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An Uphill Battle: The Impacts of Climate Change on Montane Rainforest Vertebrates



Thesis submitted by

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Green Ringtail Possum (*Pseudochirops archeri*) in Mount Lewis National Park

Photo by Supalak Siri

Publications Associated with this Thesis

Chapter Two

de la Fuente, A., Hirsch, B.T., Cernusak, L.A. and Williams, S.E. (2021). Predicting species abundance by implementing the ecological niche theory. *Ecography*, 44: 1723–1730. <https://doi.org/10.1111/ecog.05776>

Chapter Three

de la Fuente, A., Krockenberger, A., Hirsch, B.T., Cernusak, L.A., & Williams, S. E. (2022). Predicted alteration of vertebrate communities in response to climate-induced elevational shifts. *Diversity and Distributions*, 28, 1180–1190. <https://doi.org/10.1111/ddi.13514>

Chapter Four

de la Fuente, A., Navarro, A., & Williams, S. E. (2023). The climatic drivers of long-term population changes in rainforest montane birds. *Global Change Biology*, 29, 2132–2140. <https://doi.org/10.1111/gcb.16608>

Chapter Five

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Chapter Six

de la Fuente, A., Youngentob, K.N., Marsh, K.J., Krockenberger, A., Williams, S. E., Cernusak, L.A. (2024) Relationships between abiotic factors, foliage chemistry and herbivory in a tropical montane ecosystem. *Oecologia*, 206, 293–304. <https://doi.org/10.1007/s00442-024-05630-y>

Statement of the Contribution of Others

My advisory panel Stephen Williams, Andrew Krockenberger, Lucas Cernusak, and Ben Hirsch provided advice and supervision in most aspects of the thesis. Stephen Williams co-authored chapters two, three, four, and five and contributed to developing all chapters. Andrew Krockenberger co-authored chapter three and contributed to the development of chapters six and seven. Lucas Cernusak co-authored chapters two and three and contributed to chapters six and seven. Ben Hirsch is a co-author of chapters two and three.

Stephen Williams designed the monitoring surveys methodology and taught me the survey protocol, which I used during my fieldwork. Stephen, as my primary supervisor, oversaw the general development and direction of the thesis, particularly chapters two, three, four, and five. However, Lucas Cernusak took a more prevalent role as a mentor in the later stages of my PhD due to my Stephen's retirement.

Paul Nelson helped develop the soil sampling protocol for the study and helped choose the appropriate chemical assays for the development of chapters six and seven.

Alejandro Navarro contributed to chapter four by developing the models that generated the cyclone variables used in the rainforest bird population model. Alejandro Navarro also contributed to the overall development of chapter four and assisted with editing the published paper.

Kara Youngentob and Karen Ford hosted me at the Australian National University and taught me the chemical assays used to determine the nutritional quality of foliage in chapters six and seven. They oversaw all the lab work and assisted in every step of the process. They also contributed to the development of chapters six and seven and provided detailed edits and comments in all the drafts.

Michael Kearney from the University of Melbourne designed the microclimate model used in chapter seven and helped to create the mechanistic model for ringtail possums. He also contributed to the overall development of the chapter and provided detailed edits and comments in all drafts.

Natalie Briscoe from the University of Melbourne significantly contributed to all the aspects related to chapter seven. Natalie hosted me at the University of Melbourne while developing the mechanistic model and designed many aspects of the analytical design, providing excellent feedback throughout. Natalie also provided detailed edits and comments in all drafts.

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Statement of the Use of Generative AI

Generative AI technology was not used in the preparation of any part of this thesis.

Thesis Abstract

Climate change has exposed biodiversity to unprecedented conditions, with tropical ecosystems particularly vulnerable to its effects. This thesis investigates the multifaceted impacts of climate change on tropical montane ecosystems, focusing on abundance-suitability relationships, community reshuffling dynamics, population responses to climate change, biogeochemical dynamics, and the underlying physiological mechanisms driving population declines. Drawing on three decades of region-wide monitoring data in the Australian Wet Tropics, this research bridges critical gaps in our understanding of how climate change leads to biodiversity erosion in tropical montane regions, with a particular focus on rainforest birds and ringtail possums.

At the core of this thesis is the exploration of habitat suitability as a fundamental aspect of fitness, where I investigate the complex interplay between species abundance and environmental factors. By employing state-of-the-art modelling techniques and incorporating biologically relevant predictors, I demonstrate a five-fold increase in accuracy at predicting habitat suitability compared to previous efforts, uncovering key environmental factors shaping fitness for rainforest vertebrates.

Furthermore, this research investigates the escalating impacts of climate change on ecosystems through biotic disruption, revealing how dispersal differences among shifting species drive community reshuffling dynamics. By quantifying the accumulating pressure that climate change poses on communities, it becomes evident that the pace of climate-induced biodiversity erosion in montane ecosystems is often underestimated. Low-dispersal species with core populations in the uplands face imminent disruption due to the rapid warming observed along mountain slopes.

Delving into the multidimensional nature of climate change, I examine the biological responses to the press and pulse of climate trends and extreme events through the lens of population dynamics. I highlight an unequivocal link between climate change and population alteration for rainforest birds and ringtail possums. However, I uncovered substantial differences in species' abilities to track climate change, with rainforest birds primarily influenced by gradual warming and precipitation changes (presses), while low-dispersal ringtail possums succumb to extreme heatwaves (pulse). These findings underscore the urgency of proactive conservation

strategies, as climate change threatens the extinction of many endemic species within the next two decades.

Moreover, my research unravels the underlying mechanisms of climate-induced population collapse, demonstrating how climate change directly reduces animal fitness. By integrating experimental studies and ecological modelling, this study provided valuable insights into the causal links between environmental change and population declines, with a focus on rainforest ringtail possums. Specifically, it reveals that the impacts of climate change on ringtail populations are fundamentally linked to reductions in survival and recruitment resulting from increased overheating, dehydration, and reduced foraging performance. These findings offer actionable strategies for conservation and management efforts, emphasising the importance of addressing the physiological stressors exacerbated by climate change in tropical montane ecosystems.

In conclusion, my thesis underscores the urgent need for proactive conservation strategies in the face of climate-induced ecological disruptions. By leveraging long-term monitoring data and integrating advanced modelling techniques, this research advances our understanding of the complexities of climate change impacts on tropical montane ecosystems and provides a roadmap for evidence-based conservation actions. Continued investment in long-term monitoring programs is essential for addressing the ongoing challenges posed by climate change and safeguarding the resilience of montane biodiversity for future generations.

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Chapter seven

- Figure 7.1. Conceptual illustration of the study framework. Grey circles denote the diverse datasets utilised to parameterise and calibrate/validate the models. Dotted white rectangles delineate the principal models within the framework, while blue rectangles symbolise the derived parameters facilitating the integration of biophysical and biogeochemical models into the population model. Note that hourly weather data, soil, and topographic information also form part of the development of the microclimate model, but these datasets

are internally generated by the NicheMapR package (Kearney & Porter 2017) are therefore omitted in the figure. We also omitted some variables considered in the development of the population model but were not derived from the processes outlined. These include the effect of elevation on the initial population, the effect of density dependence on survival and recruitment, and the effect of the number of surveyors on detectability.

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- Figure 7.3. Conceptual summary of population dynamics for ringtail possums. Dotted lines represent the processes that led to the factors that informed population dynamics. Solid lines represent the direct effect of different predictors on population processes. Values represent the mean effect for those factors, with black values showing positive correlations while red values indicate negative effects. Subscript values represent the credible interval, describing the uncertainty around the mean effect, indicating the 5.5th and 94.5th percentiles of the sorted posterior samples. Panel A shows the results for *P. archeri*, and panel B shows the population dynamics of *H. lemuroides*.
- Figure 7.4. Summary of population trajectories for rainforest ringtail possums. Results are presented in a matrix with elevation and foliage nitrogen as its axes. Elevation categories range between 400-700 (low), 800-1100 (mid), and 1100-1350 (high). Foliage nitrogen concentration is divided into low concentration (below the 33rd percentile), mid concentration (between the 33rd and 66th percentile), and high concentration (above the 66th percentile). Pink boxes show the population state for *P. archeri*, while orange boxes show the population state for *H. lemuroides*. Plots A-D show the predicted true abundance (black) and raw count data uncorrected for detection probability (blue) for selected examples. Plots A-C show populations of *P. archeri*, while D-F represent populations for *H. lemuroides*.

Supplementary Figures

Chapter two

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- Figure S3.4. Graphical summary of the methodological framework developed for the uphill shift simulation in the Australian Wet Tropics. The top half represents the workflow followed to simulate the cost of elevational shifts. First, we defined the targeted patches based on habitat type and elevation. Then, we created different transition layers based on landscape resistance under different scenarios (from current climate +0°C to +5°C, with +1°C step). Using this background, we calculated the cost of shifting using least-cost path analysis. The bottom half represents the community re-shuffling simulation, where species are exposed to the framework developed in the top half. At each patch, we defined assemblages using species predicted potential habitat derived from SDMs. We calculated the likelihood of species within assemblages of shifting to higher elevations based on their dispersal potential (i.e., when the species dispersal potential was higher than the predicted distance between patches the shift was successful, and vice versa), this induced a community re-shuffling process that resulted in changes in community structures, measured as β -dissimilarity.
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- Figure S3.7. Change in multisite spatial β -dissimilarity along the elevational gradient in the Australian Wet Tropics. The figure represents the difference in the overall spatial β -dissimilarity (β_{jac}) across taxa and elevation between the baseline and five elevational shift scenarios (from +0°C to +5°C, with +1°C step).
- Figure S3.8. Change in multisite spatial β -dissimilarity along the elevational gradient in the Australian Wet Tropics. The figure represents the spatial change in the nestedness component (β_{jne}) across taxa and elevation

between the baseline and five elevational shift scenarios (from +0°C to +5°C, with +1°C step).

- Figure S3.9. Predominant component driving the change in β -dissimilarity in the simulated climate-induced uphill shift. Values above 0.5 indicate a change in β -dissimilarity predominantly driven by the nestedness component (β_{jne}), and values below 0.5 indicate that spatial turnover mainly influences the overall change in β -dissimilarity. Colours depict the stepwise increase in global warming from the current climate (+0°C; dark blue) to +5°C scenario (yellow), with a +1°C step.
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- Figure S3.11. Sensitivity analyses outputs. The figure shows the different output in local extinction rate obtained with $\pm 5\%$, $\pm 10\%$ (dashed line; note that there is not change between 5 and 10% so the lines corresponding to these scenarios overlap), and $\pm 50\%$ (solid line) change in species dispersal capacity compared to the observed pattern (middle solid line connecting solid dots; based on Williams et al. 2010's potential dispersal index). Colours depict the stepwise increase in global warming from the current climate (+0°C; dark blue) to +5°C scenario (yellow), with a +1°C step.

Chapter four

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- Figure S4.7. Species-specific response to climate change. Values represent the posterior mean and 95% CRI. A reference to the species code can be found in Table S4.2. Species' codes are ordered by their core elevation, with elevation increasing from bottom to top.
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Chapter five

- Figure S5.1. Elevation map of the Australian Wet Tropics bioregion with biogeographic subregions after Williams et al. 2010.
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- Figure S5.5. Formal examination of potential changepoints in population trend related to global warming (mean annual temperature trend; left panel), and extreme heatwaves (number of hot days; right panel). Black points depict observed climatic values. Coloured points represent the posterior mean value of the changepoint associated with each species, with the coloured vertical lines representing the 95% CRI. Horizontal dashed lines highlight the climatic value associated with the posterior mean of the changepoint.
- Figure S5.6. Visual examination of the synchronisation between population fluctuation and climatic trends of ringtail possums in the Australian Wet Tropics. Note that the temporal variation in climate is already accounted for in the population estimation. Thus, this figure does not explicitly represent the linear relationship between climate change and population dynamics. The linear effect of climate change on population size is reported in Figure 5.2 and Table S5.1. “MAT” stands for Mean annual temperature and the “number of hot days” is included in the model as the “extreme heatwaves” variable.
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Chapter six

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- Figure S6.2. Posterior predictive check and Bayesian p -value for the final sub-models.
- Figure S6.3. Patterns in herbivory across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.
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- Figure S6.5. Patterns in foliar N digestibility across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.
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Chapter seven

- Figure S7.1. Example of microclimate calibration on a selected number of sites and years based on daily temperatures. Each panel represent a different study location. Green lines represent the non-calibrated microclimate generated using the NicheMapR package, red lines depict the interpolated data for the region obtained from Storlei et al. (2013), and blue lines represent the calibrated microclimate.
- Figure S7.2. Validation of the microclimate adjustments. Red lines represent the calibrated microclimate generated using NicheMapR while the black lines depict the field microclimate data obtained from Leahy et al. (2022).

- Figure S7.3. Daytime den thermal buffer for *H. lemuroides*. Data represent mean den buffer potential (n = 14 dens) across hour of the day (daytime only) and month of the year. The buffer variable (y-axis) represents the average difference in temperature between the den and canopy, with positive values indicating that the ambient is hotter than inside the den.
- Figure S7.4. Green ringtail possum (*Pseudochirops archeri*) pelt with the four main fur areas highlighted by red circles.
- Figure S7.5. Observed and predicted physiological response of two rainforest ringtail possum species under control environmental conditions (metabolic chamber). Red values are derived from the endotherm model (Kearney et al., 2021) using the animal model calibrated with values showed in Table S7.3. Black values represent the measured physiological response from Krockenberger et al. (2012) and Krockenberger (unpublished). Plots in the top row correspond to *Pseudochirops archeri* while plots in the bottom row correspond to *Hemibelideus lemuroides*.
- Figure S7.6. Conceptualisation of the scenario selection approach for rainforest ringtail possums. We note differences in the exposure to the environment while resting for *Hemibelideus lemuroides*, as the species would rest in dens during the day but stay in the canopy at night. Therefore, we assumed the animal would not return to the den to rest at night between foraging events, as this behaviour was not observed in the field.
- Figure S7.7. Spatiotemporal patterns in energy requirements for two species of rainforest ringtail possums. Black lines represent the cumulative 4-days energy requirements. Red lines represent a linear model fit to visualise the overall tendency along the gradient of interest.
- Figure S7.8. Conceptualisation of data collection and integration in the biogeochemical model.
- Figure S7.9. Conceptual figure of the model integrating biogeochemical dynamics and biophysical variables into population modelling. In the biogeochemical model, all values on the left side of the bracket were included as predictor of the responses on the right side of the bracket. For example, Soil P was modelled as a function of geology, temperature, and precipitation,

while foliar total N was modelled as a function of geology, temperature, precipitation and all soil elements (N, P, C:N, Na, and K).

- Figure S7.10. Posterior predictive check and Bayesian p-value for the biogeochemical sub-models.
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- Figure S7.12. Comparison of variable effect between the two competing models for *Pseudochirops archeri*. Orange values correspond to model 1 and blue values correspond to model 2.

Location of Online Data Associated with this Thesis

Chapter Two

de la Fuente, Alejandro; Hirsch, Ben; Cernusak, Lucas; Williams, Stephen (2021). Predicting species abundance by implementing the ecological niche theory [Dataset]. Dryad. <https://doi.org/10.5061/dryad.0zpc866wv>

Chapter Three

de la Fuente, Alejandro; Krockenberger, Andrew; Hirsch, Ben; Cernusak, Lucas (2022). Predicted alteration of vertebrate communities in response to climate-induced elevational shifts [Dataset]. Dryad. <https://doi.org/10.5061/dryad.ksn02v759>

Chapter Four

de la Fuente, Alejandro; Navarro, Alejandro; Williams, Stephen (2023). The climatic drivers of long-term population changes in rainforest montane birds [Dataset]. Dryad. <https://doi.org/10.5061/dryad.hx3ffbqjj>

Chapter Five

de la Fuente, Alejandro; Williams, Stephen (2022). Climate change threatens the future of rainforest ringtail possums by 2050 [Dataset]. Dryad. <https://doi.org/10.5061/dryad.m63xsj44h>

Chapter Six

de la Fuente, Alejandro (2024). Relationships between abiotic factors, foliage chemistry and herbivory in a tropical montane ecosystem [Dataset]. Dryad. <https://doi.org/10.5061/dryad.d51c5b08s>

Chapter One - Introduction

The Urgency of Global Climate Change

The current state of global climate change, characterised by warming occurring at a pace unparalleled in the last 65 million years, presents a dire scenario (Diffenbaugh & Field 2013). Anthropogenic activities have unleashed a cascade of environmental disruptions, causing biodiversity erosion at an alarming rate (Hoegh Guldberg *et al.* 2018). As a result, habitat suitability for many species is undergoing significant shifts, compelling them to adapt, migrate, or face extinction (Berg *et al.* 2010).

The predominant response to climate change for many species is to shift their distribution, yet not all species are equipped to keep pace with these rapid changes (Chen *et al.* 2011; Pecl *et al.* 2017; Hoegh Guldberg *et al.* 2018; Pörtner *et al.* 2022). Consequently, species unable to track environmental changes face declining populations, and in many cases, outright extinction (Urban 2015). Climate-induced distributional shifts have led to severe population declines in nearly half of all studied species (Pörtner *et al.* 2022). The severity of these declines correlates with the speed at which habitat suitability diminishes as climate warms (Chen *et al.* 2011), with populations situated at the warmer edge of their environmental range often facing local extirpation (Colwell *et al.* 2008; Freeman *et al.* 2018; Urban 2018). Tropical montane ecosystems, with their exceptionally high warming velocities along mountain slopes (Chan *et al.* 2024), are particularly vulnerable, with up to 84% of all endemic species facing a high risk of extinction (Pörtner *et al.* 2022).

Climate change and the Australian Wet Tropics

The Australian Wet Tropics of North Queensland, renowned for its rich biodiversity yet highly susceptible to the impacts of global warming, serves as a pertinent case study (Williams *et al.* 2016). Projections concerning the future of this unique ecosystem under anthropogenic climate change have painted a grim picture, particularly for cooled-adapted upland endemic species (Williams, Bolitho & Fox 2003). More than 50% of these species are forecasted to face extinction due to a

complete loss of suitable climatic space. These dire predictions have spurred intensified research efforts over the past decades, with ongoing extensive region-wide surveys of numerous vertebrate taxa (Williams *et al.* 2010). Nearly twenty years later, evidence suggests that these predictions have become a reality. Recent observations of dramatic range shifts and declines of bird species in the Australian Wet Tropics (Williams & de la Fuente 2021) underscore the catastrophic impacts that climate change is having on the region's biodiversity (Williams, Bolitho & Fox 2003). The Australian Wet Tropics thus offers a unique opportunity to study the impacts of climate change. With ongoing extensive region-wide surveys dating back to the early 90's, researchers can investigate how climate change has impacted communities and populations of rainforest vertebrates over the last three decades, enabling a deep understanding of the factors and mechanisms underlying climate-driven ecological responses in tropical mountains.

To further contextualise the impacts of climate change on Australian montane rainforests, it is crucial to consider species-specific biological responses and community-level interactions. While many species in these ecosystems are shifting their distributions in response to changing climatic conditions (Williams & de la Fuente 2021), there is considerable variability in their ability to adapt, with some species more vulnerable due to specialised ecological niches or limited dispersal capacities. Understanding these differences, along with the main driving forces such as climate vulnerability and nutrient availability, is key to predicting future species dynamics. This thesis integrates experimental and ecological approaches to better understand the mechanisms behind these responses, as explored in later chapters, particularly focusing on the physiological and ecological factors shaping species' fitness and population trajectories of threatened vertebrates in the Wet Tropics.

From Predicting Extinction to Understanding the Processes

The alarming predictions about the effects of climate change on ecosystems have guided substantial research efforts towards quantifying the current state of climate-induced biodiversity erosion worldwide (Chen *et al.* 2011; Pecl *et al.* 2017; Hoegh Guldberg *et al.* 2018; Pörtner *et al.* 2022). Despite the outstanding importance

of this research, it has often focused on documenting patterns in population declines and extinctions rather than delving into the fundamental processes driving these responses. As a result, after more than three decades of intensive research effort, there remains a significant gap in understanding the underlying mechanisms leading to population declines, hindering advances in conservation and global change biology (Parmesan, Root & Willig 2000; Parmesan 2006; Pearce-Higgins *et al.* 2015). Examples like the rainforest vertebrates in the Wet Tropics underscore the urgency of addressing this question, as the fate of many species may depend on timely, targeted, and effective conservation actions.

Climate Change and Animal Fitness

Understanding the mechanisms underlying climate change impacts on animal populations has been a focal point of research, primarily through two paradigms: experimental and ecological studies. Experimental studies aim to uncover processes to infer their implications for natural populations, while ecological studies often begin with observed ecological responses to infer the underlying processes.

Experimental studies

One approach towards unravelling the causal link between climate change and population dynamics involves investigating how the environment affects animal fitness by exploring fundamental constraints on survival and recruitment (Briscoe *et al.* 2023). Building on this goal, considerable research effort has been directed towards understanding species' physiological responses under controlled experimental designs that simulate realistic climate change scenarios, such as lab conditions or common garden experiments. While these experimental studies offer valuable insights into species' mechanistic responses to warming, they do not capture the complexity of the multidimensional factors that animals must balance in nature. This limitation increases uncertainty regarding how findings from experimental designs might translate to natural populations (Briscoe *et al.* 2023).

Ecological studies

From an ecological perspective, studying animal fitness involves exploring factors contributing to habitat suitability. Central to this approach is ecological niche theory, which posits that local abundance reflects how well a site meets a species' needs across various ecological axes (Hutchinson 1957; Brown 1984). Understanding the environmental factors that fundamentally constrain species distribution and abundance can provide valuable insights into how species might respond to changes in these conditions (VanDerWal *et al.* 2009), a key point for forecasting species responses to climate change. However, the intricacies of these relationships hinder our ability to understand the underlying link between abundance and habitat suitability (He & Gaston 2007; Weber *et al.* 2017). These complexities arise because such responses are generally nonlinear, often have thresholds, and may change with novel conditions (Beissinger & Riddell 2021). Recognising this complexity, there is a growing consensus on the need to explicitly incorporate mechanisms into models of species' responses to environmental change to improve predictions and management outcomes (Urban *et al.* 2016). However, determining which mechanisms to incorporate remains a daunting task, as they could relate to various topics in ecology, evolution, and physiology, such as life history, population dynamics, dispersal, and biotic interactions (Briscoe *et al.* 2019).

Unifying Experimental and Ecological approaches

Biophysical ecology offers a promising avenue for bridging the gap between experimental studies and observed ecological responses, thereby addressing the limitations of these approaches while amplifying their strengths (Briscoe *et al.* 2023). Mechanistic models based on the principles of biophysical ecology leverage the laws of physics and chemistry to capture species thermodynamics in a given environment, including the balances of heat, water, and other aspects of energy and mass exchange. By determining the fundamental physical and chemical constraints that species must endure in their natural environment, the output of these models translates to metrics of fitness (Gates 1980), which can be naturally integrated into ecological models to mechanistically explain and predict species responses to past, present, and future climate (Buckley 2008; Kearney *et al.* 2010; Riddell *et al.* 2019;

Briscoe *et al.* 2023). Despite the potential benefits, the integration of statistical and mechanistic methods to understand and predict climate change impacts remains largely unexplored.

Thesis Objectives and Structure

The overarching goal of this thesis is to gain insights into the factors and mechanisms underlying species' responses to climate change in tropical montane ecosystems. To achieve this goal, the thesis is structured around three main objectives:

Objective one: Investigate the patterns in population responses to climate change among rainforest vertebrates in the Australian Wet Tropics.

Objective two: Unravel the climatic factors linked to population change and how they might synergise to exacerbate the impacts of warming.

Objective three: Demonstrate the mechanisms by which climate change influences population dynamics through alterations in animal fitness.

To achieve these objectives, the thesis comprises six data chapters in the format of a series of scientific publications. I focus my thesis on rainforest birds and ringtail possums of the Australian Wet Tropics given their conservation priority based on their vulnerability to climate change (Williams, Bolitho & Fox 2003; Krockenberger, Edwards & Kanowski 2012; Williams *et al.* 2016; Meade *et al.* 2018; Garnett & Baker 2021; Williams & de la Fuente 2021). Objective one is covered in chapters two to five, objective two in chapters four and five, and objective three in chapters six and seven.

Chapter two – “Predicting species abundance by implementing the ecological niche theory” (de la Fuente *et al.* 2021).

This chapter delves into the abundance-suitability relationship to demonstrate that habitat suitability can be accurately captured using ecological niche modelling. It unravels the main environmental factors that limit fitness across different rainforest endemic vertebrates, laying the groundwork for understanding the mechanisms linking climate change and abundance change in subsequent chapters.

Chapter three – “Predicted alteration of vertebrate communities in response to climate-induced elevational shifts” (de la Fuente *et al.* 2022).

Exploring an understudied aspect of climate change impacts on ecosystems, this chapter examines patterns in community reshuffling in response to climate-induced elevational shifts. It quantifies the degree of community disruption along the elevational gradient of the Australian Wet Tropics, which is predicted to increase with elevation and for communities with low dispersal capacity. This chapter sheds light on the future community dynamics of tropical montane ecosystems.

Chapter four – “The climatic drivers of long-term population changes in rainforest montane birds” (de la Fuente, Navarro & Williams 2023).

This chapter disentangles the impact of multiple climatic stressors on the populations of rainforest birds in the Australian Wet Tropics. It investigates how climatic presses and pulses synergise to drive population dynamics, providing insights into the multifaceted impacts of climate change on bird populations across elevational gradients. Broadly, "presses" are characterised by a gradual and consistent increase in climatic pressure, while "pulses" comprise extreme events that are by definition rare and low-frequency. Findings from this chapter suggest that gradual warming and precipitation changes in the region have primarily impacted rainforest bird populations, pressuring them across elevational gradients in a pattern referred to as the escalator to extinction.

Chapter five – “Climate change threatens the future of rain forest ringtail possums by 2050” (de la Fuente & Williams 2022).

Building on the insights from chapter four, this chapter examines the press-pulse effect of climate change on rainforest ringtail possum species endemic to the Wet Tropics. It assesses the risk of extinction associated with underlying factors shaping population dynamics, projecting potential future scenarios for these species. Overall, this chapter highlights the severe impact of extreme heatwaves (pulse) on the populations of ringtail possums, pushing the species to the brink of extinction.

Chapter six – “Relationships between abiotic factors, foliage chemistry and herbivory in a tropical montane ecosystem”.

This chapter marks a transition in the thesis from understanding patterns to exploring the underlying processes of climate change impacts on animal fitness. It explores the biogeochemical dynamics in the Australian Wet Tropics and its connection to herbivory, investigating what defines the nutritional landscape for folivores like the ringtail possums. I found that geology and climate are strong predictors of foliage quality, with foliage presenting 35% higher nitrogen content in trees growing on nutrient-rich basalt compared to granite and rhyolite soils.

Chapter seven – “Physiological stress explains climate change impacts on long-term population dynamics of rainforest ringtail possums”.

Integrating statistical and mechanistic methodologies, this chapter builds upon the knowledge gained in previous chapters to investigate the causal link between climate change and population declines. It demonstrates how climate change has impacted rainforest ringtail possum population dynamics primarily through reductions in fitness associated with physiological stress and food quality. In particular, extreme heatwaves have impacted survival through overheating, dehydration, and reductions in short-term foraging, while recruitment has been constrained by overall summer conditions, leading to a reduction in seasonal foraging performance.

Chapter eight – “Synthesis and future directions”

This final chapter synthesises the findings of the thesis, outlining observed patterns of climate change impact on rainforest vertebrates and the biological mechanisms by which animals respond to climate change. It contextualises these findings within the broader context of global climate change and suggests future research directions.

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Chapter Two - Predicting Species Abundance by Implementing the Ecological Niche Theory

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Abstract

Species are not uniformly distributed across the landscape. For every species, there should be few favoured sites where abundance is high and many other sites of lower suitability where abundance is low. Consequently, local abundance could be thought of as a natural expression of species response to local conditions. The correlation between abundance and environmental suitability has been well documented, and a recent meta-analysis has suggested that this relationship could be a generality. Despite the importance and potential implication of the abundance–suitability relationship, its predictive power for meaningful extrapolations has been surprisingly poorly explored. In this study, we showed how a highly predictable trend can be extracted from the abundance–suitability relationship, accurately predicting the variation in species abundance at a high spatial resolution. We produced high-quality environmental suitability estimations for 50 endemic species in the Australian Wet Tropics. Environmental suitability derived from species distribution models was related to observed abundance estimated using data from 29 years of uninterrupted monitoring effort. We used the fitted relationship to accurately predict abundance at a fine scale across the species range. Our results showed that the abundance–suitability relationship was strong for endemic species in the Australian Wet Tropics. The predictive power of our models was high, explaining, on average, 55% of the deviance across taxa. Despite interspecific variation in the strength of the abundance–suitability relationship associated with potential intrinsic estimation biases, our approach provides a powerful tool for predicting abundance across the species range at a fine scale. The potential for robust abundance predictions from occurrence-based species distribution models shown in this study are numerous, and it could have a significant impact on enhancing species conservation and management decisions.

Introduction

A widely held belief in biogeographical ecology is that local abundance reflects how well a particular site meets the needs of a species along many ecological axes (Hutchinson 1957; Brown 1984; Holt 2009). This concept is a natural extension of niche theory, formally proposed by G.E. Hutchinson in a seminal essay more than 60 years ago (Hutchinson 1957). The response of a species to local conditions could thus be measured as local abundance, with more favourable sites containing a greater proportion of the species population (Brown 1984).

Unravelling the ecological and environmental conditions that favour species persistence across their range is a central goal in ecology. Indeed, understanding the relationship between species and the environment could provide invaluable insights into forecasting species responses to climate change (VanDerWal *et al.* 2009) or predicting biological invasions (Kulhanek, Leung & Ricciardi 2011). However, estimating abundance from species distributions remains an unsolved problem (He & Gaston 2007).

A range of algorithms have been developed to forecast species distributions. These techniques, better known as ecological niche models (Peterson & Soberón 2012), use occurrence data to estimate environmental suitability as a function of ecological and environmental predictors (Hijmans & Graham 2006). The underlying mechanism that determines species occurrence is based on population demography, as presences and absences represent positive and negative population growth rates, respectively (Gaston 2003; Thuiller *et al.* 2014). In this respect, areas with higher environmental suitability should also have larger populations. This hypothesis has been called the abundance-suitability relationship, which states that environmental suitability derived from ecological niche models should explain the spatial variation in abundance over a species' geographical range (Weber *et al.* 2017). While evidence suggests that the abundance-suitability relationship could be a generality (Weber *et al.* 2017), several studies failed to detect an effect (Nielsen *et al.* 2005; Jiménez-Valverde *et al.* 2009; Filz, Schmitt & Engler 2013; Dallas & Hastings 2018), questioning the ubiquity of this relationship (Dallas & Hastings 2018).

Several factors may explain the weak abundance-suitability relationship in some studies (Estrada & Arroyo 2012). Environmental suitability predictions may be affected by the scale at which occurrence and abundance are measured (Nielsen *et*

al. 2005), and a lack of information about the entire range of a species may increase the probability of biases in sampling species abundance (Martínez-Meyer *et al.* 2013). Other potential methodological issues could be related to differences in modelling techniques and the appropriate selection of the set of predictors used to model environmental suitability (Weber *et al.* 2017). Alternatively, intrinsic species factors that may affect the estimation of abundance and/or distribution could also influence the strength of the relationship (Dallas & Hastings 2018). Among these factors, species detectability (Jiménez-Valverde 2011), availability of biological-relevant occurrences (Carrascal *et al.* 2017), and species interaction (Braz *et al.* 2020) could play a major role in estimating species habitat suitability.

Previous research in the Australian Wet Tropics (AWT) found a positive correlation between abundance and environmental suitability (VanDerWal *et al.* 2009). Yet, the power of prediction reported in the study was low (linear models explained on average only 12% of the variation in abundance), arguing that the relationship could only predict the upper limit of abundance due to the likelihood of important missing niche parameters at any given local site (VanDerWal *et al.* 2009; Weber *et al.* 2017). The relationship between environmental suitability and the upper limit of abundance may be valuable when the goal is to make inferences at a broad spatial scale without the necessity of determining abundance in all places. However, more detailed information at a finer scale is required (e.g., when planning species reintroductions), and an improvement in our models' predictive power is crucial for meaningful extrapolation of abundance information from modelled environmental suitability (Carrascal *et al.* 2015).

Here, we show that population abundance can be accurately predicted at a fine scale as a function of environmental suitability derived from ecological niche models. Due to the unavoidable triangularity of the abundance-suitability relationship derived from ecological niche models (Jiménez-Valverde, Aragón & Lobo 2021), we do not attempt to infer a precise measure of local abundance but instead produce a precise measure of the spatial variation in population size given the parameters that conform to species' environmental niches. To achieve this, we produced high-quality environmental suitability predictions using ensemble ecological niche models for 50 endemic species in the AWT. We then examined the degree, sign, and significance of the relationship between observed abundance and environmental suitability. We addressed the non-linear nature of the abundance-suitability relationship by fitting

general additive models (GAMs) using a Tweedie distribution. Lastly, we explored the potential for the abundance–suitability relationships to be influenced by species traits and sample size.

Methods

Study system

The AWT is one of the best-studied tropical rainforests worldwide (Williams 2006; VanDerWal *et al.* 2009). Long-term biodiversity monitoring has been conducted uninterruptedly since 1992, with approximately 11,650 independent surveys conducted across the region. Survey sites were established within large continuous patches of rainforest (Figure 2.1). The monitoring of birds, lizards, and frogs was conducted at independent points within the study sites, separated by a minimum distance of 0.25 km, while mammal surveys consisted of a one-kilometre-long line transect at each site ($n = 121$). Following VanDerWal *et al.* (2009), we calculated local abundance using the average relative abundance of each species derived from multiple count surveys at each location. Only independent surveys using identical standardised methodology were considered, and abundance was calculated for locations with a minimum of 3 independent replicates. A detailed protocol for species sampling methodology for abundance calculation can be found in VanDerWal *et al.* (2009).

Among all vertebrates monitored, 76 species are regionally endemic (Williams *et al.* 2010). Only regionally endemic species were included in this study to ensure that the environmental suitability predicted by ecological niche models included the species' entire range. Further, we discarded species that were not detected in standardised surveys and whose information was only obtained from opportunistic encounters, as we could not reliably estimate local abundance or determine whether the occurrences were of biological relevance. Species with sufficient abundance and occurrence information available for analyses included 12 birds, 21 frogs, 4 mammals, and 13 reptile species (Table S2.1). A detailed description of species traits and distributions can be found in Williams *et al.* (2010).

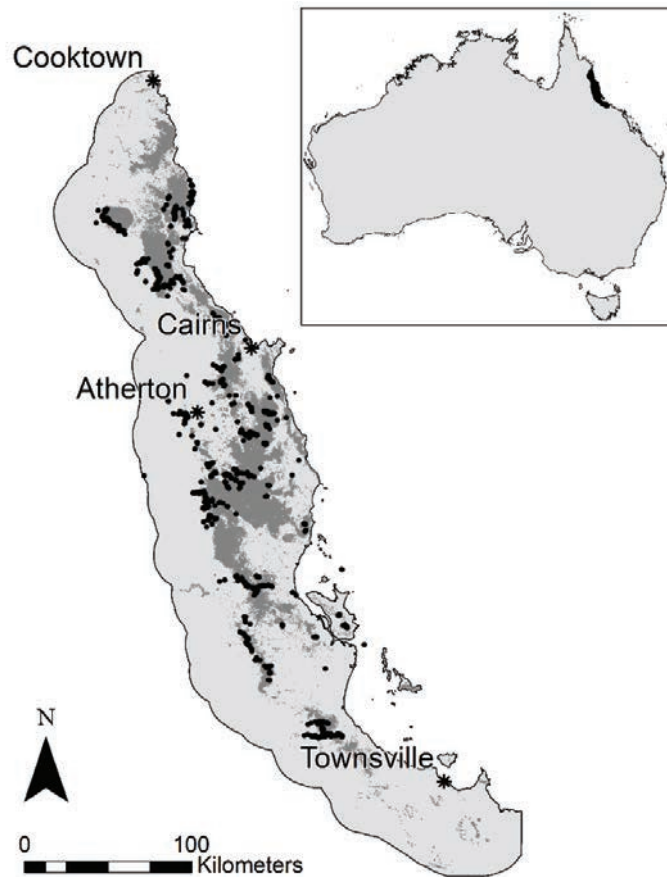


Figure 2.1. The Australian Wet Tropics bioregion and its location in Australia. Rainforest coverage is shown in dark grey. Survey sites are depicted as black dots and main towns as black asterisks.

Species occurrences were derived from a standardised sampling protocol (Figure 2.1). Absence was defined in those locations where a given species was not detected after a minimum of 10 survey replicates. Presences and absences for each species were spatially thinned to reduce potential sampling bias. The spatial thinning was implemented using a minimum nearest neighbour distance algorithm with 1000 iterations, retaining the dataset with the greatest number of records. We used a thinning distance of 0.25 km, which is the minimum distance between point sampling locations. Spatial thinning was implemented using the “thin” function within the “spThin” R package (Aiello-Lammens *et al.* 2015). Because of the reduced number of true absences in the dataset, we additionally included 7,000 background points in the analyses. These background points or pseudo-absences were implemented using the “disk” strategy, with a minimum distance of 1km to the closest occurrence, which is the

minimum distance between study sites. This approach was selected to avoid the pseudo-absences being too close (avoid pseudo-replication) or too far from the occurrences (localised sampling strategy) (Thuiller *et al.* 2013).

Predictor variables

We selected 28 potential variables to predict environmental suitability at 30 arc-second resolution ($\sim 1\text{km}^2$). These variables represented climate, topography, soil characteristics, fragmentation, forest structure, and ecosystem productivity (Table S2.3). Additionally, we provide the methods used to develop precipitation and maximum and minimum temperature seasonality variables in the Appendix.

Some predictors are likely to show a strong covariation, causing instability in parameter estimation (Dormann *et al.* 2013). We used the variance inflation factor (VIF) to detect collinearity (Naimi *et al.* 2014). We found pairs of variables that had the maximum linear correlation (greater than a correlation threshold of 0.7) and excluded the ones with the larger VIF. The process was repeated until no pair of variables with a high correlation coefficient remained. This stepwise variable selection was implemented using the “vifstep” function in the “usdm” R package (Naimi 2015).

Ensemble distribution models and environmental suitability estimation

We determined environmental suitability for each species across their entire biogeographical range by training nine different algorithms. Algorithms included surface range envelop, classification tree analysis, random forest, multivariate adaptive regression spline, flexible discriminant analysis, MaxEnt, generalised additive models, generalised boosted regression, and artificial neural networks.

We used the “biomod2” R package (Thuiller *et al.* 2013), as it offers a streamlined framework for building ensemble ecological niche models. Ensemble forecasting or consensus methods have been proven to be an efficient approach to model species ecological niche for a diverse range of species (Marmion *et al.* 2009), as identifying an appropriate species-specific model selection is usually not straightforward (Elith & Graham 2009). We selected default model tunings within “biomod2” (Hao *et al.* 2019) to be consistent with other studies and optimise ensemble modelling performance (Hao *et al.* 2020). We used 80% of the data for each species

as training data and 20% as model evaluation. This random data split ratio was iterated three times for each algorithm, resulting in a total of 27 models for each species, allowing us to account for intra- and interspecific variation among algorithms (Figure S2.3). We constructed the ensemble models using the weighted average of individual high-performance models, determined by a quality threshold of true skill statistic (TSS) = 0.7 (Allouche, Tsoar & Kadmon 2006). The weights were awarded for each method proportionally to their evaluation scores.

Abundance-suitability relationship

Empirical population estimates were related to model-predicted environmental suitability using generalized additive models (GAMs). Models were fitted using a Tweedie distribution and a log-link function. A Tweedie distribution was chosen due to the increasing tendency of abundance to be high when environmental suitability reaches high values while presenting a cluster of zeroes when environmental suitability is low (Weber *et al.* 2017; Jiménez-Valverde, Aragón & Lobo 2021). We fitted GAMs using the “mgcv” R package (Wood 2017).

We reported the predictive power of the fit between observed abundance and predicted environmental suitability as the deviance explained by the model. Spearman rank correlation coefficients (ρ) were used to quantify the abundance-environmental suitability relationship in terms of degree, sign, and significance. We applied a false discovery rate method (Benjamini & Hochberg 1995) to adjust our significance rate for multiple testing.

The effect of species potential dispersal, sample size, distribution, and body mass on the abundance-suitability relationship.

The strength of the abundance-suitability relationship may be associated with the accuracy of the estimation of both abundance and distribution. Thus, factors that strongly influence our ability to reliably estimate these parameters, such as species detectability (Jiménez-Valverde 2011), could lead to mixed results when different taxa are examined (Dallas & Hastings 2018). To examine the potential influence of intrinsic biases in estimating species abundance and/or distribution, we related the abundance-suitability correlation coefficients (ρ) to species body size, sample size, species

potential dispersal, and taxa (Williams *et al.* 2010) using multiple linear regression analysis. We expected that species with lower body size, lower potential dispersal, and species with a smaller sample size would show a weaker abundance-suitability relationship, as these factors would reduce our ability to detect species, the ability of species to occupy all potentially suitable habitats, and the quality of the data used to model the relationship, respectively.

All analyses were performed in R, version 4.0 (R Development Core Team 2020).

Results

Overall, trained ensemble ecological niche models performed well ($TSS \pm SD = 0.91 \pm 0.06$; Figure S2.3). Models accurately captured species presence (sensitivity $\pm SD = 97 \pm 3\%$) and absence (specificity $\pm SD = 94 \pm 4\%$) as a function of our predictors (Table S2.1). The relationship between observed abundance and environmental suitability derived from ecological niche models was strong across endemic species in the AWT ($\rho \pm SD = 0.58 \pm 0.14$; Figure 2.2a). Moreover, the spatial variation in observed abundance was largely explained by modelled environmental suitability (Deviance explained $\pm SD = 0.55 \pm 0.23$; Figure 2.2b), accurately predicting abundance across the species' geographical range (Figure S2.1; Figure S2.2). The significance and sign of the abundance-suitability relationship were consistent across the vertebrate taxa examined (Figure 2.2c; Table S2.2). Mammals showed the highest consistency, presenting, on average, the greatest predictive power and strength of the relationship. On the other hand, reptiles and frogs exhibited the largest interspecific variation, with deviance explained ranging from 10 to >95%. Birds systematically showed a stronger abundance-suitability relationship than frogs and reptiles, but they presented the lowest predictive power on average (Figure 2.2c).

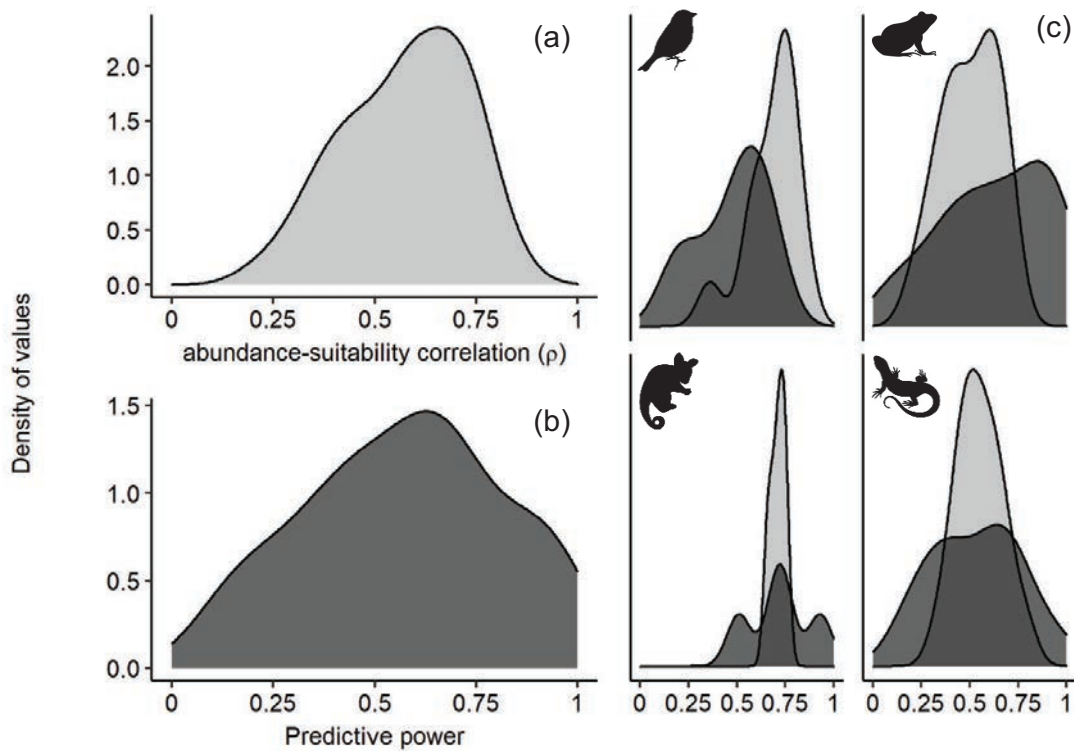


Figure 2.2. Relationship between species abundance and environmental suitability across 50 endemic vertebrates in the Australian Wet Tropics. Panel (a) shows the degree of correlation between abundance and suitability, estimated using Spearman rank correlation. Panel (b) shows the predictive power of the relationship, measured as the deviance explained by the models. Panel (c) shows an examination of the consistency of the abundance-suitability relationship across taxa.

Multiple linear regressions allowed us to measure the influence of species traits on the abundance-suitability relationship. The initial model containing the number of occurrences, species potential dispersal, taxa, and species mass ran into multicollinearity issues, and the variable “taxa” was removed due to its high VIF (VIF = 10.73). Stepwise model selection by AIC removed the variable “species mass”, considerably improving model performance. The best-performing model fits the inter-specific variation in the abundance-suitability relationship as a function of the number of occurrences and potential dispersal predictors ($F_{2,47} = 7.392$; $R^2 = 0.21$; p -value = 0.002; Table 2.1). Although both predictors showed a positive correlation with the abundance-suitability relationship as expected, only the effect of species potential

dispersal showed a statistical significance (Table 2.1), suggesting that species with a higher dispersal capacity showed a stronger abundance-suitability relationship.

Table 2.1. Multiple linear regression models on covariates related to the abundance-suitability relationship in the Australian Wet Tropics.

Coefficients	Slope $\pm$ SD	t-value	<i>p</i> -value
Intercept	0.346 $\pm$ 0.08	4.258	0.00010
Log(occurrences)	0.032 $\pm$ 0.020	1.586	0.12
Potential dispersal	0.044 $\pm$ 0.021	2.08	0.043

Discussion

In this study, we have shown that the spatial variation in species abundance can be accurately predicted at high resolution using niche theory. Our results showed a consistently strong positive correlation between species abundance and environmental suitability derived from correlative ecological niche models. However, the strength of the abundance-suitability relationship may be affected by intrinsic species traits, highlighting potential biases in estimating species abundance and distribution.

Our findings support the hypothesis that local abundance is a reflection of how species respond to local conditions (Brown 1984), which is a direct consequence of species' ecological niche (Hutchinson 1957). Habitats with higher suitability tend to hold a greater proportion of a species population (Weber *et al.* 2017). The link between demography and local conditions should be a natural result of the decrease in the probability of extinction (Araújo, Williams & Fuller 2002) and an increase in birth and survival rates in high-quality habitats (Bock & Jones 2004; Morrison, Marcot & Mannan 2012).

The effect of covariates in the abundance-suitability relationship

The strength of the abundance-suitability relationship may be influenced by our capacity to accurately determine both species abundance and distribution (Jiménez-Valverde 2011; Weber *et al.* 2017; Jiménez-Valverde, Aragón & Lobo 2021). Likewise, the estimation of these parameters could be inherently affected by species detectability (Seoane *et al.* 2005; Jiménez-Valverde 2011). The accurate estimation

of abundance and suitability could thus present challenges for elusive species (Seoane *et al.* 2005; Aubry, Raley & McKelvey 2017), for which a large sampling effort is often required (Price & Endo 1989).

Our findings showed that, in accordance with our expectations, the abundance-suitability relationship was weaker for species with smaller sample sizes. However, the effect of species' sample size was not strong enough to show statistical significance (Table 2.1). Alternatively, physical boundaries and species dispersal limitations could promote higher abundance in climatically unsuitable environments or depress abundance in some otherwise suitable areas (VanDerWal *et al.* 2009), which could potentially produce near-zero correlations between abundance and suitability (Dallas & Hastings 2018). The effect of dispersal limitation on the abundance-suitability relationship was reflected in our results. We found that species with a more limited dispersal capacity may present a weaker abundance-suitability relationship. These results could reflect the lower data quality for frogs and reptile species in our study. The higher uncertainty in the abundance-suitability relationship for these taxa could be explained by sampling biases related to the high dependence on weather conditions for the detectability of tropical ectotherms and their inherent dispersal limitations (Williams *et al.* 2010).

Prediction of the spatial variation in abundance

Previous research has shown that the abundance-suitability relationship could be described by a wedge or triangular shape. Given the anatomy of this relationship, at higher suitability, abundance can be high or low, whereas at the lowest suitability, abundance is predominantly low (VanDerWal *et al.* 2009; Jiménez-Valverde 2011; Tôrres *et al.* 2012; Carrascal *et al.* 2015; Acevedo *et al.* 2017; Lunghi *et al.* 2018; Braz *et al.* 2020; Jiménez-Valverde, Aragón & Lobo 2021). The origin of this triangular relationship could be assumed to be related to difficulties in reliably estimating environmental suitability, as abiotic conditions alone are often not enough to accurately discriminate high-quality habitats (Guisan & Thuiller 2005). Biotic components, such as species interactions, could potentially influence species distribution (Giannini *et al.* 2013; Wisz *et al.* 2013) and spatial variation in abundance (Gaston 2003; Peterson *et al.* 2011; Braz *et al.* 2020). However, biotic information is usually scarce at a large spatial scale and often not explicitly included in ecological niche models.

To what extent can we reliably estimate species abundance as a function of environmental suitability derived from ecological niche models using only abiotic information? Our findings showed that, despite the greater variation in abundance when suitability is high (Figure S2.2), a highly predictable trend can be extracted from the relationship. Furthermore, we found that using a more suitable set of predictors and a more flexible approach to fitting the non-linear relationship between abundance and suitability can yield a substantially higher predictive power and accuracy than previously reported (Figure 2.2; Table S2.2) (VanDerWal *et al.* 2009). Our study shows the importance of using biologically relevant predictors that potentially shape species populations and distribution. In contrast to VanDerWal *et al.* (2009), we developed targeted spatial variables based on known limiting factors for endemic vertebrates in the AWT. For example, a measure of the length and intensity of thermal seasonality was included (Table S2.3), which is sensible given the role of thermal physiological limitation on the distributional range of tropical montane vertebrates (Krockenberger, Edwards & Kanowski 2012). We also showed the importance of considering different algorithms to model ecological niches for a range of species from different taxa. For example, Maxent, the algorithm used by VanDerWal *et al.* (2009), showed marked limitations when modelling the niche of some species (Figure S2.3). These limitations were not observed for ensemble models in our results. In addition to providing a more accurate approximation of species habitat suitability than in previous studies, we modelled the predictive power of the abundance-suitability relationship accounting for the non-linear structure of the correlation, which allowed greater flexibility when predicting abundance for a set of species across taxa. In summary, our approach aimed to reduce the inherent triangularity nature of the abundance-suitability relationship, which resulted in a five-fold increase in prediction power compared to previous studies (VanDerWal *et al.* 2009).

The potential for robust abundance predictions from occurrence-based ecological niche models shown in this study could have numerous meaningful ecological and conservation applications. Many management plans and threatened species evaluations rely on abundance data to detect significant population changes in space and time. However, abundance data is scarce, limiting our capacity to understand ecological patterns at a population level. In this regard, the extrapolation of accurate abundance information derived from modelled environmental suitability shown here could provide invaluable insights into how species interact with the

landscape. For example, when information is limited, accurate predictions of population size in different habitats could be crucial when planning reintroductions (Malone *et al.* 2018) or identifying priority conservation areas (Wilson, Roberts & Reid 2011). Additionally, understanding how species respond to local conditions could have broad implications for conservation biology, and it could be used to predict the impact of invasive species (Kulhanek, Leung & Ricciardi 2011) or to estimate the potential impact of climate change on species distribution and abundance (VanDerWal *et al.* 2009).

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Chapter Three - Predicted Alteration of Vertebrate Communities in Response to Climate-Induced Elevational Shifts

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Abstract

Climate change is driving species to migrate to novel areas as current environments become unsuitable. As a result, species distributions have shifted uphill in montane ecosystems globally. Heterogeneous dispersal rates among shifting species could result in complex changes to community assemblages. For example, interspecific differences in dispersal ability could lead to the disruption, or creation, of species interactions and processes within communities, likely amplifying the impact of climate change on ecosystems. Here, we studied the dispersal success of vertebrate species in a tropical montane ecosystem under a climate-induced uphill shift and assessed the derived impacts on community structures. We simulated the uphill shift of 7,613 community assemblages across the elevational gradient of the Australian Wet Tropics using thermal resistance layers for movement analyses. Dispersal success was calculated as the probability of shifting given species' dispersal ability and landscape composition. We used dissimilarity indices to measure the potential changes in community structures resulting from the variability in dispersal success among migrating species. We found that dispersal success was strongly influenced by species' dispersal ability, landscape composition, and climate change. Our results suggest that the heterogeneous dispersal success among shifting species induced marked temporal changes in community assemblages along the elevational gradient. The local extinction rate (i.e., the proportion of species unable to shift) was especially remarkable at high elevations, suggesting potential mass local extinctions of upland species. Furthermore, the increasing local extinction rate with elevation resulted in substantial declines in species co-occurrence in high-altitude ecosystems. Our study highlights the escalating impact of climate change on community assemblages in response to climate-induced elevational shifts, providing a classic example of the "escalator to extinction". Future predictions of the impacts of climate change on ecosystems will benefit from improvements in understanding species interactions, population dynamics, and species potential to adapt to a changing environment.

Introduction

The geographical distribution of species depends on their environmental tolerances, dispersal constraints, and biotic interactions (Peterson *et al.* 2011). As environmental conditions change rapidly due to climate change, species must adapt, move, or face extinction (Berg *et al.* 2010). Consistent with this, climate change has induced distributional shifts (Parmesan & Yohe 2003; Chen *et al.* 2011; Freeman *et al.* 2018a) and local extinctions (Sinervo *et al.* 2010; Freeman *et al.* 2018b; Iknayan & Beissinger 2018) of many species worldwide, with the greatest observed shift in distribution associated with the interaction between global warming (Chen *et al.* 2011) and species' environmental constraints (Williams & de la Fuente 2021). Evidence demonstrates a general global pattern of uphill and poleward distributional shifts (Parmesan *et al.* 1999; Hickling *et al.* 2006; Tiberti, Mangiacotti & Bennati 2021), warning us of potential disruptions of ecological dynamics and processes (Post *et al.* 2009; Johnson *et al.* 2010). Climate-induced elevational shifts have been especially marked in tropical montane ecosystems (Chen *et al.* 2009; Freeman & Freeman 2014; Neate-Clegg *et al.* 2021), resulting in upland specialist tropical species undergoing substantial declines in abundance (Pounds, Fogden & Campbell 1999; Freeman *et al.* 2018b; Williams & de la Fuente 2021) and local extinction at high altitudes (Freeman & Freeman 2014).

Forecasting and mitigating the impacts of climate change is a major goal in conservation and global change biology, but we have generally been unsuccessful at generating comprehensive predictions or unambiguous recommendations for mitigation (Gilman *et al.* 2010). Due to the intrinsic challenges of studying species' responses to climate change, predictions have systematically focused on the direct effect of a changing environment on individual species. Studies on the response of single species to climate change are useful when studying endangered or invasive species, for which targeted conservation approaches need to be implemented (Kulhanek, Leung & Ricciardi 2011; Sousa-Silva *et al.* 2014). However, those studies usually do not provide insights into the impacts of climate change at the ecosystem level, where community "re-shuffling" could play a critical role in the response of ecosystems to the effects of climate change (Tylianakis *et al.* 2008; Gilman *et al.* 2010; Gibson-Reinemer, Sheldon & Rahel 2015).

In open communities, under climatic-induced geographical shifts, dispersal differences among species could dissolve existing species interactions, eliminating some processes and creating new ones (Ackerly 2003; Schweiger *et al.* 2008). Disrupted and novel interactions will likely alter the abundances, distributions, and extinction probabilities of species (Carpenter *et al.* 2008; Deutsch *et al.* 2008; Williams & de la Fuente 2021). In this regard, metacommunity dynamics will be dependent on dispersal restrictions under climate change (Gilman *et al.* 2010), causing extinctions of low dispersal species while favouring the range expansion of high dispersal ones.

The present study examined the effects of climate-induced uphill elevation shifts in a tropical montane ecosystem by simulating the shift of 7,613 community assemblages derived from empirical observations (Williams *et al.* 2010). We hypothesised that (1) species dispersal success under climate-induced uphill shifts would be determined by the interaction among species' dispersal ability, landscape composition, and warming. We predicted that dispersal success would decrease with elevation due to an unavoidable increase in the isolation of patches as elevation increases, creating the so-called "montane islands" (Brown 1971; Brown 1978). Further, we expected that the declining pattern in dispersal success with elevation would be exacerbated by warming, as climate change is expected to restrict species shifts (Gilman *et al.* 2010) by reducing thermo-suitable habitats for movement across the landscape (Meade *et al.* 2018). To model the likelihood of species shifting uphill, we adopted a spatially explicit approach that accounted for the interaction between species dispersal ability and landscape composition. The effect of warming on dispersal success was analysed by implementing a sequential increase in landscape resistance based on six different climate change scenarios. Given that the likelihood of species shifting depends on species dispersal ability, we also hypothesised that (2) heterogeneous dispersal rate among shifting species should result in changes in community assemblages, potentially altering species co-existence. We measured potential changes in community assemblages and species co-existence along the elevational gradient as the pairwise temporal change in β -diversity and probabilistic change in species co-occurrence. The predicted increasing tendency of temporal β -dissimilarity between assemblages and the loss of existing patterns of species co-occurrence are expected to escalate with elevation, derived from an increasing local population extinction rate towards mountaintops following a pattern known as the "escalator to extinction" (Marris 2007; Urban 2018).

Methods

Study area

The Australian Wet Tropics World Heritage Area is composed of mixed tropical rainforest in an area of approximately 7,000 km² (Figure 3.1a). The elevation varies from sea level to highlands at 1000 m, with isolated peaks reaching up to 1,620 m (Nix & Switzer 1991). The total rainforest area increases with elevation towards the midlands (600-700 m; Figure 3.1b), which are mainly dominated by tablelands. As elevation increases from the midlands, the total rainforest area decreases rapidly towards the isolated mountaintops, with less than 2% of the total rainforest area extending above 1200 m in elevation (Figure 3.1b). Compared to other habitats, rainforest coverage increases with elevation, being the predominant habitat type at high altitudes (Figure S3.1).

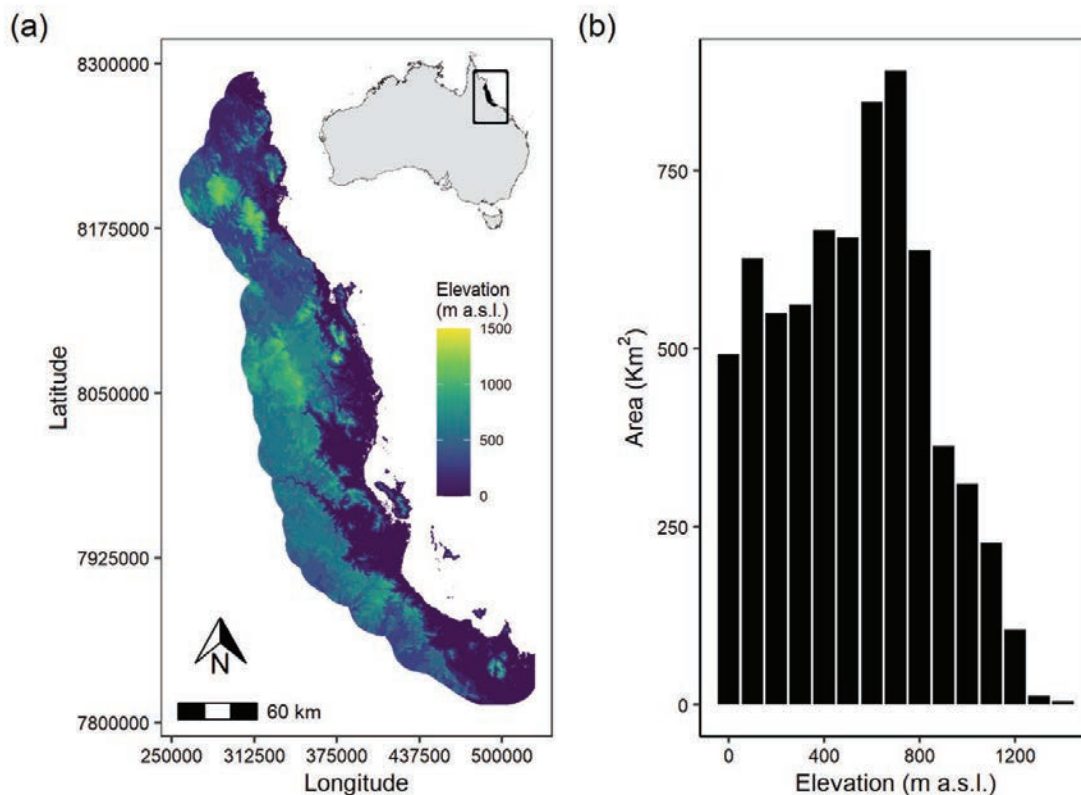


Figure 3.6. The Australian Wet Tropics World Heritage Area. (a) Elevational gradient segregated into 15 elevational bands of 100m range each. (b) Total rainforest and surrounding wet sclerophyll area at each elevational band.

Simulation set-up

Rainforest patches and elevational bands

The elevational gradient of the Australian Wet Tropics was segregated into 15 bands of 100 m width using a 3-arc-second ($\sim 90 \text{ m}^2$) resolution digital elevation model (DEM; Figure 3.1a). The reclassified elevation raster was then cropped using rainforest and adjacent wet sclerophyll (rainforest buffer areas) forest types selected from the broad vegetation groups of Queensland (Neldner *et al.* 2017). The resultant raster was thinned using a pixel clumping function, applying a "rook's case" direction to define what was considered adjacent. This approach was followed to reduce the noise produced by isolated small patches in the agricultural areas (e.g., crop edges). We defined the patches used to identify community assemblages as clumps of 100 pixels or more ($\sim 0.009 \text{ km}^2$). This filtering algorithm reduced the total number of patches at low elevations but did not affect the total rainforest area (Figure S3.2), optimising the number of biologically relevant patch sizes for vertebrate communities without significantly affecting the total area used in the simulation (Figure S3.2; Figure S3.3). Using the same algorithm, we defined a second raster with a more relaxed thinning, removing clumps of less than 10 pixels ($\sim 0.0009 \text{ km}^2$). This second raster was used to define the transition layer for movement analyses. Thus, patches that might be too small to contain a resident vertebrate assemblage could still serve as steppingstone in the transition layer, favouring movement across the matrix.

Transition layer for movement analysis

We developed a resistance layer for every elevational band and climate change scenario combination ($n = 90$). The transition layer developed for movement analysis was defined using a thermal resistance surface (Figure S3.4). The thermal resistance surface was created using a regionally-adapted thermal raster of annual mean temperature (Storlie *et al.* 2013). Values in the temperature raster were reclassified into resistance units, with a resistance unit defined as a change of 0.25°C in annual mean temperature (i.e., the maximum thermal difference between adjacent rainforest

patches). Thermal layers were elevation-specific, and the resistance gradient was calculated using the increasing deviance from the mean temperature of the elevational bands (e.g., a pixel in the temperature raster with one-degree deviation from the mean band's temperature was transformed to a pixel of four resistance units). We assigned a fixed resistance value to the matrix (i.e., cleared land) of 50% higher than the highest thermal resistance value associated with a rainforest patch, favouring the avoidance of the matrix when possible. Transition values within the transition layer were calculated using the mean thermal resistance of adjacent pixels in the thermal resistance surface, using a "rook's case" direction to define what pixels were considered adjacent. In addition to the transition layer based on current temperature, we developed five extra transition layers for each elevational band, defined by five global warming scenarios, from +1°C to +5°C with 1°C steps.

Community assemblages

Community assemblages were defined at the established rainforest patches by extracting the predicted potential habitat from species distribution models (SDMs) for 202 rainforest vertebrates in the region (Table S3.1; Table S3.2; Figure S3.5). These SDMs were developed and critically assessed by Williams *et al.* (2010) to refine the ecological realism of each species' model (Reside *et al.* 2019). The refinement of species potential distribution was based on expert opinion, species records, literature-based evidence, and empirical model validation (i.e., targeted field expeditions with approximately 11,650 independent standardised surveys).

Species dispersal capacity

Species dispersal capacity was categorised into six groups from low to very high dispersal based on the potential dispersal index developed by Williams *et al.* (2010) (Table S3.1; Figure S3.6). The index was calculated using characteristics known to influence the capacity for dispersal: flight, known movement sourced from literature, and body size. To calculate the potential dispersal index for frogs, a further category was included to identify species with a freshwater tadpole dispersal stage (Williams *et al.* 2010). Low dispersal capacity was defined by a maximum travel distance of 0.5 units in the transition layer, and very high dispersal was defined by a maximum of 16 units, with each category able to disperse double than the previous category (i.e., 0.5, 1, 2, 4, 8, and 16 units).

Data analysis

Hypothesis 1: Dispersal success under climate-induced uphill shifts

Least-cost path simulation

Using each combination of elevational band and transition layer, we calculated the least-cost path between all the patches' centroids from an elevational band and all the patches' centroids in the next higher elevational band using Dijkstra's algorithm (Dijkstra 1959). This process simulated the cost of shifting uphill for species in each patch of forest in each elevational band, resulting in a large matrix of least-cost paths containing all possible paths between rainforest patches (Figure S3.4).

Modelling dispersal success

We defined *dispersal success* as the percentage of species within an elevational band able to colonise a higher elevational band. Dispersal was considered successful when the minimum least-cost path to a higher elevational band was smaller than a threshold, defined as species dispersal capacity (Figure S3.4). For example, if the minimum least-cost path between patch A and patch B in the transition layer was four units, only species with a dispersal capacity of four or higher would be able to colonise patch B (Figure S3.4). Thus, species extinction probability at a given elevational band would result from the combination of local extinction probability of populations in all the patches at that elevation.

Change in total area

In addition to the dispersal success, we also measured the total change in area for each combination of elevation, global warming scenario, and dispersal capacity. Total area change was calculated as the difference between the total area colonised and the total area lost due to the elevational shift. In this regard, species with a high dispersal capacity would benefit from the elevational shift when the area colonised was larger than the source area. In contrast, low dispersal species would reduce their total habitat when their inability to shift to higher elevations resulted in local population extinction at the source patch.

Hypothesis 2: Change in community assemblages and species co-occurrence

Temporal β -diversity

The variation in community composition was measured as the pairwise temporal change in β -dissimilarity between assemblages in the baseline and elevational shift scenarios along the elevational gradient. Rainforest vertebrate species were segregated for analyses into the main four taxa (i.e., birds, mammals, frogs, and reptiles) to account for potential inter-taxon variation associated with inherent differences in dispersal capacity (Figure S3.6). The overall change in dissimilarity was measured as Jaccard similarity coefficient (β_{jac}). We further explored the partition of the measured dissimilarity into its turnover (β_{jtu}) and nestedness (β_{jne}) components (Baselga 2010; Baselga 2012). The partition in the temporal dissimilarity allowed us to distinguish whether the change in dissimilarity was driven by substitution of species (β_{jtu}) or loss/gain of species in a nested pattern (β_{jne}). We used the ratio between β_{jne} and β_{jac} to describe the relative contribution of each component in the change in β -dissimilarity (Dobrovolski *et al.* 2012). Ratio values above 0.5 indicated that the change in dissimilarity was driven mainly by nestedness, while a ratio below 0.5 suggested that the pattern in dissimilarity was mainly driven by spatial turnover. Additionally, we followed Baselga, Bonthoux and Balent (2015)'s approach to determine whether the observed pairwise temporal β -dissimilarity and partition values were significantly different from random expectations using a FE (Fixed patches total; Equiprobable species total) null model (Ulrich & Gotelli 2007). This null model was simulated by re-shuffling the species presence in patches while maintaining the species' frequencies constant, creating vertebrate meta-communities where species randomly go extinct or colonise higher elevations from a common regional species pool. This null model was used to randomise each elevational shift scenario at each elevational band, which were then used to recalculate the pairwise temporal change in β -dissimilarity. Null models were then compared to the observed change in β -dissimilarity using Kolmogorov-Smirnov tests. This process was iterated 1000 times for each combination of taxa, elevational band, and climate scenario using 1000 null models to assess the robustness of our simulation.

Spatial β -diversity

Spatial β -diversity studies have shown that pairwise β -diversity and multiple-site β -diversity metrics can reveal different patterns (Baselga 2013; Baselga, Bonthoux & Balent 2015). Thus, in addition to pairwise temporal β -dissimilarity analyses, we calculated multiple-site spatial dissimilarities for each scenario and baseline by computing 1000 multiple-site dissimilarity values using 25 randomly sampled patches at each elevational band. We used the dissimilarity distributions derived from this analysis and compared the resultant β -dissimilarity values with their temporal pairwise counterparts. Given that the results using the temporal and spatial approaches showed almost an identical simulation outcome, we have only presented the pairwise temporal dissimilarity findings in the results section, as our primary focus was to study changes at the population level (i.e., pairwise comparison among assemblages). Spatial β -diversity results are included in the Appendix (Figure S3.7; Figure S3.8).

Species co-occurrence

We measured the impact of the simulated elevational shifts on species co-occurrence using a probabilistic model, comparing expected vs observed species co-occurrence at each combination of taxa, elevational band, and climate change scenario (Veech 2013). A positive association between two species was determined when the observed frequency of co-occurrence was significantly large and greater than expected, while a negative association was defined by a frequency of co-occurrence significantly small and lower than expected (Veech 2013).

Sensitivity analyses

We tested the sensitivity of our simulation to different parametrisation of species dispersal capacity. We developed six scenarios where we altered species-specific dispersal capacity index by ± 5 , 10, and 50% to explore whether our inferences about assemblage changes were markedly driven by the initial species' dispersal ability rather than by the inter-specific differences in dispersal capacity.

Packages used

All analyses and spatial layer manipulations were implemented in R (R Core Team 2021) using the following packages: “raster” (Hijmans *et al.* 2015), “rgdal” (Bivand *et al.* 2021), “grainscape” (Chubaty, Galpern & Doctolero 2020), “gdistance”

(van Etten 2017), “vegan” (Oksanen *et al.* 2020), “dgof” (Arnold & Emerson 2011), “cooccur” (Griffith *et al.* 2014), and “betapart” (Baselga *et al.* 2021).

Results

Hypothesis 1: Dispersal success under climate-induced uphill shifts

The simulated climate-induced uphill shift in the Australian Wet Tropics suggested a high rate of local population extinction (i.e., the loss of a species in all the assemblages within an elevational band) and a strong reduction in the total area occupied by species (Figure 3.2). The trend in dispersal success linearly decreased with elevation and global warming scenario (Figure 3.2a). A low rate of colonisation of novel suitable habitats resulted in a marked loss in total area (Figure 3.2b), with potential extinction events of low dispersal species at high elevations. However, as expected, dispersal success increased with dispersal capacity in all the scenarios, with some species benefitting from the elevational shift when the source area was smaller than the colonised novel habitat (total area change > 0%).

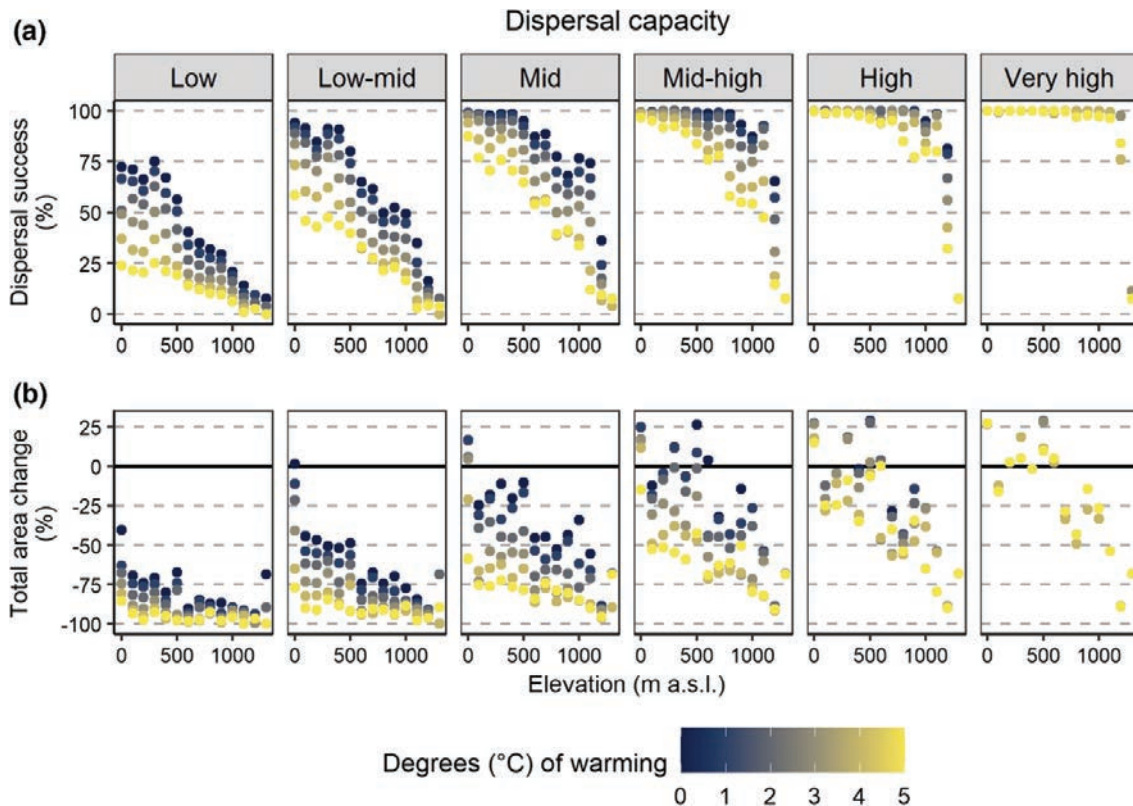


Figure 3.2. The outcome of a simulated climate-induced elevational shift across the elevational gradient in the Australian Wet Tropics. (a) Percentage of dispersal success across elevation segregated by species' dispersal capacity. (b) Total change in suitable area segregated by species dispersal capacity. Colours depict the sequential increase in global warming from the current climate (+0°C; dark blue) to +5°C scenario (yellow), with a +1°C step. The horizontal black line at 0% represents the inflection point between “winner” (increase in total area) and “loser” species. Subpanels show species dispersal capacity.

Hypothesis 2: Change in community assemblages and species co-occurrence

Change in pairwise temporal β -diversity

The effects of heterogeneous dispersal success across species, elevation, and global warming scenarios were observed in the community assemblages of the region (Figure 3.3; Figure 3.4). The pairwise temporal variation in assemblages between baseline and elevational shift scenarios resulted in a substantial increase in β -dissimilarity along the elevational gradient (Figure 3.3). As expected, the temporal variation in β -dissimilarity was dominated by the nestedness component (β_{jne}/β_{jac} , mean $\pm$ SD = 0.86 ± 0.02 ; Figure S3.9), implying a strong pattern of species loss between the baseline and the elevational shift scenarios (Figure 3.4). This pattern was particularly marked on mountaintops, with a reduced number of species able to reach areas at the mountain peaks across the region, indicated by a mass local extinction of species attempting to shift from 1200 to 1300 m and from 1300 to 1400 m elevational bands (Figure 3.4). The pattern in community changes showed high consistency across taxa (Figure 3.3; Figure 3.4). However, the increasing change in assemblages and local extinction rate tended slower for species with high dispersal capacity (i.e., birds; Figure S3.6) than for low dispersal species (i.e., frogs and reptiles; Figure S3.6), highlighting the expected influence of the interaction between landscape resistance and species' dispersal capacity.

The null model approach adopted to validate the robustness of our results showed high consistency for all taxa. The observed overall dissimilarity (β_{jac}) and nestedness component (β_{jne}) were significantly different from random expectations in all 1000 trials across scenarios, elevation, and taxa (Kolmogorov-Smirnov $D > 0.15$,

$p < 0.03$; Table S3.3). However, results did not significantly differ from null models at mountaintops for reptiles, mammals, and frogs ($D < 0.26$, $p > 0.32$ for β_{jac} ; $D < 0.50$, $p > 0.11$ for β_{jne} ; Table S3.3). The lack of significance in the overall change in β -dissimilarity and the nestedness component at 1300 m compared to the null model for these taxa could be an artefact of the combination of the low number and high isolation of patches at mountaintops. The high level of isolation combined with a low number of rainforest patches at mountaintops resulted in most assemblages (89%) being unable to shift (minimum least-cost path > highest dispersal capacity). Thus, the variation in temporal β -dissimilarity at the 1300 m elevational band for these taxa was derived from a very low number of assemblages ($n = 3$), increasing the chances of getting a similar result than when assemblage composition was assigned randomly.

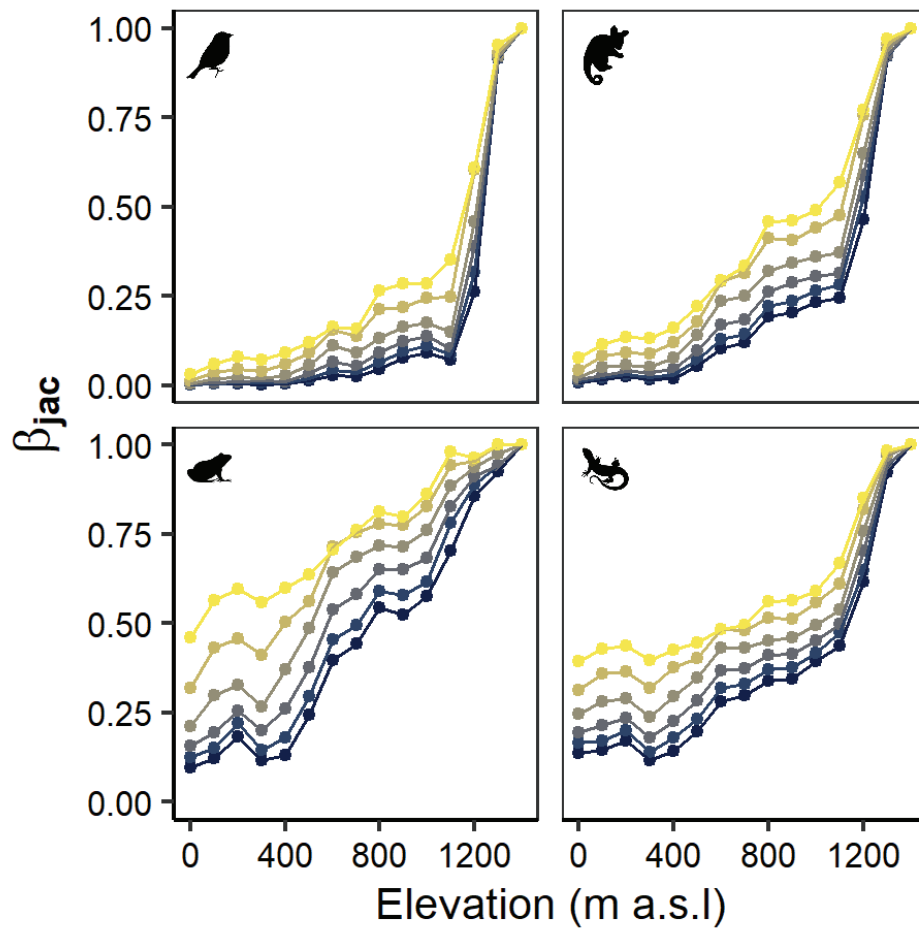


Figure 3.3. Pairwise change in temporal β -dissimilarity across taxa in the Australian Wet Tropics. The figure depicts the overall change in β -dissimilarity (β_{jac}) across the

elevational gradient. Colours depict the sequential increase in global warming from the current climate (+0°C; dark blue) to +5°C scenario (yellow), with a +1°C step.

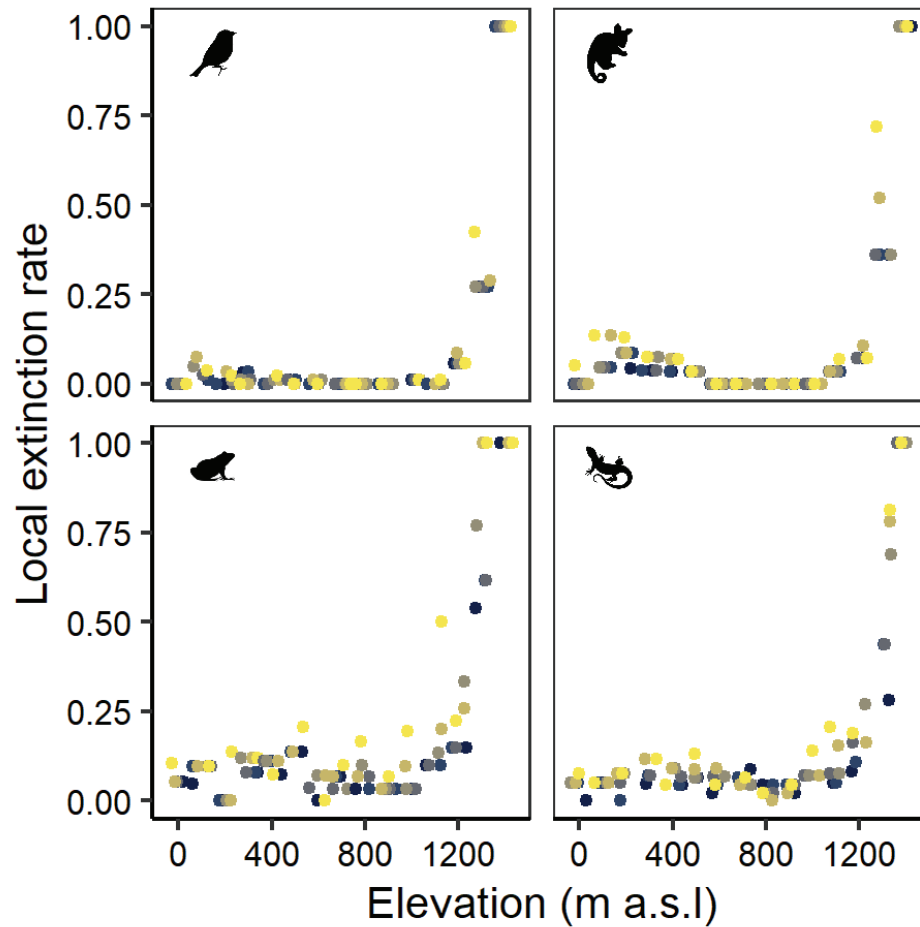


Figure 3.4. Local extinction rate derived from an uphill range shift in the Australian Wet Tropics. Values represent the percentage of species loss across taxa, elevational gradient, and climate change scenarios. Colours depict the sequential increase in global warming from the current climate (+0°C; dark blue) to +5°C scenario (yellow), with a +1°C step.

Change in species co-occurrence

The increasing rate of species local extinction across elevation was reflected in the predicted changes in species co-existence, showing high consistency across taxa. The trend in positive co-occurrence change was particularly accentuated at high elevations (>900 m), suggesting that the lower local extinction rate in the lowlands and midlands had a marginal influence on positive co-existence (Figure 3.5). However, the pattern in negative co-existence (i.e., the number of pairs of species with a high

probability of not occurring in the same community) showed higher sensitivity to low rates of local extinction than the positive co-occurrence trend (Figure 3.5; Figure 3.6), highlighting the potential disruption of species negative co-existence even at lower elevations.

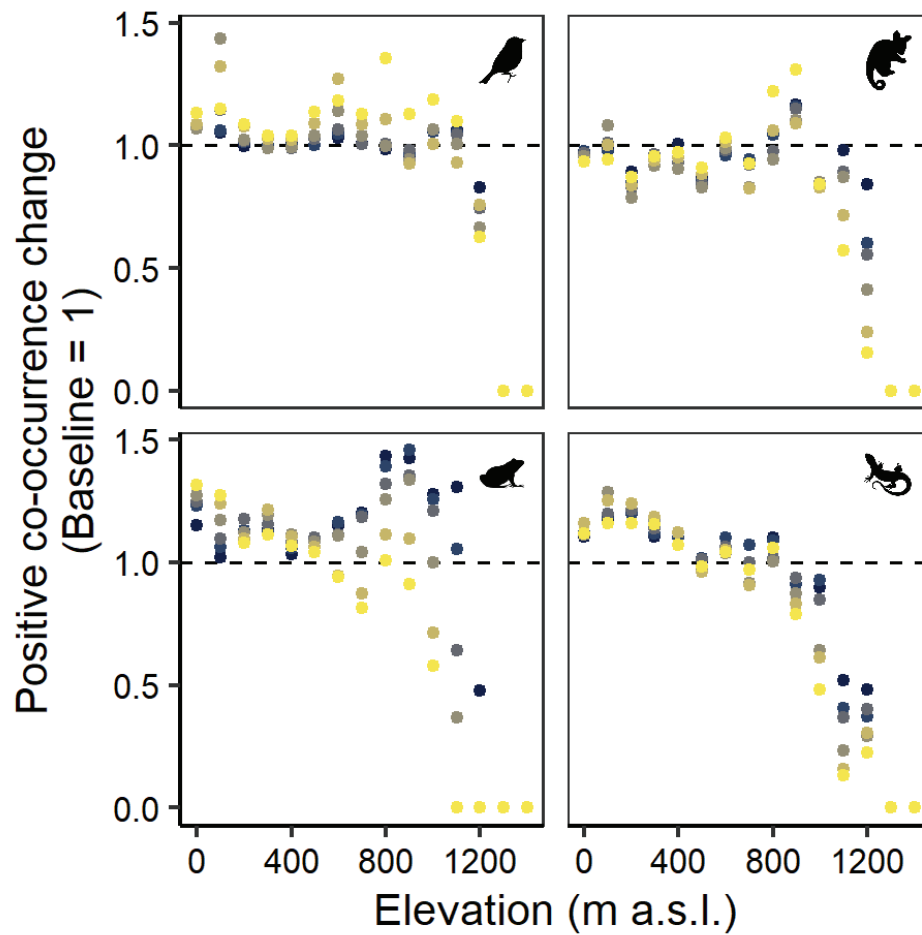


Figure 3.5. Change in positive species co-occurrence compared to the current number of probable co-existing species (baseline) across the elevational gradient. Values below the baseline threshold (horizontal dashed line) represent a decrease in co-occurrence. Colours depict the sequential increase in global warming from the current climate (+0°C; dark blue) to +5°C scenario (yellow), with a +1°C step.

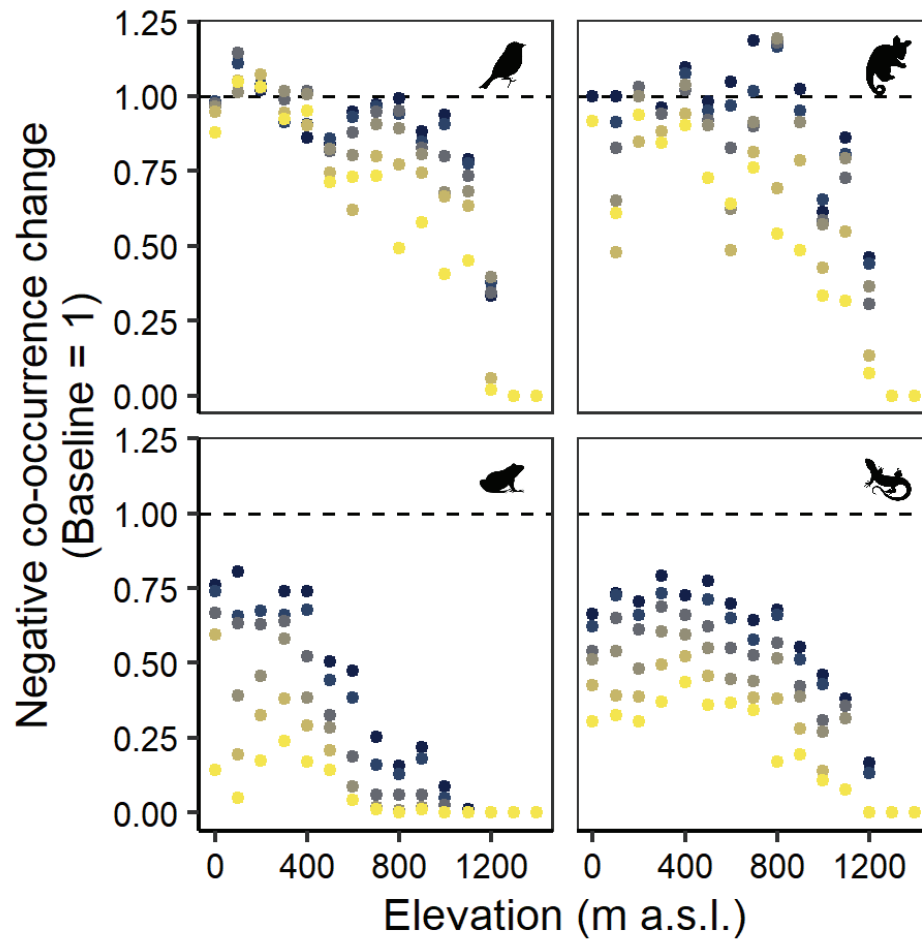


Figure 3.6. Change in negative species co-occurrence (the number of pairs of species with a high probability of not occurring in the same community) compared to the current number of probable co-existing species (baseline) across the elevational gradient. Values below the baseline threshold (horizontal dashed line) represent a decrease in co-occurrence. Colours depict the sequential increase in global warming from the current climate (+0°C; dark blue) to +5°C scenario (yellow), with a +1°C step.

Sensitivity analyses

Results from sensitivity analyses reinforced the robustness of our findings. Changes in dispersal capacity parametrisation did not substantially influence the outcome of the simulation (Figure S3.10; Figure S3.11).

Discussion

The impact of climate-induced uphill shift on communities and ecosystems

Globally, empirical studies suggest that patterns in climate-induced uphill shifts could be general across taxa (Chen *et al.* 2011). However, the ecological implications at the ecosystem level resulting from community distributional shifts have not been broadly considered. We found that an uphill shift in the Australian Wet Tropics would significantly change community assemblages and species co-existence. The observed changes in community structures evidenced the effect of heterogeneous dispersal potential among shifting species. The influence of dispersal restriction across elevations resulted in a clear pattern of increasing temporal β -dissimilarity due to a marked local extinction rate, leading to a decline in species co-occurrence across elevations. The severity of the impact of species shifting in elevation in tropical montane forests was especially noticeable in the highlands, with many species being unable to shift to the isolated mountaintops, which could lead to mass local extinctions. The ecosystem resilience to environmental changes could be further compromised due to the potential disruption of species co-existence and ecosystem processes, denoted by a marked decline in species co-occurrence along the elevational gradient. However, some species could benefit from climate-induced elevational shifts, as shown by high-dispersal species shifting to larger areas.

Escalator to extinction: response of montane communities to climate change across the elevational gradient

Our findings align with those predicted from uphill shifts, showing a classic example of the “escalator to extinction” (Marris 2007; Urban 2018). As evidenced in this study, the impact of climate change escalated exponentially towards high elevations, leading to the local extinction of 55% of the species pushed toward mountaintops. The increasing local extinction rate with elevation suggested a marked homogenisation of assemblages, denoted by a change in β -dissimilarity in a nested pattern close to 1 towards mountain peaks, and a marked reduction in species co-existence, defined by an exponential decrease in species positive co-occurrence

towards mountaintops. These findings might reflect the potential differences in community stability across elevations, with upland assemblages showing lower plasticity to a changing environment than their counterparts at lower elevations (Freeman *et al.* 2018b; Williams & de la Fuente 2021). Our results are in accordance with the projected impacts of climate change in mountain ecosystems (Williams, Bolitho & Fox 2003; Mamantov *et al.* 2021; Manes *et al.* 2021), warning of severe deterioration of montane communities, which host unique ecosystem services (Korner & Spehn 2019), and a disproportionate amount of global biodiversity (Jetz, Rahbek & Colwell 2004; Quintero & Jetz 2018). For example, many upland species in the Australian Wet Tropics are highly specialised to high elevations and rarely occur in the lowlands (Nix & Switzer 1991; Williams, Pearson & Walsh 1995; Williams *et al.* 2010). The marked local extinction rate at high elevations predicted across the Australian Wet Tropics could mean the extinction of upland specialists at the regional scale, even with the most conservative elevational shift scenario. Furthermore, the significant change in community assemblages derived from a strong pattern of local extinctions could lead to significant changes in ecological processes and interactions (Tylianakis *et al.* 2008; Gilman *et al.* 2010), potentially altering key biotic interactions and further diminishing ecosystem resilience.

Simulation assumption: a forced uphill shift

Species in montane ecosystems can show a variety of responses to climate change (Tingley *et al.* 2012; McCain & King 2014). The potential for species to adapt or even move downhill in elevation has been previously reported based on demographic responses and changes in occupancy (Moritz *et al.* 2008; Chen *et al.* 2011; Tingley *et al.* 2012; Neate-Clegg *et al.* 2021; Williams & de la Fuente 2021). However, the underlying mechanisms for species heterogeneous range shifts and demographic fluctuations could also be related to lags in response to changes in the environmental conditions (Bertrand *et al.* 2011; La Sorte & Jetz 2012; Fordham *et al.* 2016; Alexander *et al.* 2018; Lu *et al.* 2021), rather than species adaptability to climate change. Additionally, even with the potential for rapid adaptation reported for some taxa (Orizaola, Quintela & Laurila 2010; Hoffmann & Sgrò 2011; Merilä & Hendry 2014; Muir *et al.* 2014; Arietta & Skelly 2021), the observed adaptation responses are likely to be insufficient to preserve communities in their current habitats (Meester, Stoks & Brans 2018; Radchuk *et al.* 2019; Arietta & Skelly 2021). Following this logic, the

simulation performed here assumed that in each elevational shift scenario, the source patch would eventually become unsuitable for all species in the patch given the pace of global warming (Radchuk *et al.* 2019; Arias *et al.* 2021; Arietta & Skelly 2021), as the environmental conditions of the patch would shift away from the local population current climatic envelope. Under this condition, species could only colonise the next elevational band or go locally extinct. This implied that the overall change in β -dissimilarity was unavoidably driven by nestedness (i.e., $\beta_{jne}/\beta_{jac} > 0.5$; Figure S3.9), as the simulation entailed a net loss of species due to local extinction or no change at all (i.e., $\beta_{jac} = 0$).

Limitations and perspectives: towards a mechanistic approach

Our results provided compelling evidence for significant species loss due to the direct impacts of climate change, affecting ecosystems at a regional scale. The findings derived from this study highlight the importance of considering community-level elevational shift processes when studying the impact of climate change. However, some limitations in our simulation are worth noting. This study would have benefited from information on species-specific adaptation capacity, species interactions, and explicit demographic dynamics (Williams *et al.* 2008). By incorporating potential species adaptation to climate change, we could have accounted for idiosyncrasies in species shifts (Tingley *et al.* 2012), allowing for a deeper understanding of species-specific impacts of climate-induced distributional shifts. Additionally, a broader knowledge of species interactions in rainforest ecosystems would have enabled the explicit estimation of the impacts of community “re-shuffling” on disruptions of key ecosystem processes and the creation of novel interactions. Moreover, a deeper understanding of explicit migration, death, and reproductive success is needed to accurately forecast the likelihood of survival in the colonised patches. In this regard, an explicit simulation of individuals movement within patches could account for the potential under or overestimation of migration rate induced by patch size (e.g., differences between small and big species moving through a large patch), potentially providing a more robust measure of shift rates. Combined, explicit demography dynamics, adaptation capacity, and species interactions would provide a more mechanistic approach required to inform conservation decisions at the population level. Finally, we note the potential influence of synchronic habitat shifts that could affect the dispersal likelihood and establishment of migrating vertebrates.

However, synchronous vegetation movement is likely to have a negligible influence on tropical vertebrate migrations, as vegetation tends to show longer delays in response to environmental changes (Alexander *et al.* 2018; Lu *et al.* 2021) compared to the fast shift shown by vertebrates (Freeman & Freeman 2014; Williams & de la Fuente 2021). Thus, even though evidence worldwide (Chen *et al.* 2011), and specifically in the Australian Wet Tropics (Williams & de la Fuente 2021), shows that climate-induced distributional shifts in montane ecosystems tend uphill, our results could have been slightly different if the incorporation of species resilience, population dynamics, adaptation potential, and synchronisation in habitat shift were possible. Nonetheless, we are confident that the overall pattern in assemblage changes would have followed a similar trajectory, highlighting the marked vulnerability of tropical highland communities.

Conclusion

This study found marked and consistent impacts of climate-induced uphill shifts on community assemblages in the region, indicated by an escalating increase in temporal β -dissimilarity and the associated escalating decline in species co-occurrence. We also discovered that an uphill elevational shift in montane rainforests of the Australian Wet Tropics could severely impact upland ecosystems. The predicted potential mass extinction of species in the highlands of the Wet Tropics would result in the collapse of upland montane ecosystems, threatening many endemic species solely restricted to high elevations. In conclusion, our results highlight the importance of considering the community “re-shuffling” process resulting from multi-species synchronic distributional shifts. Furthermore, understanding the accumulation of individual changes in community assemblages is crucial to providing sensitive predictions at the ecosystem level, providing a more informative research input to conservation planning and management.

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Chapter Four - The Climatic Drivers of Long-Term Population Changes in Rainforest Montane Birds

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Abstract

Climate-driven biodiversity erosion is escalating at an alarming rate. The pressure imposed by climate change is exceptionally high in tropical ecosystems, where species adapted to narrow environmental ranges exhibit strong physiological constraints. Despite the observed detrimental effect of climate change on ecosystems at a global scale, our understanding of the extent to which multiple climatic drivers affect population dynamics is limited. Here, we disentangle the impact of different climatic stressors on 47 rainforest birds inhabiting the mountains of the Australian Wet Tropics using hierarchical population models. We estimate the effect of spatiotemporal changes in temperature, precipitation, heatwaves, droughts, and cyclones on the population dynamics of rainforest birds between 2000-2016. We find a strong effect of warming and changes in rainfall patterns across the elevational-segregated bird communities, with lowland populations benefiting from increasing temperature and precipitation, while upland species show an inverse strong negative response to the same drivers. Additionally, we find a negative effect of heatwaves on lowland populations, a pattern associated with the observed distribution of these extreme events across elevations. In contrast, cyclones and droughts have a marginal effect on spatiotemporal changes in rainforest bird communities, suggesting a species-specific response unrelated to the elevational gradient. This study demonstrated the importance of unravelling the drivers of climate change impacts on population changes, providing significant insight into the mechanisms accelerating climate-induced biodiversity degradation.

Introduction

Climate change has exposed biodiversity to unprecedented conditions, significantly altering ecosystem structure and resilience in most regions (Hoegh-Guldberg *et al.* 2018). In the last decades, among thousands of species spread across terrestrial, marine, and freshwater systems, half to two-thirds have shifted their range in response to warming (Chen *et al.* 2011; Pecl *et al.* 2017; Pörtner *et al.* 2022). As a result, climate-induced distributional shifts have caused severe declines in nearly half of all studied populations (Pörtner *et al.* 2022). The degree of population loss and biodiversity erosion is highest in the tropics, where local extirpation is more common than anywhere else in the world (Pörtner *et al.* 2022). Within tropical ecosystems, montane species have suffered significant losses across their lower elevational limit, increasing their geographical isolation and probability of extinction (Pounds, Fogden & Campbell 1999; Freeman *et al.* 2018; Neate-Clegg *et al.* 2021; Williams & de la Fuente 2021).

Understanding the mechanisms behind species' responses to climate change is critical in an era of increasing biodiversity loss. Most studies have focussed on quantifying the magnitude of ecological responses to climate change by studying species' range shifts (Chen *et al.* 2011). Despite the important efforts of documenting how species track global warming (Freeman *et al.* 2021), we still lack a comprehensive understanding of the extent to which different components of climate change impact natural populations (Parmesan, Root & Willig 2000; Parmesan 2006; Pearce-Higgins *et al.* 2015). By examining the mechanisms underlying climate-induced ecological responses, we can gain insights into how best to conserve and protect vulnerable species in the face of ongoing environmental changes.

In the Wet Tropics of North Queensland, Australia, rainforest bird populations have long been predicted to experience significant biodiversity loss due to climate change (Williams, Bolitho & Fox 2003). These predictions are now coming true with extraordinary spatiotemporal shifts in bird species distributions and abundance in response to climate change in just a few decades (Williams *et al.* 2016; Williams & de la Fuente 2021). Lowland species have increased their abundance by 190% at higher elevations, indicating a marked upward shift. In contrast, upland species have proportionally declined across their entire distribution, resulting in nearly 50% population loss (Williams & de la Fuente 2021). Similarly, the populations of rainforest

ringtail possums are collapsing at an alarming rate in the highlands of the region over the same period (de la Fuente & Williams 2022), evidencing the high vulnerability of tropical upland ecosystems. The accelerated biodiversity loss in the Australian Wet Tropics rapidly translated into an urgent call for conservation actions (Williams & de la Fuente 2021), with one-third of the studied species being incorporated into national and international priority conservation lists (Garnett & Baker 2021). However, adequate and targeted management plans will rely on our understanding of the mechanistic drivers impacting rainforest bird populations, as conservation strategies can markedly vary depending on the nature of the climatic stressor (Garcia *et al.* 2014).

In this study, we unravelled the drivers of climate change impacts on rainforest birds in the Australian Wet Tropics, representing a substantial advance in our understanding of how climate change leads to population changes. We analysed the long-term population dynamics of rainforest birds and their relationship with multiple climatic stressors. We used spatially and temporally explicit climate data to develop predictors capturing regional changes in temperature and precipitation. Long-term climate change included overall changes in average temperature and precipitation patterns, while short-term climatic variables accounted for extreme weather events, such as extreme heatwaves and intense droughts. Additionally, we incorporated a dynamic vegetation index that captured the apparent forest structural damage caused by tropical cyclones across the study area. We analysed the population dynamics using a hierarchical model, estimating spatiotemporal abundance changes while accounting for imperfect detection. We aimed to examine the hypothesis that regional warming is causing strong population changes across rainforest bird communities (Urban 2018; Williams & de la Fuente 2021). However, we also expected a substantial proportion of the observed population changes to be explained by a combination of multiple climatic drivers, as the effect of different climatic factors could act synergistically.

Methods

Study area

The Wet Tropics of Queensland stretches along the northeast coast of Australia, encompassing approximately 7,000 km² of mixed tropical rainforest (Figure

4.1). The outstanding biodiversity that characterises the bioregion persists in large, unfragmented areas of protected rainforest in the rugged terrain dominated by mountain ranges, tablelands, foothills, and a lowland coastal plain (Figure S4.1). The strong elevational gradient defines the biodiversity composition and ecological processes in the region (Williams, Pearson & Walsh 1995), segregating species into three predominant communities: lowland (0-300 m), midland (300-900 m), and upland community (>900 m).

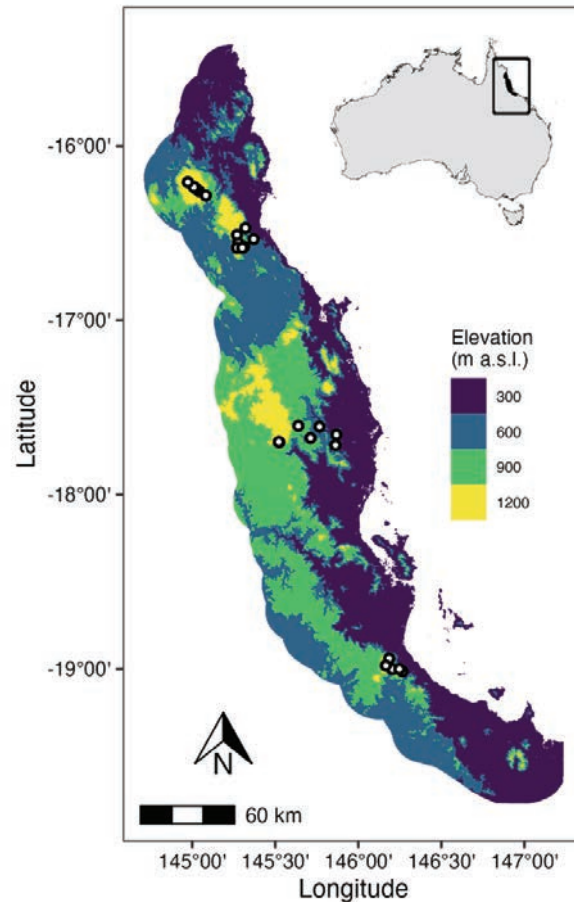


Figure 4.7. The Australian Wet Tropics World Heritage Area and its location within Australia. The colour gradient represents the main elevational bands that define species assemblages across the region. White points depict the location of the survey sites established in the four main mountain ranges of the bioregion (Table S4.1).

Population data

The bird monitoring scheme in the Australian Wet Tropics was established in 1996 and expanded in 2000 to cover a total of 124 survey locations distributed across 24 independent sites (Figure 4.1; Table S4.1). Sites were established in large, unfragmented patches of rainforest away from edges and covered the elevational gradient of the four main mountain ranges in the region (Spec Uplands, Atherton Uplands, Carbine Uplands, and Windsor Uplands). An intensive monitoring effort was conducted across all sites between 2000-2016, compiling a total of 1,977 samples in 495 independent surveys (de la Fuente, Navarro & Williams 2023). Two observers surveyed 150m long transects for 30 min within two hours of sunrise. All individual birds were identified by call or observation, and the weather conditions during the survey were recorded to account for potential detection bias. Of the 54 species monitored, analyses of spatiotemporal population dynamics were possible for 47 species with robust data across sites and years (Table S4.2). Further details of survey methods, total species observed, site characteristics, and species traits can be found in Williams *et al.* (2010a); Williams *et al.* (2010b); Williams and de la Fuente (2021).

Environmental data

Spatially and temporally explicit environmental variables were derived from gridded climatology data at 0.05° (~ 5km) resolution, using daily maximum and minimum temperature (Bureau of Meteorology 2021) and daily precipitation (Frost, Ramchurn & Smith 2018) between 1965-2019. We used a longer climatic time series compared to the ecological data (1965-2019 vs 2000-2016) to better capture the long-term regional climate change. The accuracy of the interpolated climatic grids was validated against observed data from regional weather stations (Cairns' airport, 3 m a.s.l., and Walkamin Research Station, 594 m a.s.l.), obtaining 96% and 99% correlation for temperature and precipitation data, respectively.

We developed four climatic predictors that captured long-term climatic changes and short-term seasonal extreme events across the spatiotemporal range of the study (2000-2016; Figure S4.2-S4.6). Long-term changes in mean temperature and precipitation were obtained using a 25-year window average. Short-term seasonal climatic indices (i.e., extreme heatwaves and intense droughts) were obtained by calculating the area under the curve defined between the climatic variable and a

biologically relevant threshold (de la Fuente *et al.* 2021). The threshold to define the curve was derived from the 97.5th and 2.5th percentile of daily maximum temperature and monthly precipitation across the species' climatic envelope, respectively. Thus, these indices represent the intensity and duration of extreme conditions (temperatures above 35°C and monthly precipitation below 10 mm) at a specific site and time relative to the species' environmental range, with a high index indicating intense and prolonged exposure. In contrast, a low index indicates sites close to the lowest species exposure across its distribution at a specific time (de la Fuente, Navarro & Williams 2023).

In addition to the climatic predictors, we included a spatiotemporal NDVI index generated using cloud-free images from the Landsat 5 TM and Landsat 8 OLI/TIRS satellites (Li *et al.* 2010; Foga *et al.* 2017). We created annual composites of all the images within a natural year between 1987-2021 and extracted the median values of NDVI for each 30m pixel within the Australian Wet Tropics. A detailed explanation of how the annual composites were obtained can be found in Navarro *et al.* (2021). To avoid errors associated with using single pixels (e.g., pixels that fall within roads or water features), we applied a buffer of 0.01° (~1km) around each of our study sites and calculated the median value of all the pixels within the buffer. The NDVI predictor aimed to capture the structural vegetation changes across sites impacted by tropical cyclones (Figure S4.2), accounting for potential cyclone-induced mortality and the recovery time of the rainforest canopy vegetation. Short-term extreme events and NDVI fluctuation were included in the model with 1 year delay as we expected a potential immediate effect on population dynamics (observable during the following survey season).

Statistical analysis

We used a binomial N-mixture model to analyse the temporal variation in rainforest bird populations in response to the explicit spatiotemporal effect of climatic changes (Kéry *et al.* 2009; Kéry & Royle 2020). The N-mixture model is a hierarchical model that uses replicated count data to obtain realistic ecological estimates of species abundance while accounting for imperfect detection (Royle 2004). Thus, the hierarchical model comprises two linked components, explicitly describing the ecological and observation processes (Royle 2004; Goldstein & de Valpine 2022).

The ecological process assumes that abundance (N_{it}) at site i and year t follows a Poisson distribution with mean λ_{it} :

$$N_{it} \sim \text{Poisson}(\lambda_{it})$$

The expected abundance was then modelled as the response to climate change in its multiple dimensions:

$$\log(\lambda_{it}) = \alpha + \beta_c x_{itc} + \omega_i$$

Where α defines the model's intercept, β_c represents the effect of the c -th covariate with value x_{itc} (see *Environmental data*), and ω_i accounts for the unmodelled spatial variation in abundance.

The observation process assumes that detection probability p is represented by the observed counts (y_{it}) sampled from the local population (N_{it}) in each replicate j (C_{ijt}), described by a binomial distribution:

$$C_{ijt}|N_{it} \sim \text{Binomial}(N_{it}, p_{ijt})$$

The expected detection probability was then modelled as the response to the weather conditions during the survey to account for adverse weather affecting bird detection (rain and wind; Robbins (1981)). Additionally, we included the date when the survey was conducted to account for seasonal variation in detection probability (linear and quadratic effect):

$$\text{logit}(p_{ijt}) = \alpha_t + \beta_d x_{ijtd} + \varepsilon_{ijt}$$

Where α_t defines the intercept for detection fitted for each year, β_d represents the effect of the d -th detection covariate with value x_{ijtd} , and ε_{ijt} accounts for the extra unexplained heterogeneity among surveys.

We fitted the open-population N-mixture model using Bayesian inference. Markov Chain Monte Carlo methods were used to sample the joint posterior distribution (Thompson & Brooks 2003) using JAGS software (Plummer 2003), called from R (R Core Team 2021), with the *jagsUI* package (Kellner 2021). We ran three parallel chains of 200,000 iterations each, used the first half as burn-in, and thinned the rest by one in 100 to obtain 3,000 samples of the joint posterior distribution. The sampling process led to acceptable convergence of all parameters ($\hat{R} - 1 < 0.1$, (Gelman & Hill 2006)). We examined the adequacy of the model by computing a Bayesian p -value, with values close to 0.5 (0.47 ± 0.036) indicating a good fit for all species modelled. We expressed the absence of prior information about the model parameter by implementing vague priors. We selected uniform distributions (-5, 5) for the effect of covariates, uniform distribution (0, 1) for the intercepts, and a normal distribution for the overdispersion factor in the abundance and detection model, with

a mean of 0 and precision derived from a standard deviation defined by a uniform distribution (0,100). The JAGS code is available in the Appendix.

Results

The climate of the Australian Wet Tropics has markedly changed during the last five decades. The annual mean temperature has linearly increased in the region at a rate of $0.013 \pm 0.002^{\circ}\text{C}/\text{year}$, a pattern conserved across latitude and elevation (Figure S4.3). Rainfall patterns showed high year-to-year variability within sites, resulting in a marginal overall long-term change ($0.07 \pm 0.11 \text{ mm}/\text{year}$; Figure S4.4). The derived pattern in extreme heatwaves showed marked differences across elevation but no latitude, with lowland sites showing a stronger increase in the frequency and intensity of heatwaves compared to the more stable upland sites ($0.23 \pm 0.07^{\circ}\text{C}/\text{year}$ for the lowlands; $0.07 \pm 0.02^{\circ}\text{C}/\text{year}$ for the uplands; Figure S4.5). A trend in intense droughts was not evident across the study area, although an overall marginal decrease was observed in lowland sites (i.e., precipitation has increased during the dry season; $-0.04 \pm 0.02 \text{ mm}/\text{year}$; Figure S4.6). The NDVI time series showed the predicted “valleys” associated with the two high-magnitude tropical cyclones that hit the eastern rainforest areas in the region in 2006 (cyclone Larry) and 2011 (cyclone Yasi), indicating substantial damages to the forest structure. However, the NDVI index suggested a full apparent canopy vegetation recovery within a year (Figure S4.2).

The population dynamics of rainforest birds in the Australian Wet Tropics showed strong responses to the observed spatiotemporal climatic changes (Figure 4.2). The effects of climate change on population dynamics were markedly strong at the community level (Figure 4.2), denoting a high synchronisation in the species’ responses across elevation. The synchronic responses to climate change were especially significant within mountaintops and lowland communities, while species inhabiting the midlands gradually shifted in their response across the elevational gradient (Figure 4.2). The gradual shift in the response of midland species resulted in a weak community effect, cancelling the mean community response (Figure 4.2; Figure S4.7).

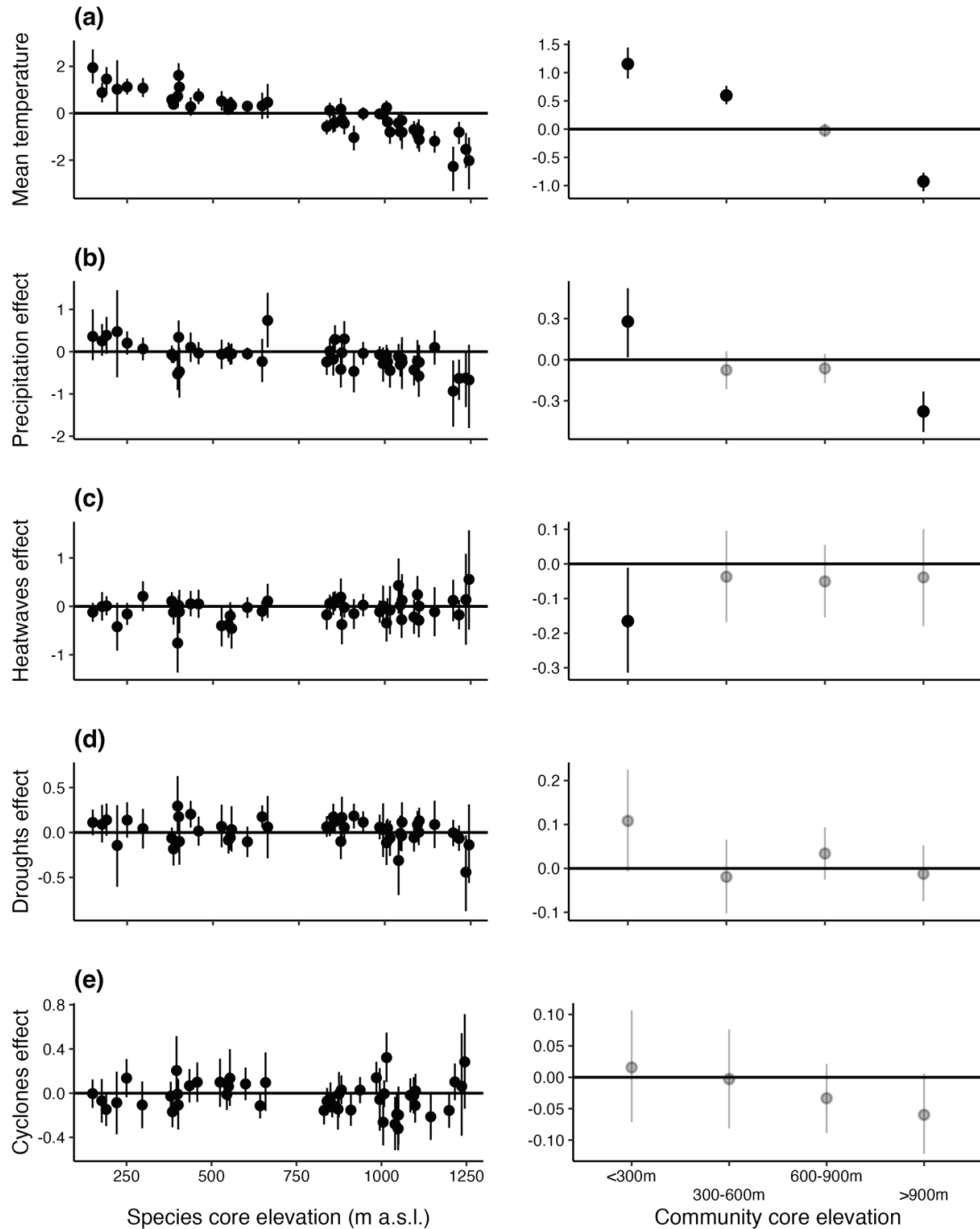


Figure 4.2. Rainforest bird communities' response to climate change in the Australian Wet Tropics. Values represent the posterior mean and 95% credible interval of the effect of the climatic variables on 47 bird species across the elevational gradient (left) and across the elevational-segregated communities (right).

Long-term changes in rainforest bird populations were strongly driven by gradual regional warming, with 72% of all rainforest birds showing a significant response to the increase in mean annual temperature (Table 4.1). The observed increase in temperature across the bioregion induced a highly symmetric response across the elevational gradient. Communities inhabiting rainforests below 600 m showed a strong positive effect to an increase in temperature, while mountaintop species showed an inverse, marked negative response to warming (Figure 4.2a). A similar pattern was observed for the impact of changes in rainfall patterns (Figure 4.2b), with communities inhabiting more seasonally drier lowland areas showing a positive response to an increase in precipitation, while communities restricted to wetter upland forests showed a negative response. Short-term extreme events showed a weaker effect on bird population dynamics (Table 4.1; Figure 4.2c, d, e). However, lowland birds revealed an overall negative response to heatwaves (Figure 4.2c), suggesting that despite the positive influence of long-term warming, lowland species could be susceptible to the observed increase in the frequency of extreme temperatures in the region. The response of rainforest birds to changes in NDVI and drought intensity showed great uncertainty among communities (Figure 4.2d, e). Thus, the local effect of cyclones and rainfall patterns during the dry season (Figure S4.2; Figure S4.6) suggested a marginal effect on the overall observed changes in rainforest bird communities across elevation.

Table 4.1. Summary response of 47 rainforest bird species to multiple climatic drivers in the Australian Wet Tropics. The overall response refers to the percentage of species sharing a positive/negative slope (posterior mean). The significant response refers to the percentage of species sharing a positive/negative slope with a 95% CRI not overlapping zero.

Climatic driver	Overall response (%)		Significant response (%)		
	Negative	Positive	Negative	Positive	Total
Mean temperature	24 (51%)	23 (49%)	18 (38%)	16 (34%)	34 (72%)
Precipitation	34 (72%)	13 (28%)	9 (19%)	1 (2%)	10 (21%)
Heatwaves	26 (55%)	21 (45%)	3 (6%)	0 (0%)	3 (6%)
Droughts	18 (38%)	29 (62%)	1 (2%)	5 (11%)	6 (13%)
Cyclones	30 (64%)	17 (36%)	7 (15%)	1 (2%)	8 (17%)

The variability in detection probability for rainforest birds was largely captured by the weather conditions during the survey. Species showed a decrease in detectability with an increase in rain and wind, as expected for survey methods relying on animal vocalisation (Figure S4.8). Additionally, the date variables showed strong but heterogeneous responses among species (Figure S4.8), indicating that the time of the season when detection was maximised was species-specific.

Discussion

Climate change is eroding the bird community of the Australian Wet Tropics at an accelerating rate. Our results indicate, with high confidence, that rainforest bird abundances have changed in response to a substantial increase in temperature, followed by changes in precipitation patterns and an increase in extreme heatwaves in the lowlands. Contrastingly, cyclones and intense droughts have a marginal effect on population dynamics at the community level. By separating the effects of multiple climatic stressors on the rainforest bird community of the Australian Wet Tropics, our results provide a substantial advance in understanding the mechanisms behind climate-induced biodiversity erosion.

The steady increase in temperature in the bioregion (0.673-0.731°C between 1965-2019) aligns with the observed global trends (Hoegh-Guldberg *et al.* 2018) and regional forecasts (Suppiah, Macadam & Whetton 2007). In line with early predictions (Williams, Bolitho & Fox 2003; Shoo, Williams & Hero 2005), our results indicate that the rapid increase in average temperature in the Australian Wet Tropics strongly affects bird communities (Figure 4.2a). Bird populations show a clear pattern of an “escalator to extinction” (Marris 2007; Urban 2018), where lowland species benefit from an early increase in temperature as they expand into higher elevations (Williams & de la Fuente 2021). Contrastingly, upland-restricted species experience a niche contraction that leads to marked population declines (Williams & de la Fuente 2021), leaving mountaintop species restricted to a smaller area with a higher risk of extinction (Urban 2018; Pörtner *et al.* 2022). These results concur with the overwhelming evidence worldwide, with 50% of all studied populations showing a decline attributable to an increase in temperature, with extirpations becoming more common (55%) in tropical ecosystems (Pörtner *et al.* 2022).

Aligning with regional climate forecasts (Suppiah, Macadam & Whetton 2007), rainfall has shown marked oscillations during the last decades in the Australian Wet Tropics. Our results suggest a tight association between long-term rainfall changes and population dynamics, potentially revealing the bottom-up effect that rainfall could impose on bird populations through primary productivity (Williams *et al.* 2010b). For example, Schuur (2003) suggests that changes in rainfall and temperature could induce contrasting patterns in productivity in tropical montane ecosystems. Thus, an increase in rainfall could reduce primary productivity in the uplands due to water saturation while increasing productivity in the lowlands due to a reduction in water stress (Clark *et al.* 2001; Schuur & Matson 2001; Girardin *et al.* 2010). This pattern matches the prediction of Albrecht's curve (Albrecht 1957), with forest productivity increasing from the seasonally drier lowlands to a maximum at intermediate precipitation levels in the midlands and then declining in the wetter uplands. The potential decrease in productivity with precipitation in the highlands of the regions could thus be related to the decline in soil fertility as precipitation exceeds potential evapotranspiration (Huston 2012; Cramer & Hoffman 2015). The expected relationship between rainfall and primary productivity in tropical mountains aligns with the inverse response to precipitation shown by lowland and mountaintop bird communities in this study (Figure 4.2b). Moreover, van de Weg *et al.* (2014) suggest that the relationship between gross primary productivity and rainfall is unrelated to drought intensity, potentially explaining the weaker link between droughts and bird population dynamics across the elevational gradient (Figure 4.2d). Thus, combined, the strong impact of long-term rainfall and the marginal effect of drought intensity on rainforest birds reinforces the expected association between primary productivity and population dynamics in tropical mountains (Williams *et al.* 2010b).

The rising number of hot days leads to more intense and frequent extreme heatwaves in the Australian Wet Tropics, which are responsible for severe population declines of tropical montane vertebrates in the region (de la Fuente & Williams 2022). Heatwaves are becoming widespread at lower elevations, aligning with the predicted early emergence of extreme temperatures in tropical ecosystems due to the low interannual temperature variability (Hoegh-Guldberg *et al.* 2018). The effect of heatwaves shows high inter-specific variability across populations, but community averages indicate an overall negative effect on lowland species (Figure 4.2c). These results suggest that extreme heatwaves could be causing rapid population declines in

lowland communities near their upper thermal limit. Interestingly, our results highlight the contrasting effects of long-term and short-term temperature changes on rainforest bird communities. On the one hand, lowland species could benefit from long-term warming due to an upward habitat expansion (de la Fuente *et al.* 2022). On the other hand, extreme heatwaves could cause direct population declines, affecting the year-to-year population fluctuation. Lowland species' sensitivity to extreme temperatures could result in an overall lowland biotic attrition (Colwell *et al.* 2008), with no species available to fill the emptying niches in lowland rainforests.

NDVI dynamics had a marginal effect on bird communities during the study period, suggesting a species-specific response unrelated to elevation. In this regard, the observed negative response to an increase in NDVI shown by some species could be related to forest gap preference (Schemske & Brokaw 1981). This pattern is well exemplified by species such as the spangled drongo (*Dicrurus bracteatus*; NDVI mean effect (95%CRI) = -0.28 (-0.52, -0.03)), which avoids dense and interior rainforest, as their feeding strategy and breeding behaviour are strongly linked to clearings (Higgins, Peter & Cowling 2006; Briggs 2016). Thus, the observed fast vegetation recovery after cyclones (Figure S4.2) could explain the negative influence of NDVI on species that benefit from forest gaps, highlighting the impact of cyclone-induced gap dynamics on the bird community structure (Schemske & Brokaw 1981).

This study demonstrates the importance of unravelling the drivers of climate change impacts on communities (Pearce-Higgins *et al.* 2015), providing significant insight into the mechanisms accelerating climate-induced biodiversity degradation (Parmesan, Root & Willig 2000; Parmesan 2006). The climate-driven biodiversity emergency is alarming in the Australian Wet Tropics World Heritage Area (Williams & de la Fuente 2021; de la Fuente & Williams 2022), a fully protected and well-managed ecosystem. The response of rainforest birds to environmental changes shown in this study is not unique. Our results align with the observed impacts of climate change across many regions and taxa (Chen *et al.* 2011; Brawn *et al.* 2017; Freeman *et al.* 2018; Neate-Clegg *et al.* 2018; Freeman *et al.* 2021; Neate-Clegg *et al.* 2021; Couet *et al.* 2022), suggesting a widespread pattern of biodiversity impoverishment in montane ecosystems worldwide (La Sorte & Jetz 2010). Near-term warming reduction in the following decades might now be beyond reach (Pörtner *et al.* 2022), threatening the imminent extirpation of mountaintop communities (Colwell *et al.* 2008; Freeman *et al.* 2018). The ubiquitous pattern of ecosystem erosion worldwide is particularly

concerning in tropical mountains, as they hold a disproportionate amount of global biodiversity (Quintero & Jetz 2018) and host unique ecosystem services (Korner & Spehn 2019).

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Chapter Five - Climate change threatens the future of rain forest ringtail possums by 2050

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Abstract

The increasing frequency and intensity of extreme weather events are escalating the pressure of warming on biodiversity. Globally, synergistic effects of multiple components of climate change have driven local extinctions and population collapses, raising concerns about the irreversible deterioration of ecosystems. Here, we disentangle the impacts of increasing temperatures and the frequency of extreme heatwaves on the population dynamics of tropical ringtail possums (family: Pseudocheiridae) endemic to the Australian Wet Tropics. We estimated long-term population dynamics of ringtail possums from 1992 to 2021 using a hierarchical population model that explicitly described the state process and accounted for imperfect detection. Using our model, we forecasted the population dynamics of ringtail possums from 2022 to 2050, propagating the estimated mechanisms governing the system. From this process, we calculated the probabilities of absolute and quasi-extinction using different population viability thresholds. We found a strong negative effect of climate change on population dynamics, particularly from extreme heatwaves, resulting in a rapid and severe decline in ringtail possum populations over the last three decades. Forecasted increases in temperature and heatwaves threaten the collapse of rainforest ringtail possums by 2050, with populations falling below viability thresholds within three decades.

Introduction

The escalating intensity of climate change poses strong pressure on global biodiversity (Hoegh-Guldberg *et al.* 2018). Species are tracking global warming by shifting their range to new suitable habitats (Chen *et al.* 2011), while species unable to shift are undergoing severe population declines (Freeman *et al.* 2018; Williams & de la Fuente 2021) and local extinctions (Sinervo *et al.* 2010; Freeman *et al.* 2018; Iknayan & Beissinger 2018). However, the magnitude of species' ecological responses to climate change is not homogeneous across the latitudinal gradient, and evidence shows that tropical ecosystems are undergoing the greatest biodiversity erosion (Freeman *et al.* 2021).

The long-term ecological response of species to climate change is generally predictable. Indeed, observed alterations in species abundance, distributions, and probability of extinction align with expectations (Urban 2015; Williams & de la Fuente 2021). However, the mechanistic drivers shaping these ecological responses could be better explained by less predictable extreme weather events, such as heatwaves (Parmesan, Root & Willig 2000; Vázquez *et al.* 2017). Heatwaves are emerging as a serious environmental threat much earlier in the tropics due to the low interannual temperature variability (Hoegh-Guldberg *et al.* 2018). The effects of heatwaves could have devastating impacts at the ecosystem level, resulting in substantial losses of suitable habitat and keystone species (Arias-Ortiz *et al.* 2018), which could have cascading effects. For example, extreme heatwaves can affect the productivity of high-quality food items, inducing mass mortalities of animal populations unable to endure extreme events due to the derived poor body conditions (Hanya *et al.* 2004; Wild *et al.* 2019). Heat stress could also impact populations by affecting different aspects of reproductive function in many species, substantially reducing reproduction success and recruitment (Hansen 2009). Moreover, temperature extremes could profoundly impact species with narrow thermal tolerance, potentially inducing direct mass mortalities and population collapses (Finlayson 1932; Welbergen *et al.* 2008).

The increasing mean annual temperature and frequency of extreme weather events are expected to synergise, having an escalating impact on tropical montane ecosystems (Colwell *et al.* 2008), where the threat that climate change poses to species with narrow environmental tolerance (Janzen 1967) is exacerbated by the limitation of upland species to shift to new suitable habitats (Marris 2007). For

example, physiological studies on green ringtail possums (*Pseudochirops archeri*) in the Australian Wet Tropics have highlighted their inability to cope with extreme heatwaves, with temperatures exceeding 30°C for more than 5 hours becoming biologically limiting for these upland species (Krockenberger, Edwards & Kanowski 2012). The synergistic effects of physiological and biogeographical constraints (i.e., the geographical isolation of mountaintops (Brown 1978)) of rainforest ringtail possums are expected to reduce their suitable habitat by 86% before the end of the century (Meade *et al.* 2018), indicative of the serious conservation concern for upland tropical ecosystems (Williams, Bolitho & Fox 2003; Williams & de la Fuente 2021).

Here, we analysed the long-term (1992-2021) population dynamics of endemic ringtail possums (*Hemibelideus lemuroides*, *Pseudochirops archeri*, *Pseudochirulus herbertensis*, and *Pseudochirulus cinereus*) in the tropical rainforests of the Australian Wet Tropics, described as the 2nd most important World Heritage Area and the 6th most important protected area globally (Le Saout *et al.* 2013). We used a Bayesian hierarchical population model that explicitly described the state process and accounted for imperfect detection in a mechanistic representation of the observation process. We explored the potential impact of climate change on population fluctuations by explicitly incorporating observed local temperature trends over the study period into the population model. We accounted for different dimensions of climate change by examining the additive effect of the long-term gradual warming and increased frequency of extreme heatwaves. The spatial differences in population dynamics were accounted for by calculating site-specific exposure to thermal stress. We forecasted population size into the future to calculate the probability of absolute and quasi-extinction probability of ringtail possums by 2050 (i.e., species declining below potential thresholds of viable population size). We predicted that climate change would strongly influence ringtail population dynamics due to their known physiological limitations to high temperatures (Krockenberger, Edwards & Kanowski 2012). However, we expected interspecific differences among ringtail species in response to different components of climate change due to potential differences in thermal tolerance and ecological traits not conserved across taxa. Finally, we expected interspecific differences in the overall population trajectory due to differences in the elevational range these species occupy. Species restricted to the highlands are expected to undergo greater population declines than species occurring at lower

elevations due to the impossibility of upland species shifting their range as they track climatic changes (i.e., "the escalator to extinction"; (Marris 2007; Urban 2018)).

Methods

Study area

The Australian Wet Tropics bioregion is composed of approximately 7,000 km² of mixed tropical rainforest (de la Fuente *et al.* 2022). The region is dominated by mountain ranges, where elevation is the predominant gradient shaping the biodiversity and ecological processes (Williams, Pearson & Walsh 1995). The elevational gradient spans from the sea level to the highlands at 1,000 m, with isolated peaks reaching up to 1,620 m (Figure S5.1; (Nix & Switzer 1991)). Despite the loss of rainforest that followed European Settlement (Woinarski 2010), large areas of continuous rainforest persist in the region within the Australian Wet Tropics World Heritage Area (Figure S4.1).

Study species

The ringtail possum community inhabiting the rainforest of the Australian Wet Tropics is composed of four species: *Hemibelideus lemuroides*, *Pseudochirops archeri*, *Pseudochirulus herbertensis* and *Pseudochirulus cinereus*. This community represent an iconic component of the Outstanding Universal Value of the Wet Tropics World Heritage Area (Williams *et al.* 2010). Ringtails are nocturnal, arboreal marsupials that feed predominantly on foliage (Goudberg 1990; Jones, Maclagan & Krockenberger 2006). They have similar morphology with average mass and body length ranging from 945-1,185 g and 268-753 mm (Winter *et al.* 2004). Their lifespan ranges from 4-6 years in the wild, with an estimated average generation time of 4 years (Springer & Kirsch 1989). The elevational and environmental range of these species overlaps greatly (Figure S5.2), except for *Pseudochirops archeri*, which has the lowest historical elevational limit (300 m a.s.l.; historical core population centred between 600-700 m (Winter *et al.* 2004; Williams *et al.* 2010)). The core population of *Hemibelideus lemuroides* and *Pseudochirulus herbertensis* is found between 800-1,000 m in elevation, with a historical elevational range spanning from 450 to >1,200 m (Winter *et al.* 2004; Williams *et al.* 2010). *Pseudochirulus cinereus* and

Pseudochirulus herbertensis are latitudinally segregated and do not overlap, with *Pseudochirulus cinereus* restricted to the highlands of northern mountain ranges above 800 m in elevation (Figure S5.2).

Ringtail possum surveys

The long-term possum monitoring scheme was established in 1992 to study the population trajectory of ringtails under the pressure of climate change. Since then, 1069 surveys have been conducted across the elevational gradient of the mountain ranges within the region. Of the 32 independent sites monitored, we selected for this study those sites with at least one observation in more than one year ($n = 19$), discarding sites that were outside the distribution of the study species. All study sites were selected to be within large patches of rainforest, avoiding habitat edges. Sites in the northern part of the Wet Tropics were not established until 2004, which explains the shorter time series analysed for *Pseudochirulus cinereus*. The combination of these sites covers approximately 94% of the available climatic space within the rainforests of the region (Williams *et al.* 2010). Study sites were defined by a 1,000 m transect on a small road/track that provided reasonable visual access to the full forest structure up to the rainforest canopy. Survey efforts and methodology have remained constant since 1992, with spotlight surveys being conducted by 2-3 observers walking at a standardised pace of 4-5 minutes of searching per 100 m with a total search time of 40-50 minutes.

Climate change covariates

Temporal climate information was obtained from Walkamin Research Station (594 m a.s.l.; (Bureau of Meteorology 2021)), located in the core of ringtails' distribution (Figure S5.2). We obtained observed mean annual temperature and yearly number of days with temperatures exceeding 35°C (97.5th percentile of maximum temperatures) between 1985-2021, allowing the examination of the impacts of climate influence in multiple dimensions: gradual global warming and increase of extreme heatwaves. Gradual warming was included to account for the long-term impact on population dynamics (Urban 2018), while the extreme heatwaves predictor accounted for rapid fluctuation in population related to ringtails' physiological limitations (Krockenberger, Edwards & Kanowski 2012). We calculated the moving average for these parameters using an 8-year window (Figure S5.3). This allowed accounting for

potential delays in population responses to a changing environment. Using the local climatic trends from Walkamin Research Station (Bureau of Meteorology 2021), we calculated the expected climate fluctuation (mean annual temperature and number of hot days) between 2022-2050 for population predictions using generalised additive models (*climatic variable ~ time*; Figure S5.4; (Wood 2011)). The models accurately captured the temporal variation in the climatic trends (deviance explained = 81.7% for mean annual temperature and 97.3% for number of hot days), indicating a robust fit for climatic forecasting (Figure S5.4).

The linearity of the expected increase in temperatures matched the predicted warming trend between 2021-2050 obtained using global climate models (Suppiah, Macadam & Whetton 2007; Arias *et al.* 2021). However, forecasting stochastic events, such as heatwaves, can be challenging. Our prediction of heatwaves was based on the assumption that, in the tropics, the frequency of heatwaves is expected to increase with global warming due to the low interannual temperature variability (Hoegh-Guldberg *et al.* 2018). Thus, following the expected linear increase in temperature between 2022-2050 and the observed linear increase in heatwaves in the last decade (2012-2021; Figure S5.3), we assumed a consistent increasing pattern in heatwave events between 2022-2050.

The spatial component of climate change was calculated as an index of climatic exposure at each study site (de la Fuente *et al.* 2021). This index was estimated as the area under the curve using interpolated monthly maximum temperature averages between 1970-2018 (Harris *et al.* 2014). The threshold to define the area under the curve was obtained from the 97.5th percentile of maximum temperature within the climate envelope of ringtail possums (Williams *et al.* 2010). Thus, the index represents the combination of both the intensity and duration of unfavourable thermal conditions for ringtail possums at a specific site relative to the species' environmental range (i.e., the conditions experienced by the species at any given point throughout their distribution), with a high index meaning intense and prolonged exposure to high temperatures. In contrast, a low index indicates sites close to the lowest exposure of the species across its distribution. Thus, the climatic exposure index provides a biologically relevant predictor for spatial differences in population size, as it accounts for the species' environmental limits and the elevational, latitudinal, and topographic gradients influencing temperature.

Population model

We adopted a dynamic binomial mixture model to analyse the temporal variation in ringtail possum populations (Kéry *et al.* 2009). These models estimate species abundance from count data while accounting for imperfect detection (Royle 2004). Detection probability is estimated using spatiotemporal replicated count surveys. This information is then used to approximate the true abundance from the variation in observed local abundance. Thus, binomial mixture models are hierarchical models composed of two linked processes: state or ecological process and observation process (Royle 2004).

The ecological process assumes that the unobserved true local population size at site i in year t (N_{it}) is described by a Poisson distribution with latent abundance λ_{it} . We accounted for the additive effect of climate change on the spatiotemporal variation in abundance by including observed and estimated climatic covariates that could influence the temporal and spatial fluctuation in ringtail possum populations:

$$N_{(it)} \sim \text{Poisson}(\lambda_{(it)})$$

$$\log(\lambda_{(it)}) = \alpha_{\text{region}} + \beta_w w_{(t)} + \beta_e e_{(t)} + \beta_{ts} ts_{(i)} + \beta_g (t - \text{midpoint})$$

Where α_{region} defines the intercept of the model (the log rate in the year 1992), β_w accounts for the effect of temporal variation in gradual regional warming (w_t), β_e accounts for the effect of temporal fluctuation in extreme temperatures (e_t), β_{ts} accounts for the effect of spatial variation in climate exposure (ts_i), and β_g accounts for the extra variation in population trajectory not explained by climate change. This temporal trend estimate was defined by subtracting the midpoint from each integer year ($t - \text{midpoint}$). Indexes define the dimension of variation for each covariate as either spatial (i) or temporal (t). We expected *a priori* potential differences in population trajectory in different sites, so we also explored the possibility of fitting a random-slope model to allow slope variation among sites. However, the model with site as a random effect did not achieve convergence, likely due to the low number of independent sites with a robust temporal representation of population fluctuation along the time series. Thus, the model developed here focussed on calculating regional summaries of the temporal fluctuation of ringtail possum populations rather than site-specific trajectories. Potential differences among sites were accounted for by the spatial climatic exposure variable, which is 96% correlated to elevation. This allowed

estimating the influence of the temporal climatic variables after accounting for potential climate-induced elevational shifts.

In addition to estimating the additive linear effect of the climatic variables on population dynamics, we explored the potential for significant thresholds of population responses to environmental conditions. The changepoint analysis was performed by adding a piecewise regression component to the temporal climatic variables of the model (i.e., global warming and extreme heatwaves). To decide whether significant changepoints in the climatic variables influenced population dynamics, we evaluated the strength of slope changes at all the potential changepoints. However, due to the low level of confidence surrounding inflection points in climatic effects (Figure S5.5), the state process in the final population dynamic model did not include the changepoint component. As the incorporation of the segmented regression structure did not influence the relationship of interest, we removed this structure to achieve a more parsimonious model while respecting the rules of marginality (McCullagh & Nelder 2019). This process achieved the structuration of the simplest model to estimate the population dynamics of ringtail possums in response to warming and heatwaves.

The observation process is the mechanistic representation of the detection process. This process assumes that detection probability p is represented by the observed counts (y_{it}) from the local population (N_{it}) in each replicate j (C_{ijt}), which is described by a binomial distribution:

$$C_{ijt}|N_{it} \sim \text{Binomial}(N_{it}, p_{ijt})$$

$$\text{logit}(p_{ijt}) = \alpha_{\text{year}(t)} + \beta_{\text{date}} \text{date}_{ijt} + \varepsilon_{ijt}$$

Where α_{year} defines the intercept for detection fitted for each year, while β_{date} accounts for the effect of the Julian date on detectability (date_{ijt} ; Figure S5.8). Additionally, we accounted for extra unexplained heterogeneity among surveys in detection probability not captured by covariates by fitting a normally distributed random effect (ε_{ijt}).

We computed the absolute and quasi-extinction probabilities for each ringtail possum species by forecasting population size into the future. We used the predicted gradual increase in mean annual temperature and increase in extreme heatwave events (Figure S5.4) to capture the variation in the forecasted population size estimations given the model (Schaub & Kery 2021). Quasi-extinction probability thresholds (i.e., minimum viable population size) were derived from the IUCN criteria

used to evaluate threatened categories (IUCN 2012). We derived the probability of each species reaching a population loss threshold of 50, 70, 80, 90 (quasi-extinction), and 100 % (absolute extinction) between 2022-2050 across the study sites. The initial population size used to calculate the minimum viable population threshold was selected *post-hoc*, using the estimated mean minimum population size prior to an observed population recovery (i.e., 1997 for *Hemibelideus lemuroides*; 1992 for *Pseudochirops archeri*; 1992 for *Pseudochirulus herbertensis*; and 2004 for *Pseudochirulus cinereus*). Thus, these quasi-extinction thresholds provided a realistic approximation of the critical minimum viable population size for ringtail possums utilised in national and international assessments of extinction risk.

We fitted the dynamic binomial mixture model using Bayesian inference. Markov Chain Monte Carlo (MCMC) methods were used to sample the joint posterior distribution (Thompson & Brooks 2003) using JAGS (Plummer 2003), called from R (R Core Team 2021), with the *jagsUI* package (Kellner 2021). We ran three parallel chains of 500,000 iterations each, used the first half as burn-in, and thinned the rest by one in 100 to obtain 7,500 samples of the joint posterior distribution. The sampling process led to acceptable convergence of all parameters ($\hat{R} - 1 < 0.1$, (Gelman & Hill 2006)). We examined the adequacy of the model by computing a Bayesian *p*-value (Kéry *et al.* 2009). Values ranging from 0.5-0.53 indicated a good fit for all species modelled. We expressed the absence of prior information about the model parameter by implementing vague priors obtained from Kéry *et al.* (2009). We selected uniform distributions (-5, 5) for α_{region} , β_w , β_e , β_{ts} , and β_{date} , uniform distribution (-1, 1) for β_g , uniform distributions (0, 1) for α_{year} , uniform distribution (0, 10) for the standard deviation of the overdispersion factor for detection, and uniform distribution (-2, 2) for the changepoint.

Results

Overall changes in population size

The population dynamics of ringtail possums in the Australian Wet Tropics showed pronounced negative responses to climate change. All species underwent marked population changes over the last 30 years, resulting in rapid population declines since 2010. Furthermore, the predicted increase in mean annual temperature

and frequency of heatwaves are expected to induce further severe population losses, threatening the collapse of the ringtail possum assemblage by 2050 (Figure 5.1). As expected, species restricted to higher elevations (i.e., *Hemibelideus lemuroides* and *Pseudochirulus herbertensis*) showed greater declines in population than species with a wider elevational range (i.e., *Pseudochirops archeri*). *Hemibelideus lemuroides* fluctuated in population size between 1992-2011, followed by a severe decline that resulted in a mean net population loss of 68.2% in only 11 years (Figure 5.1). *Pseudochirulus herbertensis* underwent a consistent population decline since 1997, showing a mean net population loss of 65.5% compared to the initial population size in 1992 (Figure 5.1). *Pseudochirops archeri* showed a strong population increase between 1992-2014, indicating an early population expansion into the uplands, with the first record of the species at sites above 1,100m in elevation in 2009. However, the population trajectory reversed in 2014, with a consistent population decline thereafter (Figure 5.1). *Pseudochirulus cinereus*, despite presenting an overall positive population growth (Figure 5.2), underwent a mean net population loss of 57.3% relative to 2004. However, the population estimates of *Pseudochirulus cinereus* showed great uncertainty (Figure 5.1), likely due to the small distributional range of the species, with population dynamics derived from only four sites (Figure S5.3).

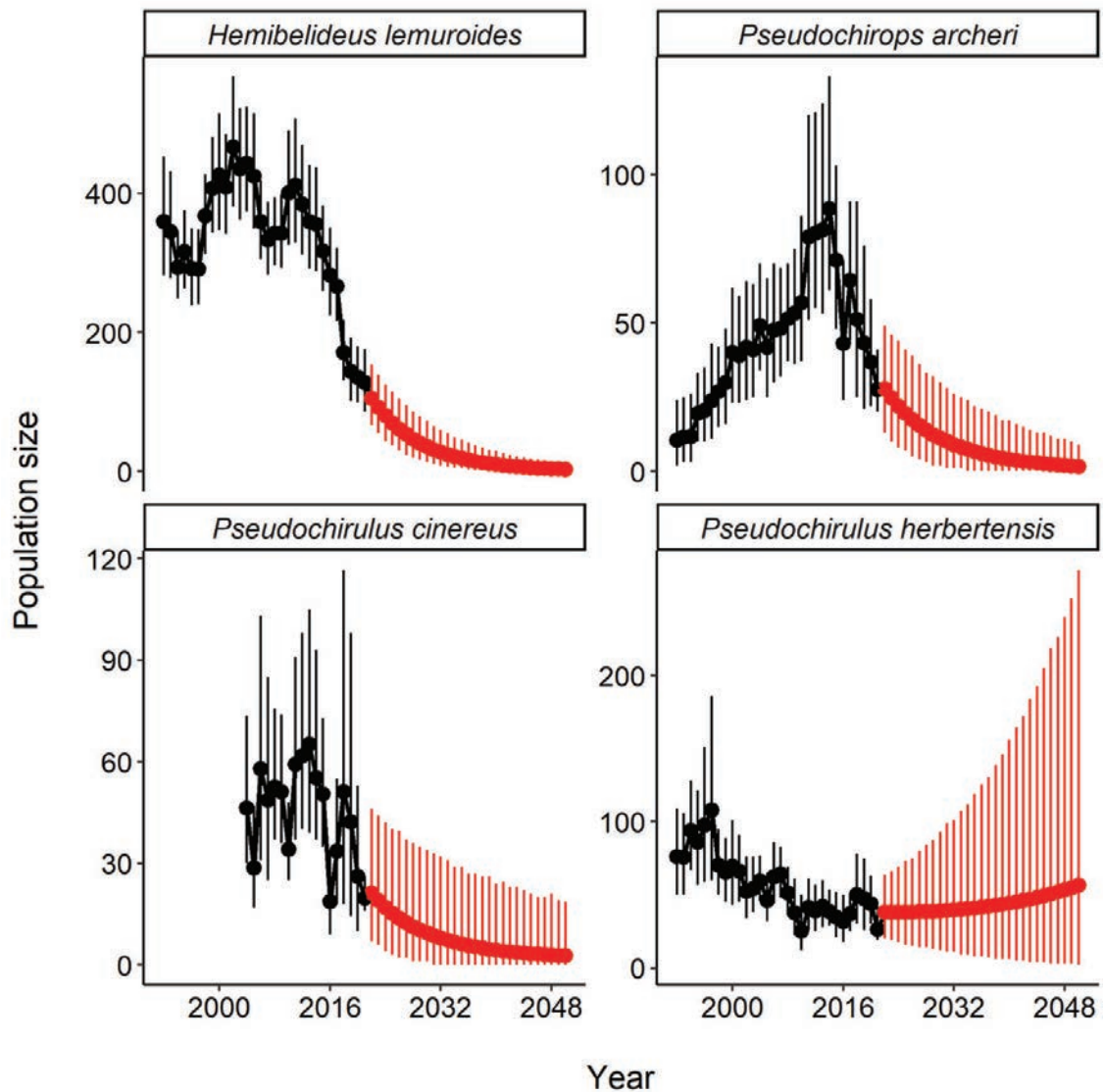


Figure 5.1. Temporal changes in ringtail possum population size between 1992-2050. Points represent the posterior mean and the 95% CRI derived from our dynamic mixture model. Black values represent the estimations derived from the observed data (1992-2021), while red values depict the predicted population size given the forecasted pace of climate change (2022-2050; Figure S5.4).

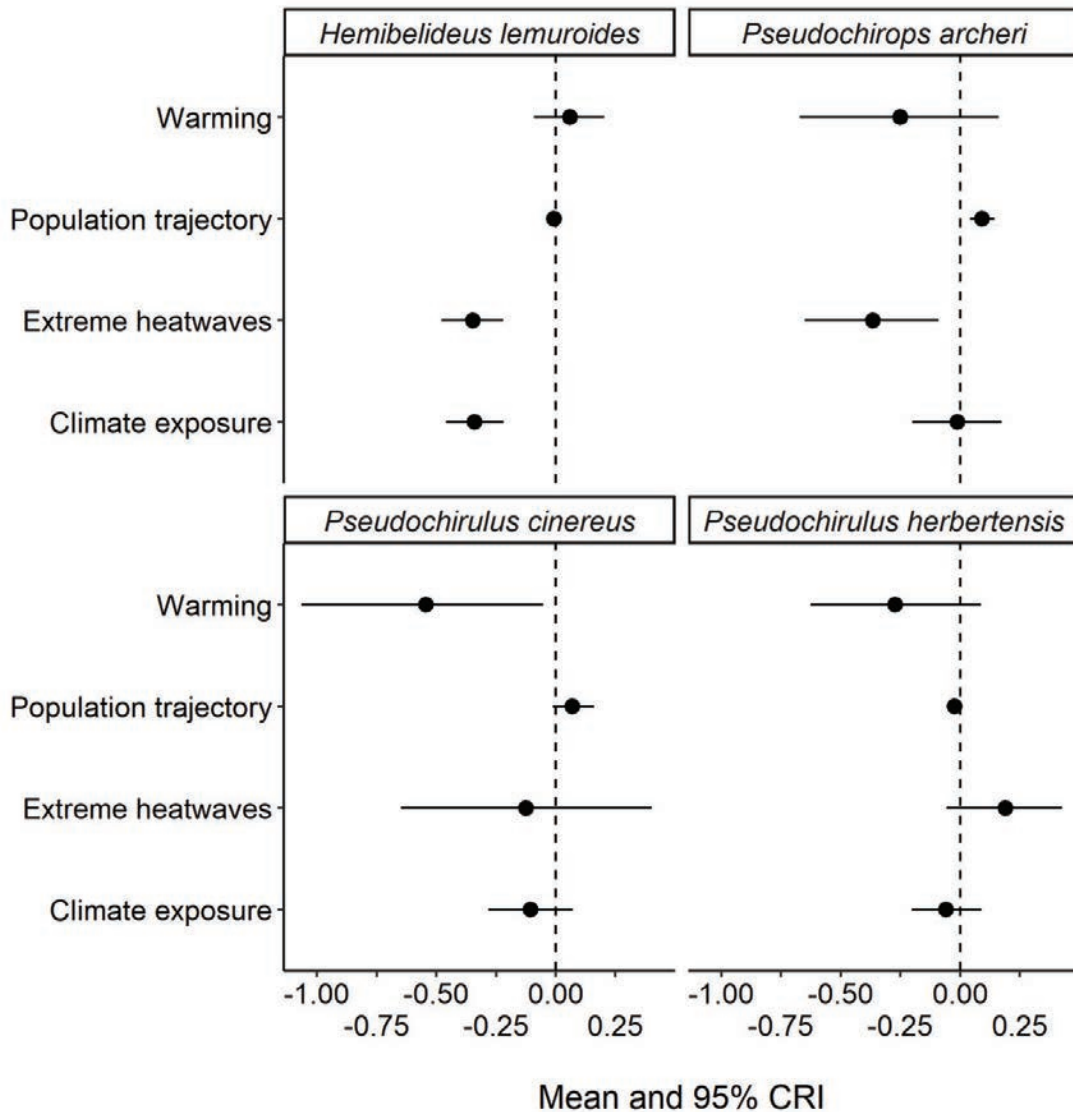


Figure 5.2. Estimated influence of each environmental variable on the observed population dynamics of each ringtail possum species. Parameter estimates based on summaries of the marginal posterior distribution. We reported the mean and 95% credible interval (CRI). The coefficients monitored represent the effect of the trend in mean annual temperature (β_w), the effect of extreme heatwaves (β_e), the overall population trajectory after accounting for temporal climatic variables (β_g), and the effect of site-specific climatic exposure (β_{ts}). A table with all model parameters can be found in the Appendix (Table S5.1). A visual representation of the relationship between the estimated population size and climatic variables can be found in figure S5.6 and S5.7. The temporal fluctuation in detectability derived from the observation process can be found in Figure S5.8.

The effect of temporal changes in the regional temperature

The temporal variation in ringtail populations was strongly correlated to regional changes in temperature (Figure 5.2; Figure S5.6; Figure S5.7). The increasing frequency of heatwaves had a strong negative effect on the population size of *Hemibelideus lemuroides* and *Pseudochirops archeri* and a weak negative influence on *Pseudochirulus cinereus* (Figure 5.2). In contrast, the increase in mean annual temperature had a strong negative correlation with *Pseudochirulus herbertensis* and *Pseudochirulus cinereus*' population dynamics and a weaker negative effect on the population size of *Pseudochirops archeri* (Figure 5.2). Interestingly, a proportion of the variation in the population dynamics was positively correlated to mean annual temperature for *Hemibelideus lemuroides* and to extreme heatwaves for *Pseudochirulus herbertensis* (Figure 5.2). *Hemibelideus lemuroides* showed a positive correlation with gradual warming in the first half of the time series, but this trend was reversed with an overall increase in temperature of $>0.27^{\circ}\text{C}$ compared to 1997 (i.e., lowest annual mean temperature; Figure S5.6). Similarly, *Pseudochirulus herbertensis* showed positive synchronisation with the early fluctuation in the number of heatwaves, but the changepoint occurred with a >1.76 increase in the number of hot days compared to 2002 (Figure S5.5; Figure S5.6). The effect of the additional temporal variability in population trajectory not captured by climatic variables was overall weaker for all species (Figure 5.2; Table S5.1), suggesting that climate change was the predominant driver of ringtails' population dynamics.

The changepoint analysis attempted to identify thresholds of significant change on the influence of the climatic variables on ringtail possum population dynamics. The changepoints associated with global warming and extreme heatwaves showed a clear pattern of temporal similarity among species (Figure S5.5). Potential changepoints induced by global warming ranged between $0.21\text{--}0.38^{\circ}\text{C}$ increase, likely occurring between 2010-2016 (Figure S5.3). Similarly, changepoints in population dynamics influenced by extreme heatwaves were closely associated with the period of linear increase in the frequency of heatwaves between 2011-2021 (Figure S5.3), with potential changes in slope induced by an increase in the number of hot days between 1.76-3.63. Despite the observed pattern in the relative influence of climatic variables (Figure S5.6), the uncertainty associated with these changepoints was high (Figure S5.5). The high uncertainty in changepoint patterns was likely related to the strong

linear effect of the climatic variable inducing negative population growth and the inherent uncertainty associated with the climatic variable inducing the early population increase (Figure 5.2).

The effect of spatial climatic exposure on abundance

The spatial variation in thermal exposure negatively influenced population size for all species, suggesting reduced ringtail populations in sites with higher exposure to extreme temperatures (i.e., at lower elevations; Figure S5.7). However, the strength of the relationship was more evident for high-elevation species (*Hemibelideus lemuroidea*, *Pseudochirulus cinereus*, and *Pseudochirulus herbertensis*; Figure 5.2, Table S5.1; Figure S5.7). The lower influence of the climatic exposure index on *Pseudochirops archeri* was expected, given the wider environmental range occupied by this species (Figure S5.3).

Extinction probability of ringtail possums between 2022-2050

Our model predicted a very high probability of continuous decline for *Hemibelideus lemuroides*, *Pseudochirops archeri*, and *Pseudochirulus cinereus* between 2022-2050. *Hemibelideus lemuroides* have already reached an average net population loss of >50% relative to 1997 (i.e., minimum population size prior to an observed recovery; Figure 5.1), with a high probability (>75%) of reaching a 70, 80 and 90% net population loss in the next 4, 8, and 13 years, respectively (Figure 5.3). This level of decline based on observed population changes currently places *Hemibelideus lemuroides* into the IUCN *Endangered* category (Criteria A2), with a high probability of them becoming *Critically Endangered* within a decade. Similarly, *Pseudochirulus cinereus* is predicted to undergo a severe net population loss, reaching a 90% decline within the next two decades. The projected response of *Pseudochirops archeri* showed delays in quasi-extinction probabilities compared to other ringtail possums due to the initial increase in population size between 1992-2014 (Figure 5.1), where the population had expanded and increased into higher elevations. Our model showed a high probability (>75%) of a 50% reduction in *Pseudochirops archeri* population (relative to 1992) and a moderate probability (>50%) of 70-80% net population loss by 2042 (Figure 5.3). Finally, despite the robust estimates of the observed population dynamics for *Pseudochirulus herbertensis*, the additive effect of climatic variables did not capture the variability in the forecasted population size

(Figure 5.1). Thus, the predicted extinction probabilities held a great uncertainty for this species (Figure 5.3). Nevertheless, based on observed population declines, *Pseudochirulus herbertensis* should be considered as *Vulnerable* under IUCN Criteria A2 (currently listed as *Least Concern* (Burnett & Winter 2016)).

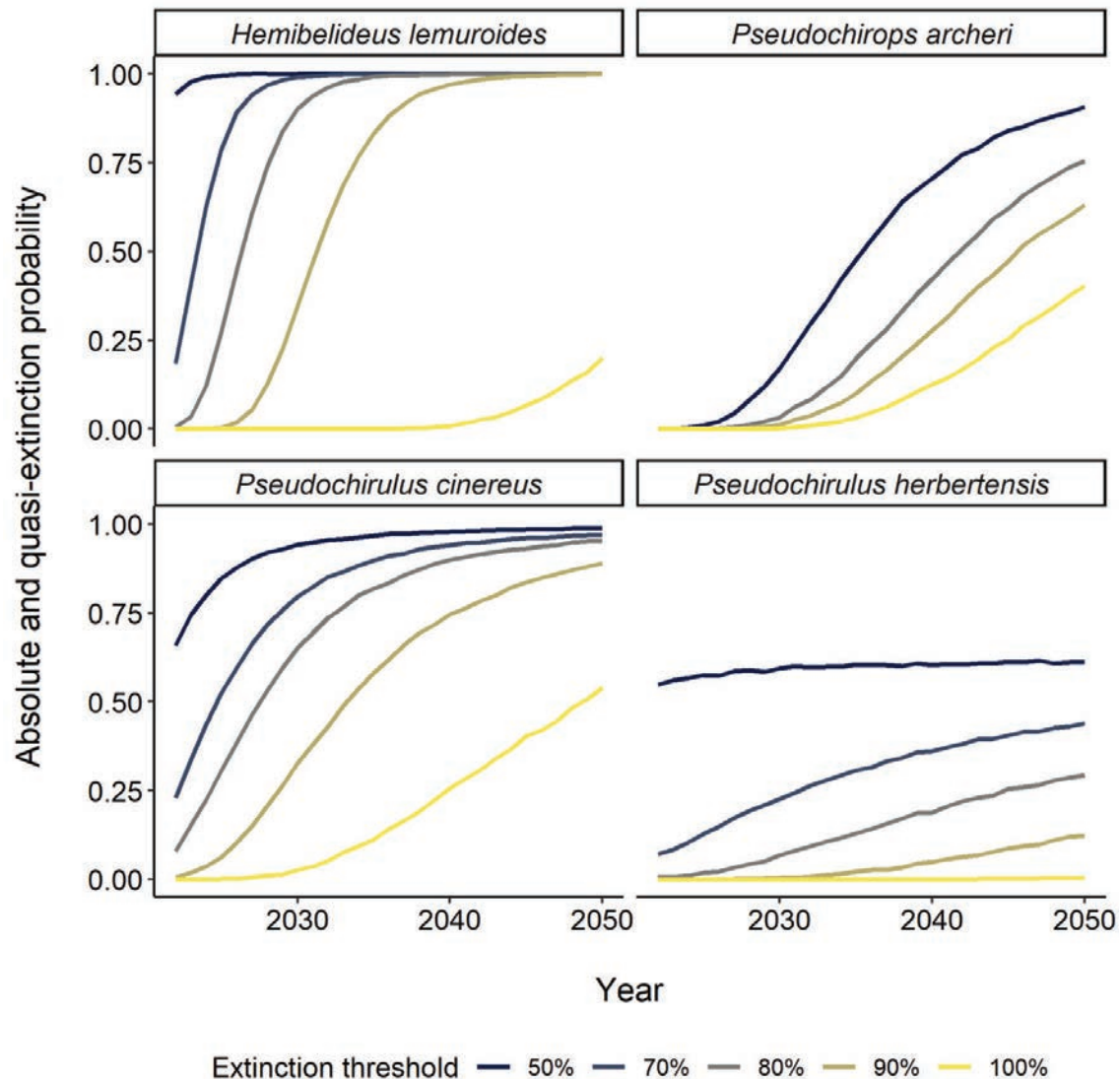


Figure 5.3. Absolute (100% population loss) and quasi-extinction probabilities (population viability threshold) of ringtail possum in the Australian Wet Tropics between 2022-2050. Extinction thresholds were derived from the IUCN threatened categories (IUCN 2012).

Discussion

Several decades of research on species response to climate change have evidenced the threat that global warming poses to communities and ecosystems worldwide (Arias *et al.* 2021). Indeed, local extinctions and community collapses have been attributed to the direct effect of climatic changes (Pounds, Fogden & Campbell 1999; Hanya *et al.* 2004; Sinervo *et al.* 2010; Freeman *et al.* 2018; Iknayan & Beissinger 2018). However, the drivers of species responses to climate change are not always evident. Our results showed the severe impact of regional warming and the increased frequency of heatwaves on ringtail possum dynamics, resulting in marked declines in population over the last 30 years. Moreover, these population losses are expected to escalate in the following decades, threatening the survival of rainforest ringtail possums by 2050.

Overall population trajectories

The overall trajectory among ringtail possums matched a priori expectations of montane species responses to global warming (Marris 2007; Urban 2018). Species restricted to high elevations showed severe population declines, with an average net population loss above 60% in 30 years. Contrastingly, species with a wider elevational range (i.e., *Pseudochirops archeri*) showed a consistent early increase in population, resulting from a population expansion into higher, cooler parts of their distribution. However, regional increases in temperature and frequency of extreme heatwaves since 2010 induced a changepoint in the trajectory of the latter population, with a linear decline thereafter. This pattern in population trajectory is not unique to ringtail possums in the region. Rainforest birds have followed a similar trend, with midland specialist species showing a steady population increase between 2000-2008, followed by a continuous decline, while upland bird species showed consistent population losses across the entire region throughout the examined period (de la Fuente *et al.* 2021). This pattern could reveal important tolerance thresholds for species with the potential to shift to new suitable habitats as they track climatic changes. Nevertheless, as our results indicated, even species adapted to a wider environmental range might not have sufficient plasticity to cope with the rapid pace of climate change (Arietta & Skelly 2021).

Spatial sensitivity to climate change

The inclusion of a spatial climatic dimension in the model allowed examining the effect of spatial variability in climatic exposure across the species distributions. Our results indicated that population dynamics were negatively influenced by exposure to intense and prolonged extreme heatwaves (Figure S5.7). Population size showed a negative correlation with increasing exposure for upland-restricted species (i.e., *Hemibelideus lemuroides*, *Pseudochirulus cinereus*, and *Pseudochirulus herbertensis*), suggesting that higher elevations species could be undergoing greater population losses at their lower elevational limit. However, the effect of climate exposure on ringtail populations was not observed on species with a wider environmental niche (i.e., *Pseudochirops archeri*). The effect of the elevational gradient on ringtails' responses to climate change aligns with the observed rapid elevational contraction of tropical montane biodiversity (Freeman *et al.* 2021), highlighting the escalating biotic perturbation and extinction risk of montane ecosystems under the pressure of climate change (La Sorte & Jetz 2010).

Temporal effect of global warming

The fluctuation in population changes in ringtail possums between 1992-2021 was largely explained by different dimensions of climate change. Our results suggested that potential evolutionary tolerance to a rapidly changing environment might not be preserved across ringtail possum species. Interestingly, species within the same family showed different responses to different climatic dimensions despite the great overlap in their environmental niche (Figure S5.3). As Meade *et al.* (2018) predicted using physiological models based on Krockenberger, Edwards and Kanowski (2012), *Pseudochirops archeri* showed the greatest response to an increase in the frequency of extreme heatwaves compared to other ringtail possums. The negative effect of heatwaves was also severe for *Hemibelideus lemuroides*, with population dynamics tracking the fluctuation in the number of hot days (Figure S5.7). Contrastingly, members of the genus *Pseudochirulus* (*P. herbertensis* and *P. cinereus*) showed a greater negative population synchronisation with a gradual increase in mean temperature. The marked differences in response to climate change among ringtail species could have profound implications for conservation. While gradual warming can be accurately predicted, and the potential impacts are also likely to be gradual, the

stochasticity related to the rapid increase in heatwaves (Hoegh-Guldberg *et al.* 2018) could have fast and devastating impacts on these vulnerable populations (Parmesan, Root & Willig 2000; Krockenberger, Edwards & Kanowski 2012).

The fate of ringtail possums

Our results showed that the escalating pace of climate change in the Australian Wet Tropics is likely to increase the pressure on rainforest ringtail possums in the following decades, threatening the species' survival. The minimum viable population analysis showed a high probability of species reaching critical declining thresholds, with populations undergoing losses of up to 90% by 2050. These projections are subject to the consistency of the observed climatic trends, although limiting warming in the following decades might now be beyond reach (Hoegh-Guldberg *et al.* 2018).

The observed trajectory of ringtail possum populations means the realisation of the predictions about climate change impacts on montane ecosystems (McDonald & Brown 1992), with an early extirpation of marginal populations likely escalating to the extinction of entire upland tropical species (Urban 2018; de la Fuente *et al.* 2022). However, as indicated by the effect of climatic exposure on populations across the elevational gradient, we could expect delays in population responses at elevations above 1,200m, where the current exposure to extreme heatwaves is low compared to lower elevations. Nevertheless, despite the potential slower degradation of populations in the mountaintops, rainforest habitat extending above 1,200m represents small areas (<2% or 136 km²; (de la Fuente *et al.* 2022)) with high isolation (i.e., "mountain islands" (Brown 1978)). Thus, the idea of remnant high-altitude rainforest areas as the sole long-term stronghold for ringtail possum populations might be limited.

This study supports the hypothesis that climate change is inducing a rapid contraction of ringtails' suitable habitat due to the increasing physiological pressure associated with thermal stress (Krockenberger, Edwards & Kanowski 2012; Meade *et al.* 2018). The severe declines that ringtail possums are undergoing might be exacerbated by climate-induced changes in the nutritional and toxicological landscape (Rothman *et al.* 2015; Beale *et al.* 2018). In this regard, the feeding rate of marsupial folivores could substantially decrease with hotter temperatures, explaining the escalating reduction in ringtails fitness with climate change (Youngentob *et al.* 2021). In this context, the effect of climate change on nutritional stress should be considered

as a potential synergistic effect increasing the direct physiological pressure induced by thermal stress (Beale *et al.* 2022). This hypothesis would align with the description of the ecological correlates of ringtail possum abundance in the Australian Wet Tropics (Kanowski *et al.* 2001), where a relationship between foliage nutritional quality and ringtail possum abundance was suggested.

Conclusion

This study has demonstrated that the imminent collapse of the rainforest ringtail possums is directly associated with climate change. We suggest that the profound biodiversity deterioration observed over the last decades in the Australian Wet Tropics (Williams & de la Fuente 2021) might be a widespread pattern in montane ecosystems worldwide (La Sorte & Jetz 2010), threatening a significant proportion of the global biodiversity (Manes *et al.* 2021). Separating the relative impacts of increasing means and extreme temperatures and identifying climatic thresholds for tipping points in population declines provides significant insights into the potential adaptation actions to minimise future impacts. Management actions associated with extreme events are potentially very different from those aimed at increasing resilience to gradual climatic changes. The relatively short temporal scale of extreme events may enable rapid and targeted management interventions that are not possible for impacts associated with longer-term changes in mean conditions.

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Chapter Six - Relationships between abiotic factors, foliage chemistry and herbivory in a tropical montane ecosystem

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Abstract

Herbivore-plant interactions are fundamental processes shaping ecosystems, yet their study is challenged by their complex connections within broader ecosystem processes, requiring a nuanced understanding of ecosystem dynamics. This study investigated the relationship between nutrient availability and insect herbivory in the Australian Wet Tropics. Our objectives were threefold. Firstly, to understand what factors influence nutrient availability for plants and herbivores across the landscape; secondly, to investigate how trees of different growth strategies respond to nutrient availability; and thirdly, to unravel how the relationship between resources and plant chemistry affects herbivory. We established a network of 25 study sites covering important abiotic gradients, including temperature, precipitation, and geology. Employing a hierarchical modelling approach, we assessed the influence of climate and geology on resource availability for plants, primarily in the form of soil nutrients. Then, we explored the influence of the above factors on the interaction between herbivory and foliage chemistry across three widespread rainforest tree species, comparing how these relationships emerged across pioneer and late successional species. Our findings suggest an overarching influence of climate and geology over soil chemistry, foliar nitrogen, and insect herbivory, both directly and indirectly. However, individual constituents of soil fertility showed marginal influence on spatial patterns of foliage chemistry once site geological origin was accounted for, suggesting an equivocal relationship between soil nutrients and foliar composition. Moreover, we found differences in the patterns that emerged across species growing in the same environment. Overall, our study demonstrates the value of integrating biogeochemical dynamics into spatial predictions of herbivory.

Introduction

Herbivory is a fundamental ecological process with far-reaching effects on ecosystem functioning. The intricate relationship between herbivores and plants cascades through key ecosystem dynamics, including food webs, community diversity, and nutrient cycling (Coley & Barone 1996; Forrister *et al.* 2019). Consequently, unravelling the dynamics of plant tolerance to herbivory, and the drivers that shape this relationship across the landscape, is crucial to decipher the ecological and evolutionary ramifications of herbivore-plant interactions (Janzen 1974; Whittaker 1979).

In attempting to explain these ecological relationships, researchers often seek clines in herbivore-plant interactions that can be captured across environmental gradients, usually associated with changes in resource availability (Endara & Coley 2011; Rasmann *et al.* 2014; Moreira *et al.* 2018). The prevailing hypothesis posits that plants growing in resource-rich environments should be able to tolerate herbivory better than plants growing in more challenging conditions (Maschinski & Whitham 1989; Whitham 1991). This hypothesis stems from the widely accepted notion that herbivory generally undermines plant fitness (Belsky 1986). The intuitive appeal of this hypothesis has laid a robust foundation for developing theories aiming to explain evolutionary links between herbivory pressure and plant defences (Coley, Bryant & Chapin 1985; Coley & Barone 1996; Endara & Coley 2011).

While conventional wisdom often suggests a negative correlation between herbivory and environmental stress, the accurate representation of these complex ecological relationships along simplified environmental gradients remains a subject of ongoing debate. For instance, Moles *et al.* (2011) challenged the prevailing idea of latitudinal gradients shaping herbivory pressure (Coley & Barone 1996), revealing that simple abiotic gradients might fail to predict variable ecological patterns across large scales. Similarly, Wise and Abrahamson (2005) demonstrated the pitfalls of using simplified resource gradients as predictors of herbivory. Their work emphasised the significance of a refined model that explores the multidimensional aspect of resource gradients for a more mechanistic understanding of the links between plant fitness and herbivory pressure (Wise & Abrahamson 2007).

In addition to resource availability, other processes can also influence plant susceptibility to herbivory. These processes can act as regulators, influencing factors

that directly affect herbivory pressure, albeit not always exerting direct control over herbivores themselves (Lynn & Fridley 2019). For example, temperature could play an important role in herbivore-plant relationships by positively impacting insect herbivore density and diversity (Moreira *et al.* 2018; Newell, Ausprey & Robinson 2023). However, temperature could also affect plant tolerance to herbivory by influencing plant defences through the regulation of edaphic chemical processes (Lynn & Fridley 2019). Overall, the comprehensive understanding of herbivore-plant interactions in natural environments might be hindered by the complex interplay of co-varying environmental factors across resource availability gradients, potentially leading to confounding effects.

Montane ecosystems are valuable natural environments for studying herbivore-plant interactions. These systems solve part of the challenge of studying variable ecological patterns across environmental gradients, as they offer strong abiotic gradients across a relatively small spatial scale, reducing the susceptibility to potential confounding effects from broad-scale factors (Pellissier *et al.* 2012; Galmán *et al.* 2018; Moreira *et al.* 2018). For instance, environmental variation across elevational gradients occurs independently of variation in day length or inter-annual variation in climate, providing a useful setting to investigate the variability in ecological relationships across space (Galmán *et al.* 2018).

This study aimed to examine the interplay of environmental gradients in regulating insect herbivory pressure in the Australian Wet Tropics across three widespread rainforest canopy tree species. Specifically, we aimed to (1) describe the abiotic drivers shaping resource availability for plants, expressed through climate and soil nutrients; (2) understand plant responses to abiotic gradients in terms of variability in foliage chemistry; (3) investigate potential correlations between insect herbivory damage, foliage nutritional chemistry and abiotic factors; (4) compare tree species with distinct growth strategies to discern contrasting responses to abiotic gradients owing to differences in potential limiting resources; and (5) unravel the indirect influence of abiotic factors on the different processes under investigation.

We predict an overarching effect of geology and climate on soil nutrients across the landscape, given the strong elevational gradient that defines montane ecosystems (Weil & Brady 2017; Galmán *et al.* 2018; Moreira *et al.* 2018; Singh Ramesh *et al.* 2023). In addition to the direct effect of abiotic factors over resource gradients, we anticipate climate and geology to propagate their influence across the ecosystem,

indirectly impacting herbivore-plant interaction through the regulation of soil nutrient availability and foliage nutritional chemistry (Lynn & Fridley 2019). If there is a direct relationship between soil and plant chemistry, then variability in plant chemistry should reflect the distribution of soil nutrients across the landscape. However, pioneer and late successional species will likely respond differently to these resource gradients, potentially reflecting their sensitivity to different limiting factors (Wise & Abrahamson 2005; Wise & Abrahamson 2007). Furthermore, we predict herbivory pressure to intensify with increasing resource availability due to the expected greater potential compensation for herbivory and lower investment in defence in resource-rich environments (Coley, Bryant & Chapin 1985; Whitham 1991; Endara & Coley 2011).

To address these aims, we first identified the main factors that could influence the variability in insect herbivory pressure in our study system: climate, geology, soil nutrients, and foliage nutritional chemistry. Then, we explicitly connected these components in a hierarchical model to study three main processes: (1) the climatic and geological influence on soil nutrients, (2) plant-soil relationships, and (3) the interaction between the amount of herbivory and plant nutritional chemistry. Following this integrated approach, we assessed the influence of the different resource gradients and climate on herbivory, both directly and indirectly.

Methods

Study system

The Australian Wet Tropics ecosystem, situated along the northeast coast of Queensland (Figure 6.1), comprises an area of approximately 7,000 km². The bioregion is characterised by a rugged landscape covered primarily by mixed tropical rainforests. Notophyll rainforest is the most extensive vegetation type, followed by mesophyll rainforest, predominantly below 400 m in elevation, and microphyll rainforest on the upper slopes and higher peaks.

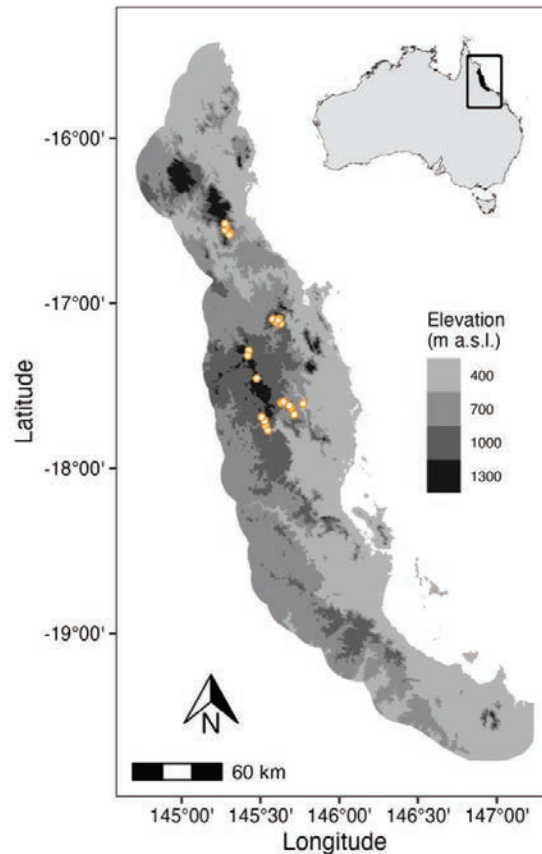


Figure 6.8. The Australian Wet Tropics bioregion and its location in Australia. The grey colour palette represents the elevational gradient of the region. Points depict the location of the 25 study sites.

The mountain ranges that shape the bioregion create a significant elevational gradient crucial in shaping biodiversity patterns and ecological processes (Williams, Pearson & Walsh 1995; Singh Ramesh *et al.* 2023). Elevation ranges from sea level to highlands at 1,000 m, with isolated peaks reaching approximately 1,620 m. Consequently, the mountain ranges in the Australian Wet Tropics define a pronounced thermal gradient spanning between 14-26 °C in mean annual temperature. The topographic features of the region also impose a longitudinal precipitation gradient, with higher rainfall near the coast (around 4,000 mm annually) and decreasing towards the western extent of the tropical rainforest distribution (approximately 1,200 mm annually). This abrupt change in rainfall occurs within 70 km of the coastline, emphasising the great variability in abiotic conditions on a relatively small spatial scale. Additionally, soil chemistry in the Wet Tropics varies markedly due to the diverse geological origins of the region. The soils primarily derive from granites, igneous rocks such as rhyolites and basalts, and metamorphic sedimentary rocks. As a result, the

bioregion presents a pronounced edaphic gradient, ranging from deep and nutrient-rich basalt-derived soils to shallow and nutrient-poor lithosols (Isbell 2016).

To capture the range of climatic and edaphic gradients of the Australian Wet Tropics, a network of 25 study sites, each approximately 1 ha, was established in notophyll rainforests, the predominant vegetation formation in the region. These study sites cover 94% of the climatic variability in the Australian Wet Tropics (Williams *et al.* 2010) and span an elevation range between 400-1,300 m. Moreover, the study site network covered the predominant soil parent material found across the mountain ranges of the Australian Wet Tropics, namely basalt, rhyolite, and granite. This study design allows for a robust examination of ecological interactions across the diverse environmental conditions present in the region. Further information about site location, geology, and climate is provided in the Appendix.

Study species

To investigate patterns in insect herbivore-plant interactions across the abiotic gradients defined above, we selected a set of canopy tree species based on their high abundance and wide distribution (see Table 6.1). These selection criteria were not intended to represent the region's rich tree biodiversity but to encompass the desirable biogeographical characteristics that allowed us to investigate the variability of ecological interactions across the landscape. Our species selection included both fast-growing generalist and slow-growing montane rainforest tree species from different families to account for potential differences in resource allocation associated with different growth strategies (Coley, Bryant & Chapin 1985; Fine, Mesones & Coley 2004). However, late successional species tend to have a more constrained geographical range than the more generalist pioneer species, resulting in an uneven sampling coverage across the abiotic gradients under investigation (Table 6.1). To cope with the differing distributional patterns when comparing the emergent relationships between growth strategies, we included two closely related species from the genus *Flindersia* to expand the sampling coverage along the abiotic gradients for late successional species (Table 6.1). Despite its limitations, this approach enabled inferring the effect of biogeochemical processes on foliage nutritional chemistry and herbivory within and between species with different growth strategies.

Table 6.2. Overview of the elevational range, habitat preference, growth strategy, sample size, and site coverage for the selected canopy tree species.

Species name	Family	Elevational range (m a.s.l.)	Habitat	Sample size	Site coverage
<i>Alphitonia petriei</i>	Rhamnaceae	0 – 1,300	Generalist; Rainforest regrowth; Pioneer species	115	100%
<i>Flindersia brayleyana</i>	Rutaceae	0 – 1,150	Well-developed montane rainforest; Late successional species	22	48%
<i>Flindersia pimenteliana</i>	Rutaceae	0 – 1,300	Well-developed montane rainforest; Late successional species	42	60%
<i>Flindersia</i> species combined	Rutaceae	0 – 1,300	Well-developed montane rainforest; Late successional species	64	84%

Insect herbivory data

Insect herbivory pressure was quantified as the proportional damage or tissue loss from attached leaves. Leaves were collected from selected canopy trees (sample height: 24.71 ± 6.28 m) during the dry seasons (April–November) of 2021 and 2022, following the methods outlined by Youngentob, Zdenek and van Gorsel (2016). Based on preliminary analyses using a reference sample (data not shown), we determined that the sampling of 20 leaves per individual tree provided an adequate sample size to measure herbivory, ensuring a complete range of apparent foliage damage across species (i.e., damage values reached a stable normal distribution within samples). To achieve the desired sample size for each tree, we randomly collected approximately 40 mature leaves from retrieved canopy branches. Half the leaves were haphazardly selected for herbivory damage measurement using the “leafbyte” image processing software (Getman-Pickering *et al.* 2020). Herbivory damage was measured only on mature leaves in this study due to the low availability of young leaves for slow-growing montane species at the sampling time. The remaining half of the leaves were snap-frozen in the field using dry ice at -80°C to preserve their chemical composition for subsequent analyses.

We focussed on quantifying the proportional leaf loss to herbivory without distinguishing the specific types of damage (i.e., chewing, sucking, or mining). This approach provided us with a general measure of insect herbivory pressure at the tree

level, allowing for an assessment of the overall impact of insect herbivores on the study tree species.

Foliage nutritional chemistry data

Measures of foliage nutritional quality for herbivores often consider the influence of nitrogen (N) as an important limiting factor due to its relatively low concentration in plant tissues (White 2012). However, the total nitrogen content in leaves may not accurately reflect the availability of this limiting factor for all herbivores. Although this study focused on insect herbivory, we also included a measure of foliar nitrogen that incorporates the influence of tannins on nitrogen digestibility (Wallis *et al.* 2012). Insects are unlikely to be affected by tannin binding due to the dissociation of tannins from proteins in the alkaline environment of insect guts (Salminen & Karonen 2011); however, the inclusion of nitrogen digestibility remains valuable in this study as it could reflect levels of tree investment in defences in the form of protein-binding tannins along abiotic and resource availability gradients.

To measure nitrogen digestibility, we followed the method outlined by DeGabriel *et al.* (2008). Briefly, this method consists of an *in vitro* digestion where paired samples are incubated in a series of buffers and enzymes. Total nitrogen and non-digestible nitrogen are measured in a Truspec Carbon/Nitrogen Analyser (LECO Corp, St. Joseph, MI), using the pre- and post-digestion samples, respectively. The index of nitrogen digestibility used in this study is then calculated as a function of the change in nitrogen and dry matter, determined by comparing samples' weight and nitrogen concentration before and after digestion, with a high index indicating a high percentage of available nitrogen relative to the total nitrogen content in the foliar tissue. Further details on the calculation of available nitrogen and lab protocol have been extensively covered in DeGabriel *et al.* (2008) and Wallis *et al.* (2012).

$$N \text{ digestibility} = \frac{(N_o * DM_o) - (N_1 * DM_1)}{(N_o * DM_o)}$$

$$Dry \text{ matter digestibility} = \frac{(DM_o) - (DM_1)}{(DM_o)}$$

Where *DM* stands for dry matter and the subscript indices represent pre-digestion (X_0) and post-digestion (X_1).

Prior to chemical analyses, foliage samples were freeze-dried and ground to pass through a 1 mm particle-size sieve. Ground samples were scanned on a Foss XDS near-infrared reflectance spectrometer. Chemical assays were performed on a

representative subset of samples, comprising 33% of our sample size, which was selected based on its near-infrared absorption spectrum and identified using Mahalanobis distance. Calibration equations were developed to predict values of foliar chemistry based on the spectra and reference values obtained from the chemical assays, following the approach outlined by Ebbers *et al.* (2002). This method allowed for a rapid, cost-effective, and non-destructive assessment of foliage nutritional chemistry by establishing a relationship between spectral information and nitrogen content (Youngentob *et al.* 2012). The calibration equations derived from this process led to a robust prediction of total nitrogen ($R^2 = 0.98$, standard error of cross-validation [SECV] = 0.06), nitrogen digestibility ($R^2 = 0.96$, SECV = 0.1259), and dry matter digestibility ($R^2 = 0.91$, SECV = 3.68). Further details about the spectral transformations and the development of the calibration equations can be found in Youngentob *et al.* (2012).

Soil chemistry data

The characterisation of soil chemistry was carried out at the site level. Our sampling design aimed to capture the heterogeneity in soil composition, deriving the average conditions to which trees were exposed at each location. We randomly selected six 150 m transects at each site with a minimum separation of 200 m between them. Along these transects, we collected soil cores every 50 m using a 65 mm Jarret-style auger. To account for the vertical variation in soil chemistry, we collected soil cores at three different depths at each sampling point (0-10 cm, 20-30 cm, and 50-60 cm). For each site and depth, samples were homogenised in the field, resulting in a total of three samples per study location. Samples were sent to the Chemistry Centre (Department of Environment and Science, Queensland Government, Brisbane, Australia) for chemical analysis promptly after collection (< 5 days).

Soil components analysed included total nitrogen and phosphorus (Kjeldahl digestion), exchangeable cations (Ca, Mg, Na, K), and organic carbon (Dumas combustion). To establish a comparable measure of soil elements across sites, we computed the mean value of each element across the vertical gradient, partly accounting for the potential effect of soil depth on nutrient acquisition (Göransson *et al.* 2006). In alignment with the study's overarching goal of understanding the interconnections within the system, our investigation focussed on specific soil elements of significant relevance in biogeochemical cycles that could, directly and

indirectly, affect herbivory pressure. These include nitrogen and phosphorus (Wright *et al.* 2005; Read *et al.* 2008; Peng *et al.* 2021; Westerland *et al.* 2023), potassium (Santiago *et al.* 2012), sodium (Kaspari 2020; Lynn, Fridley & Vandvik 2023), and the ratio between carbon and nitrogen (Weil & Brady 2017; Singh Ramesh *et al.* 2023).

Climate data

The climatic data (temperature and precipitation) was obtained from the “accuCLIM” climate layers developed for the Australian Wet Tropics (Storlie *et al.* 2013). These climate layers downscale gridded spatial climate data at 250 m resolution from empirical weather data collected between 2006-2009 at 54 rainforest sites, offering a fine-grained spatial representation of the bioregion’s climate. Our model incorporated climate variables as linear and quadratic terms, accommodating potential non-linear relationships that may emerge across the elevational gradient (Moreira *et al.* 2018).

Given the strong climatic gradient imposed by the orography of the bioregion, we expected climate to play a central role in the regulation of biogeochemical cycles (Austin & Sala 2002; Wright & Westoby 2002; Wright, Reich & Westoby 2003; Ren *et al.* 2015; Weil & Brady 2017). Additionally, we anticipated that climate would directly affect herbivory pressure through its influence on insect herbivore populations and diversity (Galmán *et al.* 2018; Newell, Ausprey & Robinson 2023).

Statistical analysis

We employed a statistical model that aimed to reflect the interconnectivity of the system by integrating climate, geology, soil element concentrations, foliage nutritional chemistry, and herbivory damage data. Our approach involved the development of a hierarchical model that mirrored the natural structure of the study system (Figure 6.2). This model enabled us to disentangle the effects of each environmental gradient on important emergent processes, such as (1) the influence of climate and geology on soil chemistry, (2) plant-soil relationships, and (3) herbivore-plant interactions. Furthermore, the hierarchical structure of the model allowed us to examine the influence of climatic and edaphic gradients throughout the ecosystem, revealing the potential impact of these abiotic factors on herbivory pressure, both directly and through the control of intermediate processes. We accounted for the inherent variation in foliar chemistry and resistance to herbivory across plant species

by implementing species-specific intercepts (Volf *et al.* 2022; Forrister *et al.* 2023). Additionally, by segregating slopes based on growth strategies—differentiating between pioneer and late successional species—we were able to compare the effect of different abiotic gradients on the processes under investigation. This combination resulted in foliage and herbivory models with a structure defined by three intercepts and two slopes per predictor (Figure 6.2). A summary of the data structure and sample size for each sub-model is provided in the Appendix.

We implemented our model in a Bayesian framework. Markov Chain Monte Carlo methods were used to sample the joint posterior distribution (Thompson & Brooks 2003) using JAGS (Plummer 2003), implemented with the jagsUI R package (Kellner 2021; R Core Team 2021). We reflected the absence of prior information about model parameters by implementing vague priors (see JAGS code in the Appendix for details). Additionally, we accounted for extra unexplained heterogeneity across sites by including a random site effect. Foliage and soil components were normally distributed, while herbivory pressure (percentage of leaf eaten) followed a beta distribution. We ran three parallel chains of 400,000 interactions, used half as burn-in, and thinned the rest by one in 100 to obtain 6,000 samples of the joint posterior distribution. The sampling process led to robust parameters convergence ($\hat{R} - 1 < 0.1$, (Gelman & Hill 2006)). We further inspected traceplots to validate good mixing and investigated the posterior predictive check by plotting the residual sums of squares for observed and simulated data. Good fitting models are expected to have values falling on a 1:1 line, suggesting a similar error structure between the observed data and the data simulated by the model (Figure S6.2). We paired the posterior predictive checks with the estimation of Bayesian p -values, with values close to 0.5 (Figure S6.2) indicating adequate model fit (Gelman, Meng & Stern 1996). Model structure and variable selection are explained in more detail in the Appendix.

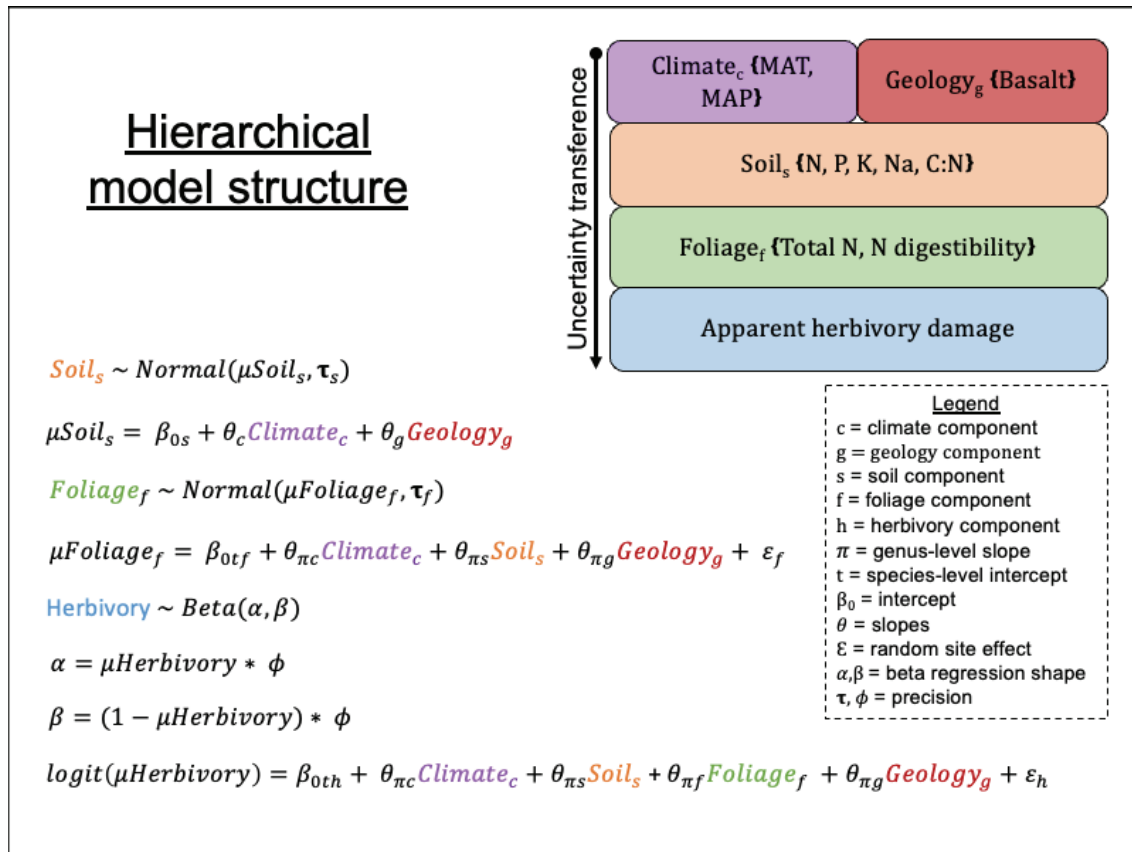


Figure 6.9. Overview of the hierarchical model developed to study herbivory pressure across environmental gradients. Colours represent the main gradients in the system. Abbreviations: Phosphorus (P); Nitrogen (N); Carbon-Nitrogen ratio (C:N); Potassium (K); Sodium (Na); Mean annual temperature (MAT); Mean annual precipitation (MAP).

Results

Spatial variability in soil nutrient

Soil nutrient availability was explained by the interplay among elevation, precipitation, and geology, the predominant environmental gradients shaping the bioregion (Figure 6.3; see *Study site*). Geology, defined by the parent materials, influenced soil element concentrations, suggesting higher nutrient concentration in sites of basaltic origin than in those derived from granite or rhyolite rocks (Figure 6.3; Figure 6.4A). Soil N and P increased with higher precipitation, while soil K and C:N decreased along the same gradient (Figure 6.3; Figure 6.4A). Temperature showed a

positive relationship with soil K but a negative association with soil Na and soil C:N (Figure 6.3; Figure 6.4A).

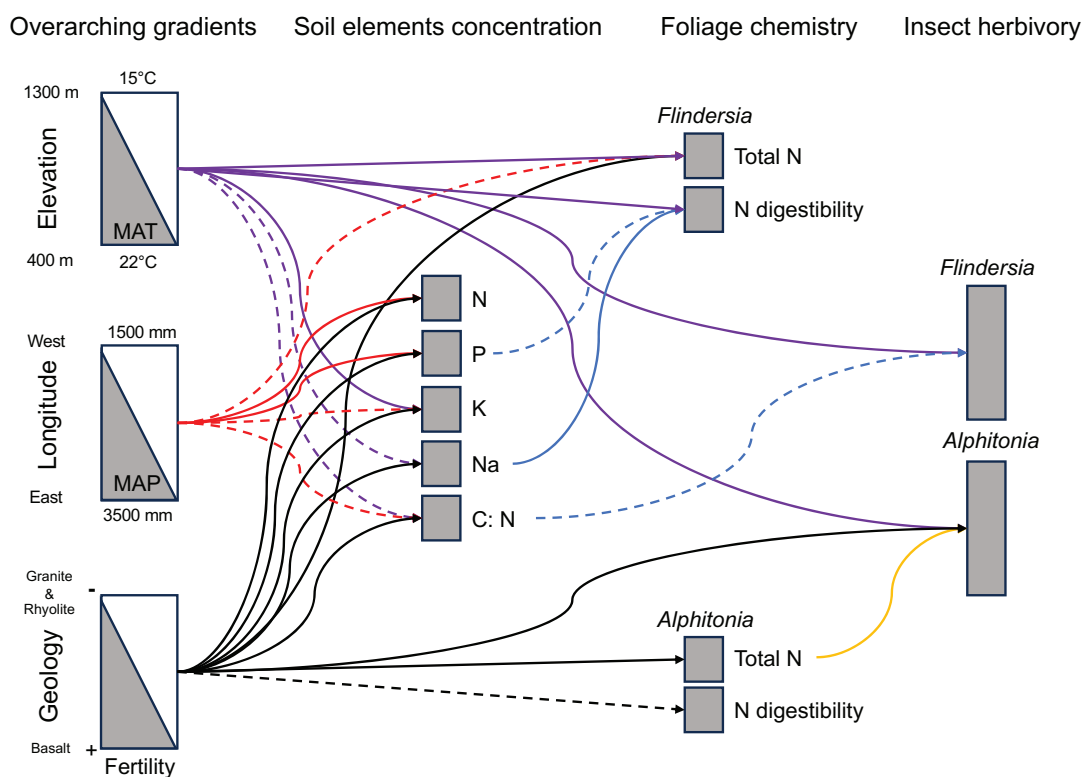


Figure 6.3. Pathways of emergent connections in the Australian Wet Tropics. This plot represents the direct and indirect associations in the ecosystem. For simplicity, only relationships that do not greatly overlap zero are included. Dashed lines represent negative relationships, while solid lines show positive associations. Colours segregate the effect of each major component in the model to ease interpretation. Abbreviations: Phosphorus (P); Nitrogen (N); Carbon-Nitrogen ratio (C:N); Potassium (K); Sodium (Na); Mean annual temperature (MAT); Mean annual precipitation (MAP). Relationships showing the overlap between the predictors and raw data are provided in Figure S6.3-6.10.

Foliage nutritional chemistry across resource gradients

We found diverging patterns in the variability of foliar chemistry across species. Specifically, *Alphitonia* showed lower N digestibility than *Flindersia*, with *Flindersia pimentaliana* exhibiting the greatest level of N digestibility across the species examined (Table S6.2). Conversely, total N was present in higher concentration in

Alphitonia than in *Flindersia*, with *Flindersia brayleyana* showing the lowest level of total N across the study species (Table S6.2).

The concentration of total N across trees was significantly influenced by geology, with individuals growing in basaltic soils showing greater levels of total N than trees growing in granite and rhyolite soils. This pattern remained consistent for *Alphitonia* and *Flindersia* (Figure 6.3; Figure 6.4B). N digestibility was negatively correlated with soil P for *Flindersia* and basaltic soils for *Alphitonia* (Figure 6.3; Figure 6.4C). A diverging pattern between *Alphitonia* and *Flindersia* was related to their response to soil Na, with *Flindersia* suggesting a positive association, while *Alphitonia* showed a marginal response (Figure 6.4C). In addition to inorganic nutrient availability, *Flindersia* also exhibited significant sensitivity to climate, suggesting an increase in total N and N digestibility with increasing temperatures and a decrease in total N with higher rainfall (Figure 6.3; Figure 6.4B-C).

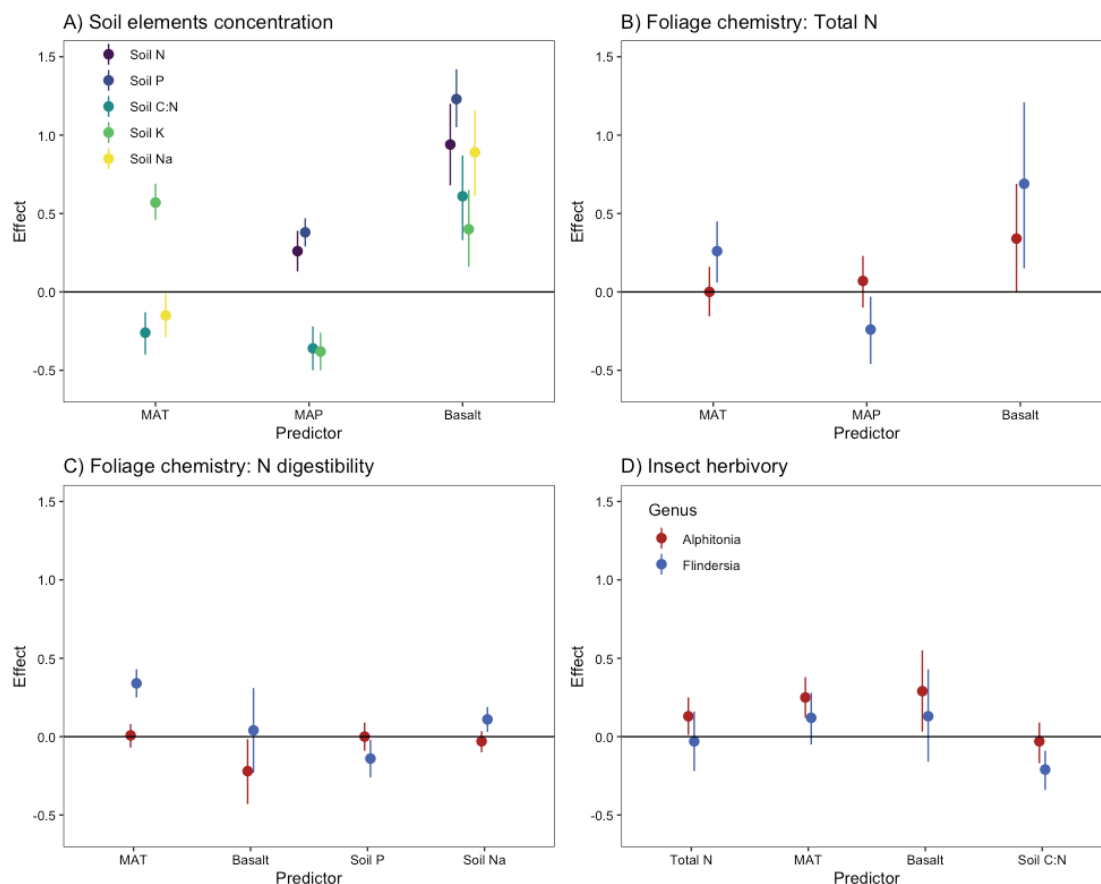


Figure 6.4. Summary plot showing the effects of different drivers on soil element concentration (A), total foliar N (B), N digestibility (C), and insect herbivory pressure (D). Values represent the posterior mean and 89% credible interval (McElreath

2020). Colours represent different soil elements in panel A and different tree genera in panel B-D. Abbreviations: Phosphorus (P); Nitrogen (N); Carbon-Nitrogen ratio (C:N); Potassium (K); Sodium (Na); Mean annual temperature (MAT); Mean annual precipitation (MAP). Relationships showing the overlap between the predictors and raw data are provided in Figure S6.3-6.10.

Patterns in herbivory damage

Herbivory pressure, measured as the proportional tissue loss from attached leaves, was low across the trees sampled, with average damage close to 4% (although individual leaf values ranged from 0.002% to 54.79%). The variability in herbivory showed no clear distinction between *Alphitonia petriei* (average = 2.5-3.3%) and *Flindersia pimentaliena* (average = 1.9-2.7%; Table S6.2). In contrast, *Flindersia brayleyana* showed generally higher levels of herbivory (average = 4.3-9.4%; Table S6.2) than *Alphitonia petriei* and *Flindersia pimentaliena*.

The variability in herbivory pressure across the landscape was influenced to some degree by all abiotic gradients but not consistently across species (Figure 6.3). *Alphitonia* showed higher levels of herbivory in sites on basalt, higher temperatures, and across trees with higher total foliar N (Figure 6.3). In a similar way, there was a negative relationship between herbivory and soil C:N and a positive relationship between herbivory and temperature for *Flindersia* species (Figure 6.3; Figure 6.4D). However, we note that the effect of temperature on herbivory for *Flindersia* showed greater uncertainty (Figure 6.4D; Figure S6.3).

Indirect effects

In addition to the direct effects described in the sections above, our result showed a variety of potential intermediate processes that emerged from the hierarchical structure of the system. Precipitation indirectly influenced N digestibility and herbivory pressure for *Flindersia* through its influence on soil P and soil C:N, respectively (Figure 6.3). Temperature, in addition to the direct relationship to foliar chemistry and herbivory pressure (Figure 6.4), also indirectly impacted N digestibility and herbivory damage for *Flindersia* by influencing soil Na and soil C:N, respectively. Lastly, geology was positively associated with herbivory damage for *Alphitonia* both directly and through its relationship to total foliar N (Figure 6.3).

Discussion

In this study, we have delved into the relationship between herbivory and resource availability across three widespread rainforest tree species in a tropical montane ecosystem, the Australian Wet Tropics. Our study has placed a particular emphasis on investigating herbivore-plant interactions within the broader context of biogeochemical dynamics. This approach has allowed us to investigate (1) what factors affect resource availability across multiple abiotic gradients, (2) how plant chemistry responds to the variation in resources, and (3) how the interplay between resource gradients and foliage nutritional chemistry correlates to patterns in insect herbivory across the landscape. Overall, our findings contribute to a deeper understanding of the intricate relationships between environmental factors, plant physiology, and herbivory dynamics in tropical montane ecosystems.

Patterns in resource availability across abiotic gradients

The climatic and geological gradients that occur across the Australian Wet Tropics showed a strong relationship to all the factors we examined. Specifically, our results suggested an interplay between climate and geology in shaping biogeochemical dynamics in montane ecosystems (Weil & Brady 2017; Singh Ramesh *et al.* 2023). Along the elevational gradient, some measured soil chemical constituents were significantly influenced by temperature. We found evidence of a negative plant-soil relationship at higher elevations, possibly related to the temperature-induced slowdown in soil microbial activity and nitrogen mineralisation (Salinas *et al.* 2011; Weil & Brady 2017). Across the longitudinal gradient, soil nutrient availability was primarily influenced by changes in rainfall. Notably, key soil nutrients, such as N and P, increased with higher precipitation, emphasising the role of rainfall in influencing nutrient availability (Austin & Sala 2002; Ren *et al.* 2015). However, rainfall could also negatively influence the concentration of some soil elements through leaching, suggested in this study by the relationship between precipitation and soil K. Independently of climatic conditions, geology showed a strong relationship to soil nutrient levels, stressing the important role of parent materials in determining the supply of rock-derived soil elements that can contribute to nutrient availability to plants (Anderson 1988).

Effect of resources availability on foliage nutritional chemistry

Foliar nutritional chemistry did not consistently correspond with broader biogeochemical processes. Despite our findings suggesting that geology was strongly correlated to soil nutrients, the positive relationship between basaltic soils and foliar nutritional chemistry could not be explained by individual constituents of soil fertility. This discrepancy might reflect the importance of understanding soil fertility as a multidimensional factor shaped by the interaction between soil nutrients and other physical or chemical properties that are associated with the underlying site geology. While this notion offers an intuitive explanation for the observed patterns (Millard 1993; Norris *et al.* 2013), it is important to acknowledge the potential influence of external variables that co-vary with geology, potentially impacting spatial variations in foliage nutritional chemistry.

In addition to the influence of geology on foliage nutritional chemistry, we found a significant climatic influence on foliar N for *Flindersia* but not for *Alphitonia*, which could reflect differences in geographical restrictions between these genera. While the generalist *Alphitonia* is widespread and well adapted to a diverse range of climatic conditions (Hyland *et al.* 2010), the more geographically constrained *Flindersia* could suffer greater fitness limitation along climatic gradients, thereby showing reduced foliar N in less favourable environments (Singh Ramesh 2023; Singh Ramesh *et al.* 2023). Moreover, our results suggested an intriguing pattern related to the relationship between N digestibility and resource gradients, where N digestibility decreased with increased soil P for *Flindersia* and basaltic soils for *Alphitonia* (Figure 6.3). This pattern did not align with our initial expectations. We propose two potential explanations for this negative relationship between N digestibility and nutrient availability.

The negative relationship between N digestibility and nutrient availability observed in this study could be related to resource-driven plant investment in defences. In resource-rich environments, plants might allocate more resources towards defences against herbivory, such as carbon-based compounds like tannins, compared to plants growing in more resource-limited conditions (Hahn & Maron 2016; Moreira *et al.* 2018; López-Goldar, Zas & Sampedro 2020). This process would result in a decrease in N digestibility but not in total N in high-resource environments, aligning with the patterns we observed in this study. An alternative explanation could be related to the presence of alkaloids in the tree species included in this study (Robertson *et al.*

2018; Al Omar *et al.* 2022), which could suggest that our measure of foliar N would capture not only protein content but also alkaloid concentration. These potential relationships warrant further investigation.

The drivers of herbivory damage

The low value in herbivory damage found in this study markedly contrasts with findings in other tropical wet forests, for which insect herbivory damage has been reported to reach values of up to 48% (Coley & Barone 1996). These differences could be attributed to a number of factors, including (1) the discrete nature of the measurement taken in this study, as opposed to continuous monitoring, preventing the determination of total leaf loss (Lowman 1985); (2) the consideration of only mature leaves, which may be less consumed by insect herbivores than young leaves (Coley & Barone 1996); (3) the lower herbivory damage on the canopy stratum of the forest, highlighting the shade/sun differences in herbivory pressure (Lowman 1985); and (4) the potential depression of insect herbivores during the dry season, when our sampling took place (Wolda 1978; Lowman 1985). While including sampling during the wet season and covering various leaf ages and forest strata could potentially yield a higher herbivory rate, our consistent sampling design provides robust insights into spatial variations in herbivory damage across multiple abiotic gradients. Additionally, it offers a comparative framework to assess how these gradients affect species with different growth strategies, as it is not confounded by changes in seasonal herbivore activity along the forest stratum or differing seasonal patterns in leaf flushing across species.

Our results suggest that herbivory damage was significantly influenced by the same abiotic factors that affected nutrient availability for soils and plants, providing some support for the compensatory continuum hypothesis, where the degree of herbivore impact changes as a function of resource availability (Maschinski & Whitham 1989; Whitham 1991). However, we found differing relationships between herbivory and other measured variables among tree species with different growth strategies, suggesting potential contrasts in factors that affect herbivory (Wise & Abrahamson 2005; Wise & Abrahamson 2007). For the pioneer species *Alphitonia petriei*, herbivory damage was primarily influenced by geology and its relationship to total foliar N (Figure 6.3), with trees growing in soils originated from basaltic rocks showing greater herbivory damage and higher foliar N than trees growing in lithosols. For late successional species of the genus *Flindersia*, soil nutrient levels impacted herbivory

pressure via the soil C:N ratio, indicating a decrease in herbivory in sites with slow N mineralisation (Weil & Brady 2017). Although these findings demonstrate some relationship between soil chemistry and the foliar nutritional landscape (Wardle *et al.* 2004), it is also notable that this relationship was not consistent across plant species. Moreover, many of the soil nutrients commonly associated with soil fertility, including N and P, showed no direct relationship to total foliar N in any species. Consistently, however, herbivore-plant interactions were significantly impacted by climate. Temperature had a strong positive relationship to herbivory for all species included in the study, potentially reflecting the positive effect of temperature on insect physiology, density, and richness along the elevational gradient (Galmán *et al.* 2018; Moreira *et al.* 2018).

Revealing hidden connections

Our analytical approach indicated that the significant effect of abiotic factors on foliage nutritional chemistry and herbivory pressure was partly explained by the cascading effect that climate and geology have on other abiotic and biotic aspects of the system (Lynn & Fridley 2019). A relevant example from our system relates to the indirect relationship between precipitation and herbivory damage in *Flindersia* species, where the effect of rainfall was only detected via its influence on soil C:N (Figure 6.3).

Conclusion

Here, we have demonstrated that herbivore-plant interactions are complex dynamics regulated by an intricate web of relationships spanning different biogeochemical processes. While our results provide some support to the notion that herbivory is affected by resource availability, species of different strategies growing under the same conditions can show differing responses to the same resources, highlighting the importance of identifying specific limiting factors rather than simpler proxies of resource availability (Wise & Abrahamson 2005). Furthermore, the regulation of herbivore-plant relationships across the landscape does not rest solely on the direct effect of limiting resources but also on the factors that regulate resource availability. These otherwise hidden links are critical for the understanding of ecosystem dynamics and should be considered when studying ecological relationships, offering a more comprehensive appreciation of the processes that govern the natural world.

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Chapter Seven - Physiological stress explains climate change impacts on long-term population dynamics of rainforest ringtail possums

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Physiological stress explains climate change impacts on long-term population dynamics of rainforest ringtail possums

Abstract

Climate change poses escalating pressure on global biodiversity, yet understanding the mechanisms linking environmental changes to ecological responses remains challenging. Given the multidimensional factors that animals must balance in nature, unravelling the biological mechanisms by which species respond to climate change demands interdisciplinary approaches. In this study, we integrate statistical and mechanistic methodologies to investigate the causal link between climate change and population declines, focusing on rainforest ringtail possums in the Australian Wet Tropics. Our framework comprises three main models. First, we developed a mechanistic model based on biophysical ecology principles, leveraging physiological, morphological, and microclimate information to capture the thermodynamics of ringtail possums. The derived output from this model consists of biophysical variables reflecting the fundamental physiological constraints of the species, including thermal stress, water loss, and foraging limitations. Second, we constructed a biogeochemical model that integrated information on climate, geology, soil nutrients, and foliage quality to determine the nutritional landscape for ringtail possums based on estimates of foliage nitrogen across three rainforest canopy trees of special importance in the species' diet. Finally, we integrated the biophysical predictors reflecting the species' physiological stress and the foliage nutritional quality derived from the biogeochemical model into an open hierarchical population model that explicitly described the dynamics of ringtail possum populations across 32 long-term monitoring sites between 1992-2022. We demonstrate that climate change has impacted rainforest ringtail possum population dynamics primarily through alterations in fitness associated with physiological stress. Specifically, climate-induced population declines resulted from a reduction in survival and recruitment linked to an increase in overheating, dehydration, and a decline in foraging performance. The extent of the physiological stress experienced by these species is influenced by the elevational gradient they occupy, potentially reaching biologically limiting levels at lower elevations, where local extinctions have been observed. This study highlights the significance of uncovering the mechanisms driving climate-induced ecological responses in wild populations. Understanding the specific causes of population declines is paramount in conservation biology, as it enables the implementation of

efficient conservation actions at the local scale, where targeted interventions are needed.

Introduction

Anthropogenic climate change has exposed ecosystems to unprecedented conditions, intensifying the pressure on global biodiversity (Hoegh-Guldberg *et al.* 2018). Notably, species responses to climate change exhibit an accelerated pace along the elevational gradient (Chen *et al.* 2011), driven by exceptionally high vertical isotherm shift velocities (Chan *et al.* 2024). Consequently, species unable to track the rapid warming along mountain slopes are undergoing severe population declines (Chen *et al.* 2011), following a pattern ominously referred to as the “escalator to extinction” (Marris 2007; Urban 2018).

The magnitude of climate-driven biodiversity erosion is particularly pronounced in tropical ecosystems (Freeman *et al.* 2021), where populations of montane species have suffered substantial losses across the lower range of their elevational limit (Pounds, Fogden & Campbell 1999; Freeman *et al.* 2018; Neate-Clegg *et al.* 2021). As a result, local extirpation in the tropics is more common than anywhere else in the world (Pörtner *et al.* 2022).

The Australian Wet Tropics of North Queensland represents a relevant example of the state of climate-induced biodiversity attrition, evidencing the pervasive impact of climate change on tropical montane ecosystems. Over three decades of monitoring efforts in this region have revealed a strong correlation between warming temperatures and population decline in rainforest vertebrates (Williams & de la Fuente 2021; de la Fuente & Williams 2022; de la Fuente, Navarro & Williams 2023). Among the most threatened species in the bioregion are endemic ringtail possums (family Pseudocheiridae), which have experienced a population collapse, pushing the species to the brink of extinction (de la Fuente & Williams 2022).

Despite the widespread evidence suggesting an unequivocal link between biodiversity loss and anthropogenic climate change, we still lack a comprehensive understanding of the mechanisms underlying climate-driven ecological responses. The question of what mechanisms link climate change to population declines remains puzzling, hindering advances in conservation and global change biology. Examples like the case of rainforest ringtail possums underscore the urgency of addressing this

question, as the fate of many species may depend on timely, targeted, and effective conservation actions.

A natural approach towards unravelling the causal link between climate change and population dynamics involves investigating how the environment affects animal fitness by exploring fundamental constraints on survival and recruitment (Briscoe *et al.* 2023). Building upon this goal, considerable research effort has been directed towards understanding species-level physiological responses under controlled experimental designs, such as lab conditions or common garden experiments, that simulate realistic climate change scenarios. For marsupial folivores like the ringtail possums, experimental studies have demonstrated their inability to cope with extreme heat, with overheating and dehydration likely limiting survival and recruitment (Krockenberger, Edwards & Kanowski 2012; Turner 2020). Additionally, climate-induced physiological stress in marsupial folivores can disrupt their feeding ecology, potentially causing a significant decrease in food intake (Beale *et al.* 2022; Beale *et al.* 2023), thereby reducing breeding success (DeGabriel *et al.* 2009; Kearney, Wintle & Porter 2010). This reduction in foraging performance can also have lethal consequences for these species due to their low muscle and fat reserves, which are required to endure extreme conditions (Rübsamen *et al.* 1984; Youngentob *et al.* 2021). While these experimental studies offer valuable insights into species' mechanistic responses to warming, they do not capture the complexity of the multidimensional factors that animals must balance in nature. This limitation increases uncertainty regarding how findings from experimental designs might translate to natural populations.

Biophysical ecology can bridge the gap between experimental studies and observed ecological responses (Briscoe *et al.* 2023). Mechanistic models based on the principles of biophysical ecology leverage the laws of physics and chemistry to capture species thermodynamics in a given environment, including the balances of heat, water, and other aspects of energy and mass exchange. By determining the fundamental physical and chemical constraints that species must endure in their natural environment, the output of these models translates to metrics of fitness (Gates 1980), which can be naturally integrated into ecological models, including population dynamics (Buckley 2008; Kearney *et al.* 2010; Riddell *et al.* 2019; Briscoe *et al.* 2023). Despite the potential benefits, the integration of statistical and mechanistic methods to understand and predict climate change impacts remains largely unexplored.

In this study, our aim was to unravel the causes of the population collapse in ringtail possum species endemic to the Australian Wet Tropics. We delved into the mechanisms underlying climate-induced population dynamics by integrating information on physiology, climate, foliage nutritional quality, and long-term abundance data. Our approach consisted of three main steps (Figure 7.1). First, we developed a mechanistic model that harnessed physiological, morphological, and microclimate data to capture the species' heat and water balances across the spatiotemporal scale of the ringtail possum monitoring program, spanning from 1992 to 2022 across 32 rainforest sites. Drawing upon the species' thermodynamics and observed feeding ecology (Goudberg 1990), we designed seven biophysical scenarios that capture daily activity patterns, resulting in a metric of potential foraging activity that accounted for biological and physiological constraints. Second, we constructed a hierarchical biogeochemical model that included information on climate, geology, soil nutrients, and foliage chemistry to determine the nutritional landscape for ringtail possums across the study sites. This nutritional landscape was based on estimates of foliage nitrogen across three rainforest canopy tree species that are of significant importance in the ringtail possums' diet. Finally, we integrated the mechanistic predictors reflecting the species' physiological stress (i.e., overheating, dehydration, and foraging performance) and foliage nutritional quality derived from the biogeochemical model into an open population model that explicitly accommodated imperfect detection. This model described the dynamics of the population by modelling the effect of physiological stress and foliage quality on survival and recruitment.

Throughout this framework, our goal was to illustrate the integration of statistical and mechanistic approaches to enhance our understanding of climate change impacts. We applied this framework to the case of rainforest ringtail possums in the Australian Wet Tropics, demonstrating how climate change has impacted these populations by inducing physiological stress and nutritional constraints (Krockenberger, Edwards & Kanowski 2012; Youngentob *et al.* 2021). We hypothesised that observed declines in population numbers have resulted from a reduction in survival and recruitment, linked to heightened physiological stress imposed by the fast-paced warming observed in the region (Suppiah, Macadam & Whetton 2007; Krockenberger, Edwards & Kanowski 2012; de la Fuente & Williams 2022). We anticipated a significant association between physiological stress and the elevational gradient occupied by ringtail possums, potentially exerting a biological

limiting pressure leading to local extinctions at lower elevations (de la Fuente & Williams 2022). Additionally, we expected climate change to have a stronger impact in sites with low nutrient availability, indicative of poorer body conditions linked to limited nutrient acquisition (Kanowski 2001; Youngentob *et al.* 2021). Finally, we aim to highlight opportunities and challenges for applying this framework more generally to other systems and to describe how outputs can be used to guide conservation efforts.

Methods

In this section, we provide a concise overview of our methodology (Figure 7.1). An extended methodology file is provided in the Appendix, where we thoroughly cover all procedures and analyses implemented in this study.

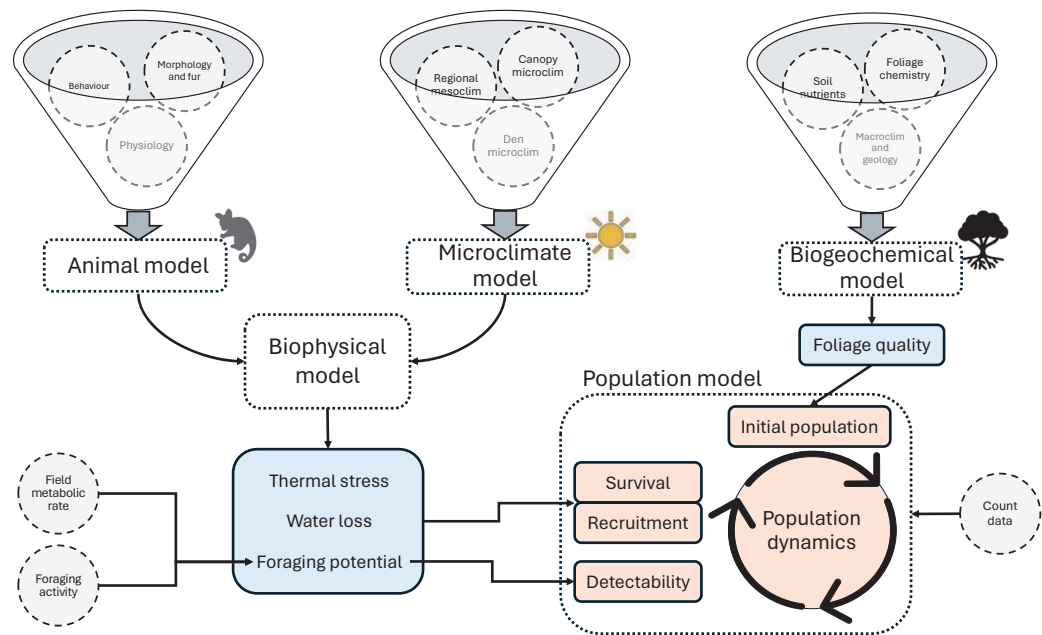


Figure 7.1. Conceptual illustration of the study framework. Grey circles denote the diverse datasets utilised to parameterise and calibrate/validate the models. Dotted white rectangles delineate the principal models within the framework, while blue rectangles symbolise the derived parameters facilitating the integration of biophysical and biogeochemical models into the population model. Note that hourly weather data, soil, and topographic information also form part of the development of the microclimate model, but these datasets are internally generated by the NicheMapR package (Kearney & Porter 2017) and are therefore omitted in the figure. We also

omitted some variables considered in the development of the population model but were not derived from the processes outlined. These include the effect of elevation on the initial population, the effect of density dependence on survival and recruitment, and the effect of the number of surveyors on detectability.

Study system

The Australian Wet Tropics (Figure 7.2) is a tropical montane ecosystem globally recognised for its significance owing to high endemism, evolutionary importance, and phylogenetic distinctiveness (Williams *et al.* 2016). Ringtail possums, endemic species to the bioregion, are medium-sized nocturnal marsupial folivores primarily inhabiting the canopy of upland rainforests. These species present discontinuous and constrained geographical ranges, possibly reflecting past fluctuations in rainforest habitats during the Pleistocene (Winter 1997). Distributional differences between the ringtail species included in this study stem from the wider elevational and latitudinal ranges presented by *Pseudochirops archeri* compared to *Hemibelideus lemuroides* (Williams *et al.* 2010). However, the core population of these species exhibit high levels of overlap, mainly centred around 700-1,000m in elevation in the Atherton Tablelands, which spans between -18° and -17° in latitude (Figure 7.2). Previous studies on the species have addressed physiological limitations (Krockenberger, Edwards & Kanowski 2012), population trends (de la Fuente & Williams 2022), feeding ecology (Goudberg 1990; Jones, Maclagan & Krockenberger 2006), and drivers of spatial distribution (Kanowski *et al.* 2001). While gaps persist in understanding their reproductive biology, based on limited field information and data from related species, it is suggested that rainforest ringtail possums reproduce during the dry season (April-November), producing a single young per year (Strahan 1995).

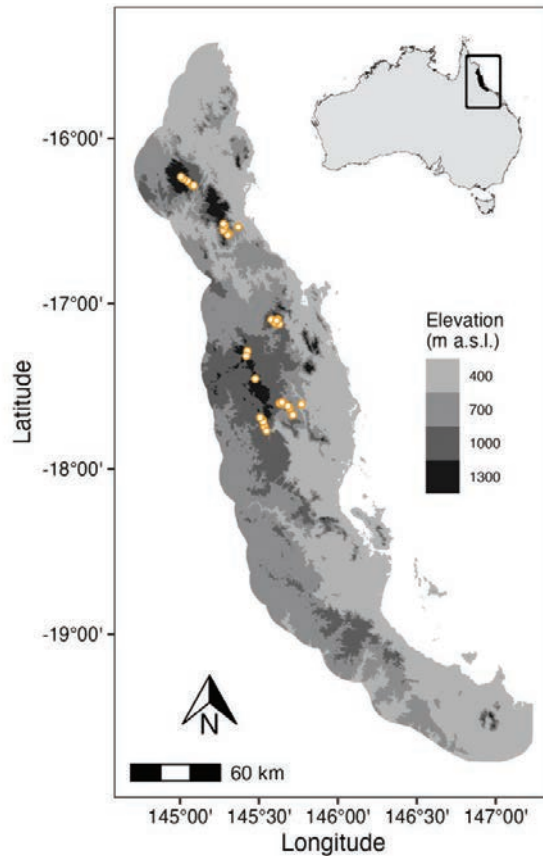


Figure 7.2. The Australian Wet Tropics bioregion and its location in Australia. The grey colour palette represents a simplified elevational gradient, with points representing the location of the long-term monitoring sites. Further details about the sites are included in the Appendix.

Biophysical ecology

Biophysical ecology employs models of microclimate, heat budgets, and thermoregulatory behaviour to describe animal fitness by capturing the fundamental interactions between organisms and their environment (Gates 1980). Consequently, the development of the biophysical models comprises generating microclimate data and designing an animal model that captures thermoregulatory behaviours. These models are then joined to solve for the physiological responses required to balance the species' heat budget in the given microclimate (Figure 7.1).

Microclimate model

Hourly microclimate data was generated across the 32 long-term study sites between 1992-2022 using the NicheMapR package (Kearney & Porter 2017),

accounting for fine-grained topographic and mesoclimatic variability in the region (Storlie *et al.* 2013). We validated the accuracy of the microclimate model in generating spatiotemporal weather data using an independent dataset consisting of hourly observed temperature across four of our study sites between 2019 and 2020 (Leahy *et al.* 2022). Additionally, microclimatic conditions were adjusted to reflect the specific environmental exposures for the species, taking into consideration the biological and behavioural characteristics of ringtail possums. For instance, we considered the exposure to vegetal substrate and sky temperature while foraging in the canopy and included daytime den buffer effect for *Hemibelideus lemuroides*. Den microclimate adjustments were implemented using hourly temperature data collected across 14 ringtail possum dens between 2007-2009, indicating a mean daytime buffer ranging between 0.25-1.5°C (Krockenberger unpublished-a). *Pseudochirops archeri* do not den in tree hollows but rather spend daylight hours curled up on a branch in the canopy (Winter, Krockenberger & Moore 2008). Therefore, we assumed full-shaded microclimate exposure for *P. archeri* during the daytime.

Animal model

The thermoregulatory behaviour of ringtail possums was captured in an animal model developed using physiological, morphological, and behavioural traits (Figure 7.1). The performance of the animal model was validated against observed metabolic data for the species (Krockenberger, Edwards & Kanowski 2012; Krockenberger unpublished-c), demonstrating the ability of the model to accurately replicate observed physiological responses under laboratory conditions (see the Appendix, “Extended methodology (II): Biophysical ecology”). We ran the animal model using the calibrated field microclimate to predict physiological responses for ringtail possum species across the 32 study sites for the period 1992-2022 (Kearney *et al.* 2021).

Activity scenarios

Seven activity scenarios were designed to mimic the daily activity and feeding ecology of the species, resulting in a physiological-derived metric that computed expected hourly activity based on biological and thermoregulatory constraints (Levy *et al.* 2016; Beale *et al.* 2023). These scenarios ranged from "resting" (i.e., non-active) to progressively more active states at 10-minute intervals, each associated with a proportional increase in metabolic cost, imposing higher physiological stress on the

animals during more active states. The overarching goal was to maximise nightly foraging potential (i.e., five hours for *P. archeri* and six hours for *H. lemuroides* (Goudberg 1990)) while minimising water loss and avoiding overheating. Considering these constraints, the animal selected the most optimal scenario each hour, resulting in an active-rest-active dynamic that prompted rest during daytime and whenever body temperature exceeded 0.5°C above their thermoneutral zone (i.e., above 36.3°C for *P. archeri* and 37.8°C for *H. lemuroides*). This foraging activity framework was informed by feeding ecology studies of captive marsupial folivores under controlled temperature conditions, where the feeding rate gradually decreased with increasing ambient temperature (Beale *et al.* 2022).

Rain mitigation effect on water loss

The biophysical model developed for this study also incorporated mechanisms to mitigate water loss stress following rainfall events. Substantial rainfall increases the availability of free water in the canopy of tropical rainforests, which strict folivores like ringtail possums can exploit by consuming wet foliage to replenish any water lost throughout the day. This compensatory mechanism was accounted for by temporarily balancing water loss to zero following significant rainfall events (daily rainfall exceeding 20 mm).

Physiological stress variables

The output derived from the biophysical model consisted of a dataset at hourly timesteps with information about water loss, energy requirements, body temperature, and potential activity for rainforest ringtail possum species across the 32 long-term monitoring sites from 1992-2022. Notably, these field physiological responses were constrained by the species' biology, physiological limits, and expected behavioural responses. To validate the performance of the animal model in the field microclimate, we corroborated physiological and behavioural predictions against field energetics data for ringtail possum species (Goudberg 1990; Krockenberger unpublished-b), suggesting high levels of accuracy (see the Appendix, "Extended methodology (II): Biophysical ecology"). Lastly, we derived annual biophysical variables from the hourly physiological response predicted in the biophysical model to match the temporal scale of our population dataset (Table 7.1). These variables captured spatiotemporal patterns in long- and short-term thermal stress, water loss, and foraging constraints

for ringtail possums (Figure 7.1). We explored the rate of change in biophysical variables across space and time to understand the effect of climate change on physiological stress by fitting linear and curvilinear models. Spatial patterns described changes in physiological stress along the elevational gradient, while temporal patterns represented the yearly rate of change between 1992-2022 across the species distribution.

Table 7.1. Description of physiological stress variables derived from the biophysical model that captures thermal, water-loss and foraging constraints. Long-term variables were calculated by summarising annual hourly data (cumulative/chronic impacts), while short-term variables were designed to capture acute stress events that occurred over hours-days.

Stress category	Scale	Definition	Units	Variable
Thermal	Long-term	Cumulative hourly stress in a year (dosage)	°C	Thermal dosage
Thermal	Short-term	Highest intensity event in a year. Thermal events are defined as 5 or more consecutive hours of stress	°C	Thermal intensity
Water loss	Long-term	Percentage of extreme stress in a year (above the 90 th percentile)	%	Long-term EWL
Water loss	Short-term	Maximum cumulative 4-days water loss	g of H ₂ O	Short-term EWL
Foraging	Long-term	Percentage of nights in a summer with a cumulative foraging time above 80% of the maximum foraging potential	%	Long-term foraging performance
Foraging	Short-term	Minimum cumulative 2-days foraging time	% of potential maximum	Short-term foraging performance

Biogeochemical dynamics

Foliage nitrogen (N) and its availability for mammalian folivores are crucial limiting factors that could influence resource acquisition, individual fitness, and population growth and distribution (White 2012). We defined the nutritional landscape for ringtail possums using metrics that captured foliage quality for folivores, including total N, available N, and tannins effect on N digestibility (DeGabriel *et al.* 2008; Wallis *et al.* 2012). Chemical assays were performed on canopy foliage samples collected across 25 of the 32 study sites for three rainforest tree species of special importance in ringtail possums' diet (Goudberg 1990; Jones, Maclagan & Krockenberger 2006). Foliage sampling was paired with soil collection across the same sites to account for

potential bottom-up effects imposed by the diverse geological origin of the Australian Wet Tropics. To capture foliage quality across the unsampled sites, we developed a hierarchical biogeochemical model that described the spatial pattern in foliage nutritional chemistry as a function of climate, geology, and soil nutrients (Figure 7.1). This approach allowed a robust stochastic imputation of soil and foliage chemistry across unsampled sites while accounting for biogeochemical dynamics (see the Appendix, “Extended methodology (III): Foliage nutritional chemistry”).

Population dynamics

To gain an understanding of the causes inducing changes in abundance over space and time, we implemented a Bayesian hierarchical population model that explicitly described the processes governing population dynamics (Dail & Madsen 2011). These models facilitate the estimation of vital rates such as survival and recruitment, as well as population growth and abundance, using simple counts of unmarked individuals replicated across space and time. Estimating vital rate parameters from counts of unmarked individuals involves a formal description of the processes driving population change over time. Temporal fluctuations in abundance at a particular location are characterised by the sum of survivors from the previous year and the number of new individuals at that site. Therefore, apparent survival encompasses mortality and emigration, while recruitment includes birth and immigration.

Our population model, based on the approach outlined by Bellier, Kéry and Schaub (2016), integrates density dependence and spatiotemporal covariates into the estimation of vital rates. This open population model allowed us to explore the effects of physiological constraints and foliage nutritional quality on population dynamics by integrating biogeochemical and biophysical processes into the population model (Figure 7.1). Spatial variation in the initial population in 1992 was modelled as a function of elevation and metrics of foliage quality, while spatiotemporal changes in recruitment and survival for the period 1993-2022 were modelled as a function of physiological stress variables. The effects of density dependence on population dynamics were tested following the model selection outlined in Bellier, Kéry and Schaub (2018), suggesting that density dependence was acting only on recruitment for both species. Further, detection probability was modelled as a response to survey effort, reflected by the number of observers in each survey, as well as the expected

levels of animal activity during the survey, predicted for the exact location and night of each survey using the biophysical model described above.

Model selection is difficult in the Bayesian framework, particularly with hierarchical models with latent states like those implemented here, where the same observed data can arise from very different combinations of latent processes (Hooten & Hobbs 2015). Therefore, to identify the most parsimonious models that described the biophysical and nutritional factors affecting the population dynamics of rainforest ringtail possums and their detection probability, we designed a five-step model selection framework that progressively identified and validated variable importance while simultaneously identifying potentially confounded predictors, resulting in the selection of the most parsimonious model explaining the dynamics of ringtail possum populations (see the Appendix, “Extended methodology (IV): Population dynamics”).

The abundance data used in the model comprises repeated yearly counts of unmarked individuals collected across 32 long-term rainforest study locations from 1992-2022. While population data were available for all four endemic ringtail possums (de la Fuente & Williams 2022), this study only included species for which we had detailed physiological information (i.e., *Hemibelideus lemuroides* and *Pseudochirops archeri*).

Results

Physiological responses

The elevational gradient that defines the abundance pattern for rainforest ringtail possums was strongly correlated to the species’ modelled physiological interactions with climate. Thermal dosage and intensity linearly decreased with elevation, while associated foraging performance showed a linear increase along the same gradient (Table 7.2). However, thermal-related physiological stress exerted a greater impact on *Pseudochirops archeri* compared to *Hemibelideus lemuroides* (Table 7.2). For instance, thermal dosage decreased at an average rate of 0.77 °C per 100 m increase in elevation for *H. lemuroides*, whereas it decreased at a rate of 29.62 °C for *P. archeri*. This discrepancy likely arises from the higher thermoneutral zone for *H. lemuroides* (37.3 °C compared to 35.8 °C for *P. archeri*), providing a greater buffer against increased temperature at lower elevations. Interestingly, the effect of

overheating on potential foraging activity was more similar between species, with *H. lemuroides* showing an average increase in annual foraging performance of 5.46% per 100 m increase in elevation, compared to the 8.81% for *P. archeri*. This could indicate that thermal stress for *H. lemuroides* is manifested through its effect on foraging activity rather than direct overheating. Lastly, results related to water stress suggested a positive linear correlation between evaporative water loss and elevation (Table 7.2). However, this pattern is likely related to the western distribution of a significant proportion of upland rainforest in the region, where rainfall decreases substantially compared to coastal low-elevational sites (from an average of 4000 mm to 1200 mm annually), possibly reducing free water availability for the ringtail possums. Temporally, climate change has intensified physiological stress for ringtail species (Table 7.2). After accounting for the effect of elevation on physiological responses, thermal stress exhibited a curvilinear (concave) pattern over time, wherein a decrease in heat stress in the early years was followed by an increase in the last decades (Table 7.2), mirroring observed heatwave patterns in the region. Conversely, short-term foraging constraints showed an inverse (convex) response, suggesting an increase in minimum foraging activity in the first half of the time series, followed by a decrease in short-term foraging performance in later years (Table 7.2). The temporal pattern in long-term foraging performance demonstrated a linear decline over time, with approximately 1% decrease in foraging performance every ten years across ringtail species. This translates to an average of 5.6 extra underperforming nights (i.e., nights in which the animal achieved less than 80% of their foraging potential) per summer across the species distribution in 2022 compared to 1992. The effects of climate change also suggested an overall escalation in water loss stress over time. For *P. archeri*, water stress showed a curvilinear (concave) pattern in short-term water loss similar to that observed for thermal stress, while long-term annual stress followed a linear temporal increase. In contrast, evaporative water loss showed a marginal temporal response for *H. lemuroides* (Table 7.2), likely reflecting the lower thermoregulatory cost associated with increased temperature for the species derived from a high thermoneutral zone.

Table 7.2. Physiological stress of ringtail possums across elevation and time.

Elevational values represent the change in physiological response (mean $\pm$ SD) per 100 m increase in elevation, while temporal values reflect the change in physiological response per 10 years. A description of the biophysical variables is

provided in Table 7.1. Trend defines whether the best fit was for linear or curvilinear change. Curvilinear change with a negative quadratic term (x^2) represents a relationship with a convex shape ($\cap$), while a positive quadratic term suggests a concave shape ($\cup$). EWL stands for evaporative water loss. Short-term foraging constraint is presented relative to each species so that if the maximum potential foraging is 100%, a positive coefficient represents the percentage closer to optimum foraging. Red values indicate effects that overlap zero.

Variable	Units	<i>Hemibelideus lemuroides</i>				<i>Pseudochirops archeri</i>			
		Elevational	Trend	Temporal	Trend	Elevational	Trend	Temporal	Trend
Thermal dosage	°C	-0.77 ± 0.25	linear	-2.82 ± 0.75 (x) 0.08 ± 0.02 (x^2)	curvilinear	-29.62 ± 6.01	linear	-41.65 ± 12 (x) 1.22 ± 0.36 (x^2)	curvilinear
Thermal intensity	°C	-0.15 ± 0.04	linear	-0.55 ± 0.14 (x) 0.015 ± 0.004 (x^2)	curvilinear	-1.1 ± 0.13	linear	-2.91 ± 0.33 (x) 0.08 ± 0.01 (x^2)	curvilinear
Short-term foraging performance	% closer to optimum	3.65 ± 0.36	linear	4.36 ± 0.95 (x) -0.12 ± 0.03	curvilinear	5.33 ± 0.41	linear	6.75 ± 1.23 (x) -0.19 ± 0.08 (x^2)	curvilinear
Long-term foraging performance	%	5.46 ± 0.84	linear	-1.23 ± 0.48	linear	8.81 ± 0.76	linear	-0.93 ± 0.48	linear
Short-term EWL	g of H ₂ O	0.56 ± 0.1	linear	0.03 ± 0.1	linear	0.39 ± 0.32	linear	-2.28 ± 0.95 (x) 0.08 ± 0.02 (x^2)	curvilinear
Long-term EWL	% extremes	1.43 ± 0.76	linear	0.11 ± 0.11	linear	1.68 ± 0.13	linear	0.22 ± 0.07	linear

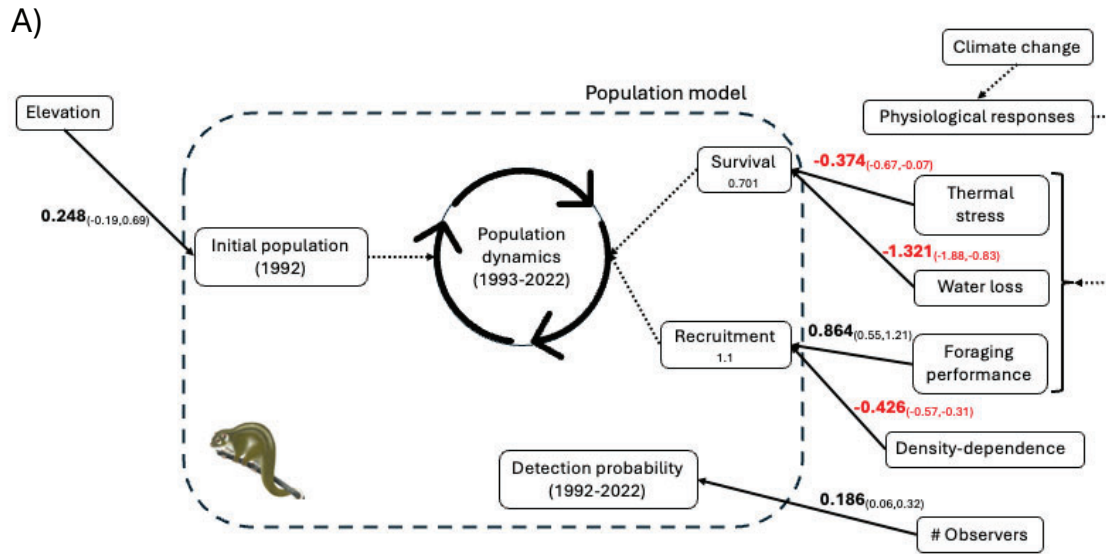
Foliage quality

Results from the biogeochemical model indicate that, after accounting for the effect of climate, the concentration of foliar nitrogen across selected tree species was significantly influenced by geology. Trees growing in basaltic soils exhibited higher levels of total nitrogen compared to those in granite and rhyolite soils. Specifically, the maximum foliar nitrogen concentration in basalt soils was $35.46 \pm 0.06\%$ (mean ± SD) higher than in granite sites and $34.62 \pm 0.1\%$ higher than in rhyolite sites. This pattern remained consistent across sampled tree species. It is noteworthy that these findings persist despite the concentration of individual soil fertility constituents (such as nitrogen, phosphorus, potassium, sodium, and the carbon-to-nitrogen ratio) showing

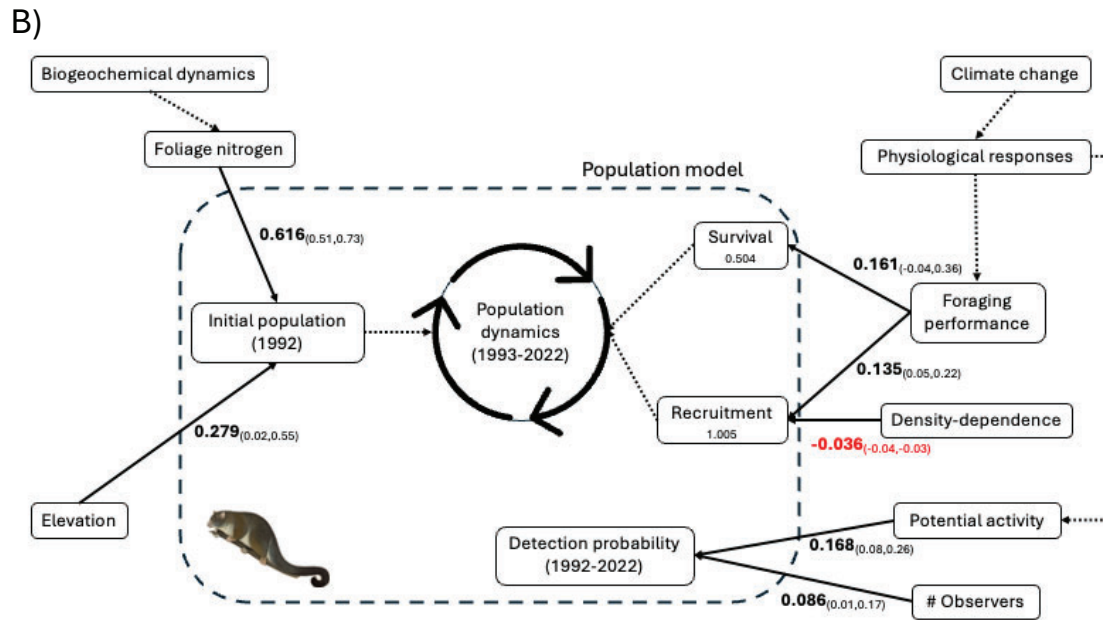
no consistent influence on foliage quality across the landscape. This discrepancy may underscore the importance of considering soil fertility as a multidimensional factor shaped by the interaction between soil nutrients and other physical or chemical properties associated with the underlying site geology. The suggested multidimensional nature of soil fertility as a driver of foliage quality is further evidenced by the fact that all individual constituents of soil fertility were present in significantly greater concentrations in soils of basaltic origin compared to granite or rhyolite (see the Appendix, “Extended methodology (III): Foliage nutritional chemistry”), stressing the important role of parent materials in determining the supply of rock-derived soil elements that can contribute to nutrient availability to plants.

Population dynamics

The impact of climate change on ringtail possum populations was accurately captured by the combined effect of habitat quality (defined by elevation and foliage nutritional chemistry), physiological stress, and the influence of density dependence on recruitment. The spatial distribution of initial abundance was positively correlated to elevation for both species (Figure 7.3), indicating that ringtail possum populations are larger in cooler upland rainforest compared to habitats found at lower elevations. After accounting for the effect of elevation, *H. lemuroides*’ abundance was positively correlated to foliage nitrogen (Figure 7.3B), suggesting that the species finds its optimum habitat in high-elevational rainforests with basaltic soils, where temperature is moderate, and foliage nutritional quality is high.



Species: *Pseudochirops archeri*



Species: *Hemibelideus lemuroides*

Figure 7.3. Conceptual summary of population dynamics for ringtail possums. Dotted lines represent the processes that led to the factors that informed population dynamics. Solid lines represent the direct effect of different predictors on population processes. Values represent the mean effect for those factors, with black values showing positive correlations while red values indicate negative effects. Subscript values represent the credible interval, describing the uncertainty around the mean effect, indicating the 5.5th and 94.5th percentiles of the sorted posterior samples.

Panel A shows the results for *P. archeri*, and panel B shows the population dynamics of *H. lemuroides*.

Spatiotemporal changes in ringtail possum populations were explained by the impact of climate-induced physiological stress on vital rates. For *P. archeri*, changes in survival were negatively correlated to thermal intensity and long-term water loss stress, while recruitment was positively affected by foraging performance (Figure 7.3A). Consequently, substantial declines in *P. archeri* populations are expected in the years following extreme summers, where overheating and dehydration could impose a severe constraint on survival, while a reduction in foraging activity could lead to a decrease in recruitment. The impact of climate change on population dynamics for *H. lemuroides* was primarily expressed through the physiological limitations imposed on foraging performance. Thus, population declines for this species are also expected following extreme summers, where heatwaves could threaten survival by limiting short-term foraging time, while a reduction in long-term foraging performance in hot years could limit the recruitment rate (Figure 7.3B). Furthermore, we detected a density-dependence constraint in recruitment for both species (Figure 7.3), suggesting potential limitations in resource availability across the landscape.

Lastly, ringtail possum detectability was significantly influenced by differences in survey effort, which varied in our study in terms of number of observers for both species (Figure 7.3). The effect of the number of observers on detection probability was stronger for the more cryptic *P. archeri*, suggesting that optimal detection for *H. lemuroides* can be achieved even with a reduced number of surveyors. Interestingly, physiological-related potential activity was the strongest factor explaining detectability for *H. lemuroides* (Figure 7.3B). This result suggests that the detection probability for the species was higher on cooler nights because of the increased foraging activity, likely reflecting the increased noise produced by animals foraging in the canopy. Importantly, this finding further enhanced our level of confidence in the biophysical model performance, suggesting it was able to accurately predict activity patterns that aligned with survey-specific patterns in detection probability.

Discussion

In this study, we investigated the causes of population decline among rainforest ringtail possums. By integrating data on physiology, climate, soil nutrients, foliage

nutritional quality, and long-term abundance, we have unravelled the mechanisms underlying climate-induced population dynamics. Our findings demonstrated that climate change has imposed significant physiological stress on ringtail possums, explaining the observed collapse in population that occurred from 1992-2022 (de la Fuente & Williams 2022). Through our modelling framework, we have tested hypotheses generated from experimental studies that measured physiological and behavioural responses under controlled conditions, demonstrating how mechanistic and statistical approaches can be integrated to elucidate how ecological responses observed in the field stem from fundamental constraints that can be measured in the lab.

Climate change in the Australian Wet Tropics

Heatwaves, characterised by a rapid increase in temperature over a short period of time, have significantly intensified in the Australian Wet Tropics over the last decades. Weather data from Walkamin Research Station (594 m a.s.l.), located approximately at the distributional centre of ringtails' geographical range, indicate a doubling in the number of extreme hot days (above 35°C) between 1992-2022 (Bureau of Meteorology 2023). However, the trajectory in extreme hot days in the Wet Tropics suggested a curvilinear trend, with a decline observed between 1997-2012, followed by an exponential increase from 2012-2022, surpassing historical records since 2016 (Bureau of Meteorology 2023). The observed heatwave pattern closely aligns with physiological responses affecting ringtail possums' fitness (Table 7.2; Figure 7.3), corroborating the findings of de la Fuente and Williams (2022), where declines in populations of *H. lemuroides* and *P. archeri* significantly correlate with observed heatwaves patterns in the region.

Impact of climate change on ringtails' fitness

Animal fitness was measured as survival and recruitment rate, which were derived from population dynamics. Survival was negatively correlated to short-term extreme heat events, while recruitment was impacted by longer-term summer conditions. This disparity suggests that fast and extreme temperature increase during heatwaves can become biologically limiting, threatening survival. However, the number of new recruits is influenced by overall conditions in the previous summer, with hot summers resulting in decreased recruitment.

For *H. lemuroides*, survival was compromised by limited foraging time, suggesting that thermoregulatory constraints restricting foraging activity during two consecutive nights could prove fatal for the species, possibly due to the low fat and muscle reserves in marsupial folivores (Rübsamen *et al.* 1984). Climate-induced foraging limitations have previously been suggested for marsupial folivores (Wagner *et al.* 2020; Beale *et al.* 2022; Beale *et al.* 2023), warning of potential lethal effects if energy and water storage become rapidly exhausted (Youngentob *et al.* 2021).

Survival limitations for *P. archeri* were related to overheating and dehydration, consistent with predictions from experimental studies (Krockenberger, Edwards & Kanowski 2012). During a heatwave, *P. archeri* stores heat to minimise evaporative water loss, a process known as facultative heterothermy (Krockenberger, Edwards & Kanowski 2012). While heterothermy allows *P. archeri* to cope with extreme heat for short durations, prolonged exposure forces substantial evaporative cooling to regulate body temperature, thus risking dehydration. Krockenberger, Edwards and Kanowski (2012) proposed that exposure to heat stress exceeding five hours could be lethal for the species if free water is not immediately available. Our results corroborate this hypothesis, indicating that water loss stress and thermal intensity, measured as the maximum annual cumulative heat stress during heatwaves lasting for five or more consecutive hours, explained observed population dynamics for *P. archeri* via effects on survival.

The impacts of climate change on recruitment suggested a similar response for both species, where the number of new recruits in a given year depended on foraging performance in the previous year. These findings imply that hot summers could impose severe constraints on foraging activity, limiting nutrient acquisition, thereby reducing reproductive success. Our results align with those of previous studies where reduced nutrient availability was linked to a decline in recruitment for marsupial folivores (DeGabriel *et al.* 2009; Kearney, Wintle & Porter 2010; Beale *et al.* 2018). For example, in the case of the related species *Petauroides volans*, protein intake has been proposed as the main limiting factor for milk production in the Wet Tropics, significantly constraining breeding potential (Kearney, Wintle & Porter 2010). In addition to foraging performance, recruitment depended on population density for both species. As density increases in an area, recruitment decreases, suggesting the presence of a limiting factor that constrains population growth. For *H. lemuroides*, these results could be related to the availability of dens, while for *P. archeri*, territoriality could affect resource

accessibility across the landscape (Krockenberger unpublished). Results on the effect of population density on recruitment align with those in DeGabriel *et al.* (2009), where irregular nutrient availability across the landscape defined reproductive success among territorial brushtail possums (*Trichosurus vulpecula*).

The population collapse of ringtail possums

The fate of ringtail possum populations is tightly linked to their position along the elevational gradient. Our results demonstrated that physiological stress is strongly influenced by elevation, suggesting that the impact of climate change could be intensified at lower elevations, where temperatures are higher, and heatwaves are more extreme and frequent. We predicted that warming might have imposed a biologically limiting amount of stress at the lower elevational range, where local extinctions have been observed at sites below 750 m in elevation for *H. lemuroides* and 600 m for *P. archeri* (Figure 7.4). Increased physiological stress at lower elevations could be exacerbated in sites characterised by low nutritional quality, where local extinctions have been observed for *H. lemuroides* at sites as high as 850 m (Figure 7.4), highlighting the role of the nutritional landscape in population dynamics (Moore *et al.* 2004; DeGabriel *et al.* 2009; Marsh *et al.* 2014). At the core of ringtails' distribution, extreme summers have shaped the dynamic of the populations, with increased physiological stress imposing constraints on the species vital rates, leading to widespread population declines in the last decades. However, populations persist in healthy numbers (compared to 1992) in optimal habitats, characterised by high-elevational rainforests with high nutritional value (Figure 7.4).

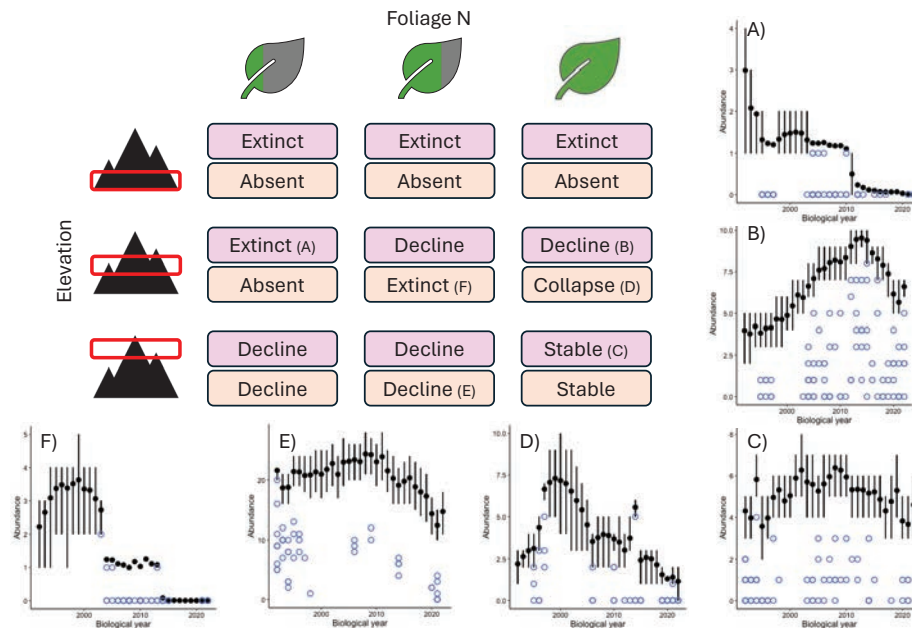


Figure 7.4. Summary of population trajectories for rainforest ringtail possums. Results are presented in a matrix with elevation and foliage nitrogen as its axes. Elevation categories range between 400-700 (low), 800-1100 (mid), and 1100-1350 (high). Foliage nitrogen concentration is divided into low concentration (below the 33rd percentile), mid concentration (between the 33rd and 66th percentile), and high concentration (above the 66th percentile). Pink boxes show the population state for *P. archeri*, while orange boxes show the population state for *H. lemuroides*. Plots A-D show the predicted true abundance (black) and raw count data uncorrected for detection probability (blue) for selected examples. Plots A-C show populations of *P. archeri*, while D-F represent populations for *H. lemuroides*.

A relevant framework to guide conservation actions

The significance of this study lies in uncovering the mechanisms driving climate-induced ecological responses in wild populations. Understanding the specific causes of population declines is paramount in conservation biology, as it enables the implementation of efficient conservation actions at the local scale, where targeted interventions are needed. For instance, if conservation actions were to be directed towards declining populations at high-elevational sites with low nutritional quality, our model suggests that population growth could be catalysed by increasing resource availability, perhaps in the form of nutritional supplements. Importantly, our framework can be adapted to simulate and compare different management options by projecting

population size given a range of possible interventions. For example, we could compare short- and long-term effects of a range of potential interventions against a control, “do nothing”, treatment to assess the effectiveness, initial vs long-term investment needed, population outcomes, and expected timeframes of potential conservation actions. Leveraging over 30 years of research effort, our approach offers invaluable guidance for implementing effective and targeted conservation efforts.

Limitations and future directions

Despite the promising results yielded by this study, there are three important caveats regarding potential modelling limitations that warrant consideration. First, there are substantial data requirements to parameterise biophysical models. Although most physiological and morphological traits can be sourced from experimental studies or museum specimens, many of the parameters related to how the animal behaves under certain field conditions must be assumed based on the best available data or expert knowledge. For example, we had to assume levels of activity and the associated metabolic costs, as well as the thresholds of physiological constraints that would induce a cease in activity. We were able to use field metabolic information to validate our assumptions for two key locations, resulting in high confidence levels, but we had to assume that individuals would show a consistent behavioural response across their distribution. Second, the foliage nutritional data used in this study were derived from samples collected across three rainforest tree species between 2021-2022, offering insights into the spatial, but not temporal, variability in nutrient availability for ringtail possums. Consequently, we were unable to capture any potential long-term decline in foliage nutritional quality, as reported for other tropical forests (Rothman *et al.* 2015). Such changes in leaf chemistry could have profound implications for the population dynamics of marsupial folivores (Beale *et al.* 2018). Investigating how foliage chemistry might have changed over the last decades in the Australian Wet Tropics would be crucial to understanding the role of nutrition in the observed population collapse. Lastly, our population model was constrained to have a simpler structure due to data limitations. Despite the intensive monitoring effort achieved over 31 years at 32 rainforest locations, the available data did not provide enough variability to thoroughly explore the interactions among different sources of spatiotemporal physiological stress and the nutritional landscape. Therefore, it is important to acknowledge that the models outlined in this study were developed using

the best available information, and they will be continually refined as additional data becomes available.

Conclusion

In conclusion, our study represents a significant advancement in our understanding of climate-driven ecological responses. We have demonstrated that the impact of climate change on population dynamics is fundamentally linked to alteration in animal fitness associated with physiological stress. For ringtail possums of the Australian Wet Tropics, the impacts of climate change are manifested through a reduction in survival and recruitment resulting from an increase in overheating, dehydration, and a reduction in foraging performance. The extent of the physiological stress experienced by these species is influenced by the elevational gradient they occupy, potentially reaching biologically limiting levels at lower elevations, where local extinctions have been observed. However, our study provides a valuable tool for managers to evaluate potential interventions, thereby guiding future conservation actions effectively.

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Chapter Eight – Synthesis and Future Directions

This thesis explored how climate change is significantly eroding tropical montane biodiversity. The first objective, addressed in chapters two, three, four, and five was to investigate patterns in population responses to climate change among rainforest vertebrates in the Australian Wet Tropics. The second objective, covered in chapters four and five was to unravel the climatic factors linked to population change and how they might synergise to exacerbate the impacts of warming. The third objective, addressed in chapters six and seven was to demonstrate the mechanisms by which climate change influences population dynamics through alterations in animal fitness. Here, I synthesise the main findings and conclusions of this thesis and present potential future research directions.

Habitat suitability as a fundamental aspect of fitness

At the heart of modern ecology lies niche theory, which posits that species abundance should reflect the suitability of their habitat across multiple ecological axes (Hutchinson 1957; Brown 1984; Holt 2009). Unravelling the fundamental conditions that favour species persistence across the landscape is thus a central goal in ecology. Yet, accurately defining habitat suitability and predicting organismal responses to environmental change pose challenges (Weber *et al.* 2017), hindering our ability to understand how abundance and habitat suitability interplay across the landscape (Nielsen *et al.* 2005; Jiménez-Valverde *et al.* 2009; Filz, Schmitt & Engler 2013; Dallas & Hastings 2018).

Given that my thesis orbits around comprehending the impacts of climate change on abundance, it was paramount to understand how abundance patterns arise across the landscape. Abundance, intricately linked to fitness, can thus be conceptualised as a function of habitat suitability (Araújo, Williams & Fuller 2002; Bock & Jones 2004; Morrison, Marcot & Mannan 2012). Chapter two explored the

relationship between abundance and habitat suitability among rainforest vertebrates in the Australian Wet Tropics. Overcoming inherent challenges associated with accurately predicting habitat suitability (Carrascal *et al.* 2017; Weber *et al.* 2017; Jiménez-Valverde, Aragón & Lobo 2021), I designed an enhanced framework leveraging biologically relevant predictors and cutting-edge modelling techniques. This refined approach resulted in a remarkable five-fold increase in prediction power of the abundance-suitability framework compared to previous studies in the region utilising the same datasets (VanDerWal *et al.* 2009). Moreover, this chapter uncovered the key environmental factors shaping habitat suitability for many rainforest vertebrates in the Wet Tropics, providing a robust foundation for subsequent investigations. For example, I found that the primary determinants defining habitat suitability for rainforest ringtail possums were exposure to extreme temperatures and soil fertility. These two variables explained approximately 80% of the variability in habitat suitability, with extreme heatwaves accounting for 50% and soil nitrogen for 30%. These insights not only informed targeted field data collection but also laid the groundwork for hypothesis testing in chapters five, six, and seven.

Escalating impacts of climate change on ecosystems through community disruption

Dispersal differences among species tracking climatic changes could result in a phenomenon known as community re-shuffling, potentially disrupting existing species interactions while fostering the emergence of novel ones (Ackerly 2003; Schweiger *et al.* 2008). Consequently, metacommunity dynamics become contingent upon species' dispersal capacities under climate change conditions, which are predicted to lead to the extinction of low-dispersal species and the range expansion of high-dispersal ones (Gilman *et al.* 2010). Despite its significance, the effect of climate-induced community disruptions remains largely understudied.

Chapter three of this thesis sheds light on the underestimated pace of climate-induced biodiversity erosion in montane ecosystems, revealing a critical gap in our understanding. By quantifying the accumulation of changes within communities, I highlighted the likelihood of climate change impacts being exacerbated by alterations in community compositions (Tylianakis *et al.* 2008). Results from this chapter indicated

a concerning trend, suggesting that species' success in tracking warming along mountain slopes diminishes with elevation, potentially resulting in the collapse of mountaintop communities even under relatively moderate warming scenarios. Moreover, the pace of community erosion varied across taxa, with those communities harbouring species of low dispersal ability, such as rainforest ringtail possums, projected to face disruption much sooner than those dominated by high-dispersal species like rainforest birds. These fundamental differences in species' ability to track climate change along mountain slopes were the foundation of the hypotheses for chapters four and five, where I delved into the observed ecological responses of bird and possum communities along the elevational gradient in the Australian Wet Tropics.

Climate change as a multidimensional stressor

While warming remains the most conspicuous effect of anthropogenic activities on the global climate (Hoegh Guldberg *et al.* 2018), climate change manifests in various forms, including changes in drought intensity (Cook, Mankin & Anchukaitis 2018), alteration in long-term precipitation patterns (Trenberth 2011), shifts in frequency and intensity of tropical cyclones (Knutson *et al.* 2010), and the escalation of regional heatwaves (Perkins-Kirkpatrick & Lewis 2020). These factors can broadly be classified into "presses", characterised by a gradual and consistent increase in climatic pressure, and "pulses", comprising extreme events that are by definition rare and low-frequency (Harris *et al.* 2018). The biological impacts of these stressors vary taxonomically and geographically, influenced by factors such as timing, severity, and duration relative to the life cycle and resilience of affected organisms. Consequently, disentangling the effects of presses and pulses becomes crucial for understanding how climate change drives biodiversity erosion (Harris *et al.* 2018).

Chapters four and five of this thesis delved into the press and pulse effects of climate change on the population dynamics of rainforest vertebrates, with a focus on birds and ringtail possums. By investigating the multidimensional impact of climate change on populations, these chapters provide significant insights into the mechanisms accelerating climate-induced biodiversity degradation (Parmesan 2006). Interestingly, substantial differences in response to presses and pulses were observed among rainforest vertebrate species. Populations of high-dispersal rainforest bird species were primarily influenced by presses, such as gradual warming and shifts in

precipitation patterns, while populations of low-dispersal ringtail possums were disproportionately impacted by extreme heatwaves. These findings align with those from chapters two and three, where predictions of rainforest vertebrate responses to climate change were linked to their dispersal abilities. Collectively, these results indicate that while warming is pushing bird species uphill in a pattern ominously referred to as the escalator to extinction, ringtail possums, unable to shift as mountain slopes warm, are succumbing to extreme heatwaves, undergoing severe declines and extirpation at lower elevations. Despite observed variations in response to different climatic stressors across taxa, consistent patterns emerge in terms of population and distributional changes, indicating that lower-elevation species are shifting uphill, presenting an early increase in population at higher elevations, while upland species face population collapse as suitable habitat diminishes with increasing elevations.

The underlying mechanisms of climate-induced population collapse

Recent developments in the press and pulse framework have substantially advanced our understanding of climate-induced ecological responses (Harris *et al.* 2018). These advancements are illustrated in chapters four and five, where the approach to the study of climate change shifts, from merely documenting declines and extinctions, to identifying the factors driving observed ecological responses. This transition lays a robust foundation for forecasting the effects of climate change on populations, revealing potential tolerance thresholds linked to population collapses (e.g., Chapter five). However, the fundamental question of what mechanisms link climate change to population declines remains puzzling, hindering advances in conservation and global change biology. Understanding the specific causes of population declines is paramount in conservation biology, as it enables the implementation of efficient conservation actions at the local scale, where targeted interventions are needed.

Using the rainforest ringtail possum as a case study, chapters six and seven focused on investigating these mechanisms by integrating all available information on species biology, ecology, and physiology. I found that the impact of climate change on ringtail possum population dynamics is intricately linked to alterations in animal fitness

associated with physiological stress and variability in the nutritional landscape. For ringtail possums in the Australian Wet Tropics, extreme heatwaves cause overheating, dehydration, and diminished foraging performance, and ultimately result in reductions in survival and recruitment. The extent of physiological stress experienced by these species is influenced by the elevational gradient they occupy, potentially reaching biologically limiting levels at lower elevations where local extinctions have been observed (Chapter five). However, the data suggest that the impact of climate-induced physiological stress along the elevational gradient could be exacerbated in areas with significantly lower foliage quality, such as those found in granite and rhyolite sites (Chapter six), where extirpations have been observed at elevations as high as 800 m, compared to the 700 m threshold observed in areas of high foliage nitrogen in basalt soils. Stable populations persist in their optimum habitat at high elevational sites with basaltic soils, where temperatures are moderate, and foliage nutritional quality is high.

Through this integrated modelling framework, I have tested hypotheses generated from experimental studies that measured physiological and behavioural responses under controlled conditions, demonstrating how mechanistic and statistical approaches can be joined to understand how ecological responses observed in the field stem from fundamental constraints that can be measured in the lab. Importantly, chapter seven provides a valuable tool for managers to evaluate potential interventions, thereby guiding future conservation actions. For instance, if conservation actions for rainforest ringtail possums are directed at high-elevational sites with low nutritional quality, models suggest that population growth could be catalysed by increasing resource availability, perhaps in the form of nutritional or water supplements. The modelling framework designed in this study can also be adapted to simulate and compare different management options by projecting population size given a range of possible interventions. For example, we could compare the short- and long-term effects of a range of potential interventions against a control, “do nothing” treatment to assess the effectiveness, initial vs long-term investment needed, population outcomes, and expected timeframes of potential conservation actions.

Key Take-Home Messages

The key findings of this thesis highlight the complexity of climate change impacts on tropical montane ecosystems, emphasising that the effects of climate

change are multidimensional and context-dependent. The following messages are central:

1. **Abundance-Suitability Relationships:** Climate change has significantly altered habitat suitability for many rainforest vertebrates. Understanding the ecological factors that shape these relationships, such as temperature extremes and soil fertility, is crucial for predicting the future distribution and abundance of species.
2. **Community Disruption and Re-shuffling:** Climate-induced community re-shuffling is a major driver of biodiversity loss in montane ecosystems, with low-dispersal species, such as ringtail possums, facing more immediate threats compared to high-dispersal species like rainforest birds. This dynamic poses risks of community collapse, especially at higher elevations.
3. **Climate Change as a Multidimensional Stressor:** The dual effects of "presses" (gradual changes like warming) and "pulses" (extreme events like heatwaves) are altering species' fitness and population dynamics. Species with limited dispersal abilities are particularly vulnerable to these pressures, especially in regions where environmental quality is already compromised.
4. **Mechanisms of Population Collapse:** The physiological stress caused by extreme heat and low foliage quality plays a key role in the population declines of rainforest species, particularly the ringtail possum. This thesis has shown that such stress, compounded by climate change, leads to significant reductions in survival and reproductive success.
5. **Management Tools for Conservation:** By integrating ecological and physiological models, this thesis provides valuable tools for managers to design effective conservation interventions. Specifically, the modelling framework developed in Chapter Seven offers a method to simulate various management strategies and assess their potential effectiveness in mitigating climate change impacts.

Conclusions and future directions

In conclusion, this thesis makes a significant contribution to our understanding of the impacts of climate change on tropical montane ecosystems. Through investigations into abundance-suitability relationships, community reshuffling

dynamics, population responses to climate change, biogeochemical dynamics, and mechanistic understanding of population declines, this thesis uncovered the intricate mechanisms driving ecological responses to environmental change. By integrating these findings, a nuanced understanding of the vulnerabilities of montane species to climate-induced stressors has been developed, along with tools for identifying key conservation priorities.

The promise of global change biology lies in its potential to provide the necessary tools for conservation and management. Moving forward, it is imperative to bridge the gap between research findings and on-the-ground conservation actions. This entails developing a framework to translate the outputs from mechanistic models into targeted and effective conservation strategies. For example, by leveraging the scientific advancements showcased in this thesis, we can inform evidence-based decision-making and prioritise interventions that maximise ecological resilience and persistence of rainforest ringtail possums. Central to this endeavour is the utilisation of integrated models capturing the complexities of climate-induced ecological responses. These models offer a powerful tool for simulating and comparing management options and projecting population sizes under various scenarios. By harnessing predictive capabilities, conservation practitioners can assess intervention efficacy and allocate resources more efficiently, and design adaptive management plans to mitigate climate change impacts. However, advancing conservation efforts requires collaborative partnerships and knowledge exchange among researchers, practitioners, policymakers, and local communities. Interdisciplinary collaborations harness collective expertise and resources to tackle complex challenges. Engaging stakeholders ensures conservation strategies align with local knowledge, values, and priorities, enhancing relevance and effectiveness.

Investing in long-term monitoring programs is paramount for advancing the field of global change biology, as demonstrated by the findings of this thesis, which relied on access to three decades of monitoring data. These datasets are invaluable assets that provide critical insights into ecological responses to environmental change over time. Without long-term data, it would be challenging to identify trends, assess the effectiveness of conservation interventions, and make informed management decisions. For these reasons, maintaining and expanding these monitoring efforts is essential for the future of conservation. Continued investment in long-term monitoring programs ensures the availability of robust datasets that are vital for understanding

and addressing the complex challenges posed by climate change and biodiversity loss.

This thesis highlights the urgent need for practical conservation strategies in the face of climate change. While most of the research in global change biology has focused on documenting biodiversity loss, this thesis took the proactive approach of developing the tools and data necessary to address these challenges head-on.

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Appendices

Appendix Chapter Two

Table S2.1. Species-specific information and covariates used in the analyses. Detailed information of the calculation of these parameters can be found in [Williams et al. \(2010\)](#).

Species code	Family	Species	Taxa	Presence	Absence	TSS	Potential dispersal	Mass (g)	Realised distribution (km ²)
ASW	Acanthizidae	Sericornis keri	Bird	151	467	0.932	3	11.9	7985.5
AUSFRYI	Microhylidae	Austrochaperina fryi	Frog	217	110	0.894	1	2.4	5205.3
AUSPLUV	Microhylidae	Austrochaperina pluvialis	Frog	163	118	0.837	1	1.1	12241.6
AUSROBU	Microhylidae	Austrochaperina robusta	Frog	327	55	0.872	1	1.7	9707.2
BHE	Meliphagidae	Lichenostomus frenatus	Bird	437	366	0.823	4	36.4	12287.3
BST	Pachycephalidae	Colluricincla boweri	Bird	339	363	0.866	5	39.1	7261.6
CARLAEV	Gekkonidae	Carphodactylus laevis	Reptile	91	61	0.837	1	21.9	8031.6
CARRUBR	Scincidae	Carlia rubrigularis	Reptile	209	20	0.887	1	3.3	15908.1
CC	Orthonychidae	Orthonyx spaldingii	Bird	397	360	0.835	4	156.5	11071.8

COPAENI	Microhylidae	Cophixalus aenigma	Frog	78	130	0.977	1	0.6	1158.5
COPBOMB	Microhylidae	Cophixalus bombiens	Frog	45	141	0.974	1	0.3	3453.7
COPCONC	Microhylidae	Cophixalus concinnus	Frog	27	148	0.999	1	1.2	163.8
COPEXIG	Microhylidae	Cophixalus exiguus	Frog	20	154	0.998	1	0.4	917.3
COPHOSM	Microhylidae	Cophixalus hosmeri	Frog	46	147	0.971	1	0.3	429.1
COPINFA	Microhylidae	Cophixalus infacetus	Frog	116	123	0.908	1	0.5	8766
COPMONT	Microhylidae	Cophixalus monticola	Frog	15	153	0.998	1	0.6	202.5
COPNEGL	Microhylidae	Cophixalus neglectus	Frog	11	152	0.995	1	1.8	244.1
COPORNA	Microhylidae	Cophixalus ornatus	Frog	515	18	0.886	1	1	11745
EULTIGR	Scincidae	Eulamprus tigrinus	Reptile	44	86	0.955	1	10.7	10109.1
FW	Acanthizidae	Oreoscopus gutturalis	Bird	295	413	0.863	3	16.6	9165.6
GLAFUSC	Scincidae	Glaphyromorphus fuscicaudis	Reptile	46	80	0.971	1	8.8	9024.6
GLAMJOB	Scincidae	Glaphyromorphus mjobergi	Reptile	13	97	0.955	1	9.4	4555.9
GNYQUEE	Scincidae	Gnypetoscincus queenslandiae	Reptile	117	44	0.928	1	6.6	9479.5
GOLDBB	Ptilonorhynchidae	Prionodura newtoniana	Bird	140	444	0.919	4	75	5523.5
HEMLEMU	Pseudocheiridae	Hemibelideus lemuroides	Mammal	262	93	0.934	2	952.5	4365.2
LAMCOGG	Scincidae	Lampropholis coggeri	Reptile	117	28	0.91	1	1.2	10178.2

LAMROBE	Scincidae	Lampropholis robertsi	Reptile	20	98	0.996	1	2	2631.4
LITGENI	Hylidae	Litoria genimaculata	Frog	296	6	0.927	2	15	16306.5
LITJUNG	Hylidae	Litoria jungguy	Frog	171	57	0.905	2	11.1	7115.3
LITNANN	Hylidae	Litoria nannotis	Frog	165	66	0.927	2	10.1	15443.2
LITRHEO	Hylidae	Litoria rheocola	Frog	208	63	0.953	2	2.3	14129.8
LITXANT	Hylidae	Litoria xanthomera	Frog	123	49	0.876	2	6.9	18376
LSOWL	Tytonidae	Tyto multipunctata	Bird	134	45	0.905	2	495	16336.6
MACHE	Meliphagidae	Xanthotis macleayana	Bird	437	372	0.769	3	32.8	19922.1
MIXCARB	Myobatrachidae	Mixophyes Carbinensis	Frog	17	86	0.952	2	38.6	1535.2
MIXCOGG	Myobatrachidae	Mixophyes Coggeri	Frog	24	78	0.901	2	76	12548.9
MIXSCHE	Myobatrachidae	Mixophyes schevilli	Frog	170	47	0.877	2	53.1	13553.9
MTHORN	Acanthizidae	Acanthiza katherina	Bird	256	398	0.899	3	8.9	6223.5
NYCDAYI	Hylidae	Nyctimystes dayi	Frog	169	73	0.912	2	6.4	16564.2
PMON	Dicruridae	Arses kaupi	Bird	224	453	0.812	4	12.6	18192.3
PSEARCH	Pseudocheiridae	Pseudochirops archeri	Mammal	325	82	0.91	2	1091.5	7689.7
PSECINE	Pseudocheiridae	Pseudochirulus cinereus	Mammal	195	104	0.981	2	1000	1705.4
PSEHERB	Pseudocheiridae	Pseudochirulus herbertensis	Mammal	271	92	0.943	2	1113.5	5011.7
SALCORN	Gekkonidae	Saltuarius cornutus	Reptile	173	26	0.9	1	38.1	11608.5
SAPBASI	Scincidae	Saproscincus basiliscus	Reptile	136	18	0.928	1	1.5	15412.5

SAPCZEC	Scincidae	Saproscincus czechurai	Reptile	24	70	0.968	1	0.8	4608.1
SAPLEWI	Scincidae	Saproscincus lewisi	Reptile	5	85	0.997	1	1.2	2428.9
SAPTETR	Scincidae	Saproscincus tetradactylus	Reptile	57	51	0.917	1	0.6	10786.6
TBBB	Ptilonorhynchidae	Scenopoeetes dentirostris	Bird	302	416	0.861	3	170	7515.5
VRIF	Paradisaeidae	Ptiloris victoriae	Bird	514	314	0.785	4	95	15118.2

Table S2.2. Species-specific abundance-suitability relationship results. Significant values are denoted with an asterisk. The effective degrees of freedom (edf) represent the linearity of the relationship. The higher the value, the higher the wiggleness of the fitted curve. Values of edf = 1 represent a linear relation.

Species code	Abundance-Suitability relationship (ρ)	Prediction power (R^2)	Model accuracy (ρ)	Effective degrees of freedom (edf)
ASW	0.75*	0.623*	0.77*	1.85
AUSFRYI	0.7*	0.663*	0.71*	3.34
AUSPLUV	0.58*	0.468*	0.58*	4
AUSROBU	0.7*	0.449*	0.72*	4.42
BHE	0.78*	0.501*	0.77*	2.5
BST	0.71*	0.492*	0.65*	1
CARLAEV	0.67*	0.45*	0.67*	3.18
CARRUBR	0.49*	0.37*	0.54*	3.82
CC	0.7*	0.61*	0.66*	2.78
COPAENI	0.66*	0.899*	0.83*	4.21
COPBOMB	0.4*	0.839*	0.41*	1
COPCONC	0.48*	0.913	0.49*	1
COPEXIG	0.28*	0.99	0.3*	2.86
COPHOSM	0.46*	0.91*	0.53*	3.99
COPINFA	0.61*	0.623*	0.61*	3.22
COPMONT	0.31*	0.95*	0.32*	1
COPNEGL	0.38*	0.921	0.4*	2.43
COPORNA	0.35*	0.12*	0.4*	3.59
EULTIGR	0.55*	0.64*	0.54*	3.47
FW	0.74*	0.5*	0.71*	1
GLAFUSC	0.63*	0.6*	0.62*	2.64
GLAMJOB	0.45*	0.693*	0.49*	1
GNYQUEE	0.55*	0.37*	0.45*	4.57
GOLDBB	0.75*	0.664*	0.76*	1
HEMLEMU	0.75*	0.71*	0.77*	2.66
LAMCOGG	0.6*	0.36*	0.56*	4.11

LAMROBE	0.53*	0.76*	0.57*	3.27
LITGENI	0.21	0.104*	0.12	2.52
LITJUNG	0.6*	0.43*	0.63*	4.79
LITNANN	0.41*	0.29*	0.37*	1.05
LITRHEO	0.62*	0.612*	0.57*	3.18
LITXANT	0.53*	0.464*	0.56*	5.64
LSOWL	0.36*	0.19*	0.11	2.72
MACHE	0.59*	0.17*	0.66*	1.01
MIXCARB	0.52*	0.68*	0.54*	1
MIXCOGG	0.7*	0.833*	0.70*	3.34
MIXSCHE	0.6*	0.322*	0.6*	1
MTHORN	0.85*	0.703*	0.84*	4.41
NYCDAYI	0.43*	0.7	0.50*	5.67
PMON	0.605*	0.29*	0.6*	1.89
PSEARCH	0.7*	0.51*	0.68*	1
PSECINE	0.66*	0.93*	0.7*	1.382
PSEHERB	0.73*	0.733*	0.73*	3.69
SALCORN	0.45*	0.201*	0.43*	1.93
SAPBASI	0.45*	0.202*	0.34*	3.54
SAPCZEC	0.67*	0.752*	0.72*	3.26
SAPLEWI	0.35*	0.95*	0.34*	1
SAPTETR	0.78*	0.593*	0.78*	2.54
TBBB	0.79*	0.577*	0.75*	1.39
VRIF	0.57*	0.375*	0.52*	2.17

Table S2.3. Potential predictors selected to model species distribution. Predictors included in the models after eliminating collinearity are in bold.

Predictor	Reference
Elevation (m)	Fick and Hijmans (2017)
Roughness	This study
Topography position index	This study
Slope (%)	This study
Terrain ruggedness index	This study

Foliage projective cover (%)	Armston <i>et al.</i> (2009)
Forest structure (categorical)	Scarth, Armston and Lucas (2014)
Height of peak plant cover density (m)	Scarth, Armston and Lucas (2014)
Average canopy height (m)	Scarth, Armston and Lucas (2014)
Canopy plant cover (%)	Scarth, Armston and Lucas (2014)
Mean annual precipitation (mm)	Storlie <i>et al.</i> (2013)
Mean annual temperature (°C)	Storlie <i>et al.</i> (2013)
Precipitation seasonality (Coefficient of Variation)	Storlie <i>et al.</i> (2013)
Precipitation seasonality (mm)	This study
Maximum temperature seasonality (°C)	This study
Minimum temperature seasonality (°C)	This study
Fragmentation (mesh size) (km²)	Chailloux, Amsallem and Chéry (2019)
Summer heat-moisture index	Wang <i>et al.</i> (2006)
Mean annual heat-moisture index	Wang <i>et al.</i> (2006)
Water deficit (%)	Harwood <i>et al.</i> (2014)
Soil pH	Viscarra Rossel <i>et al.</i> (2014b)
Soil P (%)	Viscarra Rossel <i>et al.</i> (2014d)
Soil N (%)	Viscarra Rossel <i>et al.</i> (2014c)
Soil available water capacity (%)	Viscarra Rossel <i>et al.</i> (2014a)
Australian Soil Classification (categorical)	Viscarra Rossel <i>et al.</i> (2018)
Net Primary Productivity: temperature derived	Schuur (2003)
Net Primary Productivity: precipitation derived	Schuur (2003)
Minimum Net Primary Productivity	Schuur (2003)

Environmental seasonality index calculation

Species mortality and growth rate could be highly related to the length and intensity of unfavourable conditions (Comita & Engelbrecht 2009). Consequently, diversity and abundance should be low in harsh environments and increase with environmental moderation (Menge & Sutherland 1987), shaping community assemblages (Gray 2009).

To account for environmental stress influence on species distribution and abundance pattern in our study, we considered three environmental seasonality measures: precipitation, minimum and maximum temperature (Harris *et al.* 2014). Both minimum and maximum temperatures were selected because this study included both diurnal and nocturnal animals. Therefore, we assumed that nocturnal species would be more influenced by seasonality in the minimum (i.e., night) temperatures and vice versa. Precipitation seasonality was chosen due to the strong impact of precipitation on determining rainforest distribution and floristic attributes (Kershaw 1994).

The calculation of these indices was based on the area under the curve constituted by the monthly environmental deviation from an environmental threshold. The area under the curve was calculated using the trapezoidal rule implemented with the “trapz” function within “pracma” R package (Borchers 2017). Due to all species included in this study are rainforest specialists, we chose the mean annual temperature and mean annual precipitation across rainforest habitats in the study area as our environmental threshold. As a result, the degree of environmental seasonality in each pixel was defined as a function of the stressor length and intensity, represented as the degree of deviation from the mean environmental parameter.

For temperature variables, thermal seasonality was calculated as the area under the curve from the upper monthly deviation due to an increase in temperature could have detrimental effects on rainforest species (Williams, Bolitho & Fox 2003). On the other hand, precipitation seasonality was defined using lower monthly deviation, as an increase in stress would be related to an increase in drought severity, which is a well-known driver of diversity and abundance patterns in tropical ecosystems (Williams & Middleton 2008).

Raster manipulation and analyses were done using the “raster” R package (Hijmans *et al.* 2015). All analyses were performed in R, version 4.0 (R Development Core Team 2020).

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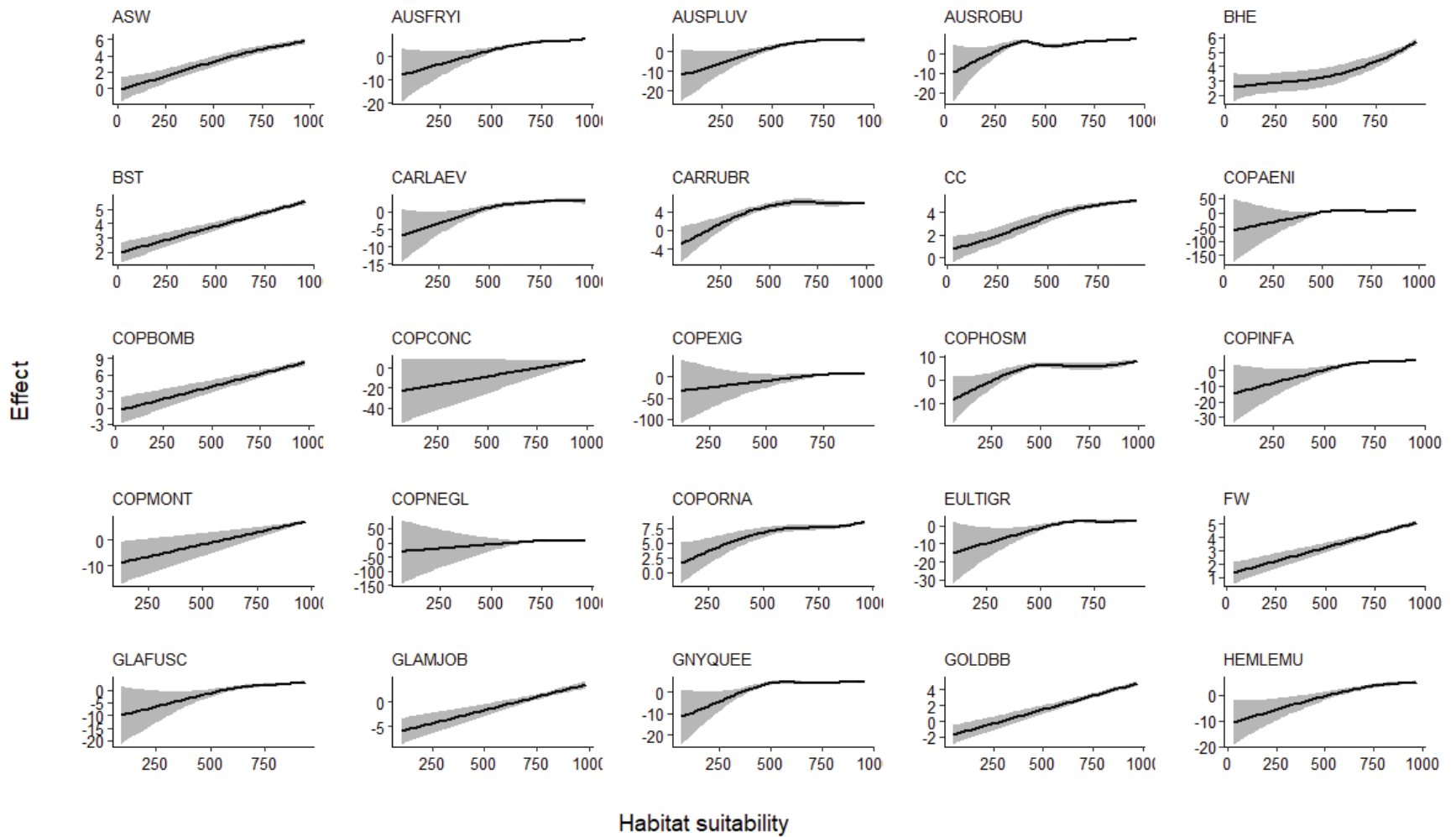


Figure S2.10. Species-specific partial plots of the abundance-suitability relationship fitted using GAMs with a Tweedie distribution and a log link function.

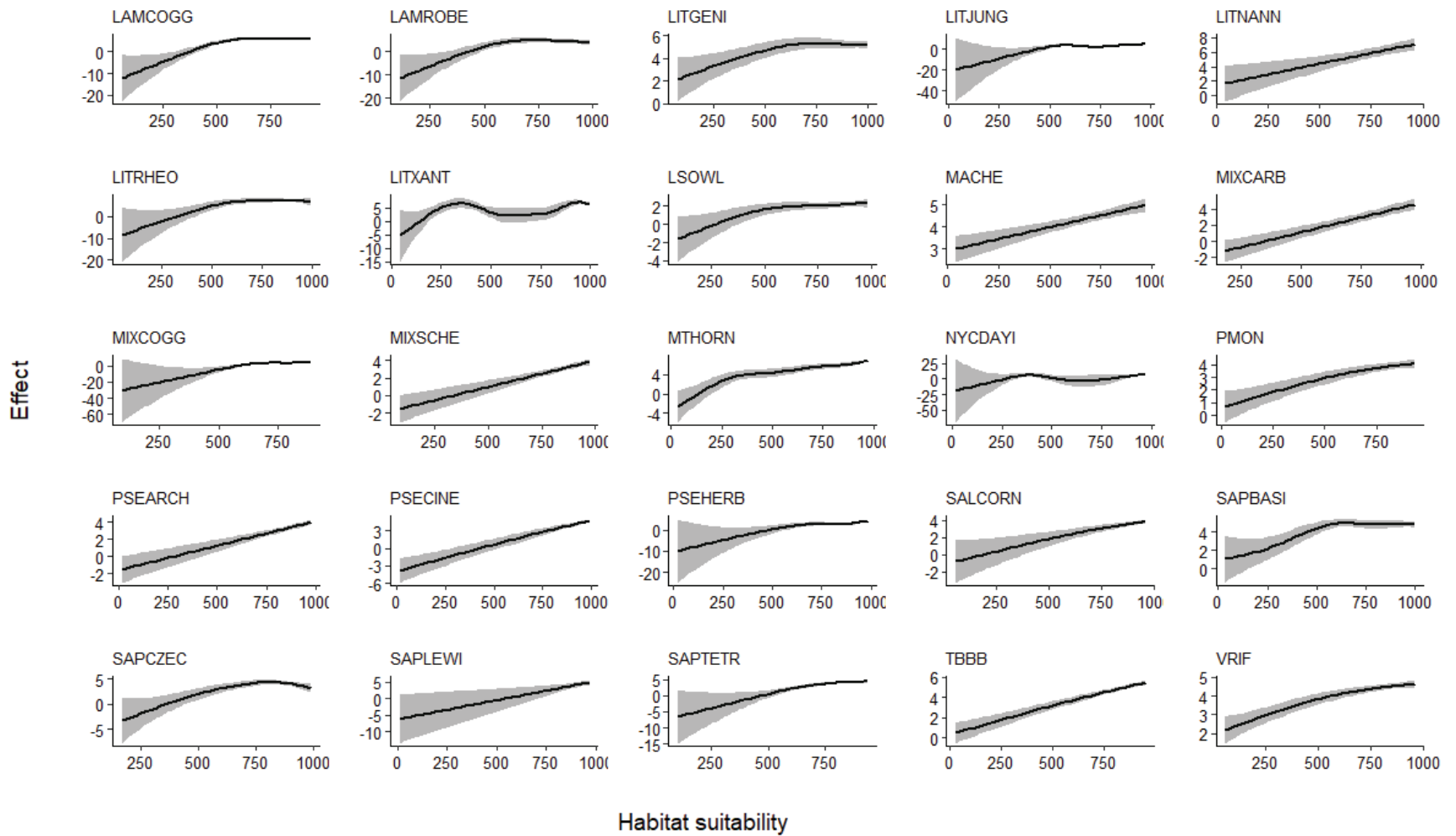


Figure S2.1. Continuation.

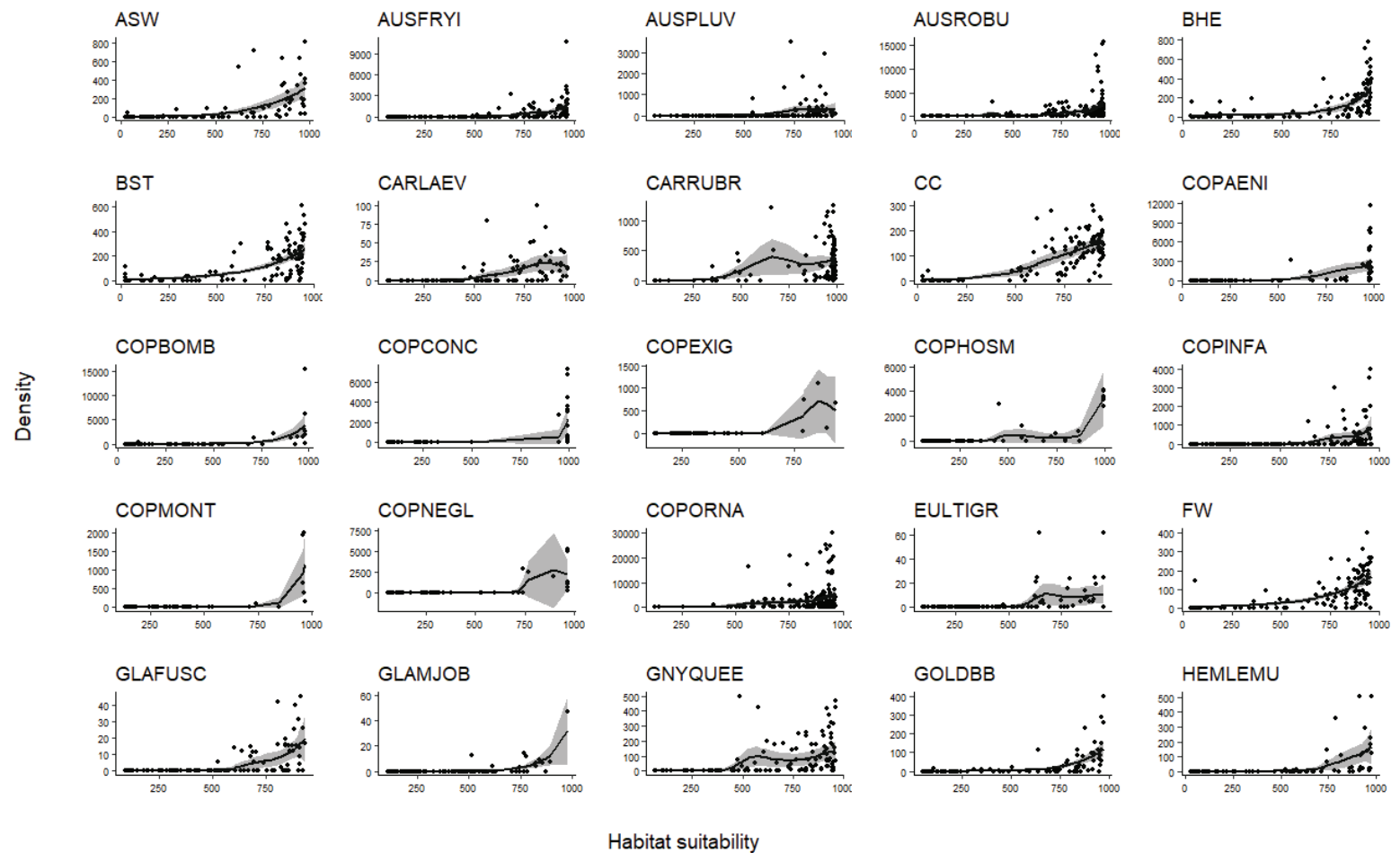


Figure S2.2. Species-specific abundance-suitability relationship. Dots represent the fitted density as a function of habitat suitability. Lines represent the fit of the relationship (with a 95% confidence interval – grey ribbons) using GAMs with a Tweedie distribution and a log link function.

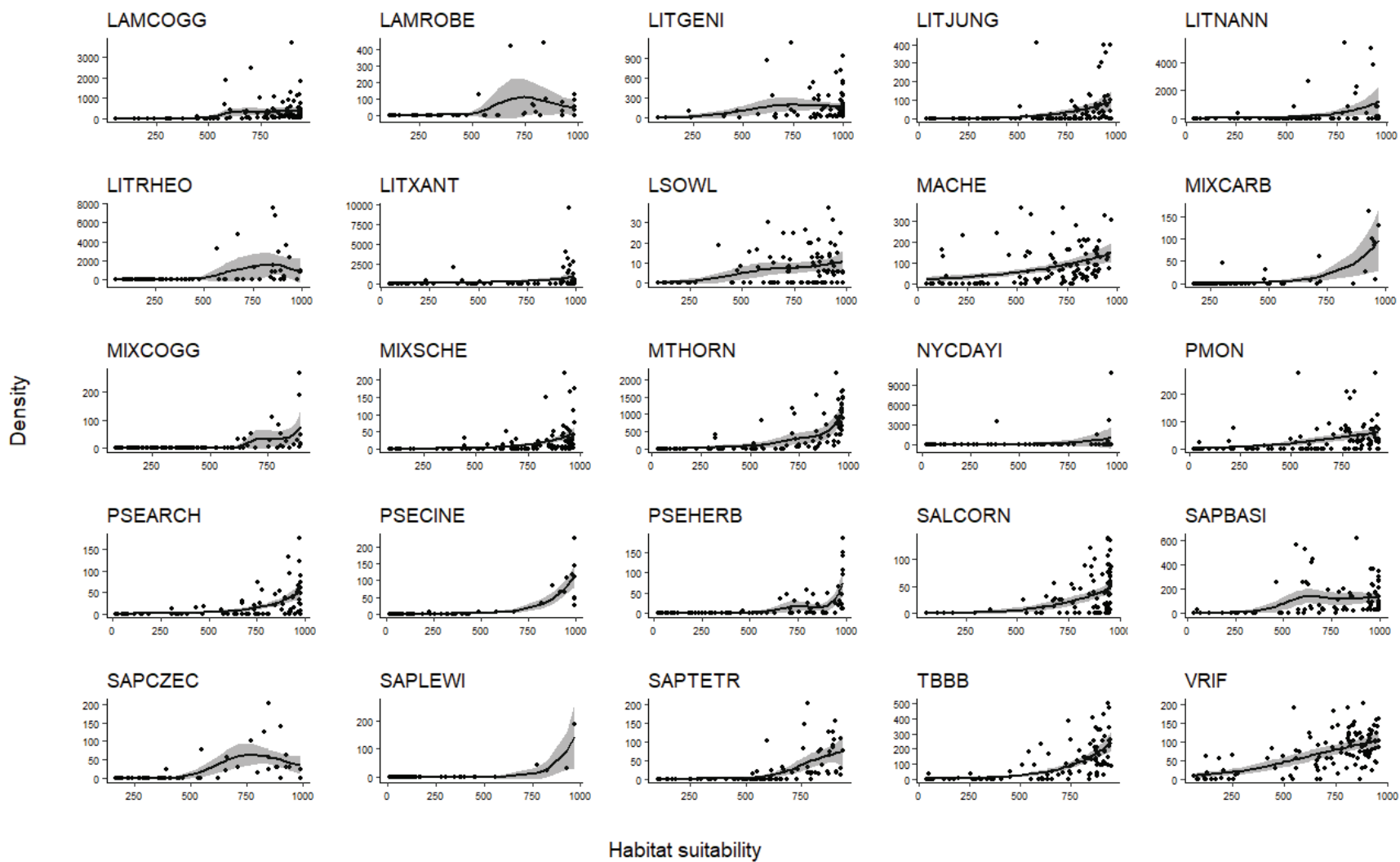


Figure S2.11. Continuation

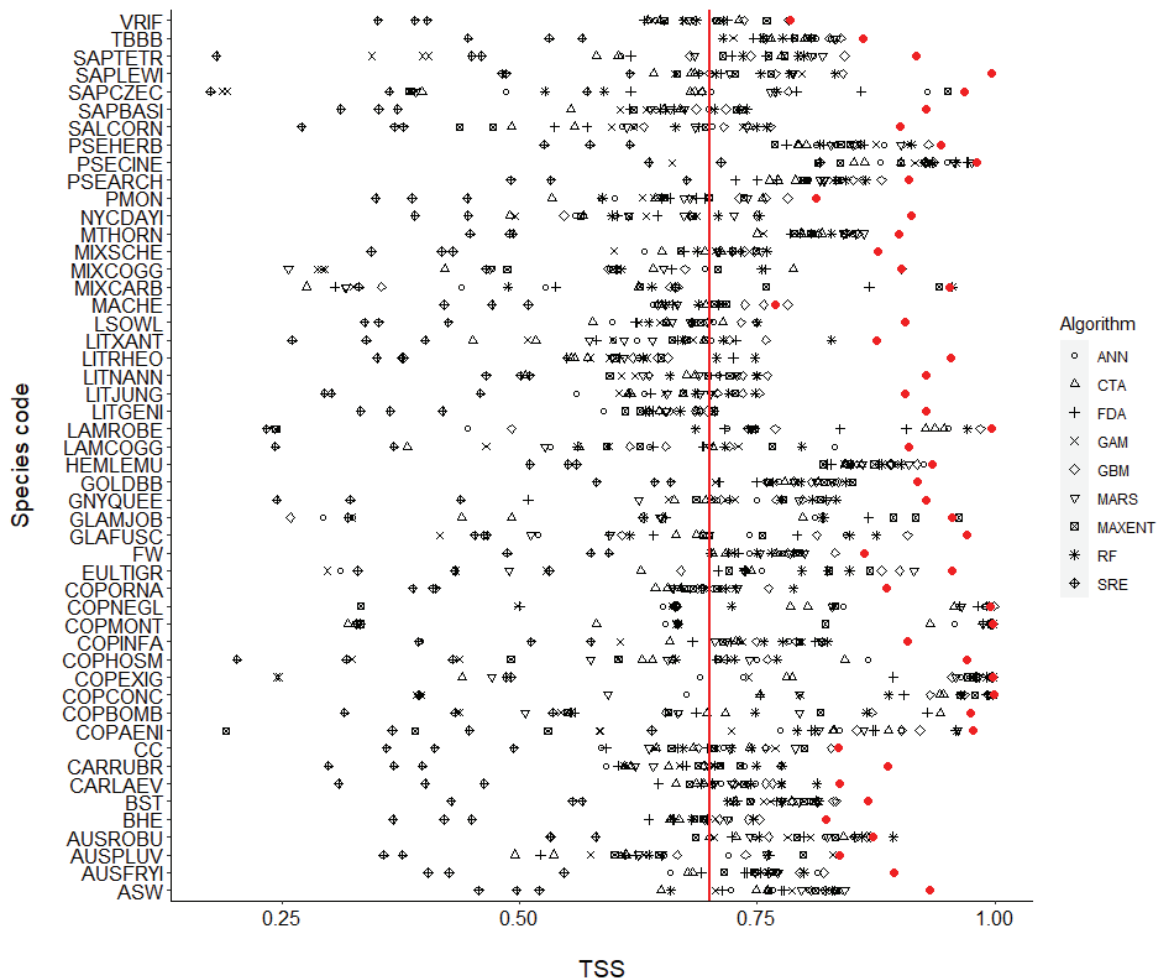


Figure S2.3. Informal comparison of individual ecological niche models and ensemble models (red points) across species in the Australian Wet Tropics. The red vertical line shows the evaluation threshold that was used to select the models for the ensemble. Models on the right of the line were used to create the final ensemble model used for analyses, while models on the left were discarded.

Appendix Chapter Three

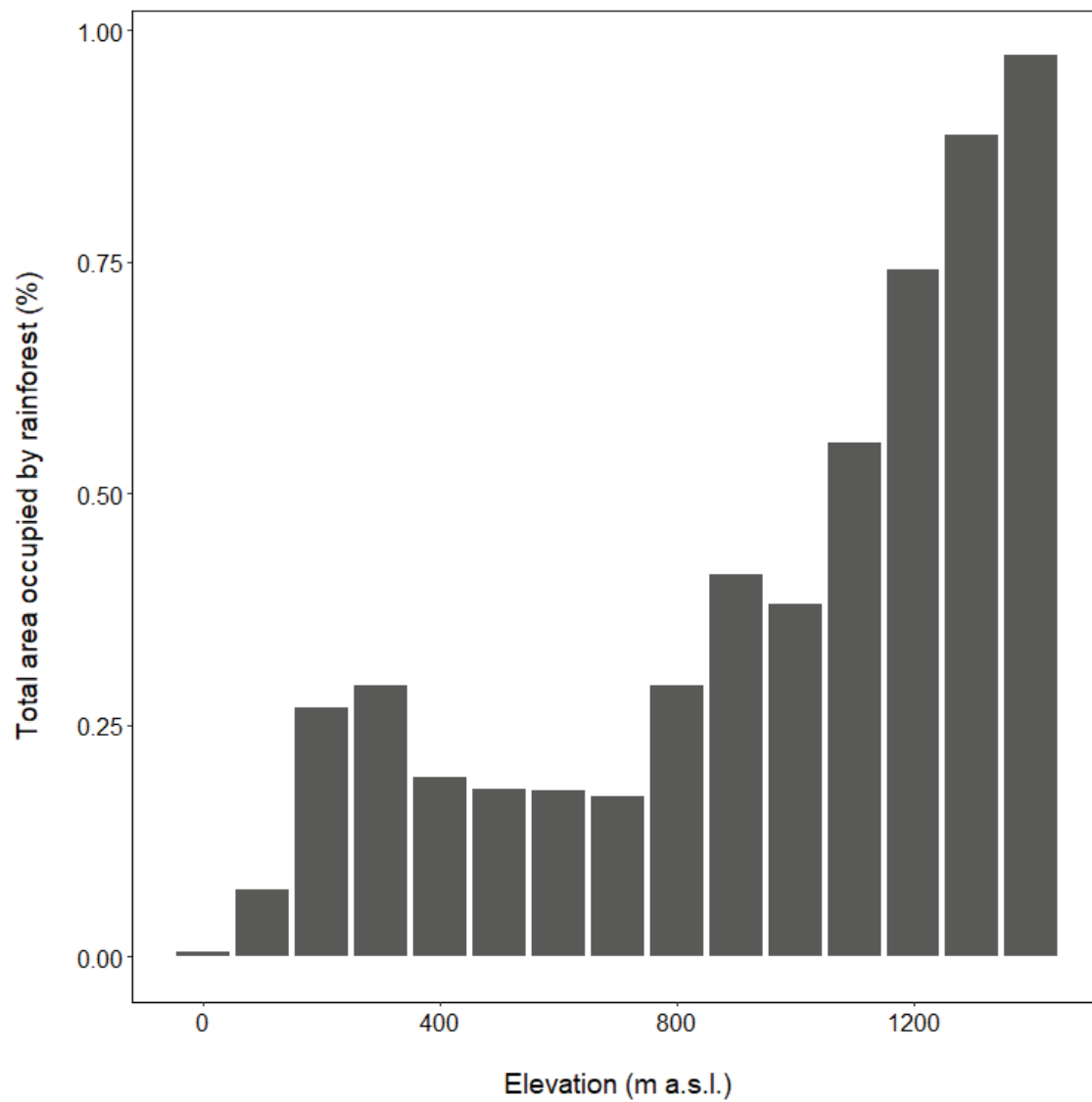


Figure S3.2. Percentage of rainforest coverage in relation to the total area across the elevational gradient in the Australian Wet Tropics.

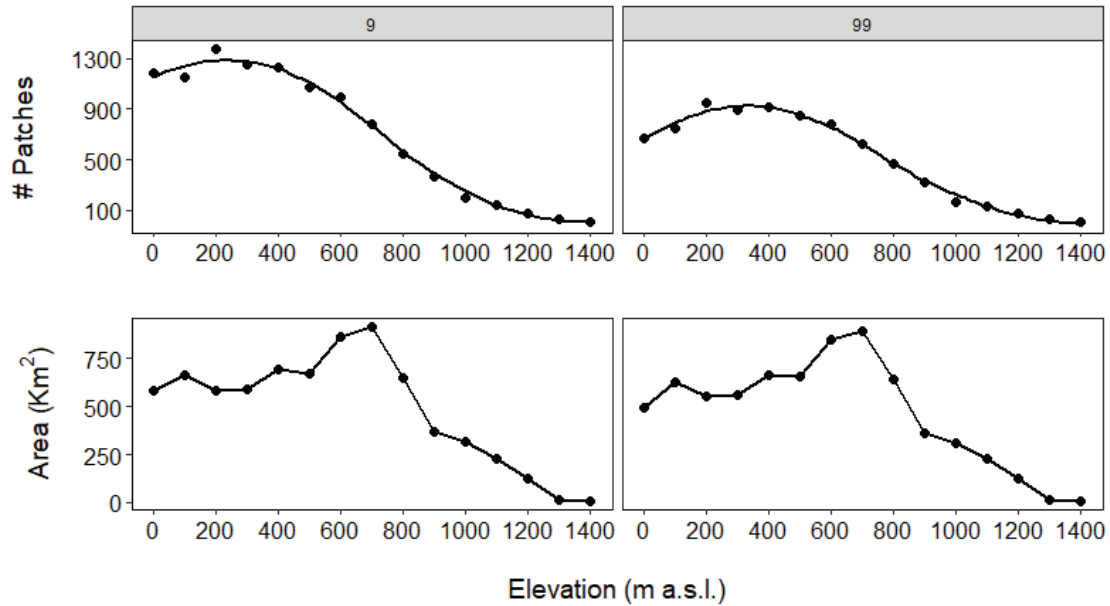


Figure S3.2. Difference in total number of rainforest patches (top row) and total area (bottom row) between thinning algorithms based on pixel clumping following a “rook’s case” to define direction. The left column shows the relaxed thinning algorithm based on patches with more than 9 pixels used to develop the transition layer. The right column shows the results of using a pixel clumping of more than 99 pixels used to define rainforest patches in the landscape. The difference in the pixel thinning algorithm was manifested in the total number of patches at low elevations, but not in the total rainforest area of the region.

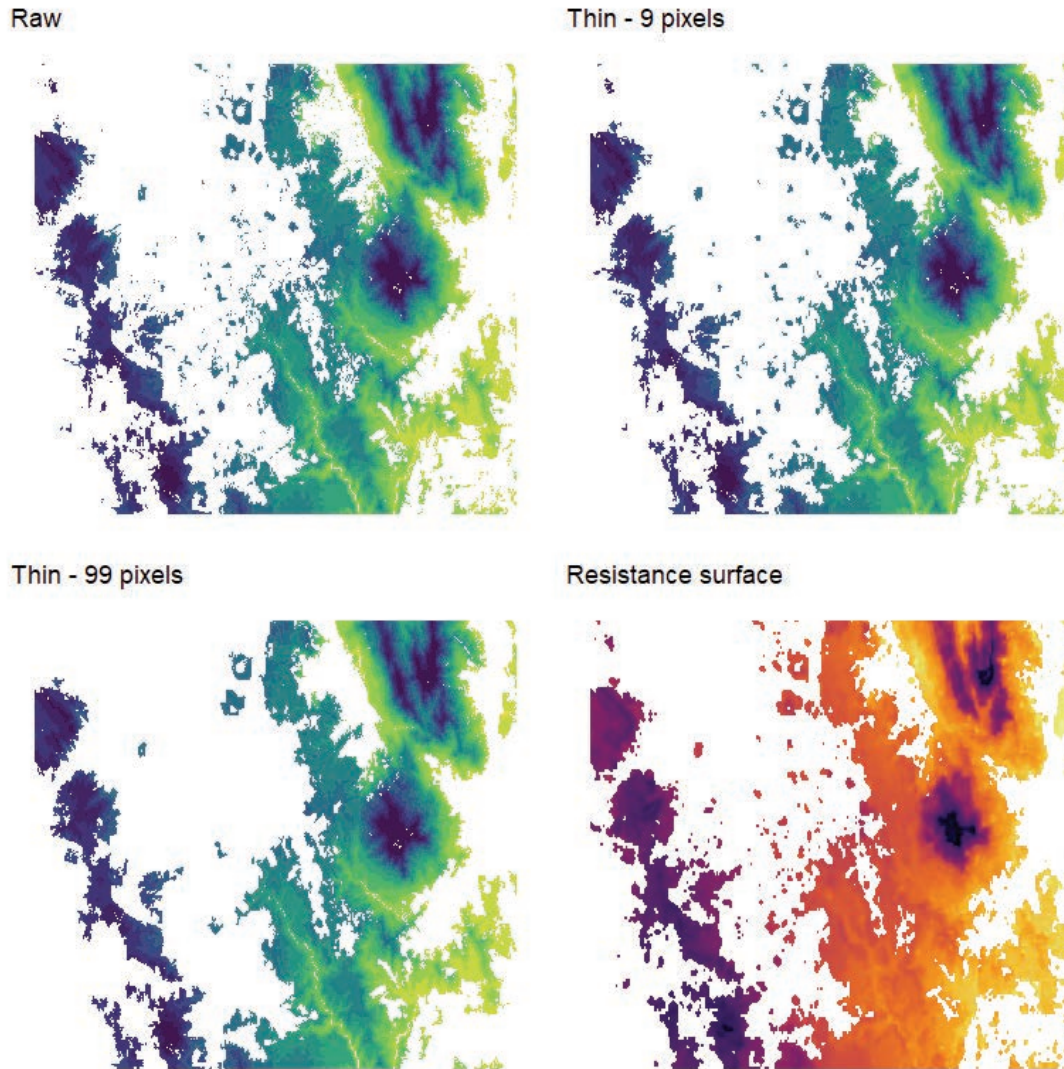


Figure S3.3. Example of the pixel thinning algorithm implemented to reduce spatial noise induced by small patches associated with agricultural areas in the Atherton Tablelands. Total number of patches derived from the broad vegetation groups of Queensland (top left). Spatial thinning retaining pixels clumps of 10 pixels or more (top right). Spatial thinning remaining pixels clumps of 100 pixels or more (bottom left). Resistance surface used for movement analysis defined by the spatial thinning with pixel clumps of 10 or more (bottom right).

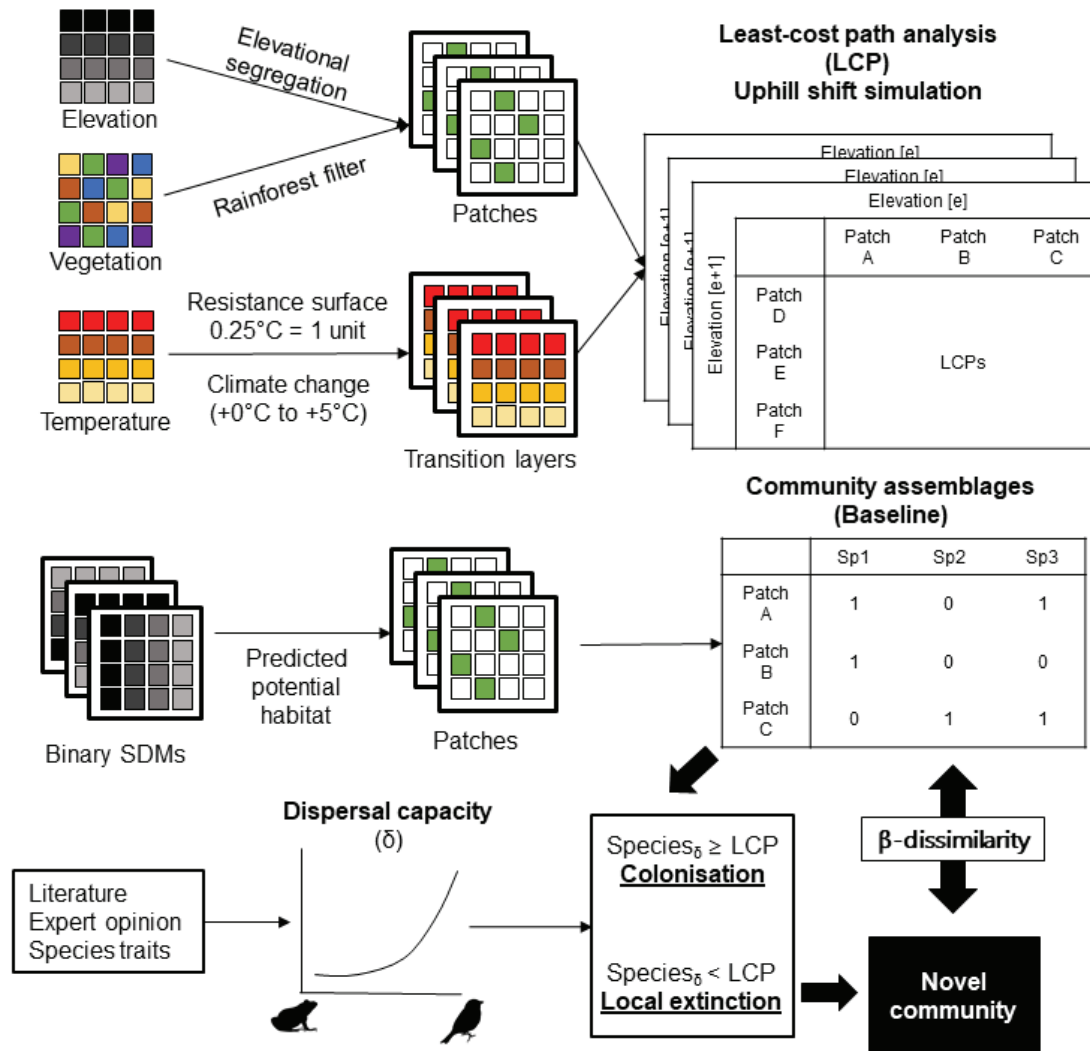


Figure S3.4. Graphical summary of the methodological framework developed for the uphill shift simulation in the Australian Wet Tropics. The top half represents the workflow followed to simulate the cost of elevational shifts. First, we defined the targeted patches based on habitat type and elevation. Then, we created different transition layers based on landscape resistance under different scenarios (from current climate +0°C to +5°C, with +1°C step). Using this background, we calculated the cost of shifting using least-cost path analysis. The bottom half represents the community re-shuffling simulation, where species are exposed to the framework developed in the top half. At each patch, we defined assemblages using species predicted potential habitat derived from SDMs. We calculated the likelihood of species within assemblages of shifting to higher elevations based on their dispersal

potential (i.e., when the species dispersal potential was higher than the predicted distance between patches the shift was successful, and vice versa), this induced a community re-shuffling process that resulted in changes in community structures, measured as β -dissimilarity.

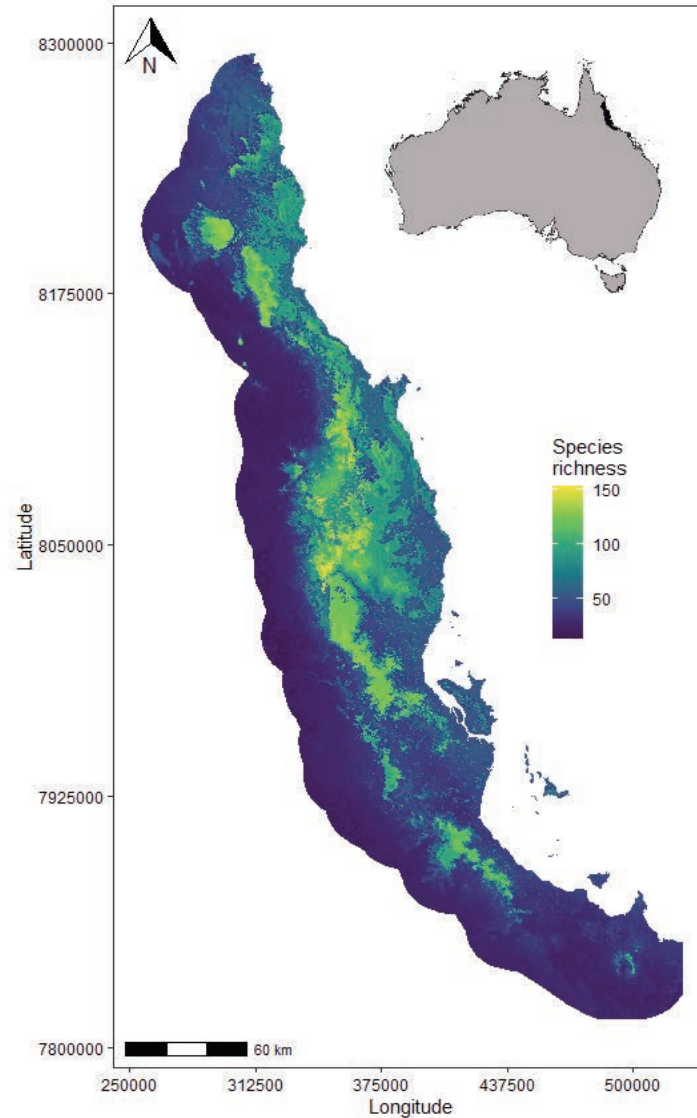


Figure S3.5. Richness distribution of vertebrate species in the Australian Wet Tropics. The map represents the accumulation of species from a pool of 202 vertebrates in each 250m² cell.

Table S3.1. Vertebrate species of the Australian Wet Tropics included in the simulation. The table includes information about species' family, taxa, dispersal capacity (obtained from Williams et al. 2010), percentage of patches occupied before the simulation, and percentage of patches occupied after each elevational shift scenario.

Taxa	Family	Scientific name	Common name	Species code	Dispersal capacity	Patches occupied before shift (%)	Patches occupied after shift (%)					
						Initial	Current climate	1°C	2°C	3°C	4°C	5°C
BIRD	Megapodiidae	<i>Alectura lathamii</i>	Australian Brush Turkey	ABT	4	0.644	0.626	0.618	0.604	0.576	0.537	0.503
MAMM	Dasyuridae	<i>Antechinus adustus</i>	Rusty Antechinus	ANTADUS	0.5	0.085	0.026	0.022	0.018	0.012	0.010	0.009
MAMM	Dasyuridae	<i>Antechinus flavipes</i>	Yellow-footed Antechinus	ANTFLAV	1	0.291	0.171	0.155	0.132	0.104	0.084	0.078
MAMM	Dasyuridae	<i>Antechinus godmani</i>	Atherton Antechinus	ANTGODM	1	0.141	0.061	0.055	0.045	0.032	0.023	0.024
BIRD	Acanthizidae	<i>Sericornis keri</i>	Atherton Scrubwren	ASW	2	0.138	0.101	0.092	0.083	0.069	0.053	0.051
FROG	Microhylidae	<i>Austrochaperina fryi</i>	Cricketer Chirper	AUSFRYI	0.5	0.162	0.074	0.065	0.054	0.044	0.029	0.017
FROG	Microhylidae	<i>Austrochaperina pluvialis</i>	White-browed Chirper	AUSPLUV	0.5	0.594	0.301	0.267	0.226	0.175	0.122	0.084
FROG	Microhylidae	<i>Austrochaperina robusta</i>	Peeling Chirper	AUSROBU	0.5	0.258	0.087	0.074	0.059	0.043	0.033	0.032

BIRD	Alcedinidae	<i>Alcedo azurea</i>	Azure Kingfisher	AZK	4	0.890	0.873	0.865	0.850	0.821	0.777	0.739
BIRD	Muscicapidae	<i>Zoothera lunulata</i>	Bassian Thrush	BASTH	4	0.170	0.154	0.150	0.141	0.124	0.104	0.093
BIRD	Halcyonidae	<i>Tanysiptera sylvia</i>	Buff-breasted Paradise-Kingfisher	BBPK	16	0.566	0.566	0.566	0.566	0.565	0.566	0.565
BIRD	Artamidae	<i>Cracticus quoyi</i>	Black Butcherbird	BBUT	4	0.758	0.754	0.749	0.741	0.724	0.695	0.654
BIRD	Campephagidae	<i>Coracina lineata</i>	Barred Cuckoo-Shrike	BCS	8	0.530	0.528	0.527	0.526	0.520	0.506	0.488
BIRD	Cuculidae	<i>Cacomantis variolosus</i>	Brush Cuckoo	BCUC	8	0.790	0.790	0.789	0.788	0.782	0.770	0.756
BIRD	Dicruridae	<i>Monarcha melanopsis</i>	Black-faced Monarch	BFMON	16	0.490	0.489	0.489	0.489	0.489	0.487	0.484
BIRD	Estrildidae	<i>Erythrura trichroa</i>	Blue-faced Parrot-Finch	BFPF	4	0.317	0.310	0.306	0.299	0.282	0.263	0.244
BIRD	Acanthizidae	<i>Gerygone mouki</i>	Brown Gerygone	BGER	4	0.632	0.620	0.612	0.598	0.569	0.525	0.490
BIRD	Meliphagidae	<i>Lichenostomus frenatus</i>	Bridled Honeyeater	BHE	8	0.332	0.325	0.324	0.322	0.316	0.302	0.287
REPT	Colubridae	<i>Boiga irregularis</i>	Brown Tree Snake	BOIRRE	16	0.873	0.872	0.872	0.872	0.872	0.870	0.868
BIRD	Strigidae	<i>Ninox novaeseelandiae</i>	Southern Boobook	BOO	8	0.632	0.627	0.627	0.625	0.618	0.601	0.581
BIRD	Columbidae	<i>Macropygia amboinensis</i>	Brown Cuckoo-Dove	BPIG	8	0.748	0.741	0.740	0.738	0.730	0.714	0.693

BIRD	Pachycephalidae	<i>Colluricincla boweri</i>	Bowers Shrike-Thrush	BST	16	0.271	0.267	0.267	0.267	0.267	0.263	0.261
REPT	Elapidae	<i>Cacophis churchilli</i>		CACCHUR	8	0.396	0.388	0.387	0.385	0.378	0.362	0.343
MAMM	Canidae	<i>Canis lupus dingo</i>	Dingo	CANLUPU	16	0.978	0.975	0.975	0.975	0.974	0.970	0.968
REPT	Gekkonidae	<i>Carphodactylus laevis</i>	Chameleon Gecko	CARLAEV	1	0.318	0.210	0.193	0.164	0.133	0.109	0.090
REPT	Scincidae	<i>Carlia rhomboidalis</i>		CARRHOM	0.5	0.009	0.005	0.005	0.004	0.002	0.002	0.001
REPT	Scincidae	<i>Carlia rubrigularis</i>	Northern Red-throated Skink	CARRUBR	0.5	0.823	0.441	0.397	0.341	0.267	0.188	0.135
BIRD	Casuariidae	<i>Casuarus casuarus</i>	Southern Cassowary	CASS	16	0.327	0.327	0.327	0.327	0.326	0.326	0.326
BIRD	Ptilonorhynchidae	<i>Ailuroedus melanotis</i>	Spotted Catbird	CAT	8	0.650	0.643	0.642	0.640	0.634	0.618	0.596
BIRD	Cuculidae	<i>Cacomantis castaneiventris</i>	Chestnut-breasted Cuckoo	CBCUC	8	0.208	0.206	0.206	0.205	0.204	0.202	0.195
BIRD	Cuculidae	<i>Scythrops novaehollandiae</i>	Channel-billed Cuckoo	CBILCUC	16	0.496	0.496	0.496	0.496	0.496	0.494	0.493
BIRD	Orthonychidae	<i>Orthonyx spaldingii</i>	Chowchilla	CC	4	0.424	0.405	0.397	0.384	0.357	0.317	0.289
MAMM	Burramyidae	<i>Cercartetus caudatus</i>	Long-tailed Pygmy Possum	CERCAUD	1	0.240	0.130	0.117	0.101	0.083	0.068	0.058

REPT	Scincidae	<i>Coeranoscincus frontalis</i>		COEFRON	2	0.237	0.185	0.171	0.155	0.132	0.107	0.102
FROG	Microhylidae	<i>Cophixalus aenigma</i>	Tapping Nursery-Frog	COPAENI	0.5	0.029	0.009	0.008	0.006	0.005	0.003	0.001
FROG	Microhylidae	<i>Cophixalus bombiens</i>	Windsor Nursery-Frog	COPBOMB	0.5	0.050	0.020	0.018	0.015	0.013	0.009	0.005
FROG	Microhylidae	<i>Cophixalus concinnus</i>	Beautiful Nursery-Frog	COPCONC	0.5	0.003	0.001	0.001	0.001	0.001	0.001	0.000
FROG	Microhylidae	<i>Cophixalus exiguus</i>	Bloomfield Nursery-Frog	COPEXIG	0.5	0.011	0.007	0.006	0.004	0.004	0.002	0.000
FROG	Microhylidae	<i>Cophixalus hosmeri</i>	Pipping Nursery-Frog	COPHOSM	0.5	0.013	0.003	0.003	0.002	0.002	0.001	0.001
FROG	Microhylidae	<i>Cophixalus infacetis</i>	Buzzing Nursery-Frog	COPINFA	0.5	0.311	0.164	0.145	0.122	0.091	0.062	0.046
FROG	Microhylidae	<i>Cophixalus mcdonaldi</i>	Southern Nursery-Frog	COPMCDO	0.5	0.008	0.005	0.005	0.004	0.002	0.002	0.001
FROG	Microhylidae	<i>Cophixalus monticola</i>	Mountain Top Nursery-Frog	COPMONT	0.5	0.004	0.000	0.000	0.000	0.000	0.000	0.000
FROG	Microhylidae	<i>Cophixalus neglectus</i>	Tangerine Nursery-Frog	COPNEGL	0.5	0.005	0.002	0.002	0.002	0.001	0.001	0.001
FROG	Microhylidae	<i>Cophixalus ornatus</i>	Common Nursery-Frog	COPORNA	0.5	0.431	0.179	0.159	0.133	0.102	0.072	0.056
BIRD	Psittacidae	<i>Platycercus elegans</i>	Crimson Rosella	CROS	4	0.163	0.147	0.145	0.138	0.125	0.103	0.093
BIRD	Artamidae	<i>Strepera graculina</i>	Pied Currawong	CURR	16	0.401	0.397	0.397	0.397	0.397	0.393	0.391
REPT	Scincidae	<i>Cyclodomorphus gerrardii</i>	Pink-tongued Lizard	CYCGERR	1	0.858	0.648	0.612	0.557	0.478	0.393	0.327

MAMM	Petauridae	<i>Dactylopsila trivirgata</i>	Striped Possum	DACTRIV	4	0.850	0.830	0.821	0.806	0.774	0.724	0.678
MAMM	Dasyuridae	<i>Dasyurus maculatus</i>	Spotted-tailed Quoll	DASMACU	16	0.107	0.102	0.102	0.102	0.102	0.100	0.099
BIRD	Psittacidae	<i>Cyclopsitta diophthalma</i>	Double-eyed Fig-Parrot	DEFP	4	0.724	0.716	0.711	0.700	0.677	0.642	0.604
REPT	Elapidae	<i>Demansia psammophis</i>	Yellow-faced Whipsnake	DEMPSAM	8	0.071	0.071	0.071	0.071	0.070	0.069	0.069
MAMM	Macropodidae	<i>Dendrolagus bennettianus</i>	Bennett's Tree-kangaroo	DENBENN	8	0.118	0.117	0.117	0.117	0.117	0.116	0.111
REPT	Colubridae	<i>Dendrelaphis calligastra</i>	Northern Tree Snake	DENCALL	4	0.557	0.553	0.552	0.549	0.539	0.523	0.498
MAMM	Macropodidae	<i>Dendrolagus lumholtzi</i>	Lumholtz's Tree-kangaroo	DENLUMH	8	0.105	0.100	0.099	0.097	0.092	0.084	0.077
REPT	Colubridae	<i>Dendrelaphis punctulata</i>	Common Tree Snake	DENPUNC	8	0.864	0.863	0.863	0.862	0.856	0.843	0.829
BIRD	Meliphagidae	<i>Myzomela obscura</i>	Dusky Honeyeater	DUHE	4	0.867	0.861	0.855	0.844	0.821	0.783	0.743
BIRD	Columbidae	<i>Chalcophaps indica</i>	Emerald Dove	ED	8	0.849	0.846	0.845	0.843	0.837	0.820	0.800
REPT	Scincidae	<i>Egernia frerei</i>	Major Skink	EGEFRER	1	0.549	0.433	0.408	0.372	0.321	0.259	0.199
BIRD	Meliphagidae	<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	ESB	8	0.256	0.248	0.247	0.245	0.242	0.230	0.213
REPT	Scincidae	<i>Eulamprus brachysoma</i>		EULBRAC	0.5	0.196	0.126	0.114	0.097	0.074	0.052	0.042
REPT	Scincidae	<i>Eulamprus frerei</i>		EULFRER	1	0.002	0.001	0.001	0.001	0.001	0.001	0.001

REPT	Scincidae	<i>Eulamprus quoyii</i>	Eastern Water Skink	EULQUOY	0.5	0.663	0.365	0.328	0.280	0.218	0.154	0.114
REPT	Scincidae	<i>Eulamprus tigrinus</i>		EULTIGR	0.5	0.253	0.096	0.085	0.071	0.055	0.038	0.026
BIRD	Eupetidae	<i>Psophodes olivaceus</i>	Eastern Whipbird	EWB	4	0.518	0.500	0.492	0.478	0.449	0.408	0.376
BIRD	Acanthizidae	<i>Gerygone palpebrosa</i>	Fairy Gerygone	FGER	2	0.650	0.632	0.625	0.609	0.580	0.529	0.473
BIRD	Oriolidae	<i>Sphecotheres viridis</i>	Figbird	FIG	8	0.624	0.624	0.624	0.623	0.619	0.610	0.603
BIRD	Cuculidae	<i>Cacomantis flabelliformis</i>	Fan-tailed Cuckoo	FTCUC	16	0.642	0.638	0.638	0.638	0.638	0.635	0.632
REPT	Elapidae	<i>Furina ornata</i>	Orange-naped Snake	FURORNA	0.5	0.467	0.329	0.299	0.260	0.206	0.148	0.111
REPT	Elapidae	<i>Furina tristis</i>	Brown-headed Snake	FURTRIS	0.5	0.048	0.032	0.030	0.026	0.022	0.017	0.011
BIRD	Acanthizidae	<i>Oreoscopus gutturalis</i>	Fernwren	FW	2	0.287	0.224	0.207	0.188	0.161	0.131	0.124
BIRD	Cuculidae	<i>Chrysococcyx russatus</i>	Gould's Bronze-Cuckoo	GBCUC	8	0.307	0.307	0.307	0.306	0.306	0.305	0.303
BIRD	Dicruridae	<i>Rhipidura fuliginosa</i>	Grey Fantail	GFAN	2	0.933	0.851	0.825	0.789	0.726	0.642	0.587
BIRD	Accipitridae	<i>Accipiter novaehollandiae</i>	Grey Goshawk	GGH	16	0.674	0.670	0.670	0.670	0.670	0.667	0.665
BIRD	Meliphagidae	<i>Meliphaga gracilis</i>	Graceful Honeyeater	GHE	2	0.801	0.767	0.752	0.728	0.683	0.617	0.554

BIRD	Petroicidae	<i>Heteromyias albispecularis</i>	Grey-headed Robin	GHR	2	0.436	0.368	0.348	0.323	0.284	0.240	0.225
REPT	Scincidae	<i>Glaphyromorphus clandestinus</i>	Mt Elliot skink	GLACLAN	0.5	0.001	0.000	0.000	0.000	0.000	0.000	0.000
REPT	Scincidae	<i>Glaphyromorphus fuscicaudis</i>	Grey-tailed Skink	GLAFUSC	0.5	0.530	0.273	0.247	0.210	0.164	0.115	0.081
REPT	Scincidae	<i>Glaphyromorphus mjobergi</i>		GLAMJOB	0.5	0.150	0.037	0.031	0.024	0.017	0.012	0.010
REPT	Scincidae	<i>Gnypetoscincus queenslandiae</i>	Prickly Forest Skink	GNYQUEE	0.5	0.449	0.199	0.177	0.147	0.113	0.080	0.055
BIRD	Ptilonorhynchidae	<i>Prionodura newtoniana</i>	Golden Bowerbird	GOLDBB	4	0.113	0.098	0.096	0.090	0.080	0.065	0.057
BIRD	Pachycephalidae	<i>Pachycephala pectoralis</i>	Golden Whistler	GOLDW	8	0.416	0.409	0.408	0.405	0.399	0.383	0.367
BIRD	Pachycephalidae	<i>Pachycephala simplex</i>	Grey Whistler	GREYW	8	0.683	0.683	0.683	0.682	0.678	0.672	0.667
MAMM	Pseudocheiridae	<i>Hemibelideus lemuroides</i>	Lemuroid Ringtail Possum	HEMLEMU	2	0.099	0.069	0.060	0.052	0.041	0.030	0.031
REPT	Elapidae	<i>Hemiaspis signata</i>	Black-bellied Swamp Snake	HEMSIGN	4	0.180	0.164	0.162	0.156	0.144	0.126	0.116
BIRD	Meliphagidae	<i>Philemon buceroides</i>	Helmeted Friarbird	HFB	16	0.330	0.330	0.330	0.330	0.330	0.330	0.330
REPT	Agamidae	<i>Hypsilurus boydii</i>	Boyd's Forest Dragon	HYPBOYD	2	0.531	0.471	0.451	0.427	0.388	0.339	0.303
MAMM	Potoroidae	<i>Hypsiprymnodon moschatus</i>	Musky Rat-kangaroo	HYPMOSC	2	0.330	0.281	0.266	0.246	0.215	0.179	0.154

BIRD	Cuculidae	<i>Eudynamys scolopacea</i>	Common Koel	KOEL	16	0.386	0.386	0.386	0.386	0.386	0.384	0.385
BIRD	Psittacidae	<i>Alisterus scapularis</i>	Australian King Parrot	KP	16	0.342	0.338	0.338	0.338	0.338	0.334	0.332
REPT	Scincidae	<i>Lampropholis coggeri</i>		LAMCOGG	0.5	0.679	0.347	0.312	0.265	0.206	0.144	0.101
REPT	Scincidae	<i>Lampropholis mirabilis</i>		LAMMIRA	0.5	0.006	0.004	0.004	0.003	0.002	0.001	0.001
REPT	Scincidae	<i>Lampropholis robertsi</i>		LAMROBE	0.5	0.030	0.006	0.005	0.004	0.003	0.002	0.002
BIRD	Cuculidae	<i>Chrysococcyx minutillus</i>	Little Bronze-Cuckoo	LBCUC	16	0.970	0.967	0.967	0.967	0.967	0.963	0.961
BIRD	Acanthizidae	<i>Gerygone magnirostris</i>	Large-billed Gerygone	LBGER	4	0.199	0.198	0.198	0.198	0.197	0.194	0.183
BIRD	Acanthizidae	<i>Sericornis magnirostris</i>	Large-billed Scrubwren	LBSW	2	0.806	0.730	0.705	0.673	0.619	0.544	0.485
BIRD	Meliphagidae	<i>Meliphaga lewinii</i>	Lewin's Honeyeater	LEWHE	2	0.483	0.411	0.390	0.362	0.318	0.268	0.255
FROG	Myobatrachidae	<i>Limnodynastes peronii</i>	Striped Marshfrog	LIMPERO	1	0.410	0.329	0.310	0.281	0.239	0.199	0.182
FROG	Hylidae	<i>Litoria fallax</i>	Eastern Sedgefrog	LITFALL	1	0.336	0.276	0.262	0.242	0.211	0.180	0.160
FROG	Hylidae	<i>Litoria genimaculata</i>	Green-eyed Treefrog	LITGENI	1	0.807	0.595	0.558	0.504	0.434	0.351	0.276
FROG	Hylidae	<i>Litoria infrafrenata</i>	White-lipped Treefrog	LITINFR	1	0.495	0.426	0.407	0.380	0.337	0.276	0.211
FROG	Hylidae	<i>Litoria jungguy</i>		LITJUNG	1	0.779	0.597	0.564	0.515	0.448	0.367	0.286

FROG	Hylidae	<i>Litoria lorica</i>	Armoured Mistfrog	LITLORI	1	0.223	0.171	0.159	0.145	0.129	0.097	0.071
FROG	Hylidae	<i>Litoria nannotis</i>	Waterfall Frog	LITNANN	1	0.743	0.549	0.516	0.465	0.399	0.326	0.257
FROG	Hylidae	<i>Litoria nyakalensis</i>	Mountain Mistfrog	LITNYAK	1	0.443	0.297	0.273	0.239	0.200	0.161	0.133
FROG	Hylidae	<i>Litoria revelata</i>	Whirring Treefrog	LITREVE	1	0.101	0.045	0.040	0.031	0.021	0.015	0.017
FROG	Hylidae	<i>Litoria rheocola</i>	Common Mistfrog	LITRHEO	1	0.565	0.432	0.406	0.369	0.320	0.258	0.193
FROG	Hylidae	<i>Litoria xanthomera</i>	Northern Orange-eyed Treefrog	LITXANT	1	0.635	0.452	0.423	0.375	0.317	0.258	0.208
BIRD	Alcedinidae	<i>Alcedo pusilla</i>	Little Kingfisher	LK	2	0.472	0.447	0.438	0.423	0.389	0.352	0.332
BIRD	Tytonidae	<i>Tyto multipunctata</i>	Lesser Sooty Owl	LSOWL	4	0.491	0.473	0.466	0.452	0.423	0.387	0.364
BIRD	Pachycephalidae	<i>Colluricincla megarhyncha</i>	Little Shrike-Thrush	LST	4	0.929	0.921	0.914	0.901	0.872	0.829	0.784
BIRD	Meliphagidae	<i>Xanthotis macleayana</i>	Macleay's Honeyeater	MACHE	2	0.798	0.735	0.714	0.684	0.633	0.563	0.503
MAMM	Muridae	<i>Melomys cervinipes</i>	Fawn-footed Melomys	MELCERV	1	0.657	0.478	0.448	0.408	0.349	0.282	0.238
FROG	Myobatrachidae	<i>Mixophyes Carbinensis</i>		MIXCARB	1	0.031	0.013	0.011	0.009	0.008	0.006	0.005
FROG	Myobatrachidae	<i>Mixophyes Coggeri</i>		MIXCOGG	1	0.451	0.344	0.324	0.294	0.253	0.203	0.156

FROG	Myobatrachidae	<i>Mixophyes schevilli</i>	Northern Barred Frog	MIXSCHE	1	0.262	0.142	0.128	0.108	0.086	0.068	0.060
REPT	Boidae	<i>Morelia kinghorni</i>	Amethystine Python	MORKING	16	0.394	0.394	0.394	0.394	0.393	0.392	0.393
REPT	Boidae	<i>Morelia spilota</i>	Jungle Carpet Python	MORSPIL	16	0.081	0.081	0.081	0.081	0.081	0.081	0.081
BIRD	Sturnidae	<i>Aplonis metallica</i>	Metallic Starling	MSTAR	16	0.433	0.433	0.433	0.433	0.432	0.433	0.433
BIRD	Dicaeidae	<i>Dicaeum hirundinaceum</i>	Mistletoebird	MTB	8	0.994	0.989	0.988	0.985	0.977	0.960	0.938
BIRD	Acanthizidae	<i>Acanthiza katherina</i>	Mountain Thornbill	MTHORN	2	0.147	0.104	0.095	0.085	0.073	0.055	0.053
MAMM	Vespertilionidae	<i>Murina florium</i>	Flute-nosed bat	MURFLOR	8	0.292	0.288	0.288	0.286	0.281	0.271	0.258
MAMM	Vespertilionidae	<i>Myotis adversus</i>	Large-footed myotis	MYOADVE	8	0.833	0.831	0.831	0.830	0.824	0.811	0.797
REPT	Gekkonidae	<i>Nactus cheverti</i>		NACCHEV	0.5	0.177	0.117	0.107	0.094	0.077	0.056	0.033
BIRD	Pittidae	<i>Pitta versicolor</i>	Noisy Pitta	NPIT	16	0.826	0.823	0.823	0.823	0.823	0.820	0.818
FROG	Hylidae	<i>Nyctimystes dayi</i>	Australian Lace-lid	NYCDAYI	1	0.567	0.418	0.394	0.357	0.307	0.250	0.187
MAMM	Pteropodidae	<i>Nyctimene robinsoni</i>	Eastern tubenosed bat	NYCROBI	16	0.748	0.747	0.747	0.747	0.746	0.744	0.742
BIRD	Oriolidae	<i>Oriolus sagittatus</i>	Olive-backed Oriole	OBO	16	0.196	0.196	0.196	0.196	0.196	0.196	0.196
BIRD	Cuculidae	<i>Cuculus saturatus</i>	Oriental Cuckoo	OCUC	16	0.055	0.055	0.055	0.055	0.055	0.055	0.055

BIRD	Megapodiidae	<i>Megapodius reinwardt</i>	Orange-footed Scrubfowl	OFSF	2	0.734	0.680	0.661	0.635	0.591	0.527	0.466
MAMM	Ornithorhynchidae	<i>Ornithorhynchus anatinus</i>	Platypus	ORNANAT	8	0.733	0.726	0.725	0.722	0.715	0.698	0.676
MAMM	Peramelidae	<i>Perameles nasuta</i>	Long-nosed Bandicoot	PERNASU	4	0.601	0.582	0.575	0.560	0.530	0.487	0.459
BIRD	Podargidae	<i>Podargus papuensis</i>	Papuan Frogmouth	PFROG	8	0.647	0.646	0.646	0.646	0.644	0.640	0.630
REPT	Gekkonidae	<i>Phyllurus amnicola</i>	Mt.Elliot Leaf-tail gecko	PHYAMNI	1	0.004	0.003	0.003	0.003	0.003	0.002	0.002
REPT	Gekkonidae	<i>Phyllurus gulbaru</i>	Gulbaru Gecko	PHYGULB	0.5	0.087	0.054	0.048	0.037	0.027	0.022	0.022
REPT	Agamidae	<i>Physignathus lesueurii</i>	Eastern Water Dragon	PHYLESU	1	0.789	0.598	0.562	0.510	0.439	0.361	0.292
BIRD	Columbidae	<i>Ducula bicolor</i>	Pied Imperial Pigeon	PIPIG	16	0.109	0.109	0.109	0.109	0.109	0.109	0.109
BIRD	Dicruridae	<i>Arses kaupi</i>	Pied Monarch	PMON	4	0.801	0.789	0.782	0.768	0.740	0.696	0.655
MAMM	Muridae	<i>Pogonomys mollipilosus</i>	Prehensile-tailed Rat	POGMOLL	1	0.969	0.743	0.701	0.639	0.552	0.450	0.366
MAMM	Pseudocheiridae	<i>Pseudocheirops archeri</i>	Green Ringtail Possum	PSEARCH	2	0.190	0.144	0.131	0.117	0.096	0.074	0.073
MAMM	Pseudocheiridae	<i>Pseudochirulus cinereus</i>	Daintree River Ringtail Possum	PSECINE	2	0.027	0.019	0.017	0.014	0.011	0.008	0.007

MAMM	Pseudocheiridae	<i>Pseudochirulus herbertensis</i>	Herbert River Ringtail Possum	PSEHERB	2	0.144	0.105	0.094	0.082	0.065	0.050	0.049
REPT	Elapidae	<i>Pseudechis porphyriacus</i>	Red-bellied Black Snake	PSEPORP	16	0.363	0.360	0.360	0.360	0.359	0.355	0.353
MAMM	Pteropodidae	<i>Pteropus alecto</i>	Black flying-fox	PTEALEC	16	0.303	0.303	0.303	0.303	0.303	0.303	0.303
MAMM	Pteropodidae	<i>Pteropus conspicillatus</i>	Spectacled flying-fox	PTECONS	16	0.463	0.463	0.463	0.463	0.462	0.460	0.460
BIRD	Petroicidae	<i>Tregellasia capito</i>	Pale-yellow Robin	PYR	2	0.833	0.760	0.736	0.704	0.649	0.575	0.515
REPT	Typhlopidae	<i>Ramphotyphlops polygrammicus</i>		RAMPOLY	0.5	0.911	0.527	0.475	0.410	0.324	0.232	0.170
FROG	Ranidae	<i>Rana daemeli</i>	Australian Bullfrog	RANDAEM	1	0.365	0.317	0.304	0.285	0.258	0.208	0.151
MAMM	Muridae	<i>Rattus fuscipes</i>	Bush Rat	RATFUSC	2	0.284	0.241	0.230	0.216	0.189	0.160	0.151
MAMM	Muridae	<i>Rattus leucopus</i>	Cape York Rat	RATLEUC	2	0.387	0.365	0.358	0.348	0.333	0.300	0.251
BIRD	Meropidae	<i>Merops ornatus</i>	Rainbow Bee-eater	RBBE	16	0.871	0.871	0.871	0.871	0.870	0.869	0.868
BIRD	Columbidae	<i>Ptilinopus regina</i>	Rose-crowned Fruit-Dove	RCFD	16	0.788	0.788	0.788	0.788	0.787	0.786	0.783
BIRD	Dicruridae	<i>Rhipidura rufifrons</i>	Rufous Fantail	RFAN	16	0.968	0.964	0.964	0.964	0.963	0.960	0.958
MAMM	Rhinolophidae	<i>Rhinolophus megaphyllus</i>	Eastern horseshoe bat	RHIMEGA	8	0.922	0.916	0.915	0.912	0.904	0.887	0.865

REPT	Elapidae	<i>Cryptophis nigrescens</i>	Eastern Smalleyed Snake	RHINIGR	8	0.544	0.538	0.537	0.534	0.527	0.510	0.494
BIRD	Psittacidae	<i>Trichoglossus haematodus</i>	Rainbow Lorikeet	RL	16	0.977	0.974	0.974	0.974	0.973	0.970	0.968
BIRD	Rallidae	<i>Rallina tricolor</i>	Red-necked Crake	RNCR	4	0.648	0.644	0.641	0.636	0.623	0.601	0.574
BIRD	Strigidae	<i>Ninox rufa</i>	Rufous Owl	ROWL	8	0.389	0.388	0.387	0.385	0.379	0.368	0.358
REPT	Gekkonidae	<i>Saltuarius cornutus</i>	Northern Leaf-tailed Gecko	SALCORN	1	0.521	0.358	0.334	0.295	0.249	0.202	0.158
REPT	Scincidae	<i>Saproscincus basiliscus</i>		SAPBASI	0.5	0.540	0.269	0.241	0.206	0.160	0.113	0.084
REPT	Scincidae	<i>Saproscincus czechurai</i>	Czechura's Litter Skink	SAPCZEC	0.5	0.088	0.023	0.020	0.016	0.011	0.008	0.006
REPT	Scincidae	<i>Saproscincus lewisi</i>		SAPLEWI	0.5	0.077	0.043	0.038	0.032	0.025	0.017	0.010
REPT	Scincidae	<i>Saproscincus tetradactylus</i>	Four-toed Litter Skink	SAPTETR	0.5	0.423	0.218	0.194	0.164	0.127	0.091	0.066
BIRD	Ptilonorhynchidae	<i>Ptilonorhynchus violaceus</i>	Satin Bowerbird	SATBB	8	0.113	0.106	0.105	0.103	0.101	0.095	0.085
BIRD	Cuculidae	<i>Chrysococcyx lucidus</i>	Shining Bronze- Cuckoo (Golden)	SBCUC	16	0.488	0.485	0.485	0.485	0.485	0.481	0.479
BIRD	Psittacidae	<i>Trichoglossus chlorolepidotus</i>	Scaly- breasted Lorikeet	SBL	16	0.826	0.823	0.823	0.823	0.823	0.819	0.818

BIRD	Meliphagidae	<i>Myzomela sanguinolenta</i>	Scarlet Honeyeater	SCARHE	8	0.648	0.646	0.646	0.645	0.640	0.629	0.619
BIRD	Cacatuidae	<i>Cacatua galerita</i>	Sulphur-crested Cockatoo	SCC	16	0.996	0.993	0.993	0.993	0.993	0.989	0.987
BIRD	Dicruridae	<i>Dicrurus bracteatus</i>	Spangled Drongo	SD	16	0.946	0.946	0.946	0.946	0.945	0.944	0.942
BIRD	Zosteropidae	<i>Zosterops lateralis</i>	Silvereye	SE	8	0.959	0.958	0.957	0.954	0.948	0.932	0.913
BIRD	Columbidae	<i>Ptilinopus superbus</i>	Superb Fruit-Dove	SFD	16	0.918	0.917	0.917	0.917	0.916	0.912	0.910
MAMM	Dasyuridae	<i>Sminthopsis leucopus</i>	White-footed Dunnart	SMILEUC	1	0.009	0.005	0.004	0.003	0.002	0.001	0.002
BIRD	Dicruridae	<i>Monarcha trivirgatus</i>	Spectacled Monarch	SMON	16	0.869	0.866	0.866	0.866	0.865	0.861	0.859
REPT	Colubridae	<i>Stegonotus cucullatus</i>	Slaty-grey Snake	STECUCU	8	0.821	0.815	0.814	0.812	0.804	0.787	0.766
FROG	Myobatrachidae	<i>Taudactylus acutirostris</i>	Sharp-snouted Dayfrog	TAUACUT	1	0.267	0.161	0.147	0.129	0.110	0.084	0.063
FROG	Myobatrachidae	<i>Taudactylus rheophilus</i>	Northern Tinkerfrog	TAURHEO	1	0.051	0.022	0.019	0.016	0.013	0.010	0.009
BIRD	Ptilonorhynchidae	<i>Scenopoeetes dentirostris</i>	Tooth-billed Bowerbird	TBBB	4	0.249	0.232	0.226	0.214	0.193	0.165	0.150
REPT	Scincidae	<i>Techmarscincus jigurru</i>	Bartle Frere Skink	TECJIGU	0.5	0.002	0.000	0.000	0.000	0.000	0.001	0.001
MAMM	Macropodidae	<i>Thylogale stigmatica</i>	Red-legged Pademelon	THYSTIG	4	0.376	0.359	0.353	0.339	0.314	0.280	0.260

BIRD	Columbidae	<i>Lopholaimus antarcticus</i>	Topknot Pigeon	TPIG	16	0.353	0.348	0.348	0.348	0.348	0.344	0.343
MAMM	Phalangeridae	<i>Trichosurus vulpecula j.</i>	Coppery Brushtail Possum	TRIJOHN	4	0.054	0.053	0.052	0.048	0.041	0.033	0.032
REPT	Elapidae	<i>Tropidechis carinatus</i>	Rough-scaled Snake	TROCARI	8	0.179	0.171	0.170	0.168	0.164	0.152	0.135
REPT	Colubridae	<i>Tropidonophis mairii</i>	Keelback	TROMAIR	4	0.513	0.511	0.511	0.509	0.502	0.489	0.478
MAMM	Muridae	<i>Uromys caudimaculatus</i>	Giant White-tailed Rat	UROCAUD	4	0.530	0.521	0.515	0.502	0.479	0.448	0.425
MAMM	Muridae	<i>Uromys hadrourus</i>	Masked White-tailed Rat	UROHADR	2	0.069	0.054	0.050	0.045	0.040	0.032	0.027
REPT	Varanidae	<i>Varanus scalaris</i>	Spotted Tree Monitor	VARSCAL	2	0.399	0.348	0.332	0.312	0.279	0.241	0.231
REPT	Varanidae	<i>Varanus varius</i>	Lace Monitor	VARVARI	4	0.667	0.659	0.657	0.649	0.629	0.600	0.576
MAMM	Vespertilionidae	<i>Vespadelus pumilus</i>	Eastern forest bat	VESPUMI	8	0.205	0.205	0.204	0.204	0.203	0.201	0.200
BIRD	Paradisaeidae	<i>Ptiloris victoriae</i>	Victoria's Riflebird	VRIF	4	0.670	0.653	0.646	0.631	0.602	0.558	0.518
BIRD	Campephagidae	<i>Lalage leucomela</i>	Varied Triller	VT	2	0.905	0.847	0.826	0.794	0.738	0.662	0.601
BIRD	Petroicidae	<i>Poecilodryas superciliosa</i>	White-browed Robin	WBR	2	0.016	0.016	0.016	0.016	0.016	0.015	0.016
BIRD	Acanthizidae	<i>Sericornis frontalis</i>	White-browed Scrubwren	WBSW	2	0.125	0.105	0.100	0.092	0.075	0.061	0.066

BIRD	Artamidae	<i>Artamus leucorhynchus</i>	White-breasted Woodswallow	WBWS	16	0.312	0.312	0.312	0.312	0.312	0.312	0.312
BIRD	Dicruridae	<i>Monarcha leucotis</i>	White-eared Monarch	WEMON	2	0.704	0.673	0.659	0.635	0.594	0.534	0.477
BIRD	Columbidae	<i>Columba leucomela</i>	White-headed Pigeon	WHPIG	8	0.262	0.255	0.254	0.252	0.249	0.236	0.220
BIRD	Columbidae	<i>Ptilinopus magnificus</i>	Wompoo Fruit-Dove	WOMP	8	0.817	0.815	0.814	0.812	0.806	0.789	0.769
BIRD	Apodidae	<i>Collocalia spodiopygius</i>	White-rumped Swiftlet	WRSW	4	0.584	0.566	0.560	0.552	0.532	0.500	0.461
BIRD	Apodidae	<i>Hirundapus caudacutus</i>	White-throated Needletail	WTNT	16	0.775	0.771	0.771	0.771	0.770	0.767	0.765
BIRD	Climacteridae	<i>Cormobates leucophaeus</i>	White-throated Treecreeper	WTTC	4	0.368	0.349	0.343	0.330	0.304	0.267	0.245
BIRD	Dicruridae	<i>Machaerirhynchus flaviventer</i>	Yellow-breasted Boatbill	YBBB	4	0.825	0.811	0.804	0.789	0.761	0.716	0.672
BIRD	Oriolidae	<i>Oriolus flavocinctus</i>	Yellow Oriole	YO	8	0.322	0.322	0.322	0.321	0.321	0.320	0.318
BIRD	Meliphagidae	<i>Meliphaga notata</i>	Yellow-spotted Honeyeater	YSHE	2	0.763	0.722	0.708	0.687	0.645	0.579	0.522

BIRD	Acanthizidae	<i>Sericornis citreogularis</i>	Yellow- throated Scrubwren	YTSW	2	0.260	0.204	0.189	0.174	0.148	0.119	0.116

Table S3.2. Species distribution across the elevational gradient in the Australian Wet Tropics. The table represent the number of parches occupied by each species at each elevational band.

Species Code	Elevation (m a.s.l.)														
	0	100	200	300	400	500	600	700	800	900	1000	1100	1200	1300	1400
ABT	477	446	438	443	556	642	565	448	344	226	123	101	66	24	7
ANTADUS	0	0	0	1	2	22	70	128	212	131	57	18	3	0	0
ANTFLAV	1	7	15	32	73	178	365	441	421	308	162	126	67	23	0
ANTGODM	0	0	1	3	8	42	154	267	252	135	85	78	35	3	7
ASW	0	0	0	2	6	48	119	174	199	160	120	119	73	27	7
AUSFRYI	36	60	72	105	136	151	174	120	99	82	61	59	51	24	0
AUSPLUV	462	469	552	518	513	508	492	367	281	147	83	72	38	12	6
AUSROBU	0	4	13	70	173	239	337	375	330	197	103	79	31	3	7
AZK	651	703	853	800	796	697	622	512	430	300	168	135	75	27	7
BASTH	0	0	0	2	8	58	145	270	304	201	114	94	66	24	7
BBPK	589	663	810	737	649	429	243	106	56	17	6	2	0	0	1
BBUT	654	718	901	848	832	715	553	356	166	27	2	0	0	0	0
BCS	5	34	210	505	647	678	622	522	401	251	94	40	20	6	0
BCUC	654	745	935	860	809	638	559	336	229	131	65	49	7	0	0
BFMON	42	30	100	415	620	624	556	476	393	244	103	81	39	3	6
BFPF	157	134	158	260	356	353	318	235	209	102	59	43	21	9	0
BGER	56	146	407	607	692	698	671	560	435	287	134	91	31	0	0
BHE	3	2	4	23	186	399	433	421	384	275	163	129	75	27	7

BOIIRRE	661	746	943	876	850	725	654	497	383	226	58	18	3	1	5
BOO	5	44	283	520	715	778	751	595	450	316	159	119	59	18	1
BPIG	466	508	595	562	675	651	606	536	417	289	159	125	75	27	7
BST	0	0	3	3	36	279	445	408	341	234	119	96	66	25	7
CACCHUR	2	11	13	68	194	398	562	571	462	320	170	135	75	27	7
CANLUPU	631	733	945	892	918	839	764	601	444	307	158	126	62	22	7
CARLAEV	0	24	81	168	340	444	429	342	300	159	76	42	14	3	0
CARRHOM	3	1	4	1	3	6	9	11	8	12	6	3	2	0	0
CARRUBR	505	593	749	723	743	730	646	519	413	288	144	115	68	26	5
CASS	472	517	455	187	130	89	126	202	141	118	34	11	5	1	0
CAT	267	355	487	549	645	641	566	476	385	248	136	99	64	25	7
CBCUC	138	131	161	193	207	214	180	132	71	65	33	28	19	9	0
CBILCUC	447	433	497	464	514	436	387	218	193	105	54	30	0	0	0
CC	23	64	101	215	312	495	549	472	376	259	139	115	71	27	7
CERCAUD	64	43	13	34	96	165	268	321	300	215	116	95	66	24	7
COEFRON	1	8	20	78	164	216	249	303	280	201	118	92	47	22	7
COPAENI	0	0	0	0	2	9	25	47	25	25	23	20	31	15	0
COPBOMB	1	2	8	21	43	49	47	14	14	49	46	44	27	16	0
COPCONC	0	0	0	0	0	1	1	1	2	3	2	3	5	3	0
COPEXIG	0	0	7	8	17	14	19	15	2	1	2	1	0	0	0
COPHOSM	0	0	0	0	0	0	0	1	15	11	16	17	25	12	0
COPINFA	232	257	352	336	319	300	217	150	124	38	15	16	1	1	6
COPMCDO	0	0	0	0	3	6	9	11	8	12	6	3	2	0	0

COPMONT	0	0	0	0	0	0	0	0	0	0	1	3	17	9	0
COPNEGL	0	0	0	1	2	2	0	1	1	1	6	8	7	2	7
COPORNA	85	119	183	265	358	435	432	432	389	256	143	101	59	15	7
CROS	0	0	0	1	5	8	79	233	279	237	156	133	75	27	7
CURR	0	4	6	13	164	479	619	583	458	316	170	135	75	27	7
CYCGERR	374	494	675	757	838	819	764	615	463	320	170	135	75	27	7
DACTRIV	484	571	717	699	751	750	709	596	459	318	170	135	75	27	7
DASMACU	34	18	2	1	6	12	38	97	107	160	120	110	73	27	7
DEFP	642	699	864	749	682	583	446	308	270	136	69	56	8	0	0
DEMPSAM	2	15	41	41	56	72	155	87	42	24	7	1	0	0	0
DENBENN	79	100	132	127	108	96	91	50	18	27	17	31	14	12	0
DENCALL	520	584	714	635	594	488	313	183	103	73	22	11	0	0	0
DENLUMH	0	0	0	3	12	27	81	120	163	134	90	88	56	15	7
DENPUNC	644	749	946	886	908	783	663	482	351	139	24	4	2	0	0
DUHE	665	749	946	886	913	827	705	524	299	78	4	1	0	0	0
ED	586	658	813	780	746	690	666	557	426	295	124	80	33	9	1
EGEFRER	415	499	573	506	485	461	428	371	226	150	46	16	5	1	0
ESB	0	0	1	1	8	41	314	474	402	297	166	134	75	27	7
EULBRAC	23	90	139	175	170	233	230	194	121	74	20	8	6	2	4
EULFRER	0	0	0	0	0	1	0	1	1	1	1	1	1	1	5
EULQUOY	325	465	575	577	618	571	539	470	372	258	125	101	40	12	0
EULTIGR	207	181	179	121	163	193	215	195	124	115	82	68	54	24	7
EWB	68	103	188	344	508	615	591	498	394	269	145	119	71	27	7

FGER	664	746	936	861	782	498	296	130	28	6	0	0	0	0	0
FIG	634	678	725	562	523	468	384	328	289	138	22	1	0	0	0
FTCUC	69	180	316	566	706	709	683	561	448	306	148	102	66	24	7
FURORNA	380	432	571	549	572	445	362	198	42	6	1	0	0	0	0
FURTRIS	186	127	46	5	0	0	0	0	0	0	0	0	0	0	0
FW	0	3	3	5	109	357	450	402	328	215	115	96	71	27	7
GBCUC	569	602	659	356	101	17	5	12	4	8	5	0	0	0	0
GFAN	444	618	862	859	906	839	778	617	461	318	169	134	74	26	1
GGH	282	370	645	724	737	657	520	386	297	207	111	112	53	23	7
GHE	658	743	932	878	894	823	699	372	86	9	2	0	0	0	0
GHR	3	7	58	198	398	554	536	496	394	283	158	127	75	27	7
GLACLAN	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0
GLAFUSC	341	370	439	458	531	529	446	336	216	164	77	54	45	24	7
GLAMJOB	0	0	0	2	6	25	143	244	271	162	105	92	64	24	7
GNYQUEE	192	251	334	306	394	451	420	325	279	168	106	95	64	25	7
GOLDBB	0	0	0	1	2	3	15	101	233	197	114	96	64	25	7
GOLDW	0	2	6	106	315	519	572	529	420	296	165	129	75	27	7
GREYW	644	739	929	858	834	616	375	153	34	12	3	2	2	0	0
HEMLEMU	0	0	0	2	5	30	101	130	168	89	82	84	51	13	0
HEMSIGN	1	0	0	8	31	114	219	260	222	198	113	97	73	27	7
HFB	613	622	525	272	183	108	70	82	19	15	6	1	0	0	0
HYPBOYD	373	368	338	326	392	469	475	415	374	260	115	85	44	9	0
HYPMOSC	176	172	204	189	227	293	352	286	258	144	84	53	50	23	0

KOEL	318	347	433	429	450	345	245	128	121	86	28	8	0	0	0
KP	0	2	6	66	219	415	468	426	369	259	144	122	75	27	7
LAMCOGG	292	390	628	628	672	640	575	473	364	219	112	94	59	23	0
LAMMIRA	3	1	4	1	3	5	8	9	6	5	0	0	0	0	0
LAMROBE	0	0	0	1	2	3	1	4	17	18	32	57	63	27	7
LBCUC	644	708	884	867	914	841	781	618	460	299	159	125	64	24	0
LBGER	572	525	379	36	1	0	0	0	0	0	0	0	0	0	0
LBSW	473	584	745	754	734	669	596	511	399	280	156	126	74	27	7
LEWHE	0	2	7	116	431	676	716	577	451	309	161	128	74	25	2
LIMPERO	111	181	267	320	434	439	433	331	246	182	84	64	24	3	0
LITFALL	331	225	232	272	378	314	325	226	136	83	28	10	0	0	0
LITGENI	434	534	743	716	710	654	638	568	448	302	163	132	72	26	7
LITINFR	648	672	755	609	439	342	192	56	40	17	2	0	0	0	0
LITJUNG	555	651	788	762	734	681	557	408	298	197	113	90	64	24	7
LITLORI	172	173	248	234	192	155	135	99	63	63	49	48	40	24	0
LITNANN	297	579	816	675	573	549	582	561	444	267	138	97	59	22	0
LITNYAK	84	113	220	326	421	446	456	370	332	229	143	128	72	27	7
LITREVE	0	0	0	1	2	7	87	131	188	158	94	75	26	1	0
LITRHEO	573	597	694	552	484	398	374	254	188	82	45	33	22	2	0
LITXANT	163	365	581	521	498	509	558	557	438	294	148	120	62	22	0
LK	441	313	383	438	508	474	412	351	179	81	14	3	0	0	0
LSOWL	2	40	192	375	496	552	535	487	419	267	145	121	75	27	7
LST	653	749	945	886	915	838	775	605	453	234	21	2	0	0	0

MACHE	580	639	803	772	748	684	627	511	379	217	78	30	5	0	0
MELCERV	260	274	410	493	569	634	655	558	452	316	164	123	65	24	7
MIXCARB	0	0	0	0	0	1	2	15	38	46	42	45	33	16	0
MIXCOGG	31	138	358	460	464	497	455	379	258	173	82	59	46	25	7
MIXSCHE	1	2	8	13	92	259	407	340	291	213	137	123	73	27	7
MORKING	415	311	329	313	328	384	365	247	156	92	39	15	4	0	0
MORSPIL	5	2	4	9	17	50	129	186	152	57	4	3	1	0	0
MSTAR	649	655	715	508	388	239	109	33	1	0	0	0	0	0	0
MTB	667	750	946	888	917	841	781	617	457	318	166	131	74	16	1
MTHORN	0	0	0	1	4	27	88	220	247	204	118	106	69	27	7
MURFLOR	0	3	44	137	239	323	334	281	324	241	130	109	43	15	0
MYOADVE	663	734	899	816	806	714	623	443	333	195	71	36	8	0	0
NACCHEV	376	317	348	187	83	32	6	1	0	0	0	0	0	0	0
NPIT	569	666	828	786	768	704	626	510	375	220	104	58	52	17	7
NYCDAYI	569	611	688	483	416	371	320	263	264	162	82	69	20	2	0
NYCROBI	578	658	815	755	717	621	508	375	308	178	78	66	29	10	0
OBO	153	227	277	239	220	156	102	62	20	25	6	2	0	0	0
OCUC	174	92	55	39	31	12	5	2	6	4	0	0	0	0	0
OFSF	646	690	821	761	720	595	502	331	276	132	55	47	13	1	0
ORNANAT	505	576	673	610	550	516	520	487	422	311	170	134	75	27	6
PERNASU	104	144	294	404	495	657	712	588	458	313	169	134	74	26	1
PFROG	565	602	776	676	617	500	410	289	193	150	68	55	20	5	0
PHYAMNI	0	0	0	0	1	3	5	6	4	7	2	0	0	0	0

PHYGULB	7	19	37	63	96	106	122	123	56	31	5	0	0	0	0
PHYLESU	557	620	703	611	628	631	614	533	442	309	157	112	63	24	0
PIPIG	401	327	94	6	2	0	0	0	0	0	0	0	0	0	0
PMON	554	644	776	751	734	675	618	518	399	250	98	57	19	4	0
POGMOLL	622	703	895	876	914	837	770	593	447	310	166	134	75	27	7
PSEARCH	0	1	1	7	46	127	228	296	282	192	108	90	52	20	0
PSECINE	0	0	0	0	0	0	0	1	23	49	42	45	34	14	0
PSEHERB	0	0	0	5	18	95	201	224	219	141	89	68	25	3	7
PSEPORP	16	41	77	141	216	372	431	470	379	251	149	121	74	26	2
PTEALEC	495	540	685	395	174	18	1	0	0	0	0	0	0	0	0
PTECONS	551	537	544	360	299	266	273	232	189	128	75	52	17	3	0
PYR	454	636	801	780	774	724	656	541	399	260	136	100	61	22	0
RAMPOLY	667	750	946	890	914	819	730	535	348	175	74	61	28	1	0
RANDAEM	514	503	547	426	332	238	149	48	14	3	3	1	0	0	2
RATFUSC	1	3	15	103	198	283	372	431	277	195	107	83	62	26	7
RATLEUC	498	491	534	408	302	234	166	124	64	51	19	14	22	14	3
RBBE	667	750	944	885	904	796	692	494	363	122	13	1	0	0	0
RCFD	622	727	909	804	736	659	592	473	288	151	30	5	2	0	0
RFAN	656	742	928	872	877	805	723	602	455	310	167	130	74	25	1
RHIMEGA	578	710	925	867	877	808	689	547	405	271	143	111	63	21	7
RHINIGR	143	195	298	421	471	534	520	475	429	297	153	121	60	22	0
RL	666	749	944	887	909	830	754	593	449	310	153	116	58	23	0
RNCR	647	727	904	800	707	556	338	173	37	35	7	0	0	0	0

ROWL	11	45	135	211	363	434	491	416	357	228	128	104	34	6	0
SALCORN	164	173	277	323	450	514	519	466	419	290	156	121	63	22	7
SAPBASI	285	306	411	438	485	513	505	438	365	234	95	25	5	2	6
SAPCZEC	0	0	0	1	2	7	18	66	139	143	105	93	66	26	7
SAPLEWI	81	88	95	86	64	52	52	38	12	6	4	4	5	3	0
SAPTETR	334	311	375	357	368	388	385	305	239	125	25	3	1	2	6
SATBB	0	0	0	1	3	4	16	101	173	208	124	125	75	27	7
SBCUC	1	10	41	279	546	657	568	531	436	307	156	101	60	20	0
SBL	414	565	802	769	774	721	664	496	429	293	156	125	63	21	0
SCARHE	102	286	553	650	724	680	632	500	394	250	99	49	12	1	0
SCC	663	750	946	892	917	841	781	618	462	319	169	133	71	23	0
SD	662	746	940	877	900	825	753	595	427	282	115	79	1	0	0
SE	643	746	937	882	914	838	777	611	447	306	124	63	12	1	0
SFD	557	708	875	845	846	792	708	582	436	297	156	114	61	11	4
SMILEUC	0	0	0	0	2	5	8	13	24	11	4	2	0	0	0
SMON	614	676	824	789	764	704	660	550	410	273	142	114	70	23	0
STECUCU	618	658	798	744	706	664	588	470	367	256	158	130	70	24	1
TAUACUT	0	14	107	185	194	232	230	214	243	229	151	130	72	26	2
TAURHEO	0	0	0	1	2	3	5	14	54	67	71	73	64	24	7
TBBB	0	0	2	3	31	211	403	392	326	217	116	96	66	25	7
TECJIGU	0	0	0	0	0	1	0	1	1	1	1	1	1	1	5
THYSTIG	1	21	59	134	243	302	454	504	441	310	163	128	73	25	1
TPIG	10	5	4	84	223	408	461	453	394	274	147	115	72	27	7

TRIOHN	0	0	0	0	1	5	34	59	139	99	48	24	1	0	0
TROCARI	7	5	1	15	26	55	130	184	265	258	170	135	75	27	7
TROMAIR	416	556	751	696	587	405	254	158	56	26	3	0	0	0	0
UROCAUD	363	355	360	385	419	470	467	416	370	234	99	51	36	10	0
UROHADR	2	1	8	19	31	73	114	124	43	20	22	20	31	13	1
VARSCAL	13	56	133	264	383	501	517	460	348	242	85	26	4	1	4
VARVARI	307	408	609	651	670	623	562	436	330	255	113	77	33	5	0
VERANNU	3	4	65	134	234	245	324	218	152	111	42	23	3	0	0
VRIF	196	342	546	635	680	656	588	504	395	252	132	95	61	22	0
VT	667	750	946	887	915	836	763	570	400	147	7	2	0	0	0
WBR	25	47	35	12	3	0	1	0	0	0	0	0	0	0	0
WBSW	0	0	0	0	2	11	141	244	251	193	69	27	11	0	0
WBWS	423	365	377	342	320	250	140	77	31	38	11	3	2	0	0
WEMON	506	655	834	805	822	726	526	346	112	29	1	0	0	0	0
WHPIG	8	1	2	22	82	221	375	403	329	230	124	99	66	24	7
WOMP	553	633	775	758	734	680	638	538	421	262	115	82	28	0	0
WRSW	594	602	650	477	386	329	358	321	247	168	107	103	71	27	7
WTNT	475	521	675	666	731	694	637	490	386	258	145	122	67	23	7
WTTC	0	1	3	19	162	390	561	521	437	305	163	131	74	27	7
YBBB	570	665	816	773	745	685	646	532	391	235	105	72	36	9	0
YO	653	677	700	336	82	0	0	0	0	0	0	0	0	0	0
YSHE	643	700	860	811	801	671	537	382	230	140	28	5	4	0	0
YTSW	0	0	1	3	56	288	389	359	327	220	119	108	75	26	7

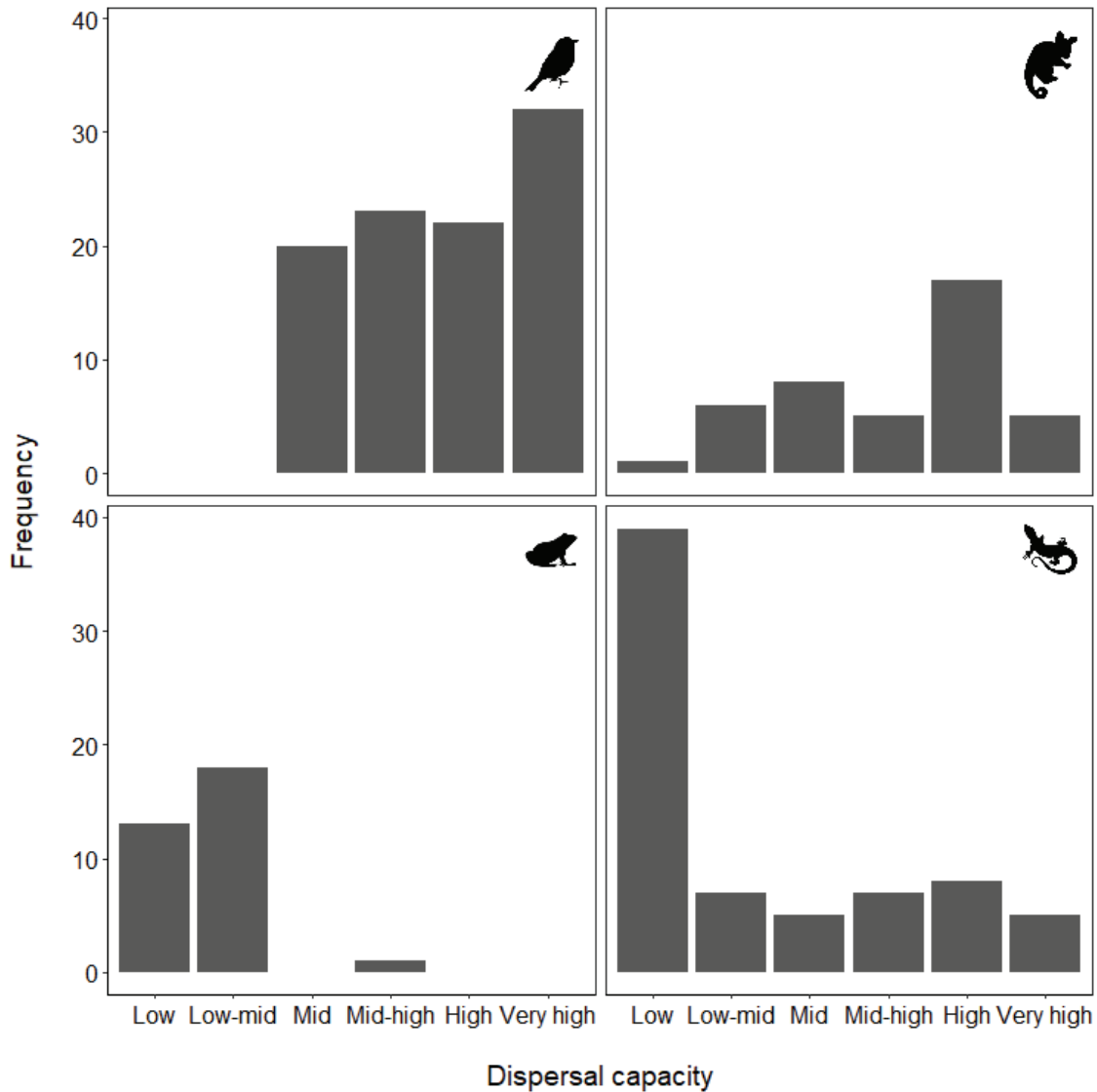


Figure S3.6. Distribution of dispersal capacity values across taxa. See table S3.1 for species-specific values.

Changes in multi-site spatial β -diversity

Multiple-site dissimilarity analysis produced similar results to the pairwise temporal dissimilarity, showing an increasing change in assemblages with elevation, both in overall β -dissimilarity (β_{jac} ; Figure S3.8) and the nestedness component (β_{jne} ; Figure S3.9). In addition, multi-site spatial dissimilarity analysis allowed a visual comparison of the change in spatial β -dissimilarity between the baseline (observed assemblages) and elevational shift scenarios along the elevational gradient. Similarly to pairwise temporal β -dissimilarity analyses, the change in spatial β -dissimilarity was

particularly accentuated at mountaintops (Figure S3.8). The turning point in β -dissimilarity at high elevations was defined by an increase in the nestedness component (Figure S3.9), with the pattern driven by a local mass extinction of species shifting to mountaintops (local extinction rate between 25-100%; Figure 3.4).

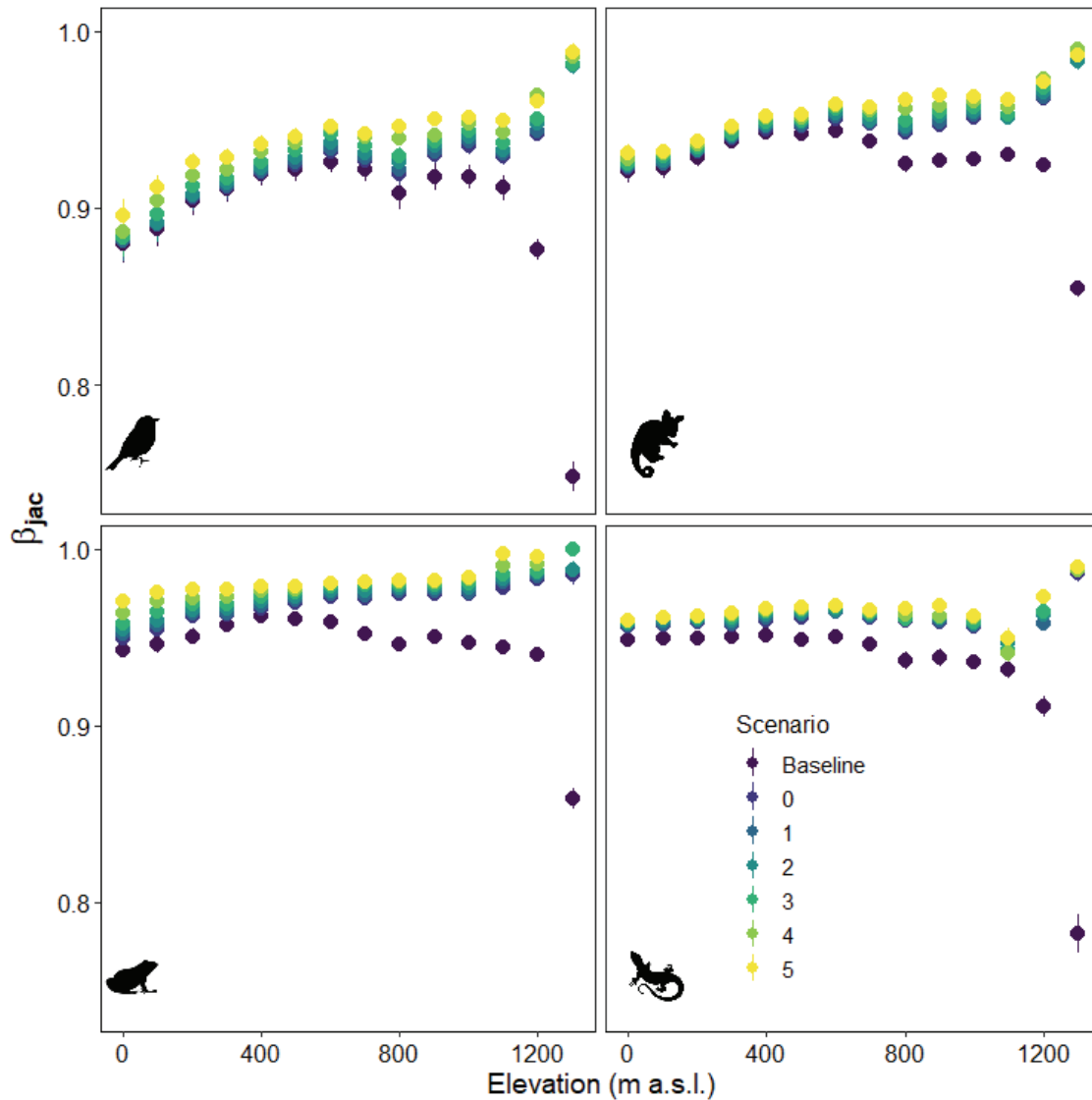


Figure S3.7. Change in multisite spatial β -dissimilarity along the elevational gradient in the Australian Wet Tropics. *The figure represents the difference in the overall spatial β -dissimilarity (β_{jac}) across taxa and elevation between the baseline and five elevational shift scenarios (from +0°C to +5°C, with +1°C step).*

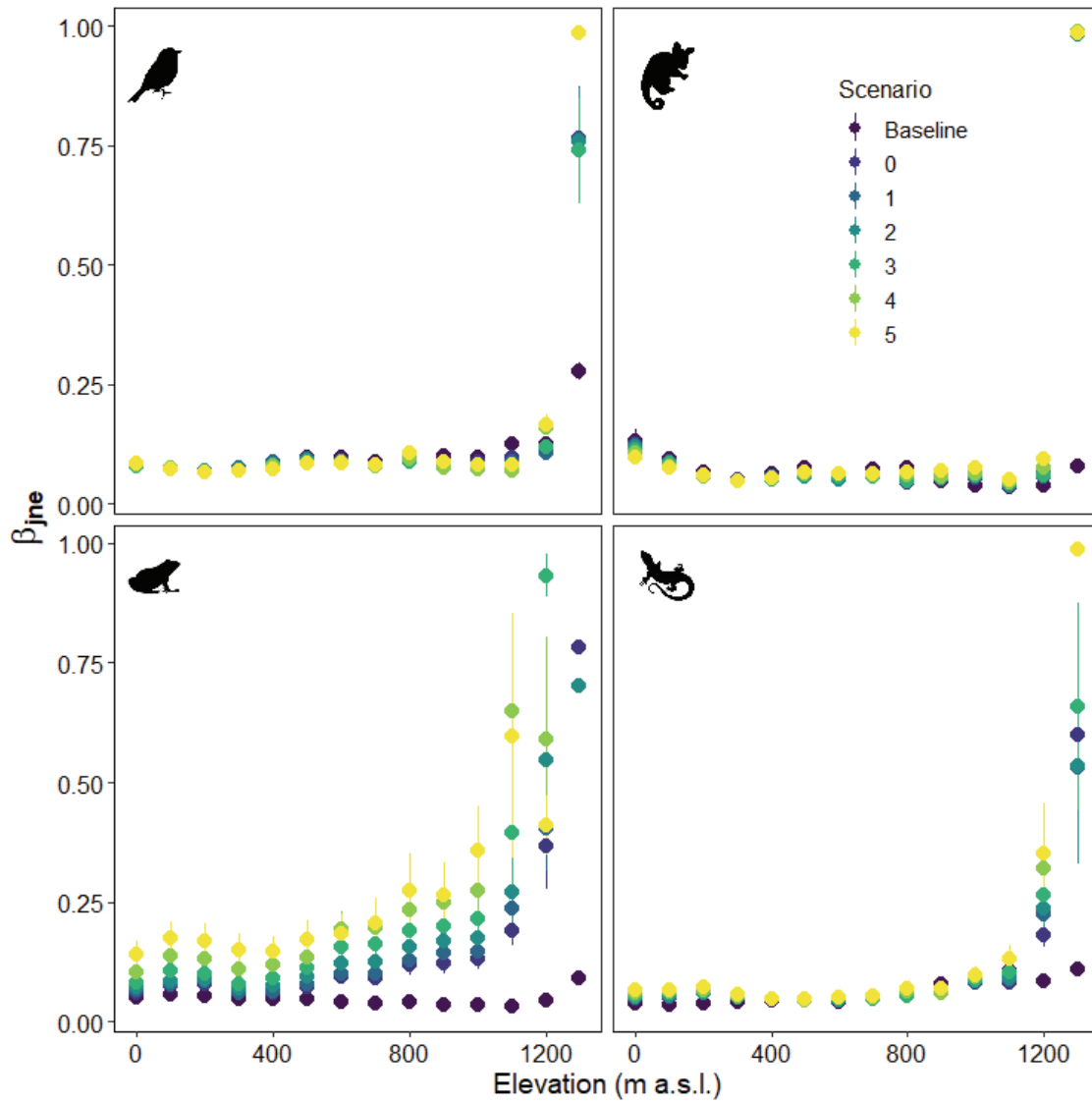


Figure S3.8. Change in multisite spatial β -dissimilarity along the elevational gradient in the Australian Wet Tropics. *The figure represents the spatial change in the nestedness component (β_{jne}) across taxa and elevation between the baseline and five elevational shift scenarios (from +0°C to +5°C, with +1°C step).*

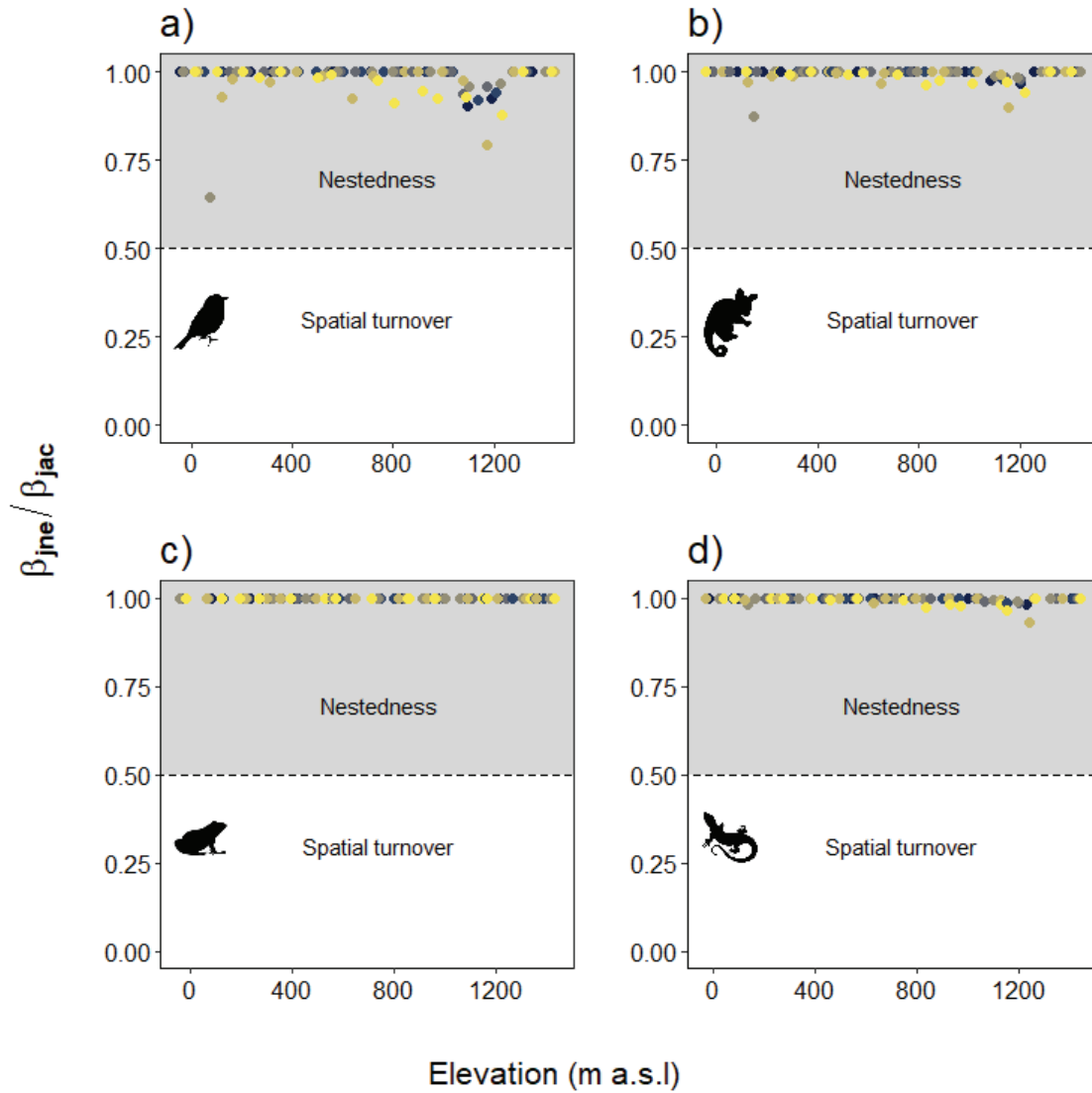


Figure S3.9. Predominant component driving the change in β -dissimilarity in the simulated climate-induced uphill shift. Values above 0.5 indicate a change in β -dissimilarity predominantly driven by the nestedness component (β_{jne}), and values below 0.5 indicate that spatial turnover mainly influences the overall change in β -dissimilarity. Colours depict the stepwise increase in global warming from the current climate (+0°C; dark blue) to +5°C scenario (yellow), with a +1°C step.

Table S3.3. Kolmogorov-Smirnov test results across taxa, elevation, and climate change scenario.

Taxa	Elevation	Climate change scenario (degrees increased)	K-S test			
			B _{jac}		B _{jne}	
			D (min)	p-value (max)	D (min)	p-value (max)
FROG	0	0	0.9009	0	0.722	0
FROG	100	0	0.8812	0	0.7288	0
FROG	200	0	0.8695	0	0.7208	0
FROG	300	0	0.9163	0	0.7692	0
FROG	400	0	0.9344	0	0.7535	0
FROG	500	0	0.8882	0	0.6794	0
FROG	600	0	0.7682	0	0.6043	0
FROG	700	0	0.7544	0	0.5423	0
FROG	800	0	0.6242	0	0.5458	0
FROG	900	0	0.5875	0	0.5372	0
FROG	1000	0	0.6	0	0.485	4.51E-14
FROG	1100	0	0.6	0	0.3024	0.0001
FROG	1200	0	0.52	3.12E-09	0.5135	0.0007
FROG	1300	0	0.1852	0.743	0.5	0.774
FROG	0	1	0.8814	0	0.7163	0
FROG	100	1	0.8653	0	0.7171	0
FROG	200	1	0.8511	0	0.7139	0
FROG	300	1	0.9007	0	0.7565	0
FROG	400	1	0.9147	0	0.7227	0
FROG	500	1	0.8536	0	0.6436	0
FROG	600	1	0.7183	0	0.5898	0
FROG	700	1	0.7092	0	0.4972	0
FROG	800	1	0.5637	0	0.5728	0
FROG	900	1	0.5563	0	0.527	0
FROG	1000	1	0.5412	0	0.4354	1.29E-10
FROG	1100	1	0.5185	3.33E-16	0.3276	7.22E-05
FROG	1200	1	0.5067	8.70E-09	0.5429	0.003
FROG	1300	1	0.1481	0.928	0.5	0.785
FROG	0	2	0.8604	0	0.6719	0

FROG	100	2	0.8425	0	0.6648	0
FROG	200	2	0.8265	0	0.6971	0
FROG	300	2	0.8808	0	0.7382	0
FROG	400	2	0.8712	0	0.6708	0
FROG	500	2	0.7977	0	0.627	0
FROG	600	2	0.6453	0	0.5441	0
FROG	700	2	0.6252	0	0.4623	0
FROG	800	2	0.4924	0	0.583	0
FROG	900	2	0.4938	0	0.51	0
FROG	1000	2	0.4647	2.22E-16	0.4112	8.48E-09
FROG	1100	2	0.5037	2.66E-15	0.3997	9.14E-06
FROG	1200	2	0.44	9.89E-07	0.5079	0.015936963
FROG	1300	2	0.1481	0.928	0.4444	0.903
FROG	0	3	0.8289	0	0.6229	0
FROG	100	3	0.8052	0	0.659	0
FROG	200	3	0.7811	0	0.6817	0
FROG	300	3	0.8384	0	0.7	0
FROG	400	3	0.804	0	0.6199	0
FROG	500	3	0.6953	0	0.6061	0
FROG	600	3	0.5314	0	0.4857	0
FROG	700	3	0.5105	0	0.4412	0
FROG	800	3	0.4773	0	0.4841	0
FROG	900	3	0.4656	0	0.5716	0
FROG	1000	3	0.4647	2.22E-16	0.3635	2.13E-06
FROG	1100	3	0.5111	9.99E-16	0.4722	9.09E-06
FROG	1200	3	0.3467	0.0002	0.46	0.049
FROG	1300	3	0.0741	0.999	0.5	1
FROG	0	4	0.7869	0	0.5585	0
FROG	100	4	0.7264	0	0.6043	0
FROG	200	4	0.7099	0	0.6272	0
FROG	300	4	0.7528	0	0.642	0
FROG	400	4	0.6879	0	0.5615	0
FROG	500	4	0.5858	0	0.5492	0
FROG	600	4	0.4456	0	0.4156	0
FROG	700	4	0.4394	0	0.439	0

FROG	800	4	0.5119	0	0.4537	0
FROG	900	4	0.4844	0	0.506	0
FROG	1000	4	0.4588	5.55E-16	0.3934	1.12E-05
FROG	1100	4	0.4222	7.06E-11	0.4673	0.001
FROG	1200	4	0.2933	0.003	0.4762	0.263
FROG	1300	4				
FROG	0	5	0.7118	0	0.5444	0
FROG	100	5	0.6142	0	0.5865	0
FROG	200	5	0.5747	0	0.5944	0
FROG	300	5	0.6314	0	0.5919	0
FROG	400	5	0.5839	0	0.5346	0
FROG	500	5	0.5417	0	0.504	0
FROG	600	5	0.4353	0	0.4208	0
FROG	700	5	0.4394	0	0.4403	0
FROG	800	5	0.5119	0	0.4446	0
FROG	900	5	0.4688	0	0.3403	3.33E-08
FROG	1000	5	0.4941	0	0.4803	5.89E-07
FROG	1100	5	0.3037	7.82E-06	0.4626	0.017
FROG	1200	5	0.24	0.026	0.4545	0.003
FROG	1300	5				
BIRD	0	0	0.9925	0	0.8906	0
BIRD	100	0	0.992	0	0.896	0
BIRD	200	0	0.9947	0	0.9101	0
BIRD	300	0	0.9955	0	0.935	0
BIRD	400	0	0.9891	0	0.9401	0
BIRD	500	0	0.9822	0	0.9407	0
BIRD	600	0	0.9782	0	0.9283	0
BIRD	700	0	0.9677	0	0.9208	0
BIRD	800	0	0.9482	0	0.8985	0
BIRD	900	0	0.9531	0	0.7688	0
BIRD	1000	0	0.8824	0	0.7824	0
BIRD	1100	0	0.9111	0	0.837	0
BIRD	1200	0	0.6533	2.50E-14	0.4953	2.61E-08
BIRD	1300	0	0.3333	0.01	0.3519	0.138
BIRD	0	1	0.991	0	0.8936	0

BIRD	100	1	0.988	0	0.8947	0
BIRD	200	1	0.9947	0	0.9186	0
BIRD	300	1	0.9955	0	0.9316	0
BIRD	400	1	0.988	0	0.9379	0
BIRD	500	1	0.9715	0	0.93	0
BIRD	600	1	0.9795	0	0.895	0
BIRD	700	1	0.9709	0	0.9063	0
BIRD	800	1	0.9309	0	0.8531	0
BIRD	900	1	0.9594	0	0.7219	0
BIRD	1000	1	0.8824	0	0.7412	0
BIRD	1100	1	0.9111	0	0.7926	0
BIRD	1200	1	0.64	9.11E-14	0.4405	1.16E-06
BIRD	1300	1	0.3704	0.049	0.3519	0.138
BIRD	0	2	0.9895	0	0.8876	0
BIRD	100	2	0.984	0	0.8893	0
BIRD	200	2	0.9873	0	0.9049	0
BIRD	300	2	0.9899	0	0.9283	0
BIRD	400	2	0.9793	0	0.9292	0
BIRD	500	2	0.9561	0	0.9015	0
BIRD	600	2	0.959	0	0.8553	0
BIRD	700	2	0.9661	0	0.8643	0
BIRD	800	2	0.9244	0	0.7646	0
BIRD	900	2	0.9594	0	0.6781	0
BIRD	1000	2	0.8647	0	0.7118	0
BIRD	1100	2	0.8963	0	0.7481	0
BIRD	1200	2	0.6133	1.12E-12	0.2884	0.004
BIRD	1300	2	0.4074	0.023	0.331	0.221
BIRD	0	3	0.991	0	0.8936	0
BIRD	100	3	0.976	0	0.888	0
BIRD	200	3	0.9736	0	0.8922	0
BIRD	300	3	0.9641	0	0.8957	0
BIRD	400	3	0.9597	0	0.8998	0
BIRD	500	3	0.9371	0	0.86	0
BIRD	600	3	0.9052	0	0.7862	0
BIRD	700	3	0.9499	0	0.7868	0

BIRD	800	3	0.9071	0	0.6587	0
BIRD	900	3	0.9094	0	0.5875	0
BIRD	1000	3	0.8353	0	0.6176	0
BIRD	1100	3	0.8815	0	0.6	0
BIRD	1200	3	0.4133	5.45E-06	0.3216	0.001
BIRD	1300	3	0.7037	3.12E-06	0.4615	0.451
BIRD	0	4	0.9715	0	0.8786	0
BIRD	100	4	0.9533	0	0.8653	0
BIRD	200	4	0.926	0	0.8488	0
BIRD	300	4	0.9417	0	0.8632	0
BIRD	400	4	0.9477	0	0.8464	0
BIRD	500	4	0.9253	0	0.8102	0
BIRD	600	4	0.8771	0	0.6927	0
BIRD	700	4	0.9176	0	0.6866	0
BIRD	800	4	0.8337	0	0.5227	0
BIRD	900	4	0.7969	0	0.4656	0
BIRD	1000	4	0.7647	0	0.4647	2.22E-16
BIRD	1100	4	0.8667	0	0.4222	7.06E-11
BIRD	1200	4	0.4267	2.35E-06	0.3794	4.75E-05
BIRD	1300	4	0.7037	3.12E-06	0.5833	0.324
BIRD	0	5	0.94	0	0.8561	0
BIRD	100	5	0.8907	0	0.8053	0
BIRD	200	5	0.9049	0	0.7812	0
BIRD	300	5	0.9249	0	0.8072	0
BIRD	400	5	0.9281	0	0.7941	0
BIRD	500	5	0.9205	0	0.7212	0
BIRD	600	5	0.8579	0	0.6466	0
BIRD	700	5	0.8853	0	0.6446	0
BIRD	800	5	0.73	0	0.4492	0
BIRD	900	5	0.6906	0	0.4469	0
BIRD	1000	5	0.7	0	0.3647	3.03E-10
BIRD	1100	5	0.637	0	0.2741	7.89E-05
BIRD	1200	5	0.48	6.26E-08	0.3516	0.0002
BIRD	1300	5	0.6296	4.49E-05	0.5362	0.430
MAMMAL	0	0	0.9685	0	0.7946	0

MAMMAL	100	0	0.9613	0	0.7733	0
MAMMAL	200	0	0.9281	0	0.7368	0
MAMMAL	300	0	0.9585	0	0.7668	0
MAMMAL	400	0	0.9619	0	0.8115	0
MAMMAL	500	0	0.9181	0	0.7628	0
MAMMAL	600	0	0.9014	0	0.6504	0
MAMMAL	700	0	0.8837	0	0.63	0
MAMMAL	800	0	0.8099	0	0.4428	0
MAMMAL	900	0	0.7063	0	0.4188	0
MAMMAL	1000	0	0.7765	0	0.4	3.08E-12
MAMMAL	1100	0	0.8	0	0.4074	3.71E-10
MAMMAL	1200	0	0.5333	1.09E-09	0.2754	0.007
MAMMAL	1300	0	0.1111	0.996	0.1481	0.972
MAMMAL	0	1	0.964	0	0.8081	0
MAMMAL	100	1	0.948	0	0.7653	0
MAMMAL	200	1	0.9101	0	0.7167	0
MAMMAL	300	1	0.9496	0	0.759	0
MAMMAL	400	1	0.9488	0	0.7898	0
MAMMAL	500	1	0.8909	0	0.7295	0
MAMMAL	600	1	0.8668	0	0.6031	0
MAMMAL	700	1	0.8708	0	0.5622	0
MAMMAL	800	1	0.7775	0	0.3931	0
MAMMAL	900	1	0.6719	0	0.3688	0
MAMMAL	1000	1	0.7294	0	0.3235	3.74E-08
MAMMAL	1100	1	0.7778	0	0.2963	1.43E-05
MAMMAL	1200	1	0.48	6.26E-08	0.3058	0.002
MAMMAL	1300	1	0.0741	0.999	0.1795	0.884
MAMMAL	0	2	0.955	0	0.8036	0
MAMMAL	100	2	0.9227	0	0.732	0
MAMMAL	200	2	0.8985	0	0.6924	0
MAMMAL	300	2	0.9361	0	0.7399	0
MAMMAL	400	2	0.9172	0	0.7418	0
MAMMAL	500	2	0.8553	0	0.6631	0
MAMMAL	600	2	0.8412	0	0.5262	0
MAMMAL	700	2	0.8142	0	0.4814	0

MAMMAL	800	2	0.7214	0	0.3348	0
MAMMAL	900	2	0.6469	0	0.3	6.21E-13
MAMMAL	1000	2	0.7118	0	0.2882	1.47E-06
MAMMAL	1100	2	0.7407	0	0.2667	0.0001
MAMMAL	1200	2	0.3467	0.0002	0.3898	2.63E-05
MAMMAL	1300	2	0.1111	0.996	0.1442	0.986
MAMMAL	0	3	0.934	0	0.7856	0
MAMMAL	100	3	0.8827	0	0.6827	0
MAMMAL	200	3	0.8689	0	0.6279	0
MAMMAL	300	3	0.9002	0	0.6794	0
MAMMAL	400	3	0.8867	0	0.6623	0
MAMMAL	500	3	0.8209	0	0.573	0
MAMMAL	600	3	0.7887	0	0.4238	0
MAMMAL	700	3	0.7658	0	0.3651	0
MAMMAL	800	3	0.6544	0	0.2743	1.44E-15
MAMMAL	900	3	0.5938	0	0.2719	1.07E-10
MAMMAL	1000	3	0.6176	0	0.2706	7.86E-06
MAMMAL	1100	3	0.6222	0	0.2815	4.53E-05
MAMMAL	1200	3	0.28	0.006	0.392	2.31E-05
MAMMAL	1300	3	0.1852	0.743	0.1875	0.999
MAMMAL	0	4	0.8876	0	0.7346	0
MAMMAL	100	4	0.8387	0	0.588	0
MAMMAL	200	4	0.833	0	0.5476	0
MAMMAL	300	4	0.852	0	0.5964	0
MAMMAL	400	4	0.866	0	0.5556	0
MAMMAL	500	4	0.777	0	0.4626	0
MAMMAL	600	4	0.7311	0	0.3457	0
MAMMAL	700	4	0.6947	0	0.2892	0
MAMMAL	800	4	0.5659	0	0.2203	3.48E-10
MAMMAL	900	4	0.5344	0	0.2844	1.15E-11
MAMMAL	1000	4	0.5588	0	0.2647	1.34E-05
MAMMAL	1100	4	0.5556	0	0.3259	1.18E-06
MAMMAL	1200	4	0.2533	0.016	0.4623	2.72E-07
MAMMAL	1300	4	0.1852	0.743	0.2727	0.995
MAMMAL	0	5	0.8231	0	0.6072	0

MAMMAL	100	5	0.772	0	0.4573	0
MAMMAL	200	5	0.7738	0	0.4218	0
MAMMAL	300	5	0.8251	0	0.4832	0
MAMMAL	400	5	0.8192	0	0.4434	0
MAMMAL	500	5	0.72	0	0.4211	0
MAMMAL	600	5	0.7119	0	0.3329	0
MAMMAL	700	5	0.6624	0	0.2779	0
MAMMAL	800	5	0.5032	0	0.2462	1.29E-12
MAMMAL	900	5	0.5	0	0.2969	1.13E-12
MAMMAL	1000	5	0.5	0	0.3118	1.33E-07
MAMMAL	1100	5	0.4667	3.41E-13	0.3481	1.57E-07
MAMMAL	1200	5	0.24	0.027	0.4893	4.05E-08
MAMMAL	1300	5	0.1111	0.996	0.4444	0.766
REPTILE	0	0	0.8726	0	0.7601	0
REPTILE	100	0	0.8507	0	0.7427	0
REPTILE	200	0	0.7791	0	0.6744	0
REPTILE	300	0	0.8464	0	0.7455	0
REPTILE	400	0	0.8301	0	0.7244	0
REPTILE	500	0	0.8007	0	0.6251	0
REPTILE	600	0	0.7362	0	0.484	0
REPTILE	700	0	0.7286	0	0.4556	0
REPTILE	800	0	0.6004	0	0.3564	0
REPTILE	900	0	0.5688	0	0.3281	2.22E-15
REPTILE	1000	0	0.5412	0	0.2824	2.60E-06
REPTILE	1100	0	0.4296	3.01E-11	0.2519	0.0004
REPTILE	1200	0	0.2	0.044	0.299	0.003
REPTILE	1300	0	0.2593	0.324	0.3333	0.188
REPTILE	0	1	0.8456	0	0.7271	0
REPTILE	100	1	0.808	0	0.704	0
REPTILE	200	1	0.7526	0	0.6501	0
REPTILE	300	1	0.8184	0	0.7141	0
REPTILE	400	1	0.8094	0	0.671	0
REPTILE	500	1	0.7639	0	0.567	0
REPTILE	600	1	0.6901	0	0.4289	0
REPTILE	700	1	0.6947	0	0.3716	0

REPTILE	800	1	0.5637	0	0.3283	0
REPTILE	900	1	0.5344	0	0.3125	5.36E-14
REPTILE	1000	1	0.5118	0	0.2471	6.23E-05
REPTILE	1100	1	0.437	1.27E-11	0.2519	0.0004
REPTILE	1200	1	0.1867	0.050	0.3008	0.002
REPTILE	1300	1	0.2222	0.518	0.375	0.111
REPTILE	0	2	0.7916	0	0.6822	0
REPTILE	100	2	0.724	0	0.6213	0
REPTILE	200	2	0.703	0	0.5994	0
REPTILE	300	2	0.7747	0	0.6783	0
REPTILE	400	2	0.7778	0	0.5937	0
REPTILE	500	2	0.7343	0	0.4899	0
REPTILE	600	2	0.6517	0	0.3764	0
REPTILE	700	2	0.6349	0	0.315	0
REPTILE	800	2	0.5184	0	0.3499	0
REPTILE	900	2	0.5031	0	0.325	4.22E-15
REPTILE	1000	2	0.5	0	0.2529	3.78E-05
REPTILE	1100	2	0.3852	4.00E-09	0.2667	0.000135457
REPTILE	1200	2	0.1467	0.039529826	0.2864	0.004629614
REPTILE	1300	2	0.1852	0.743544609	0.2125	0.770434434
REPTILE	0	3	0.7181	0	0.6102	0
REPTILE	100	3	0.6413	0	0.548	0
REPTILE	200	3	0.6332	0	0.5127	0
REPTILE	300	3	0.7141	0	0.5762	0
REPTILE	400	3	0.7255	0	0.4749	0
REPTILE	500	3	0.6655	0	0.4116	0
REPTILE	600	3	0.6453	0	0.4277	0
REPTILE	700	3	0.6139	0	0.3635	0
REPTILE	800	3	0.4773	0	0.3823	0
REPTILE	900	3	0.4531	0	0.3688	0
REPTILE	1000	3	0.4706	1.11E-16	0.2765	4.55E-06
REPTILE	1100	3	0.363	3.78E-08	0.2963	1.43E-05
REPTILE	1200	3	0.2667	0.009655899	0.2747	0.007521349
REPTILE	1300	3	0.0741	0.999999462	0.1818	0.999975987
REPTILE	0	4	0.6027	0	0.4873	0

REPTILE	100	4	0.556	0	0.4107	0
REPTILE	200	4	0.5856	0	0.3879	0
REPTILE	300	4	0.6424	0	0.4372	0
REPTILE	400	4	0.6634	0	0.3627	0
REPTILE	500	4	0.5991	0	0.3594	0
REPTILE	600	4	0.6146	0	0.452	0
REPTILE	700	4	0.5687	0	0.3942	0
REPTILE	800	4	0.4557	0	0.4341	0
REPTILE	900	4	0.3875	0	0.4156	0
REPTILE	1000	4	0.4118	6.07E-13	0.2882	1.47E-06
REPTILE	1100	4	0.2889	2.56E-05	0.3407	3.12E-07
REPTILE	1200	4	0.3067	0.001729045	0.3302	0.000626643
REPTILE	1300	4	0.1111	0.996255192	0.3333	0.963945244
REPTILE	0	5	0.5232	0	0.3538	0
REPTILE	100	5	0.5053	0	0.3573	0
REPTILE	200	5	0.5106	0	0.3636	0
REPTILE	300	5	0.583	0	0.37	0
REPTILE	400	5	0.5882	0	0.3965	0
REPTILE	500	5	0.5694	0	0.4009	0
REPTILE	600	5	0.5903	0	0.4456	0
REPTILE	700	5	0.5606	0	0.3877	0
REPTILE	800	5	0.4212	0	0.432	0
REPTILE	900	5	0.4094	0	0.375	0
REPTILE	1000	5	0.3706	1.45E-10	0.3235	3.74E-08
REPTILE	1100	5	0.2741	7.89E-05	0.2963	1.43E-05
REPTILE	1200	5	0.28	0.00558957	0.3028	0.002261097
REPTILE	1300	5	0.0741	0.999999462	0.3333	0.979363114

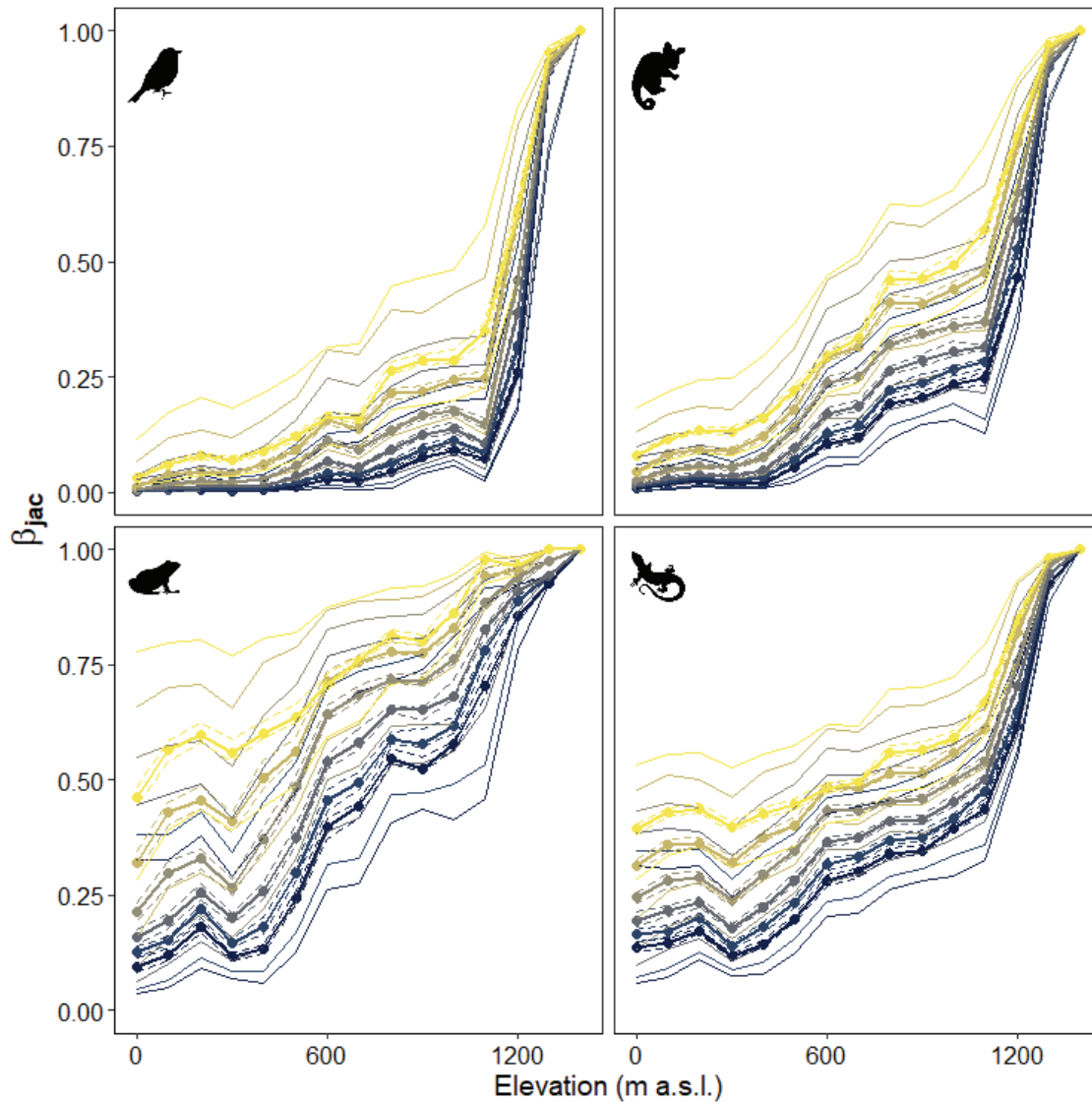


Figure S3.10. Sensitivity analyses outputs. The figure shows the different output in the overall pairwise temporal β -dissimilarity (β_{jac}) obtained with $\pm 5\%$, $\pm 10\%$ (dashed line; note that there is not change between 5 and 10% so the lines corresponding to these scenarios overlap), and $\pm 50\%$ (solid line) change in species dispersal capacity compared to the observed pattern (middle solid line connecting solid dots; based on Williams et al. 2010's potential dispersal index). Colours depict the stepwise increase in global warming from the current climate ($+0^{\circ}\text{C}$; dark blue) to $+5^{\circ}\text{C}$ scenario (yellow), with a $+1^{\circ}\text{C}$ step.

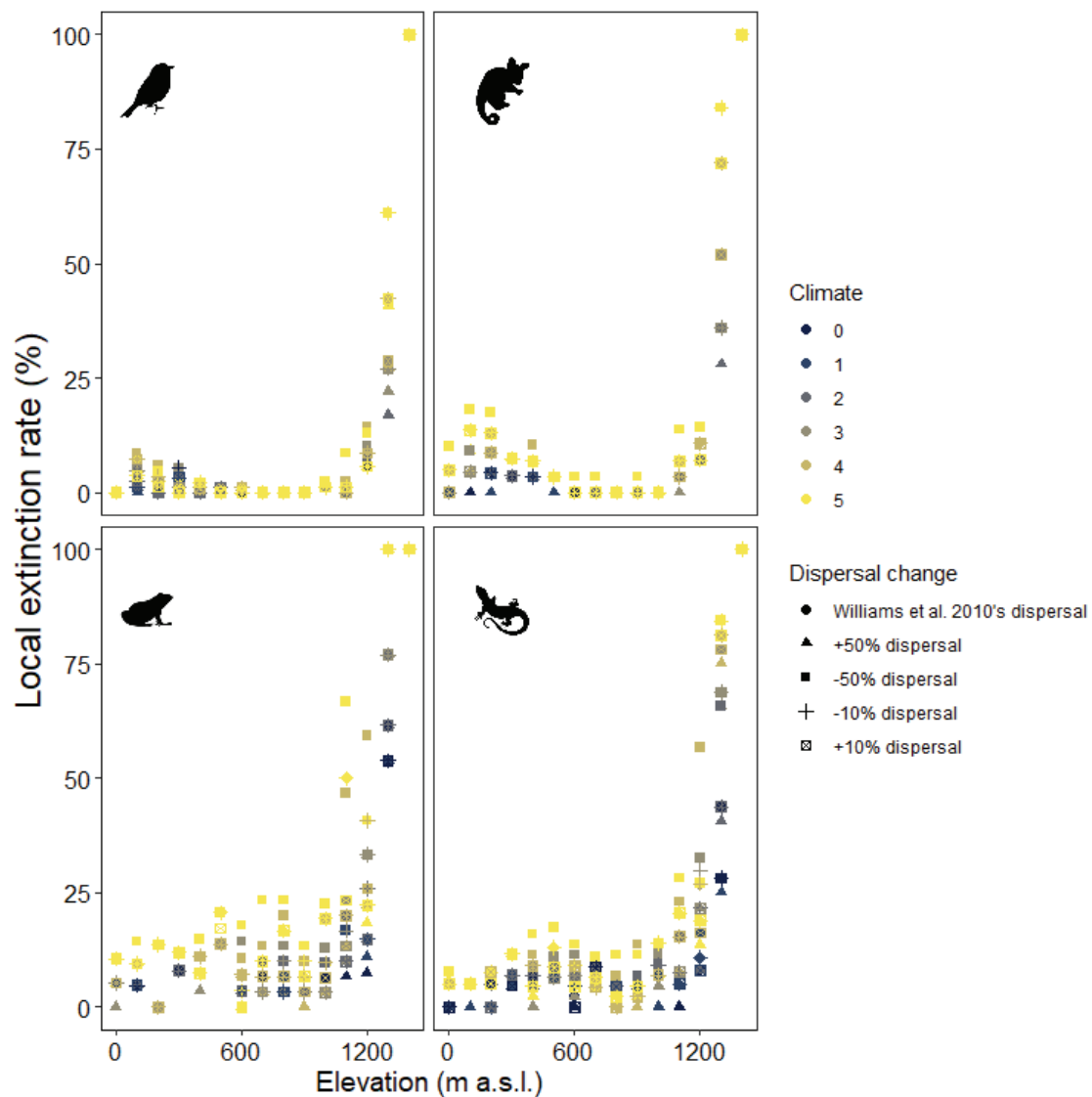


Figure S3.11. Sensitivity analyses outputs. The figure shows the different output in local extinction rate obtained with $\pm 5\%$, $\pm 10\%$ (dashed line; note that there is not change between 5 and 10% so the lines corresponding to these scenarios overlap), and $\pm 50\%$ (solid line) change in species dispersal capacity compared to the observed pattern (middle solid line connecting solid dots; based on Williams et al. 2010's potential dispersal index). Colours depict the stepwise increase in global warming from the current climate ($+0^{\circ}\text{C}$; dark blue) to $+5^{\circ}\text{C}$ scenario (yellow), with a $+1^{\circ}\text{C}$ step.

Appendix Chapter Four

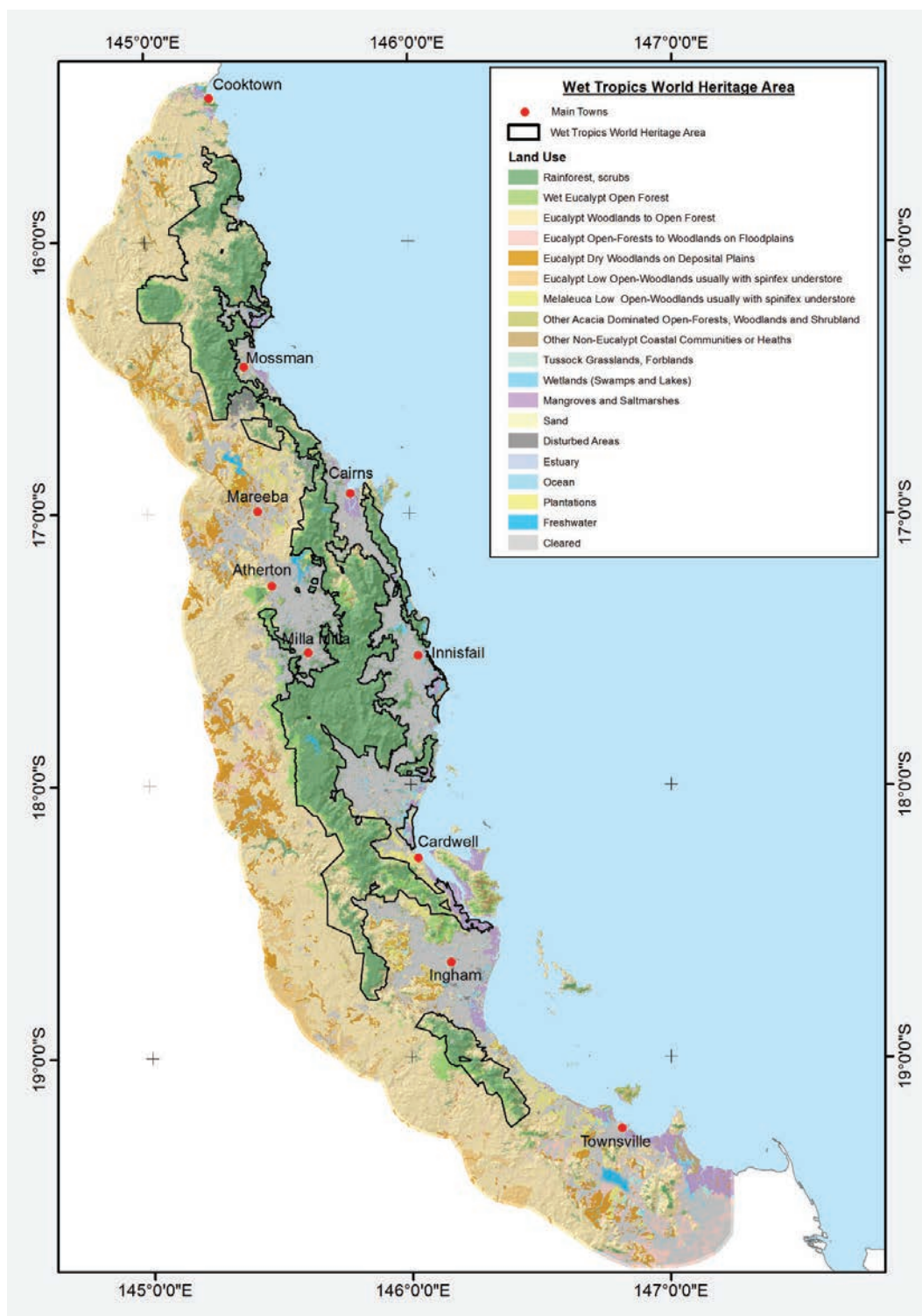


Figure S4.1. Vegetation map of the Australian Wet Tropics bioregion with the Wet Tropics World Heritage Area (Williams *et al.* 2010).

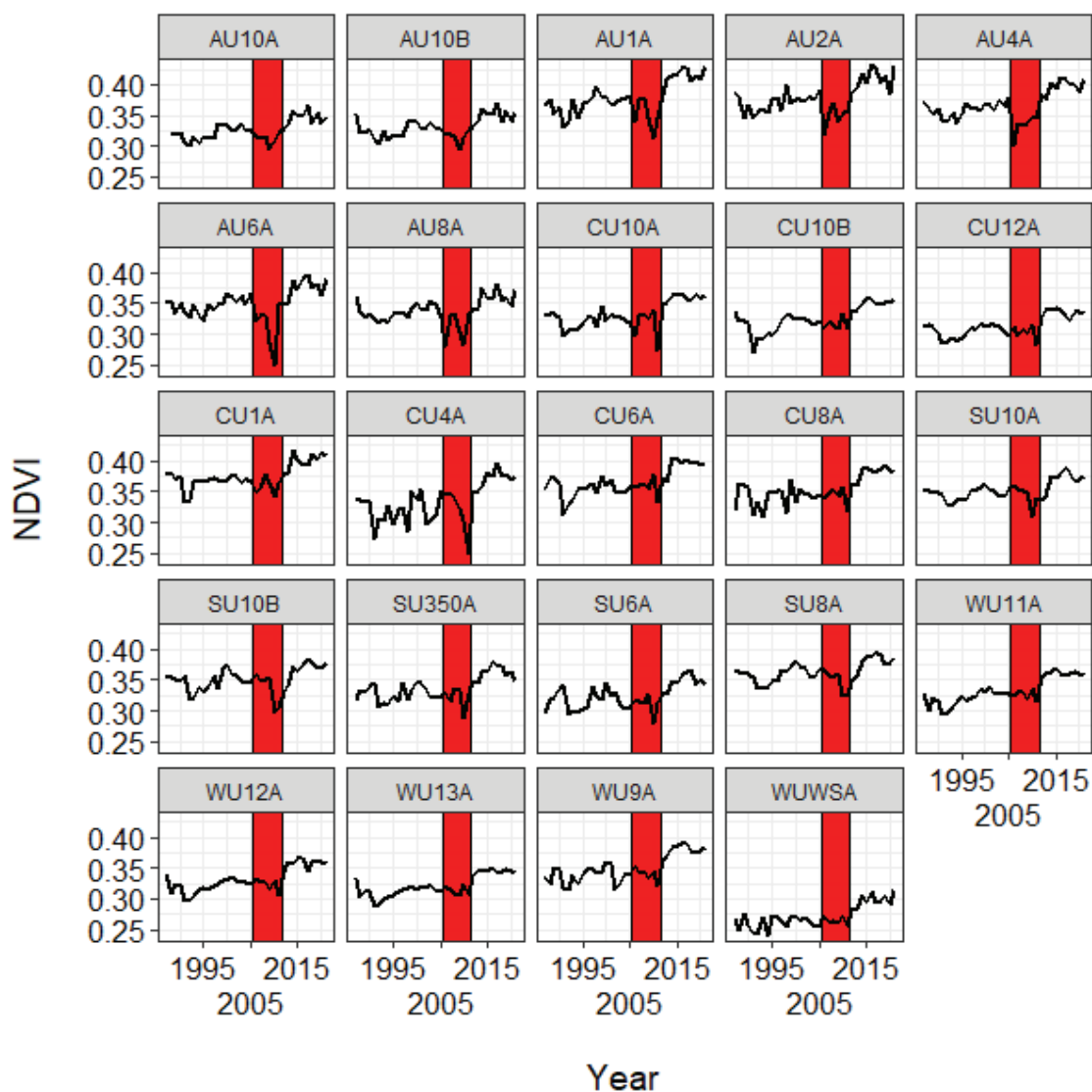


Figure S4.2. Long-term NDVI changes across the study sites within the Australian Wet Tropics. The red rectangles represent the interval between the two major cyclones that affected the region during the study period (cyclone Larry in 2006 and cyclone Yasi in 2011).

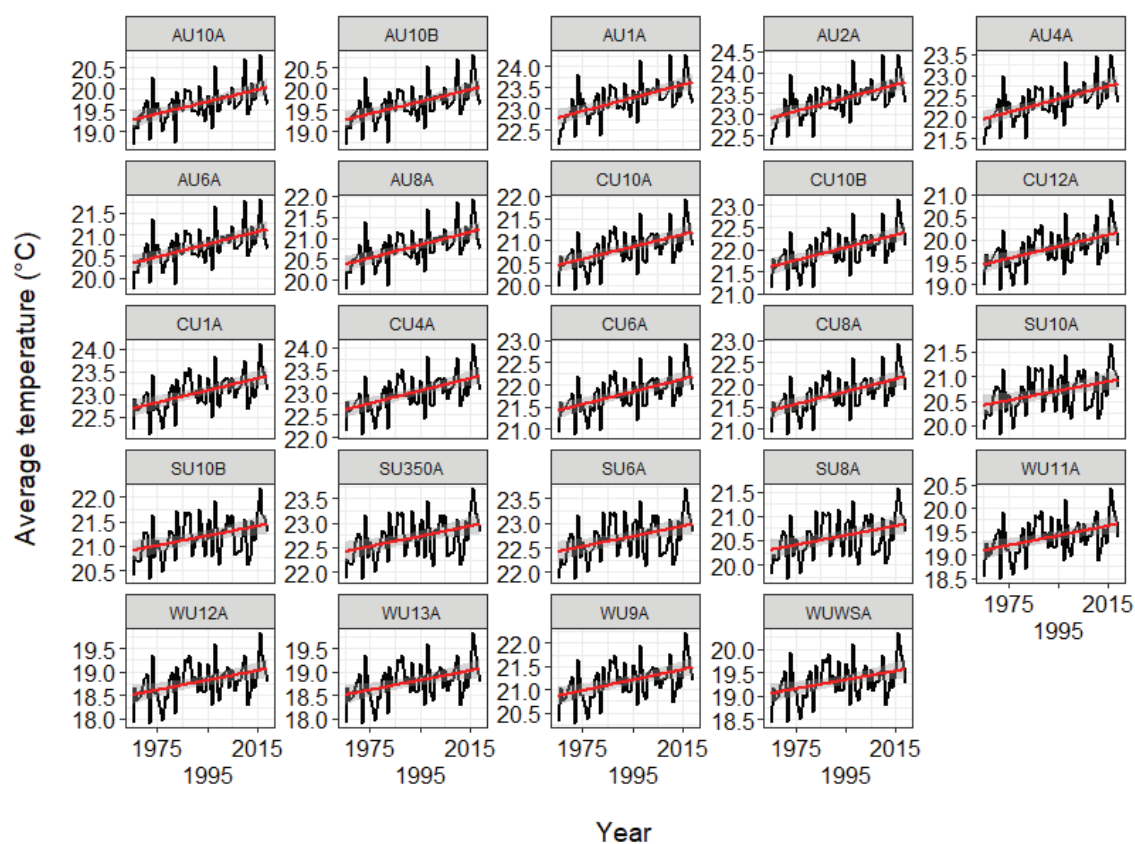


Figure S4.3. Long-term change in average temperature across the study sites within the Australian Wet Tropics. The red line represents the long-term trend.

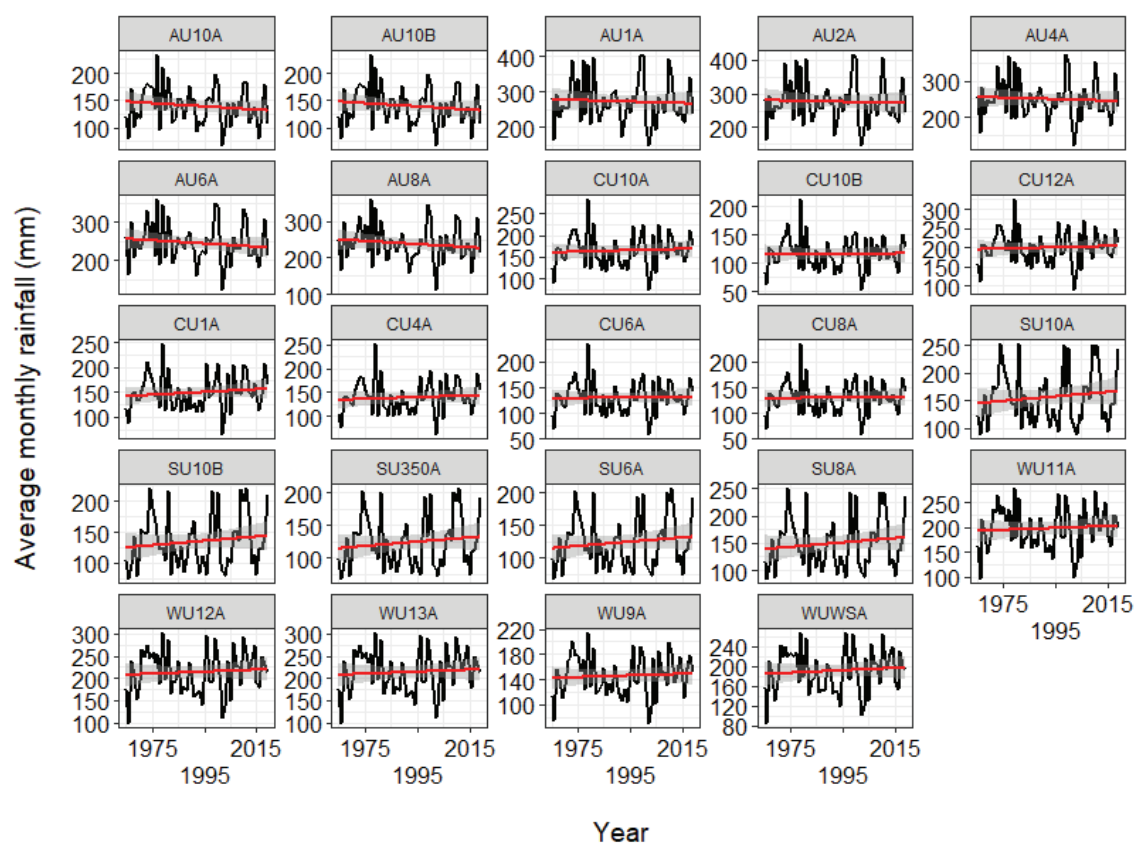


Figure S4.4. Long-term change in average rainfall across the study sites within the Australian Wet Tropics. The red line represents the long-term trend.

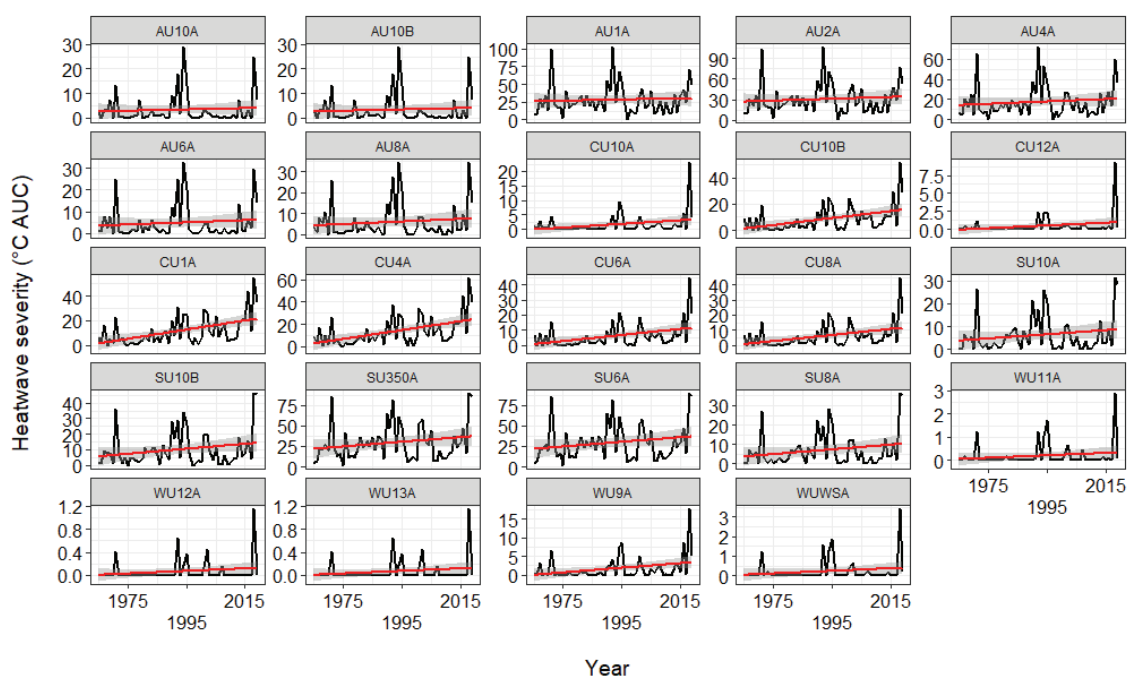


Figure S4.5. Long-term change in extreme heatwaves across the study sites within the Australian Wet Tropics. The red line represents the long-term trend.

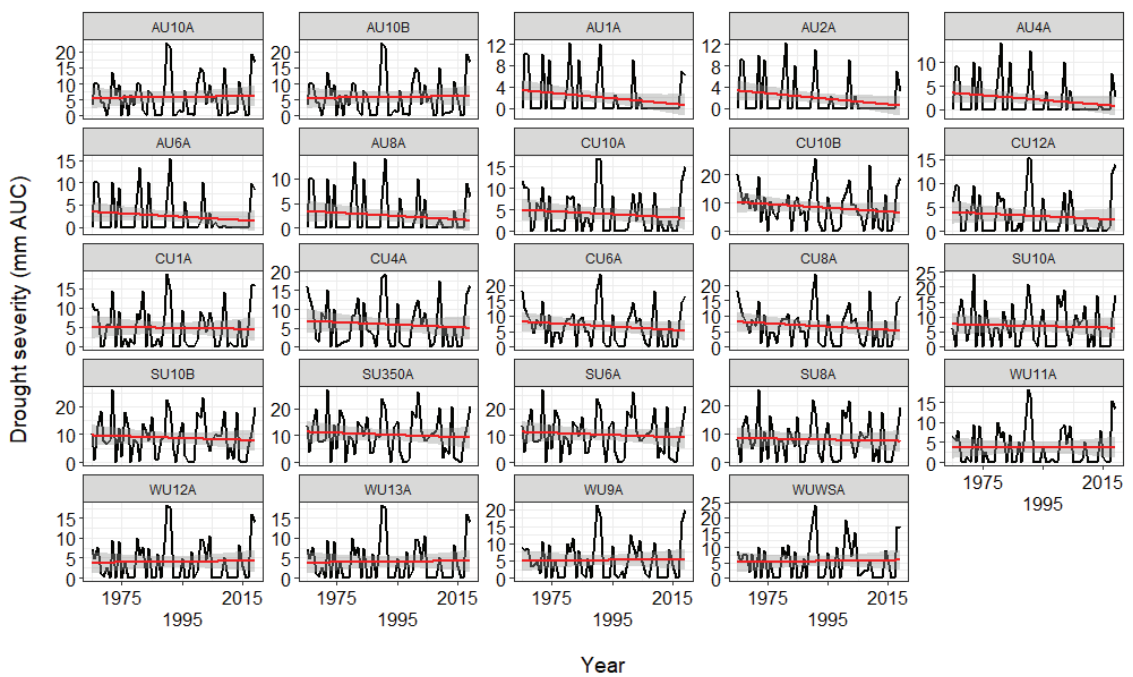


Figure S4.6. Long-term change in extreme droughts across the study sites within the Australian Wet Tropics. The red line represents the long-term trend.

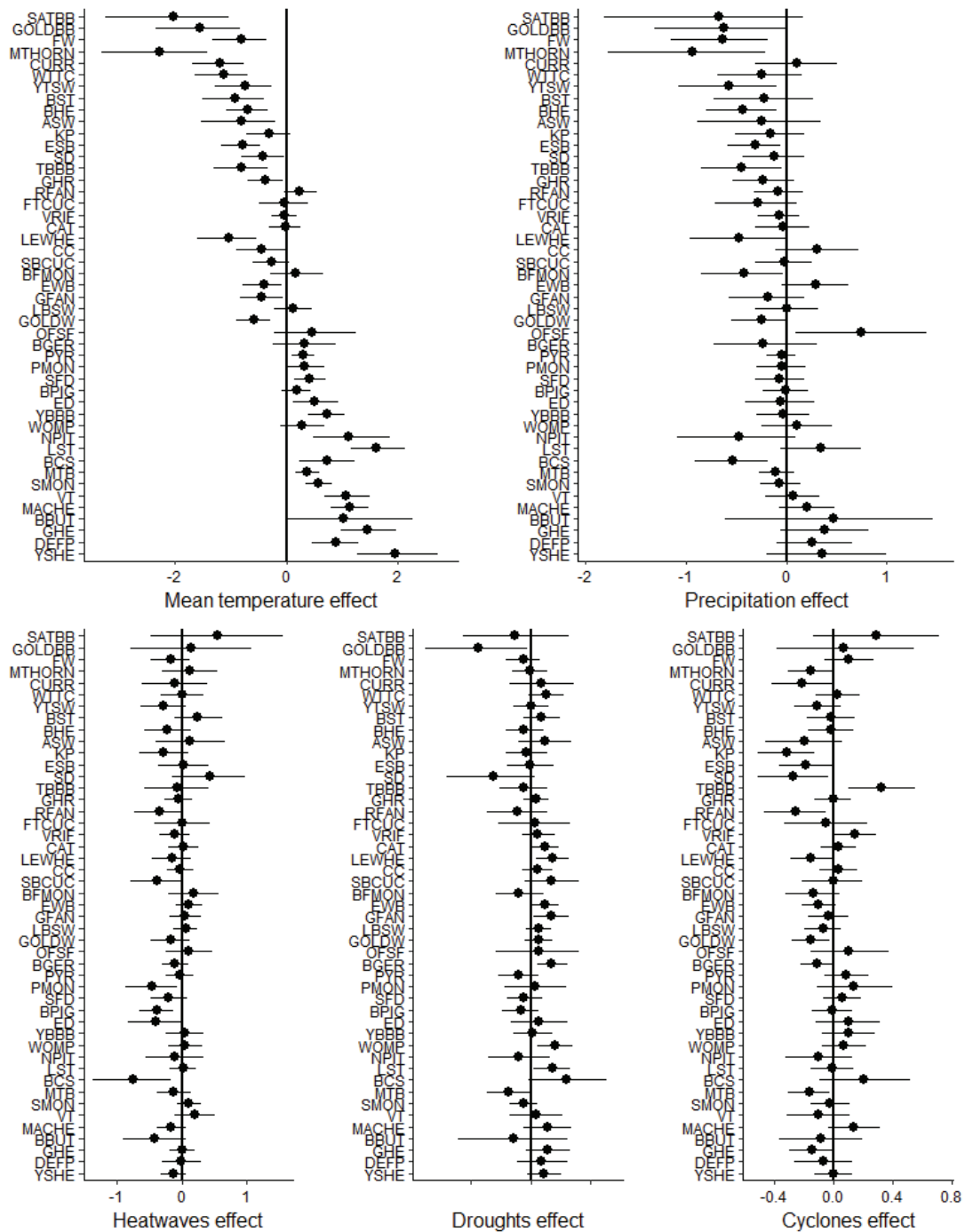


Figure S4.7. Species-specific response to climate change. Values represent the posterior mean and 95% CRI. A reference to the species code can be found in Table S4.2. Species' codes are ordered by their core elevation, with elevation increasing from bottom to top.

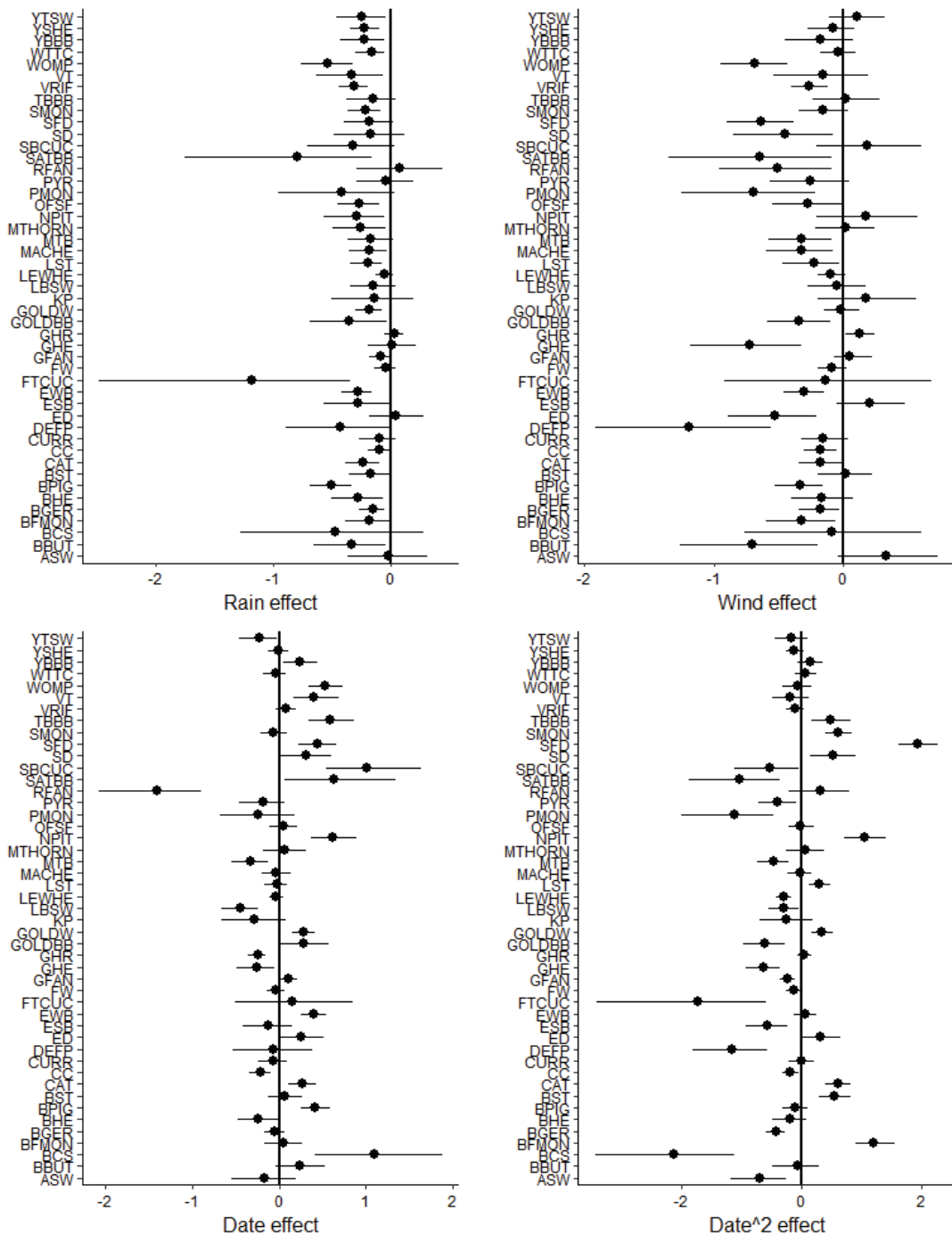


Figure S4.8. Species-specific effect of weather and season (linear - “Date”- and quadratic - “Date^2”- effect) on detection probability. Values represent the posterior mean and 95% CRI. A reference to the species code (y axis) can be found in table S2.

Table S4.1. Site location within the main mountain ranges included in the study (subregions) and across the elevational range.

Site ID	Subregion	Elevation (m a.s.l.)
AU10A	Atherton Uplands	1049
AU10B	Atherton Uplands	977
AU1A	Atherton Uplands	84
AU2A	Atherton Uplands	199
AU4A	Atherton Uplands	423
AU6A	Atherton Uplands	613
AU8A	Atherton Uplands	799
CU1	Carbine Uplands	152
CU4A	Carbine Uplands	432
CU6A	Carbine Uplands	595
CU8A	Carbine Uplands	766
CU10A	Carbine Uplands	969
CU10B	Carbine Uplands	988
CU12A	Spec Uplands	1168
SU350A	Spec Uplands	349
SU6A	Spec Uplands	591
SU8A	Spec Uplands	810
SU10A	Spec Uplands	978
SU10B	Spec Uplands	874
WU9A	Windsor Uplands	890
WU11A	Windsor Uplands	1074
WU12A	Windsor Uplands	1195
WU13A	Windsor Uplands	1275
WUWSA	Windsor Uplands	1138

Table S4.2. Rainforest bird species of the Australian Wet Tropics included in the study.

Family	Scientific name	Common name	Species code
Acanthizidae	<i>Sericornis keri</i>	Atherton Scrubwren	ASW
Artamidae	<i>Cracticus quoyi</i>	Black Butcherbird	BBUT

Campephagidae	<i>Coracina lineata</i>	Barred Cuckoo-Shrike	BCS
Dicruridae	<i>Monarcha melanopsis</i>	Black-faced Monarch	BFMON
Acanthizidae	<i>Gerygone mouki</i>	Brown Gerygone	BGER
Meliphagidae	<i>Lichenostomus frenatus</i>	Bridled Honeyeater	BHE
Columbidae	<i>Macropygia amboinensis</i>	Brown Cuckoo-Dove	BPIG
Pachycephalidae	<i>Colluricincla boweri</i>	Bowers Shrike-Thrush	BST
Ptilonorhynchidae	<i>Ailuroedus melanotis</i>	Spotted Catbird	CAT
Orthonychidae	<i>Orthonyx spaldingii</i>	Chowchilla	CC
Artamidae	<i>Strepera graculina</i>	Pied Currawong	CURR
Psittacidae	<i>Cyclopsitta diophthalma</i>	Double-eyed Fig-Parrot	DEFP
Columbidae	<i>Chalcophaps indica</i>	Emerald Dove	ED
Meliphagidae	<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	ESB
Eupetidae	<i>Psophodes olivaceus</i>	Eastern Whipbird	EWB
Cuculidae	<i>Cacomantis flabelliformis</i>	Fan-tailed Cuckoo	FTCUC
Acanthizidae	<i>Oreoscopus gutturalis</i>	Fernwren	FW
Dicruridae	<i>Rhipidura fuliginosa</i>	Grey Fantail	GFAN
Meliphagidae	<i>Meliphaga gracilis</i>	Graceful Honeyeater	GHE
Petroicidae	<i>Heteromyias albispecularis</i>	Grey-headed Robin	GHR
Ptilonorhynchidae	<i>Prionodura newtoniana</i>	Golden Bowerbird	GOLDBB
Pachycephalidae	<i>Pachycephala pectoralis</i>	Golden Whistler	GOLDW
Psittacidae	<i>Alisterus scapularis</i>	Australian King Parrot	KP
Acanthizidae	<i>Sericornis magnirostris</i>	Large-billed Scrubwren	LBSW
Meliphagidae	<i>Meliphaga lewinii</i>	Lewin's Honeyeater	LEWHE
Pachycephalidae	<i>Colluricincla megarhyncha</i>	Little Shrike-Thrush	LST
Meliphagidae	<i>Xanthotis macleayana</i>	Macleay's Honeyeater	MACHE
Dicaeidae	<i>Dicaeum hirundinaceum</i>	Mistletoebird	MTB
Acanthizidae	<i>Acanthiza katherina</i>	Mountain Thornbill	MTHORN
Pittidae	<i>Pitta versicolor</i>	Noisy Pitta	NPIT
Megapodiidae	<i>Megapodius reinwardt</i>	Orange-footed Scrubfowl	OFSF
Dicruridae	<i>Arses kaupi</i>	Pied Monarch	PMON
Petroicidae	<i>Tregellasia capito</i>	Pale-yellow Robin	PYR
Dicruridae	<i>Rhipidura rufifrons</i>	Rufous Fantail	RFAN
Ptilonorhynchidae	<i>Ptilonorhynchus violaceus</i>	Satin Bowerbird	SATBB
Cuculidae	<i>Chrysococcyx lucidus</i>	Shining Bronze-Cuckoo (Golden)	SBCUC
Dicruridae	<i>Dicrurus bracteatus</i>	Spangled Drongo	SD
Columbidae	<i>Ptilinopus superbus</i>	Superb Fruit-Dove	SFD
Dicruridae	<i>Monarcha trivirgatus</i>	Spectacled Monarch	SMON
Ptilonorhynchidae	<i>Scenopoeetes dentiostri</i>	Tooth-billed Bowerbird	TBBB
Paradisaeidae	<i>Ptiloris victoriae</i>	Victoria's Riflebird	VRIF
Campephagidae	<i>Lalage leucomela</i>	Varied Triller	VT
Columbidae	<i>Ptilinopus magnificus</i>	Wompoo Fruit-Dove	WOMP
Climacteridae	<i>Cormobates leucophaeus</i>	White-throated Treecreeper	W TTC
Dicruridae	<i>Machaerirhynchus flaviventer</i>	Yellow-breasted Boatbill	YBBB

Meliphagidae	<i>Meliphaga notata</i>	Yellow-spotted Honeyeater	YSHE
Acanthizidae	<i>Sericornis citreogularis</i>	Yellow-throated Scrubwren	YTSW

References

Williams, S., VanDerWal, J., Isaac, J., Shoo, L.P., Storlie, C., Fox, S., Bolitho, E.E., Moritz, C., Hoskin, C.J. & Williams, Y.M. (2010) Distributions, life-history specialization, and phylogeny of the rain forest vertebrates in the Australian Wet Tropics. *Ecology*, **91**, 2493-2493.

JAGS code

```

model {
#####
# 1. Priors #
#####
#####
#### 1.1 random effects ####
#####
#=== 1.1.1. detectability
for(t in 1:nyears){
  p0[t] ~ dunif(0,1)
  alpha0[t] <- log(p0[t]/(1-p0[t])) # intercept detection
}
#=== 1.1.2. site random effect
for(i in 1:nsites){
  eps[i] ~ dnorm(0, tau.site) # overdispersion
}
#####
#### 1.2. hyperparameters ####
#####
#=== 1.2.1. detectability hyperpriors
tau.lp <- 1 / (sigma.p * sigma.p)
sigma.p ~ dunif(0, 100)
#=== 1.2.2. site random effect
tau.site <- 1 / (sigma.site * sigma.site)
sigma.site ~ dunif(0, 100)
#####
#### 1.3. slopes priors ####
#####
#=== 1.3.1. abundance covs
beta0 ~ dunif(0,1)
beta.tmean ~ dunif(-5,5)

```



```

beta.rainfall ~ dunif(-5,5)
beta.seasonality ~ dunif(-5,5)
beta.hot ~ dunif(-5,5)
beta.cyclone ~ dunif(-5,5)

#=== 1.3.2. detectability covs
alpha.wind ~ dunif(-5,5)           # Wind effect on detectability
alpha.rain ~ dunif(-5,5)           # Rain effect on detectability
alpha.date ~ dunif(-5,5)           # date effect on detectability
alpha.date2 ~ dunif(-5,5)          # date quadratic
#####

# 2. Likelihood #
#####
#####

#=== 2.1. Ecological model for true abundance #
#####

for (i in 1:nsites){
  for(t in 1:nyears){
    N[i,t] ~ dpois(lambda[i,t])
    log(lambda[i,t]) <- beta0 +      # intercept
      beta.tmean * tmean[i,t] +     # spatio-temporal tmean
      beta.rainfall * rainfall[i,t] + # spatio-temporal rainfall
      beta.seasonality * seasonality[i,t] + # spatio-temporal drought
      beta.hot * hot35[i,t] +        # spatio-temporal extreme temperature
      beta.cyclone * cyclone[i,t] +  # dynamic NDVI
      eps[i]

#####

#=== 2.2. Observation model for replicated counts #
#####

for (j in 1:nreps){
  C[i,j,t] ~ dbin(p[i,j,t], N[i,t])
  p[i,j,t] <- exp(lp[i,j,t])/(1+exp(lp[i,j,t]))
  lp[i,j,t] ~ dnorm(mu.lp[i,j,t], tau.lp)
  mu.lp[i,j,t] <- alpha0[t] + alpha.wind * wind[i,j,t] + # wind effect on detection
    alpha.rain * rain[i,j,t] + # rain effect on detection
    alpha.date * date[i,j,t] + # date effect on detection
    alpha.date2 * pow(date[i,j,t], 2) # date quadratic
}
}
}

#####

#=== 2.3. Derived quantity #
#####

#=== 2.3.1. Total abundance across all surveyed sites
for (t in 1:nyears){
  totalN[t] <- sum(N[,t])

```

```

}
#####
# 3. Bayesian p-value #
#####
for(t in 1:nyears){
  for(i in 1:nsites){
    for(j in 1:nreps){
      #=== 3.1 Actual data
      eval[i,j,t] <- N[i,t]*p[i,j,t] # Expected value
      sd.resi[i,j,t]<-sqrt(eval[i,j,t]*(1-p[i,j,t])) +0.5
      E[i,j,t]<-(C[i,j,t]-eval[i,j,t])/ sd.resi[i,j,t]
      E2[i,j,t] <- pow(E[i,j,t],2)
      #=== 3.2. Replicate data sets
      C.new[i,j,t]~dbin(p[i,j,t],N[i,t])
      E.new[i,j,t]<-(C.new[i,j,t]-eval[i,j,t])/sd.resi[i,j,t]
      E2.new[i,j,t] <- pow(E.new[i,j,t], 2)
    }
  }
}
fit <- sum(E2[,,]) # Sum up squared resi for actual data set
fit.new <- sum(E2.new[,,]) # Sum up for replicate data sets
}

```

Appendix Chapter Five

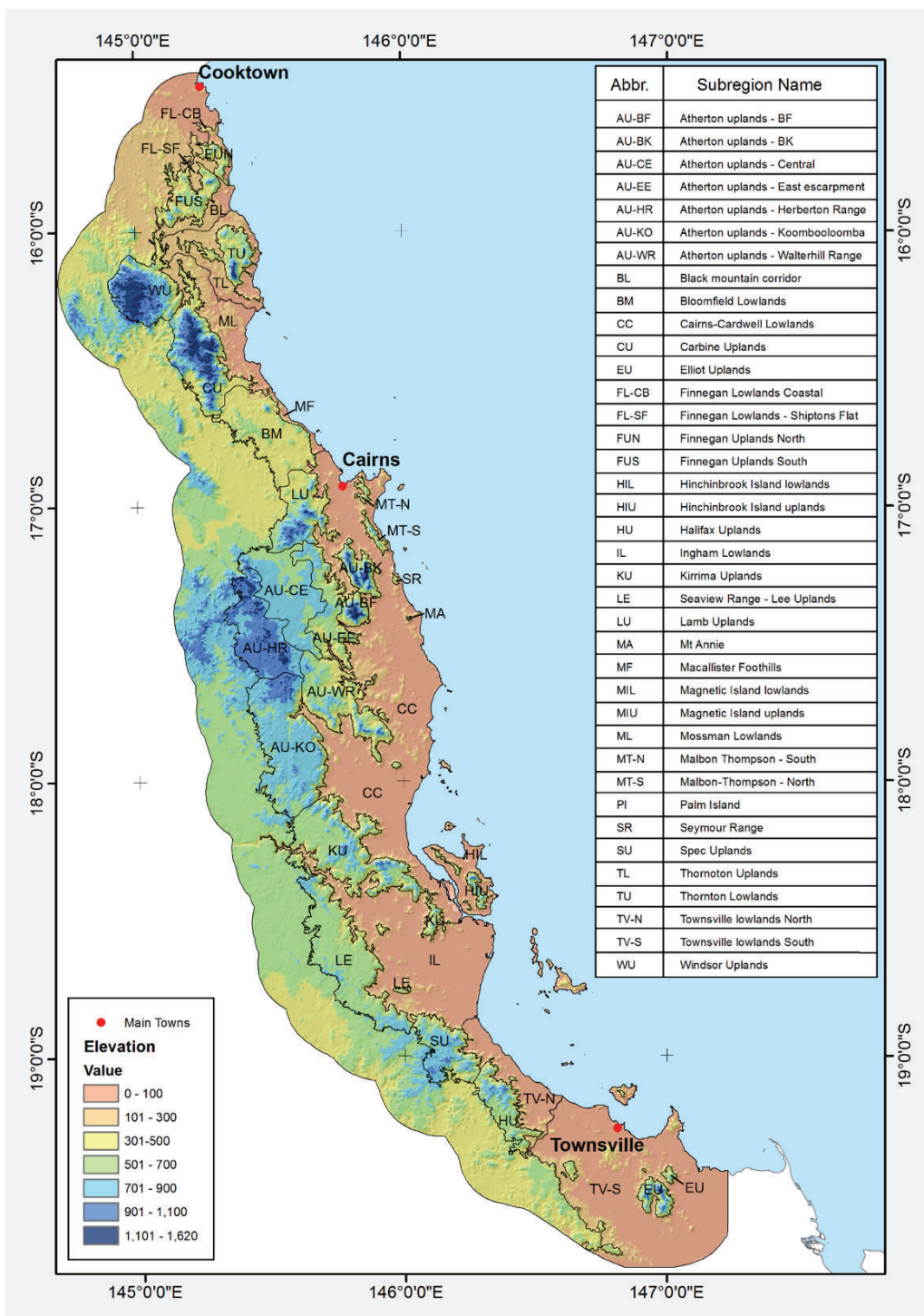


Figure S5.1. Elevation map of the Australian Wet Tropics bioregion with biogeographic subregions after Williams et al. 2010.

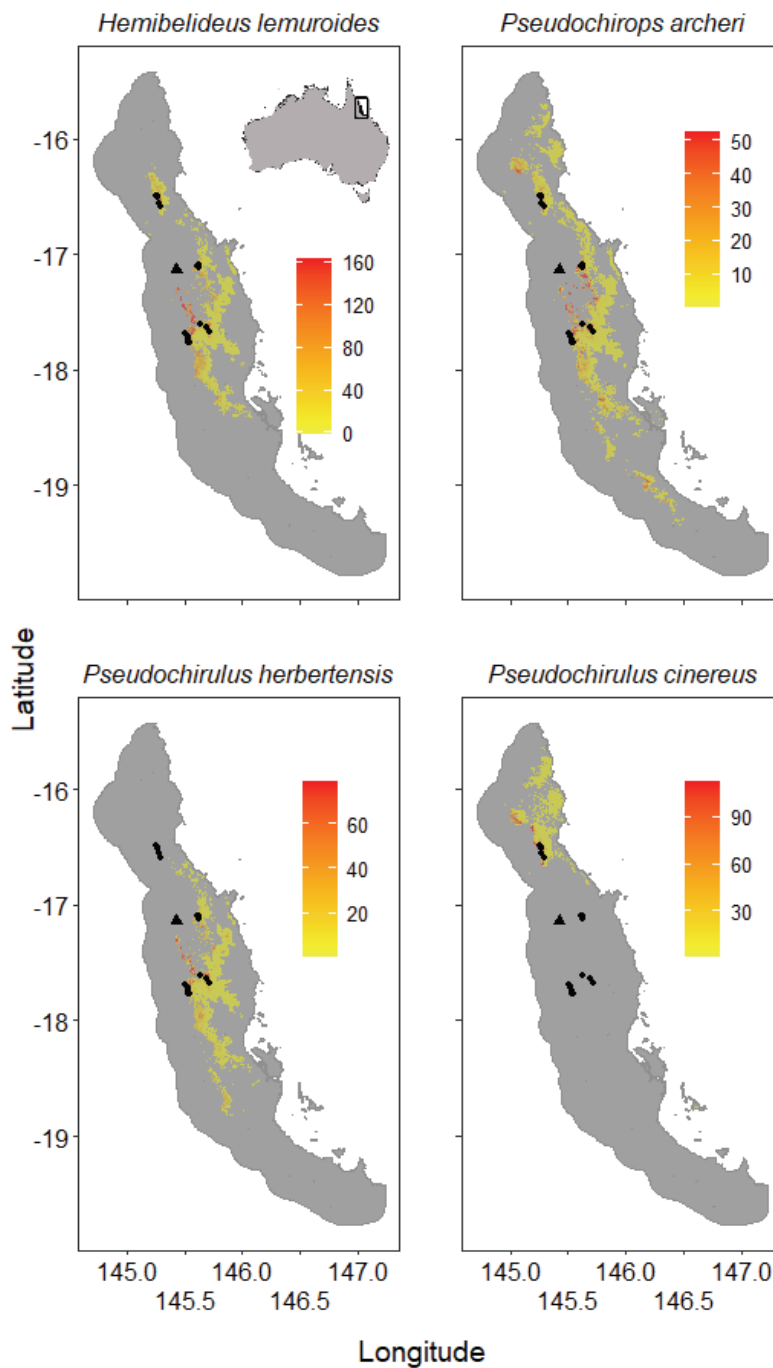


Figure S5.2. Distribution of ringtail possums in the Australian Wet Tropics obtained from 357-408 occurrence points. The colour gradient represents the predicted population size derived from environmental suitability (de la Fuente et al., 2021).

Points depict the long-term study sites included in the analysis. The triangle represents the location of Walkamin Research Station, from where the climate data was obtained.

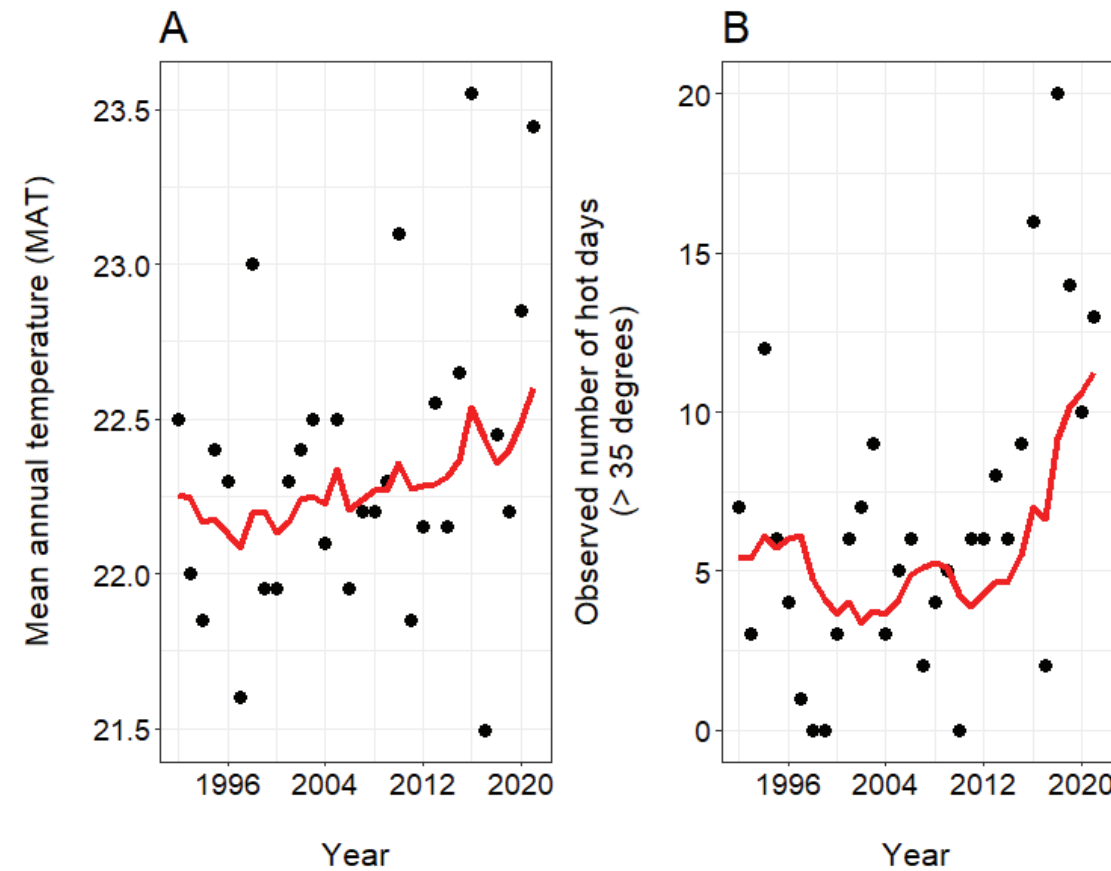


Figure S5.3. Temperature fluctuation in Walkamin Research Station (594 m a.s.l.) between 1992-2021. Panel A shows the temperature in mean annual temperature. Panel B shows the fluctuation in number of hot days per year ($>35^{\circ}\text{C}$). Points represent the observed value, and the red line depicts the 8-years moving average (between 1985-2021).

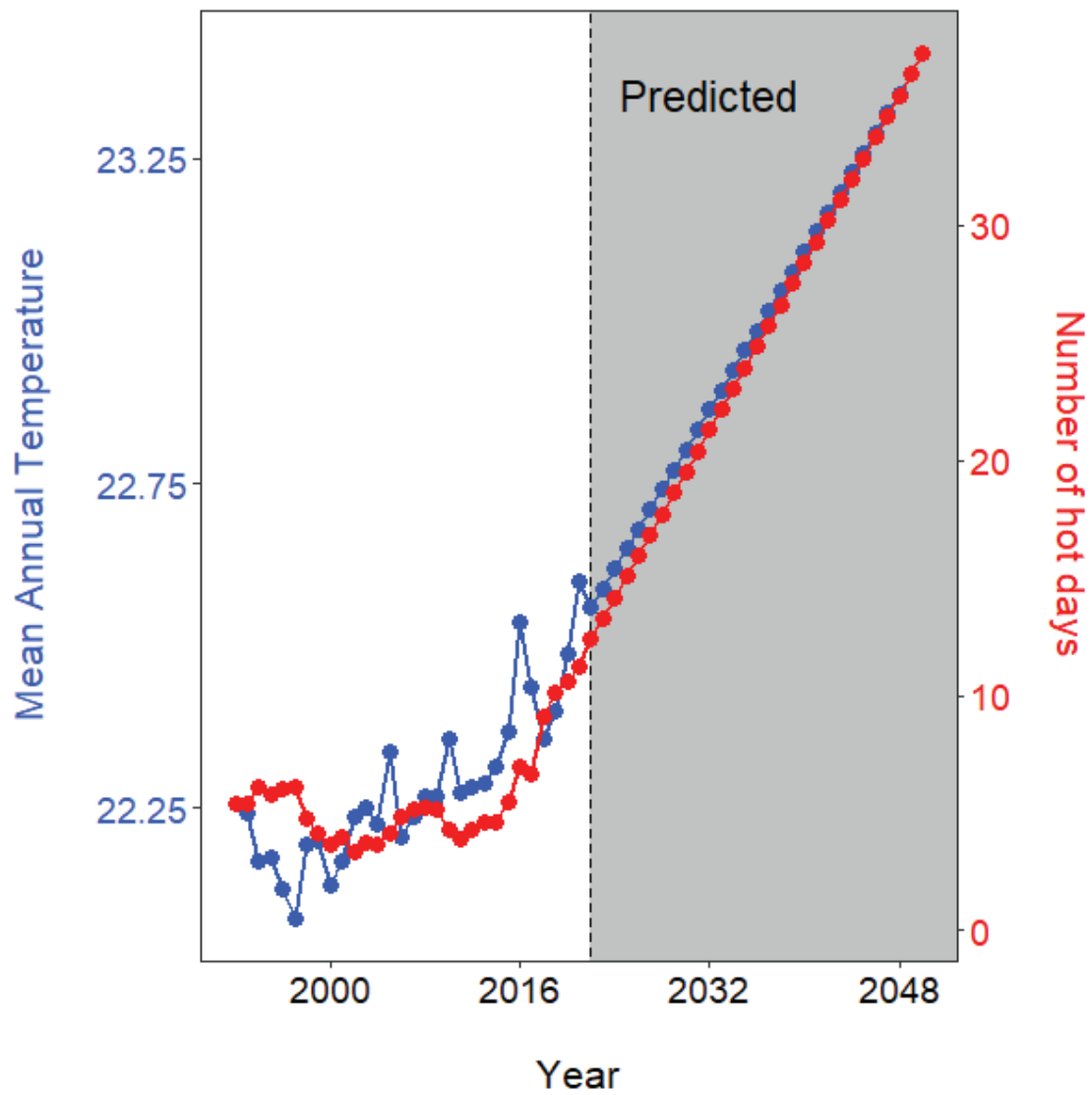


Figure S5.4. Observed and predicted temperature fluctuation in Walkamin Research Station between 1992-2050. Predicted values were obtained by fitting a general additive model to the observed temperature trajectory.

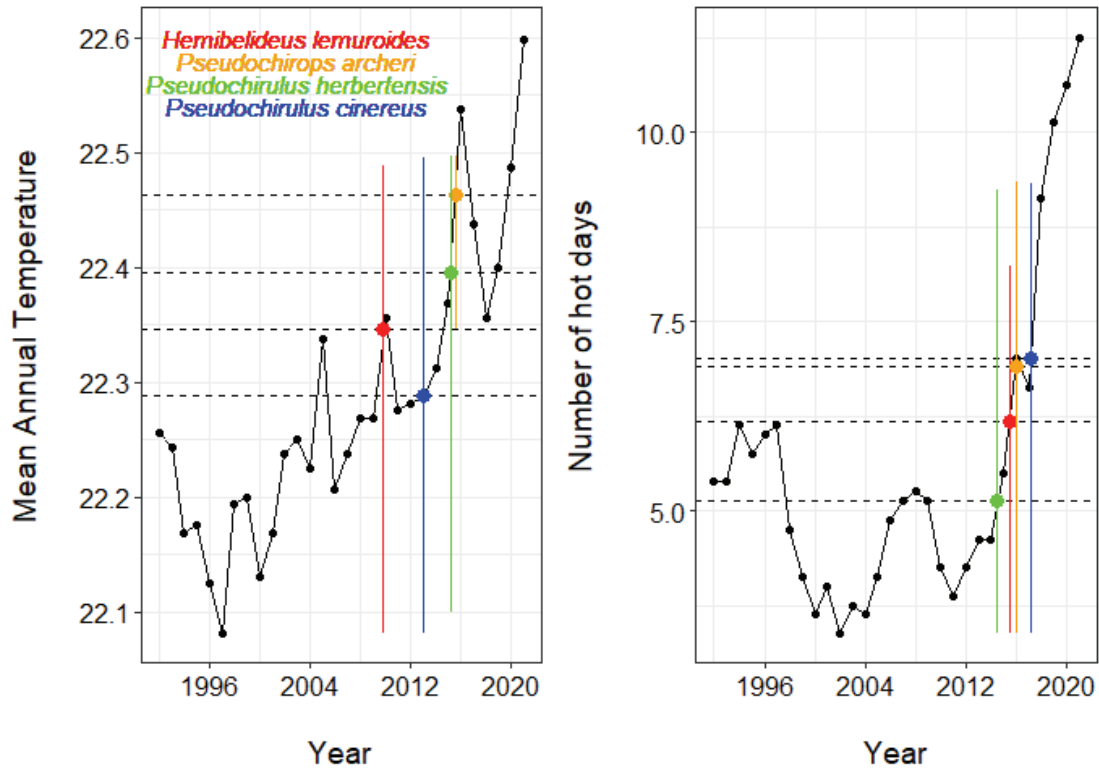


Figure S5.5. Formal examination of potential changepoints in population trend related to global warming (mean annual temperature trend; left panel), and extreme heatwaves (number of hot days; right panel). Black points depict observed climatic values. Coloured points represent the posterior mean value of the changepoint associated with each species, with the coloured vertical lines representing the 95% CRI. Horizontal dashed lines highlight the climatic value associated with the posterior mean of the changepoint.

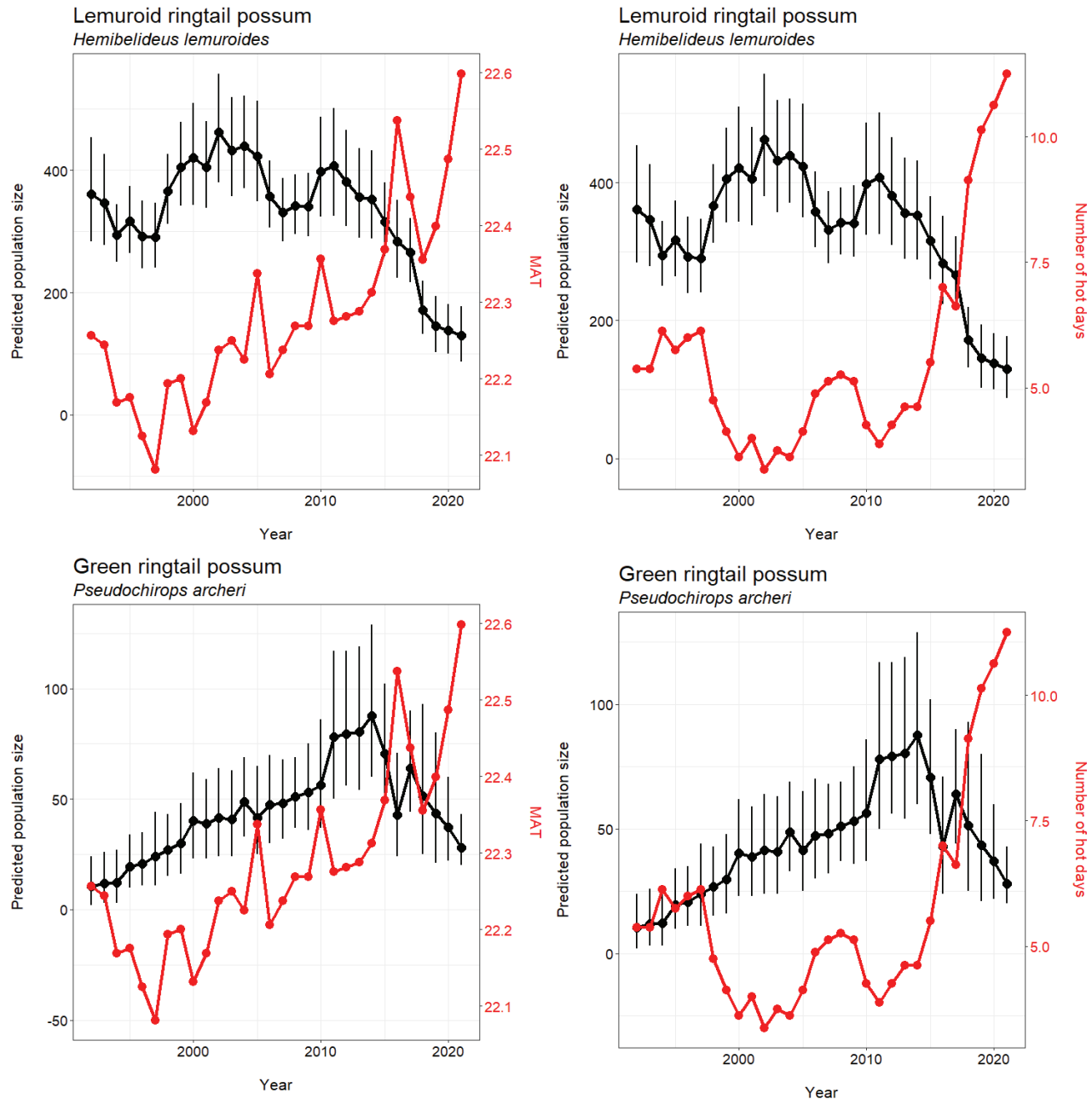


Figure S5.6. Visual examination of the synchronisation between population fluctuation and climatic trends of ringtail possums in the Australian Wet Tropics. Note that the temporal variation in climate is already accounted for in the population estimation. Thus, this figure does not explicitly represent the linear relationship between climate change and population dynamics. The linear effect of climate change on population size is reported in Figure 5.2 and Table S5.1. “MAT” stands for Mean annual temperature and the “number of hot days” is included in the model as the “extreme heatwaves” variable.

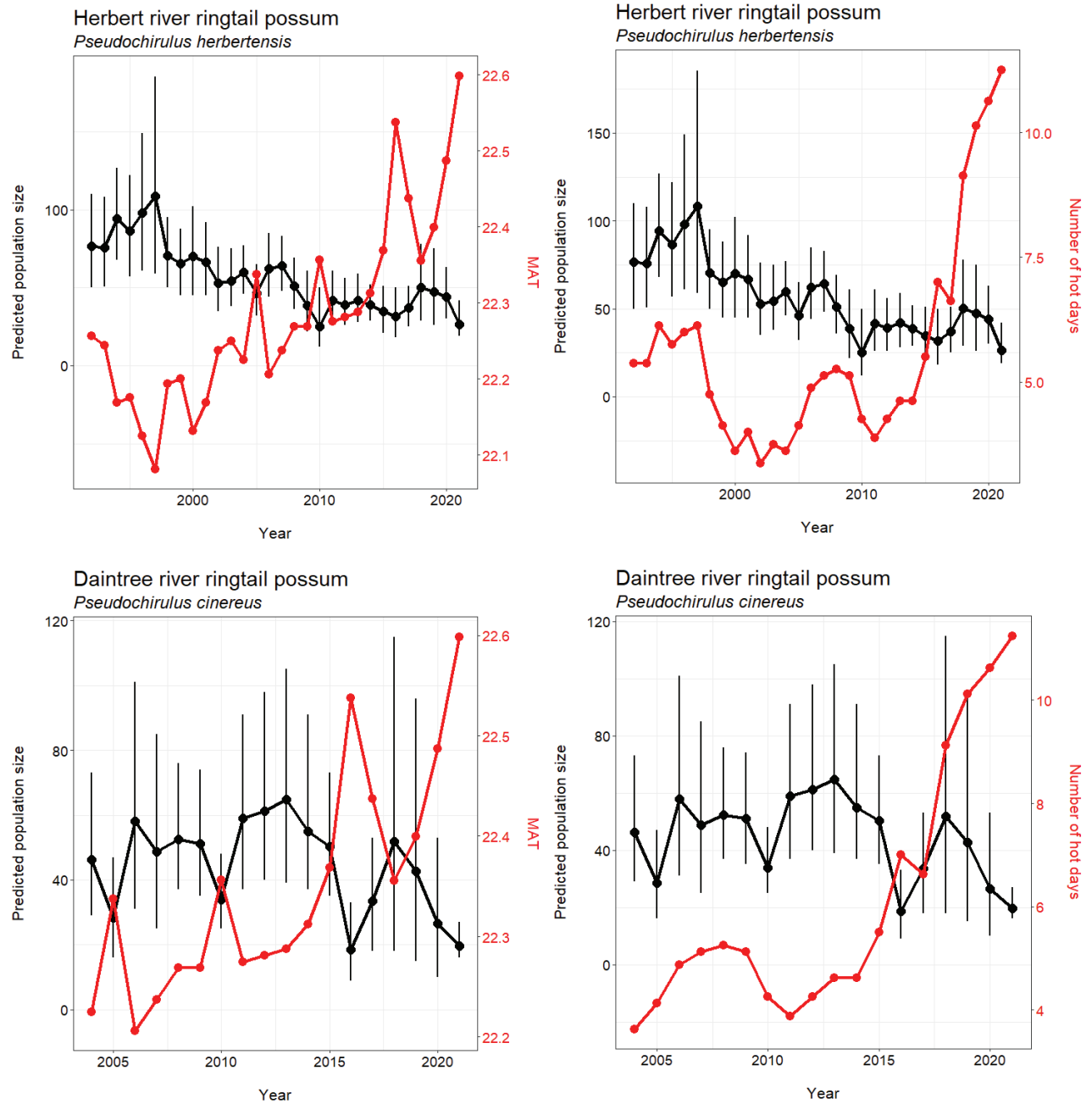


Figure S5.6. Continuation.

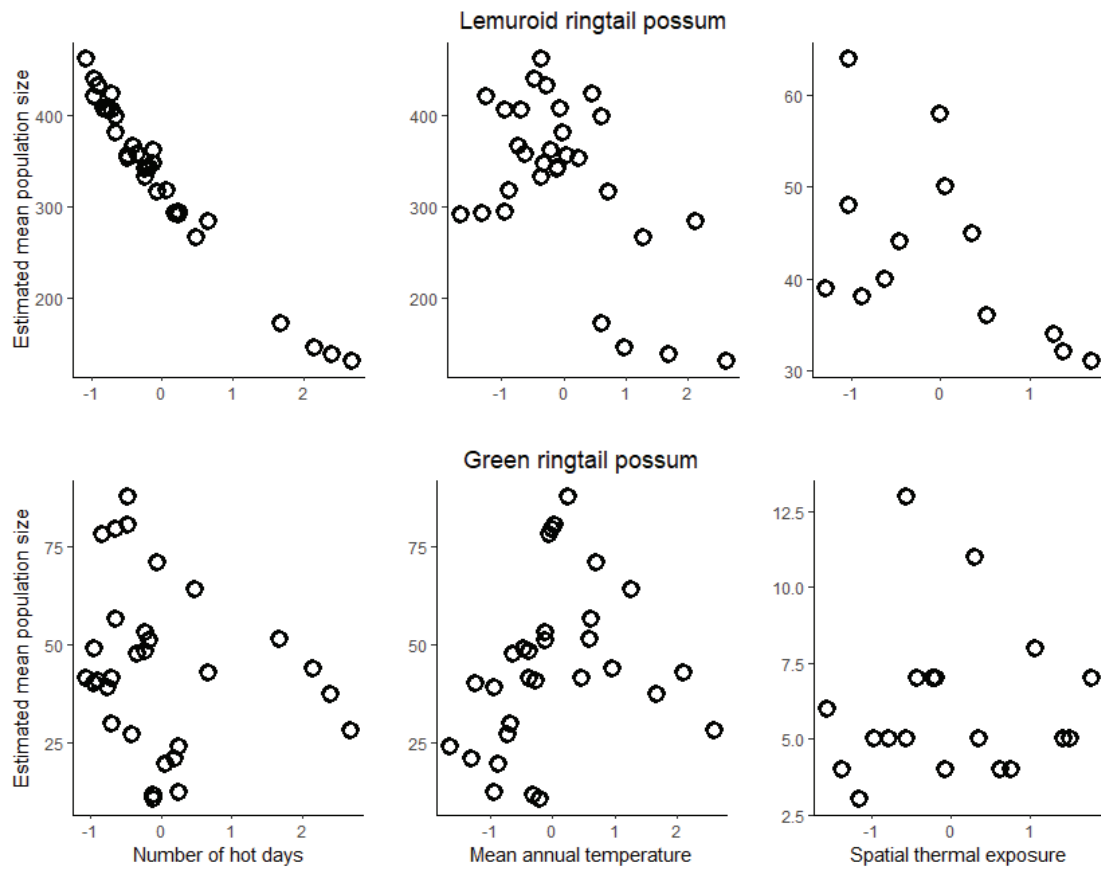


Figure S5.7. Relationship between ringtail possum population dynamics and climate change in the Australian Wet Tropics. Note that the y-axis represents the posterior mean of annual total population size. Thus, that value already accounts for the influence of climate change. The strength and uncertainty of the impact of climate change on population size is reported in Figure 5.2 and Table S5.1.

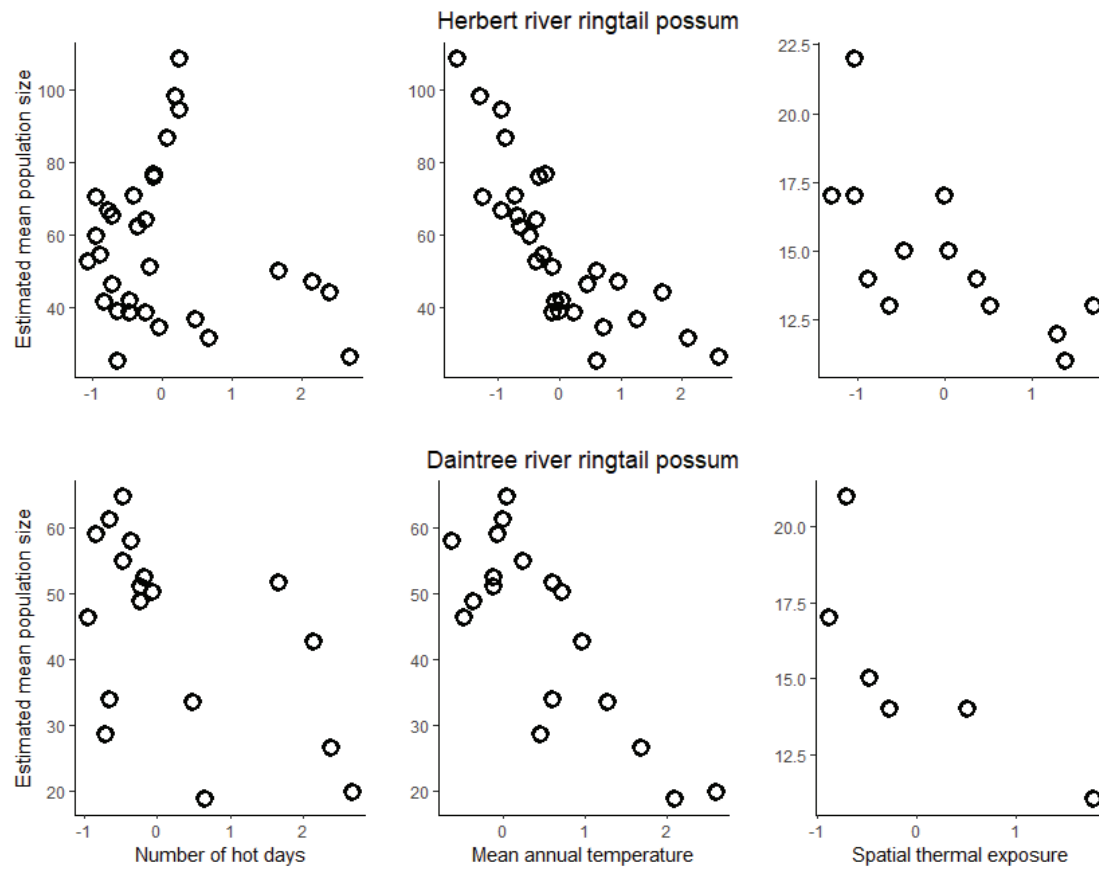


Figure S5.7. Continuation.

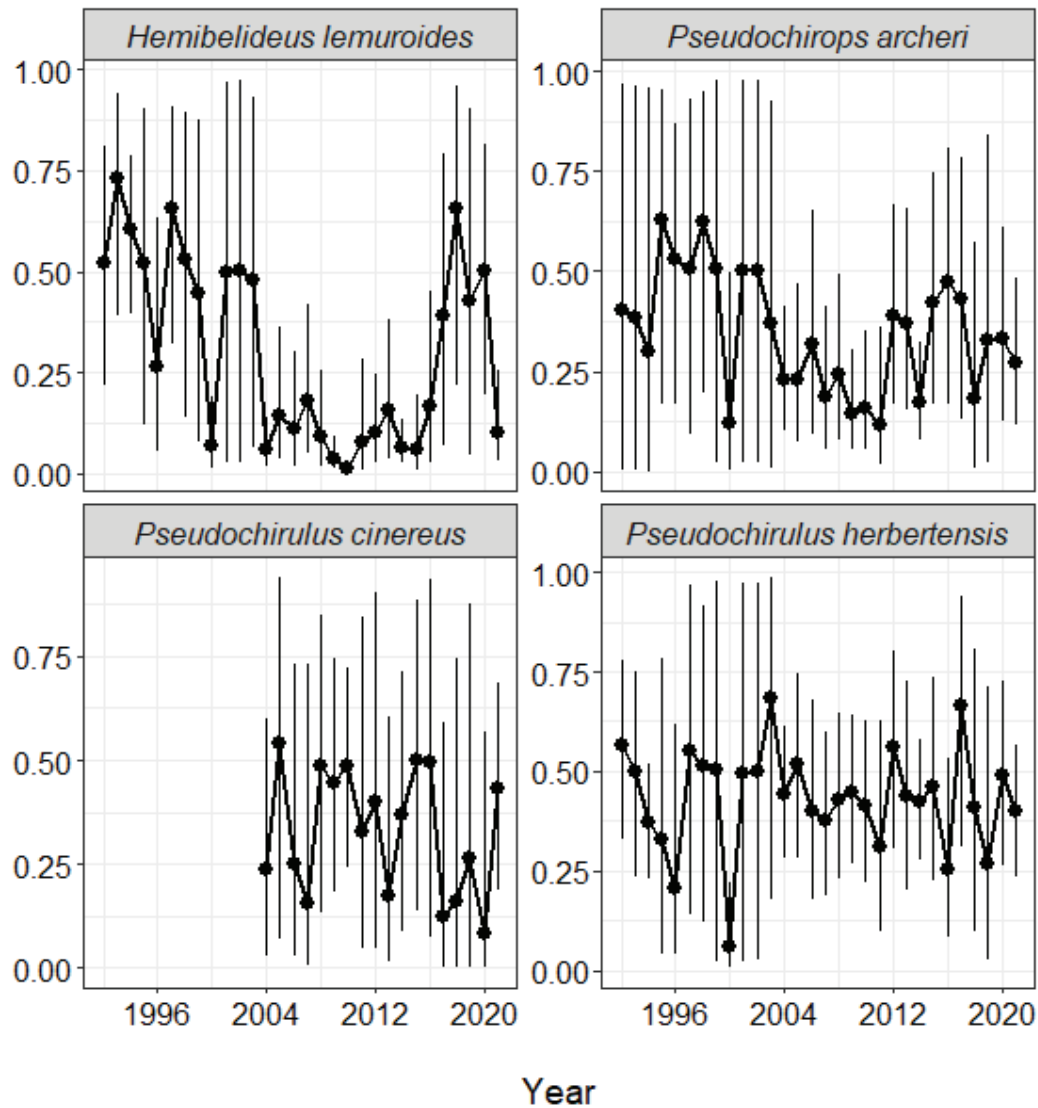


Figure S5.8. Temporal variation in detection probability of ringtail possums between 1992-2021 derived from the binomial mixture population model.

Table S5.1. Parameter estimates based on summaries of the marginal posterior distribution. We reported the mean, 95% credible interval, and the proportion of the posterior distribution that shared the same sign as the mean (f). The coefficients monitored represent the intercept for abundance (*intercept*), the effect of the trend in mean annual temperature (β_w), the effect of extreme heatwaves (β_e), the overall population trajectory after accounting for temporal climatic variables (β_g), the effect of site-specific climatic exposure on abundance (β_{ts}), the effect of Julian date on detectability (β_{date}), and overdispersion of detection (Sigma p). The temporal

fluctuation in detectability derived from the observation process can be found in Figure S5.8.

Coefficients	Posterior mean (95% CRI)							
	<i>H. lemuroides</i>	f	<i>P. archeri</i>	f	<i>P. herbertensis</i>	f	<i>P. cinereus</i>	f
Intercept	2.76 (2.66, 2.86)	1	0.685 (0.445, 0.936)	1	1.01 (0.84, 1.19)	1	1.60 (0.55, 1.90)	1
β_w	0.06 (-0.09, 0.20)	0.78	-0.25 (-0.67, 0.16)	0.88	-0.27 (-0.63, 0.09)	0.93	-0.54 (-1.06, -0.05)	0.98
β_g	-0.01 (-0.02, 0.01)	0.78	0.09 (0.04, 0.14)	1	-0.02 (-0.05, 0.004)	0.95	0.07 (-0.01, 0.16)	0.95
β_e	-0.35 (-0.48, -0.22)	1	-0.37 (-0.65, -0.09)	0.99	0.19 (-0.06, 0.43)	0.93	-0.125 (-0.65, 0.40)	0.685
β_{ts}	-0.34 (-0.46, -0.22)	1	-0.01 (-0.20, 0.17)	0.55	-0.06 (-0.20, 0.09)	0.79	-0.11 (-0.28, 0.07)	0.88
β_{date}	0.24 (-0.058, 0.53)	0.94	0.1 (-0.17, 0.37)	0.76	-0.245 (-0.53, 0.03)	0.96	0.004 (-0.51, 0.495)	0.51
Sigma p	2.85 (2.52, 3.22)	1	1.66 (1.24, 2.17)	1	1.75 (1.40, 2.17)	1	2.23 (1.64, 2.905)	1

JAGS code

```
{
# Priors
for(t in 1:nyears){
  p0[t] ~ dunif(0,1)
  alpha0[t] <- log(p0[t]/(1-p0[t]))
}
tau.lp <- 1 / (sigma.p*sigma.p)
sigma.p ~ dunif(0,10)
beta.date ~ dunif(-5,5)
beta0 ~ dunif(-5,5)
beta.tmean ~ dunif(-5,5)
beta.trend ~ dunif(-1,1)
beta.nts ~ dunif(-5,5)
beta.hot ~ dunif(-5,5)
# Likelihood
# Ecological model for true abundance
for (i in 1:nsites){
  for(t in 1:nyears){
    N[i,t] ~ dpois(lambda[i,t])
    log(lambda[i,t]) <- beta0 + beta.tmean * t.wind[t] + beta.trend * (t-15.5) + beta.hot * hot[t] + beta.nts * nts[i]
    # Observation model for replicated counts
    for (j in 1:nsurveys){
      C[i,j,t] ~ dbin(p[i,j,t], N[i,t])
      p[i,j,t] <- exp(lp[i,j,t])/(1+exp(lp[i,j,t]))
      lp[i,j,t] ~ dnorm(mu.lp[i,j,t], tau.lp)
      mu.lp[i,j,t] <- alpha0[t] + beta.date * date[i,j,t]
    } }
    # Derived quantity: Total abundance across all surveyed sites
    for (t in 1:nyears){
      totalN[t] <- sum(N[,t])
    }
    # extinction probability
    for(t in 1:nyears){
      for(d in 1:5){ # absolute and quasi extinction thresholds (50,70,80, 90, and 100% decline)
        # "D" is threshold derived from the minimum population size prior a recovery. This needs to be provided as data.
        # for Lemuroids ringtail possums D <- c(145,87,58,29,0)
        # for Green ringtail possums D <- c(5.25,2.95,2.1,1.05,0)
        # for Herbert river ringtail possums D <- c(38.27, 23,15.31,7.65,0)
        # for Daintree river ringtail possums D <- c(23.14, 13.88,9.25,4.63,0)
        quasi_extinction[d,t] <- step(D[d] - totalN[t])
      } }
    # Computation of fit statistic
    for(t in 1:nyears){
```

```

for(i in 1:nsites){
  for(j in 1:nsurveys){
    # Actual data
    eval[i,j,t] <- N[i,t]*p[i,j,t] # Expected value
    sd.resi[i,j,t] <- sqrt(eval[i,j,t]*(1-p[i,j,t])) + 0.5
    E[i,j,t] <- (C[i,j,t]-eval[i,j,t])/sd.resi[i,j,t]
    E2[i,j,t] <- pow(E[i,j,t],2)
    # Replicate data sets
    C.new[i,j,t] ~ dbin(p[i,j,t],N[i,t])
    E.new[i,j,t] <- (C.new[i,j,t]-eval[i,j,t])/sd.resi[i,j,t]
    E2.new[i,j,t] <- pow(E.new[i,j,t], 2)
  } }
fit <- sum(E2[,,])
fit.new <- sum(E2.new[,,])
}

```

Changepoint version of the model used in analysis

```

{
  # Priors
  for(t in 1:nyears){
    p0[t] ~ dunif(0,1)
    alpha0[t] <- log(p0[t]/(1-p0[t]))
  }
  tau.lp <- 1 / (sigma.p*sigma.p)
  sigma.p ~ dunif(0,10)
  beta.date ~ dunif(-5,5)
  beta0 ~ dunif(-5,5)
  for(c in 1:2){
    beta.tmean[c] ~ dunif(-5,5)
    beta.hot[c] ~ dunif(-5,5)
  }

  for(i in 1:nyears){
    C1[i] <- 1 + step(t.wind[i] - t.change)
    C2[i] <- 1 + step(hot[i] - hot.change)
  }

  beta.trend ~ dunif(-1,1)
  beta.nts ~ dunif(-5,5)
  hot.change ~ dunif(min.hot, max.hot) # maximum a minimum value of the "hot" predictor. The position of the
  changepoint should be constraint to the range of the variable
  t.change ~ dunif(min.tmean, max.tmean)
  # Likelihood
  # Ecological model for true abundance
  for (i in 1:nsites){

```

```

for(t in 1:nyears){
  N[i,t] ~ dpois(lambda[i,t])
  log(lambda[i,t]) <- beta0 + beta.tmean[C1[t]] * (t.wind[t] - t.change) +
    beta.trend * (t-15.5) +
    beta.hot[C2[t]] * (hot[t] - hot.change) +
    beta.nts * nts[i]

  # Observation model for replicated counts
  for (j in 1:nsurveys){
    C[i,j,t] ~ dbin(p[i,j,t], N[i,t])
    p[i,j,t] <- exp(lp[i,j,t])/(1+exp(lp[i,j,t]))
    lp[i,j,t] ~ dnorm(mu.lp[i,j,t], tau.lp)
    mu.lp[i,j,t] <- alpha0[t] + beta.date * date[i,j,t]
  } }

  # Derived quantity: Total abundance across all surveyed sites
  for (t in 1:nyears){
    totalN[t] <- sum(N[,t])
  }

  # extinction probability
  for(t in 1:nyears){
    for(d in 1:5){ # absolute and quasi extinction thresholds (50,70,80, 90, and 100% decline)
      quasi_extinction[d,t] <- step(D[d] - totalN[t])
    } }

  # Computation of fit statistic
  for(t in 1:nyears){
    for(i in 1:nsites){
      for(j in 1:nsurveys){
        # Actual data
        eval[i,j,t] <- N[i,t]*p[i,j,t] # Expected value
        sd.resi[i,j,t] <- sqrt(eval[i,j,t]*(1-p[i,j,t])) + 0.5
        E[i,j,t] <- (C[i,j,t]-eval[i,j,t])/ sd.resi[i,j,t]
        E2[i,j,t] <- pow(E[i,j,t],2)

        # Replicate data sets
        C.new[i,j,t] ~ dbin(p[i,j,t], N[i,t])
        E.new[i,j,t] <- (C.new[i,j,t]-eval[i,j,t])/sd.resi[i,j,t]
        E2.new[i,j,t] <- pow(E.new[i,j,t], 2)
      } }

    fit <- sum(E2[,t])
    fit.new <- sum(E2.new[,t])
  }
}

```


Appendix Chapter Six

Variable selection and model structure

We performed a pairwise correlation analysis to evaluate the degree of association among the potential predictors examined in this study (Figure S6.2). Notably, we found a high correlation between dry matter and N digestibility ($r = 0.98$) and between basalt and granite parent materials ($r = -0.77$). Since the N digestibility index already encompassed information about changes in dry matter digestibility, we proceeded with only N digestibility for constructing the hierarchical model. Similarly, because 88% of the sites were either derived from basalt or granite, basaltic geological origin already included information about granite soils (i.e., basalt = 0). Therefore, we proceeded with basalt as a predictor in subsequent models. Further, we found a high correlation between basalt and soil P ($r = 0.8$). Since both parameters inform different aspects of resource availability gradients, we initially included both predictors in the foliage and herbivory models. However, we only retained the predictor that increased predictive accuracy following the variable selection approach described below.

Our model encompassed eight interconnected sub-models: five soil models (i.e., one for each element), two foliage models (i.e., total N and N digestibility), and one herbivory model. The propagation of uncertainty followed the directionality of the relationships among the components of the system, expressed by the hierarchical structure of the model (Figure 6.2). To achieve a more parsimonious model, we employed variable selection, aiming to maximise predictive accuracy while adhering to the principles of marginality (McCullagh 2019). Variable selection was performed following the leave-one-out selection method using the “loo” package (Vehtari *et al.* 2020), an appropriate approach for variable selection in hierarchical models (Hooten & Hobbs 2015).

Following the hierarchical interconnections within our model, we initiated the variable selection process by evaluating the impact of climate and geology on soil chemistry, followed by the effect of climate, geology, and soil nutrients on foliage chemistry, and then the effect of all the above factors on herbivory pressure. This sequential approach facilitated a coherent understanding of the direct and indirect influences of all predictors across various model components while reducing the

probability of mistakenly eliminating a predictor with an important role in shaping the system. A summary variable selection table is provided in the Appendix (Table S6.1).

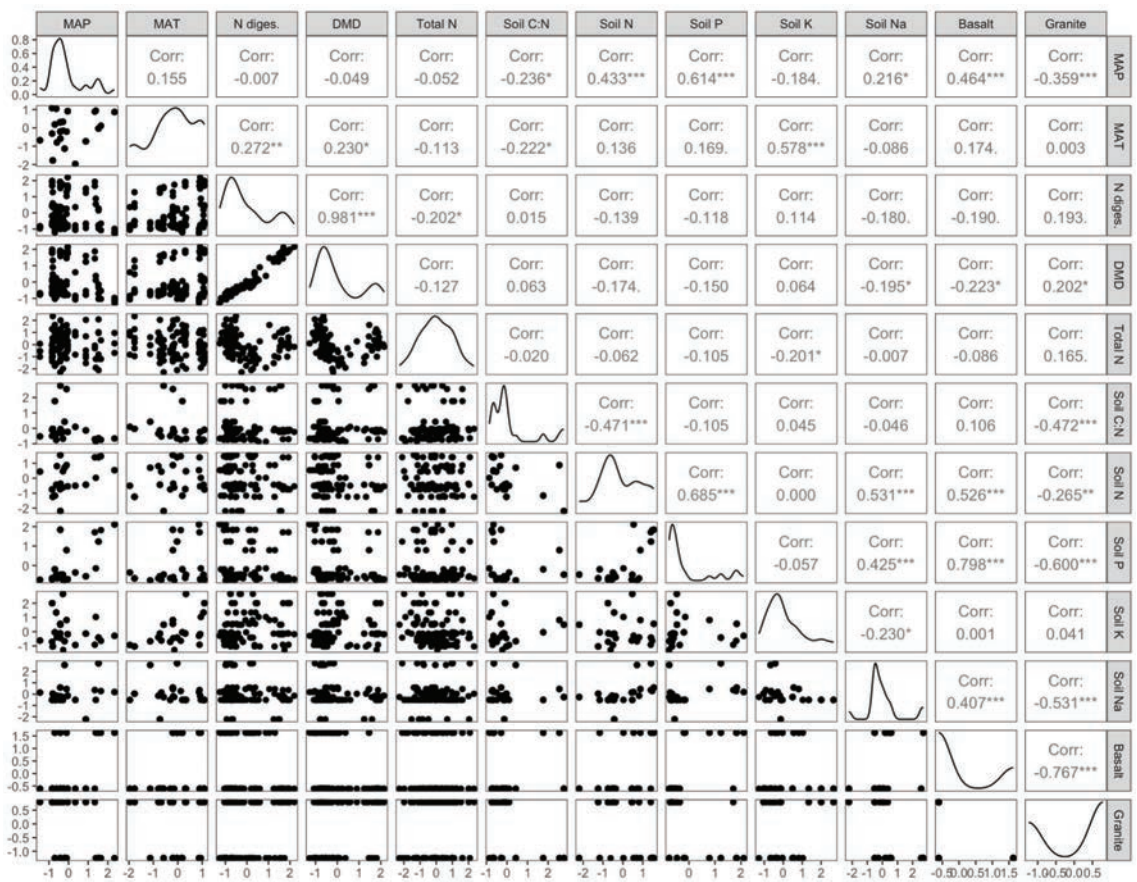


Figure S6.1. Pairwise correlation among potential model predictors. The main diagonal plots show the distribution of values for each variable. Scatterplots below the diagonal represent the raw relationship between pairs of variables, while values above the diagonal indicate the level of correlation of such predictors, with the level of significance following traditional notation (*95%; **99%; ***99.99%).

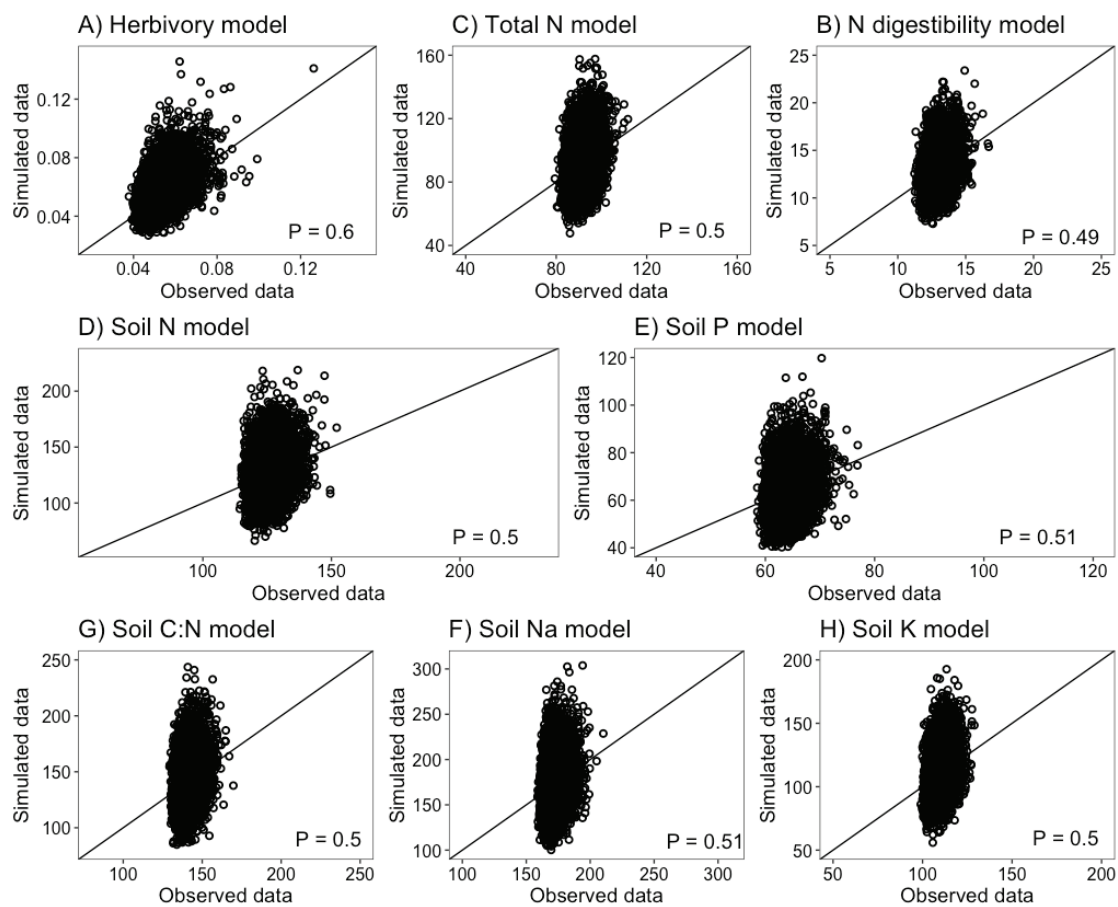


Figure S6.2. Posterior predictive check and Bayesian p -value for the final sub-models.

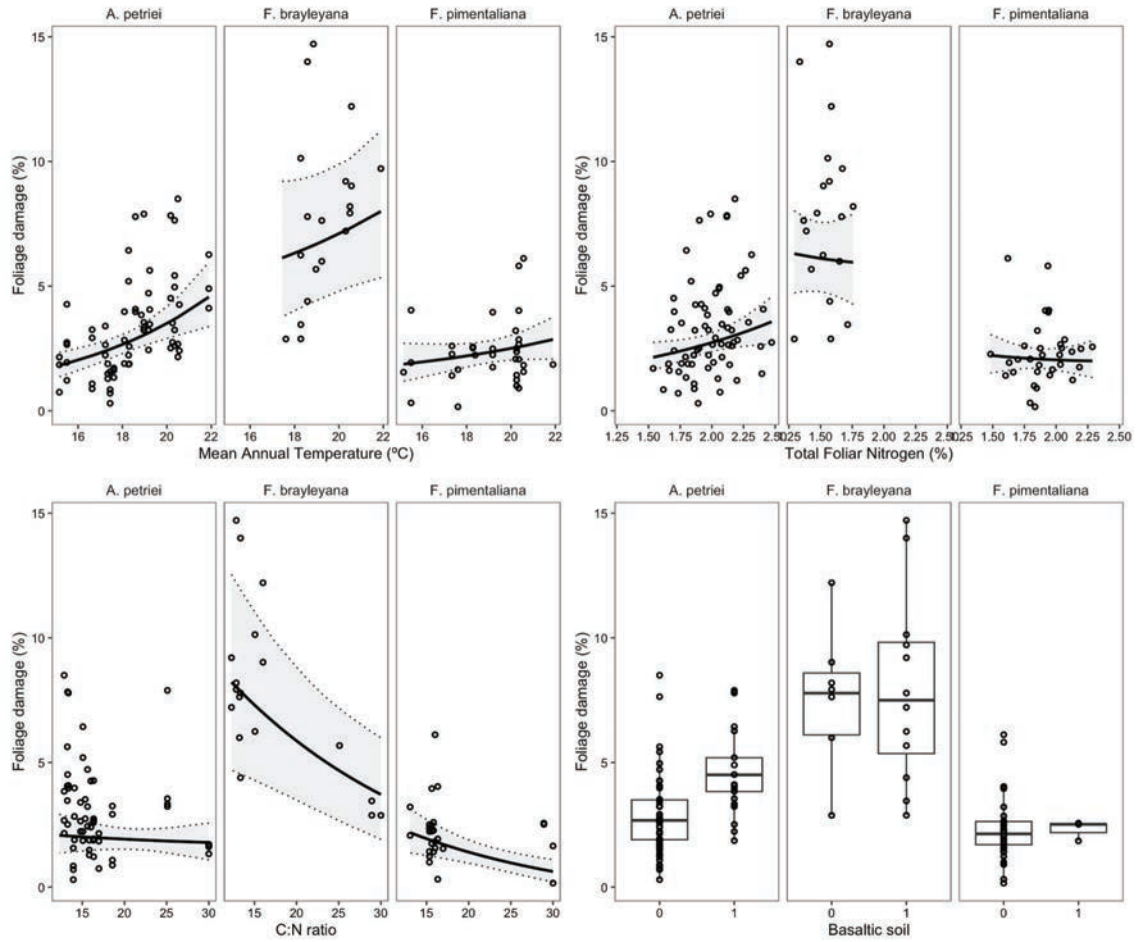


Figure S6.3. Patterns in herbivory across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.

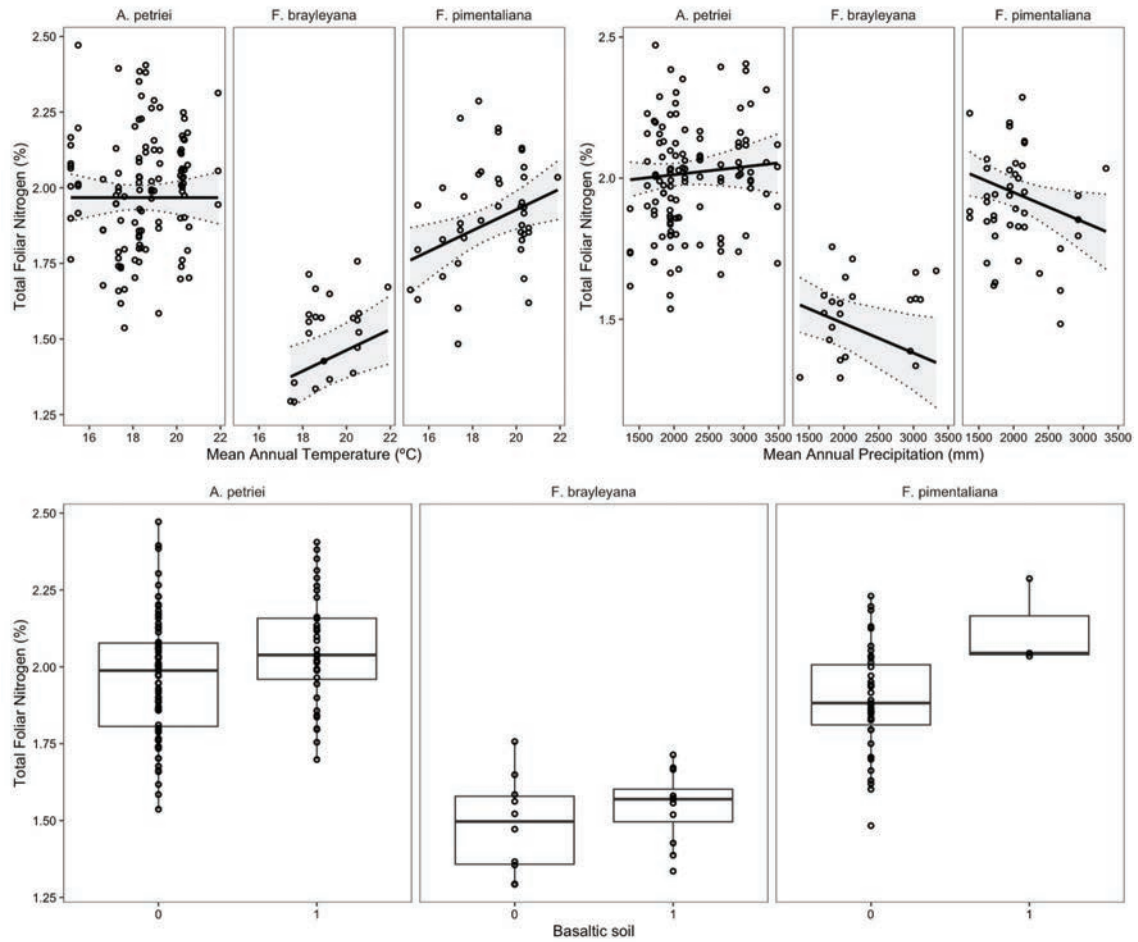


Figure S6.4. Patterns in foliar total N across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.

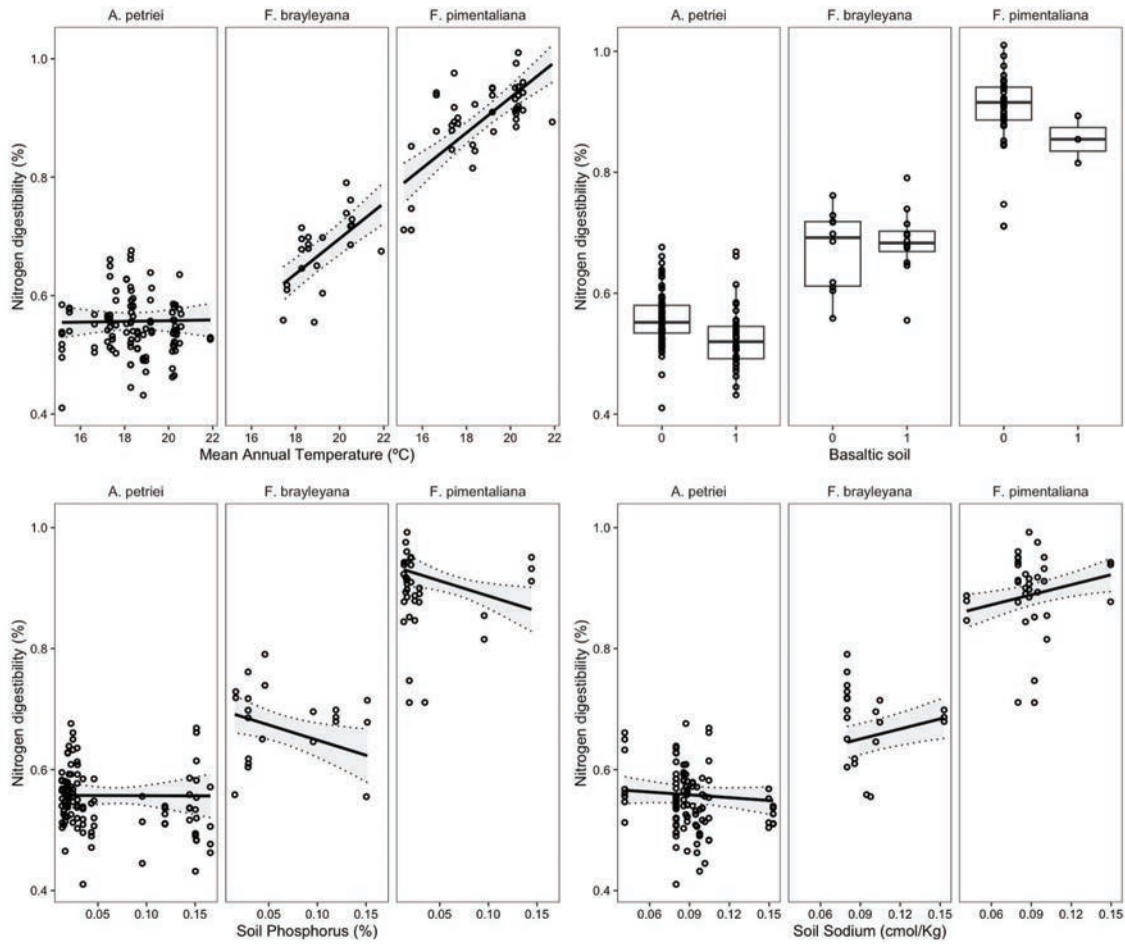


Figure S6.5. Patterns in foliar N digestibility across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.

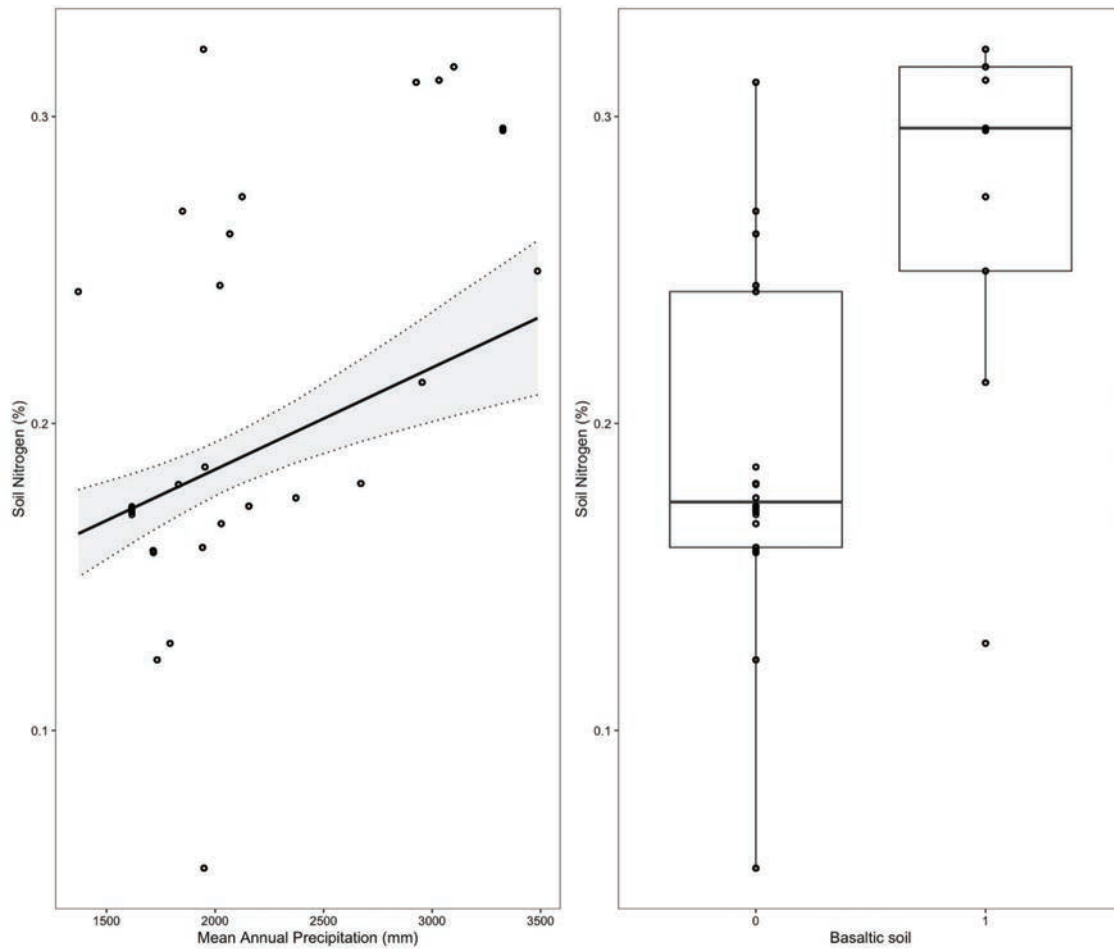


Figure S6.6. Patterns in soil N across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.

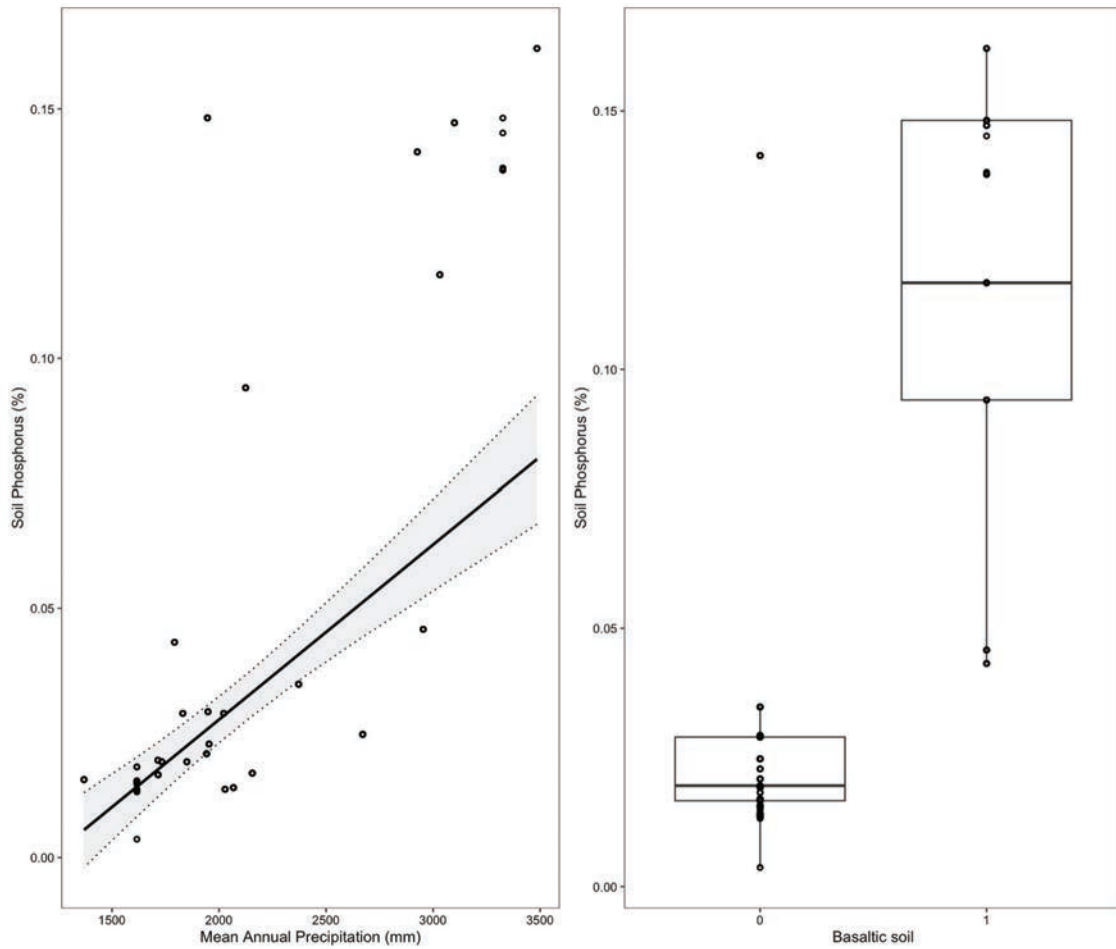


Figure S6.7. Patterns in soil P across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.

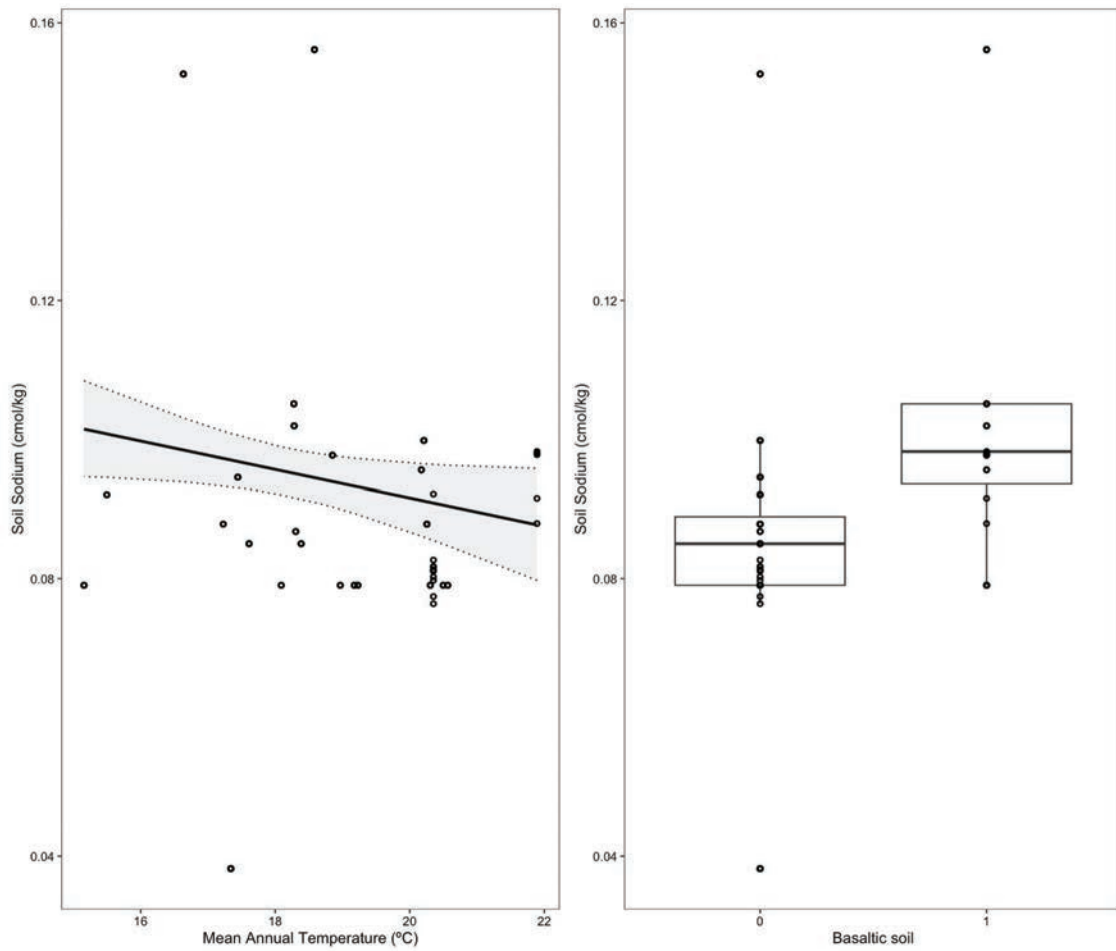


Figure S6.8. Patterns in soil Na across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.

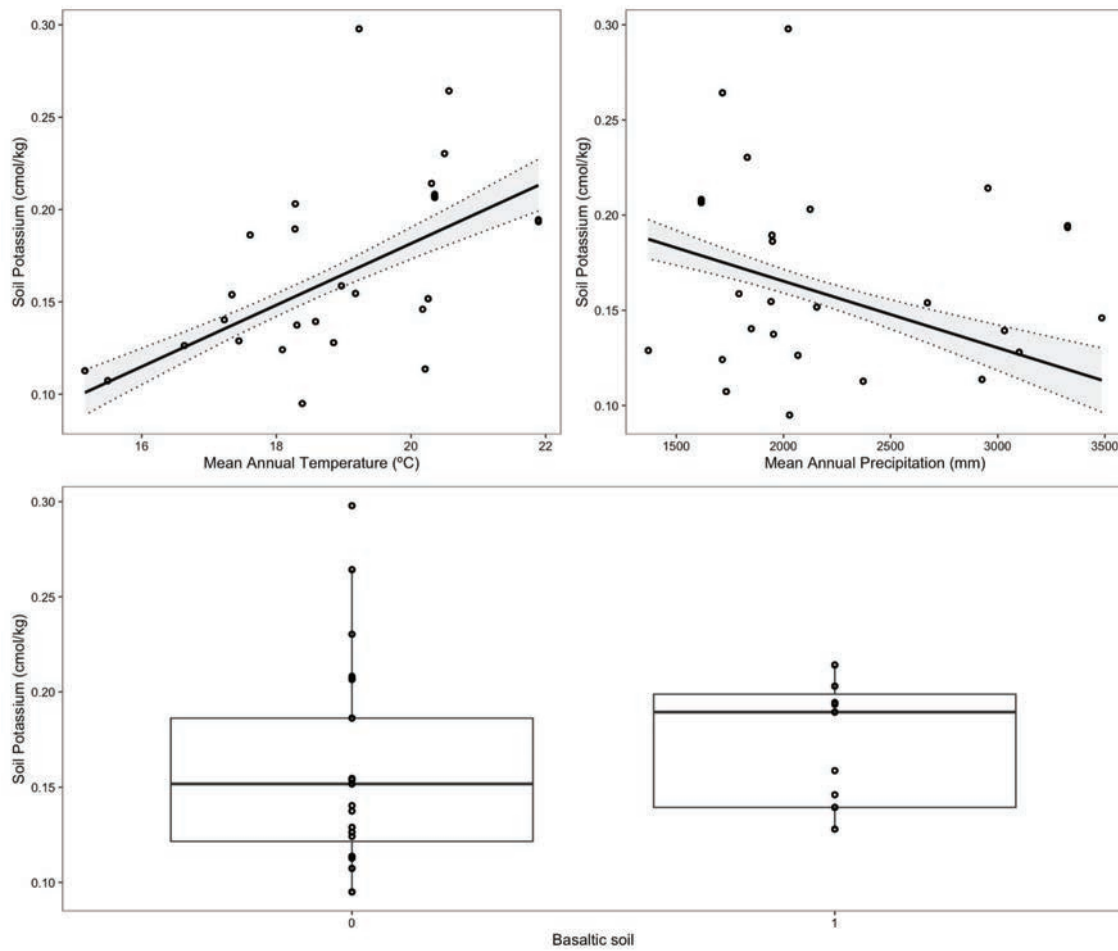


Figure S6.9. Patterns in soil K across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.

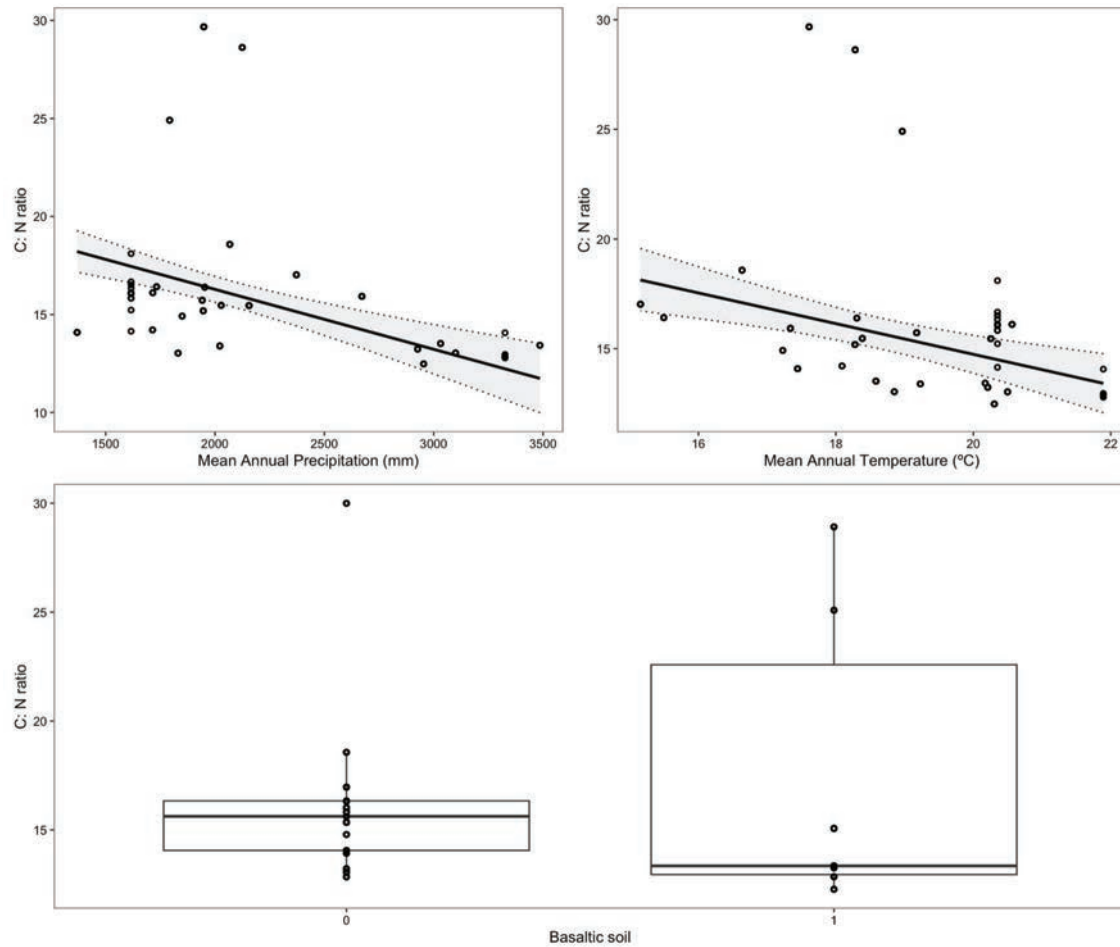


Figure S6.10. Patterns in soil C:N ratio across selected gradients. Predictive line shows the average effect with the shade area representing the 89% CI.

Table S6.1. Variable selection results comparing the expected predictive accuracy (theoretical expected log pointwise predictive density or ELPD) between most complex version of each sub-model and the stepwise removal of predictors with marginal effect. A positive difference in predictive value (Δ ELPD) suggest that the removal of that predictor increased the predictive accuracy of the model. For sub-models with only “Most Complex” competing model, no variable removal improved predictive accuracy, meaning that the most complex model performed best.

Hierarchy	Sub-model	Competing model	ELPD LOO	Δ ELPD
Soil	Soil Na	Most Complex	-263.3	
		Remove MAP	-262.3	1
	Soil K	Most Complex	-222.6	

Foliage	Soil CN	Most Complex	-244.3	
	Soil P	Most Complex	-174.1	
		Remove MAT	-173.9	0.2
	Soil N	Most Complex	-232.9	
		Remove MAT	-232.3	0.6
	Total N	Most Complex	-209.9	
		Remove Soil Na	-208.1	1.8
		Remove Soil K	-207	1.1
		Remove Soil CN	-205.5	1.5
		Remove Soil N	-204.2	1.3
		Remove Soil P	-204	0.2
	N digestibility	Most Complex	-38	
		Remove Soil K	-36.7	1.3
		Remove Soil CN	-35.5	1.2
		Remove MAP	-33.9	1.6
		Remove Soil N	-33.8	0.1
Herbivory	Damage	Most Complex	435.7	
		Remove Soil P	437	1.3
		Remove N digestibility	441.5	4.5
		Remove Soil Na	442.7	1.2
		Remove Soil K	442.8	0.1
		Remove MAP	443.6	0.8
		Remove Soil N	444	0.4

Table S6.2. Model intercepts. Values are reported as the mean and 89% credible interval (CI).

Model	Species	Mean	Lower CI	Upper CI
Herbivory (%)	<i>Alphitonia petriei</i>	2.9	2.5	3.3
Herbivory (%)	<i>Flindersia brayleyana</i>	6.6	4.3	9.4
Herbivory (%)	<i>Flindersia pimentaliana</i>	2.3	1.9	2.7
N digestibility (Fraction 0-1)	<i>Alphitonia petriei</i>	0.56	0.54	0.57
N digestibility (Fraction 0-1)	<i>Flindersia brayleyana</i>	0.66	0.63	0.68
N digestibility (Fraction 0-1)	<i>Flindersia pimentaliana</i>	0.89	0.88	0.91
Total N (%)	<i>Alphitonia petriei</i>	1.97	1.93	2.01
Total N (%)	<i>Flindersia brayleyana</i>	1.42	1.33	1.51
Total N (%)	<i>Flindersia pimentaliana</i>	1.88	1.83	1.93
Soil N (%)		0.19	0.18	0.2
Soil P (%)		0.034	0.03	0.039
Soil C: N (ratio)		15.73	15.07	16.39
Soil K (cmol/kg)		0.16	0.153	0.165
Soil Na (cmol/kg)		0.084	0.081	0.088

Table S6.3. Summary of sample size and treatment of the datasets used in each sub-model.

Sub-model	Scale	Data collected	Data treatment	Sample size for the model
Soil	Site	For each of the 25 sites, three samples were collected at three different depths	Chemical concentration for each soil element was averaged across the vertical gradient	25
Foliage	Tree	243 canopy trees were collected for three different species	Chemical assays were performed on a representative subsample (33%) selected based on near-infrared spectroscopy techniques. Chemical profiles for the remaining samples were predicted using calibrated equations (see Materials and methods)	243
Herbivory	Tree	An average of 20 individual leaves were sampled across 243 canopy trees	Herbivory damage was averaged at the tree level based on the 20 individual measures per tree	243
Climate	Site	Data retrieved from spatial climate layers	Mean annual temperature and	25

precipitation were
extracted from spatial
layers adjusted for the
region (see Materials
and methods)

Table S6.4. Site description.

Site ID	Geology	Elevation (m)	Latitude	Longitude	Mean Annual Precipitation (mm)	Mean Annual Temperature (°C)
AU10A	basalt	940	-17.7062	145.5267	1946.19382	18.2770004
AU4A	basalt	410	-17.608226	145.769781	3325.91078	21.8910008
AU6A	basalt	630	-17.673722	145.71513	2953.89001	20.3050003
AU7A	granite	690	-17.631963	145.693306	2926.42775	20.2099991
AU7B	basalt	750	-17.618911	145.68341	3485.48296	20.1720009
AU8A	basalt	850	-17.603419	145.632515	3099.89512	18.8500004
AU8B	basalt	820	-17.597161	145.646271	3031.61144	18.5830002
AUAC	basalt	830	-17.743289	145.534109	2124.41302	18.2810001
AUAD	basalt	760	-17.770123	145.547467	1792.43365	18.9659996
AUSR	rhyolite	900	-17.7154	145.5267	2028.3956	18.3850002
CU10A	granite	1050	-16.556704	145.276664	2671.55869	17.3390007
CU11	granite	1120	-16.529514	145.284013	1732.86775	15.4960003
CU12A	granite	1190	-16.516485	145.275519	2372.22501	15.1569996
CU6A	granite	630	-16.577398	145.309423	1616.30773	20.3509998
CU8A	granite	805	-16.584539	145.303007	2155.69822	20.2539997
G5	rhyolite	1040	-17.688477	145.507957	1948.67603	17.6100006
HRG1	rhyolite	1160	-17.454248	145.476429	2067.48736	16.6340008
HRG3	granite	1230	-17.286008	145.426695	1369.47718	17.4430008
HRG3A	granite	1170	-17.316392	145.419989	1849.89389	17.2269993
LU10	granite	990	-17.102851	145.590055	1941.90305	19.1749992
LU11	granite	1090	-17.092501	145.618886	1953.35974	18.3050003
LU12	granite	1180	-17.096672	145.577881	1714.58576	18.0890007
LU7	granite	705	-17.124248	145.629435	1831.17529	20.4969997
LU8	granite	760	-17.117477	145.602962	1715.59607	20.5629997
LU9	granite	900	-17.103734	145.611918	2022.01865	19.2280006

References

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- McCullagh, P. (2019) *Generalized linear models*, Second edn. Routledge.
- Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P.-C., Paananen, T. & Gelman, A. (2020) loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. *R package version*, **2**, 12.

JAGS code

```
#####  
# Likelihood #  
#####  
  
for(i in 1:n) {  
  
# Herbivory model  
  
y[i] ~ dbeta(alpha[i], beta[i])  
alpha[i] <- mu[i] * phi  
beta[i] <- (1-mu[i]) * phi  
logit(mu[i]) <- a_hr[spp_intercept[i]] + ### intercepts  
    ### Climate  
    b.mat_hr[genus_slope[i]] * mat[i] +  
    ### Soil  
    b.cn_hr[genus_slope[i]] * cn[i]+  
    ### Geology  
    b.basalt_hr[genus_slope[i]] * basalt[i]+  
    ### Foliage  
    b.totalN_hr[genus_slope[i]] * total_N[i]+  
    ### Random effect  
    r.site[site[i]]  
  
# residuals (for posterior predictive check)  
res.herb[i] <- pow((y[i] - mu[i]),2)  
y.new[i] ~ dbeta(alpha[i], beta[i])  
res.herb.new[i] <- pow((y.new[i] - mu[i]),2)  
  
# log-likelihood (for model comparison)  
hr_loglik[i] <- logdensity.beta(y[i], alpha[i], beta[i])  
  
# Foliage model  
  
# Sub-model N digestibility  
availN[i] ~ dnorm(mu_avail[i], prec_avail)  
mu_avail[i] <- a_availN[spp_intercept[i]] + ### intercepts  
    ### Climate  
    b.mat_availN[genus_slope[i]] * mat[i] +  
    ### Soil  
    b.p_kj_availN[genus_slope[i]] * p_kj[i] +  
    b.na_availN[genus_slope[i]] * na[i] +
```

```

#### Geology
b.basalt_availN[genus_slope[i]] * basalt[i]+
#### Random effect
eps_availN[site[i]]

# residuals (for posterior predictive check)
res.availN[i] <- pow((availN[i] - mu_avail[i]), 2)
availN.new[i] ~ dnorm(mu_avail[i], prec_avail)
res.availN.new[i] <- pow((availN.new[i] - mu_avail[i]),2)

# log-likelihood (for model comparison)
availN_loglik[i] <- logdensity.norm(availN[i], mu_avail[i], prec_avail)

# Sub-model total_N
total_N[i] ~ dnorm(mu_total_N[i], prec_total_N)
mu_total_N[i] <- a_total_N[spp_intercept[i]]+ #### intercepts
#### Climate
b.map_total_N[genus_slope[i]] * map[i] +
b.mat_total_N[genus_slope[i]] * mat[i] +
#### Geology
b.basalt_total_N[genus_slope[i]] * basalt[i]+
#### Random effect
eps_total_N[site[i]]

# residuals (for posterior predictive check)
res.total_N[i] <- pow((total_N[i] - mu_total_N[i]),2)
total_N.new[i] ~ dnorm(mu_total_N[i], prec_total_N)
res.total_N.new[i] <- pow((total_N.new[i] - mu_total_N[i]),2)

# log-likelihood (for model comparison)
totalN_loglik[i] <- logdensity.norm(total_N[i], mu_total_N[i], prec_total_N)

# Soil model (likelihood)
# Submodel Soil N
n_kj[i] ~ dnorm(mu_n_kj[i], prec_n_kj)
mu_n_kj[i] <- a_n_kj + #### intercept
#### Climate
b.map_n_kj * map[i] +
## Geology effect
b.basalt_n_kj * basalt[i]

# residuals (for posterior predictive check)

```



```

res.n_kj[i] <- pow((n_kj[i] - mu_n_kj[i]),2)
n_kj.new[i] ~ dnorm(mu_n_kj[i], prec_n_kj)
res.n_kj.new[i] <- pow((n_kj.new[i] - mu_n_kj[i]),2)

# log-likelihood (for model comparison)
n_loglik[i] <- logdensity.norm(n_kj[i], mu_n_kj[i], prec_n_kj)

# Submodel Soil P
p_kj[i] ~ dnorm(mu_p_kj[i], prec_p_kj)
mu_p_kj[i] <- a_p_kj + ### intercept
      ### Climate
      b.map_p_kj * map[i] +
      ## Geology effect
      b.basalt_p_kj * basalt[i]

# residuals (for posterior predictive check)
res.p_kj[i] <- pow((p_kj[i] - mu_p_kj[i]),2)
p_kj.new[i] ~ dnorm(mu_p_kj[i], prec_p_kj)
res.p_kj.new[i] <- pow((p_kj.new[i] - mu_p_kj[i]),2)

# log-likelihood (for model comparison)
p_loglik[i] <- logdensity.norm(p_kj[i], mu_p_kj[i], prec_p_kj)

# Submodel Soil C:N
cn[i] ~ dnorm(mu_cn[i], prec_cn)
mu_cn[i] <- a_cn + ### intercept
      ### Climate
      b.map_cn * map[i] +
      b.mat_cn * mat[i] +
      ## Geology effect
      b.basalt_cn * basalt[i]

# residuals (for posterior predictive check)
res.cn[i] <- pow((cn[i] - mu_cn[i]),2)
cn.new[i] ~ dnorm(mu_cn[i], prec_cn)
res.cn.new[i] <- pow((cn.new[i] - mu_cn[i]),2)

# log-likelihood (for model comparison)
cn_loglik[i] <- logdensity.norm(cn[i], mu_cn[i], prec_cn)

# Submodel Soil K

```

```

k[i] ~ dnorm(mu_k[i], prec_k)
mu_k[i] <- a_k + ### intercept
      ### Climate
      b.map_k * map[i] +
      b.mat_k * mat[i] +
      ## Geology effect
      b.basalt_k * basalt[i]

# residuals (for posterior predictive check)
res.k[i] <- pow((k[i] - mu_k[i]),2)
k.new[i] ~ dnorm(mu_k[i], prec_k)
res.k.new[i] <- pow((k.new[i] - mu_k[i]),2)

# log-likelihood (for model comparison)
k_loglik[i] <- logdensity.norm(k[i], mu_k[i], prec_k)

# Submodel Soil Na
na[i] ~ dnorm(mu_na[i], prec_na)
mu_na[i] <- a_na + ### intercept
      ### Climate
      b.mat_na * mat[i] +
      ## Geology effect
      b.basalt_na * basalt[i]

# residuals (for posterior predictive check)
res.na[i] <- pow((na[i] - mu_na[i]),2)
na.new[i] ~ dnorm(mu_na[i], prec_na)
res.na.new[i] <- pow((na.new[i] - mu_na[i]),2)

# log-likelihood (for model comparison)
na_loglik[i] <- logdensity.norm(na[i], mu_na[i], prec_na)
}

#####
# Priors #
#####

phi ~ dgamma(.1,.1)

# Species-specific Intercepts
for(sp in 1:nspp_intercept){

  a_hr[sp] ~ dnorm(0,.001)
  a_availN[sp] ~ dnorm(0,.001)
  a_total_N[sp] ~ dnorm(0,.001)

```

```

}

# Soil intercepts
a_n_kj ~ dnorm(0,.001)
a_p_kj ~ dnorm(0,.001)
a_cn ~ dnorm(0,.001)
a_k ~ dnorm(0,.001)
a_na ~ dnorm(0,.001)

# Genus-specific Slopes

for(sp in 1:ngenus_slope){

  # Slopes Herbivory model

  ### Climate
  b.mat_hr[sp] ~ dnorm(0,1.0E-6)
  ### Soil
  b.cn_hr[sp] ~ dnorm(0,1.0E-6)
  ### Foliage
  b.totalN_hr[sp] ~ dnorm(0,1.0E-6)
  ###Geology
  b.basalt_hr[sp] ~ dnorm(0,1.0E-6)

  # Slopes Foliage model

  # N digestibility
  ### Climate
  b.mat_availN[sp] ~ dnorm(0,1.0E-6)
  ### Soil
  b.p_kj_availN[sp] ~ dnorm(0,1.0E-6)
  b.na_availN[sp] ~ dnorm(0,1.0E-6)
  ###Geology
  b.basalt_availN[sp] ~ dnorm(0,1.0E-6)

  # total_N
  ### Climate
  b.map_total_N[sp] ~ dnorm(0,1.0E-6)
  b.mat_total_N[sp] ~ dnorm(0,1.0E-6)
  ###Geology
  b.basalt_total_N[sp] ~ dnorm(0,1.0E-6)

}

```

```

# Slopes soil

# Submodel soil N
b.map_n_kj ~ dnorm(0,1.0E-6)
b.basalt_n_kj ~ dnorm(0,1.0E-6)

# Submodel soil P
b.map_p_kj ~ dnorm(0,1.0E-6)
b.basalt_p_kj ~ dnorm(0,1.0E-6)

# Submodel soil C:N
b.map_cn ~ dnorm(0,1.0E-6)
b.mat_cn ~ dnorm(0,1.0E-6)
b.basalt_cn ~ dnorm(0,1.0E-6)

# Submodel soil K
b.map_k ~ dnorm(0,1.0E-6)
b.mat_k ~ dnorm(0,1.0E-6)
b.basalt_k ~ dnorm(0,1.0E-6)

# Submodel soil Na
b.mat_na ~ dnorm(0,1.0E-6)
b.basalt_na ~ dnorm(0,1.0E-6)

# Precision hierarchical models
prec_avail ~ dgamma(0.01, 0.01)
prec_total_N ~ dgamma(0.01, 0.01)
prec_n_kj ~ dgamma(0.01, 0.01)
prec_p_kj ~ dgamma(0.01, 0.01)
prec_cn ~ dgamma(0.01, 0.01)
prec_k ~ dgamma(0.01, 0.01)
prec_na ~ dgamma(0.01, 0.01)

#####
# Random effects #
#####

# herbivory model
for(s in 1:nsites){ r.site[s] ~ dnorm(0, tau.site) }
sd.site <- 1 / sqrt(tau.site)
tau.site ~ dgamma(0.01, 0.01)

# N digestibility

```

```

for(i in 1:nsites){ eps_availN[i] ~ dnorm(0, tau_availN) }
tau_availN ~ dgamma(0.01, 0.01)
sd_availN <- 1 / sqrt(tau_availN)

# total_N
for(i in 1:nsites){ eps_total_N[i] ~ dnorm(0, tau_total_N) }
tau_total_N ~ dgamma(0.01, 0.01)
sd_total_N <- 1 / sqrt(tau_total_N)

#####
# Sum of residuals (for Posterior Predictive Checks) #
#####

fit.herb <- sum(res.herb[])
fit.herb.new <- sum(res.herb.new[])

fit.availN <- sum(res.availN[])
fit.availN.new <- sum(res.availN.new[])

fit.total_N <- sum(res.total_N[])
fit.total_N.new <- sum(res.total_N.new[])

fit.n_kj <- sum(res.n_kj[])
fit.n_kj.new <- sum(res.n_kj.new[])

fit.p_kj <- sum(res.p_kj[])
fit.p_kj.new <- sum(res.p_kj.new[])

fit.cn <- sum(res.cn[])
fit.cn.new <- sum(res.cn.new[])

fit.k <- sum(res.k[])
fit.k.new <- sum(res.k.new[])

fit.na <- sum(res.na[])
fit.na.new <- sum(res.na.new[])

```

Appendix Chapter Seven

Extended methodology (I): Microclimate

Microclimate generation

Microclimate information for the region was derived from the ERA5 weather data (Maclean, Mosedale & Bennie 2019; Kearney *et al.* 2020) using the NicheMapR package (Kearney & Porter 2017). We computed hourly microclimate between 1990-2022 for each of the 32 study locations, accounting for local topography and vegetation effects. We generated the microclimate data for two shade scenarios: 0% (full exposure to radiation; on top of the rainforest canopy) and 90% shade (limited exposure to radiation; under the canopy), which allowed for a realistic representation of the microclimate available for ringtail possums. These canopy dwellers can be exposed to 0% shade during foraging activities but remain close to full shade while resting under the canopy.

Microclimate validation

Step 1: Calibration

The first step in the microclimate validation was to test for inconsistencies in the generated microclimate related to potential unaccounted complex topographic features of the region. This process involved validating the expected pattern in temperature along the elevational gradient using climate layers calibrated explicitly for the Australian Wet Tropics (Storlie *et al.* 2013). Briefly, these climate layers downscale gridded spatial climate data at 250 m resolution from empirical weather information collected between 2006-2009 across 54 rainforest sites (including 29 of the 32 sites in this study), offering a fine-grained representation of the bioregion's climate. We compared daily maximum and minimum temperatures between the gridded climatic layers and the generated microclimate using root mean square error metrics, with acceptable levels of error established around 1°C.

Results from this comparison indicated a systematic bias in the generated microclimate (Table S7.1; "ERA5 not adjusted"), suggesting potential inconsistencies in the topographic corrections imposed by the microclimate model. These inconsistencies were especially pronounced in sites with high slopes close to

mountaintops. To mitigate these discrepancies, we designed a conditional adjustment factor based on site-specific differences between expected and predicted temperatures, using daily temperature values between 1990-2016 (Storlie *et al.* 2013). The calibration factor accounted for the time of the day and seasonal temperature differences associated with changes in solar radiation. This adjustment was implemented within the microclimate model, extending the calibration to other microclimatic factors affected by temperature. We re-ran the microclimate model with the integrated calibration factor and re-analysed the discrepancy between expected and generated temperature patterns. Calibrated results showed satisfactory levels of spatiotemporal match between expected and generated temperature data (Table S7.1 “ERA5 adjusted”; Figure S7.1).

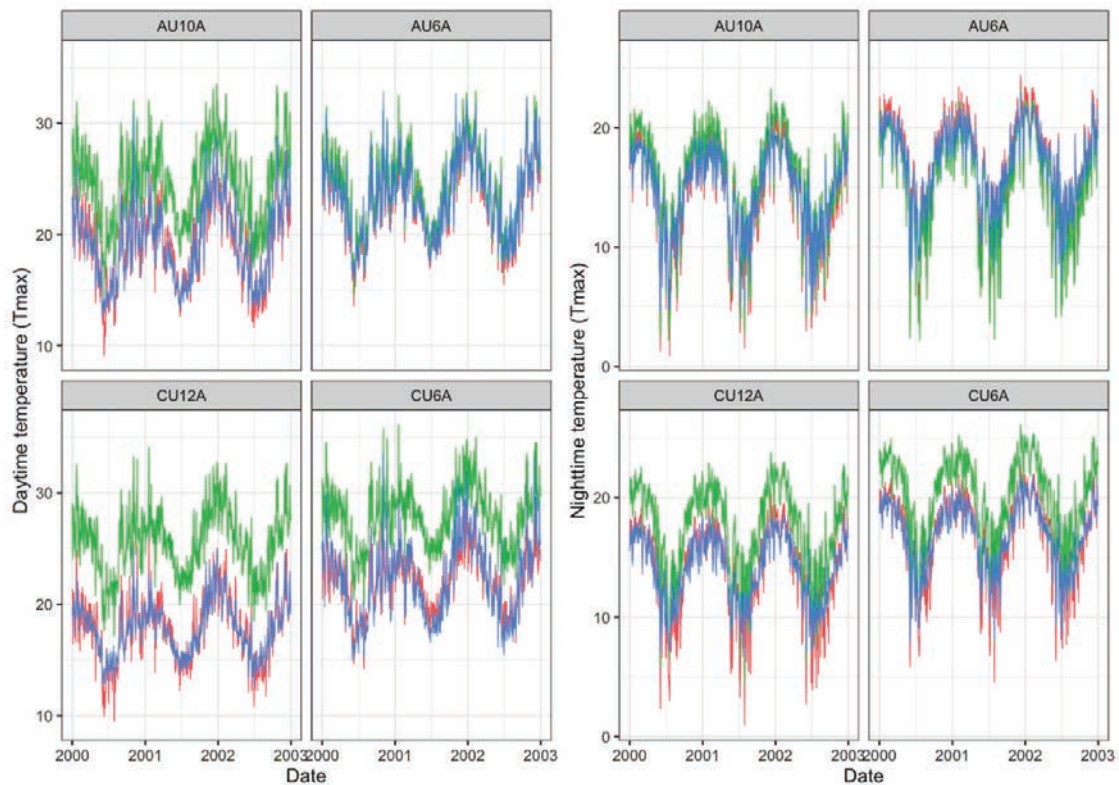


Figure S7.1. Example of microclimate calibration on a selected number of sites and years based on daily temperatures. Each panel represent a different study location. Green lines represent the non-calibrated microclimate generated using the NicheMapR package, red lines depict the interpolated data for the region obtained from Storlei et al. (2013), and blue lines represent the calibrated microclimate.

Table S7.1. Root Mean Square Error metric for the two-step calibration method implemented to adjust microclimate data to observed values. Example for the wet season is defined between December-April, and the dry season ranges from May-November.

Step	Validation dataset	RMSE (ERA5 not adjusted)	RMSE (ERA5 adjusted)	Resolution	Length	Sites
Calibration	Storlei et al., 2013	5.303553	1.204323	Daily (tmax)	385698 days	32
Calibration	Storlei et al., 2013	2.368044	1.137534	Daily (tmin)	385698 days	32
Calibration	Storlei et al., 2013	5.328379	1.185908	Daily (tmax) dry season	178048 days	32
Calibration	Storlei et al., 2013	2.30999	1.271569	Daily (tmin) dry season	178048 days	32
Calibration	Storlei et al., 2013	5.268963	1.229381	Daily (tmax) wet season	128512 days	32
Calibration	Storlei et al., 2013	2.446199	0.9201148	Daily (tmin) wet season	128512 days	32
Validation	Leahy et al., 2022	2.566441	0.8159706	Hourly	55561 hours	4

Step 2: Corroboration

We further validated the calibrated microclimate by cross-referencing it with an independent dataset (Leahy *et al.* 2022), encompassing hourly temperature recordings collected in the field between 2019 and 2020 across four study sites. We computed the root mean square error metric to quantify the discrepancy between the datasets. The results of this validation demonstrated satisfactory levels of agreement between observed and predicted hourly microclimate data for all sites with available observed data, confirming the precision and reliability of the implemented calibration factor (Table S7.1; Figure S7.2).

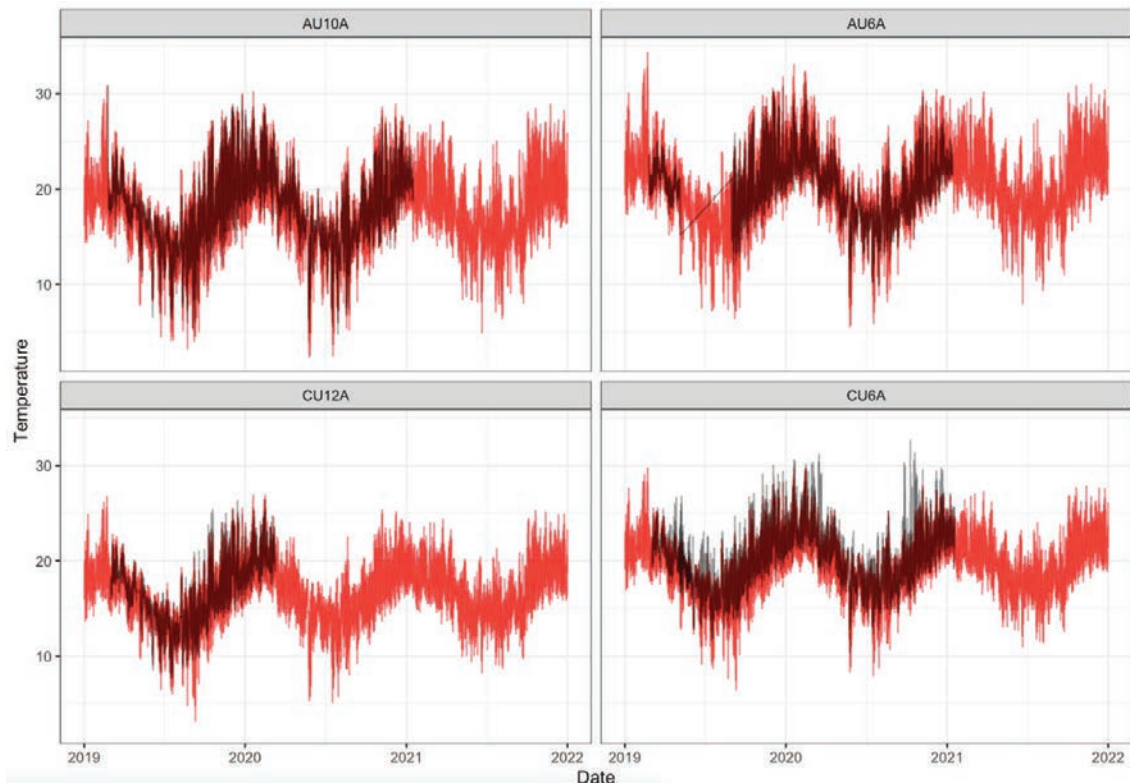


Figure S7.2. Validation of the microclimate adjustments. Red lines represent the calibrated microclimate generated using NicheMapR while the black lines depict the field microclimate data obtained from Leahy *et al.* (2022).

Night-time microclimate adjustment for canopy foragers

Microclimatic conditions in the canopy can vary depending on the exposure to sky temperatures. We accounted for non-continuous exposure of the animal to unshaded microclimate while foraging in the canopy by computing sky temperature as a weighted average between actual non-shaded exposure to sky temperature and foliage temperature (i.e., the temperature of the foliage surrounding the animal while foraging). Weights were assigned assuming that ringtails' foraging activity occurs, on average, 70% on top of the canopy (full sky exposure) and 30% under the canopy (exposed to foliage temperature). For this purpose, foliage temperature was obtained using an extension of the ectotherm model (Kearney & Porter 2020) that uses leaf temperature calculations based on equation 14.1 from Campbell and Norman (2000). Details on leaf functional traits used to compute leaf temperature can be found in Table S7.2.

Table S7.2. Leaf functional traits used in the foliage temperature model.

Functional trait	Value (units)
Leaf vapor conductance (abaxial)	0.2 mol/m ² /s
Leaf vapor conductance (adaxial)	0 mol/m ² /s
Maximum leaf vapor conductance (abaxial)	0.3 mol/m ² /s
Maximum leaf vapor conductance (adaxial)	0 mol/m ² /s
Base leaf vapor conductance when stomata closed	0.01 (μmol H ₂ O) / (m ² s Pa)
Ratio of b axis:a axis for ellipsoid	0.0025
Ratio of c axis:a axis for ellipsoid	0.1176
Emissivity of the substrate	0.95
Emissivity of the leaf	0.97
Solar absorptivity of the leaf	0.8
Radiation configuration factor to sky	0.5
Radiation configuration factor to substrate	0.5
Convective enhancement factor	1.4
Percent of leaf conducting to the ground	0%
Geometry	ellipsoid

Daytime den buffer

Rainforest ringtail possums differ in their daytime exposure to microclimatic conditions due to differences in shelter usage. *Hemibelideus lemuroides* actively rest in tree hollows during the day, while *Pseudochirops archeri* spends daylight hours curled up on a branch in the canopy (Winter, Krockenberger & Moore 2008). To account for the potential daytime buffer that dens can offer to *H. lemuroides*, we used an unpublished dataset of microclimate differences between actively used dens and forest canopy (Krockenberger, unpublished). This dataset was collected at one of our study sites using dataloggers that continuously recorded temperature every 30 min between 2007-2009. A pair of dataloggers were placed at 14 identified den locations. One of the dataloggers was located inside the den, attached to a metal wire so that the logger was placed away from the opening of the den while preventing its contact with the tree surface. The paired control logger was placed 10-20 cm from the den entrance and collected canopy temperature simultaneously. Using this dataset, we computed the hourly average temperature difference between canopy and dens, controlling by month to account for seasonal temperature changes (Figure S7.3). Using this information, we adjusted daytime temperature exposure for *H. lemuroides* by subtracting the buffer effect from daytime hourly temperature. Further, we assumed dens to buffer the species against wind exposure and assumed air movement inside

the den was close to zero (0.001 m/s). This approach resulted in adjusted daytime microclimate data for *H. lemuroides*, assuming consistency in den characteristics and buffer potential across the species distribution.

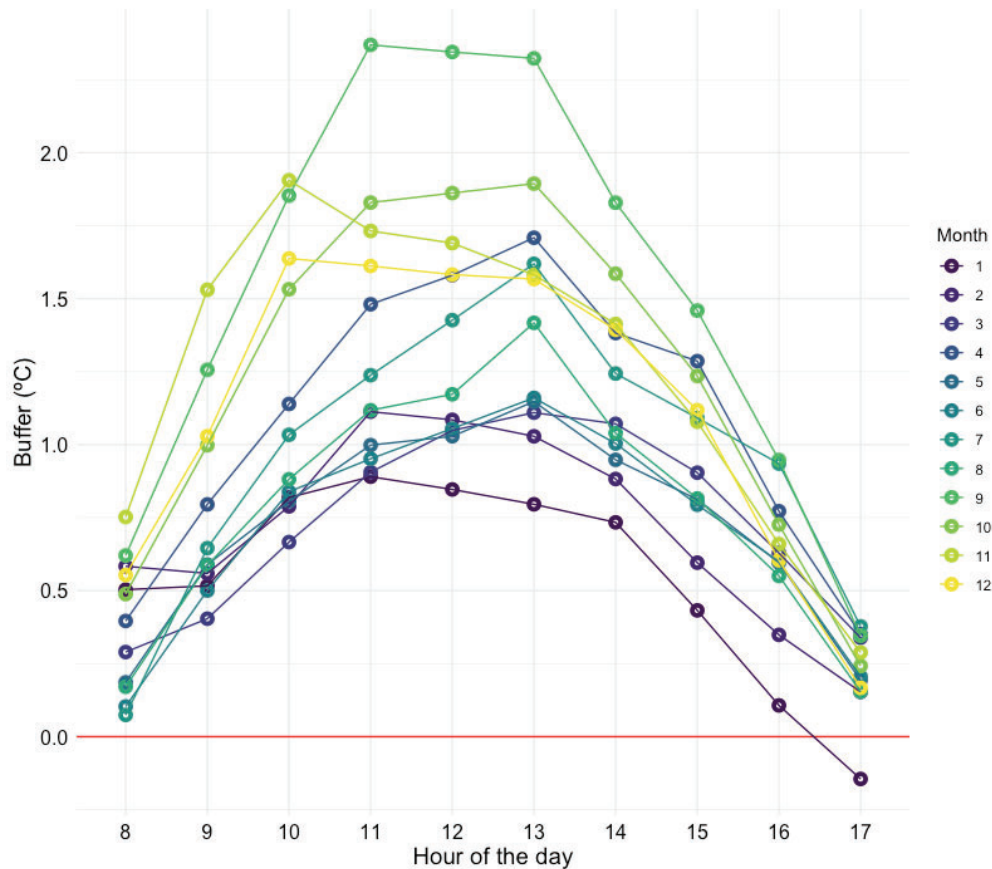


Figure S7.3. Daytime den thermal buffer for *H. lemuroides*. Data represent mean den buffer potential ($n = 14$ dens) across hour of the day (daytime only) and month of the year. The buffer variable (y-axis) represents the average difference in temperature between the den and canopy, with positive values indicating that the ambient is hotter than inside the den.

Extended methodology (II): Biophysical ecology

Animal model

Morphology and fur properties

One crucial aspect of developing a robust animal model is to accurately capture the morphological features and fur properties of the animal, as these functional traits significantly influence its interactions with the environment. In the case of ringtail possums, we adopted a cylindrical geometry, enabling them to fully curl into a ball,

with a ventral-to-dorsal surface ratio of 1:1. Fur properties were measured from specimens housed in the Queensland Museum (Brisbane), including 20 individuals of *Pseudochirops archeri* and 17 individuals of *Hemibelideus lemuroides*. An additional seven individuals of *Pseudochirops archeri* were measured from specimens stored at James Cook University (Cairns).

Measurements conducted at the museum included fur depth and hair length across distinct areas of the individuals (head, dorsal, ventral, and flank; Figure S7.4) using digital callipers. However, measurements of hair diameter and density, which necessitate damaging the fur, were only feasible for the specimens at James Cook University, encompassing seven individuals of *Pseudochirops archeri*. For *Hemibelideus lemuroides*, similar values were assumed due to the unavailability of direct measurements.

To accurately represent the uneven fur properties of the dorsal region (head, dorsal fur, and flank), we calculated a weighted average, with weights being assigned based on proportional surface area (0.5 dorsal fur, 0.4 flanks, and 0.1 head). A summary of the morphological and fur properties included in the models are provided in Table S7.3.

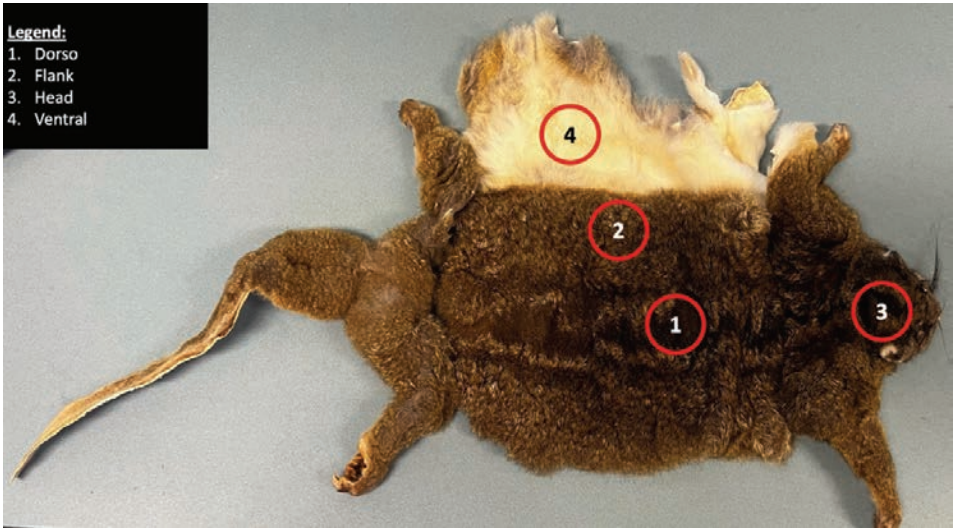


Figure S7.4. Green ringtail possum (*Pseudochirops archeri*) pelt with the four main fur areas highlighted by red circles.

Table S7.3. Summary of parameters included in the biophysical model. Note that “JCU specimens” refers to the specimens of *Pseudochirops archeri* stored at James Cook University.

Component	Species	Variable (units)	Value	Source

Fur	<i>Pseudochiro ps archeri</i>	Dorsal hair length (m)	0.0234	QLD museum + JCU specimens
		Ventral hair length (m)	0.0074	QLD museum + JCU specimens
		Dorsal hair diameter (m)	9.93E-06	JCU specimens
		Ventral hair diameter (m)	9.43E-06	JCU specimens
		Dorsal fur depth (m)	0.0194	QLD museum
		Ventral fur depth (m)	0.001	QLD museum
		Dorsal hair density (1/m ²)	85992878	JCU specimens
		Ventral hair density (1/m ²)	51392322	JCU specimens
		Dorsal fur reflectivity (fractional 0-1)	0.383	Borrowed from Koalas (Briscoe <i>et al.</i> 2014)
		Ventral fur reflectivity (fractional 0-1)	0.523	Borrowed from Koalas (Briscoe <i>et al.</i> 2014)
	<i>Hemibelideu s lemuroides</i>	Dorsal hair length (m)	0.0247	QLD museum
		Ventral hair length (m)	0.01494	QLD museum
		Dorsal hair diameter (m)	9.93E-06	Borrowed from <i>P. archeri</i>
		Ventral hair diameter (m)	9.43E-06	Borrowed from <i>P. archeri</i>
		Dorsal fur depth (m)	0.0217	QLD museum
		Ventral fur depth (m)	0.00171	QLD museum
		Dorsal hair density (1/m ²)	55992877.9	Borrowed from Koalas (Briscoe <i>et al.</i> 2014)
		Ventral hair density (1/m ²)	31392321	Borrowed from Koalas (Briscoe <i>et al.</i> 2014)
		Dorsal fur reflectivity (fractional 0-1)	0.383	Borrowed from Koalas (Briscoe <i>et al.</i> 2014)
		Ventral fur reflectivity (fractional 0-1)	0.523	Borrowed from Koalas (Briscoe <i>et al.</i> 2014)
Physiology	<i>Pseudochiro ps archeri</i>	Percentage of wet skin surface	2.5	Expert opinion
		Maximum percentage of wet skin surface	40	Expert opinion
		Intervals by which skin wetness increases (%)	0.15	Expert opinion
		Percentage of surface area for evaporation that is skin (e.g., licking paws)	4	Expert opinion
		Q10	1.8	Expert opinion
		Basal heat generation (W)	2.67	Calculated
		Offset between air temperature and breath (°C)	Calculated as a function of air temperature	Derived from Krockenberger, Edwards and Kanowski (2012)
		O ₂ extraction efficiency (%)	20	Default
		Panting increment steps	0.015	Default
		Maximum panting rate (multiplier on air flow through the lungs)	2	Expert opinion
		Multiplier on basal metabolic rate at maximum panting level	1	Default
		Initial thermal conductivity (W m ⁻¹ K ⁻¹)	0.9	Default
		Maximum thermal conductivity (W/mK)	2.8	Default
		Increase in thermal conductivity per iteration (W/m°C)	0.1	Default
		Core temperature (TC) (°C)	35.8	Krockenberger, Edwards and Kanowski (2012)
		Maximum TC (°C)	40.8	Krockenberger, Edwards and Kanowski (2012)
		Intervals by which TC increases	0.04	Expert opinion
		Minimum metabolic rate (KJ/day)	231	Calculated
	<i>Hemibelideu s lemuroides</i>	Percentage of wet skin surface	1.5	Expert opinion
		Maximum percentage of wet skin surface	40	Expert opinion
		Intervals by which skin wetness increases (%)	0.15	Expert opinion

		Percentage of surface area for evaporation that is skin (e.g., licking paws)	4	Expert opinion
		Q10	1.8	Expert opinion
		Basal heat generation (W)	2.35	Estimated
		Offset between air temperature and breath (°C)	Calculated as a function of air temperature	Derived from Krockenberger (unpublished)
		O ₂ extraction efficiency (%)	20	Default
		Panting increment steps	0.015	Default
		Maximum panting rate (multiplier on air flow through the lungs)	2	Expert opinion
		Multiplier on basal metabolic rate at maximum panting level	1	Default
		Initial thermal conductivity (W m ⁻¹ K ⁻¹)	0.9	Default
		Maximum thermal conductivity (W/mK)	2.8	Default
		Increase in thermal conductivity per iteration (W/m ² °C)	0.1	Default
		Core temperature (TC) (°C)	37.3	Krockenberger (unpublished)
		Maximum TC (°C)	40.8	Krockenberger (unpublished)
		Intervals by which TC increases	0.02	Default
		Minimum metabolic rate (Kj/day)	191	Calculated
General morphology	<i>Pseudochirops archeri</i>	Fat percentage	10	Expert opinion
		Mass (Kg)	1.17	Krockenberger, Edwards and Kanowski (2012)
		Ratio of length:height when resting	1.1	Expert opinion
		Maximum possible ration long and short axis	6	Expert opinion
		Fraction surface area that is ventral fur	0.5	Expert opinion
		Fraction of surface area touching the substrate	0.07	Expert opinion
		Uncurling rate	0.1	Expert opinion
	<i>Hemibelides lemuroides</i>	Fat percentage	10	Expert opinion
		Mass (Kg)	0.92	Krockenberger (unpublished)
		Ratio of length:height when resting	1.1	Expert opinion
		Maximum possible ration long and short axis	6	Expert opinion
		Fraction surface area that is ventral fur	0.5	Expert opinion
		Fraction of surface area touching the substrate	0.07	Expert opinion
		Uncurling rate	0.1	Expert opinion

Physiological data

Physiological data for ringtail possums were sourced from studies by Professor Andrew Krockenberger and collaborators. These studies measured physiological responses under controlled environmental conditions (i.e., metabolic chambers) in wild individuals. In these experiments, individual ringtail possums were exposed to chamber temperatures ranging between 5 and 35 °C, with a sequential thermal increase after a period of adaptation. Among the multiple measures taken during the experiment, the most relevant for our study included metabolic rate measured as oxygen consumption, body temperature, and evaporative water loss. Physiological responses were collected for individuals of both species (*Pseudochirops archeri* and

Hemibelideus lemuroides) captured at the same location and during the same year and season. However, only the results for *Pseudochirops archeri* are currently published (Krockenberger, Edwards & Kanowski 2012). A summary of the physiological parameters used in the biophysical model can be found in Table S7.3.

In addition to the physiological responses to increasing heat, further physiological studies have been conducted to understand energy requirements in rainforest ringtail possums using double-labelled water methods. Double-labelled water techniques measure energy expenditure in free-living animals, providing a useful framework for inferring energy balance in wild animals (Foley *et al.* 1990). Energy requirements were measured for free-living individuals of *Hemibelideus lemuroides* (Goudberg 1990) and for *Pseudochirops archeri* (Krockenberger, unpublished), reporting field metabolic rates of 546 KJ/day and 383 KJ/day. These additional datasets provide an ideal framework to corroborate the accuracy of the biophysical model by comparing expected and observed field metabolic rates.

Thermoregulatory sequence

The thermoregulatory sequence outlines the steps the animal follows in the model to regulate its body temperature, considering factors such as morphology, fur properties, physiological limits, and behaviour. The sequence was designed and fine-tuned based on the observed behavioural and physiological responses of the animal under controlled metabolic chamber conditions. The thermoregulatory sequence for ringtail possums involved (1) seeking shade and reducing metabolic rate to resting level, (2) increasing body temperature, (3) increasing flesh thermal conductivity, (4) uncurling to allow heat dissipation through ventral exposure, (5) panting, (6) wetting fur through licking. This sequence illustrates the adaptive strategies ringtail possums employ to maintain optimal body temperature levels in response to environmental conditions.

Animal model validation: metabolic chamber

We developed and calibrated an animal model for each species using the morphological features, fur properties, baseline physiological parameters, and the thermoregulatory sequence outlined above. To assess the realism of these models, we compared the predicted physiological responses with those documented in physiological experiments conducted on *Pseudochirops archeri* (Krockenberger, Edwards & Kanowski 2012) and *Hemibelideus lemuroides* (Krockenberger,

unpublished). To predict physiological responses, we employed the endotherm model within the NicheMapR package (Kearney *et al.* 2021), implemented under the same environmental conditions reported for the metabolic chamber in both studies. Despite the expected variability resulting from differences in heat sensitivity among individual ringtail possums, our predictions mirrored the physiological response observed in these controlled conditions (Figure S7.5).

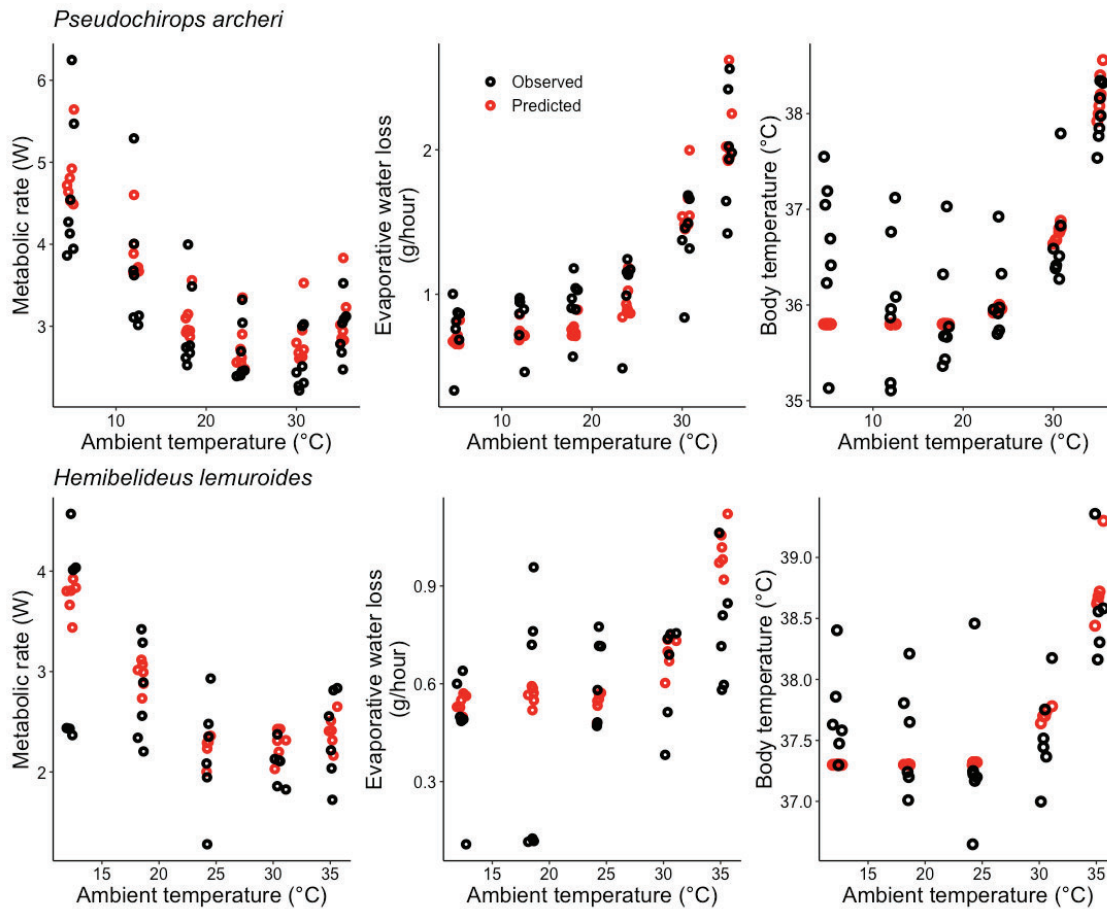


Figure S7.5. Observed and predicted physiological response of two rainforest ringtail possum species under control environmental conditions (metabolic chamber). Red values are derived from the endotherm model (Kearney *et al.* 2021) using the animal model calibrated with values showed in Table S7.3. Black values represent the measured physiological response from Krockenberger, Edwards and Kanowski (2012) and Krockenberger (unpublished). Plots in the top row correspond to *Pseudochirops archeri* while plots in the bottom row correspond to *Hemibelideus lemuroides*.

Field simulations of heat, energy, and water budgets

The next step involved integrating the animal and microclimate model to understand the spatiotemporal physiological responses of rainforest ringtail possums under field conditions in the last 32 years. The biophysical model was implemented using the endotherm model (Kearney *et al.* 2021).

Rain mitigation effect on water loss

Following rainfall, the availability of free water in the environment increases in tropical rainforests. Strict folivores, like ringtail possums, can take advantage by consuming wet foliage, replenishing any water lost throughout the day. However, the canopy's elevated position exposes vegetation to stronger winds than ground level, hastening water evaporation. To account for some of the factors limiting free water availability following rainfall, we defined a conservative threshold of 20 mm of rainfall beyond which water stress could be alleviated. We assumed that daily rainfall surpassing 20 mm can saturate the foliage and surrounding environment, providing ample moisture for folivores even if the rain stopped during the day. Furthermore, we assumed that because of high humidity and lush vegetation in tropical rainforests, free water in the canopy could persist after substantial rain for at least another night, propagating the effect of water stress mitigation. Within our model, we accounted for this compensatory mechanism by temporarily balancing water loss to zero following significant rainfall events.

Feeding ecology data

Foraging activity is crucial for understanding population dynamics as it directly influences resource acquisition, individual fitness, and population growth and distribution. Indeed, constraints in feeding activity have been associated with increasing temperatures for marsupial folivores (Beale *et al.* 2018; Beale *et al.* 2022; Beale *et al.* 2023), suggesting negative implications for population dynamics in the context of climate change (Youngentob *et al.* 2021).

In the biophysical model, foraging activity is not directly calculated, but it is considered a derived product from the activity limitation imposed by physiological constraints (Levy *et al.* 2016; Kearney *et al.* 2018; Briscoe *et al.* 2022). To estimate the potential foraging activity associated with the predicted physiological responses, we used field information on feeding activity obtained from Goudberg (1990). The maximum reported foraging time served as the upper boundary for potential feeding

activity under optimal conditions. According to field observations, *Hemibelideus lemuroides* exhibited a maximum foraging time of up to 6 hours per night, while *Pseudochirops archeri* displayed a maximum of 5 hours. It is important to acknowledge potential uncertainty in the maximum feeding activity for *Pseudochirops archeri*, attributable to low detectability and abundance at the study site where this research was conducted.

Activity scenarios

To accurately represent ringtail possums' physiological responses, we developed seven different activity scenarios that aimed to capture a significant proportion of the daily activity budget for the species. These scenarios ranged from "resting under full shade/inside den" to progressively more active states at 10-minute intervals, mirroring foraging behaviour. Activity scenarios had an associated proportional increase in metabolic cost, imposing higher physiological stress on the animal when selecting more active scenarios (Table S7.4). This incremental foraging activity was derived from feeding ecology studies of captive marsupial folivores under controlled temperature conditions, where the animal gradually decreased in feeding with an increase in ambient temperature (Beale *et al.* 2022).

Table S7.4. Summary of activity scenarios implemented in the study. Metabolic multiplier refers to the increase in basal heat generation derived from each activity level. For instance, a metabolic multiplier of 2 means that the animal doubles the basal heat generation for that scenario.

Species	Scenario	Hourly activity (minutes)	Metabolic multiplier
<i>Pseudochirops archeri</i>	1	0 (resting)	1
<i>Pseudochirops archeri</i>	2	10	1.5
<i>Pseudochirops archeri</i>	3	20	2
<i>Pseudochirops archeri</i>	4	30	2.5
<i>Pseudochirops archeri</i>	5	40	3
<i>Pseudochirops archeri</i>	6	50	3.5
<i>Pseudochirops archeri</i>	7	60	6
<i>Hemibelideus lemuroides</i>	1	0 (resting)	1
<i>Hemibelideus lemuroides</i>	2	10	2
<i>Hemibelideus lemuroides</i>	3	20	3
<i>Hemibelideus lemuroides</i>	4	30	4
<i>Hemibelideus lemuroides</i>	5	40	5
<i>Hemibelideus lemuroides</i>	6	50	6
<i>Hemibelideus lemuroides</i>	7	60	7

Considering the physiological responses in each scenario, the animal selected the optimal activity state for each hour while respecting the species' biology and physiological limitations. For instance, restriction to foraging was imposed when body temperature raised 0.5 °C above the thermoneutral zone (i.e., above 36.3°C for *Pseudochirops archeri* and 37.8°C for *Hemibelideus lemuroides*), leading the animal to select the resting scenario to avoid overheating. We further enforced selecting the resting scenario during the daytime, as rainforest ringtail possums are strictly nocturnal. Total cumulative foraging time was also limited to the maximum foraging potential known for the species (see "Feeding ecology data"). Following these constraints, the animal selected the most optimal hours of the night for foraging, aiming to maximise the foraging potential while minimising energy requirements or water loss (after accounting for the rain mitigation effect). Based on this selection approach, the model naturally avoided selecting unrealistic scenarios, like 50-60 min of continuous activity within the hour, resulting in active-rest-active dynamics (Figure S7.6).

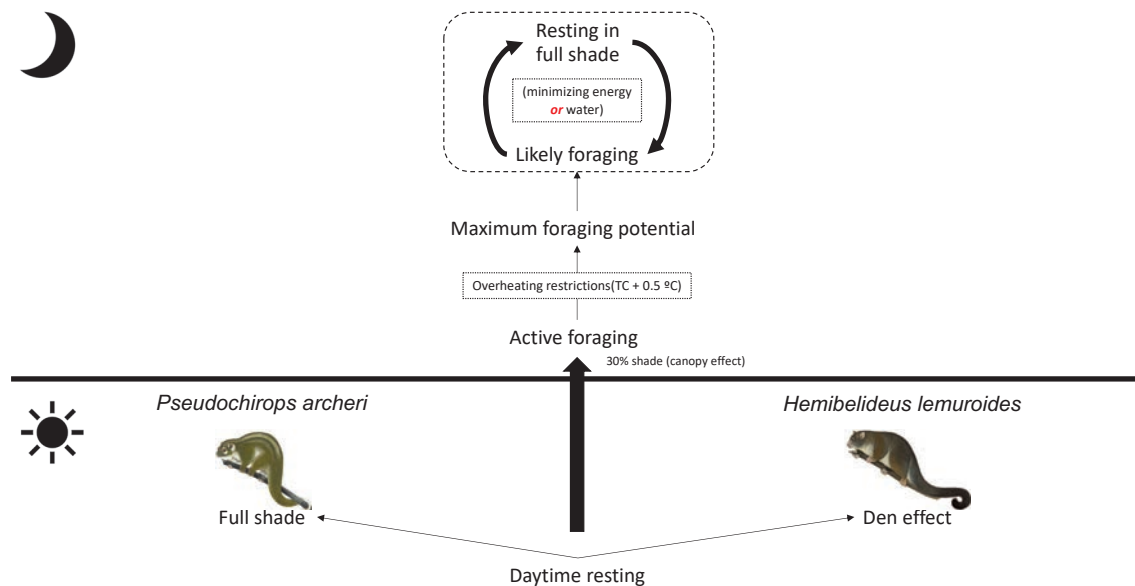


Figure S7.6. Conceptualisation of the scenario selection approach for rainforest ringtail possums. We note differences in the exposure to the environment while resting for *Hemibelideus lemuroides*, as the species would rest in dens during the day but stay in the canopy at night. Therefore, we assumed the animal would not return to the den to rest at night between foraging events, as this behaviour was not observed in the field.

Biophysical model validation through field metabolic rate

We validated the prediction accuracy of our model by comparing predicted energy requirements for each species to observed values in free-living animals (i.e., field metabolic rate). For this purpose, we used our model to predict field metabolic rates for rainforest ringtail possums during the same days and at the exact location that those measured in the field (see “Physiological data”). We note, however, that field metabolic data for *Hemibelideus lemuroides* was collected in 1986, but our microclimate model was generated between 1990-2022. Thus, for this species, we selected the same days of the month for that location but in the year 1990. Additionally, we compared the predicted field metabolic rate for *Hemibelideus lemuroides* to data from a close relative, *Petauroides volans*, as a complementary validation approach.

Our results showed exceptional levels of accuracy. The predicted field metabolic rate for *Pseudochirops archeri* was 381.37 KJ/day compared to 383 KJ/day measured during the same days and location (Krockenberger, unpublished), while for *Hemibelideus lemuroides* predicted field metabolic rate was 533.55 KJ/day compared to 546 KJ/day measured for the species in 1986 (Goudberg 1990) or 521 KJ/day for its close relative (Foley *et al.* 1990). These values indicated an average metabolic multiplier of 1.59 for *Pseudochirops archeri* and 2.43 for *Hemibelideus lemuroides*.

Physiological stress variables

The biophysical model output provides a detailed hourly description of the physiological responses of rainforest ringtail possums across 32 study locations from 1990 to 2022. However, since population models operate on an annual timescale, it was necessary to upscale the relevant biophysical variables for their integration into population dynamics. Moreover, given that summer, the most challenging period physiologically for ringtail possums (Krockenberger, Edwards & Kanowski 2012; Meade *et al.* 2018), straddles two calendar years (November to March), we adjusted our annual metrics—including both population data and physiological responses—to align with “biological years”. These biological years were defined as starting from April rather than January, preceding the birth season for rainforest ringtail possums (Strahan 1995). Therefore, biophysical predictors were included in the population model with one year delay. Because summer stress occurs at the end of the biological year, the derived physiological stress can only impact population dynamics in the following year.

Annual biophysical predictors were designed to capture both the long-term effect of physiological stress and short-term extreme events. Biophysical predictors encompassed four different categories of physiological stress: thermal stress, water loss, energy requirements, and foraging constraints, resulting in a total of eight biophysical predictors (i.e., two predictors per category: long- and short-term stress). Thermal stress was defined as a significant increase in body temperature, with stress values indicating the amount of heat that surpassed a stress threshold each hour. The thermal stress threshold was established as 0.5 °C above the species' thermoneutral zone, consistent with foraging limitation thresholds (refer to "Activity scenarios"). Long-term thermal stress (thermal dosage) was calculated as the cumulative sum of hourly thermal stress over a biological year. Short-term thermal stress was computed by identifying significant stress events in a year, defined as five or more consecutive hours of thermal stress, a limit proposed for the species (Krockenberger, Edwards & Kanowski 2012; Meade *et al.* 2018). Each event's intensity was quantified as cumulative thermal stress, with the most intense event in a year serving as an indicator of extreme short-term thermal stress. Annual predictors for water loss and energy requirements were computed similarly, with long-term values derived from the average duration of stress exceeding the 90th percentile threshold for each species during the year. Short-term water loss and energy requirement stress were assessed as a 4-day cumulative stress, selecting the maximum value in the year. Long-term foraging success was defined as the proportion of nights in a year when the animal achieved 80% or more of its maximum potential foraging, while short-term foraging limitation was defined as the minimum value in a 2-day cumulative foraging time. The shorter cumulative time window used in foraging predictors compared to water and energy stress is attributable to the ringtail possums' limited reserve capacity, relying on continuous foraging for survival. Consequently, a low 48-hour cumulative foraging time was deemed a threat to animal survival. A summary of biophysical predictors is provided in Table S7.5.

Table S7.5. Description of physiological stress variables derived from the biophysical model.

Stress category	Scale	Definition	Units
Thermal	Long-term	Cumulative hourly stress in a year (dosage)	°C
Thermal	Short-term	Highest intensity event in a year. Thermal events are five or more consecutive hours of stress	°C

Water loss	Long-term	Percentage of extreme stress in a year (above the 90 th percentile)	%
Water loss	Short-term	Maximum cumulative four-days water loss	g of H ₂ O
Energy requirement	Long-term	Percentage of extreme stress in a year (above the 90 th percentile)	%
Energy requirements	Short-term	Maximum cumulative four-days energy requirements	KJ
Foraging	Long-term	Percentage of nights in a year with a cumulative foraging time above 80% of the maximum foraging potential	%
Foraging	Short-term	Minimum cumulative two-days relative foraging time	% of potential maximum

The potential confounding effects of energy requirements and elevation

Rainforest ringtail possums abundance increases significantly along the elevational gradient in the Australian Wet Tropics (Kanowski *et al.* 2001; Krockenberger, Edwards & Kanowski 2012; de la Fuente & Williams 2022). However, energy requirements also escalate along the elevational gradient due to the decrease in temperature (Figure S7.7), resulting in a positive correlation between ringtail possum population density and energy demands. Temporally, the effects of climate change in the region have significantly raised temperatures in the last decades (de la Fuente *et al.* 2022). Regional warming has consequently caused a decline in energy requirements over time, potentially resulting in a positive correlation with population dynamics for these species (Figure S7.7). Due to these confounding effects, we refrained from using energy requirement stress as a predictor in the population models.

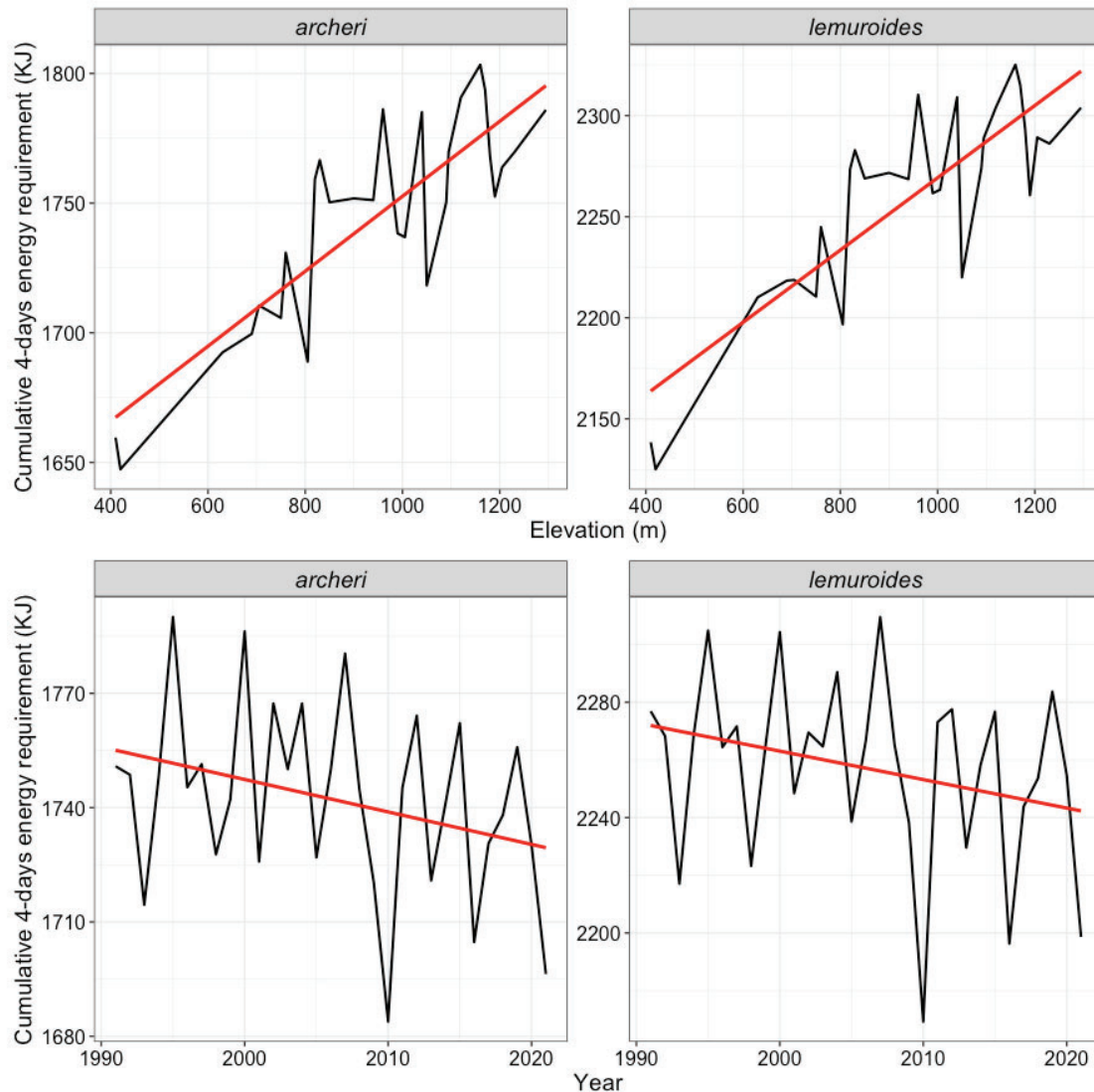


Figure S7.7. Spatiotemporal patterns in energy requirements for two species of rainforest ringtail possums. Black lines represent the cumulative 4-days energy requirements. Red lines represent a linear model fit to visualise the overall tendency along the gradient of interest.

Extended methodology (III): Foliage nutritional chemistry

Foliage data

To study the spatial patterns in nutritional quality, we selected three abundant and widespread canopy tree species considered important in rainforest ringtail possums' diet (Goudberg 1990; Jones, Maclagan & Krockenberger 2006). These selection criteria were not intended to represent the region's rich tree biodiversity or

ample ringtail possums' diet but to encompass the desirable biogeographical characteristics that allowed us to investigate the variability of foliage quality across the landscape for some important trees species in ringtails' diet (Table S7.6). These species included *Alphitonia petriei*, *Flindersia brayleyana*, and *Flindersia pimenteliana*.

Table S7.6. Overview of the elevational range, habitat preference, growth strategy, sample size, and site coverage for the selected canopy tree species.

Species name	Family	Elevational range (m a.s.l.)	Habitat	Sample size	Site coverage
<i>Alphitonia petriei</i>	Rhamnaceae	0 – 1,300	Generalist; Rainforest regrowth; Pioneer species	115	100%
<i>Flindersia brayleyana</i>	Rutaceae	0 – 1,150	Well-developed montane rainforest; Late successional species	22	48%
<i>Flindersia pimenteliana</i>	Rutaceae	0 – 1,300	Well-developed montane rainforest; Late successional species	42	60%

Foliage samples were collected from selected canopy trees (sample height: 24.71 ± 6.28 m) during the dry seasons (April-November) of 2021 and 2022, following the methods outlined by Youngentob, Zdenek and van Gorsel (2016). Foliage material from retrieved canopy branches was snap-frozen in the field using dry ice at -80°C to preserve their chemical composition for subsequent analyses.

Foliage nutritional chemistry

Measures of foliage nutritional quality for herbivores often consider the influence of nitrogen (N) as a significant limiting factor due to its relatively low concentration in plant tissues (White 2012). However, the total nitrogen content in leaves may not always accurately reflect the availability of this limiting factor for all herbivores. To account for some of the factors influencing nitrogen availability for ringtail possums across the landscape, we also included a measure of foliar nitrogen that incorporates the influence of tannins and fibre on nitrogen digestibility (Wallis *et al.* 2012). A summary of the foliage nutritional predictors considered in the model is provided in Table S7.7.

To measure the effect of tannins on nitrogen digestibility, we followed the method outlined by DeGabriel *et al.* (2008). This method consists of an in vitro digestion where paired samples are incubated in a series of buffers and enzymes. Total nitrogen and non-digestible nitrogen are measured in a Truspec Carbon/Nitrogen Analyser (LECO Corp, St. Joseph, MI), using the pre- and post-digestion samples, respectively. Available nitrogen is then calculated as a function of the change in nitrogen and dry matter, determined by comparing samples' weight and nitrogen concentration before and after digestion. Paired samples are digested in a solution with and without polyethylene glycol (PEG) to measure the binding capacity, a functional measure of tannins (Silanikove *et al.* 1996). The effect of tannins on nitrogen availability was derived from the difference in available nitrogen in samples digested with and without PEG. Further details on the calculation of available nitrogen, tannins effect, and lab protocol have been extensively covered in DeGabriel *et al.* (2008) and Wallis *et al.* (2012).

Before chemical analyses, foliage samples were freeze-dried and ground to pass through a 1 mm particle-size sieve. Ground samples were scanned on a Foss XDS near-infrared reflectance spectrometer. Chemical assays were performed on a representative subset of samples, comprising 33% of our sample size, which was selected based on its near-infrared absorption spectrum and identified using Mahalanobis distance. Calibration equations were developed to predict values of foliar chemistry based on the spectra and reference values obtained from the chemical assays, following the approach outlined by Ebbers *et al.* (2002). This method allowed for a rapid, cost-effective, and non-destructive assessment of foliage nutritional chemistry by establishing a relationship between spectral information and nitrogen content (Youngentob *et al.* 2012). The calibration equations derived from this process led to a robust prediction of total nitrogen ($R^2 = 0.98$, standard error of cross-validation [SECV] = 0.06), non-PEG available nitrogen ($R^2 = 0.96$, SECV = 0.1259), PEG available nitrogen ($R^2 = 0.99$, SECV = 0.07), and dry matter digestibility ($R^2 = 0.91$, SECV = 3.68). Further details about the spectral transformations and the development of the calibration equations can be found in Youngentob *et al.* (2012).

Table S7.7. Summary of foliage nutritional predictors considered in the population model.

Variable	Description	Units

Total N	General measure of total nitrogen content in foliar tissue prior digestion	%
Available N	Measure of nitrogen availability for ringtail possums after digestion	%
Tannins effect	Amount of available nitrogen bound to PEG	%

Soil data

The characterisation of soil chemistry was carried out at the site level. Our sampling design aimed to capture the heterogeneity in soil composition, deriving the average conditions trees were exposed at each location. We randomly selected six 150 m transects at each site with a minimum separation of 200 m between them. Along these transects, we collected soil cores every 50 m using a 65 mm Jarret-style auger. To account for the vertical variation in soil chemistry, we collected soil cores at three different depths at each sampling point (0-10 cm, 20-30 cm, and 50-60 cm). For each site and depth, samples were homogenised in the field, resulting three samples per study location. Samples were sent to the Chemistry Centre (Department of Environment and Science, Queensland Government, Brisbane, Australia) for chemical analysis promptly after collection (< 5 days). Soil components analysed included total nitrogen and phosphorus (Kjeldahl digestion), exchangeable cations (Ca, Mg, Na, K), and organic carbon (Dumas combustion). To establish a comparable measure of soil elements across sites, we computed the mean value of each element across the vertical gradient, partly accounting for the potential effect of soil depth on nutrient acquisition (Göransson *et al.* 2006).

Climate data

The climatic data used in the biogeochemical model was obtained from the “accuCLIM” climate layers developed for the Australian Wet Tropics (Storlie *et al.* 2013). Climate information included annual temperature and precipitation across the 32 study locations, averaged between 1990 and 2016. The “Microclimate validation” section explains this dataset in more detail.

Biogeochemical model

Foliage nutritional chemistry and soil composition were measured across 78% of the study sites (25/32; Table S7.8). However, to construct a comprehensive population model, predictions of foliage quality were required for all 32 study sites. To

achieve this, we employed a hierarchical biogeochemical model to capture the spatial pattern in foliage quality by integrating bottom-up processes that influence nutritional chemistry across the landscape (Figure S7.8). This method allowed for the stochastic imputation of missing soil element concentration and foliage nutritional chemistry based on climate, soil nutrients, and geological information.

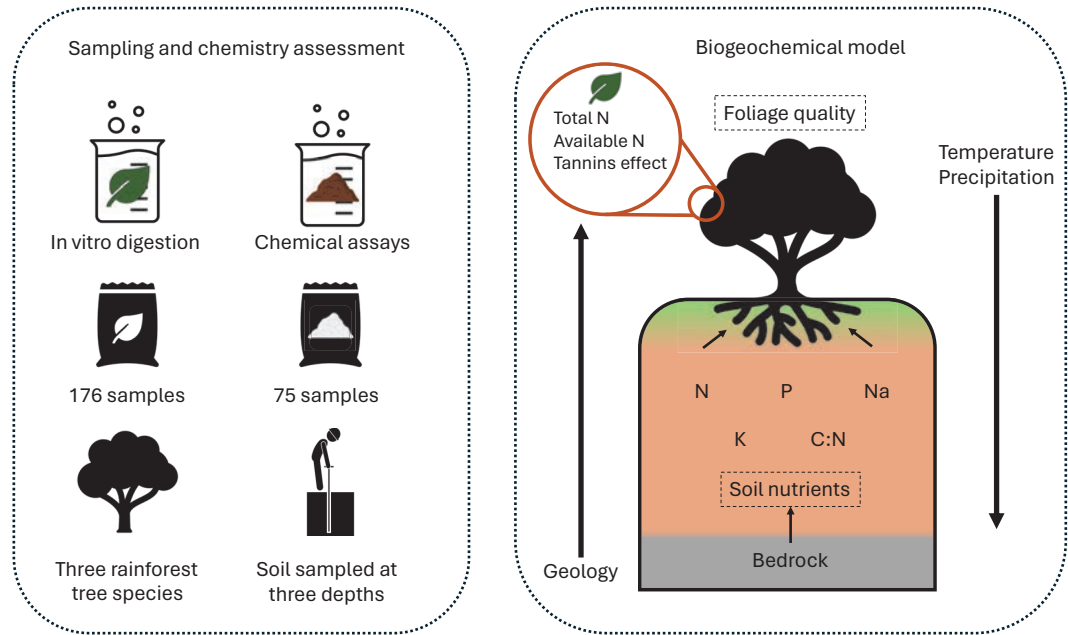


Figure S7.8. Conceptualisation of data collection and integration in the biogeochemical model.

Table S7.8. Description of the 32 long-term monitoring sites for rainforest ringtail possum populations.

Site ID	Geology	Elevation (m)	Latitude	Longitude	Mean Annual Precipitation (mm)	Mean Annual Temperature (°C)	Soil and foliage chemistry
AU10A	basalt	940	-17.7062	145.5267	1946.19382	18.2770004	observed
AU4A	basalt	410	-17.608226	145.769781	3325.91078	21.8910008	observed
AU6A	basalt	630	-17.673722	145.71513	2953.89001	20.3050003	observed
AU7A	granite	690	-17.631963	145.693306	2926.42775	20.2099991	observed
AU7B	basalt	750	-17.618911	145.68341	3485.48296	20.1720009	observed
AU8A	basalt	850	-17.603419	145.632515	3099.89512	18.8500004	observed
AU8B	basalt	820	-17.597161	145.646271	3031.61144	18.5830002	observed
AUAC	basalt	830	-17.743289	145.534109	2124.41302	18.2810001	observed
AUAD	basalt	760	-17.770123	145.547467	1792.43365	18.9659996	observed
AUSR	rhyolite	900	-17.7154	145.5267	2028.3956	18.3850002	observed
CU10A	granite	1050	-16.556704	145.276664	2671.55869	17.3390007	observed
CU11	granite	1120	-16.529514	145.284013	1732.86775	15.4960003	observed
CU12A	granite	1190	-16.516485	145.275519	2372.22501	15.1569996	observed

CU6A	granite	630	-16.577398	145.309423	1616.30773	20.3509998	observed
CU8A	granite	805	-16.584539	145.303007	2155.69822	20.2539997	observed
G5	rhyolite	1040	-17.688477	145.507957	1948.67603	17.6100006	observed
HRG1	rhyolite	1160	-17.454248	145.476429	2067.48736	16.6340008	observed
HRG3	granite	1230	-17.286008	145.426695	1369.47718	17.4430008	observed
HRG3A	granite	1170	-17.316392	145.419989	1849.89389	17.2269993	observed
LU10	granite	990	-17.102851	145.590055	1941.90305	19.1749992	observed
LU11	granite	1090	-17.092501	145.618886	1953.35974	18.3050003	observed
LU12	granite	1180	-17.096672	145.577881	1714.58576	18.0890007	observed
LU7	granite	705	-17.124248	145.629435	1831.17529	20.4969997	observed
LU8	granite	760	-17.117477	145.602962	1715.59607	20.5629997	observed
LU9	granite	900	-17.103734	145.611918	2022.01865	19.2280006	observed
CU4A	granite	420	-16.53464	-16.53464	2712.895	23.409	predicted
AU10B	basalt	960	-17.69998	145.5211	1958.961	18.282	predicted
WU10A	granite	1005	-16.28245	-16.28245	1601.59	17.774	predicted
WU11A	granite	1095	-16.25920	-16.25920	2457.223	17.169	predicted
WU12A	granite	1205	-16.24498	-16.24498	1555.7	16.804	predicted
WU13A	granite	1295	-16.23247	-16.23247	2077.12	16.78	predicted
WU9A	granite	940	-16.28514	-16.28514	1789.44	18.94	predicted

This multilevel model comprised five soil sub-models representing nutrient availability for plants: Na, N, P, K, and the C:N ratio (Wright *et al.* 2005; Read *et al.* 2008; Santiago *et al.* 2012; Weil & Brady 2017; Kaspari 2020; Peng *et al.* 2021; Lynn, Fridley & Vandvik 2023; Singh Ramesh 2023; Westerland *et al.* 2023). Soil element concentrations were modelled hierarchically as functions of climate variables (mean annual temperature and precipitation) and the geological origin of each site (basalt, granite, or rhyolite). In conjunction with soil nutrient predictions, these factors informed three foliar nutritional sub-models: total N, available N, and tannins effect (Figure S7.9). The transference of uncertainty from soil predictions to foliage chemistry predictions was implemented directly through the Bayesian hierarchical model, with each model level being fit simultaneously. Species variability in foliar chemistry was accounted for by incorporating species-specific intercepts and slopes. The sample size for each model is provided in Table S7.9 and a description of the study sites is provided in Table S7.8. The biogeochemical model can be formalised as follow:

$$\begin{aligned}
 \text{Soil}_{i,\text{element}} &\sim \text{Normal}(\mu_{i,\text{element}}, \tau_{\text{element}}) \\
 \mu_{i,\text{element}} &= \alpha_{\text{element}} + \beta_{\text{element}} * X_i(\text{climate \& geology}) \\
 \text{Foliage}_{i,\text{tr},s,\text{component}} &\sim \text{Normal}(\mu_{i,\text{tr},s,\text{component}}, \tau_{s,\text{component}})
 \end{aligned}$$

$$\mu_{i,tr,s,component} = \alpha_{s,component} + \beta_{s,component} \\ * X_{i,s,component}(Soil\ elements, climate \& geology)$$

Soil element concentration $Soil_{i,element}$ at site i is modelled as a normal distributed variable with mean $\mu_{i,element}$ and precision $\tau_{element}$. The mean soil element concentration is then modelled as a function of climate and geology. Foliage component (total N, available N, and tannins effect) $Foliage_{i,tr,s,component}$ at each site i , tree tr , and species s , is also modelled as a normal distributed variable with mean $\mu_{i,tr,s,component}$ and precision $\tau_{s,component}$. The mean for each foliage nutritional chemistry component is then modelled as a function of soil element concentration, climate, and geology.

Table S7.9. Summary of sample size and treatment of the datasets used in each sub-model.

Sub-model	Scale	Data collected	Data treatment	Sample size for the model
Soil	Site	For each of the 25 sites, three samples were collected at three different depths	Chemical concentration for each soil element was averaged across the vertical gradient	25
Foliage	Tree	179 canopy trees were collected for three different species	Chemical assays were performed on a representative subsample (33%) selected based on near-infrared spectroscopy techniques.	179
Climate	Site	Data retrieved from spatial climate layers	Mean annual temperature and precipitation were extracted from spatial layers adjusted for the region	32

The overall nutritional value for ringtail possums at a site was determined based on the maximum total/available N and the minimum tannins impact, as we assumed that ringtail possums would selectively forage optimal trees to achieve maximum diet quality while minimising metabolic costs. Biogeochemical dynamics were directly integrated into the population model, enabling the transfer of uncertainty derived from the predictive error in the soil and foliage models (Figure S7.9).

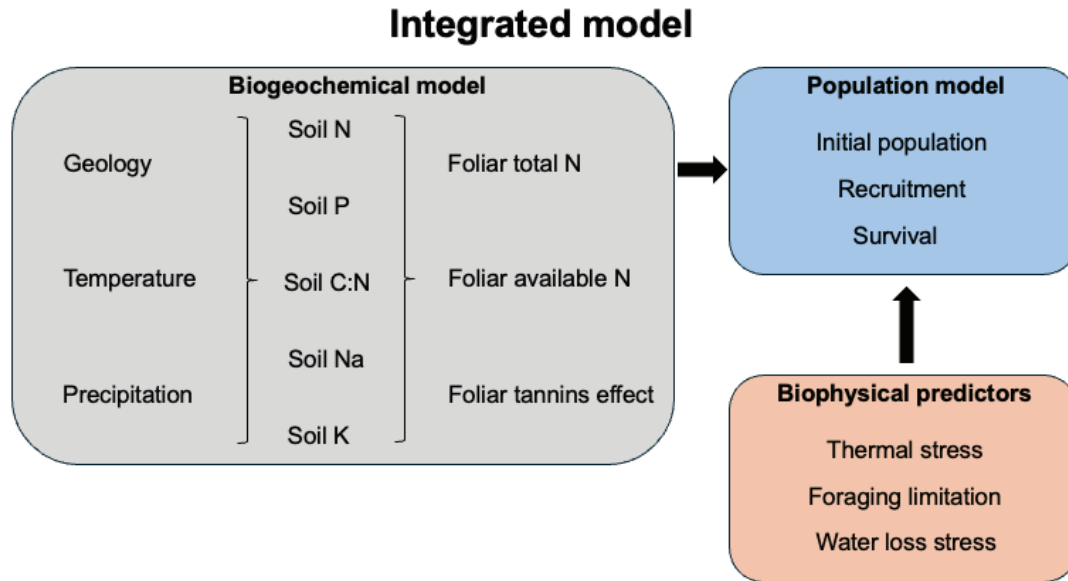


Figure S7.9. Conceptual figure of the model integrating biogeochemical dynamics and biophysical variables into population modelling. In the biogeochemical model, all values on the left side of the bracket were included as predictor of the responses on the right side of the bracket. For example, Soil P was modelled as a function of geology, temperature, and precipitation, while foliar total N was modelled as a function of geology, temperature, precipitation and all soil elements (N, P, C:N, Na, and K).

Markov Chain Monte Carlo methods were used to sample the joint posterior distribution (Thompson & Brooks 2003) using JAGS (Plummer 2003), implemented with the jagsUI R package (Kellner 2021; R Core Team 2021). We reflected the absence of prior information about biogeochemical model parameters by implementing normally distributed vague priors. We ran three parallel chains of 400,000 interactions, used half as burn-in, and thinned the rest by one in 100 to obtain 6,000 samples of the joint posterior distribution. The sampling process led to robust parameters convergence ($\hat{R} - 1 < 0.1$, (Gelman & Hill 2006)). We further inspected traceplots to validate good mixing and investigated the posterior predictive check by plotting the residual sums of squares for observed and simulated data. Good fitting models are expected to have values falling on a 1:1 line, suggesting a similar error structure between the observed data and the data simulated by the model (Figure S7.10). We paired the posterior predictive checks with the estimation of Bayesian p-values, with values close to 0.5 indicating adequate model fit (Gelman, Meng & Stern

1996). The JAGS code used to implement the integrated biogeochemical and population model can be found below.

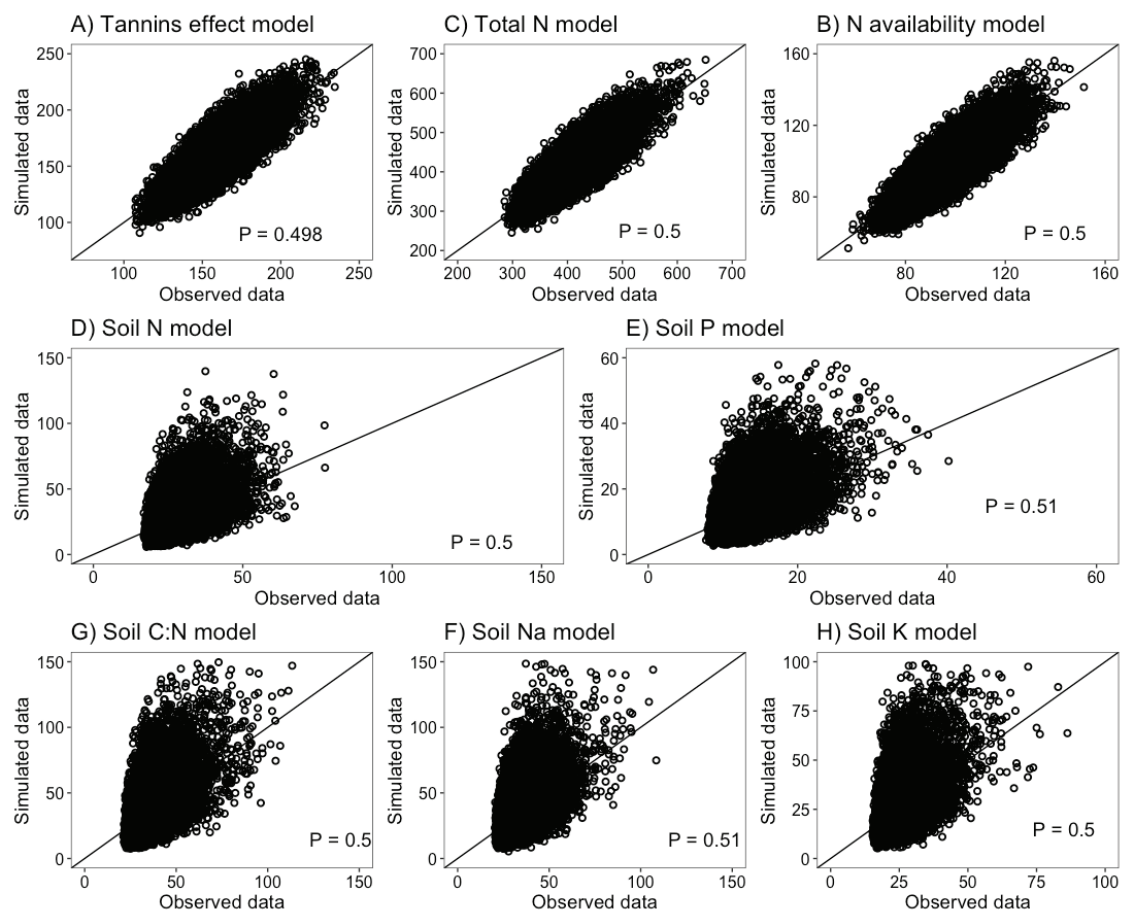


Figure S7.10. Posterior predictive check and Bayesian p-value for the biogeochemical sub-models.

Results from the biogeochemical model are extensively discussed in a separate paper currently under review. However, we offer a matrix displaying the associations among factors influencing biogeochemical dynamics in the Wet Tropics (Table S7.10). Overall, our model captured the drivers of soil and foliage chemistry across the landscape, resulting in robust predictions of soil nutrients and foliage quality for the seven unsampled study sites.

Table S7.10. Association matrix showing the significant relationships driving biogeochemical dynamics in the Wet Tropics. Rows represent responses and columns predictors, with the sign indicating a positive (+) or negative (-) effect.

	Temperature	Precipitation	Soil N	Soil P	Soil C:N	Soil K	Soil Na	Basalt origin
Soil N		+						+

Foliage sub- models	Soil P		+			+
	Soil C:N	-	-			+
	Soil K	+	-			+
	Soil Na	-				+
	Total N	+	-			+
	Available N	+		-	+	-
	Tannins				-	-

Extended methodology (IV): Population dynamics

Population data

The long-term spotlight monitoring scheme in the Australian Wet Tropics was established in 1992 to investigate the ecology and population trends of rainforest ringtail possums under the influence of climate change pressures (Williams, Pearson & Walsh 1995; Williams *et al.* 2010; de la Fuente & Williams 2022). By the end of 2022, a total of 974 spotlight surveys were conducted across 32 rainforest locations. These survey sites were selected to cover the entire elevation gradient across the species distribution, prioritising locations within large rainforest patches while avoiding habitat edges. We note that not all locations were surveyed yearly due to the extensive spatial scale covered by the study site network, resulting in an uneven temporal survey effort (Table S7.11).

Table S7.11. Temporal survey coverage across the 32 study locations.

Site ID	Elevation (m)	Temporal coverage (% of years with at least 1 survey)
AU10A	940	84
AU4A	410	55
AU6A	630	61
AU7A	690	45
AU7B	750	26
AU8A	850	71
AU8B	820	13
AUAC	830	42
AUAD	760	35
AUSR	900	19
CU10A	1050	52
CU11	1120	10
CU12A	1190	48
CU6A	630	42
CU8A	805	52

G5	1040	29
HRG1	1160	19
HRG3	1230	16
HRG3A	1170	6
LU10	990	16
LU11	1090	42
LU12	1180	16
LU7	705	39
LU8	760	16
LU9	900	42
CU4A	420	35
AU10B	960	29
WU10A	1005	13
WU11A	1095	36
WU12A	1205	16
WU13A	1295	32
WU9A	940	32

Surveys were conducted along 1000-meter line transects on small roads or tracks, ensuring reasonable visual access to the entire forest structure up to the canopy, where significant ringtail possum activity occurs. We aimed to maintain a consistent survey effort throughout the 31 years of monitoring by adopting a standardised pace of 4-5 minutes of active searching per 100 meters, resulting in a consistent total search time ranging between 40 and 50 minutes per survey. However, the number of observers fluctuated over the years, averaging 2.7 ± 1.7 surveyors. This variation in the number of observers was accommodated in the model to account for the potential effect on the species' detection. Whenever possible, surveys were replicated multiple times within the same week to address potential variation in detection probability. While survey effort was not restricted to a specific season, accessibility to sites was occasionally limited by weather conditions, leading to most surveys being conducted between April and November, corresponding with the dry season.

Population model

We employed an extension of the classic N-mixture population model (Royle 2004) incorporating a formal description of population dynamics (Dail & Madsen 2011) to explore the impact of physiological stress and foliar nutritional chemistry on the vital rates of rainforest ringtail possums. These models facilitate the estimation of vital rates

such as survival and recruitment, as well as population growth and abundance, using simple counts of unmarked individuals replicated across space and time. Importantly, they explicitly account for imperfect detection, enhancing the accuracy of the estimations (Kéry *et al.* 2009; Kéry & Royle 2020). Additionally, these models are suited to deal with missing years and variability in survey efforts (Kéry & Royle 2020), providing a robust framework to analyse population data for rainforest ringtail possums.

Our population model, based on the approach outlined by Bellier, Kéry and Schaub (2016), integrates density dependence and spatiotemporal covariates into the estimation of vital rates. This strategy helps mitigate estimation bias when the parametric assumptions of constant probability of survival and recruitment are violated, particularly in cases of declining populations (Dail & Madsen 2011). The effects of density dependence on population dynamics were tested following the model selection outlined in Bellier, Kéry and Schaub (2018), suggesting that density dependence was acting only on recruitment for both species.

Estimating vital rate parameters from counts of unmarked individuals involves a formal description of the processes driving population change over time. Our model assumes a pre-breeding census (Caswell 2000) where population growth rate is the sum of survival and recruitment. Temporal fluctuations in abundance at a particular location are characterised by the sum of survivors from the previous year and the number of new individuals at that site. Therefore, apparent survival encompasses mortality and emigration, while recruitment includes birth and immigration. The hierarchical model can be formalised as follow:

$$\begin{aligned}
 N_{i,1} &\sim \text{Poisson}(\lambda_{i,1}) \text{ (Initial population in year 1992)} \\
 R_{i,t} &\sim \text{Poisson}(N_{i,t-1} \gamma_{i,t}) \text{ (Recruitment between 1993 – 2022)} \\
 S_{i,t} &\sim \text{Binomial}(N_{i,t-1}, \phi_{i,t}) \text{ (Survival between 1993 – 2022)} \\
 N_{i,t} &= R_{i,t} + S_{i,t} \text{ (Population between 1993 – 2022)} \\
 C_{i,j,t} &\sim \text{Binomial}(N_{i,t}, \rho_{i,j,t}) \text{ (Observation proccess between 1992 – 2022)} \\
 \log(\lambda_{i,1}) &= \lambda_0 + \beta_a * X_{i,a} \text{ (Initial abundance)} \\
 \text{logit}(\rho_{i,j,t}) &= \rho_0 + \beta_d * X_{i,j,t,d} + \varepsilon_{i,j,t} \text{ (Detection probability)} \\
 \log(\gamma_{i,t}) &= \gamma_0 + \beta_r * X_{i,t,r} \text{ (Recruitment rate)} \\
 \text{logit}(\phi_{i,t}) &= \phi_0 + \beta_s * X_{i,t,s} + (N_{i,t-1} - \bar{N}) \text{ (Survival rate)}
 \end{aligned}$$

Population size, $N_{i,1}$, at site i in the first year (1992) is assumed to be a Poisson random variable with expected abundance $\lambda_{i,1}$. The expected abundance is then modelled as a response of spatial factors, the effect of which is determined by β_a . The number of surviving individuals from one year to the next, $S_{i,t}$, is modelled as a binomial distribution with success probability being apparent survival $\phi_{i,t}$. The number of recruits, $R_{i,t}$, is assumed to be drawn from a Poisson distribution with a mean defined by recruitment rate $\gamma_{i,t}$. Apparent survival and recruitment rate are then modelled as a function of physiological stress variables, with density dependence ($N_{i,t-1} - \bar{N}$) additionally influencing the recruitment rate for these species. Starting in year 1993, population size is derived from the sum of new recruits and survivors from the previous year, so that population size has the Markov property. Lastly, the observation process is determined by the observed counts $C_{i,j,t}$ at site i , survey j , and year t . The observed counts are assumed to be drawn from a binomial distribution with success probability $\rho_{i,j,t}$, which corresponds with the detection probability. Detection probability is then modelled as a function of the number of observers and potential activity while accounting for extra unexplained heterogeneity among surveys ($\varepsilon_{i,j,t}$). Potential change in detection probability over time is also accounted for by including a year-segregated intercept ($\rho 0_t$). A summary of the predictors considered in each model is provided in Table S7.12.

The population model was integrated into the same Bayesian framework as the biophysical model. Thus, these models shared the same characteristics related to their implementation and posterior sampling using JAGS. Vague priors were used throughout the model to express the absence of prior information for the modelled parameters (see JAGS code). The sampling process led to acceptable convergence of all parameters ($\hat{R} - 1 < 0.1$, (Gelman & Hill 2006)). Traceplots and posterior predictive validations indicated a good model fit (Figure S7.11), leading to a Bayesian p-value close to 0.5 (Gelman, Meng & Stern 1996). The JAGS code used to implement the integrated biogeochemical and population model can be found below.

Table S7.12. Summary of predictors considered for each model level.

Predictor	Scale	Level
Elevation	Spatial	Initial abundance
Total foliar N	Spatial	Initial abundance
Available foliar N	Spatial	Initial abundance

Tannins effect	Spatial	Initial abundance
Water loss (long- and short-term)	Spatiotemporal	Survival and recruitment
Thermal stress (long- and short-term)	Spatiotemporal	Survival and recruitment
Foraging performance (long- and short-term)	Spatiotemporal	Survival and recruitment
Density dependence	Spatiotemporal	Survival and recruitment
Number of observers	Survey level	Detection
Potential activity	Survey level	Detection

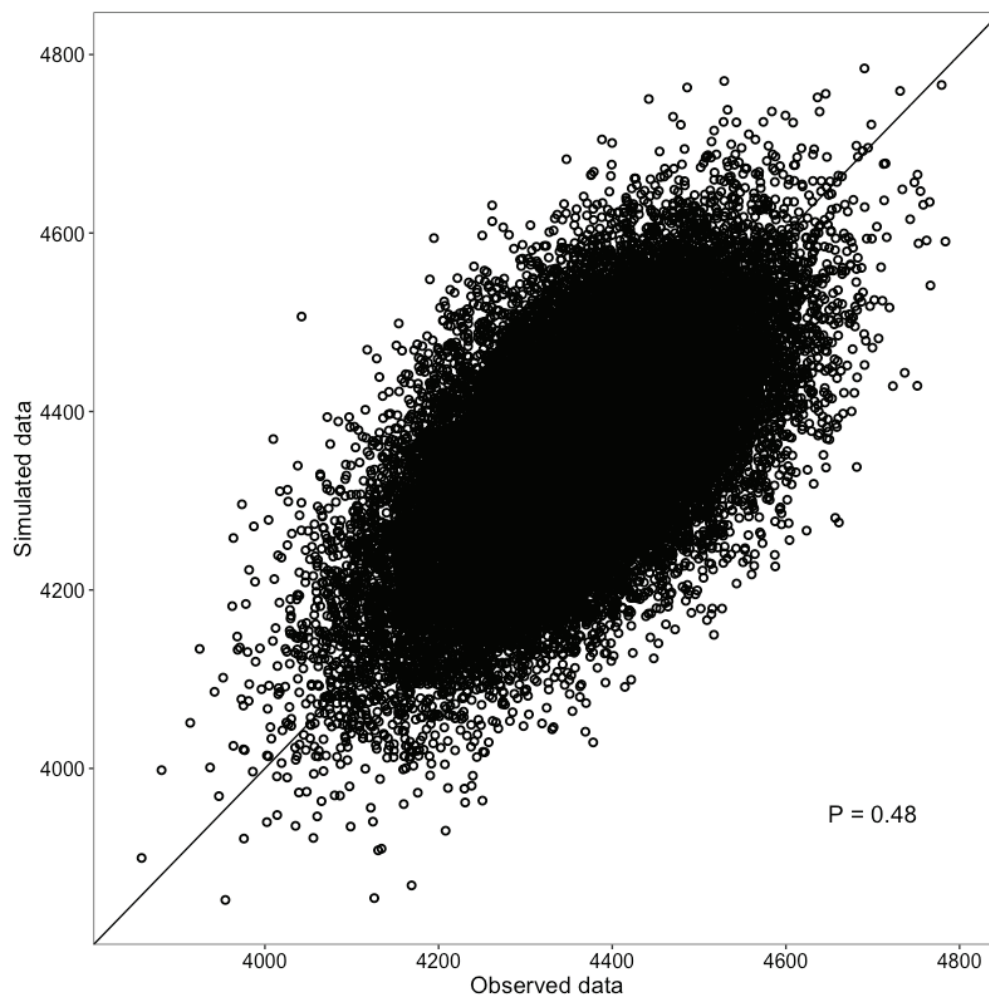


Figure S7.11. Posterior predictive check for the population model.

Detectability and foraging potential

In modelling animal populations, it is common practice to incorporate the survey date as a covariate in the detection process (Kéry *et al.* 2009). This approach is justified by the fact that many animals exhibit seasonal patterns of activity. By including the date as a linear and quadratic covariate, these seasonal patterns can be captured, potentially explaining detection probability in the model (Kéry *et al.* 2009). However, in

this study, we have explicitly captured the hourly potential activity for the species within the biophysical model (see “Activity scenarios”). Consequently, we explicitly accounted for the effect of activity on detection by computing the total expected activity for each ringtail possum species at the exact location and night where the surveys were conducted. We expected a positive correlation between animal activity and our ability to detect the species.

Model selection

Model selection is difficult in the Bayesian framework, particularly with hierarchical models with latent states like those implemented here, where the same observed data can arise from very different combinations of latent processes (Hooten & Hobbs 2015). To decide what variables were important in explaining the population dynamics (initial abundance, recruitment, and survival), we followed a variable selection that included five steps.

Step 1: Correlation matrix

In the first step, we conducted a correlation matrix analysis to identify pairs of highly correlated variables, which could potentially lead to multicollinearity issues. Variables with a correlation coefficient exceeding 0.7 were deemed unsuitable for inclusion in the same model (Table S7.13; Table S7.14). In subsequent steps, variable selection was implemented while respecting the correlation coefficient threshold defined here.

Table S7.13. Correlation matrix for spatial-only predictors

	Elevation	Total foliar N	Available foliar N	Tannins effect
Elevation		-0.09	-0.11	0.08
Total foliar N			0.27	0.44
Available foliar N				-0.72

Table S7.14. Correlation matrix for spatiotemporal biophysical predictors. LT correspond to long-term while ST correspond to short-term variables. Purple values correspond to *Hemibelideus lemuroides* while black values correspond to *Pseudochirops archeri*.

	Water loss (LT)	Water loss (ST)	Thermal stress (LT)	Thermal stress (ST)	Foraging performance (LT)	Foraging performance (ST)
Water loss (LT)		0.16/0.51	-0.52/-0.22	-0.61/-0.23	0.87/0.8	0.78/0.59

Water loss (ST)	0.01/-0.19	0.11/-0.18	0.23/0.45	0.08/0.35
Thermal stress (LT)		0.87/0.94	-0.62/-0.21	-0.60/-0.29
Thermal stress (ST)			-0.67/-0.22	-0.75/-0.3
Foraging performance (LT)				0.86/0.7

Step 2: Defining the initial population model

In the second step, we aimed to determine what spatial variables best explained the initial population size for each species (Table S7.12). We constructed models incorporating all possible combinations of variables while keeping the dynamic components of the model (survival and recruitment) constant. This process resulted in two potential initial abundance models for each species, one informed by elevation, total N, and available N, while the other model included elevation, total N, and tannins effect, avoiding highly correlated variables in the same model (Table S7.13). To determine the significance of each spatial variable, we employed a conservative threshold. Variables demonstrating an effect with a posterior probability exceeding 0.8 were retained for further analysis, while variables with higher uncertainty were considered unimportant in explaining spatial patterns in abundance for these species (Table S7.15). This process yielded a robust representation of the spatial pattern in abundance for rainforest ringtail possums, with elevation and total foliar N explaining the initial population of *Hemibelideus lemuroides*, while only elevation was retained in the initial population model for *Pseudochirops archeri*.

Table S7.15. Summary of variables retained after the second step of the model selection. Crossed variables represent those variables deemed unimportant as their posterior probabilities were below 0.8.

<i>Hemibelideus lemuroides</i>	<i>Pseudochirops archeri</i>
Elevation	Elevation
Total foliar N	~~Total foliar N~~
~~Available foliar N~~	~~Available foliar N~~
~~Tannins effect~~	~~Tannins effect~~

Step 3: Identifying unimportant biophysical variables

The predictors derived from the biophysical model represented different aspects of physiological stress for rainforest ringtail possums. However, some of these stress factors are inherently linked (and in some cases highly correlated), as they result from the same environmental conditions affecting the animal. For example, thermal stress in a particular year may coincide with a corresponding water loss effect, as thermoregulatory processes often involve the use of water for cooling. In this step, we focussed on discerning what factors were potentially limiting animal fitness and thereby influencing population dynamics. For instance, following the example above, we needed to identify what factor was limiting population growth in that example year: overheating or dehydration. Since recruitment and survival are parallel processes connected in the model, non-limiting variables would show instability when paired with different factors because of the different domains of the available variability in the data they could explain. For instance, in the example above, if dehydration is the limiting factor, then water stress would consistently show a strong impact on population dynamics, while thermal stress would show an influence only when paired with variables that do not compete to explain the same variability in the data.

To systematically explore the influence of different factors on vital rates, we ran all potential combinations of univariate models for survival and recruitment ($n = 64$). We retained those variables that consistently influenced either process of population dynamics. Throughout this variable selection process, we also accounted for the effect of density dependence on recruitment for both species (see "Population model" section). Variables demonstrating a consistent influence were those with an effect exceeding a posterior probability threshold of 0.8. This process showed that only foraging performance variables were limiting for *Hemibelideus lemuroides*, while only short-term water loss was unimportant in explaining the population dynamics of *Pseudochirops archeri* (Table S7.16).

Table S7.16. Summary of variables retained after the third step of the model selection. Crossed variables represent those variables deemed unimportant based on the posterior probability threshold of 0.8. LT refers to long-term and ST refers to short-term.

<i>Hemibelideus lemuroides</i>	<i>Pseudochirops archeri</i>

~~Water loss (LT)~~	Water loss (LT)
~~Water loss (ST)~~	~~Water loss (ST)~~
~~Thermal stress (LT)~~	Thermal stress (LT)
~~Thermal stress (ST)~~	Thermal stress (ST)
Foraging performance (LT)	Foraging performance (LT)
Foraging performance (ST)	Foraging performance (ST)
Density dependence (recruitment only)	Density dependence (recruitment only)

Step 4: Potential additive effect of biophysical factors

In the fourth step, we explored the potential additive effects of biophysical variable pairs in explaining the spatiotemporal patterns of recruitment and survival. For *Hemibelideus lemuroides*, the variable selection was concluded in the third step due to the high correlation between the foraging performance variables (Table S7.14). The best univariate combination of these variables in the dynamic part of the model was selected for the final model of this species. However, for *Pseudochirops archeri*, we investigated all potential models integrating two biophysical variables in each process while still considering the influence of density dependence on recruitment. This process resulted in a total of 15 potential combinations. Following the approach outlined in step three, we tracked the effect of each variable on the survival and recruitment processes for each model. Variables demonstrating consistent poor predictive power (posterior probability lower than 0.8) for either process were considered non-limiting variables. The results from this step indicated no additive effect of any pair of biophysical variables explaining recruitment for *Pseudochirops archeri*. However, four variables consistently showed an additive effect on survival (Table S7.17).

Table S7.17. Summary of variables retained after the fourth step of the model selection for *Pseudochirops archeri*. Crossed variables represent those variables deemed unimportant based on the posterior probability threshold of 0.8. LT refers to long-term and ST refers to short-term.

<i>Survival</i>	<i>Recruitment</i>
Water loss (LT)	Water loss (LT)
Thermal stress (LT)	~~Thermal stress (LT)~~
Thermal stress (ST)	~~Thermal stress (ST)~~
Foraging performance (LT)	Foraging performance (LT)
~~Foraging performance (ST)~~	Foraging performance (ST)
	Density dependence

Step 5: Final model for Pseudochirops archeri

Results from the previous step showed that the survival process was defined by the additive effect of multiple combination of two biophysical variables, while the recruitment process was defined by one among three potential biophysical variables in association with the density dependence effect (Table S7.17). We tested for all possible two-variable combinations in the survival process and one biophysical variable plus density dependence in the recruitment process. Consistent with previous steps, we retained only models in which all variables showed a consistent effect with a posterior probability greater than 0.8. Of the 11 competing models, only two suggested robust predictions of population dynamics:

Model 1

Survival ~ Thermal stress (LT) + Foraging performance (LT)

Recruitment ~ Water stress (LT) + Density dependence

Model 2

Survival ~ Thermal stress (ST) + Water stress (LT)

Recruitment ~ Foraging performance (LT) + Density dependence

The two final models for *Pseudochirops archeri* showed very similar structure and predictive power. The differing characteristics between the models relate to the position of foraging performance and water stress in their influence on population dynamics. Although the variable effects were robust in both cases with a posterior probability greater than 0.95 (traditionally considered statistically significant), differences in effect size allowed us to select between the two models (Figure S7.12). Comparative analysis of the effect sizes of different parameters revealed that water loss had a greater impact when included in the survival process, whereas the effect of foraging performance was stronger when influencing recruitment. Consequently, based on the effect size of these variables, model 2 indicated a potentially better fit. Therefore, we selected it as the final model for *Pseudochirops archeri*.

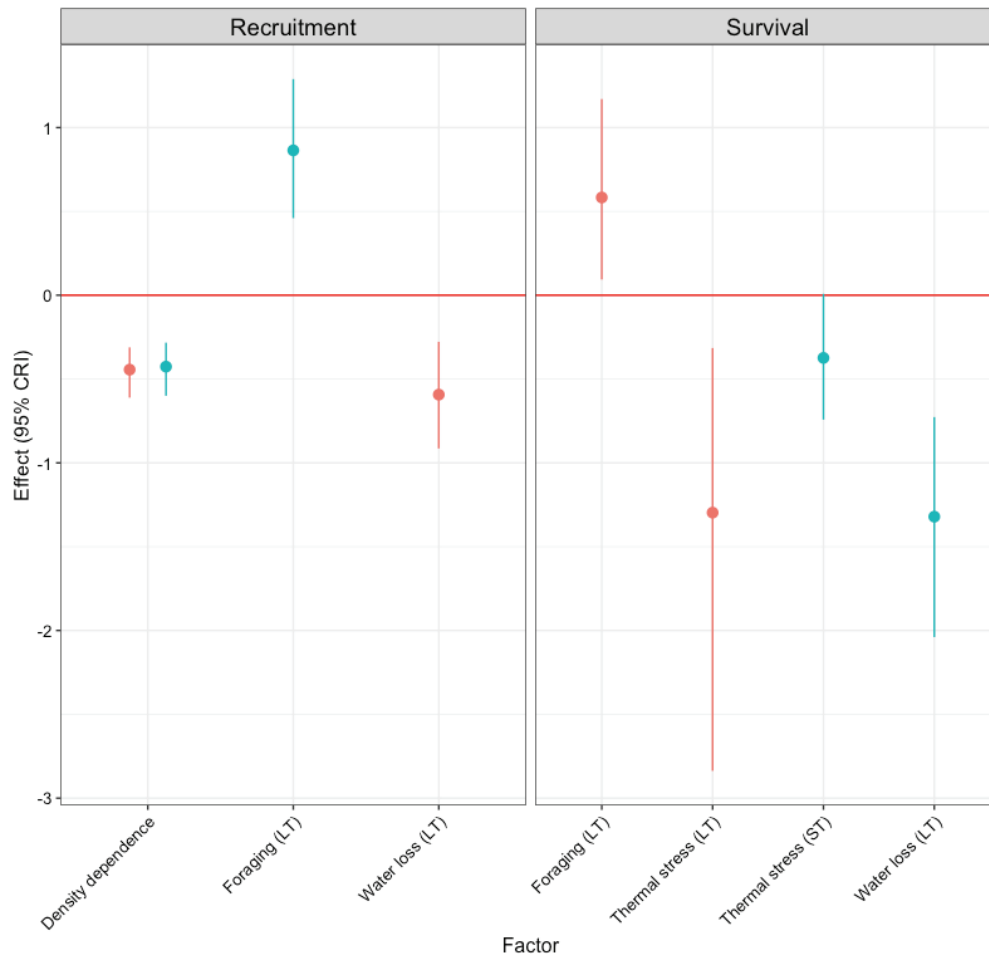


Figure S7.12. Comparison of variable effect between the two competing models for *Pseudochirops archeri*. Orange values correspond to model 1 and blue values correspond to model 2.

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JAGS code

The following code correspond to the final model for the species *Hemibelideus lemuroides*. Code for *Pseudochirops archeri* only differ in the covariate included in the population model resulted from model selection.

Code:

```
#####
# SUPERMODEL 1 - CLIMATE - SOIL – FOLIAGE #
#####

#####
# Likelihood #
#####

for(s in 1:nsites){

  # Soil model (likelihood)

  # Submodel Soil N

  n_kj[s] ~ dnorm(mu_n_kj[s], prec_n_kj)

  mu_n_kj[s] <- a_n_kj + ### intercept
    ### Climate
    b.map_n_kj * map[s] +
    b.mat_n_kj * mat[s] +
    ### Geology
    b.basalt_n_kj * basalt[s]

  # residuals Soil N
  res.n_kj[s] <- pow((n_kj[s] - mu_n_kj[s]),2)
```

```
n_kj.new[s] ~ dnorm(mu_n_kj[s], prec_n_kj)
res.n_kj.new[s] <- pow((n_kj.new[s] - mu_n_kj[s]),2)
```

```
# Submodel Soil P
```

```
p_kj[s] ~ dnorm(mu_p_kj[s], prec_p_kj)
```

```
mu_p_kj[s] <- a_p_kj + ### intercept
### Climate
b.map_p_kj * map[s] +
b.mat_p_kj * mat[s] +
### Geology
b.basalt_p_kj * basalt[s]
```

```
# residuals Soil P
```

```
res.p_kj[s] <- pow((p_kj[s] - mu_p_kj[s]),2)
p_kj.new[s] ~ dnorm(mu_p_kj[s], prec_p_kj)
res.p_kj.new[s] <- pow((p_kj.new[s] - mu_p_kj[s]),2)
```

```
# Submodel Soil C: N
```

```
cn[s] ~ dnorm(mu_cn[s], prec_cn)
```

```
mu_cn[s] <- a_cn + ### intercept
### Climate
b.map_cn * map[s] +
b.mat_cn * mat[s] +
### Geology
b.basalt_cn * basalt[s]
```

```
# residuals Soil C: N
```

```
res.cn[s] <- pow((cn[s] - mu_cn[s]),2)
cn.new[s] ~ dnorm(mu_cn[s], prec_cn)
res.cn.new[s] <- pow((cn.new[s] - mu_cn[s]),2)
```

```
# Submodel Soil K
```

```
k[s] ~ dnorm(mu_k[s], prec_k)
```

```
mu_k[s] <- a_k + ### intercept
### Climate
b.map_k * map[s] +
b.mat_k * mat[s] +
### Geology
b.basalt_k * basalt[s]
```

```

# residuals Soil K
res.k[s] <- pow((k[s] - mu_k[s]),2)
k.new[s] ~ dnorm(mu_k[s], prec_k)
res.k.new[s] <- pow((k.new[s] - mu_k[s]),2)

# Submodel Soil Na

na[s] ~ dnorm(mu_na[s], prec_na)

mu_na[s] <- a_na + ### intercept
### Climate
b.map_na * map[s] +
b.mat_na * mat[s] +
### Geology
b.basalt_na * basalt[s]

# residuals Soil Na
res.na[s] <- pow((na[s] - mu_na[s]),2)
na.new[s] ~ dnorm(mu_na[s], prec_na)
res.na.new[s] <- pow((na.new[s] - mu_na[s]),2)

for(z in 1:nspp){

  for(r in 1:nrep){

    # Sub-model avail

    avail[s,z,r] ~ dnorm(mu_avail[s,z,r], prec_avail)

    mu_avail[s,z,r] <- a_availN[z] + # intercept
    ### Climate
    b.map_availN[z] * map[s] +
    b.mat_availN[z] * mat[s] +
    ### Soil
    b.n_kj_availN[z] * n_kj[s] +
    b.p_kj_availN[z] * p_kj[s] +
    b.cn_availN[z] * cn[s]+
    b.k_availN[z] * k[s]+
    b.na_availN[z] * na[s]+
    ### Geology
    b.basalt_availN[z] * basalt[s]+
    ### Random effect
    eps_availN[s]

```



```

# residuals
res.avail[s,z,r] <- pow((avail[s,z,r] - mu_avail[s,z,r]),2)
avail.new[s,z,r] ~ dnorm(mu_avail[s,z,r], prec_avail)
res.avail.new[s,z,r] <- pow((avail.new[s,z,r] - mu_avail[s,z,r]),2)

# Sub-model tannins

tannins[s,z,r] ~ dnorm(mu_tannins[s,z,r], prec_tannins)

mu_tannins[s,z,r] <- a_tannins[z]+ ### Random intercept
### Climate
b.map_tannins[z] * map[s] +
b.mat_tannins[z] * mat[s] +
### Soil
b.n_kj_tannins[z] * n_kj[s] +
b.p_kj_tannins[z] * p_kj[s] +
b.cn_tannins[z] * cn[s]+
b.k_tannins[z] * k[s]+
b.na_tannins[z] * na[s] +
### Geology
b.basalt_tannins[z] * basalt[s]+
### Random effect
eps_tannins[s]

# residuals
res.tannins[s,z,r] <- pow((tannins[s,z,r] - mu_tannins[s,z,r]),2)
tannins.new[s,z,r] ~ dnorm(mu_tannins[s,z,r], prec_tannins)
res.tannins.new[s,z,r] <- pow((tannins.new[s,z,r] - mu_tannins[s,z,r]),2)

# Sub-model total_N

total[s,z,r] ~ dnorm(mu_total_N[s,z,r], prec_total_N)

mu_total_N[s,z,r] <- a_total_N[z]+ ### Random intercept
### Climate
b.map_total_N[z] * map[s] +
b.mat_total_N[z] * mat[s] +
### Soil
b.n_kj_total_N[z] * n_kj[s] +
b.p_kj_total_N[z] * p_kj[s] +
b.cn_total_N[z] * cn[s]+
b.k_total_N[z] * k[s]+
b.na_total_N[z] * na[s]+
### Geology
b.basalt_total_N[z] * basalt[s]+

```

```

    ### Random effect
    eps_total_N[s]

# residuals
res.total_N[s,z,r] <- pow((total[s,z,r] - mu_total_N[s,z,r]),2)
total_N.new[s,z,r] ~ dnorm(mu_total_N[s,z,r], prec_total_N)
res.total_N.new[s,z,r] <- pow((total_N.new[s,z,r] - mu_total_N[s,z,r]),2)

}
}
}

#####
# Priors #
#####

for(z in 1:nspp){

  for(a in 1:nage){

    ### Intercepts
    a_availN[z] ~ dnorm(0, 0.001)
    a_tannins[z] ~ dnorm(0, 0.001)
    a_total_N[z] ~ dnorm(0, 0.001)

    ### Slopes

    # AvailN
    b.map_availN[z] ~ dnorm(0,1.0E-6)
    b.mat_availN[z] ~ dnorm(0,1.0E-6)
    b.n_kj_availN[z] ~ dnorm(0,1.0E-6)
    b.p_kj_availN[z] ~ dnorm(0,1.0E-6)
    b.cn_availN[z] ~ dnorm(0,1.0E-6)
    b.k_availN[z] ~ dnorm(0,1.0E-6)
    b.na_availN[z] ~ dnorm(0,1.0E-6)
    b.basalt_availN[z] ~ dnorm(0,1.0E-6)

    # Tannins
    b.map_tannins[z] ~ dnorm(0,1.0E-6)
    b.mat_tannins[z] ~ dnorm(0,1.0E-6)
    b.n_kj_tannins[z] ~ dnorm(0,1.0E-6)
    b.p_kj_tannins[z] ~ dnorm(0,1.0E-6)
    b.cn_tannins[z] ~ dnorm(0,1.0E-6)
    b.k_tannins[z] ~ dnorm(0,1.0E-6)
    b.na_tannins[z] ~ dnorm(0,1.0E-6)

```

```

b.basalt_tannins[z] ~ dnorm(0,1.0E-6)

# total_N
b.map_total_N[z] ~ dnorm(0,1.0E-6)
b.mat_total_N[z] ~ dnorm(0,1.0E-6)
b.n_kj_total_N[z] ~ dnorm(0,1.0E-6)
b.p_kj_total_N[z] ~ dnorm(0,1.0E-6)
b.cn_total_N[z] ~ dnorm(0,1.0E-6)
b.k_total_N[z] ~ dnorm(0,1.0E-6)
b.na_total_N[z] ~ dnorm(0,1.0E-6)
b.basalt_total_N[z] ~ dnorm(0,1.0E-6)

}
}

# Intercepts
a_n_kj ~ dnorm(0, 0.001)
a_p_kj ~ dnorm(0, 0.001)
a_cn ~ dnorm(0, 0.001)
a_k ~ dnorm(0, 0.001)
a_na ~ dnorm(0, 0.001)

# Slopes soil

# Submodel soil N
b.map_n_kj ~ dnorm(0,1.0E-6)
b.mat_n_kj ~ dnorm(0,1.0E-6)
b.basalt_n_kj ~ dnorm(0,1.0E-6)
# Submodel soil P
b.map_p_kj ~ dnorm(0,1.0E-6)
b.mat_p_kj ~ dnorm(0,1.0E-6)
b.basalt_p_kj ~ dnorm(0,1.0E-6)
# Submodel soil C:N
b.map_cn ~ dnorm(0,1.0E-6)
b.mat_cn ~ dnorm(0,1.0E-6)
b.basalt_cn ~ dnorm(0,1.0E-6)
# Submodel soil K
b.map_k ~ dnorm(0,1.0E-6)
b.mat_k ~ dnorm(0,1.0E-6)
b.basalt_k ~ dnorm(0,1.0E-6)
# Submodel soil K
b.map_na ~ dnorm(0,1.0E-6)
b.mat_na ~ dnorm(0,1.0E-6)
b.basalt_na ~ dnorm(0,1.0E-6)

```

```

# Precision hierarchical models
prec_avail ~ dgamma(0.01, 0.01)
prec_tannins ~ dgamma(0.01, 0.01)
prec_total_N ~ dgamma(0.01, 0.01)
prec_n_kj ~ dgamma(0.01, 0.01)
prec_p_kj ~ dgamma(0.01, 0.01)
prec_cn ~ dgamma(0.01, 0.01)
prec_k ~ dgamma(0.01, 0.01)
prec_na ~ dgamma(0.01, 0.01)

#####
# Random effects hierarchical models #
#####

# AvailN
for(i in 1:nsites){ eps_availN[i] ~ dnorm(0, tau_availN) }
tau_availN ~ dgamma(0.01, 0.01)
sd_availN <- 1 / sqrt(tau_availN)

# Tannins
for(i in 1:nsites){ eps_tannins[i] ~ dnorm(0, tau_tannins) }
tau_tannins ~ dgamma(0.01, 0.01)
sd_tannins <- 1 / sqrt(tau_tannins)

# total_N
for(i in 1:nsites){ eps_total_N[i] ~ dnorm(0, tau_total_N) }
tau_total_N ~ dgamma(0.01, 0.01)
sd_total_N <- 1 / sqrt(tau_total_N)

#####
# Derived site pred for pop model#
#####

# sum of residuals

fit.availN <- sum(res.avail[,,])
fit.availN.new <- sum(res.avail.new[,,])

fit.total_N <- sum(res.total_N[,,])
fit.total_N.new <- sum(res.total_N.new[,,])

fit.tannins <- sum(res.tannins[,,])
fit.tannins.new <- sum(res.tannins.new[,,])

```

```

fit.n_kj <- sum(res.n_kj[])
fit.n_kj.new <- sum(res.n_kj.new[])

fit.p_kj <- sum(res.p_kj[])
fit.p_kj.new <- sum(res.p_kj.new[])

fit.cn <- sum(res.cn[])
fit.cn.new <- sum(res.cn.new[])

fit.k <- sum(res.k[])
fit.k.new <- sum(res.k.new[])

fit.na <- sum(res.na[])
fit.na.new <- sum(res.na.new[])

for(s in 1:nsites){
  n_site[s] <- n_kj[s]
  p_site[s] <- p_kj[s]
  k_site[s] <- k[s]
  cn_site[s] <- cn[s]

  avail_site[s] <- max(avail[s,])
  total_site[s] <- max(total[s,])
  tannins_site[s] <- min(tannins[s,])
}

#####
# SUPERMODEL 2 - POPULATION AND DETECTION #
#####

#####
#PRIORS #
#####

# Intercept abundance/survival/recruitment

mean_lambda ~ dunif(0,100)
mean_phi ~ dunif(0,1)
mean_gamma ~ dunif(0,3)

# Random year intercept detection

for(t in 1:NYEARS){

```

```

p0[t] ~ dunif(0,1)

alpha0[t] <- log(p0[t]/(1-p0[t])) # intercept detection

}

tau.lp <- 1 / (sigma.p * sigma.p)

sigma.p ~ dunif(0, 100)

# Slopes

# Prior for covariate effect

for(j in 1:ncovs){
  b[j] ~ dnorm(0,0.01) # change the priors to see if this works better than the dunif() one
}

# Slopes detection

alpha.obs ~ dunif(-5,5)
alpha.activity ~ dunif(-5,5)

#####
#Likelihood #
#####

for(i in 1:NSITES){ # open NSITES loop

#####
# STATE PROCESS: INITIAL CONDITION #
#####

N[i,1] ~ dpois(lambda[i])

log(lambda[i]) <- mean_lambda + b[1] * nts[i] + b[2] * total_site[i]

#####
# STATE PROCESS: TRANSITION MODEL #
#####

for(t in 1:(NYEARS-1)){ # open NYEARS-1 loop

S[i,t+1] ~ dbin(phi[i,t], N[i,t])      # Aparent survival

```

```

logit(phi[i,t]) <- mean_phi + b[3] * foraging_cum[i,t]

R[i,t+1] ~ dpois(N[i,t] * gamma[i,t])    # per-capita recr. = 'autoreg'

log(gamma[i,t]) <- mean_gamma + b[4] * foraging_success[i,t] + b[5] * (N[i,t] - Nm)

N[i,t+1] <- S[i,t+1] + R[i,t+1]

} # close NYEARS-1 LOOP

#####
# OBSERVATION PROCESS #
#####

for(t in 1:NYEARS){ # open NYEARS loop

  for(j in 1:NREPLICATES){ # open NREPLICATES loop

    C[i,j,t] ~ dbin(p[i,j,t], N[i,t])

    p[i,j,t] <- exp(lp[i,j,t]) / (1 + exp(lp[i,j,t]))

    lp[i,j,t] ~ dnorm(mu.lp[i,j,t], tau.lp)

    mu.lp[i,j,t] <- alpha0[t] + alpha.obs * obs[i,j,t] + alpha.activity * activity[i,j,t]

    # residuals

    eval[i,j,t] <- N[i,t] * p[i,j,t] # Expected value

    sd.resi[i,j,t] <- sqrt(eval[i,j,t] * (1 - p[i,j,t])) + 0.5

    E[i,j,t] <- (C[i,j,t] - eval[i,j,t]) / sd.resi[i,j,t]

    E2[i,j,t] <- pow(E[i,j,t], 2)

    C.new[i,j,t] ~ dbin(p[i,j,t], N[i,t])

    E.new[i,j,t] <- (C.new[i,j,t] - eval[i,j,t]) / sd.resi[i,j,t]

    E2.new[i,j,t] <- pow(E.new[i,j,t], 2)

```

```
    } # close NREPLICATES loop
  } # close NYEARS loop
} # close NSITES loop
fit <- sum(E2[,,])
fit.new <- sum(E2.new[,,])

# Sum up squared resi for actual data set
# Sum up for replicate data set
```