduces variability around suitable conditions into the model.
Product	Continuous	Product of two variables	In combination with linear (and quadratic) features, the distribution is constrained where the covariance of the variables is the same expectation of the covariance at each sample location. Introduces interactions between variables.
Threshold	Continuous	Step function in relation to threshold, where above and below the threshold have a different response (piecewise constant spline)	Distribution is constrained so that the proportion of values for a variable designated above the selected threshold is the same expectation as the proportion over the sample locations.
Hinge	Continuous	Linear response in relation to threshold, where above and below the threshold have a different response with the slope being either negative or positive (piecewise linear spline)	Distribution is constrained in the same manner as a linear feature, but values below the threshold are held constant.
Discrete or Category	Categorical	A binary feature for categorical variables; the number of categorical features matches the number of categorical variable values given.	The only feature designated for categorical variables, the constraint is that the proportion of the values for a categorical variable across the predicted distribution is the same expectation as the proportion of sample locations with that value.

Maxent generates several thresholds, the default being 0.5, which can be used to define a cut-off point where below that value is considered unsuitable for the species (Phillips *et al.* 2006; Phillips & Dudik 2008). It is often necessary to identify areas where the species is likely to be absent (the habitat is unsuitable), and selecting a threshold is used to do this (Pearson 2007). In a binary prediction, thresholds are related to sensitivity (true positive or presence fraction) and specificity (the true negative or absence fraction). Models that have high sensitivity indicate low omission (false absences) and generate a more relaxed model in that all locations where a species has been recorded are included. Selecting a high threshold (more strict) reduces the risk of identifying sites that a species is likely to be absent by identifying areas with high suitability, although some locations where a species has been observed may be omitted (Pearson 2007). In this thesis, I have applied the 'balance threshold' that minimizes 6 x training omission rate + 0.4 x cumulative threshold + 1.6 x fractional predicted area which is a more relaxed threshold. This threshold was selected as it has previously ranked consistently as the best threshold value for species in this region (VanDerWal *et al.* 2009a; Williams *et al.* 2010).

Maxent automatically generates an AUC value (see Chapter 1) for each model run and generates an ROC plot which can be used in model evaluation. A plot of training omission versus predicted area is also presented to see how well the predicted omission rate matches the test omission rate drawn from the Maxent distribution (Phillips *et al.* 2006; Phillips & Dudik 2008). It is important to note that, as Maxent is using only presence data and background data without the use of absence data, then the commission rate (fraction of false presences) is not used here (Phillips *et al.* 2006; Phillips & Dudik 2008). Rather the 'fractional predicted area' is uses, which is the fraction of the study area where presence is predicted. This then violates the assumption that the maximum achievable AUC score is 1, and the AUC values presented by Maxent will be less than one.

Importance of variables

Maxent also includes analyses for determining which variables matter most in model building. During model training, variables that contribute to model building are assessed by attributing the gain of that iteration to the environmental variables that a particular feature depends on (with each iteration the coefficient only a single feature is modified) (Phillips *et al.* 2006; Phillips & Dudik 2008). The contributions of all variables across all iterations are then presented as a (relative) percentage contribution to the overall model run. There is an option to include a jack-knife analysis of variables included in which tests each variable in comparison with all other variables, with each variable tested alone, and with each excluded in turn and model run with remaining variables (Phillips *et al.* 2006; Phillips & Dudik 2008).

Maxent outputs also include response curves for each environmental variable, with the shape of the curve dependent on the types of features (described above; Table Appendix A.1) selected in the model run (Phillips *et al.* 2006; Phillips & Dudik 2008). These curves are visual representations of how the prediction is affected by each environmental variable. The plots generated represent the relationship of the predicted probability of presence of a species across the full range of conditions available for that given variable. This gives us an idea of the values for a particular variable that are conducive to high suitability for the modelled species. Response curves are created in two ways; 1) how each model changes when one environmental variable is altered and the others are maintained at their average value, and 2) each model run only with that single environmental variable, without any of the other variables included (Phillips *et al.* 2006; Phillips & Dudik 2008). Confidence intervals are not provided with these response curves as each is a product of only one Maxent 'run'.

Clamping

When generating predictions, in particular onto new environments (i.e. climate change), novel conditions may arise that did not occur in the original study area. An example provided in the Maxent tutorial (see above, Phillips *et al.* 2006; Phillips & Dudik 2008) using the Brown-throated Sloth (*Bradypus variegatus*) shows the maximum temperature recorded at a species occurrence was 35°C and the sampling region rarely reaches 36°C so there is no knowledge on if the species can tolerate such temperatures. In future scenarios representative of climate change, this study area will now experience higher temperatures that exceed those known at present and used in model training. This problem of novel environments, or extrapolation, is a limitation of such modelling techniques and Maxent has a built in 'clamping' feature to address this. Clamping identifies any environmental variables that are outside of the range experience during training and constrains (resetting the values) the features so that they are within the training range (put at the limit of this range). This prevents Maxent from extrapolating and predicting high suitability onto novel conditions. Maxent also includes a fade by clamping feature which allows for some extrapolation onto novel environments, but in a constrained manner so that extrapolation is faded as predictions stray from known conditions (Phillips *et al.* 2006; Phillips & Dudik 2008). This is useful in future scenarios as it is likely that some of these novel environments, at least those close to present conditions, may be suitable.

Limitations

Maxent suffers from limitations common of presence-only modelling, including the reliance on an unbiased sample, uncertainty when projecting onto novel environments, and the inability to use available absence data where reliable (Peterson *et al.* 2007; Phillips 2008; Elith & Leathwick 2009; Elith *et al.* 2011). In addition, species distribution models assume a species is in equilibrium with their environment and that environmental information alone limits a species (Elith & Leathwick 2009). However, there is a growing literature that deals with these assumptions and limitations, allowing researchers to account for them in their models. As highlighted earlier in this review, target group background sampling (Phillips *et al.* 2009) and selection of background data from a buffer within a defined region (VanDerWal *et al.* 2009a) can be used for addressing sampling bias, and fade by clamping can be introduced into Maxent to deal with projections onto novel space (Phillips & Dudik 2008). In addition, models are becoming more complex and introducing dynamic parameters such as weather data (Chapter 5, Reside *et al.* 2010) and biotic interactions (Chapter 4, Araújo & Luoto 2007) so that model outputs are more realistic.

Conclusion

This review was provided as a general overview of the Maxent modelling algorithm commonly used in SDM research. It has been included in this thesis so that the necessary background and technical information needed for a full understanding of the methodologies have been provided. I have tried to cover all aspects of Maxent that are relevant to the research presented here, although this modelling technique is complex and not all aspects were able to be covered here. As mentioned in the outset of this review, there are several sources from the literature that provide a more extensive review and explanation of this algorithm which I suggest for further reading (Phillips & Dudík 2004; Phillips *et al.* 2006; Phillips 2008; Phillips & Dudik 2008; Phillips *et al.* 2009; Elith *et al.* 2011).

Appendix B : Probability of detection of northern bettongs at Mt Zero-Taravale[1][2]

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[1] **Bateman BL**, Johnson CN (in prep) Using probability of detection to determine survey effort and population decline of the northern bettong. To be submitted to *Wildlife Research*

[2] Please note references for Appendix B listed in main reference section

I conducted a trapping survey of the northern bettong (*Bettongia tropica*) at the Australian Wildlife Conservancy (AWC) conservation sanctuary of Mt Zero-Taravale from 2006-2009. The aim of this survey was to improve the basis for the conservation and management of this northern bettong population after its discovery in 1997 extended the geographic range of the species by 300 km (D. Storch personal communication; McIlwee & Freeman 1998). Northern bettongs were recorded on Mt Zero-Taravale from 1997 – 2003, with a 18 month survey hiatus before the commencement of my trapping survey (Middleton & Legge 2007). Survey work was based on live cage-trapping of animals based on trapping grids across the sanctuary (Figure Appendix B.1).

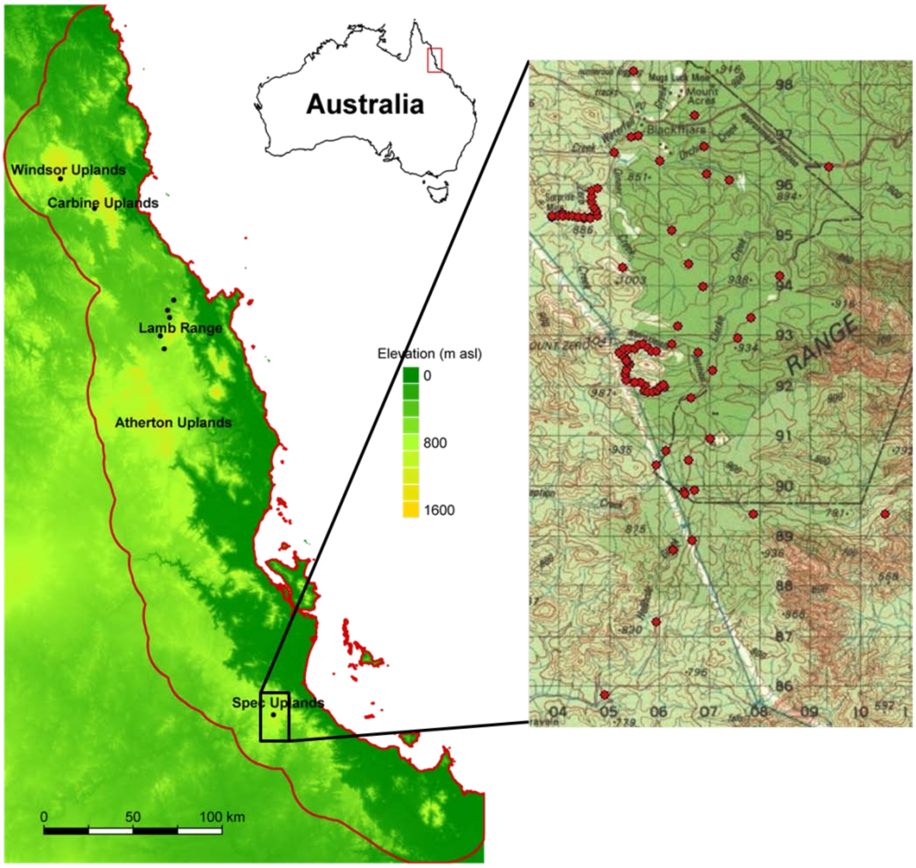

Figure Appendix B.1. Location of all trapping grids within Mt Zero-Taravale Sanctuary and location of study site in Wet Tropics region of Australia. Red dots represent locations of northern bettong trapping grids surveyed from 2006-2009.

A total of 3636 trapnights during the survey period resulted in the failure to detect the northern bettong at Mt Zero-Taravale. In addition, this decline coincided with a replacement of the northern bettong by the rufous bettong in several trapping sites; in 1997, no rufous bettongs were captured during trapping surveys, however 38 were captured during my trapping survey. To assess the possibility of a local extinction, or severe population contraction, of northern bettongs at Mt Zero-Taravale I have utilized the concept of detectability using the binomial probability distribution (presence/absence data).

$$p[Y=K] = [N\ k]\ P^{k}\,(1-P)^{N-k}$$ (Reed 1996)

N= number of visits, adapted here to be number of trapnights*
k= number of successful captures
P= probability of success (detection)
p= Statistical Confidence

The interest is in the case that k is equal to 0, representing zero captures, from N number of trapnights (*trapnights are equivalent to the number of traps used times the number of nights surveyed). I am interested in three aspects of this, 1) being the number of visits needed to be statistically confident the species does not occur at a site 2) show statistically if there has been a decline in detection of the species at a site and, 3) if there has been a decline in detection, what probability of detection would we assume with 95% confidence over N trapnights with zero captures.

In 1997 eight individual northern bettongs were captured in nine successful trappings over 378 trap nights on the Mt. Zero-Taravale (McIlwee & Freeman 1998):

Probability of Detection: 9 trappings/378 trapnights= 0.024= 2.4%

$$N_{min} = \log(\alpha) / \log(1-P)$$

N_{min} = minimum number of trapnights needed for detection
α = statistical confidence level
P= probability of detection (from 0 to 10%)

$$N_{min} = \log(0.05)/\log(1-0.024)$$
$$N_{min} = 140.05, \text{ with } 95\% \text{ confidence}$$

A minimum number of 140 trapnights is needed to detect northern bettongs at the detection levels from 1998 (Figure Appendix B.2). I have conducted 3636 trapnights at Mt Zero-Taravale with zero captures of northern bettongs from 2006-2009.

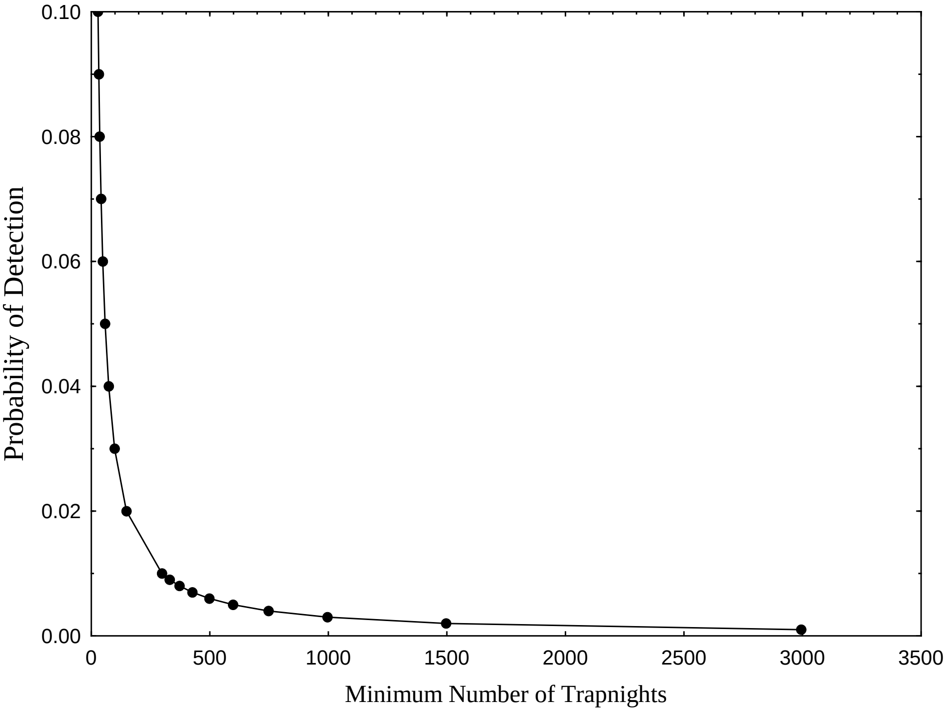

Figure Appendix B.2. The minimum number of trapnights needed to detect a species given probability of detection (from 0 to 10%).

From 2006-2009, I have conducted 3636 trapnights at Mt Zero-Taravale and successfully trapped zero northern bettongs.

H_0: P = 0.024, the probability of detection has remained the same since
1998
H_1: P< 0.024, the probability of detection has decreased since
1998

$$p[k=0] = [3636 \text{ choose } 0]\ 0.024^{0}\ (1-0.024)^{3636}$$
$$p= (0.976)^{3636}$$
$$p= 4.36 \text{ E-}39$$

Therefore, the null hypothesis, p = 0.024, the probability of detection has remained the same since 1998, may be rejected. There has been a significant and severe decline of the detectability of the northern bettong at Mt. Zero/Taravale since 1998.

$$p(k=0)= 0.05= (3636 \text{ choose } 0)\ x^{0}\ (1-x)^{3636}$$
$$0.05= (1-x)^{3636}$$
$$x = 0.00082$$
$$\text{Detectability} = 0.0008$$

With the captures of zero northern bettongs in 2006-2009 over 3636 trapnights, we can be 95% (p = 0.05) confident the capture success (detectability) has declined to 0.08%. More recent surveys (2008-2010) have also failed to detect the northern bettong at Mt Zero-Taravale, including comprehensive camera trapping surveys (Kanowski *et al.* 2010a; Kanowski *et al.* 2010b). This is indicative of a major decline in the detection of the species at Mt Zero-Taravale, translating to either a large contraction of the species range and population or possible local extinction.

Appendix C : Top models from generalized linear modelling in Chapter 5

Table Appendix C.1. Top Models selected using the Bayesian information criterion (BIC) for northern bettong core versus northern bettong southern range edge. All temperature variables are in °C and rainfall variables are in mm. Variability is represented by standard deviation (SD) and averages by the mean (x). BIC model weights (w_i) and model accuracy values are presented.

Variable	**Variable**	**Variable**	**BIC**	w_i	**Accuracy**
Minimum Temperature SD			11.96	0.54	1
Minimum Temperature SD	Daily Rainfall of Drought		17.94	0.03	1
Minimum Temperature SD	Temperature Range SD		17.94	0.03	1
Minimum Temperature SD	Length of Drought SD		17.94	0.03	1
Minimum Temperature SD	Number of Droughts		17.94	0.03	1
Minimum Temperature SD	Length of Drought x		17.94	0.03	1
Minimum Temperature SD	Number of Heat Waves		17.94	0.03	1
Minimum Temperature SD	Rainfall SD		17.94	0.03	1
Minimum Temperature SD	Minimum Rainfall Drought		17.94	0.03	1
Minimum Temperature SD	Heat Wave Length x		17.94	0.03	1
Minimum Temperature SD	Rainfall SD		17.94	0.03	1
Minimum Temperature SD	Heat Wave Length SD		17.94	0.03	1
Minimum Temperature SD	Temperature Range x		17.94	0.03	1
Minimum Temperature SD	Maximum Temperature SD		17.94	0.03	1
Minimum Temperature SD	Maximum Temperature x		17.94	0.03	1
Minimum Temperature SD	Minimum Temperature SD		17.94	0.03	1
Minimum Temperature SD	Total Degree Days > 28°C		17.94	0.03	1
Minimum Temperature SD	Rainfall of Drought x		17.94	0.03	1

Table Appendix C.2. Top Models selected using the Bayesian information criterion (BIC) for northern bettong versus the rufous bettong. All temperature variables are in °C and rainfall variables are in mm. Variability is represented by standard deviation (SD) and averages by the mean (x). BIC model weights (w_i) and model accuracy values are presented.

Variable	**Variable**	**Variable**	**Variable**	**Variable**	**BIC**	w_i	**Accuracy**
Minimum Temperature SD	Rainfall SD	Length of Heat Wave x	Length of Drought x	Daily Rainfall of Drought	318.30	0.29	0.97
Minimum Temperature SD	Maximum Temperature x	Rainfall SD	Length of Drought x	Daily Rainfall of Drought	320.10	0.12	0.97
Minimum Temperature SD	Maximum Temperature x	Rainfall SD			320.85	0.08	0.97
Minimum Temperature SD	Maximum Temperature x	Rainfall SD	Daily Rainfall of Drought		321.60	0.06	0.97
Minimum Temperature SD	Rainfall SD	Length of Heat Wave x	Daily Rainfall of Drought		321.72	0.05	0.97
Minimum Temperature SD	Rainfall SD	Length of Heat Wave x	Number of Droughts	Daily Rainfall of Drought	321.77	0.05	0.97
Minimum Temperature SD	Maximum Temperature x	Rainfall SD	Number of Droughts	Daily Rainfall of Drought	322.40	0.04	0.97
Minimum Temperature SD	Temperature Range x	Temperature Range SD	Rainfall SD		322.49	0.04	0.97
Minimum Temperature SD	Rainfall SD	Length of Heat Wave x	Rainfall of Drought x	Daily Rainfall of Drought	323.23	0.02	0.97
Minimum Temperature SD	Maximum Temperature x	Temperature Range SD	Rainfall SD		323.89	0.02	0.97
Minimum Temperature x	Minimum Temperature SD	Rainfall SD	Daily Rainfall of Drought		324.15	0.02	0.97
Minimum Temperature SD	Maximum Temperature x	Rainfall SD	Rainfall of Drought x	Daily Rainfall of Drought	324.15	0.02	0.97
Minimum Temperature x	Minimum Temperature SD	Temperature Range x	Temperature Range SD	Rainfall SD	324.28	0.01	0.97
Minimum Temperature SD	Maximum Temperature x	Temperature Range x	Temperature Range SD	Rainfall SD	324.28	0.01	0.97
Minimum Temperature SD	Rainfall SD	Total Degree Days > 28°C	Length of Drought x	Daily Rainfall of Drought	324.38	0.01	0.97
Minimum Temperature SD	Maximum Temperature x	Temperature Range SD	Rainfall SD	Daily Rainfall of Drought	324.78	0.01	0.97
Minimum Temperature x	Minimum Temperature SD	Rainfall SD	Length of Drought x	Daily Rainfall of Drought	325.09	0.01	0.97

Table Appendix C.3. Top Models selected using the Bayesian information criterion (BIC) for northern bettong presence versus northern bettong absence in the southern range edge. All temperature variables are in °C and rainfall variables are in mm. Variability is represented by standard deviation (SD) and averages by the mean (x). BIC model weights (w_i) and model accuracy values are presented.

Variable	**Variable**	**Variable**	**Variable**	**BIC**	w_i	**Accuracy**
Maximum Temperature SD	Rainfall x	Number of Droughts		14.95	0.18	1.00
Rainfall x	Rainfall of Drought x	Minimum Rainfall of Drought		14.95	0.18	1.00
Minimum Temperature x	Rainfall of Drought x	Minimum Rainfall of Drought		14.95	0.18	1.00
Minimum Temperature x	Number of Heat Waves	Total Degree Days > 28°C	Daily Rainfall of Drought	18.69	0.03	1.00
Minimum Temperature x	Temperature Range x	Length of Drought x	Length of Drought SD	18.69	0.03	1.00
Maximum Temperature x	Temperature Range x	Length of Drought x	Length of Drought SD	18.69	0.03	1.00
Minimum Temperature x	Temperature Range SD	Rainfall x	Rainfall of Drought x	18.69	0.03	1.00
Minimum Temperature x	Minimum Temperature SD	Length of Drought x	Length of Drought SD	18.69	0.03	1.00
Rainfall x	Number of Heat Waves	Rainfall of Drought x	Minimum Rainfall of Drought	18.69	0.03	1.00
Rainfall x	Length of Drought SD	Rainfall of Drought x	Minimum Rainfall of Drought	18.69	0.03	1.00
Minimum Temperature x	Rainfall x	Rainfall of Drought x	Minimum Rainfall of Drought	18.69	0.03	1.00
Length of Heat Wave SD	Length of Drought x	Length of Drought SD	Minimum Rainfall of Drought	18.69	0.03	1.00
Minimum Temperature x	Length of Drought SD	Rainfall of Drought x	Minimum Rainfall of Drought	18.69	0.03	1.00
Rainfall SD	Number of Heat Waves	Rainfall of Drought x	Minimum Rainfall of Drought	18.69	0.03	1.00
Number of Heat Waves	Rainfall of Droughts x	Minimum Rainfall of Drought	Daily Rainfall of Drought	18.69	0.03	1.00
Maximum Temperature SD	Number of Heat Waves	Rainfall of Drought x	Minimum Rainfall of Drought	18.69	0.03	1.00
Minimum Temperature x	Maximum Temperature SD	Rainfall of Drought x	Minimum Rainfall of Drought	18.69	0.03	1.00
Minimum Temperature x	Rainfall of Drought x			20.14	0.01	0.98
Minimum Temperature x	Rainfall SD	Rainfall of Drought x		21.43	0.01	0.95

Appendix D : Animated figures (Chapter 5)[1]

Animated Figure 5.1. Generalised Linear Modelling top variable weather models in geographical space from 1980 - 2006 for northern bettongs core (Lamb Range; ‘stable bettong weather’) versus northern bettongs southern range edge (Coane Range); The core, Lamb Range, represents ‘stable northern bettong weather’ represented by red here and the southern range edge, the Coane Range weather, is represented by green.

Animated Figure 5.2. Generalised Linear Modelling top variable weather models in geographical space from 1980 - 2006 for northern bettongs versus rufous bettongs Northern bettong ‘weather’ is represented by green, rufous bettong ‘weather’ represented by red, and the niche overlap zone between these species is identified by yellow-tan**.**

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[1] See C.D. for data

Appendix E : Small-mammal species richness and abundance along a tropical altitudinal gradient: an Australian example[1,2]

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[1] **Bateman, B. L.**, Kutt, A. S., Vanderduys, E. P. & Kemp, J. E. 2010. Small-mammal species richness and abundance along a tropical altitudinal gradient: an Australian example. *Journal of Tropical Ecology* 26:139-149.

[2] Please note references for Appendix E listed in main reference section

Rationale for inclusion in thesis

I have included this article in the appendix of my thesis as the data collection took place in conjunction with my PhD research. One of my northern bettong survey sites was located on Mt Lewis, within the Australian Wildlife Conservancy's Brooklyn Sanctuary. Despite considerable effort no northern bettongs were captured during any of the survey periods. My co-authors and I published this article on the other mammal species we did capture.

The following article is already published and is presented here with minor formatting changes. All references are listed within the main reference section.

Abstract

This study examined patterns in the species richness and abundance of small non-volant mammals along a tropical altitudinal gradient in north-eastern Australia. We investigated whether a mid-altitudinal peak in diversity was apparent, and if it occurred, whether it was determined by particular environmental conditions. We sampled a small-mammal assemblage at 17 sites distributed along an altitude-environmental gradient from savanna (350 m) to rain-forest vegetation (1000 m). Over four separate occasions (5100 trap-nights) we recorded seventeen species of mammal with 416 captures. A positive non-linear relationship between altitude and mammal species richness and abundance was observed, peaking at the 800-900 m range. Many species were distributed across a range of altitudes, while others were strongly associated with particular habitat conditions. There was a distinct reduction in abundance and species richness at low altitudes associated with the less complex vegetation, lower productivity and possible anthropogenic effects. Key findings were; that small-mammal richness peaked towards the summit of the gradient and not at one-half the maximum altitude predicted by the mid-domain effect; contrasting conditions and greatest vegetation juxtaposition had the greatest influence on the patterns recorded; and that local idiosyncratic influences such as habitat factors, land management and historical biogeography are significant.

Introduction

Montane ecosystems are ideal for investigating processes that determine species assemblage along environmental gradients. Altitudinal gradients are particularly important, as there is a strong relationship between changing altitude and changing environmental variables such as climate and vegetation (Körner 2007). Vegetation pattern can exhibit rapid changes over short distances within a single montane system, with corresponding changes in species assemblage (Bullock *et al.* 1995; van Ingen *et al.* 2008) These zones of rapid transition support high concentrations of species, a trend which is especially true in the tropics (Heaney 2001). Therefore these gradients act as natural experiments that can provide key insights into important ecological concepts such as the relationship between environmental heterogeneity and local or regional species diversity (Hutchinson 1959; Schmida & Wilson 1985). However there is only moderate consensus on what factors explain patterns of diversity along these gradients, despite commonality in biogeography and vegetation pattern observed on different continents (Rowe 2009).

Many studies of assemblages along altitudinal gradients have identified peaks in species richness at mid-altitudes, a phenomenon that occurs across many regions and taxa (Rahbek 1995, 1997; Lacher & Alho 2001; Nor 2001; Sanchez-Cordero 2001; Colwell *et al.* 2004; McCain 2004). In particular, non-volant small mammals often display mid-altitudinal peaks in species richness, especially within tropical systems (Heaney 2001; Nor 2001; McCain 2005). These peaks are predicted to occur at either points of optimal environmental conditions, at mid-domains where species overlap, or locations where distinct vegetation communities occur in close proximity (Lomolino 2001; Currie &

Kerr 2008). The mid-domain effect, where species richness is concentrated at mid-altitude due to spatial constraints and hard boundaries, is often cited as influencing patterns of species richness (Colwell *et al.* 2004; McCain 2004). However, such mid-domain effects often coincide with ideal climate position along the gradient or are strongly collinear with environmental gradients (Hawkins *et al.* 2005; Currie & Kerr 2008). More recent studies support the environmental hypothesis, where environmental variables such as climate, topography, and productivity drive species patterns (H-Acevedo & Currie 2003; McCain 2007b, a; Rahbek *et al.* 2007; Currie & Kerr 2008; 2009). Although there are varying hypotheses on the underlying cause of the mid-altitudinal peak, a simple universal explanation may be difficult to attain due to local environmental idiosyncrasies such as historical biogeography, regional climate nuances and local anthropogenic impacts (Rowe 2009).

Many climatic patterns along altitudinal gradients are consistent, such as reduction in temperature and radiation with increasing altitude, whereas others such as precipitation, are less predictable (Körner 2007). Many mountain regions display their own unique moisture gradients which interact with local soil nutrient availability and historical fire patterns to create local vegetation patterns (Webb 1968; Lacher & Alho 2001; Körner 2007). Vegetation structure and habitat complexity, as determined by climatic conditions, will have a strong influence on small-mammal community assemblage and thus communities are likely to be in part determined by such climatic gradients (Williams & Marsh 1998; Sanchez-Cordero 2001). There is a well-established link between local and regional species diversity patterns and increasing structural complexity of vegetation (Recher 1969), though in many altitude-gradient studies the effect of climate is often considered more influential (Heaney 2001).

Studies of the pattern of small mammals along gradients within Australian montane systems are lacking in the literature and it is not known whether non-volant small mammals follow this same mid-altitudinal peak pattern. Australian rain forests are an important addition to case studies of altitude patterns as they are very limited in distribution, have a high proportion of endemic species, and contain very sharp gradients from wet rain forest to extensive dry tropical savannas (Bowman 2000). It is necessary to encompass all regions and continents when addressing patterns in global diversity. In particular the tropical rain forest of Queensland has been cited as an excellent candidate for such studies (Colwell *et al.* 2004).

We examined the patterns of small-mammal assemblage along an altitude gradient in tropical Queensland, Australia and investigated key competing hypotheses associated with mountain gradients: (1) there is a mid-altitudinal peak in diversity (species richness and abundance); (2) there is no apparent peak at mid-altitude, but rather species patterns are associated with environmental conditions. We evaluated the distribution of small-mammal species recorded along the gradient, and examine whether there are strong relationships between species diversity patterns and altitude, vegetation type, habitat complexity, and/or local effects.

Methods

Study area

The study sites are located on Mt Lewis (16°30’S, 145°12’E) in tropical north-eastern Queensland. The property was operated as a pastoral lease for many years, but has been owned and managed for conservation (as the Brooklyn Sanctuary) by the Australian Wildlife Conservancy since 2004. The sites occur along an altitudinal gradient that ranges from a plateau of open savanna woodlands (300 m) to upland (>1000 m) tropical rain forest to the east. Rainfall varies from typical tropical savanna rainfall of <600 mm y^{-1} to the west through to >3000 mm y^{-1} at upland sites (Webb 1968; van Ingen *et al.* 2008) . Climate data derived from *ANUCLIM* software indicate that annual mean temperature ranges between ~22 °C at the base of the mountain to ~19 °C at the top, with rainfall seasonality (coefficient of variation of mean monthly precipitation) varying from ~115 to ~80 correspondingly (ANUCLIM, version 5.1, Fenner School, Australian National University).

There were seventeen sampling sites located along the altitudinal gradient on two adjacent ridgelines; ten sites were located on a walking track that follows a ridgeline. These ten sites encompass a vegetation and altitudinal gradient from 620 m to 1000 m (Figure 1). Seven sites were located along an adjacent ridge; these seven sites encompass the entire accessible portion of this ridgeline, a gradient from 350-700 m (Figure 1).

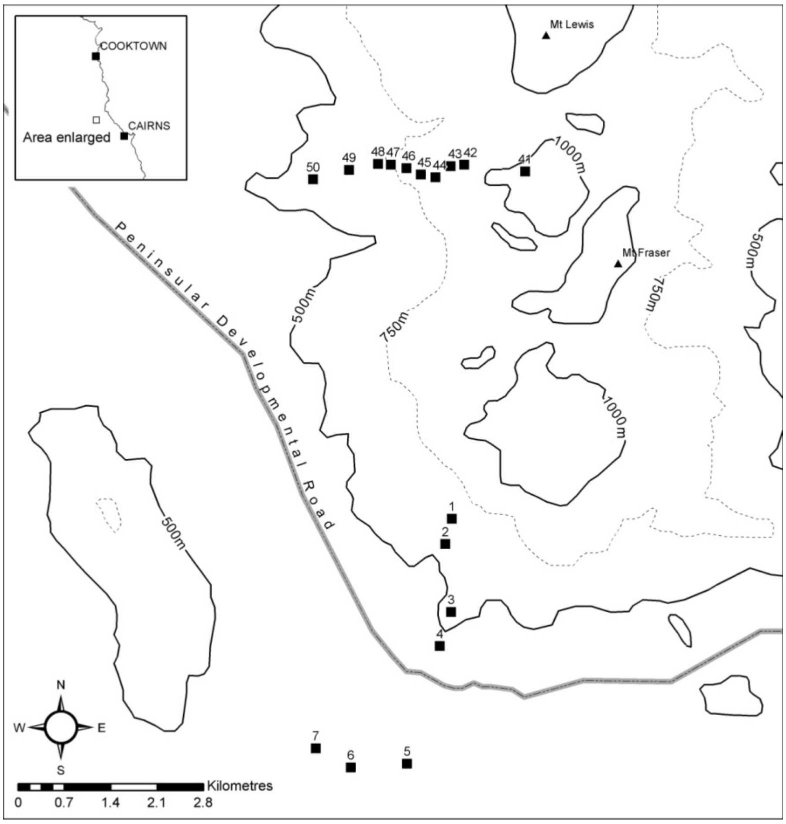

Figure 1. Location of sites and gradient sampled, and location of Brooklyn Station in Queensland.

Sample sites were located on the ground with reference to vegetation mapping for the region (Sattler & Williams 1999) and physical reconnaissance. Sites were located within a mapped vegetation polygon, and where possible, at least 500 m from each other and at least 200 m from the nearest obvious ecotone or edge between vegetation types. In two cases where the pattern in vegetation change was rapid, the edge of one quadrat was only 300 m from the start of the next. Sample sites were 100 × 100 m in size and marked by three permanent steel fence posts at 0, 50 and 100 m points that run down the ridgeline. Two reflective tags were placed on trees at 50 m on both sides and perpendicular to the 0 m mark which is labelled with a large reflective tag and site number. Sites were grouped into Broad Vegetation Groups as allocated to vegetation mapping units by the Queensland Herbarium (Accad *et al.* 2008). Brief vegetation descriptions based on the quadrats and the number of sites sampled in each type are presented in Table 1.

Mammal sampling

Small mammals were sampled over a 6-d, five-night period on four separate occasions (May 2006, November 2006, April 2007 and November 2007). Trapping occurred within the 100 × 100-m quadrat, and comprised of five baited treadle cage traps (three 300 × 300 × 600-mm and two 200 × 200 × 400-mm treadle traps) and ten baited Elliott (100 × 100 × 300-mm aluminium box) traps. The cages were placed at 0, 50 and 100 m ridgeline markers, with two additional cages placed perpendicular and on either side to the 0-m cage, 50 m from this point. The Elliott traps were placed at 10-m intervals, along the perpendicular arm, running down either side of the ridge line. Elliott and cage traps were baited with peanut butter, honey, oats, vanilla or pistachio essence; alternative traps were also baited with dog biscuits. One cage trap at each site was baited with chicken to target *Dasyurus* spp. (quolls). Traps were checked in the morning between 06h00 and 10h00. Each animal trapped was identified and released. In this study we were concerned with differences in the relative abundance (sensu Martin & McIntye 2007) of mammal species along the altitudinal and vegetation gradient, and not absolute counts such as ‘known to be alive’ estimates; thus we did not undertake mark-capture measurements.

Table 1. The description of the broad vegetation groups sampled along the altitudinal gradient. Broad vegetation groups follow naming protocols of the Environmental Protection Agency (2007b). The broad floristic description of each habitat is as follows: RFE = Complex notophyll vine forest and ecotone woodland of *Eucalyptus grandis*, with understorey rain forest elements, WTOF = *E. resinifera, E. reducta, Corymbia intermedia, Syncarpia glomulifera, Allocasuarina torulosa* and *Banksia aquilonia* tall open forest, DOF = *Eucalyptus reducta, E. portuensis, E. tereticornis, Corymbia intermedia, C. citriodora, C. stockeri* open forest, DOW = *Eucalyptus cullenii, E. portuensis, Corymbia stockeri* low open woodland and DAW = *Eucalyptus platyphylla* and *E. leptophleba* open woodland.

Site	Habitat	Altitude (m)	Altitude Band
B41	Rain forest and ecotone (RFE)	1000	>900
B42		940	
B43	Wet tall open forest (WTOF)	890	800-900
B44		870	
B45		850	
B46		810	
B47	Dry open forest (DOF)	780	700-800
B48		740	
B49		700	
B01		680	600-700
B02		650	
B50	Dry open woodland (DOW)	620	
B03		550	500-600
B04		550	
B05	Dry alluvial woodland (DAW)	350	300-500
B06		350	
B07		350	300-500

Common names, scientific names and authorities for fauna follow Clayton. (2006). Scientific names and authorities for plants follow Bostock & Holland (2007). However, there is some uncertainty regarding the species of *Sminthopsis* (Dasyuridae). Preliminary genetic analyses of specimens collected at high- and low-altitude sites, were in conflict with morphological characteristics of the species. Until this can be satisfactorily resolved we will refer to the two morphotypes as *Sminthopsis* sp. A (high-altitude species) and *Sminthopsis* sp. B (low-altitude species), though the putative species for each is *S. murina*.

Vegetation sampling

Structural and habitat variables were measured following the methods outlined in (Neldner *et al.* 2004) sampled along the 100-m transect line running perpendicular to the ridge line. Canopy heights and crown cover for each stratum were measured using a line intercept method (Neldner *et al.* 2004). A 100-m tape was laid down and the vertical projection onto the tape of the start and finish of each crown by species and strata was recorded. A vertical sighting tube was used to ensure that crown intercepts were vertically projected. The total length of crown was divided by the total length of the tape to give an estimate of percentage crown cover. Height of each stratum was measured using a clinometer and measurements were taken at the 0-, 50- and 100-m points of the 100-m tape and averaged. The ground cover (% live vegetation cover, rock cover) was visually estimated using five 1-m^2 quadrats placed at the 35-, 45-, 55-, 65- and 75-m marks of the tape. Site score represents the average of the five quadrats.

Analysis

For grouping and analysis of the data, we selected altitude bands over broad vegetation types. From convention, studies of mountain gradients are generally couched in the language of changes along altitude, and altitude is a convenient corollary of environmental gradients. To reconcile the use of altitude bands as representative of the environmental gradients, we tested via Spearman rank correlations the relationship between altitude, broad vegetation group category (numbered 1-6, with 1 the uplands vegetation group, and 6 the lowland vegetation group) and vegetation structural measures. We also tested the strength of the altitude band and broad vegetation groups to categorise variation in mammal assemblage via analysis of similarity (ANOSIM) (Primer version 6.1.11, Primer-E Ltd). ANOSIM tests *a priori* categorisation of multivariate data by non-parametric permutation applied to the underlying similar matrix. The larger output value R (rank similarities) the greater the separation of replicates between groups. We used fourth-root transformed Bray-Curtis similarity matrices derived from the mammal abundance data.

I investigated the adequacy of our sampling effort via sample-based (observed) rarefaction curves and estimate-based rarefaction curves (Chao2 estimates). We plotted the number of observed species and estimated species per altitudinal band (300, 500, 600, 700, 800 and 900+ m) against the number of trapping days consecutive over the four survey periods (1-20 d), using the module DIVERSE in Primer. If the curves approached the asymptote, those sites were considered sufficiently sampled. To account for variation among altitudinal bands, observed species accumulation curves were compared against the non-parametric randomization estimator Chao2 (McCain 2004) also using DIVERSE in Primer.

The relationship between altitude and the total abundance of small mammals, abundance of selected species (*Melomys cervinipes, Melomys burtoni, Rattus fuscipes, Dasyurus hallucatus* and *Zyzomys argurus*) and total species richness (pooled over all four sampling periods), were examined via generalised linear modelling (Crawley 1993) testing linear, non-linear and polynomial distributions (STATISTICA, version 6. StatSoft, Inc., www.statsoft.com). For each comparison we tested whether the linear, non-linear or polynomial fit best represented the relationship by examining the resultant residual sum of squares (linear regression), or percentage deviance explained (non-linear and polynomial regression). The percentage deviance explained is the difference between the model with the explanatory term included (e.g. altitude), against the model with the explanatory variable excluded.

The altitudinal distribution of each small-mammal species recorded was examined using weighted maximum-minimum, mean and standard error range plots, weighting each distribution by total abundance for each species at each altitude. Weighting adjusts the contribution of individual cases (e.g. altitudes) within the range plots in proportion to the values of a selected variable (e.g. abundance of mammal).

The variation in the mean abundance and richness of all species across the altitude bands, were examined using non-parametric (Kruskal-Wallis) one-way analysis of variance. We also tested variation of individual species abundance (data pooled across the four sample periods) for all small mammals recorded in more than three sites, and variation in habitat complexity (cover and height) also using non-parametric ANOVA.

Two-dimensional ordination using semi-strong hybrid multi-dimensional scaling (SSHMDS) derived from Bray-Curtis association (dissimilarity) indices were used to investigate variation in the assemblage composition (Belbin 1991). Three-dimensional ordination was forsaken due to low improvement in the stress, and the increase in complexity of the interpretation of the pattern sites for little gain in clarity. Ordinations used range-transformed total abundance data pooled over the four sampling periods. No clustering was undertaken; rather we used the altitude bands as the group classification, recognising that this is strongly correlated to vegetation and habitat change along the gradient (ANOSIM Global R = 0.74).

Principal axis correlation (PCC) was used to examine the correlation between environmental measures with the ordination pattern. PCC is a multi-linear regression program designed to identify how a set of attributes can best be fitted to an ordination space (Belbin 1993). The resultant output identifies the direction of best fit and a correlation coefficient. A Monte Carlo randomisation technique (MCAO) using 999 permutations was undertaken to test the statistical significance of the correlation coefficient of each vector (Belbin 1993). We tested the vegetation cover and height measures as environmental vectors to examine which were strongly correlated to the ordination pattern.

Results

There was strong correlation between altitude and broad vegetation group (R = 0.98), canopy cover (R = 0.59), subcanopy cover (R = 0.49), shrub cover (R = 0.76), canopy height (R = 0.79) and subcanopy height (R = 0.75). The *a priori* categorisation of the small-mammal assemblage using altitude bands was strong (Global R = 0.74) as it was for broad vegetation groups (Global R = 0.65). These results reinforce our contention that altitude is a strong surrogate for environmental variation along the gradient, and variation in the mammal assemblage composition. Subsequent analysis used altitude bands for grouping sites, recognising that this is in effect an environmental gradient.

Species accumulation curves for all altitudinal bands were all approaching the asymptote suggesting the sampling effort per site was adequate and suitable to examine patterns of species richness along the gradient. However the Chao2-estimated species richness suggested that for the 800-m band, the species richness was potentially underestimated compared to the samples for the other altitude band (Figure 2).

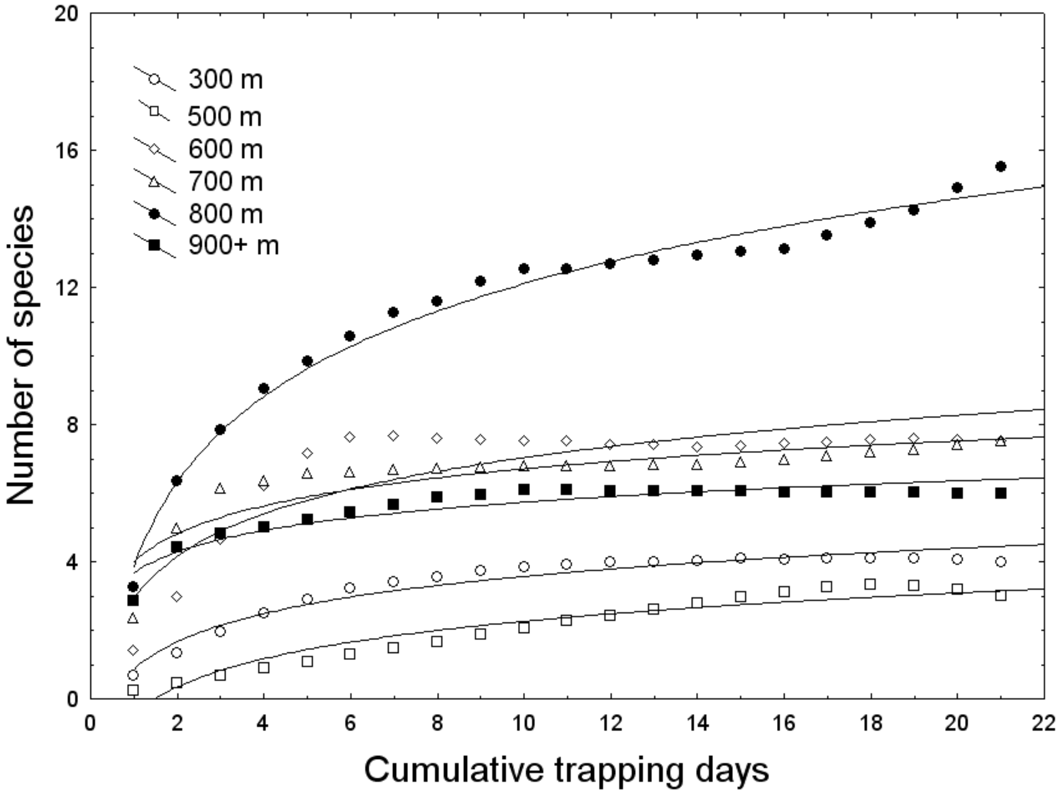

Figure 2. Estimated species accumulation curves (Chao 2) for the small-mammal species richness across six altitudinal bands (in metres). Cumulative trapping days are the four survey periods assessed combined in sequence.

The relationship between species richness and altitude was best characterised by a non-linear relationship (per cent deviance explained = 41%) (Figure 3a), as was the relationship between abundance and altitude (per cent deviance explained = 91%) (Figure 3b). Investigation of the pattern between individual abundance and altitude indicated a strong non-linear relationship between the rodents *M. cervinipes* and *R. fuscipes* and altitude (percent deviance explained = 88% and 66% respectively) (Figure 4a), and moderate polynomial relationships between *D. hallucatus* (32%), *M. burtoni* (20%) and *Z. argurus* (36%) (Figure 4b).

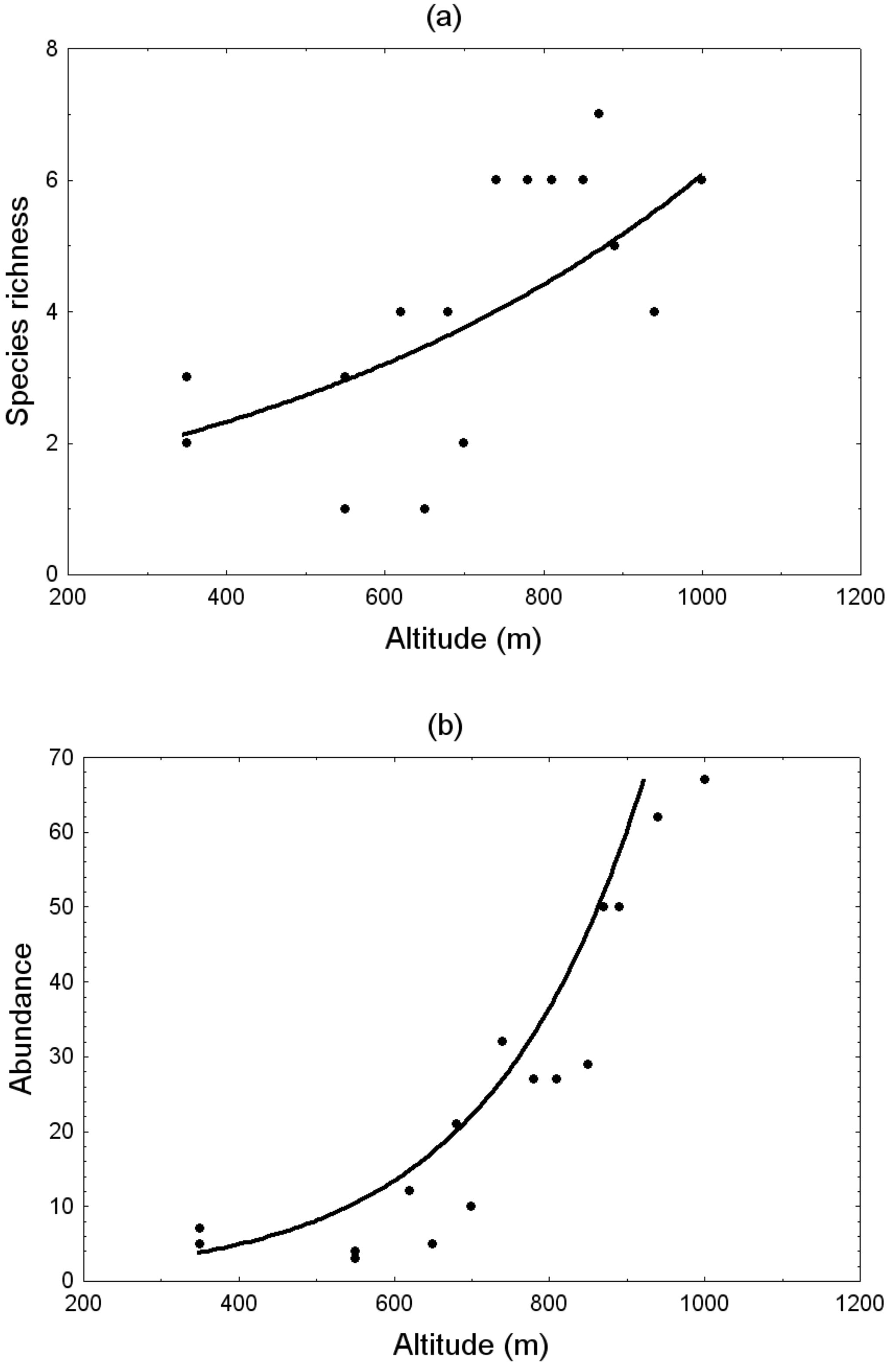

Figure 3. The relationship between the distribution of total mammal abundance (pooled over the four surveys) and species richness across the altitude gradient as identified via generalised linear modelling. Relationship with species richness ($y = e^{(0.21 + (0.0016\ x))}$) (a). A normal distribution with a log-link function was used. Relationship with abundance ($y = e^{(-0.40 + (0.005\ x))}$) (b). A normal distribution with a log-link function was used.

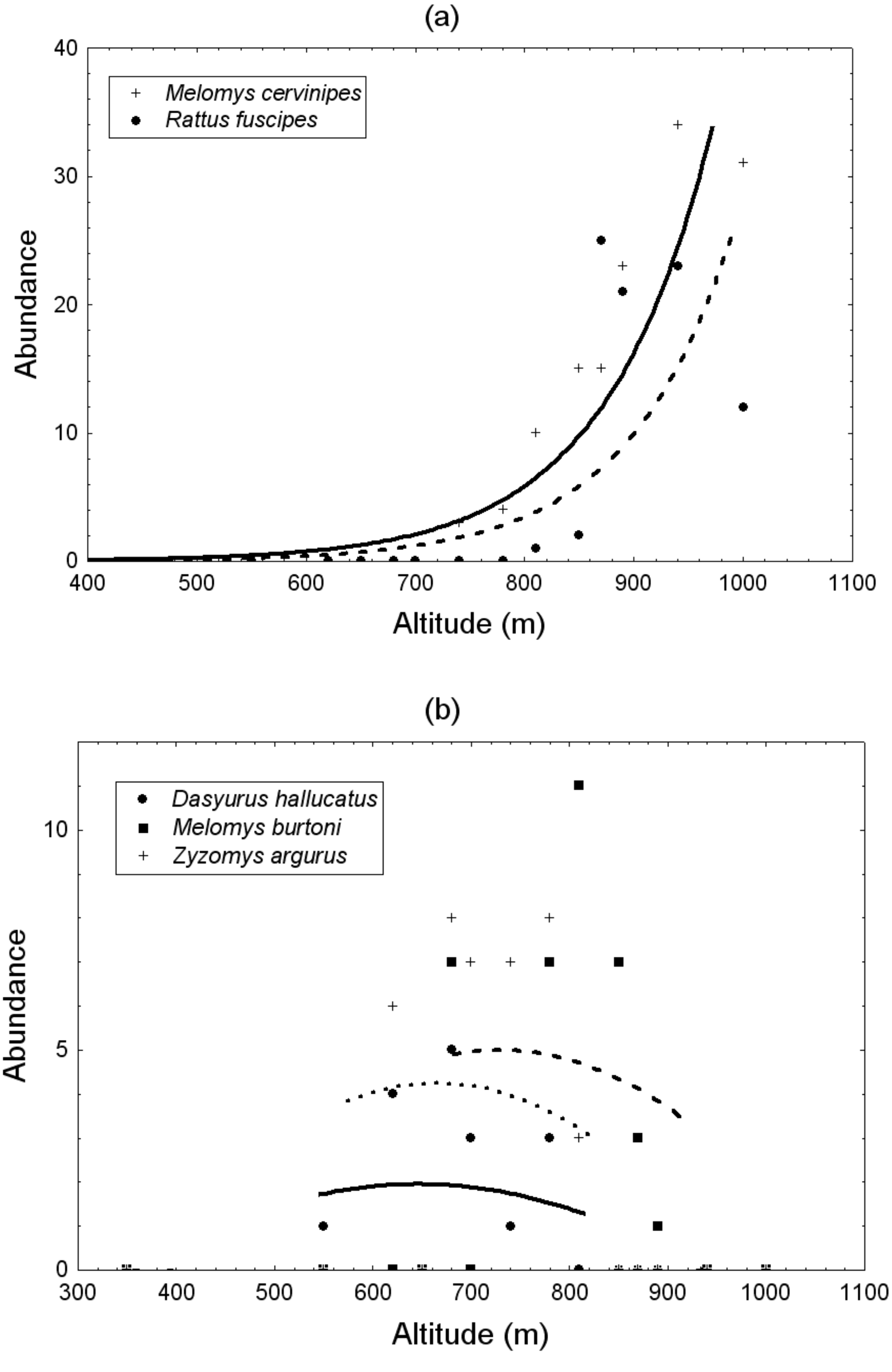

Figure 4**.** The relationship between the distribution of total mammal abundance (pooled over the four surveys), for selected species across the altitude gradient as identified via generalised linear modelling. Relationship with *Melomys cervinipes* ($y = e^{(-6.4 + (0.01x))}$) and *Rattus fuscipes* ($y = e^{(-7.2 + (0.011x))}$) abundance (a). A Poisson distribution with a log-link function was used. Relationship with *Dasyurus hallucatus* ($y = -7.8 + 0.03x - 2.3(10^{-5})x^2$), *Zyzomys argurus (*$y = -17.6 + 0.07x - 4.9(10^{-5})x^2$) and *Melomys burtoni* ($y = -18.6 + 0.06x - 4.4(10^{-5})x^2$) abundance (b). A polynomial distribution was used.

Seventeen species of mammal representing three families (Dasyuridae, 5 species; Peramelidae, 2 spp.; Muridae, 10 spp.) were recorded from 416 captures and 5100 trap-nights along the altitudinal gradient (Table 2). The most abundant species were *M. cervinipes*, *M. burtoni*, *R. fuscipes* and *Z. argurus*. The least abundant were *Perameles nasuta, Rattus sordidus* and *Rattus leucopus*. Five species were restricted to one altitude, though two of these (*R. leucopus* and *R. sordidus*) were represented only by a single capture (Figure 5). The remaining eleven species occupied sites over a range of altitudes with *M. cervinipes*, *M. burtoni, R. fuscipes, Isoodon macrourus, D. hallucatus* and *Pseudomys delicatulus* being the most cosmopolitan species, distributed between 200-300 m of altitude (Figure 5).

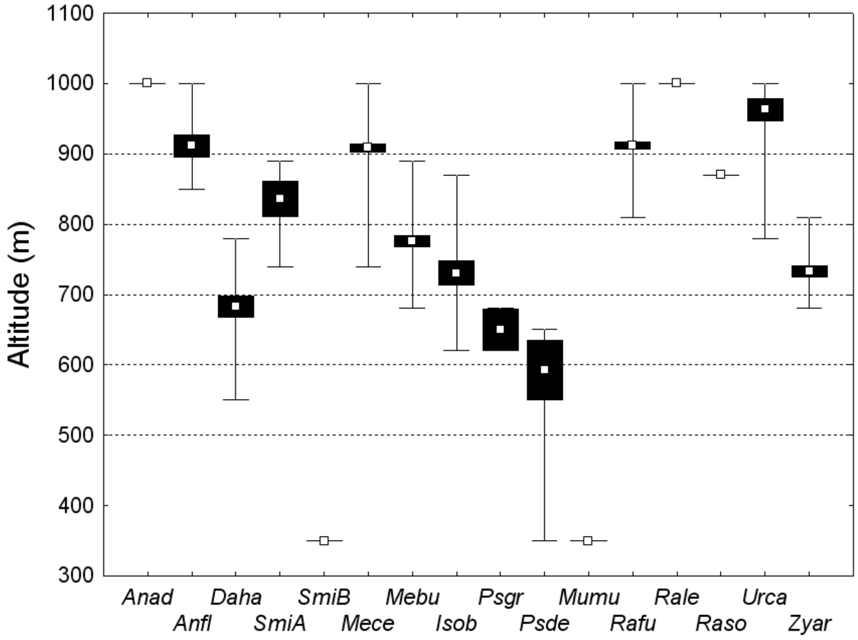

Figure 5. The mean, SE and range of altitudinal distribution of each small-mammal species recorded in this study. Each distribution is weighted by total abundance; that is weighting adjusts the contribution of individual cases (e.g. altitudes) within the range plots in proportion to the values of a selected variable (e.g. abundance of mammal). Species codes are as follows; *Anad = Antechinus adustus, Anfl = Antechinus flavipes, Daha = Dasyurus hallucatus, SmiA = Sminthopsis* sp. A, *SmiB* = *S.* sp. B, *Mebu =, Melomys burtoni, Mece = M. cervinipes, Mumu = Mus musculus, Psde = Pseudomys delicatulus, Psgr = P. gracilicaudatus, Rafu = Rattus fuscipes, Rale = R. leucopes, Raso = R. sordidus, Urca = Uromys caudimaculata, Zyar = Zyzomys argurus. Perameles nasuta* was recorded from a single individual from a single site and as such is not illustrated.

The distribution of species across the altitude bands, indicated that the most species-rich vegetation (total pooled data for all four surveys) was the 800-m band (11 species), followed by 700-m (7 spp. species) and the >900-m and 600-m bands (6 spp.). The total abundance, also pooled data for all four surveys was clearly highest in the 800-m (156 captures) and >900-m bands (128 captures) (Table 2). Mean site abundance was highest in the >900-m band (64.5 ± 2.5) and lowest declining steadily to the dry alluvial woodland (5.7 ± 0.7). Sites in dry open woodland and dry alluvial woodland had the lowest species richness (2.0-2.6) and mammal abundance was also low (3.5 and 5.7 respectively, Table 2). There was significant variation in species abundance across the altitude bands for five species; *M. cervinipes* (H = 14.8, P = 0.01) and *R. fuscipes* (H = 15.1, P = 0.009) most abundant in the high-altitude sites; *Z. argurus* (H = 11.3, P = 0.04) and *D. hallucatus* (H = 10.7, P = 0.05) in the mid-altitude sites and *Mus musculus* (H = 15.8, P = 0.007) in the low-altitude sites (Table 2).

The change in structure and dominant vegetation composition up the altitudinal gradient was from woodland dominated by two to three *Eucalyptus* spp., through diverse myrtaceous (*Eucalyptus*, *Corymbia*, *Banksia*) forest (dominated by 6 spp.), to rain forest at the top of the mountain (Table 1). In terms of habitat structure and complexity, there were significant changes in canopy and subcanopy height from the low-altitude sites (16.3 m for canopy, 7.0 m for subcanopy) to the >900-m band (28.5 m for canopy, 16.5 m for subcanopy) (Table 2). Canopy and subcanopy cover was highest in the > 900-m and 800-m bands (68%-64.5% for canopy, 28.5%-23.5% for subcanopy), declining sharply down the gradient to 38.7% (canopy) and 7.0% (subcanopy) at the bottom (Table 2). Shrub cover was significantly higher in the 700-m, 800-m and >900-m bands. Ground cover and height did not vary markedly along the gradient, but rock cover was significantly higher in the 600-m and 700-m bands.

Environmental vector fitting on the ordination (not illustrated) suggested that there were strong relationships between the small-mammal composition with canopy height ($r^2 = 0.57$), subcanopy height ($r^2 = 0.60$), rock cover ($r^2 = 0.43$), and canopy cover ($r^2 = 0.40$). The gradient for canopy height, subcanopy height and canopy cover broadly followed an axis of change from low-altitude to high-altitude sites (which also represents the shift from dry open woodlands through to the wet tall open forest and rain forest).The rock-cover gradient runs perpendicular to these axes, and identifies a mid- to low-altitude zone of rock outcropping (600-700 m).

Table 2. Species richness, abundance and habitat measures and individual species abundances for altitude bands. n = number of sites that a species was recorded. Data tabulated (with adjacent number in parentheses) are the mean scores and SE. Other data are totals. Variation in mean site richness, abundance, habitat measures and species was examined using non-parametric analysis of variance (Kruskal-Wallis). H is the test statistic for this ANOVA.

Factors	n	300-499 m	500-599 m	600-699 m	700-799 m	800-899 m	>900 m	H	P
Number of sites		3	2	3	3	4	2		
Richness		4.0	3.0	6.0	7.0	11.0	6.0		
Abundance		17.0	7.0	38.0	69.0	156.0	129.0		
Mean site species richness		2.6 (0.3)	2.0 (1.0)	3.0 (1.0)	4.7 (1.3)	6.0 (0.4)	5.0 (1.0)	9.6	0.09
Mean site abundance		5.7 (0.7)	3.5 (0.5)	12.7 (4.6)	23.0 (6.6)	39.0 (6.4)	64.5 (2.5)	14.1	0.02
Canopy height (m)		16.3 (0.7)	8.5 (0.5)	13.7 (2.4)	16.7 (0.3)	23.8 (3.5)	28.5 (6.5)	13.7	0.01
Subcanopy cover (%)		9.3 (4.7)	11.0 (0.0)	22.3 (6.2)	21.3 (14.4)	54.5 (11.7)	48.0 (38.0)	6.4	0.27
Subcanopy height (m)		7.0 (1.0)	4.0 (1.0)	5.0 (0.6)	8.0 (0.0)	13.5 (3.7)	16.5 (1.5)	12.9	0.02
Shrub cover (%)		0.0	1.5 (0.5)	8.3 (3.3)	15.7 (2.2)	17.8 (6.6)	12.5 (2.5)	11.1	0.05
Shrub height (m)		1.0 (0.0)	1.35 (0.2)	0.39 (0.3)	0.8 (0.2)	1.3 (0.2)	1.3 (0.5)	4.9	0.42
Ground cover (%)		38.6 (7.8)	46.0 (2.0)	20.7 (7.5)	16.7 (6.7)	40.0 (7.5)	32.5 (22.5)	6.6	0.25
Ground cover height (m)		0.6 (0.0)	0.2 (0.4)	0.3 (0.0)	0.23 (0.0)	0.4 (0.1)	0.8 (0.5)	8.6	0.12
Rock cover (%)		0.0	4.0 (0.0)	18.0 (8.7)	20.0 (7.6)	9.3 (4.3)	2.0 (0.0)	11.3	0.04
Dasyuridae									
Antechinus adustus	1	0.0	0.0	0.0	0.0	0.0	2.5 (2.5)		
Antechinus flavipes	4	0.0	0.0	0.0	0.0	1.3 (0.9)	1.5 (0.5)	10.2	0.07
Dasyurus hallucatus	6	0.0	0.5 (0.5)	3.0 (1.5)	2.3 (0.7)	0.0	0.0	10.7	0.05
Sminthopsis sp. A	3	0.0	0.0	0.0	0.3 (0.3)	1.0 (0.7)	0.0	5.3	0.38
Sminthopsis sp. B	1	1.0 (1.0)	0.0	0.0	0.0	0.0	0.0		
Muridae									
Melomys burtoni	7	0.0	0.0	2.3 (2.3)	8.3 (5.2)	5.5 (2.2)0	0.0	9.4	0.09
Melomys cervinipes	8	0.0	0.0	0.0	2.3 (1.2)	15.7 (2.7)	32.5 (1.5)	14.8	0.01
Mus musculus	3	3.6 (0.9)	0.0	0.0	0.0	0.0	0.0	15.8	0.007
Pseudomys delicatulus	3	0.3 (0.3)	0.5 (0.5)	1.7 (1.7)	0.0	0.0	0.0	4.0	0.54

Pseudomys gracilicaudatus	6	0.7 (0.7)	2.5 (0.5)	0.7 (0.3)	0.0	0.25	0.0	8.9	0.11
Rattus fuscipes	6	0.0	0.0	0.0	0.0	12.3 (6.3)	17.5 (5.5)	15.1	0.009
Rattus leucopes	1	0.0	0.0	0.0	0.0	0.0	1.0		
Rattus sordidus	1	0.0	0.0	0.0	0.0	0.75	0.0		
Uromys caudimaculata	4	0.0	0.0	0.0	0.7 (0.7)	0.3 (0.3)	9.5 (6.5)	10.3	0.06
Zyzomys argurus	6	0.0	0.0	4.7 (2.4)	7.3 (0.3)	0.8 (0.8)	0.0	11.3	0.04
Peramelidae									
Isoodon macrourus	6	0.0	0.0	0.3 (0.3)	1.7 (0.9)	1.0 (0.4)	0.0	7.6	0.17
Perameles nasuta	1	0.0	0.0	0.0	0.0	0.25 (0.25)	0.0		

Discussion

In this study, we found that richness of small non-volant mammals peaked towards the summit of the gradient and not at one-half the maximum altitude predicted by the mid-domain effect (McCain 2005; Currie & Kerr 2008). Such skews in richness peaks towards higher altitudes are indicative of climatic influences which are often associated with changes in vegetation (McCain 2005). Peak richness occurred at the point of optimal environmental conditions (high productivity and structural diversity) and the zone of rapid transition between distinct vegetation communities.

The altitudinal gradient of this study is situated on the western fall of the upland wet tropical region and provides a zone of rapid transition from dry savanna woodlands at lower altitude, through to high-rainfall areas with true rain forest on the mountain tops (Webb 1968; Harrington & Sanderson 1994). Temperature, precipitation, productivity and vegetation cover have been shown to influence patterns of species richness (H-Acevedo & Currie 2003; Williams & Middleton 2008) and richness often increases with increasing precipitation and humidity (O'Brien 1998; Nor 2001). In tropical regions, such as north-east Australia, species richness may be limited by precipitation (Nor 2001; H-Acevedo & Currie 2003) and variation in productivity is influenced more so by rainfall patterns, in particular precipitation seasonality, than temperature (Williams & Middleton 2008 and references therein). The savannas of this region are characterized by high seasonality of precipitation, and decreasing precipitation seasonality is observed with increasing altitude towards the wet-forest habitats (Woinarski *et al.* 2005; Williams & Middleton 2008). The increasing precipitation, decreasing precipitation seasonality, structural complexity and mammal diversity of the high-altitude habitats from this study is consistent with previous studies in the Australian wet tropics region (Williams & Marsh 1998). The small-mammal assemblage described here, appears to support the environmental hypothesis that predicts peak richness where climate is the most favourable rather than a geographic or mid-domain effect (Currie & Kerr 2008). This is consistent with other recent studies where climate has been shown to be an important influence on species diversity patterns (H-Acevedo & Currie 2003; McCain 2007a, b; 2009). Species abundance also increased with increasing altitude, a typical relationship where high abundance is strongly related to high productivity, in this case associated with rain-forest vegetation (Williams *et al.* 2002).

Unlike other gradient studies, there was no clear evidence of any major point of species disjunction (Lacher & Alho 2001; van Ingen *et al.* 2008), and, instead a gradual overlap and replacement of species was observed. The key point of change was where the savanna and rain-forest vegetation were adjacent, and these transition zones between dry and wet forests tend to be sources of diversity due to increased landscape complexity (Lacher & Alho 2001; Lomolino 2001). Such richness peaks at transition zones are common in tropical altitudinal gradients of small non-volant mammals, and often occur where communities from adjacent zonal habitats overlap in species ranges (Heaney 2001; Lomolino 2001; Nor 2001; Rickart 2001; Sanchez-Cordero 2001). This suggests that species diversity along the gradient in this study is not only a function of local conditions within one vegetation type, but also of neighbouring resources in adjacent types. A mass effect occurs where there are marginal habitat patches that are suitable yet suboptimal, which allows temporal and spatial variation in habitat occupation (Williams *et al.* 2002). The rapid transition of habitat types along altitudinal gradient only enhances this effect.

Outside tropical environments, patterns of mammal composition through conifer forest to desert, indicated that temporal and habitat variation was as influential as altitude change (Kelt 1999). This suggests that, despite some universal patterns associated with altitude gradients, there are regional idiosyncratic influences on mammal pattern such as biogeography, landscape context, level of disturbance, and habitat extent and structural diversity of the transect in question. We found this to be the case in our study too; that is the strong relationship between saxicolous small-mammal species (*D. hallucatus*, *Z. argurus*) and rock cover within the 600-m and 700-m altitudinal bands. In this case substrate, not vegetation type, was influential on species pattern. Local habitat variation within gradient can control assemblage pattern, quite apart from altitude, climate or vegetation change (Kelt 1999).

The sudden depletion of the mammal assemblage below 600 m is partly influenced by the occurrence of feral predators and the historical poor management of Australian rangelands (Johnson 2006; Kutt & Woinarski 2007). Some species unrecorded in this study (the rodents *Rattus tunneyi*, *Mesembriomys gouldi* and the dasyurid *Planigale maculata*), might have be absent for reasons of natural rarity, or reduced abundance due to range contractions in north-eastern Australia caused by land management (Braithwaite & Brady 1993; Braithwaite & Griffiths 1996; Kutt & Woinarski 2007). Where *R. tunneyi* occurs in high numbers, it is easily caught by the methods utilised in this survey, so its absence from the transect at low altitudes is probably a factor of land management (Braithwaite & Griffiths 1996). On the other hand *M. gouldi* is an arboreal rodent that is extremely trap-shy; its absence might be a trapping artefact. Similarly the very small dasyurid *P. maculata* is widely distributed and disturbance-tolerant but more readily recorded through pitfall trapping (A. Kutt pers. obs.). Other species captured at higher altitudes on this transect that should occur in the lower-altitude savanna woodlands (*M. burtoni, P. gracilicaudatus, D. hallucatus, I. macrourus*) were absent, and this is function of species-specific effects ((i.e. ingestion by D. hallucatus of cane toad and its fatal toxin(Burnett 1997)) , or broader land-management impacts on these species (Woinarski *et al.* 2001).

The two species recorded in the dry open and alluvial woodlands *P. delicatulus* and the introduced *M. musculus*, are adapted to disturbed sites being able to persist in sites with sparse ground cover (*P. delicatulus*) or highly modified environments (*M. musculus*) (Braithwaite & Brady 1993; Kutt & Woinarski 2007). From a global perspective, lowland and upland sites on altitude gradients tend to be the most disturbed montane communities, and thus species poor (Rahbek 1995; Nogues-Bravo *et al.* 2008). This modification of habitats alters natural diversity patterns along such gradients, making it more difficult to discern any patterns in diversity which may exist (Nogues-Bravo *et al.* 2008). Similarly the low-altitude sites on the gradient, and the associated low species richness may simply be a function of low environmental suitability and productivity (i.e. low rainfall, simple structural diversity) (Rowe 2009), which is compounded by poor land management (Kutt & Woinarski 2007).

This study examined sites from 300 m to 1000 m, omitting sites between 1000 m and 1250 m (the peak of this mountain range) as well as sites within the

400-m altitudinal band. Recent work has shown that omission of part of any gradient can allow for observations of only an element of the true pattern (Nogues-Bravo *et al.* 2008). It is generally accepted that peaks of species richness are expected to occur between 1000 and 2500-m, and beyond a certain altitude, there is a decrease in habitat heterogeneity and in most cases a decline in mammal species richness resulting in a mid-altitude peak in species richness (Heaney 2001; Mena & Vázquez-Domínguez 2005). This is the case for most mountains that have longitudinal montane gradients (<300 m to > 1900 m) (Rahbek 1997; Goodman & Rasolonandrasana 2001; Mena & Vázquez-Domínguez 2005). Regardless, the maximum potential height of Mt Lewis (our study area) is only 1250 m and the minimum at 300 m. As the study site is considered to be a small site (100-1000 km^2) and Mt Lewis is a small mountain (<1250 m), what variation does present is most likely a factor of vegetation type and biotic interactions rather than altitude and climate at such a scale, and such mountains are expected to have little variation in species richness (Körner 2000; Heaney 2001; Hortal *et al.* 2008). As the regions of the gradient left out of this survey display consistent vegetation characteristic to the sites sampled within this survey we are confident the range we encompassed will reflect true species patterns of this mountain.

Conclusion

In this study, we found a peak in species richness of small non-volant mammals towards the summit of the altitude gradient at the point of optimal environmental conditions and greatest vegetation juxtaposition. With increasing altitude, the steep gradient caused a gradual overlap and replacement of species and increasing species diversity was observed. I suggest that our study identifies a more typical ecological concept; that is there is a relationship between local habitat, resource heterogeneity and species richness supporting the environmental hypothesis rather than a mid-domain effect. Similarly species richness was influenced by local effects, such as the relationship between certain species (e.g. saxicolous) and habitat resources (e.g. rock outcrop), and a combination of anthropogenic effects and low primary productivity (e.g. lower rainfall) at the lowest altitude sites.

I support the contention that, despite some universal patterns associated with altitude gradients, there are regional idiosyncratic influences on mammal pattern such as biogeography, landscape context, level of disturbance, and habitat extent and structural diversity of the transect in question. However our study only provides one example from Australia, and it is imperative that more such studies are conducted in other transect and in different environmental conditions (e.g. alpine Australia), to observe how altitudinal and environmental gradients vary both regionally and across taxa. These natural experiments that provide data on how species patterns change with changing climate (e.g. reduced rainfall, increased temperatures and rainfall seasonality) and landscape effects (e.g. fire frequency) will provide significant information with respect to the resilience or adaptability of fauna patterns to changing global environmental conditions.

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