Constructing network models to predict spatial and temporal shifts in the ecological community of the Australian Wet Tropics

By

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Declaration

I certify that this thesis:

1. does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any university

2. and the research within will not be submitted for any other future degree or diploma without the permission of Flinders University; and

3. to the best of my knowledge and belief, does not contain any material previously published or written by another person except where due reference is made in the text.

Signed.........S. Doherty.........

Date.............21st May 2025............

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Contents

Abstract

Predicting how trophic cascades and coextinction influence extinction risk in ecological communities has steadily gained traction over the last few decades, because they are likely to play increasingly important roles under future changing environmental conditions predominantly in freshwater and marine ecosystems. Terrestrial ecosystems have comparatively received less attention given their higher complexity and the dearth of data needed to assess these hidden extinction pathways. Thus, predicting how cascades and coextinctions affect the extinction risk of species in terrestrial ecosystems at fine spatio-temporal scales using empirical data is required, particularly if we are to mitigate such threats. The overarching aim of my thesis was to quantify how anthropogenic threats might influence the extinction risk of vertebrate species in a terrestrial ecosystem at a fine spatio-temporal scale through the processes of trophic cascades and coextinctions. My research specifically examines how climate change may affect the extinction risk of vertebrate species in the Australian Wet Tropics through coextinction and trophic cascades. I developed a novel framework to represent terrestrial food webs more accurately than previous models generating more realistic simulations of trophic cascades under future environmental perturbations. By applying this approach to the Australian Wet Tropics, I provide a comprehensive, ecosystem-wide assessment of extinction risk in terrestrial communities. My research showed that analysing both alpha and beta diversity alongside multidimensional trait space provided a useful way to define terrestrial vertebrate communities across latitudinal and elevational gradients in the Australian Wet Tropics. Although compositional differences appeared, particularly across latitude, the trait-based analyses showed that these communities occupied broadly similar functional spaces. In contrast, distinct differences in both composition and trait space emerged between low- and high-elevational areas. Consequently, these findings suggested that the studied vertebrates largely function as a single community across this bioregion, with marking distinctions emerging only between low- and high-elevation zones based on their functional characteristics. Building on this foundation, I showed how combining such community boundaries with machine-learning algorithms

facilitated the construction and analysis of multi-taxa trophic network models. This approach revealed structural differences associated with elevation while highlighting overarching similarities in predator-prey dynamics, and their potential links to extinction risks. Through simulations incorporating basal resources (plants and invertebrates), I demonstrated that bottom-up trophic cascades, particularly in constructed high-elevation networks, could amplify the extinction risk of vertebrate species by pushing ecosystems past tipping points. Coextinction thresholds and resource loss severity emerged as determinant factors in species persistence. Finally, I assessed potential climate-induced coextinctions under multiple future scenarios towards the end of this century, showing that direct climate impacts could rival or exceed coextinction rates, especially in highland vertebrate communities where limited space constrain species' adaptive potential. These results highlight the need for conservation strategies that extend beyond *ad hoc* responses and single-species management to account for broader ecological consequences of species loss, ensuring more effective biodiversity protection in an increasingly fragile biosphere.

Publications

Chapter 1 is published in a peer-reviewed journal where I am the first author:

> **Doherty, S.**, Saltré, F., Llewelyn, J., Strona, G., Williams, S. E., & Bradshaw, C. J. A. (2023). Estimating coextinction threats in terrestrial ecosystems. Global Change Biology, 29, 5122–5138. https://doi.org/10.1111/gcb.16836

I also co-authored one other peer-reviewed journal article separate from my doctoral thesis:

> Llewelyn, J., Strona, G., Dickman, C.R., Greenville, A.C., Wardle, G.M., Lee, M.S.Y., **Doherty, S.**, Shabani, F., Saltré, F. and Bradshaw, C.J.A. (2023), Predicting predator–prey interactions in terrestrial endotherms using random forest. Ecography, 2023: e06619. https://doi.org/10.1111/ecog.06619

At time of writing, I am preparing all other chapters for publication. As such, style or formatting across chapters might be different. All other chapters are sole authored, with support provided by Frédérik Saltré, John Llewelyn, Stephen E. Williams, and Corey J. A. Bradshaw, as per the Flinders University's HDR supervisor policy.

Introduction

Over the past 550 million years, Earth has experienced five mass extinction events (Dirzo et al., 2022), each leading to at least 75% of global biodiversity going extinct and requiring hundreds of thousands to millions of years for recovery (Erwin, 2001; Kirchner & Weil, 2000). We are now likely witnessing a sixth mass extinction, one that is both unprecedented in speed and scale, and driven predominantly by anthropogenic changes to the biosphere (Crutzen, 2006, 2016). The current proposed epoch, known as the Anthropocene, is marked by rapid and destructive environmental changes associated with industrialisation, deforestation, pollution, invasive species, and anthropogenic climate change (Ceballos, Ehrlich, & Ehrlich, 2015; Ceballos, Ehrlich, Barnosky, et al., 2015). This moment in history represents a dramatic and urgent turning point, with the potential to alter irrevocably the natural world and the future of humanity itself. One cannot overstate the gravity of this situation; it demands immediate and profound action to avoid catastrophic outcomes (Bradshaw et al., 2021).

The tropical rain forests of the Australian Wet Tropics (Figure 1) provide an ideal system to study extinction risk in terrestrial communities. The unique combination of a limited area covering just < 900,000 hectares of land (DCCEEW, 2023), high biodiversity and endemism (UNESCO World Heritage Centre, 2024), and extensive research over several decades has afforded an exceptional opportunity to investigate extinction risks at a fine spatio-temporal scale (i.e., focusing on specific regions and shorter time periods, such as local habitats and seasonal changes) necessary for planning tangible management outcomes (Nicholson et al., 2009). Further, the biodiversity crisis reaches its utmost urgency when considering tropical rain forests, which have been predicted to host at least 50% of the world's total number of species (Dinerstein et al., 2017; Wilson, 1988), while simultaneously being among the most threatened habitats (e.g., Matricardi et al., 2020).

Formed during the era of the super-continent Gondwana approximately 50-100 million years ago when forests covered much of Australia and parts of Antarctica (UNESCO World Heritage Centre, 2024), the Wet Tropics are today located in north-eastern Queensland and encompass a narrow stretch of coastal plains and ranges, including segments of the Great Dividing Range. The region extends for approximately 450 kilometres from Black Mountain in the north to Mount Elliot in the south. Within the bioregion lies the renowned Wet Tropics World Heritage Area. This region supports more biodiversity than any other terrestrial location in Australia, and is the largest expanse of rain forest in the country (WTMA, 2023). Globally, these rain forests are among the oldest extant rain forest communities (WTMA, 2023) and are ranked among the top 0.1% of the most important protected areas (Osipova et al., 2020).

Figure 1. Mount Lewis looking southeast over the tropical rain forests of the Australian Wet Tropics World Heritage Area (credit: Seamus Doherty).

Despite covering only 0.12% of Australia's total land area, the Wet Tropics contain approximately 45% of Australia's terrestrial vertebrate species, including 40% of birds, 30% of mammals, 29% of frogs, and 21% of reptiles (Williams et al., 2016; WTMA, 2024b). Of these, some of the more well-known species include Australia's heaviest bird and evolutionary relic, the southern cassowary (*Casuarius casuarius*, Gunduy), Boyd's forest dragon (*Lophosaurus boydii*, Jalbil), known for its remarkable tree-climbing and camouflage abilities, the majestic bird-of-paradise Victoria's riflebird (*Lophorina victoriae*), the large white-lipped tree frog (*Litoria infrafrenata*), and the elusive Lumholtz tree kangaroo (*Dendrolagus lumholtzi*, Muppie) (Figure 2). Amongst the diverse array of vertebrate species, the Wet Tropics are also home to over 2,800 described vascular plant species, including 19 of the 29 ancient lineages of primitive flowering plants (Metcalfe & Ford, 2008). The region also hosts a large diversity of invertebrate species, including 60% of Australia's described butterflies and 21% of cycad species (WTMA, 2024b). Some of the other interesting invertebrates found in this region include the gargantuan stick insect (*Ctenomorpha gargantua*), the giant petaltail (*Petalura ingentissima*), and the Hercules moth (*Cosinocera hercules*) (Figure 2).

Figure 2. Species of the Australian Wet Tropics - Top left: Giant stick insect (*Ctenomorpha gargantua*) (credit: Seamus Doherty), top middle: Boyd's forest dragon (*Lophosaurus boydii,* Jalbil) (credit: Charles J. Sharp licensed under CC BY-SA 4.0), top right: Idiotfruit tree (*Idiospermum australiense*) (credit: CSIRO licensed under CC BY 3.0), bottom left: Lumholtz tree kangaroo (*Dendrolagus lumholtzi,* Muppie) (credit: Rolf Lawrenz licensed under CC BY 4.0), bottom middle: Southern cassowary (*Casuarius casuarius*, Gunduy) (credit: Naomi Lacroix licensed under the Pexels License), and bottom right: White-lipped tree frog (*Litoria infrafrenata*) (credit: JJ. Harrison licensed under CC BY-SA 3.0).

The region is also home to at least 20 recognised Indigenous groups spanning 120 clans, who have continuously occupied the area for at least the last 5,000 years (Cosgrove et al., 2007; Pannell & Johnson, 2006), and probably much longer (Bradshaw et al., 2023; Clarkson et al., 2017) — it is the only place in Australia where Indigenous peoples have permanently occupied a tropical rain forest area (WTMA, 2024a). This region is also the only place in the world where two World Heritage areas meet, where its land connects to the Great Barrier Reef, containing the world's most extensive collection of coral reefs (Weber et al., 2021). For these reasons, the Wet Tropics are integral to Australia's ecological and cultural legacy and are considered of 'Outstanding Universal Value' (UNESCO World Heritage Centre, 2024).

To assess the extinction risks faced by such important ecosystems, researchers have traditionally relied on single-species population and distribution models to evaluate the direct impacts of threats like habitat loss and climate change on species extinction risks, which generally evaluate species as disconnected entities (Araújo & Luoto, 2007). However, because species are members of ecological communities consisting of a network of interacting, interdependent species, the extinction of one species can lead to the indirect extinction of another, potentially initiating an ecological cascade that causes further coextinctions within a community (Garcia et al., 2014). Consequently, there is increasing recognition of the role that biotic interactions play in influencing species' extinction risks both now and in the future (Strona & Bradshaw, 2018; Strona & Bradshaw, 2022). Yet, the conventional approach of assessing vulnerability for species individually has limited ability to incorporate biotic interactions and physical processes (Elith & Leathwick, 2009). For instance, although correlative species distribution models can indirectly incorporate species interactions, they are unable to forecast or simulate changes in these interactions under shifting environmental conditions (Carmel et al., 2013). These limitations could underestimate the true extent of environmental threats because they do not account for coextinction processes and their influence on the extinction risk of entire communities (Strona & Bradshaw, 2018). While some studies have attempted to address these gaps by modelling multispecies dynamics (Säterberg et al., 2013), such efforts remain the exception rather than the norm.

Ecological network modelling based on network theory offers an alternative approach to quantify extinction risks that can inherently consider interactions among constituent species (Delmas et al., 2019; Pocock et al., 2012). This approach has gained traction as a flexible mathematical method for understanding biotic interactions within parameterised networks, enabling a more robust assessment of extinction risks (Delmas et al., 2019). By incorporating species interactions within a community, these models can simulate coextinctions with greater realism (Geary et al., 2020; Lau et al., 2017; Pocock et al., 2012) than the aforementioned methodologies. Network models can help elucidate ecosystem-wide impacts (e.g., environmental shifts) and forecast the outcomes of different management strategies, making them particularly effective for examining extinction drivers and their cascading effects (Säterberg et al., 2013; Wallach et al., 2017).

Consequently, network modelling is an invaluable tool for predicting and mitigating future biodiversity loss and changes, ultimately aiding in developing more effective environmental management and policy decisions (Desjardins-Proulx et al., 2017; Harvey et al., 2017; Moir & Brennan, 2020). For instance, network modelling has been applied to identify which species should be targets to restore ecological functions and community stability in a terrestrial ecosystem threatened by habitat loss (Pocock et al., 2012). Despite the potential of network modelling to predict extinction risks, this approach has primarily been applied to aquatic communities (e.g., Dunne et al., 2016; Thompson & Townsend, 2004) while being seldom used in terrestrial systems. This discrepancy is due to the comparatively higher complexity of trophic structure and predator-prey relationships (e.g. Arditi & Ginzburg, 2012) found in terrestrial ecosystems, combined with a lack of necessary diet data to estimate network connectivity (e.g. Davis et al., 2012), leaving the vulnerability of species to coextinction in such communities unclear.

Given the importance of understanding and mitigating the extinction risks of individual species and entire ecological communities both now and in the future, this thesis aims to use the Australian Wet Tropics as a case study to show how network modelling can be applied to evaluate these risks. By focusing on this unique ecosystem, the research I present in this thesis seeks to provide insights into coextinction risks in terrestrial ecosystems at an unprecedentedly fine and complex spatio-temporal scale. My overall aim is, therefore, to provide insights and understanding that generalise to other terrestrial ecosystems globally.

Thesis outline

The aim of my thesis is to quantify how anthropogenic threats might influence the extinction risk of vertebrate species in a terrestrial ecosystem at a fine spatio-temporal scale through the processes of trophic cascades and coextinctions. This research specifically addressed the question: *How might climate change effect the extinction risk of vertebrate species through the processes of coextinction and trophic cascades in the Australian Wet Tropics?* I designed each chapter of the thesis as a standalone paper, but with each still contributing to a cohesive body of work. While each chapter builds on the knowledge developed in preceding chapters (Figure 1), this interconnected structure generated some intentional redundancies between chapters to ensure clarity and context within each individual study.

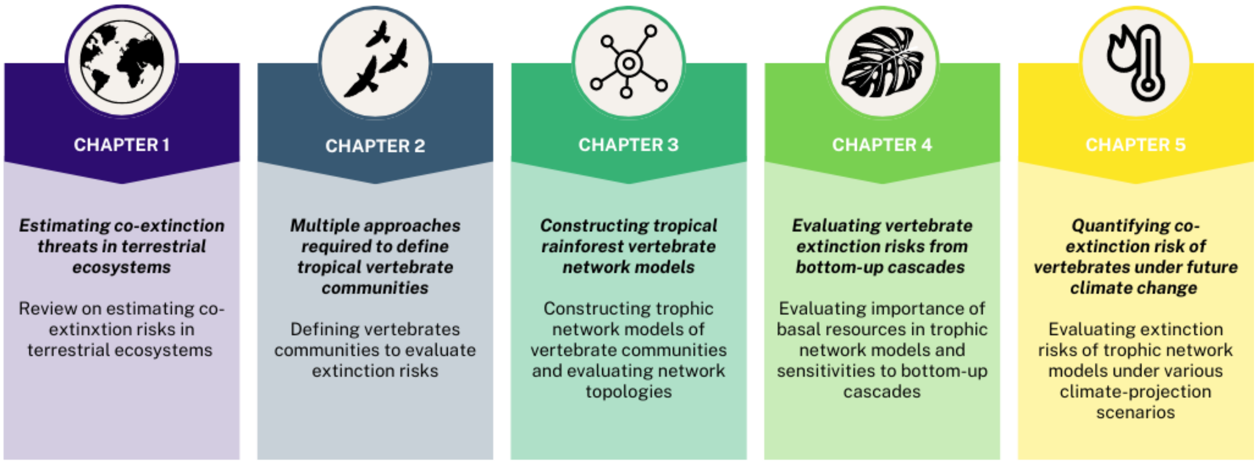

Figure 1. Overview of chapter outline for thesis.

In **Chapter 1**, I review research on coextinction threats, highlighting the knowledge gaps and challenges in assessing such threats, focusing on terrestrial ecosystems at fine spatio-temporal scales (Figure 1). I discuss the implications of earlier research focusing on direct environmental effects and emphasise the need to consider the complex dynamics of trophic cascades and coextinctions. The chapter introduces a novel approach to building ecological network models that represent real-world food webs and explores how these models can simulate potential indirect effects of primary extinctions and various environmental perturbations. By improving the accuracy of extinction risk estimates, the chapter discusses how this framework can predict how environmental disturbances influence entire ecological communities and help identify species at risk of coextinction or serving as catalysts for such events. Indeed, the chapter further discusses how the proposed framework can be applied to guide effective conservation interventions to minimise extinctions, integrating biotic interactions and network dynamics to predict community responses to global change more effectively.

In **Chapter 2**, I used a standardised approach to differentiate ecological communities as a necessary precursor to representing identified communities as network models to predict extinction risks. The chapter focuses on ecological communities in the Australian Wet Tropics bioregion, using taxonomic and functional composition tools to delineate communities (Figure 1). This chapter explores questions relating to whether species diversity and trait-space analyses can be used to differentiate communities in the Wet Tropics, testing empirically whether it is justifiable to group this bioregion as one community or treat sub-regions as separate communities according to latitude and/or elevation. Here, I hypothesise that community composition does not beget functional diversity and that variation in community diversity and trait space are more pronounced across elevational gradients compared to latitudinal gradients.

In **Chapter 3,** I build trophic network models of defined, low- and high-elevation vertebrate communities in the Australia Wet Tropics and assess their network topologies (Figure 1). Here, I investigate whether trophic interactions can be inferred between vertebrate species using a random forest (machine-learning) approach. The chapter also analyses if resultant trophic network model topologies differ between low- and high-elevation vertebrate communities, and how this might relate to extinction risks. Here, I hypothesise that networks should differ in both complexity and predator-prey dynamics.

In **Chapter 4**, I add trophic links from vertebrates to plant and invertebrate prey nodes in the low- and high-elevation network models developed in Chapter 3. I use these models to evaluate the role bottom-up cascades can play in affecting extinction vulnerability in these communities (Figure 1). In this chapter, I test whether it is possible to identify when vertebrate communities collapse and if this tipping point beyond which collapse occurs depends on the underlying assumptions regarding basal resources. I also evaluate how species coextinction thresholds and the number of basal resources removed in simulations affect the number of total primary and secondary vertebrate extinctions. Finally, I identify which vertebrates are the most and the least vulnerable to extinction across each scenario simulated. I hypothesise that lower coextinction thresholds and higher rates of basal resource removal increase secondary extinctions (when a species goes extinct due to the loss of another species it relies on) compared to primary extinctions. The chapter also proposes that different vertebrate taxonomic classes have varying vulnerabilities to secondary extinctions across different scenarios. Further, the chapter identifies which threatened species are more prone to primary extinction than secondary extinction.

In **Chapter 5**, I use the network models built in Chapter 4 (i.e., including vertebrates, invertebrates, and plants) to evaluate the role trophic cascades and coextinctions could play in future climate change-linked vertebrate extinctions in the Wet Tropics (Figure 1). In this chapter, I asked how important coextinction cascades are to future vertebrate species extinction risk, whether the prevalence/importance (in terms of the number of extinctions) of climate change-induced cascades is influenced by the capacity of species to shift their elevational range and rewire trophic interactions, whether certain vertebrate trophic levels and taxonomic groups are more vulnerable to climate change-induced cascades than others, and whether any of these groups are also disproportionately important for maintaining ecosystem stability. I hypothesise that coextinctions will be most prevalent under moderate climate change scenarios because under extreme climate-change scenarios, most extinctions will be due to species surpassing their thermal limits (i.e., primary extinctions), whereas under the best-case future climate scenario, few/no species will go extinct. I also hypothesise that coextinction rates increase with trophic level, and lower-level species play an important role in initiating such cascades. Further, I hypothesise that communities whose species cannot shift to higher elevations will face higher extinction rates, but that the capacity to shift to higher elevations will offer little long-term relief under worst-case/extreme climate-change scenarios.

Finally, I hypothesise that communities unable to rewire trophic interactions after prey loss will experience higher coextinction risk than those that can rewire.

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Literature review

Estimating coextinction threats in terrestrial ecosystems

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Keywords

Ecological network models, Trophic cascades, Coextinctions, Climate change, Terrestrial ecosystems, Conservation.

Highlights

- Among other anthropogenic threats, climate change is expected soon to become the primary driver of species extinctions.
- Because ecological communities underlie dense networks of biotic interactions, threats that directly affect some species often have secondary effects on others in the same community.

Quantifying these relationships is, therefore, necessary to predict community-level responses (trophic cascades and coextinctions) to changed environmental conditions.

- Little research has quantified these effects in real-world terrestrial ecosystems due to data limitations, and this has likely led to underestimating extinction risk in terrestrial communities.
- By proposing a novel framework, we aim to improve the accuracy of identifying coextinction risks in terrestrial ecosystems and provide better estimates of community-level responses to environmental changes.
- Our framework offers the potential to guide conservation efforts and mitigate future biodiversity loss in terrestrial ecosystems by identifying species coextinction risks.

Abstract

The biosphere is changing rapidly due to human endeavour. Because ecological communities underlie networks of interacting species, changes that directly affect some species can have indirect effects on others. Accurate tools to predict these direct and indirect effects are therefore required to guide conservation strategies. However, most extinction-risk studies only consider the direct effects of global change — such as predicting which species will breach their thermal limits under different warming scenarios — with predictions of trophic cascades and coextinction risk remaining mostly speculative. To predict the potential indirect effects of primary extinctions, data describing community interactions and network modelling can estimate how extinctions cascade through communities. While theoretical studies have demonstrated the usefulness of models in predicting how communities react to threats like climate change, few have applied such methods to real-world communities. This gap partly reflects challenges in constructing trophic network models of real-world food webs, highlighting the need to develop approaches for quantifying coextinction risk more accurately. We propose a framework for constructing ecological network models representing real-world food webs in terrestrial ecosystems, and subjecting these models to coextinction scenarios triggered by probable future environmental perturbations. Adopting our framework will improve estimates of how environmental perturbations affect whole ecological communities. Identifying species at risk of coextinction (or those that might trigger coextinctions) will also guide conservation interventions aiming to reduce the probability of coextinction cascades and additional species losses.

Introduction

Over the last 50 years, much of the biosphere has been destroyed or degraded (Díaz et al., 2020) as a result of human endeavour. Unsustainable land use, resource-intensive agriculture, invasive species, emerging diseases, and natural resource extraction have degraded environments and exacerbated the impacts of natural disasters (e.g., droughts and fires) (Heleno, Ripple, & Traveset, 2020; Shukla et al., 2019). Among current pressures, climate change is one of the greatest threats to biodiversity (Newbold, 2018), with expectations that it will soon become the primary driver of species extinctions (Urban, 2015). According to the Intergovernmental Panel on Climate Change (Allen et al., 2019), even under the unlikely lowest rates of projected warming (SSP1-1.9: < 2 °C above pre-industrial temperatures by 2100) (Masson-Delmotte et al., 2021), climate change is expected to disrupt ecological communities and processes beyond natural variation, degrading their structure (Holmgren, Hirota, van Nes, & Scheffer, 2013), composition (de la Fuente, Krockenberger, Hirsch, Cernusak, & Williams, 2022), and function (Garcia, Cabeza, Rahbek, & Araújo, 2014; Seddon, Macias-Fauria, Long, Benz, & Willis, 2016). Together, human modification of the biosphere will likely continue in the short term, and amplify the effects of climate change in the long term.

Ecological communities — assemblages of species living together in a particular area — are simultaneously threatened by anthropogenic climate change and other perturbations (Barnosky et al., 2011; Pecl et al., 2017), with these changes having already simplified the structure and complexity of most ecological communities (Heleno et al., 2020; Ledger, Brown, Edwards, Milner, & Woodward, 2013; Woodward et al., 2012), and modified species' distributions, body size, abundance, and seasonal movements (Eduardo S Brondizio, Josef Settele, S Díaz, & Hien T Ngo, 2019; Eduardo S Brondizio, Josef Settele, Sandra Díaz, & Hien T Ngo, 2019; Ernakovich et al., 2014; Hatfield & Prueger, 2015; Shukla et al., 2019). Natural communities are organised into multiple **networks** (see Glossary) where species are linked to one another based on different kinds of ecological interactions, such as those between plants and pollinators, predators and prey, and hosts and parasites. Both the species in a community and the interactions among them are necessary for sustaining biodiversity overall, and are a fundamental component in determining how communities respond to ecological disruption (Ives & Carpenter, 2007; Suttle, Thomsen, & Power, 2007). It is because of these interactions and interdependencies, however, that threats directly affecting some species often also have secondary effects on others in the same community (Ripple et al., 2016; Strona & Bradshaw, 2018). Therefore, quantifying how species interact within their community and modelling how biodiversity loss can propagate through network links (ecological cascades) are important to predict entire community responses to future environmental conditions.

The component of climate change expressed as global warming directly affects species by challenging their thermal tolerances (Hickling, Roy, Hill, Fox, & Thomas, 2006), with predictions of how it threatens species relying primarily on estimating when temperatures will breach these tolerance limits. However, the indirect effects of these threats on communities through species interactions (Dorresteijn et al., 2015) are less clear. For example, if a species depends on the persistence of another, the extinction of the latter can cause the former to become *coextinct* which can in turn, elicit a trophic cascade leading to more **coextinctions** in a community (Garcia et al., 2014). These cascades are generally either ***bottom-up*** (affecting consumers losing their food resources) or ***top-down*** (affecting resources losing their consumers) (Feit, Dempster, Jessop, Webb, & Letnic, 2020; Letnic, Koch, Gordon, Crowther, & Dickman, 2009), potentially disrupting entire ecological communities and increasing the overall rate of extinction.

These changes to species assemblages often involve the arrival of new species (e.g., invasive or naturally range-expanding) that have never interacted with endemic species, generating new interactions (Wallingford et al., 2020). Measuring the cascading implications of invading alien species will become increasingly important as no-analogue climate change will engender no-analogue communities (Williams, Jackson, & Kutzbach, 2007). Most research on trophic networks (food webs) has focused on examining the effects of environmental perturbations on trophic guilds (Feit et al., 2020), with many examples documented in marine (Batten, Ruggerone, & Ortiz, 2018) and freshwater (Jones et al., 2017) environments. Yet, there has been little focus on terrestrial ecosystems, suggesting that we have underestimated extinction risks in that realm. Understanding the effects of environmental perturbations from a more complete ecological perspective will provide greater insights into how ecosystems respond to climate change and other pressures, thereby guiding more effective conservation strategies.

In this review, we probe into the complexities of characterising and measuring species interactions and community responses to environmental change, while highlighting the intricacies of defining ecological communities and the consequential implications of developing comprehensive food webs. This exploration is underpinned by a critical assessment of the limitations, issues, and methods associated with quantifying and modelling biotic interactions. To enhance our understanding of biotic interactions in ecosystem-level processes and consequences, we introduce a novel framework for constructing ecological network models that can capture food webs more realistically within terrestrial ecosystems. We further discuss how this framework can allow researchers to simulate trophic cascades that are influenced by plausible future environmental perturbations, with a focus on advancing environmental policies and management of terrestrial biodiversity (Fig. 1).

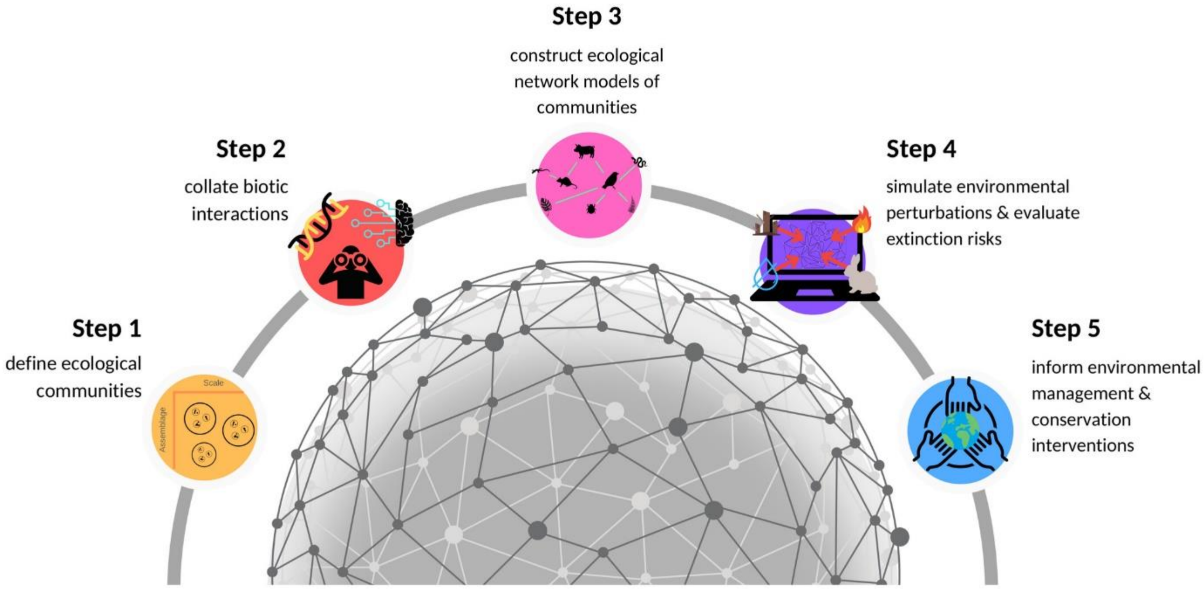

Figure 1. Main steps for estimating coextinction risks in terrestrial ecosystems. The process involves five primary steps: (**1**) **define ecological communities** — identify specific biotic components that make up a community of interest, e.g., a list of species observed in a given space and time (see 'Incomplete food webs'). (**2**) **collate biotic interaction data** — gather pre-existing data on biotic interactions within defined communities (Fig. 2); gaps filled by (*i*) collecting new interaction data, e.g., by making field observations or running feeding trials, and/or (*ii*) inferring interactions using, e.g., machine-learning algorithms (see 'Inferring biotic interactions'). (**3**) **construct ecological network models** of defined communities based on collated biotic interaction data; modelling communities can apply network theory to make realistic networks (see 'Modelling species interactions and community change'). (**4**) **simulate environmental perturbations**, e.g., use models to simulate probable future environmental perturbations and apply these disturbances to the network models to investigate the trophic cascades they trigger (see 'Simulating trophic cascades in ecological networks'). **(5) inform environmental management & conservation interventions**, e.g., identifying conservation target such as key species that, if lost, could have significant detrimental effects on communities (see 'Implications for management and conservation').

Challenges in measuring species interactions and community responses to environmental change

Our understanding of why some species in a community interact and others do not is relatively nascent (Blanchet, Cazelles, & Gravel, 2020), compared to what we now understand about species distributions, despite this information being essential to predict community change (Bartomeus et al., 2016). Indeed, measuring interactions and determining how they change through time as part of complex, interconnected structures are challenging endeavours

(Jordano, 2016). This is made even more difficult because most trophic interactions include > 2 species (Golubski, Westlund, Vandermeer, & Pascual, 2016), and current and historical interaction data are sparse (Hortal et al., 2015). Data describing phenotypic plasticity and genetic variation that permit species some capacity for adjustment or adaptation in terms of the species with whom they interact, and the strength/importance of these interactions are also rare. This rarity thereby weakens inferences on the extent to which food webs can ‘rewire’ (e.g., develop new interactions between previously non-interacting species or shift the strength/importance of pre-existing interactions) following the loss or gain of species in a community (Gilljam, Curtsdotter, & Ebenman, 2015). Moreover, this paucity of information prevents discriminating potential and realised interactions (Strona & Veech, 2017), further masking how ecological communities might respond to environmental changes.

Anthropogenic threats can affect interactions among species in terrestrial ecosystems. However, data regarding the impacts of such threats on interactions among species are rare, largely due to the difficulty of distinguishing the effects of human-driven environmental change, such as climate change, from changes attributed to natural stochasticity (McCann, 2007). For example, while we know that climate change can alter plant-herbivore interactions by directly and indirectly inducing greater food consumption by herbivores (Lemoine, Drews, Burkepile, & Parker, 2013), comprehensive data documenting these impacts is scarce (Tylianakis, Didham, Bascompte, & Wardle, 2008). Despite these challenges, recent research has begun to examine the potential for extinction cascades in marine and freshwater ecosystems (Donohue et al., 2017). Global estimates of species extinction rates from climate change initially excluded coextinctions (Thomas et al., 2004), but recent research has attempted to include their contribution (Hughes, 2013; Strona & Bradshaw, 2018; Strona & Bradshaw, 2022). However, this empirical research has predominantly focused on marine and freshwater ecosystems (Anaya-Rojas et al., 2019; Donohue et al., 2017; Hayden, Harrod, Sonninen, & Kahilainen, 2015; A. D. M. Smith et al., 2011) because aquatic communities include species with predictable, linear relationships between predator and prey body sizes (Arditi & Ginzburg, 2012), and many studies (especially in fisheries) provided detailed diet information from gut-content and stable-isotope analyses (Davis, Blanchette, Pusey, Jardine, & Pearson, 2012). Aquatic ecosystems (e.g., lakes) also tend to function as **quasi-closed systems** with more distinct trophic levels than in terrestrial ecosystems (J. A. Estes, Tinker, Williams, & Doak, 1998), making the former easier to model. In contrast, coextinction processes in terrestrial systems remain poorly understood and have garnered comparatively less attention (Strona & Bradshaw, 2018).

The sparser literature on terrestrial ecosystems have contrarily focused more on networks of plants and pollinators (Dallas & Cornelius, 2015), and plants and herbivores (Pearse & Altermatt, 2013); even the few studies on terrestrial predator-prey networks are concentrated mainly on specific taxonomic groups such as invertebrates, mammals, or birds (Letnic et al., 2009). Further, most terrestrial networks consider only top-down effects, with few exceptions (Kagata, Nakamura, & Ohgushi, 2005; Scherber et al., 2010), likely due to the complexity and lack of data on basal resources (e.g., plants and invertebrates) needed to predict bottom-up processes. For example, the reintroduction of wolves (*Canis lupus*) in Yellowstone National Park in the USA elicited a trophic cascade, positively increasing woody browse species and bison (*Bison bison*), while simultaneously decreasing elk (*Cervus canadensis*), the wolf's prey (Ripple & Beschta, 2012). Most other terrestrial ecological networks have been constructed to estimate the impacts of invasive species because of the availability of research funding for investigating the economic costs of their impacts (Bradshaw et al., 2021; Crystal-Ornelas et al., 2021). For example, the invasion of the cane toad (*Rhinella marina*) across mainland Australia (Doody et al., 2015), and the yellow crazy ant (*Anoploepis gracilipes*) on oceanic archipelagos (Sugden, 2003), have caused both trophic cascades and species compositional changes in their respective communities. Despite the challenges and limitations in quantifying the effects of coextinction cascades in terrestrial ecosystems, additional research is necessary to predict future community change and assist conservation interventions.

Incomplete food webs

Model food webs are simplified representations of real food webs constructed to study the dynamics of an ecosystem or test hypotheses about how it functions (Susanne, Raul, Maria, Andrey, & Michaela, 2015). However, despite their efficacy, these models have inherent limitations for capturing the complexities of real ecosystems. Such food web models, that quantify the trophic interactions among species or feeding guilds, provide an objectively useful starting point to predict community responses to environmental change (Pringle & Hutchinson, 2020) and to estimate extinction risk more generally (Llewelyn et al., 2022; Strona & Bradshaw, 2018). Yet, the intricate nature of real food webs makes the construction of realistic models for entire communities challenging. Indeed, it is not logistically practicable to record all the interactions among species in complex communities, especially due to variations in species composition and interactions through space and time. By virtue of this variation, the few detailed food webs that have been built are necessarily incomplete at one spatial and/or temporal scale or another, such as at the microhabitat or seasonal scale, making most available empirical food webs snapshots that are not necessarily loyal to ecological reality — an observation supported by the scarcity of relevant literature on terrestrial food webs (Pocock, Evans, & Memmott, 2012). Although many data on species interactions exist (e.g., open-access databases like *Global Biotic Interactions — GloBI*) (Bohan et al., 2017; Carscallen, Vandenberg, Lawson, Martinez, & Romanuk, 2012; Poelen, Simons, & Mungall, 2014), these data often refer to a few known pairwise interactions with a focus on individual species, and cannot therefore be used to build complete food webs (Fig. 2).

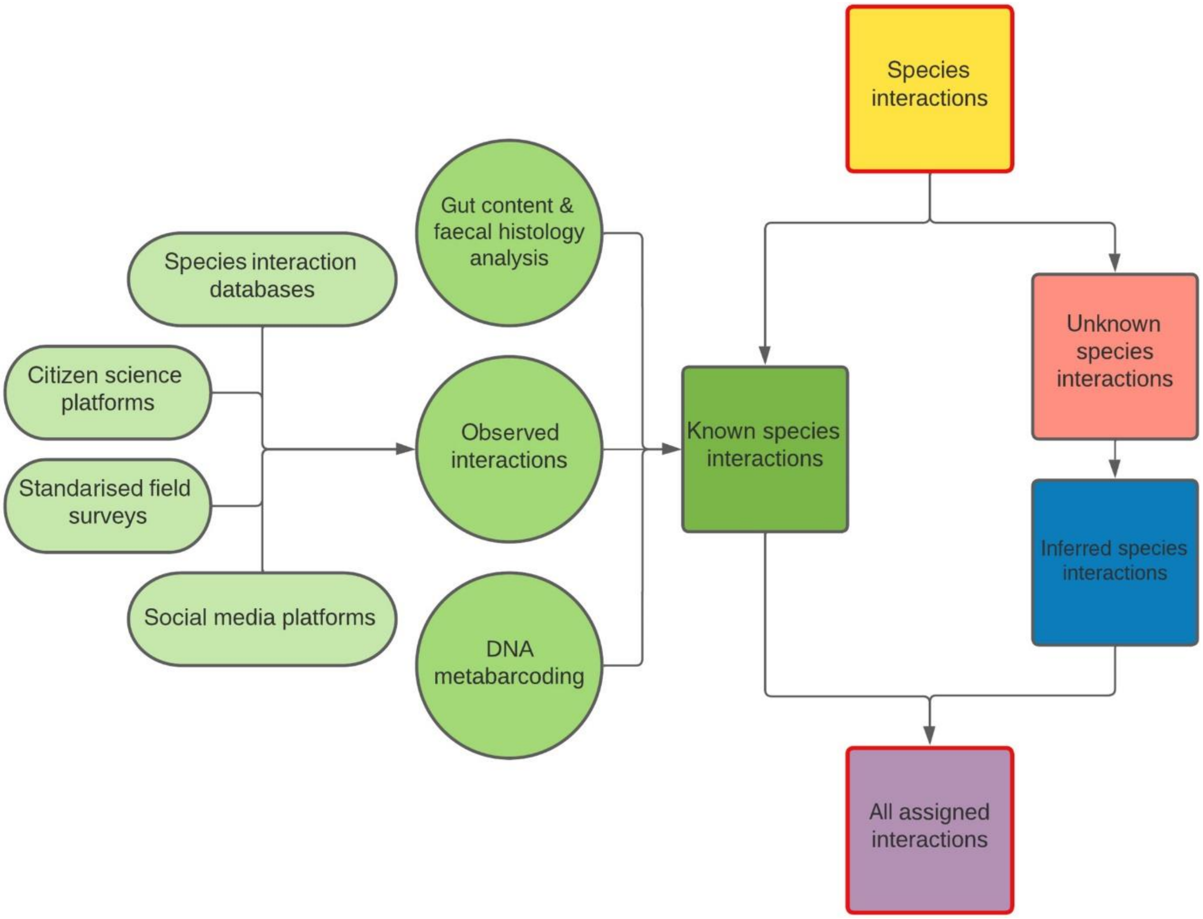

Figure 2. Sources, gaps, and pathways for interaction data. For species interactions (yellow: start), known interactions (green) are typically derived from one of three sources: (*i*) observed interactions (e.g., *GloBi*, *iNaturalist*, *Mangal*, and *Facebook*), (*ii*) gut contents and faecal histology (e.g., Carscallen et al., 2012), or (*iii*) DNA metabarcoding (e.g., Bohan et al., 2017). Several interrelating factors have made classifying the interactions for most species difficult (red). Methods to infer interactions (blue) (e.g., Desjardins-Proulx, Laigle, Poisot, & Gravel, 2017) have been used to address this gap, including supervised machine-learning methods. Known biotic interaction data derived from various sources, combined with methods to address unknown interactions, can provide a more comprehensive list of all assigned (or potential) interactions (purple: finish) within an ecological community.

Despite the higher taxonomic resolution of contemporary data used in food web models (Ings et al., 2009), the prediction accuracy of these models remains hindered by persistent issues and limitations, particularly the lack of a standard method for defining a 'community' (Herrando-Pérez, Brook, & Bradshaw, 2014; Herrando-Pérez, Delean, Brook, & Bradshaw, 2012; Krebs, 1985). Ideally, one can quantify trophic interactions among species without considering how its associated community is defined, but clearly defining the community can help researchers ensure that all relevant species are considered, and standardise the terminology used to describe trophic interactions. Furthermore, a well-defined characterisation of the community structure offers insight into the intricate trophic relationships between various species in a complex food web (e.g., better characterising the relationships or interdependencies between different trophic levels).

While ecological communities can be defined simplistically as “all organisms within a prescribed area” (Diamond, 1986), there is a more nuanced understanding that acknowledges temporal scales and the variability of species' presence and their contribution to community processes within these boundaries. For instance, some definitions describe a community as the “… group of species that occur together in space and time”, indicating that temporal scale is an equally important component of the definition (Harper, Begon, & Townsend, 1990; Stroud et al., 2015). Among the various methods for defining a community, spatio-temporal movement data are required when defining boundaries (Harper et al., 1990; Stroud et al., 2015) because implicit temporal averaging means that not all species are always present in a defined area, such that membership and relative importance vary through time. In terms of categorical boundaries, a community can also be defined by a taxonomic group (e.g., mammals), or by a group of species serving a specific ecological function or role (e.g., herbivores) (Begon, Townsend, & Harper, 2006). This is often defined artificially to suit a study’s criteria or by outlining the boundary where separately defined communities (i.e., using the aforementioned definitions) overlap. This boundary can be defined, often in combination, by the number of species observed in a given area (Cadotte & Tucker, 2017), biotic interactions (K. Dodds & A. Nelson, 2006), diversity indices or rank-abundance diagrams (Begon et al., 2006; Shaheen, Ullah, Khan, & Harper, 2012), pattern limits (e.g., checkerboarding) (Cody, MacArthur, & Diamond, 1975), comparing local and regional species richness (Szava-Kovats, Ronk, & Pärtel, 2013), species traits (Kraft & Ackerly, 2014), and/or by functional trait diversity (Lamanna et al., 2014), or using other variables (Begon & Townsend, 2020).

The careful consideration of methods for defining a community should be an essential first step, with elements such as structure, biotic interactions, spatio-temporal scale, and the specific research questions asked playing important roles in this determination. This process demands collecting as much data as possible, taking into account the spatial and temporal scale of the study. The resultant improvement in the accuracy and reliability of model outputs can ultimately reveal more practical and effective conservation strategies for at-risk communities. But obtaining comprehensive data on trophic interactions within ecological communities can be challenging due to the lack of clear boundaries and the difficulties in collecting data describing interactions. Historically, the primary method for assigning biotic interactions was via directly observed relationships in terrestrial ecosystems (e.g., through standardised field surveys, feeding trials, and gut/faecal content analyses) (Carmel et al., 2013) (Fig. 2). However, collecting empirical interaction data is usually costly and onerous, meaning that incomplete data are often used to construct entire networks (Lau, Borrett, Baiser, Gotelli, & Ellison, 2017). The questionable accuracy of such networks have been compounded by sampling biases (Blüthgen, 2010) and an unknown proportion of misidentified species (Egli, LeVan, & Work, 2020), meaning that past inferences made from trophic networks need to be interpreted with caution (Bortolus, 2008).

The presence of cryptic species, which are commonly found across a variety of taxonomic groups and regions (Struck et al., 2018), can undermine the realism of resultant networks (Pringle & Hutchinson, 2020). For example, treating two morphologically identical species as a single species (i.e., by observation) (Parker, 2004) (M. A. Smith et al., 2008). Cryptic interactions (those that are not easily observed) generally missed by conventional field surveys (e.g., interaction observation, scat analyses) can arise from intraspecific variation in size, behaviour, habitat, and activity (Pringle & Hutchinson, 2020). Furthermore, cryptic, non-consumptive predator-prey interactions (e.g., the mere presence of predators creating ‘landscapes of fear’) in ecological communities can potentially limit the distribution, habitat use, and abundance of species, and therefore, the interactions in a community (Pringle et al., 2019).

Considering that most interactions among species are infrequent and fluctuate across diverse spatial and temporal scales (Parker, 2004), they are not likely detected by short-term or seasonal field surveys. Although an interaction might be rare, it can still potentially alter community processes (Arditi & Ginzburg, 1989; Leitão et al., 2016), especially if it involves top predators (Duffy, 2003). Additionally, intraspecific variation (e.g., phenotypic plasticity) can indirectly modify the true expression of an individual’s diet (e.g., ontogenetic shifts, behavioural specialisation, habitat-restrictive prey availability) (Pringle & Hutchinson, 2020), but it is so far unclear if such variation affects the accuracy of inferred trophic interactions, and therefore, the ecological realism of constructed networks.

Due to uneven taxonomic/disciplinary foci and research specialisations, the quantification of ecological interactions, especially in terrestrial ecosystems, often falls short, exacerbating the existing methodological limitations and data gaps in species interactions. For example, there are geographical biases in study location and a disproportionate focus on functions indirectly related to interactions *per se* (e.g., invasion biology) (Cameron et al., 2019). Although alternative methods to observational field surveys have been developed (e.g., faecal microhistology and dietary databasing), such methods are labour-intensive, exceed the budget and time frames of most studies, and have limited resolution and accuracy (Pringle & Hutchinson, 2020). While other methods, such as DNA metabarcoding, are emerging, they can be costly (Bohan et al., 2017). Citizen science and public platforms are also a potential source of species interaction data (Maritz & Maritz, 2020), but these too have their own issues with quality control (Anhalt-Depies, Stenglein, Zuckerberg, Townsend, & Rissman, 2019) and coverage. Together, these methodological limitations create data gaps in species interactions that have flow-on consequences for inferring high-resolution trophic networks and quantifying the relationships between biotic components in communities (mainly terrestrial). However, the increasing accessibility and development of new technologies will provide more relevant data.

Inferring biotic interactions

Awareness of the importance of biotic interactions in determining species' responses to environmental change has motivated a recent surge in modelling ecological communities and associated methods to infer species interactions (Gravel, Poisot, Albouy, Velez, & Mouillot, 2013). However, due to the limitations in documenting new interactions, such as those between previously non-co-occurring species, predicting potential interactions is necessary to predict and potentially manage the impacts of changing environments, and the consequences of emerging alien species.

Earlier methods to infer trophic interactions were generally derived from predator-prey body-size relationships (Gravel et al., 2013; Warren & Lawton, 1987), but these inferences are limited in ecosystems with poorly resolved diversity, or for whose interactions are not easily described by such relationships, particularly in terrestrial ecosystems. This limitation has spawned the development of alternative techniques for inferring biotic interactions. Examples include calculating the probability of interactions among species using functional traits (e.g., morphological, physiological, behavioural) or phylogeny as a proxy of these traits (Morales-Castilla, Matias, Gravel, & Araújo, 2015), or abundance data to infer pairwise interactions among species. However, these methods are also limited by the data available to construct matching relationships empirically (Bartomeus et al., 2016). Co-occurrence data have been used to infer species interactions (Ibarra-Cerdena, Valiente-Banuet, Sanchez-Cordero, Stephens, & Ramsey, 2017), but these have been criticised as poor proxies (Blanchet et al., 2020; Yackulic, Korman, Yard, & Dzul, 2018). Joint species distribution models can also be adapted to infer species interactions based on environmental conditions and presence/absence or abundance data. By combining multispecies occurrences with hypothesised environmental predictors, these models can assess the residual probability of co-occurrence after controlling for environmental conditions (Momal, Robin, & Ambroise, 2020), although co-occurrence is not always evidence of direct interaction (Anhalt-Depies et al., 2019; Blanchet et al., 2020), and such models require expansive datasets (Sinclair, White, & Newell, 2010). Trait-matching using generalised linear models (Desjardins-Proulx et al., 2017; Pichler, Boreux, Klein, Schleuning, & Hartig, 2020) can also infer species interactions, although other methods often have higher predictive capacity (Caron, Maiorano, Thuiller, & Pollock, 2022).

To alleviate issues of data scarcity and inference limitations, newly emerging tools such as supervised machine-learning algorithms have become popular means for predictive interactions for different network types (Murphy, 2012). In particular, *k*-nearest neighbour and **random forest** have been applied to infer species interactions accurately by using both trait and observed trophic interaction/non-trophic interaction data (Desjardins-Proulx et al., 2017; Llewelyn et al., 2022; McConkey & Brockelman, 2011), providing a tool to predict novel species interactions under environmental change (Pomeranz, Thompson, Poisot, & Harding, 2019).

Despite supervised algorithms like random forest requiring extensive training data to be used effectively and having uncertainties about their ability to infer trophic interactions in highly **nested** networks, machine learning remains one of the most promising methods available for inferring biotic interactions (Desjardins-Proulx, Poisot, & Gravel, 2019). While predicting individual interactions can provide insight into the dynamics of food webs, the methods used might not be sufficient for quantifying the overall food web structure of communities (Poisot, 2023). Predicting interactions alone does not necessarily reveal the real position of each species in a food web, nor the relationships between species that are not directly linked by trophic interactions. For example, methods that perform well when inferring species interactions might not do as well when inferring whole community structures (Poisot, 2023). Deciding which methods to use should depend on whether inferring more realistic trophic interactions or constructing more realistic food web structures are more important for addressing particular research aims.

Another issue beyond inferring just the potential interactions between biotic components is assessing the importance of those relationships, because quantifying the strength of interactions is necessary to attribute ecosystem dynamics and predict their responses to perturbation.(Laska & Wootton, 1998). For example, the strength of a predator's interaction with a prey species depends on many components, including predator abundance (Yousef, Yousef, & Maji, 2021). However, how interaction strength is measured can complicate its quantification. For example, interaction strength can refer to different aspects of ecological relationships, from the increase in fitness (e.g., thermal tolerance) that a species experiences in a mutualistic association (Xie et al., 2013)**,** to the influence of cross-species reproductive disturbances and competitive struggles for resources (Kishi & Nakazawa, 2013)**.** This multiplicity of measures and the inherent variability of ecological interactions poses a challenge to their comparison of, and integration into model food webs, with choice depending on the assumptions underpinning particular ecological theories or the method of quantification applied. Although empirical data such as field observations quantifying interaction frequency and intensity (Wootton & Emmerson, 2005) can be used to infer an interaction strength between species, alternative approaches are necessary when such data are not available (as is often the case). Various mechanistic models can account for such effects, including those that use traits to incorporate the frequency of prey items in predator diets (Pocock, Schmucki, & Bohan, 2021), or those based on bioenergetic-mechanistic models that link the energy flow between species and describe how they acquire and transform resources into traits (e.g., body size) that influence relationships (Passoni et al., 2022).

Although the previous examples are valid methods to quantify interaction strengths, one should carefully consider the underlying assumptions when evaluating coextinction risks. Assuming the strength of interaction between any two species remains constant through time and regardless of changes in the ecological community in which they occur, as well as assuming that interactions between species are linear and that their strength is invariant to the densities of interacting species (Vázquez, Ramos-Jiliberto, Urbani, & Valdovinos, 2015) need to be determined. However, methods outlined to quantify interaction strengths demonstrate situations where these assumptions are not always met, and might, therefore, not fully mimic reality. For example, ignoring the synergistic or antagonistic, non-additive effects of environmental perturbations on species interactions — i.e., the effect of ≥ 2 species interacting is not equal to the sum of their individual effects — can modify estimated extinction risk (Thompson, MacLennan, & Vinebrooke, 2018).

Modelling species interactions and community change

Analytical, correlative, and numerical simulation models are becoming more tractable and popular for describing structure and processes within ecosystems, and to predict community changes arising from environmental perturbations (Strona & Bradshaw, 2018). Network models, such as those representing relationships between individual species (Llewelyn et al., 2022), can represent trophic, mutualistic, competitive, or other interactions within a community, or be simplistic representations of pre-existing or existing ecosystems typically based on unweighted interaction links (Geary et al., 2020).

Basic predator-prey models describing the dynamic relationship between two guilds have long been used to characterise species interactions (Lotka, 1910). Such models have traditionally been based on standard predator-prey differential equations like the Lotka-Volterra to quantify the effects of biodiversity loss on the vulnerability of communities to secondary extinctions (Sanders, Thébault, Kehoe, & Frank van Veen, 2018), and the subsequent compensatory Rosenzweig-MacArthur (Rosenzweig & MacArthur, 1963) and ratio-dependent Arditi-Ginzburg variants (Arditi & Ginzburg, 1989), to model ecological systems (Åkesson et al., 2021; Nonaka & Kuparinen, 2021). These models highlight the importance of accounting for trophic interactions between organisms when modelling ecosystems (McCann, 2007).

Single-species population and distribution models have been used to predict the implications of anthropogenic climate change (Araújo & Luoto, 2007), yet their inherent limitations prevent a comprehensive assessment of species extinction risk. These types of models do not consider biotic interactions and physical processes (Elith & Leathwick, 2009) (Fig. 3), and therefore, only provide a limited assessment of species vulnerability (Carmel et al., 2013); the exception is some studies modelling multispecies dynamics (Säterberg, Sellman, & Ebenman, 2013). Correlative species distribution models can include interactions, but they cannot predict variation in these interactions under changing environmental conditions. As a result, such models cannot account for coextinction processes and are likely to underestimate extinction risks under future climate change (Strona & Bradshaw, 2018).

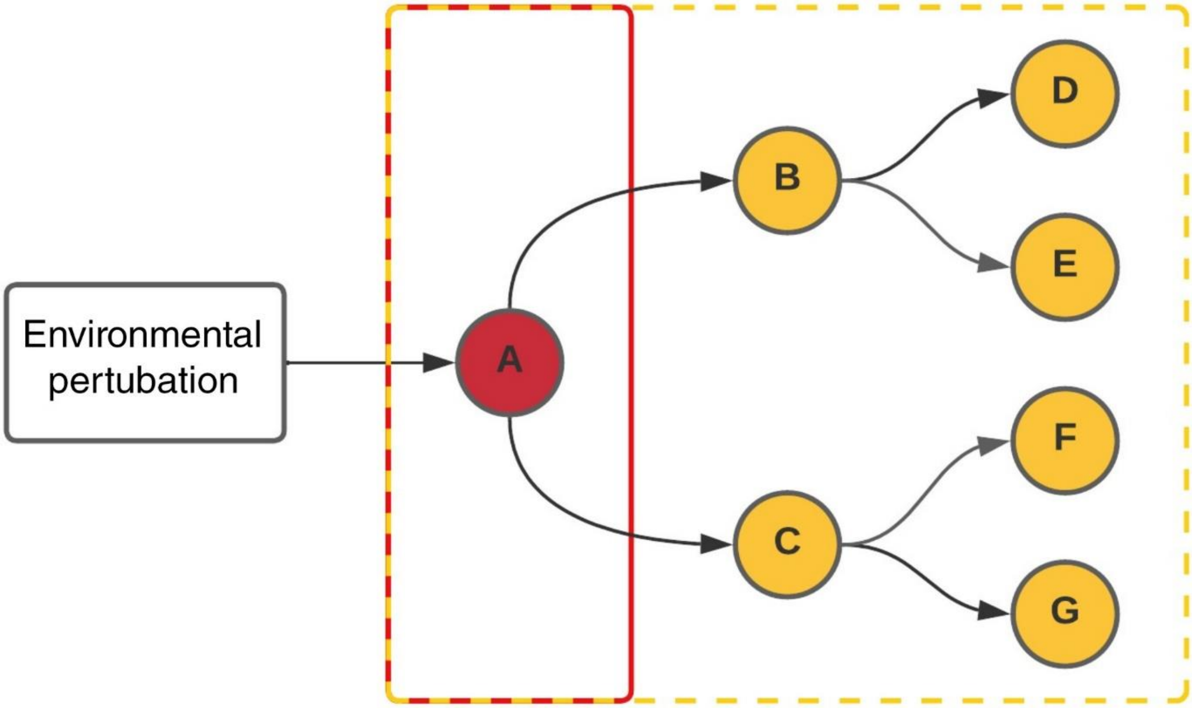

Figure 3. Single- *versus* multiple-species extinction models. Extinction estimates based on single-species models (solid red box) (e.g., species distribution models) can only predict direct effects caused by environmental perturbations (e.g., climate change) (red circle 'A' representing a primary extinction). These models consider each species as a disconnected entity and do not account for the indirect effects of species coextinctions and population changes. In contrast, multiple-species models (e.g., network-based models) (dotted yellow box) consider both direct (red circles: primary extinctions) and indirect effects (yellow circles: coextinctions and population changes). For example, a decline in the population of one species (B) can lead to the coextinction of other species (D and E) that depend on B for food or other resources. By accounting for these indirect effects, multiple-species models provide a more accurate and comprehensive analysis of the impact of environmental perturbations on ecosystems and the risk of species extinctions.

As an alternative modelling tool, ecological network models based on network theory include interactions by using a flexible mathematical framework accounting for a specified number of biotic components and relationships within a parameterised network (i.e., species interactions can be **weighted** or **unweighted**) (Delmas et al., 2019). These models can be defined as a network (*G*) comprised of **nodes** (*N*) and **edges** or links (*E*) (Geary et al., 2020; Landi, Minoarivelo, Brännström, Hui, & Dieckmann, 2018), formulated generically as $G = (N, E)$, that represent one or more interactions between nodes (Lau et al., 2017). These models are typically represented as **bipartite networks** (Geary et al., 2020), although can also be used to represent trophic interactions among species in a community (Pocock et al., 2012).

Ecological network models representing biotic interactions can test hypotheses about variation in food web structure and resilience to perturbation (Säterberg et al., 2013). Because these models ideally encapsulate most nodes in a community and identify (and possibly quantify) the interactions among them, ecological network models can simulate coextinctions more realistically than other types of models (Geary et al., 2020) (Fig. 3), with many examples of network models applied to reveal ecosystem-wide effects or predict the relative impacts of different management scenarios (Wallach et al., 2017). Ecological network modelling can be applied not only to evaluate multiple extinction drivers in addition to coextinction effects (e.g., invasive species and land-use changes) (Strona & Bradshaw, 2022), they also assess how these stressors might, in turn, affect different parts of the same network. Further, the graphical representation of species interactions in ecological network models can be more effectively used to explore the potential for cascading effects and other nonlinear interactions arising from anthropogenic threats. This is more useful compared to other mechanistic frameworks that can represent ecological communities, such as the Madingley model (Flores, Kortsch, Tittensor, Harfoot, & Purves, 2019) that is more suited to studying ecological processes and dynamics on species populations (e.g., competition) and how these affect communities. Although network models attempt to represent entire ecological communities, they too have operational limitations beyond the availability and quality of the constituent data. Model nodes representing entire populations are necessarily oversimplified, given that these might not account for all the associated qualities of a biotic component. For example, when a node represents an individual species, all associated traits (e.g., phylogeny, morphology, physiology) are encapsulated by this single node and can never fully represent the real-world variation within the species. This limitation can generate errors in inferred network dynamics and responses (Bolnick et al., 2011). Population dynamics (e.g., age structure, density compensation) within nodes are usually ignored, either because they can make a network unwieldy, or because of data gaps for all species within the community, preventing network models from weighting nodes by variation in abundance and its influence on extinction risk

(Wilmers, 2007). However, community viability models where particularly influential nodes are expanded to account for population structure and abundance could potentially increase the ecological realism of network models. Further, it is possible to attach dynamical models to important nodes in a network. For example, in predator-prey systems with large fluctuations in abundances, such as cycling predator-prey dynamics (e.g., hare *Lepus americanus*–lynx *Lynx canadensis*) (Elton, 1924), dynamical models can be used to modify edge weights when those fluctuations occur. This approach would enable network models to capture more of the complexity of fluctuating interactions between species. Beyond population dynamics, accounting for spatial and temporal dynamics associated with various ecological processes is also important for modelling biotic interactions. However, dividing community spatial units according to temporal processes that vary interaction potential, such as migration patterns, seasonal changes, or disturbances, can be challenging. For instance, the migration of one species could fundamentally alter the ecological interactions within a given spatial unit (Bauer & Hoye, 2014), introducing new complexities into the community when that species is present. Likewise, natural disasters such as bushfires, floods, or other extreme events can alter food webs (e.g., by facilitating biological invasions) (Spencer, Barton, Ripple, & Newsome, 2020), leading to different dynamics that temporally static models are not able to capture. To account for such temporal variability in community composition, one could potentially iteratively modify a species' ability to interact as a proxy for time (e.g., through shifting migration patterns) (Rickbeil et al., 2019), and by simulating the rate of movement (e.g., through elevation change) (Freeman, Scholer, Ruiz-Gutierrez, & Fitzpatrick, 2018), by coupling network models with species distribution models. Of course, higher model complexity increases data requirements (e.g., ontogenetic variation in traits) (Lau et al., 2017). Modelling a subset of interactions within a community, although useful for quantifying binary relationships (Dallas & Cornelius, 2015), can also limit the utility of network models. For example, focusing only on trophic interactions disregards the potential offsetting effects of other interaction types, such as host-parasite (García-Callejas, Molowny-Horas, & Araújo, 2018) or plant-pollinator relationships (Bartomeus, Saavedra, Rohr, & Godoy, 2021), which could also bias estimates of extinction risk (Lafferty et al., 2008). A more realistic approach would ideally include multiple interaction types simultaneously (Hutchinson et al., 2019). Such ‘multiplex’ networks could theoretically encapsulate most interaction types among species in a community, account for spatio-temporal heterogeneity, context dependency (Stella, Andreazzi, Selakovic, Goudarzi, & Antonioni, 2016), and characterise the structure, function, dynamics, and coextinction risk of entire ecosystems (Pilosof, Porter, Pascual, & Kéfi, 2017). For example, a multiplex approach has been used to produce a framework for a multispecies food web model that allows for non-trophic interactions as functional classes (Kéfi et al., 2012). However, because most interaction types (e.g., plant-seed dispersers) are not linked explicitly to trophic interactions, they cannot be applied easily to all species in a community. Although some multiplex networks can bypass this problem by including both trophic (e.g., predator-prey relationships) and non-trophic (e.g., mutualistic partnerships) interaction networks represented as separate layers and interconnected by shared species (Pilosof et al., 2017) (Fig. 4), they require expansive datasets to build (Strona, 2022). For example, non-trophic interactions such as predator interference (e.g., ‘landscape of fear’ exclusion of potential prey) (Brown, Laundré, & Gurung, 1999) can modify the functional relationships between predators and prey beyond simple inference of potential trophic interaction. Accounting for such phenomena that modify the shape of the functional response (Kéfi et al., 2012) would require different network topologies to those inferred solely from trophic inference.

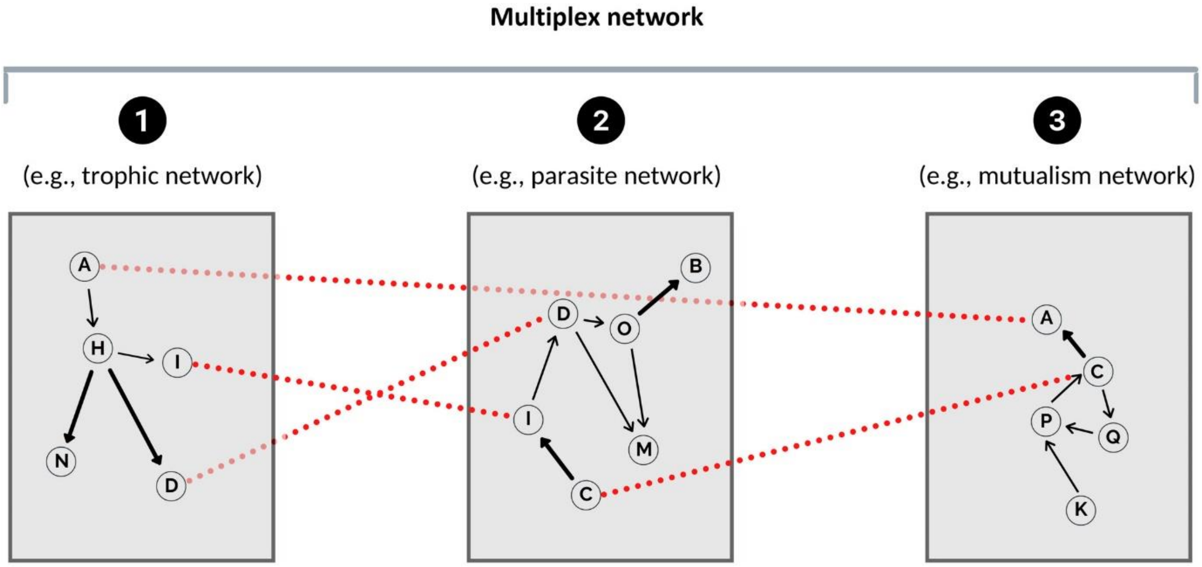

Figure 4. A theoretical multiplex network. A multiplex network can include two or more network layers (e.g. layers 1, 2, and 3). Using a model based on network theory, nodes (represented as letters) can be used to characterise biotic components such as species or functional groups, while edges or links represent their interactions within each interaction network. For example, nodes 'D' and 'I' could represent shared prey or host species from predation and parasitic networks, respectively. These nodes could be connected by 'C' as a shared host in both the parasite and mutualism networks, connecting all biotic components trophically, either directly or indirectly. The thickness of the black arrows representing these interactions can be weighted according to ecological effect. However, full-community multiplex networks are difficult to construct because they require extensive datasets that are unavailable for most systems. Interactions between networks can be linked by shared species, but no current theory exists for weighting links between trophic and non-trophic networks (indicated by red dotted lines).

General consumer-resource models, which are fundamentally based on the direct relationships between consumer and resource species (MacArthur, 1970), have also been designed to integrate multiple interaction types (Lafferty et al., 2015). Furthermore, there is still no unifying theory to account for the trait space a species occupies, and therefore, no method for weighting the links between species in different networks (Fig. 4). Developing methods to allow node parameters to affect different types of interactions with other parts of the network, with additional consideration to spatial and temporal influences, is a clear avenue for development.

While methods have been developed to quantify coextinction risk across non-trophic interactions networks (Dallas & Cornelius, 2015), few studies have constructed complex networks consisting of multiple, mutualistic networks (e.g., facilitation, pollination, seed dispersal) (Valiente-Banuet & Verdú, 2013), or interaction types (e.g., predation, mutualistic, parasitic interactions) (Pocock et al., 2012). In contrast, most research on ecological networks has focused on comparatively simplified, empirically based parasitic (e.g., host-parasite) (Dallas & Cornelius, 2015) and mutualistic (e.g., plant-pollinator) networks (Koh, Sodhi, & Brook, 2004), with no current framework developed for quantifying the coextinction risk for many other non-trophic interaction networks.

Simulating trophic cascades in ecological networks

Simulation models are a common tool applied to predict relative extinction risk, encompassing diverse methodologies and approaches. These approaches range from simple statistical models to estimate secondary extinctions as an effect of primary extinctions, to modelling coextinctions and trophic cascades accounting for the rewiring of interaction matrices (Colwell, Dunn, & Harris, 2012). Various hypothetical and empirically based coextinction simulation models have been constructed across different biome and interaction network types (Strona & Bradshaw, 2018), with a particular focus on simulating primary and secondary extinctions in **unipartite** and bipartite networks (Dallas & Cornelius, 2015; Lian Pin Koh et al., 2004; Strona & Bradshaw, 2018; Valiente-Banuet & Verdú, 2013).

While showing that the primary extinction of a species can precipitate the secondary extinction of others, the process of predicting relative extinction risk is a more complex task. Computer simulations and network theory are modern tools that can evaluate extinction risk (Traveset, Tur, & Eguíluz, 2017), facilitated by simulations in large-scale studies (Baumgartner, Almeida-Neto, & Gomes, 2020) and by supervised inferences of the relationships between biotic components (Poisot, Stouffer, & Kéfi, 2016). Simulations are generally constructed under a set of user-defined assumptions, with extinction risk for a given species estimated from different exposures to a theoretical list of different conditions (Baumgartner et al., 2020). However, the main challenges limiting the realism of such simulations is devising realistic assumptions to trigger secondary extinctions for species in a network, and the difficulty of accounting for the effects of complex trophic and non-trophic interactions.

Coextinction simulations, conventionally derived from probability-based coextinction models (L. P. Koh et al., 2004; Memmott, Waser, & Price, 2004), provide estimations of potential species extinctions linked to the loss of associated species. Such simulations rely on the premise that affiliated extinctions occur in a random sequence, typically within bipartite networks, and have since developed into an array of more advanced methods. These include topological models that simulate coextinction when a non-basal species loses all or the majority of other species in the food chain that it relies upon (J. A. Dunne, Williams, & Martinez, 2002), stochastic models that also account for variation in demographic dependencies among species (Vieira & Almeida-Neto, 2015), and hybrid coextinction models that combine topological and simulation models for different species types (Traveset et al., 2017) to estimate complex extinction probabilities based on the removal and persistence of nodes. Other approaches include the dependent random-search coextinction model (Baumgartner et al., 2020) that improves the realism of extinction estimates by accounting for how extinction processes affect not only node removal, but also how their interactions change or are rewired following node extinctions where novel interactions are designated randomly 'depending' on similarities among nodes.

Although many existing simulation models can account for processes of coextinction and trophic cascades, several complications and limitations need to be addressed. Techniques to simulate coextinctions are usually designed for specific studies or network types (Dunn, Harris, Colwell, Koh, & Sodhi, 2009; L. P. Koh et al., 2004). For example, simulations designed for bipartite networks with two trophic guilds cannot normally accommodate the multiple trophic levels making up entire food webs. Much of the research in community ecology has also attempted to estimate the resilience of ecological networks under various perturbations (Dallas & Cornelius, 2015; Wilmers, 2007), as opposed to quantifying the coextinction risk of specific nodes within networks. Moreover, simulation methods that can be applied to networks with multiple trophic guilds are primarily restricted to simulating hypothetical scenarios that are focused on either top-down or bottom-up trophic cascades, but not both (Llewelyn et al., 2022; Strona & Bradshaw, 2018).

While many existing simulation models consider processes of coextinction and trophic cascades, the functional importance of different species within a community can potentially alter how inferred linkages emerge (Brodie et al., 2014). Functional importance can be quantified by relative position within a trait hypervolume — i.e., all traits (e.g., morphology, behaviour, life history) (Kissling et al., 2018) represented by all species within a given space and time. These traits together represent the functional diversity or richness of a particular hypervolume (Lundgren et al., 2020; Pimiento et al., 2020) describing the community's total trait variation (Roscher et al., 2012). The more trait redundancy in the hypervolume, the greater a community's resilience to perturbation, and therefore, its potential to resist extinction cascades (Lundgren et al., 2021). Species-level trait databases (Pimiento et al., 2020) analysed using Gower similarity or dissimilarity matrices (Gower, 1971) can be used to construct such trait hypervolumes (Lundgren et al., 2020; McLean et al., 2019) that contextualise community composition and interaction potential based on their functional compatibility. The position of species within a network can also be used as a measure of functional importance (Bello, Schleuning, & Graham, 2023), although different measures (e.g., degree, which surmises the total number of edges connected to a node) reflect different aspects of 'importance' (Cirtwill et al., 2018).

By ascertaining the functional importance of species within a community, we are equipped to determine the functional compatibility and potential interactions between species. This process can reveal which traits play important roles in facilitating interactions with other species (Lavorel & Garnier, 2002). Further, estimating the functional importance of a species within a community can reveal emergent properties of the relative functional roles of specific taxonomic groups (Dehling & Stouffer, 2018). Species that are functionally unique or that contribute disproportionately more to the functional diversity of a community are more likely to form foundational linkages within that community (James A Estes, Heithaus, McCauley, Rasher, & Worm, 2016). The loss of such species might therefore have a higher relative probability of eliciting cascades.

Implications for management and conservation

Not considering most biotic interactions in an ecosystem likely underestimates future extinction risk (Strona & Bradshaw, 2018), and therefore, network-based analyses provide a relevant framework to clarify ecosystem-level processes and consequences (Harvey, Gounand, Ward, & Altermatt, 2017). Quantifying, inferring, and simulating biotic interactions give deeper insights into how anthropogenic threats will erode entire ecosystems via coextinctions (Desjardins-Proulx et al., 2017; Pomeranz et al., 2019; Tylianakis et al., 2008). As climate disruption compounds other extinction drivers like habitat loss (Benton, Bieg, Harwatt, Pudasaini, & Wellesley, 2021) and invasive species (Essl et al., 2020), network models offer a useful way to explore the potential ecosystem-wide effects of future biodiversity loss and change, by simulating emerging interactions and the loss of existing interactions that can rearrange species assemblages in otherwise unpredictable ways. Measuring how the topology of interactions within a community degrades in response to perturbations can also identify the extent to which resilience to future environmental change declines concomitantly (Strona & Bradshaw, 2022).

Single-species management frameworks have historically dominated environmental decision-making (Lindenmayer et al., 2007), but sensible environmental policy relies on identifying and avoiding environmental tipping points (Hillebrand et al., 2020) (i.e., events that depend on species' interactions and multiple scales of complexity) (Landi et al., 2018; Wolanski & McLusky, 2011). Comprehensive ecological network models can represent these interactions over different scales of complexity, and so improve the accuracy of predictions, enabling policies that will have a higher probability of avoiding negative tipping points (J. Dunne & Pascual, 2006). Ecological network modelling might better inform environmental management by simulating possible outcomes under a broad set of assumptions; for example, network models can be applied to predict and mitigate the effects of biological invasions on native communities, or even possibly to evaluate different intervention strategies and avoid ineffective species translocations (Morris, Brook, Moseby, & Johnson, 2021). Extended outcomes of this type of research could also assist with recognising coextinction risk in threatened-species assessments and policies (Moir & Brennan, 2020). As such, ecological network modelling is poised to add considerable power to the management of biodiversity (Schuwirth et al., 2019), although in practical applications, there are many issues relating to model feasibility, data availability, and communication transparency that could limit the utility of these methods (Schuwirth et al., 2019).

Conclusions

The trophic complexity of some terrestrial ecosystems and the spatial and temporal uncertainties of community boundaries have made resolving trophic networks difficult. Combined with the dearth of empirical data on species interactions (Momal et al., 2020) and the difficulty and costs associated with collecting such data (Pringle & Hutchinson, 2020), quantifying how species interact within a community remains a challenge. Comprehensive research for constructing trophic networks that realistically model ecological interdependencies, coupled with robust methods for quantifying extinction risk, are still needed to predict and manage the indirect effects of climate change and other anthropogenic threats. More research to test assumed processes and inference accuracy will make these approaches more realistic, guiding current and future decisions in the management of terrestrial ecosystems (see 'Outstanding questions').

Outstanding questions

- How do anthropogenic threats like climate change affect the extinction risk of vertebrate species through the processes of coextinction and trophic cascades at fine spatio-temporal scales? Previous research has tended to focus on either marine or freshwater ecosystems, with comparatively little research on terrestrial ecosystems. Understanding how anthropogenic threats affect these communities, specifically between multi-trophic and non-trophic networks at fine spatio-temporal scales will be necessary for effective multispecies conservation.
- Can machine-learning algorithms be used to infer all predator-prey interactions for vertebrates in terrestrial communities? Although many trophic networks have been constructed, few studies have attempted to model all the interactions in entire (and diverse) terrestrial systems, with many difficulties surrounding the quantification of trophic relationships between species.
- How might a change in a community's detail (e.g., intraspecific variation) and composition affect how trophic cascades and coextinctions occur in coextinction

models? Identifying all potential trophic interactions among species in an ecosystem is a complex element that is typically neglected in many coextinction models that instead progressively remove species and ignore how species may rewire their interactions when other species are lost or join the community. Further, basal resources (e.g., invertebrates and plants) in terrestrial network models are typically ignored or clumped due to a dearth of data, developing a gap in our understanding of the dynamics of food webs.

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Conflict of interest

All authors declare that they have no conflicts of interest.

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Glossary

bipartite network

An interacting relationship between two groups of species, such as that between plants and pollinators within a biological community.

coextinction

The cascading process in which the primary extinction of a species results in the secondary extinction of another, dependent species.

edge

In an ecological network model, edges represent the relationship (e.g., biomass flow, trophic interaction) between nodes.

nestedness

The pattern in which species interactions within a network are organised such that less-connected species tend to interact with only a subset of the species that are more connected. This results in a nested structure, where the interactions of the less-connected species are a subset of those of the more connected species.

networks

A complex system of interactions between different biotic components, where the interactions can be direct or indirect and can involve a variety of mechanisms and functions. These components can include individual organisms, populations, communities, or ecosystems, and they can be connected through different types of relationships, such as mutualism, predation, parasitism, competition, or facilitation.

node

In an ecological network model, nodes can represent a biotic component (e.g., species, functional groups) connected by *edges*.

random forest

A supervised machine-learning algorithm based on ensemble learning that uses input data to construct and merge decision trees to predict an outcome.

single-species management frameworks

A management strategy that specifically focuses on conserving individual species, excluding other associated or dependent species from direct intervention.

top-down and bottom-up trophic cascades

The process by which species going extinct at one trophic level (consumers) causes species occupying lower trophic levels (resources) also to go extinct (top-down), or *vice versa* (bottom-up).

unweighted and weighted relationships

A weighted interaction link is a relationship between two species in which a numerical value represents the strength of the interaction; an unweighted link does not account for interaction strength.

unipartite network

An interacting relationship such as predation in which only one group of species interacts with all other species within a biological community.

quasi-closed ecosystem

An ecosystem that functions as if it is closed to external influences, with little exchange of matter or energy with its surroundings.

Chapter 2

Multiple approaches required to define tropical vertebrate communities

Abstract

Understanding which species interact within a 'community' is essential to predict responses to environmental change. However, what defines an ecological community is a complex question with no standardised definition. As a consequence, communities have been defined using many different techniques. In this chapter, we discuss the use of both *alpha* and *beta* diversity indices and multidimensional trait space to define terrestrial vertebrate communities to evaluate their risk to anthropogenic threats (e.g., climate change) in the future. Using the Wet Tropics bioregion as a case study, our results suggest that *alpha and beta* diversity indices can be used to differentiate vertebrate communities across latitude and elevation to a degree, whilst analysis of multidimensional trait space suggests that these communities are functionally analogous. Specifically, defining vertebrate communities by their functional composition may help protect functional groups and, therefore, maintain the resilience of these communities to environmental perturbations. However, completely ignoring species composition may lead to the extinction of vulnerable species, which may lead to the loss of endemic species and facilitate invasions by other species. Alternatively, solely focusing on species composition may also be disadvantageous as even highly differentiated communities may not be comprehensively described as disconnected entities, as indicated in this case study. Thus, evaluating how to define vertebrate communities in terrestrial environments depends on the study's objectives and the availability of data.

Introduction

Anthropogenic threats such as climate change, species invasions, and habitat modification compromise biodiversity at a global scale (Kerr et al., 2015; Seddon et al., 2016), with expectations to impact every level of terrestrial ecological community structures and functions (Seddon et al., 2016; Suttle et al., 2007; Warren et al., 2001; Woodward et al., 2012). In addition to understanding the direct impact of these threats and mechanisms that drive biodiversity patterns across different spatio-temporal scales, identifying how these impacts propagate (i.e., flow-on effects) through ecological communities via biotic interactions (i.e., direct and indirect effects) is critical to predict their ecological implications accurately. Without considering these flow-on effects, we are likely to underestimate ecological impacts on these communities vastly (Strona & Bradshaw, 2018). Therefore, there is a pressing need to firstly revist how ecological communities are differentiated using various approaches to facilitate studies evaluating their extinction risk.

Species assemblages are connected to their neighbouring assemblages through species/propagule dispersal, geneflow, interactions, and the transfer of nutrients and resources, making it difficult to define boundaries between communities (Leibold et al., 2004). The definition of ecological communities has been debated and evolved through time, progressing from broad, generalised terms focused on the occupancy of species in a specific area (Diamond, 1986; Roughgarden & Diamond, 1986), to more factual definitions focused on the importance of accounting for spatial and temporal scales (Harper et al., 1990; Mittelbach & McGill, 2019; Stroud et al., 2015). However, practically defining the physical boundaries of a community (i.e., where one community starts and another ends) is more complex because such arbitrary boundaries are unlikely to exist, and if they do, are exceptionally rare because species vary in membership and relative importance. However, clear definitions are required for practical applications of assessing extinction risk in communities, because without them, important biotic processes (e.g., interactions between rare species) could be overlooked and lead to underestimation of extinction risk (Strona & Bradshaw, 2018). Very often, the research question drives the definition of communities to meet research criteria more objectively, there have been many ways to both measure and describe boundaries between ecological communities. Recent studies defined communities using species composition attributes, such as basing this on a single taxonomic group or interaction type, or by evaluating their alpha and beta diversity by measuring their species richness, diversity, and evenness (Begon & Townsend, 2020; Shaheen et al., 2012; Suttle et al., 2007; Tilman, 1982). For example, rank-abundance diagrams (Tokeshi, 1993), gradient, and ordination analyses were used to describe boundaries in community patterns (Begon & Townsend, 2020). Multidimensional trait space analysis, which can represent the functional traits of all of the species found within a given space and time (Lundgren et al., 2020; Pimiento et al., 2020), can be combined with methods quantifying species composition (Karkarey et al., 2022), to define communities based on their functional diversity, and identify their responses to environmental changes. Yet, there is still no unified approach to differentiate terrestrial ecological communities, combined with practical discussion of the application of these defined spatial and temporal boundaries, for evaluating their extinction risk in response to environmental perturbations for the purposes of conservation.

The biodiverse montane rain forests of the Australian Wet Tropics bioregion in north-east Queensland, Australia (Bertzky et al., 2013; Le Saout et al., 2013) has been extensively surveyed (S. E. Williams et al., 2010; S. E. Williams et al., 2010), providing a model system for studying ecological communities and responses to anthropogenic impacts. Anthropogenic climate change is expected to be the greatest driver of biodiversity loss in this region in the coming decades (Korner & Spehn, 2019), with > 50% of vertebrate species predicted to become locally extinct by 2100 (Williams et al., 2003). Montane rain forests are some of the most vulnerable ecosystems globally (Nogués-Bravo et al., 2007), largely due to their constituent species' high endemism and specialisation to narrow temperature ranges (La Sorte & Jetz, 2010; Laurance et al., 2011; Mamantov et al., 2021). While studies in the Australian Wet Tropics have defined some vertebrate communities using abundance and distribution metrics (S. E. Williams et al., 2010), no approach has been employed for differentiating vertebrate communities for the purpose of community vulnerability to environmental change. Identifying community structure and functions is an essential first step for predicting community responses to threats and implementing relevant conservation strategies.

In this chapter, I aim to use a comprehensive approach to differentiate between discrete ecological communities identified in the Wet Tropics bioregion for the purposes of evaluating their extinction risk and assess how species diversity and trait space vary among putative communities as a function of spatial variation in climate. I address two main questions: *i*) Can species diversity and trait space be used to differentiate communities in the Australian Wet Tropics; and *ii*) Is it justifiable to group this bioregion as one community, or is it more appropriate to divide it into latitudinal and/or altitudinal communities. More specifically, I investigate if diversity-based community differences are also portrayed in trait-based differences among identified communities. As supported by contemporary conservation practises (Cadotte, 2011; Cadotte et al., 2011; Leuzinger & Rewald, 2021), conserving trait space is considered more important than conserving taxonomic diversity for maintaining community resilience as this directly correlates to preserving functional diversity, a key factor in sustaining ecosystems functions and services (Balvanera et al., 2006). I hypothesise that community composition does not beget functional diversity and, therefore, trait space should be considered when evaluating community resilience, as well as that community differences in diversity and trait space should be more distinct across elevational space (Janzen, 1967) as opposed to over latitudinal space.

Methods

I accessed 3,055,261 species occurrence records collected by S. Williams and colleagues (James Cook University, Townsville) between 1997 and 2015 across the Australian Wet Tropics in standardised vertebrate field surveys. I used the ArcGIS® Pro (version 2.7) multivariate clustering tool based on *k*-means unsupervised machine-learning algorithm (non-requiring of classified features to train) (Likas et al., 2003) to identify natural clusters, by evaluating the optimal number of clusters ('sites' henceforth) (Figure 1) by comparing a pseudo F-statistic for clustering mixtures from 2 through 30 within the dataset using geographic location of each observational point. This analysis identified a total of 164 vertebrate species commonly recorded in tropical rain forest areas across all highland (aka 'upland') (> 850 m above sea level) and lowland (≤ 450 m above sea level) areas, excluding all other species found exclusively in midland areas (≥ 451 – 850 m above sea level) or those not commonly found in these areas due to not being species core habitat (as defined by S. Williams et al. (2010) as species with ≥ 3 degree of rain forest specialisation).

Biodiversity indices

I completed all statistical analyses using R v4.0.0 (R Core Team, 2021) and the `vegan` package (Oksanen et al., 2013), except for otherwise stated. To differentiate species composition between the identified sites across both latitudinal and altitudinal space, I used a combination of different indices to measure alpha diversity (α-diversity), defined as the species diversity of a community. Specifically, I estimate the alpha diversity in both highland (> 850m above sea level) and lowland (≤ 450 m above sea level) areas to maximise the effect size to detect differences in communities by evaluating their upper and lower most distributions (Guo et al., 2013). I also used different indices to measure beta diversity (β-diversity), defined as the difference in species diversity between two or more communities, to evaluate differences in diversity at varying spatial scales. Specifically, I calculated species richness (S) at each site and elevation range as the sum of all species found within each area. I compared species richness among sites to the total number of known vertebrate species in each taxonomic class for the entire Wet

Tropics bioregion. I also assessed the spatial sample-based rarefaction for each site and elevation using the `mobr` R package (McGlinn et al., 2021), in which I accumulated species by order of their spatial proximity to the original focal plot to assess sampling effort. Further, I also calculated the Shannon-Wiener diversity index (H', (Shannon & Weaver, 1949)):

$$H' = \sum_{i=1}^{s} p_i \log_e p_i$$

where p_i = the proportion (n/N) of individuals of the i^{th} species (n) divided by the total number of individuals found (N) and s = the total number of species, to measure both total abundance and evenness of species found in each site and elevational range. As an alternative measure, I also calculated the Simpson's diversity index (Simpson, 1949) to measure the number of species and their relative abundances:

$$\gamma \ = \ 1 - \sum_{i=1}^{s} \left(\frac{n_i(n_i - 1)}{N(N-1)} \right) = 1 - \sum p_i^2$$

Additionally, I calculated Pielou's species evenness (Pielou, 1966), which measures how evenly distributed each species is, defined as a sum of the total number of observations made, as well as relative abundance for each site and elevational range:

$$J' = H'/\log_e(S)$$

To also measure community dissimilarity among sites, I calculated the Jaccard coefficient:

$$d_j(A,B) = 1 - J(A,B) = \frac{|\mathrm{A} \cap \mathrm{B}| - |\mathrm{A} \cup \mathrm{B}|}{|\mathrm{A} \cup \mathrm{B}|}$$

where *A* and *B* represent two sites, ∩ represent the intersection and ∪ represent the union between these sites. I calculated the coefficient for all highland areas among sites, all lowland areas among sites, and all low and highland areas among sites. I completed a resampling randomisation test for each analysis to evaluate for non-randomness (permutations = 10,000). Finally, to calculate pairwise comparisons of sites and identify the most influential species (≥ 70% of the differences) by site based on the decomposition of Bray-Curtis dissimilarity, I ran a SIMPER analysis for each site and between, including between low and highland areas within each site.

To assess the relationships between these analysed diversity indices and different bioclimatic variables, I applied generalised linear models (GLMs). Specifically, I sourced bioclimatic variables from a time series of daily temperature maxima and minima maps from 1950–2021, downscaled to the Wet Tropics World Heritage Area, and mapped at a spatial resolution of 0.0025° (~ 250 m) (Storlie et al., 2013). I then applied this model followed by a variance inflation-factor analysis to identify any multicollinearity among covariates in the bioclimatic dataset. Next, I employed a Moran's I test to check for spatial autocorrelation among bioclimatic variables. I used the resulting independent bioclimatic variables identified in these analyses (mean diurnal range, isothermality, temperature seasonality, precipitation seasonality, and precipitation of the warmest quarter) as predictors in generalised linear models (GLMs). I fitted each model separately for each diversity metric (Shannon, Simpson, Jaccard, and species richness) derived from pairwise site comparisons. Because different biodiversity indices can respond differently to environmental variables, I modelled each index separately to account for potential variation in their relationships.

For Shannon, Simpson, and Jaccard diversity indices, I assumed Gaussian error distributions with identity links:

$$Y_{\mathrm{i}} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_5 + \varepsilon_{\mathrm{i}}$$

For species richness, I assumed a Gamma error distribution with a log link:

$$log(E[Y_{\mathrm{i}}]) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_5$$

where Y_{i} represents the diversity metric for each pairwise site comparison, and X_1 to X_5 represent each of the independent bioclimatic variables evaluated.

I repeated this process for each model combination, ranking the resulting models using Akaike's Information Criterion corrected for small samples (AIC$_c$), implemented with the `MuMIn` R package (Burnham & Anderson, 2003). Model selection based on AIC$_c$ penalises models for unnecessary complexity, thereby mitigating risks of over-parameterisation and redundancy among predictors. For the highest-ranked models, I also calculated d^2 for each of the independent bioclimatic variables to measure goodness of fit using the `modEvA` R package (Barbosa et al., 2016).

Multidimensional trait space analysis

To represent both the functional traits and compare the functional roles, as well as the functional roles occupied by species considered at risk of extinction, for all 164 vertebrate species identified across the sites, I collected 30 traits, including physiology, diet, functional morphology, life history, and behaviour traits, from the dataset provided by S. Williams et al. (2010) (traits used can be viewed and downloaded at https://doi.org/10.6084/m9.figshare.c.3303180.v1). Furthermore, I georeferenced elevation ranges using a digital elevation model (30 m spatial resolution), collecting missing data from other online, peer-reviewed sources or estimated using allometric equations. For the latter, I estimated maximum longevity (ω) for volant mammals and birds as $\omega = 10^{0.89+0.13\ log_{10}\ M}$ (Bradshaw et al., 2021), and ω for non-volant mammals and birds as $\omega = \ 7.02M^{0.174}$ (Healy et al., 2014), where M equals the average mass (g) for each species. Applying the same bioclimatic variables used to assess the relationships between the different diversity indices, I overlaid the bioclimatic dataset onto the vertebrate occurrence database from the Kirrama, Atherton, Carbine, Bellenden Ker, and Thornton subregions of the Wet Tropics bioregion (the same subregions identified in the site areas) from 1993–2013 (Figure 1), where I averaged each bioclimatic variable using values from each observation point a species was recorded. Minimum and maximum values, however, were provided for the hottest and coldest months, respectively recorded across this period. I used the same method for all binary and continuous species traits, inputting them into vectors and fitting them to the species trait space. Following this, I characterised multidimensional trait volumes using a weighted principal coordinates analysis (PcoA) for each site and for all the species across all the sites. I categorised all categorical traits into binary values and $\log_{10}$-transformed all continuous variables with a skewed distribution (De Bello et al., 2021). I averaged each trait and calculated a Gower dissimilarity index to combine all traits and weight them evenly. I fitted $\log_{10}$-transformed maximum temperature of the warmest month and minimum temperature of the coldest month as non-multicollinear bioclimatic variables (those with non-significant intercorrelation) onto the species trait space to show which variables correlated the most. I applied a randomisation test for each analysis to identify any patterns of non-randomness in trait variability explained for the first three PcoA axis (permutations = 10,000). This same process was also completed for all species considered as most likely to go extinct by selecting species' whose conservation status are classified at risk (≥ near threatened) as defined by the Australian Environment Protection and Biodiversity Conservation Act 1999, or when data was not available, by the Nature Conservation Act 1992. A randomisation test was also completed to assess whether the loss of vulnerable species caused a greater reduction in trait space than the random loss of the same number of species for each analysis (permutations = 10,000) (see Appendix Figure A5).

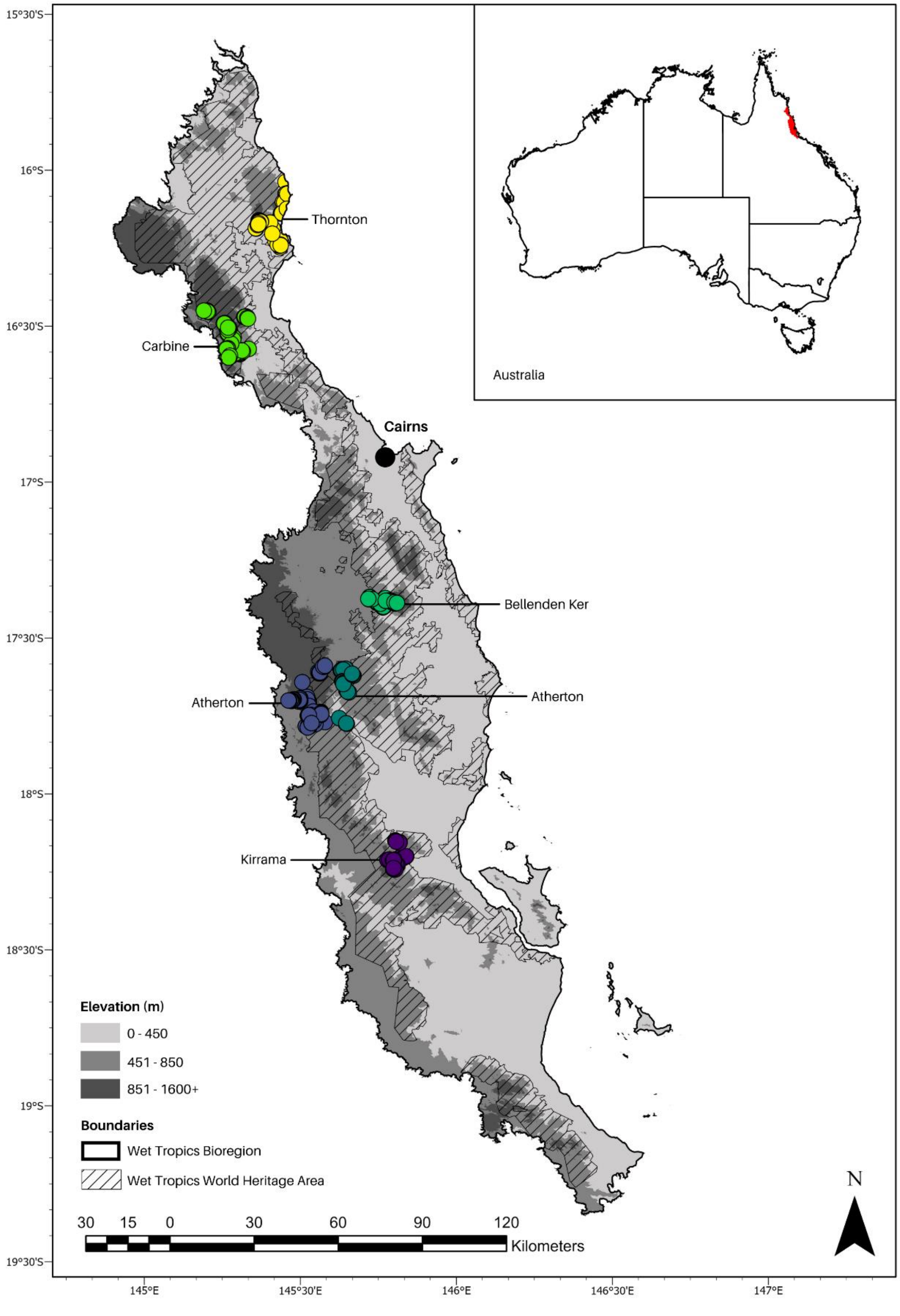

Figure 1. Map of the location of each identified site (coloured circles) in the Wet Tropics bioregion.

Results

Multivariate clustering identified 28 clusters, of which eight main clusters had data in low- (0–450 m), mid- (451–850 m), and high- (851–1600+ m) altitudinal bands. Out of these eight, I identified six main clusters (Figure 1) that had ≥ 10,000 occurrence records to analyse.

Biodiversity indices

Among the 6 identified sites, species richness (S) differed (Figure 2; mean ± SD = 115 ± 12, $p < 0.001$), but was consistently lower in each site than across the whole bioregion (164 species) whereas the proportion of species within each vertebrate taxonomic class was approximately proportional among sites (Figure 2a), although sites 2 and 4 showed probable under-sampling (refer to Appendix Figure A2 to A4 for spatial sample-based rarefaction analysis). Highland areas (> 850m above sea level) overall had higher species richness ($p < 0.001$) than lowland areas (≤ 450 m above sea level) ($p < 0.001$) (Figure 2b) (refer to Appendix Figure A1 for analysis by elevation and taxonomic class), except for site 6 which had fewer ($\Delta_S = S_{highland} - S_{lowland} = -66$) in highland areas relative to lowland areas.

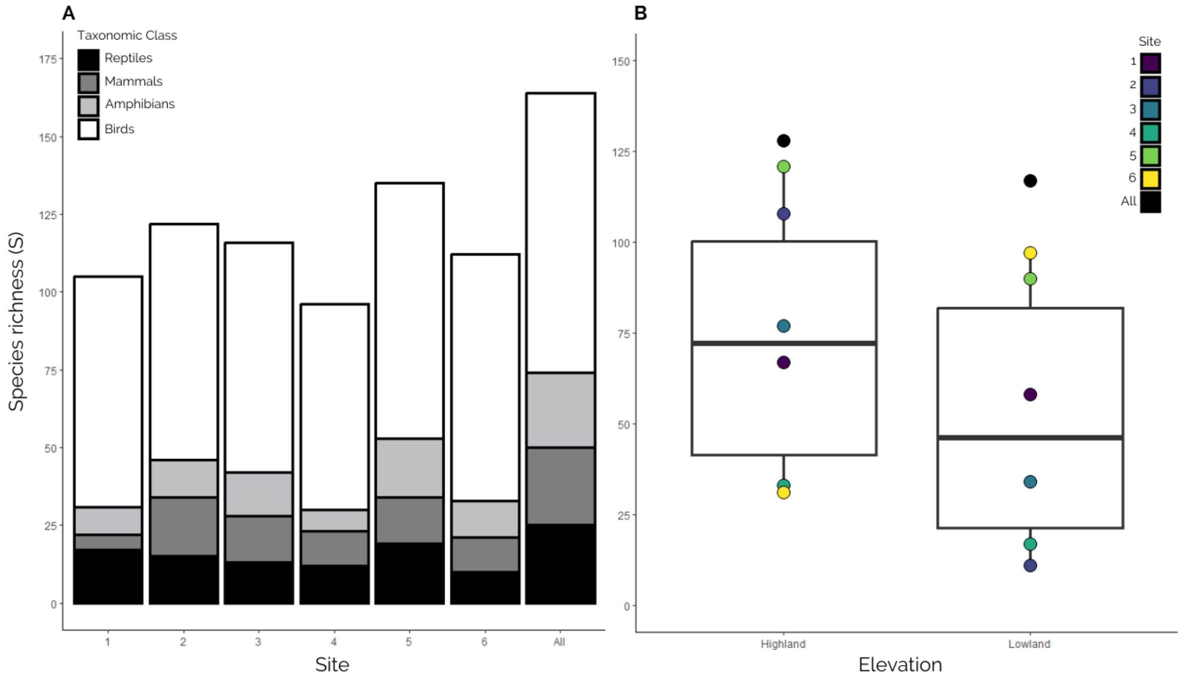

Figure 2. Vertebrate species richness (S) for six sites (1 = Kirrama, 2 = Atherton (a), 3 = Atherton (b), 4 = Bellenden Ker, 5 = Carbine, and 6 = Thornton) (A) across the Australian Wet Tropics, and (B.) split between highland (> 850m above sea level) and lowland (≤ 450 m above sea level) areas.

Species evenness, which measures the distribution of abundance, was highest in site 3 ($J' = 0.61$) (Atherton Tablelands), with lower species evenness across all other sites ($J' = 0.31 \pm 0.13$) ($p < 0.01$), which was similar to evenness for the whole bioregion ($J' = 0.38$) (Figure 3a). Species evenness across all sites was lower in highland areas ($J' = 0.37 \pm 0.26$, $p < 0.01$) than in lowland areas ($J' = 0.83 \pm 0.11$, $p < 0.01$) (similar to the whole bioregion: $J' = 0.42$ and 0.77 for high and lowland areas, respectively) (Figure 3b), except in site 3 which showed higher evenness in highland areas in site 3 ($J' = 0.72$) compared to lowland areas ($J' = 0.41$). Amphibians were disproportionally detected in each site, except sites 3 (Atherton tablelands) and 4 (Bellenden Ker), which showed a more proportionate, lower detectability of different vertebrate taxonomic classes (see Appendix Figure A1).

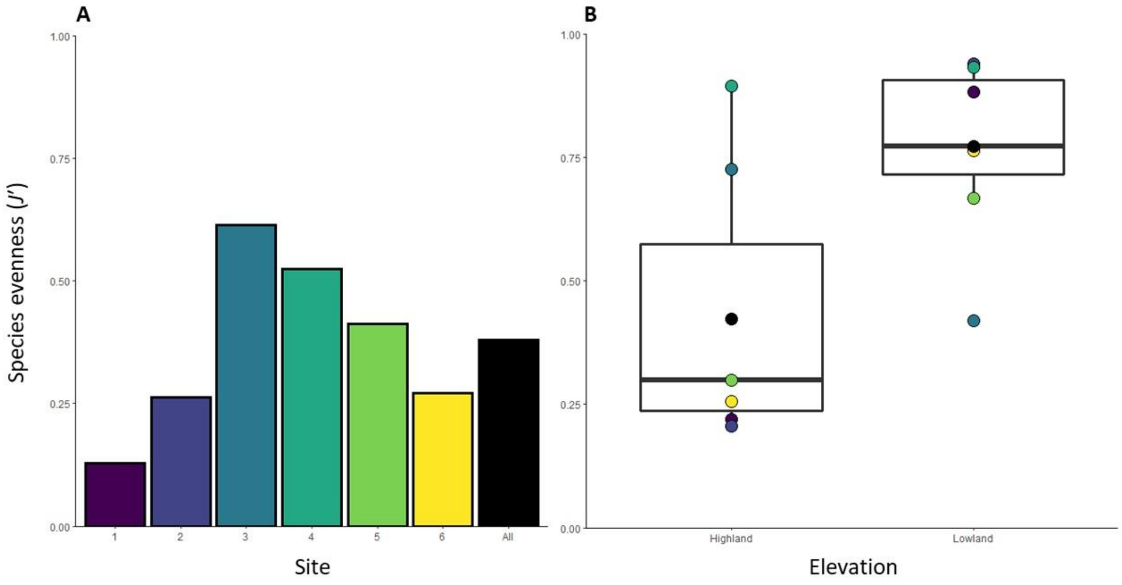

Figure 3. Pielou's species evenness J' among the six identified sites (1 = Kirrama, 2 = Atherton (a), 3 = Atherton (b), 4 = Bellenden Ker, 5 = Carbine, and 6 = Thornton) in the Australian Wet Tropics (A) and between elevations (B) (highland: > 850 m above sea level; lowland: ≤ 450 m above sea level).

The Shannon-Wiener diversity index was highest in site 3 (*H*′ = 2.95), and lower across both individual sites (*H*′ = 1.53 ± 0.66) ($p < 0.0001$) and the bioregion (*H*′ = 1.90) (Figure 4a). All sites consistently showed lower diversity in highland areas (*H*′ = 1.75 ± 1.00, $p < 0.0001$) than in lowland areas (*H*′ = 3.08 ± 0.52, $p < 0.0001$) (Figure 4b), except for sites 3 and 4, which showed lower diversity in highland areas (*H*′ = 3.15 and 3.12, respectively) compared to lowland areas (*H*′ = 1.47 and 2.64, respectively).

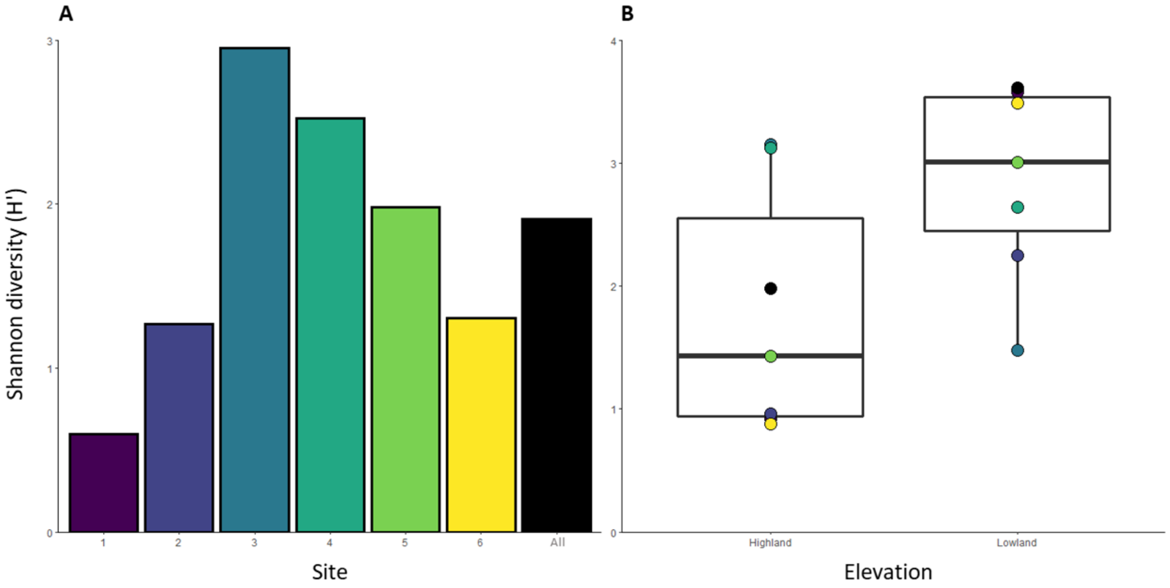

Figure 4. Shannon-Wiener diversity *H*′ among the six identified sites (1 = Kirrama, 2 = Atherton (a), 3 = Atherton (b), 4 = Bellenden Ker, 5 = Carbine, and 6 = Thornton) in the Australian Wet Tropics (A) and elevation (B) (highland: > 850 m and lowland: ≤ 450 m above sea level).

Simpson's diversity showed similar trends ($p < 0.001$) (Figure 5), with site 3 having the highest diversity ($\gamma = 0.85$). All sites consistently showed higher diversity in lowland areas ($\gamma = 0.91 \pm 0.04$, $p < 0.001$) compared to highland areas ($\gamma = 0.47 \pm 0.06$, $p < 0.001$), except for sites 3 and 4 which showed lower diversity in lowland areas ($\gamma = 0.56$ and 0.91) compared to highland areas ($\gamma = 0.91$ and 0.94). Similar patterns occurred across the entire bioregion ($\gamma = 0.96$ and 0.74, respectively), albeit with a larger negatively skewed interquartile range in highland areas (Figure 4b).

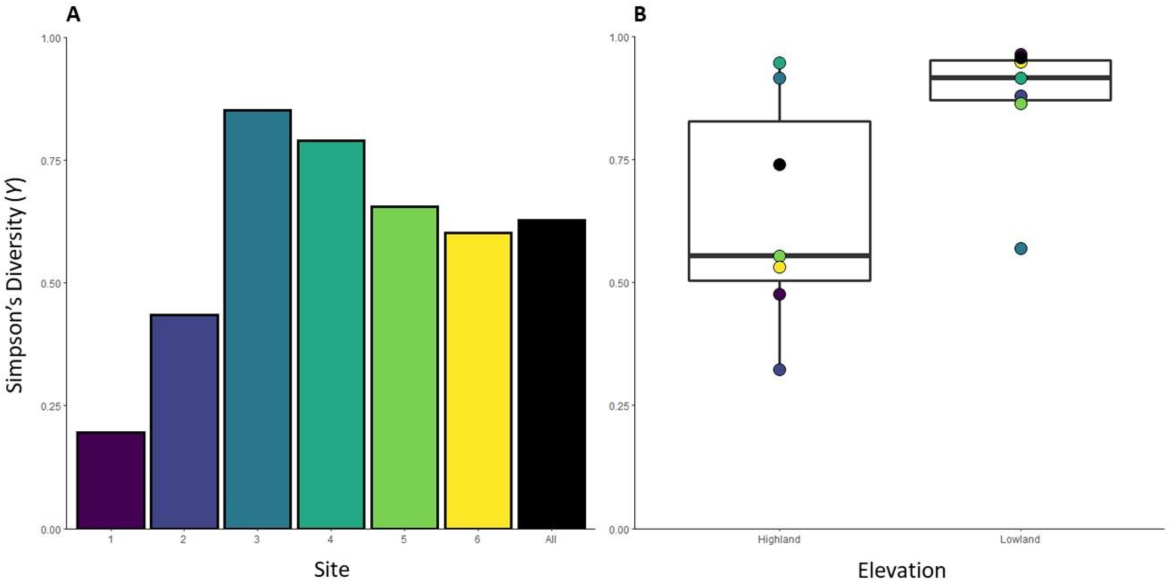

Figure 5. Simpson's diversity γ among the six identified sites (1 = Kirrama, 2 = Atherton (a), 3 = Atherton (b), 4 = Bellenden Ker, 5 = Carbine, and 6 = Thornton) in the Australian Wet Tropics (A) and elevations (B) (highland > 850m above sea level; lowland = ≤ 450 m above sea level).

Jaccard's distance was lower among ($d_j = 0.32 \pm 0.05$, $p < 0.001$) (Figure. 6a) than within sites (across elevation) ($d_j = 0.67 \pm 0.17$, $p < 0.001$). Site 2 had the highest dissimilarity (0.91) among other sites (Figure 7). Among sites, Jaccard's distance was weakly correlated with geographic distance (Figure 6b), with amphibians (*Cophixalus* spp. in 56% of sites comparisons) attributing to ≥ 70% of the Bray-Curtis dissimilarity (see Appendix Table 1). Jaccard's distance was higher overall in lowland areas ($d_j = 0.71 \pm 0.16$, $p < 0.001$) compared to highland areas ($d_j = 0.55 \pm 0.15$, $p < 0.001$) between sites, except for site 6 ($d_j = 0.52$ and 0.62, respectively) (Figure 7). The species contributing most to Bray-Curtis dissimilarity between lowland and highland areas within sites were also associated with higher species richness within sites than across sites (see Appendix Tables 1 and 2).

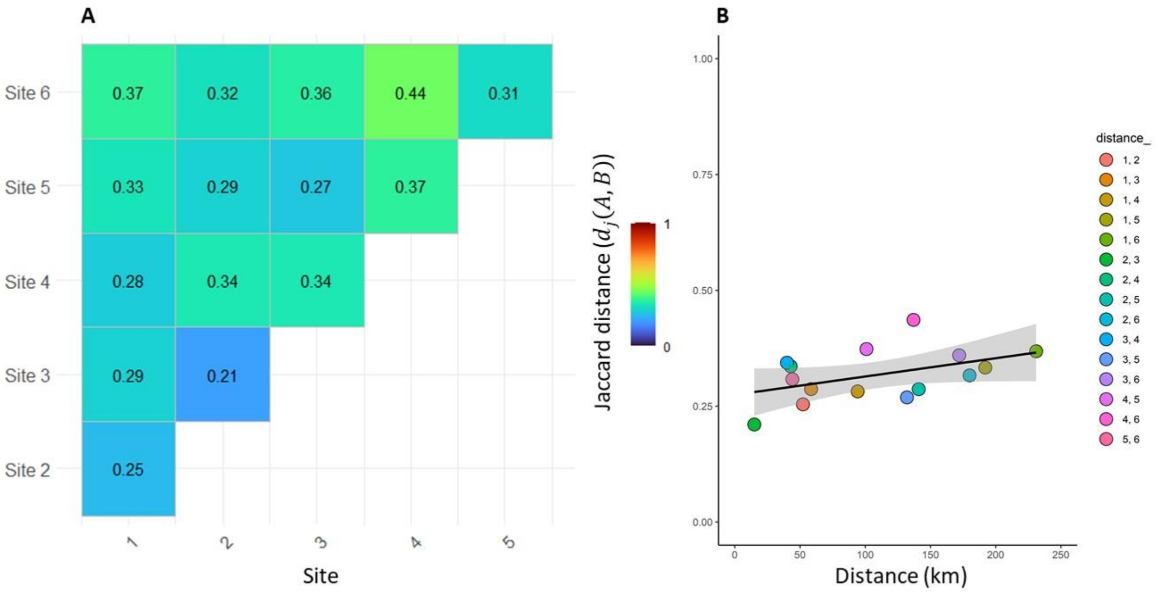

Figure 6. Jaccard distance d_j (A) among site pairs (1 = Kirrama, 2 = Atherton (a), 3 = Atherton (b), 4 = Bellenden Ker, 5 = Carbine, and 6 = Thornton) and between elevations (highland: > 850m above sea level; lowland: ≤ 450 m above sea level), (B) and relative to geographic distance (km).

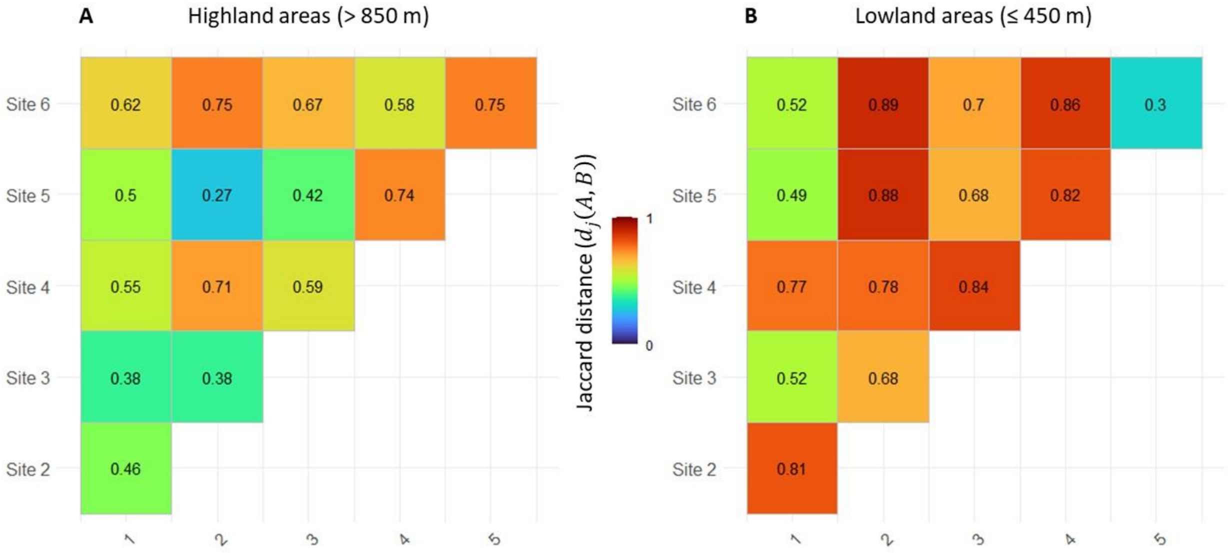

Figure 7. Jaccard distance $d_j(A,B) = 1 - J(A,B) = \frac{|A\cap B| - |A\cup B|}{|A\cup B|}$ between (A) highland and (B) lowland areas across sites (1 = Kirrama, 2 = Atherton (a), 3 = Atherton (b), 4 = Bellenden Ker, 5 = Carbine, and 6 = Thornton).

GLM results and climate variables

Of the environmental variables, species richness was most strongly correlated with precipitation of the warmest quarter ($d^2 = 0.112$) across sites (Table 6). Isothermality was most strongly correlated with species evenness ($d^2 = 0.114$) among sites (Table 7). Isothermality was also the bioclimatic variable most strongly correlated with Shannon-Wiener diversity ($d^2 = 0.113$) among sites (Table 3). Mean diurnal temperature range was most strongly correlated to Simpson's diversity ($d^2 = 0.129$) among sites (Table 4). Precipitation of the warmest quarter was most strongly correlated with Jaccard's dissimilarity ($d^2 = 0.340$) among sites (Table 5).

Multidimensional trait space analysis

The first three axes of the principal coordinates analysis explained 12.7% of the trait variability for all species (Figure 8). The first axis (Dim1) was most strongly correlated with minimum elevation ($r = 0.750$; $p < 0.001$) and maximum temperature of the warmest month ($r = -0.573$; $p < 0.001$). The second axis (Dim2) was most strongly correlated with minimum temperature of the coldest month ($r = 0.466$; $p < 0.001$) and maximum elevation ($r = -0.297$; $p < 0.001$), whilst the third axis (Dim3) was most strongly correlated with mean temperature of the driest quarter ($r = 0.655$; $p < 0.001$) and maximum elevational range ($r = -0.396$; $p < 0.001$). Birds showed the greatest trait space variability, followed by reptiles, mammals, and amphibians. When compared against all species minus those considered most vulnerable to extinction (see appendix Figure A6), only 9.81% of trait variability (a 22.64% reduction) was explained by the first three axes of the principal coordinates analysis ($p < 0.01$). Further analysis of trait spaces compared across sites, trait pattern and variability were shown to be similar except for site 5 (Carbine subregion; Figure 9).

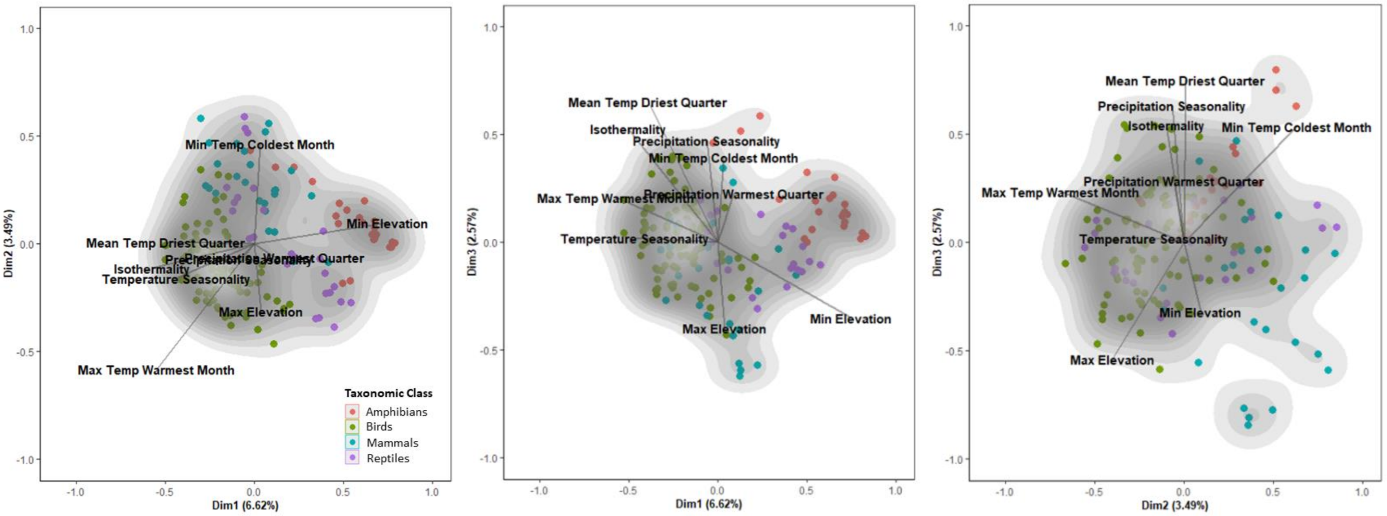

Figure. 8. Trait space for all site species categorised by taxonomic class (first three principal coordinates axes = 12.68%; *p* < 0.001). Vector lines show how different bioclimatic variables correlate with the trait space.

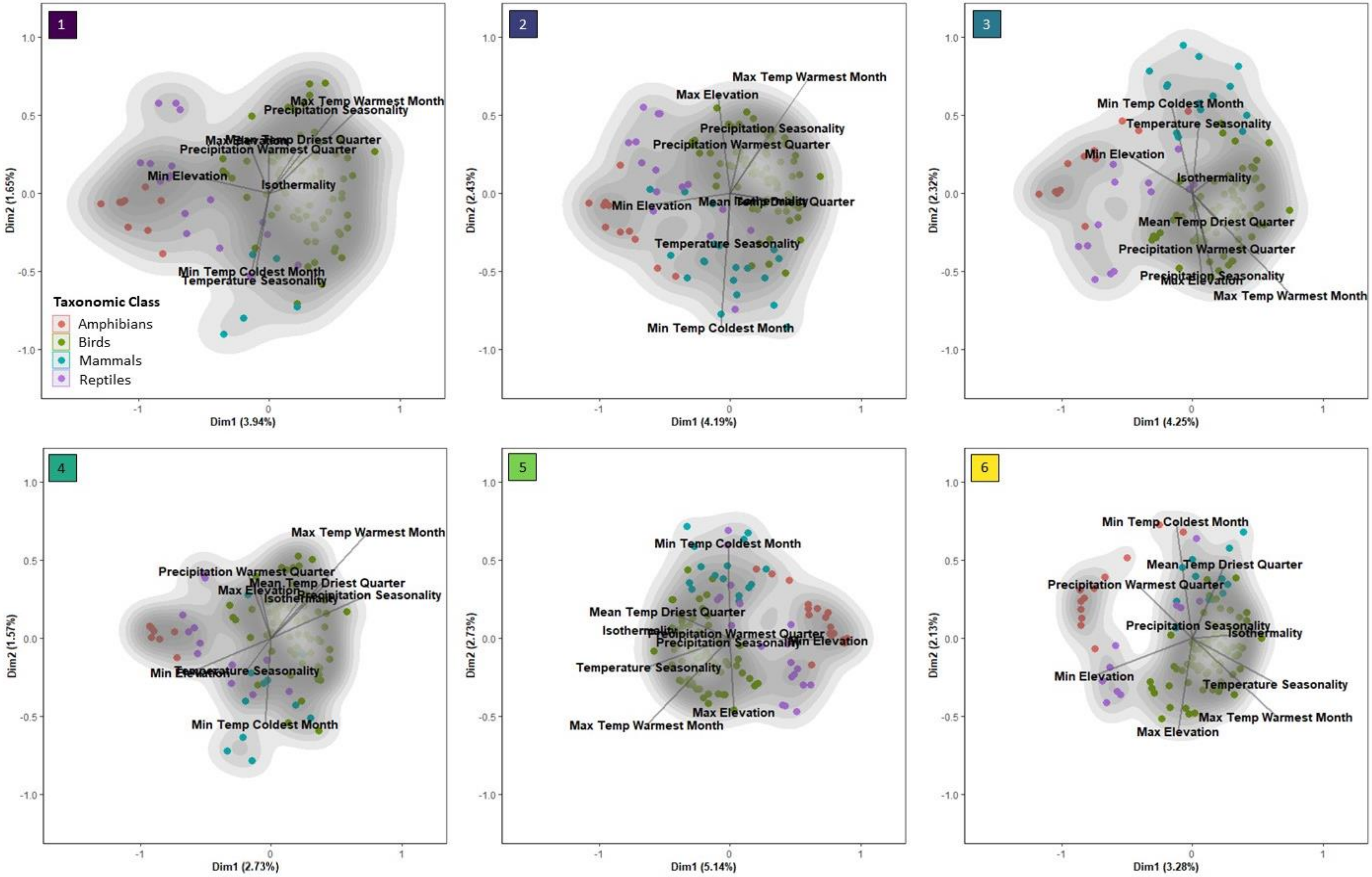

Figure. 9 Trait space represented by each of the six identified sites (1 = Kirrama, 2 = Atherton (a), 3 = Atherton (b), 4 = Bellenden Ker, 5 = Carbine, and 6 = Thornton) in Australian Wet Tropics. Species are categorised by taxonomic class (first two PcoA axes, *p* = .001). Vector lines show how different bioclimatic variables correlate with the trait space.

Discussion

Using the Wet Tropics bioregion as a case study, my results suggest that analysis of both alpha and beta diversity and multidimensional trait space can be used to define terrestrial vertebrate communities both latitudinally and between elevational bands across the bioregion. My results do not support the hypothesis that diversity-based community differences are also portrayed in trait-based differences, and instead support the narrative that although compositional differences can be observed latitudinally across the Australian Wet Tropics bioregion, occupied trait space is highly similar. These results, however, do support the hypothesis that community differences in terms of composition and trait space are more distinct across elevational gradients then across latitudinal space. These results suggest that all analysed vertebrates can be considered as one community across the studied parts of this bioregion, only distinguishing between low- and high-elevational areas as described by their occupied trait spaces.

Differences seen in communities are consistent with previous findings in the Wet Tropics bioregion showing that patterns in assemblage composition change both across elevations and latitudinally among vertebrate groups (Williams et al., 1995), including birds (S. E. Williams et al., 2010), mammals (Nix & Switzer, 1991), amphibians (McDonald, 1992), and reptiles (Covacevich & Couper, 1994), particularly between the North and South of the subregion, as divided by the Black Mountain Corridor; a rugged, high-elevation terrain that creates a physical barrier to the movement of species (Joseph et al., 1995; Taberlet, 1998).

Differences in community composition between low- and high-elevation areas are particularly prominent, because rain forest specialists that are regionally endemic are more distinctly displayed in highland areas — a pattern credited to the selection of cool-adapted species to rain forest refugia within this bioregion (Nix & Switzer, 1991). These differences are consistent with patterns observed in many tropical montane rain forests, where elevational diversity gradients (Rahbek, 1995) have the most substantial influence on diversity (as measured by species richness and composition). These findings are consistent with Janzen's mountain pass hypothesis (Janzen, 1967), stating that tropical environments with high regional endemicity of rain forest specialists and limited thermal tolerances have more distinct vertebrate communities across elevational gradients than communities across latitudinal space.

However, analysis of species richness at the alpha diversity scale for lowland areas in sites 2 and 4 should be interpreted with caution due to probable under-sampling (see Appendix Figure A2 to A4).

Results show that species occupy different functional spaces with some overlap, as depicted by their associated taxonomic class (Figure 9). Specifically, birds consistently occupied larger trait spaces and higher functional diversity. This result supports the high proportion of generalist birds found in this subregion, particularly lowland assemblages (Williams & de la Fuente, 2021). Conversely, reptiles, mammals, and amphibians occupied smaller trait spaces and lower functional diversity, respectively, a finding also supported by the high level of regionally restricted endemic rain forest specialists found across the Australian Wet Tropics (Williams et al., 1995; Williams, 1997), particularly for frogs which display an exceptionally high degree of specialisation (Williams & Hero, 1998). Therefore, many functional roles occupied across the bioregion can be provided by different species, potentially indicating high redundancy within communities (Biggs et al., 2020; Gorczynski & Beaudrot, 2021). The consistent patterns in the species trait space at varying spatial scales suggest that no benefit would be gained by distinguishing communities by sites; instead, it could be more biologically meaningful to define vertebrate communities at the bioregional scale.

The filtering of vertebrates found across the bioregion from the expansion and contraction of rain forest refugia (Nix & Switzer, 1991; Williams & Pearson, 1997) could explain why species might be able to serve these similar functional roles. The trait space for site 5 (Carbine subregion) (Figure 9), although still showing a similar level of explained trait variability and correlation to bioclimatic variables, was different to all other sites. The difference in trait space likely arises because of the high diversity of vertebrates in this area (specifically, birds, mammals, and reptiles) (Covacevich & Couper, 1994; McDonald, 1992; Williams et al., 1995; Winter & Winter, 1984). Researchers hypothesise that such high diversity results from the ecotonal habitats created by overlapping Atherton and Thornton subregions — two separate communities considered epicentres of vertebrate diversity in the bioregion (Winter & Winter, 1984). This explanation is supported by the high species richness in the Carbine subregion (Figure 2) that strongly influences the position of functional spaces when combined with all species across the bioregion. Removing species classified as most vulnerable to extinction showed that the functional composition of species across the bioregion could reduce the total amount of trait variability explained (see Appendix Figure A6). Volancy (see Appendix Figure A5), among other functional traits not measured in this study, may be irreplaceably lost if species currently listed as vulnerable were to become extinct (see Appendix Figure A5). This result could filter a higher proportion of arboreal species across the bioregion; a trait in vertebrates attributed to greater resilience to temperature constraints imposed by forecasted climate change in the Wet Tropics (Scheffers & Williams, 2018). Future research should seek to evaluate whether species can adapt to different functional roles when other species occupy their prototypical niche space or when niche space is made vacant by the loss of other species, which could help identify whether functional redundancy is also practical for maintaining resilience in a community. Bioclimatic variables most correlated for each site when comparing alpha and beta diversity were also shown to correlate with trait space (Figure 8 and 9), appearing to influence species niche as outlined by each species associated taxonomic class.

A limitation of the trait space analysis is; however, a deficiency of statistical power as only a small percentage of trait variability (< 13%) is explained for the functional traits that were measured, potentially undermining the significance of these results. Theoretically, other methods (Guillerme et al., 2020) of multidimensional trait space analysis may explain all trait variability, although this is yet to develop for analysing species' functional diversity. Furthermore, analysis of trait space is not embedded in ecological theory and is therefore likely limited by its application to explain tangible differences in functional diversity.

Defining community boundaries across the Wet Tropics bioregion using multidimensional trait spaces by treating all species as one connected unit might be more important for protecting functional groups than individual species and maintaining resilience to perturbation (Toussaint et al., 2021). Focusing on functional diversity would be more practical (e.g., instead of investing money to save highly specialised endemic species) for maintaining community resilience to environmental perturbations and, therefore, for conserving vertebrate populations in different terrestrial bioregions. Describing a community based on its functional composition might also be more practical for understanding how distinct groups interact trophically. This method can also be helpful in identifying functionally unique species, as losing them can otherwise reduce the functional diversity of the community. However, for applications such as ecological network modelling that can be specifically employed for the use of evaluating the extinction risk of communities, nodes may represent functional groups instead of individual species, simplifying the need to gather further data on the nodes and their edges in these simulations. Entirely disregarding community composition, however, could exacerbate the extinction risk of the most endemic species and promote the future invasion of widespread species, leading to the loss of evolutionary potential to adapt to future environmental changes. Conversely, although analysis of species composition could serve to distinguish communities latitudinally or across elevational gradients, defined communities cannot be described as completely disconnected entities. Further, species present in each defined 'community' do or likely will interact at some spatial or temporal scale, and therefore, defining this fictitious boundary will likely depend on both the specific goals and the availability of data to test hypotheses.

Although it is important to consider the extent of an ecological community to account for meaningful spatial and temporal scales, regardless of which methods one uses, it might also be vital to consider how these scales affect a community's ability to qualify for protection under environmental legislation (Nicholson et al., 2009), such as Australia's current Environment Protection and Biodiversity Conservation Act 1999 (Fraser et al., 2019). Specifically, protection depends on how a community matches the criteria for being classified as threatened (Fraser et al., 2017), as well as how effectively a community can be managed and conserved (Nicholson et al., 2009; Saunders et al., 2021), which is important for identifying the extent to which some anthropogenic threats affect the environment.

Appendix

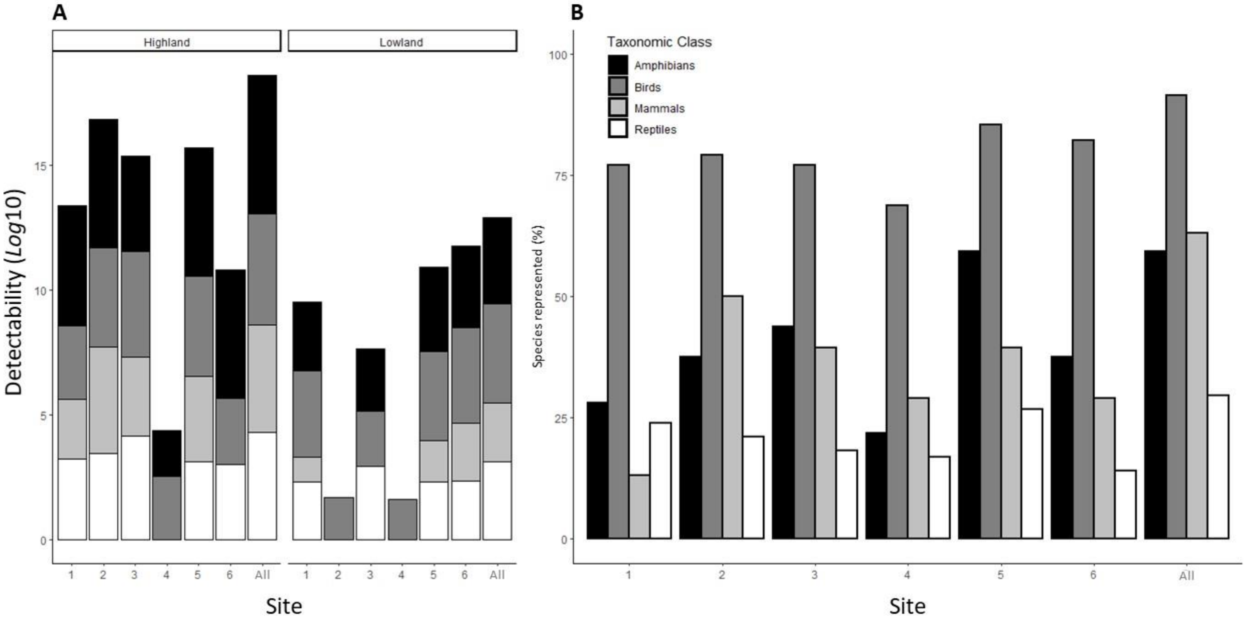

Figure A1. (A) Total abundance of species found in each site, categorised by taxonomic class and elevation (highland = > 850m above sea level, lowland = ≤ 450 m above sea level). (B) Number of vertebrate species found in each site representative of the total number of known vertebrate species who have a ≥ 3 degree of rain forest specialisation found in the Wet Tropics categorised by taxonomic class.

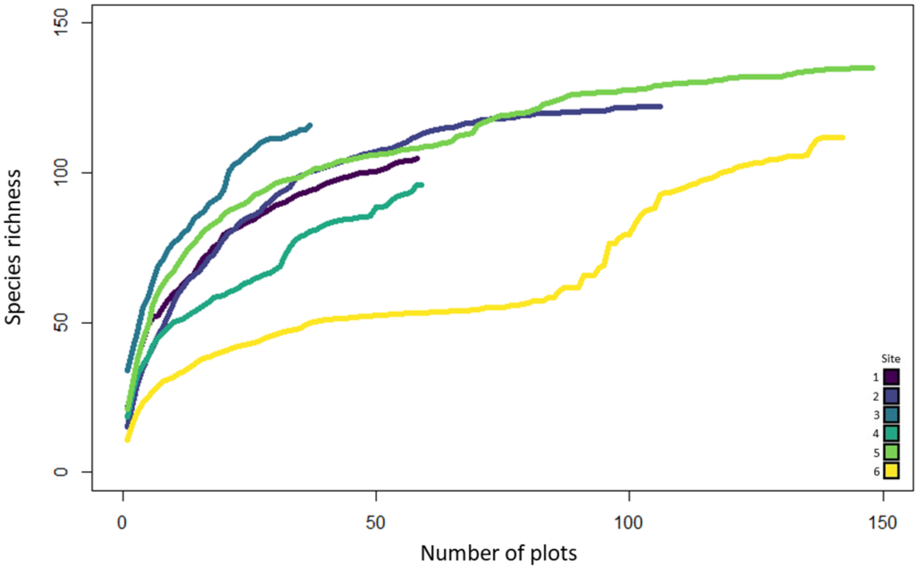

Figure A2. Spatial sample-based rarefaction in which species are accumulated by including spatially proximate plots first in each site.

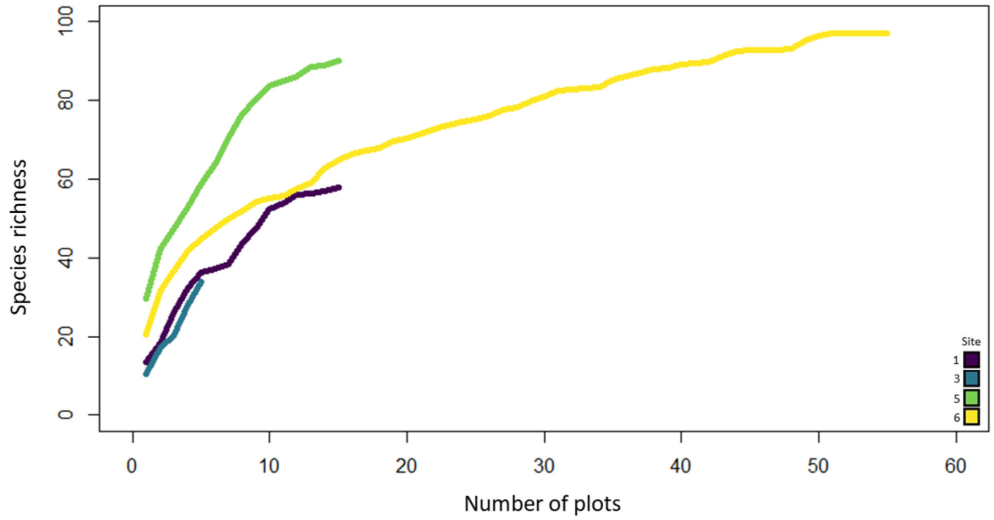

Figure A3. Spatial sample-based rarefaction in which species are accumulated by including spatially proximate plots first in each site for lowland areas (≤ 450 m above sea level). Note sites 3 and 4 are missing due to having only one surveyed plot each.

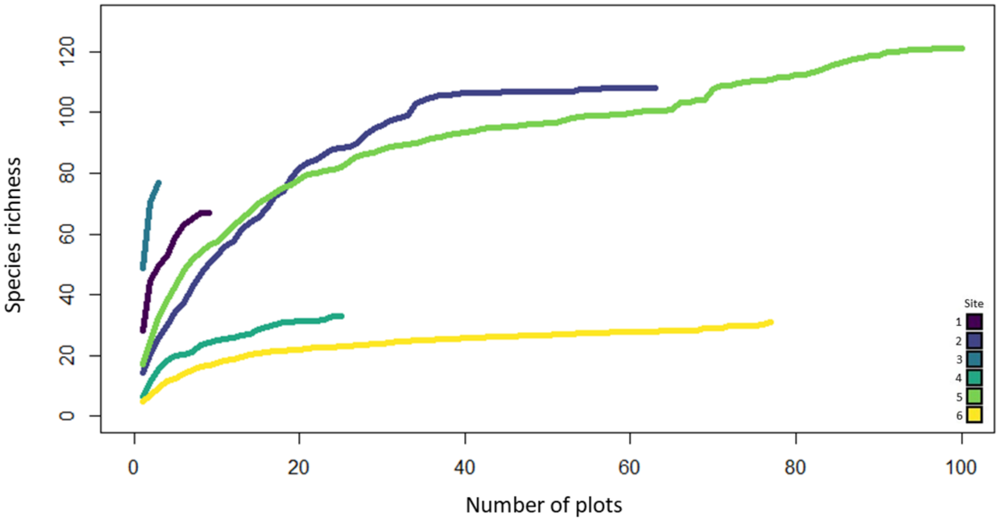

Figure A4. Spatial sample-based rarefaction in which species are accumulated by including spatially proximate plots first in each site for highland areas (> 850m above sea level).

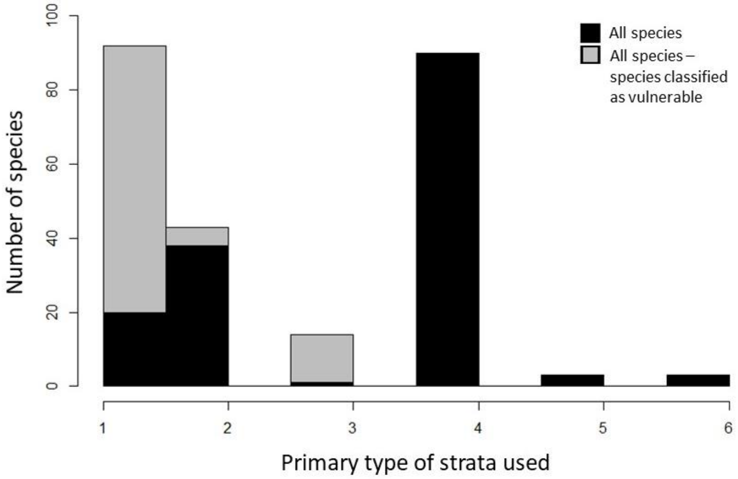

Figure A5. Histogram showing the primary type of habitat strata used by species across all sites. Black portions of the bars represent at-risk species (defined as those listed as ≥ Near Threatened under the Environment Protection and Biodiversity Conservation Act 1999 [EPBC Act] or the Nature Conservation Act 1992); grey portions indicate species not classified as threatened or at risk. Primary strata categories are: 1 = arboreal, 2 = terrestrial, 3 = freshwater, 4 = volant, 5 = arboreal/terrestrial, 6 = freshwater/terrestrial. When considering all species (i.e., including at-risk species), volant is the most common primary stratum. However, when considering only non-at-risk species, arboreal becomes the most frequent.

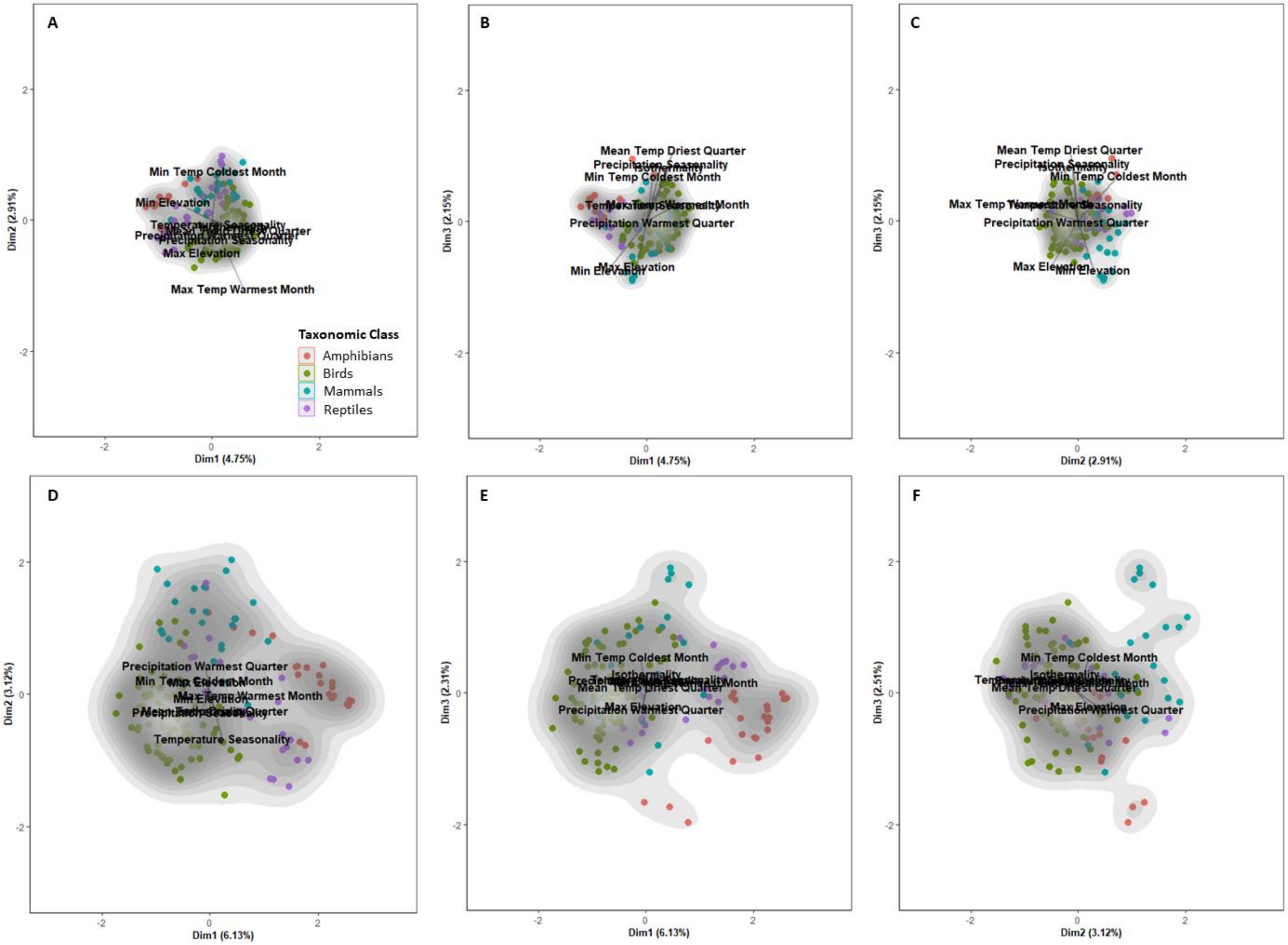

Figure A6. Trait space (A, B, C) represented by all sites species minus species classified with an at-risk conservation status (≥ Near threatened). Trait space (D, E, F) represent random sampling of same number of species. All species are categorised by taxonomic class (first three PcoA axis, *p* = 0.0004). Vector lines show how different environmental variables correlate with the trait space.

Table 1. SIMPER analysis showing the most influential species (≥ 70% difference) to Bray-Curtis dissimilarity between sites. SD = Standard deviation of species contribution. Ratio = Average to SD ratio. Ava/Avb = Average contribution for each pairwise comparison. Cumsum = Ordered cumulative contribution.

Species	Average	Sd	Ratio	Ava	Alb	Cumsum	Site comparison
Cophixalus orotus	0.221962	NA	NA	538505	311984	0.714032	1, 2
Cophixalus orotus	0.410516	NA	NA	538505	37827	0.485484	1, 3
Lampropholis coggeri	0.169035	NA	NA	17213	223374	0.685389	1, 3
Hemibelideus lemuroides	0.034173	NA	NA	0	41679	0.725803	1, 3
Cophixalus orotus	0.811261	NA	NA	538505	7976	0.92897	1, 4
Cophixalus orotus	0.349082	NA	NA	538505	11120	0.366543	1, 5
Cophixalus hosmeri	0.33958	NA	NA	0	513030	0.723109	1, 5
Cophixalus orotus	0.347975	NA	NA	538505	0	0.35418	1, 6
Cophixalus aenigma	0.31428	NA	NA	0	486360	0.674064	1, 6
Cophixalus concinnus	0.220066	NA	NA	0	340560	0.898054	1, 6
Cophixalus orotus	0.264185	NA	NA	311984	37827	0.34825	2, 3
Lampropholis coggeri	0.211032	NA	NA	4376	223374	0.626434	2, 3
Carlia rubrigularis	0.023631	NA	NA	974	25497	0.657584	2, 3
Gerygone mouki	0.01389	NA	NA	1204	15618	0.675894	2, 3
Psophodes olivaceus	0.013171	NA	NA	1212	14880	0.693256	2, 3
Bolemoreus freotus	0.013028	NA	NA	1048	14568	0.71043	2, 3
Cophixalus orotus	0.643987	NA	NA	311984	7976	0.806978	2, 4
Cophixalus hosmeri	0.386058	NA	NA	0	513030	0.412073	2, 5
Cophixalus orotus	0.226402	NA	NA	311984	11120	0.653732	2, 5

Cophixalus monticola	0.087938	NA	NA	0	116860	0.747595	2, 5
Cophixalus aenigma	0.356137	NA	NA	0	486360	0.363166	2, 6
Cophixalus concinnus	0.249375	NA	NA	0	340560	0.617463	2, 6
Cophixalus orotus	0.22845	NA	NA	311984	0	0.850422	2, 6
Lampropholis coggeri	0.330855	NA	NA	223374	1316	0.382162	3, 4
Hemibelideus lemuroides	0.062046	NA	NA	41679	36	0.453829	3, 4
Cophixalus orotus	0.044476	NA	NA	37827	7976	0.505203	3, 4
Carlia rubrigularis	0.03635	NA	NA	25497	1100	0.54719	3, 4
Gerygone mouki	0.022161	NA	NA	15618	744	0.572788	3, 4
Psophodes olivaceus	0.021348	NA	NA	14880	552	0.597446	3, 4
Bolemoreus freotus	0.020859	NA	NA	14568	568	0.62154	3, 4
Sericornis magnirostra	0.019287	NA	NA	13641	696	0.643819	3, 4
Rhipidura fuliginosa	0.018982	NA	NA	13104	364	0.665744	3, 4
Heteromyias albispecularis	0.018207	NA	NA	12792	572	0.686775	3, 4
Gnypetoscincus queenslandiae	0.015647	NA	NA	14634	4132	0.704849	3, 4
Cophixalus hosmeri	0.335756	NA	NA	0	513030	0.414031	3, 5
Lampropholis coggeri	0.145623	NA	NA	223374	865	0.593602	3, 5
Cophixalus monticola	0.07648	NA	NA	0	116860	0.687912	3, 5
Cophixalus aenigma	0.053358	NA	NA	0	81530	0.753709	3, 5
Cophixalus aenigma	0.310824	NA	NA	0	486360	0.322848	3, 6
Cophixalus concinnus	0.217646	NA	NA	0	340560	0.548913	3, 6
Lampropholis coggeri	0.1427	NA	NA	223374	84	0.697134	3, 6
Austrochaperio fryi	0.03489	NA	NA	24	54618	0.733374	3, 6

Cophixalus hosmeri	0.533124	NA	NA	0	513030	0.563575	4, 5
Cophixalus monticola	0.121437	NA	NA	0	116860	0.691949	4, 5
Cophixalus aenigma	0.084723	NA	NA	0	81530	0.781511	4, 5
Cophixalus aenigma	0.486813	NA	NA	0	486360	0.497255	4, 6
Cophixalus concinnus	0.340877	NA	NA	0	340560	0.845444	4, 6
Cophixalus hosmeri	0.276433	NA	NA	513030	0	0.321498	5, 6
Cophixalus aenigma	0.218132	NA	NA	81530	486360	0.57519	5, 6
Cophixalus concinnus	0.183502	NA	NA	0	340560	0.788607	5, 6

Table 2. SIMPER analysis showing the most influential species (≥ 70% difference) to Bray-Curtis dissimilarity between low and highland elevations within sites. SD = Standard deviation of species contribution. Ratio = Average to SD ratio. Ava/Avb = Average contribution for each pairwise comparison. Cumsum = Ordered cumulative contribution.

Species	Average	Sd	Ratio	Ava	Avb	Cumsum	Site comparison
Cophixalus ornatus	0.627143	NA	NA	74	43715	0.639813	1 (lowland), 1 (highland)
Austrochaperina robusta	0.271804	NA	NA	21	18935	0.917108	1 (lowland), 1 (highland)
Cophixalus ornatus	8.17E-01	NA	NA	0	142734	0.817884	2 (lowland), 2 (highland)
Lampropholis coggeri	2.01E-01	NA	NA	0	8232	0.213874	3 (lowland), 3 (highland)
Carlia rubrigularis	1.11E-01	NA	NA	876	5416	0.331826	3 (lowland), 3 (highland)
Cophixalus ornatus	9.69E-02	NA	NA	256	4232	0.435126	3 (lowland), 3 (highland)
Austrochaperina robusta	4.37E-02	NA	NA	0	1792	0.481684	3 (lowland), 3 (highland)
Psophodes olivaceus	3.12E-02	NA	NA	0	1280	0.514939	3 (lowland), 3 (highland)
Rhipidura fuliginosa	2.67E-02	NA	NA	0	1096	0.543414	3 (lowland), 3 (highland)
Gnypetoscincus queenslandiae	2.46E-02	NA	NA	0	1008	0.569603	3 (lowland), 3 (highland)
Bolemoreus frenatus	2.42E-02	NA	NA	0	992	0.595375	3 (lowland), 3 (highland)
Hemibelideus lemuroides	2.36E-02	NA	NA	0	968	0.620525	3 (lowland), 3 (highland)
Heteromyias albispecularis	2.20E-02	NA	NA	0	904	0.644011	3 (lowland), 3 (highland)
Gerygone mouki	2.15E-02	NA	NA	6	888	0.666927	3 (lowland), 3 (highland)
Acanthiza katherina	2.14E-02	NA	NA	0	880	0.68979	3 (lowland), 3 (highland)
Sericornis magnirostra	2.14E-02	NA	NA	3	880	0.712575	3 (lowland), 3 (highland)
Cophixalus neglectus	0.083665	NA	NA	0	42	0.097674	4 (lowland), 4 (highland)
Strepera graculina	0.067729	NA	NA	0	34	0.269767	4 (lowland), 4 (highland)
Cormobates leucophaea	0.061753	NA	NA	2	33	0.34186	4 (lowland), 4 (highland)

Austrochaperina robusta	0.057769	NA	NA	0	29	0.409302	4 (lowland), 4 (highland)
Pachycephala pectoralis	5.38E-02	NA	NA	0	27	0.472093	4 (lowland), 4 (highland)
Macropygia phasianella	0.045817	NA	NA	1	24	0.525581	4 (lowland), 4 (highland)
Acanthiza katherina	0.045817	NA	NA	0	23	0.57907	4 (lowland), 4 (highland)
Ptilinopus superbus	0.035857	NA	NA	4	22	0.62093	4 (lowland), 4 (highland)
Sericornis magnirostra	0.035857	NA	NA	5	23	0.662791	4 (lowland), 4 (highland)
Psophodes olivaceus	0.027888	NA	NA	1	15	0.695349	4 (lowland), 4 (highland)
Amblyornis newtonianus	0.027888	NA	NA	0	14	0.727907	4 (lowland), 4 (highland)
Cophixalus hosmeri	6.18E-01	NA	NA	2	102602	0.632798	5 (lowland), 5 (highland)
Cophixalus monticola	1.41E-01	NA	NA	0	23372	0.776948	5 (lowland), 5 (highland)
Cophixalus aenigma	5.27E-01	NA	NA	0	80664	0.528099	6 (lowland), 6 (highland)
Cophixalus concinnus	3.71E-01	NA	NA	0	56760	0.899702	6 (lowland), 6 (highland)

Table 3. Gaussian generalised linear model for Shannon diversity (**p* < 0.01).

Model parameter	Estimate	SE	P	D^2
Intercept (Shannon diversity)	-1.091	0.460	0.042*	0.613
Mean Diurnal Range	-3.945	2.943	0.213	0.077
Isothermality	66.473	41.011	0.140	0.113
Temperature Seasonality	-0.226	1.452	0.880	0.001
Precipitation Seasonality	-0.394	1.090	0.726	0.006
Precipitation of Warmest Quarter	-0.380	0.683	0.591	0.013

Table 4. Gaussian generalised linear model for Simpson's diversity (**p* < 0.01).

Model parameter	Estimate	SE	P	D^2
Intercept (Simpson's diversity)	-0.303	0.119	0.311*	0.576
Mean Diurnal Range	-1.255	0.759	0.1329	0.129
Isothermality	17.319	10.582	0.1362	0.127
Temperature Seasonality	-0.142	0.375	0.7143	0.007
Precipitation Seasonality	0.167	0.281	0.5670	0.017
Precipitation of Warmest Quarter	0.028	0.176	0.8762	0.001

Table 5. Gaussian generalised linear model for Jaccard distance (****p* < 0.000).

Model parameter	Estimate	SE	P	D^2
Intercept (Jaccard distance)	0.282	0.027	2.31e-06***	0.368
Mean Diurnal Range	0.010	0.171	0.953	0.000
Isothermality	2.526	2.380	0.316	0.079
Temperature Seasonality	-0.021	0.084	0.808	0.004

Precipitation Seasonality	0.026	0.063	0.688	0.012
Precipitation of Warmest Quarter	-0.060	0.040	0.165	0.160

Table 6. Gamma generalised linear model for species richness (***p* < 0.001).

Model parameter	**Estimate**	**SE**	**P**	**D²**
Intercept (Species richness)	0.054	0.016	0.001**	0.225
Mean Diurnal Range	-0.018	0.089	0.845	0.003
Isothermality	-0.914	1.472	0.550	0.027
Temperature Seasonality	0.052	0.056	0.375	0.062
Precipitation Seasonality	-0.029	0.039	0.468	0.039
Precipitation of Warmest Quarter	-0.057	0.058	0.352	0.112

Table 7. Gaussian generalised linear model for species evenness (**p* < 0.01).

Model parameter	**Estimate**	**SE**	**P**	**D²**
Intercept (Species evenness)	-0.225	0.095	0.042*	0.611
Mean Diurnal Range	-0.811	0.610	0.217	0.077
Isothermality	13.770	8.504	0.140	0.114
Temperature Seasonality	-0.048	0.301	0.877	0.002
Precipitation Seasonality	0.082	0.226	0.724	0.006
Precipitation of Warmest Quarter	-0.080	0.142	0.585	0.014

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Chapter 3

Constructing tropical rain forest vertebrate network models

Abstract

This chapter explores constructing and analysing trophic ecological network models for vertebrates in the Australian Wet Tropics, focusing on variations between low- and high-elevation communities. A random forest machine-learning algorithm was employed to construct networks of communities using empirical data. Analyses of models reveal both differences and similarities in network topology between communities, emphasising the role of elevation on predator-prey dynamics. The findings offer a nuanced view as a resource of how vertebrate species interact trophically within complex communities, how this might relate to extinction risk, and as an example of how terrestrial communities, which comprise multiple different taxonomic classes, can be modelled.

Introduction

Quantifying how biotic interactions influence species' responses to environmental change is an essential research pathway, given the mounting biodiversity crisis (Díaz et al., 2019; Pecl et al., 2017). If species interactions and the indirect effects of primary extinctions are not considered, the impacts of probable future disturbances can be considerably underestimated (Säterberg et al., 2013). Fortunately, more and better performing computational models are becoming available to characterise ecosystem structures and dynamics and forecast shifts in communities due to environmental perturbations (Strona & Bradshaw, 2018; Strona & Bradshaw, 2022).

Among these methods, network models describe the structure of biotic interactions in ecological communities as a mathematical framework to incorporate both direct and indirect effects of disturbances on species (Delmas et al., 2019), thereby providing a means to test hypotheses about how disturbances affect food-web topology and stability (Säterberg et al., 2013). While there is now an abundance of complex network models built from observed interactions (Momal et al., 2020; Pichler et al., 2020), relatively few investigations have modelled interactions across the full breadth of terrestrial vertebrate systems, as the majority of research has concentrated on communities within freshwater (Jones et al., 2017), marine (Batten et al., 2018), or invertebrate (Desjardins-Proulx et al., 2017; Laigle et al., 2018) communities

This dearth of network models for terrestrial ecosystems primarily arises because documenting which species do and do not interact is logistically challenging — interactions can be fleeting, rare, and difficult to observe (Desjardins-Proulx et al., 2017; Parker, 2004; Pringle & Hutchinson, 2020). To address this gap in available interaction data, different methods have been developed to infer biotic interactions using other types of more readily available data (Momal et al., 2020; Morales-Castilla et al., 2015). Machine-learning algorithms (Desjardins-Proulx et al., 2019) to infer biotic interactions in terrestrial ecosystems (Desjardins-Proulx et al., 2017; Pichler et al., 2020) have greatly enhanced inference capabilities, enabling more realistic assessments of food-web structures in terrestrial communities, and facilitating the prediction of trophic cascades and coextinctions more effectively than alternative methods (e.g., rule-based or mechanistic models) (Geary et al., 2020).

This study focused on vertebrate communities in the Australian Wet Tropics bioregion to demonstrate how to construct trophic network models for complex terrestrial communities. Results from Chapter 2 found that vertebrate communities differed in terms of diversity and functional trait space between low- (< 450 m) and high- (> 850 m) elevation sites; therefore, these defined communities are modelled separately here. By creating ecologically plausible network models of these vertebrate communities and analysing their trophic properties, resources can be developed to assist other researchers and natural resource managers predict and manage threats to biodiversity in this bioregion. More broadly, these communities provide an example of how network models can represent trophic relationships in complex terrestrial ecosystems in other regions.

This chapter aims to infer trophic interactions (including all 165 identified vertebrates) for both low- and high-elevation communities in the Australia Wet Tropics bioregion, and to assess the resulting network structures/topologies. Following the low- and high-elevation communities defined in Chapter 2, I ask whether (*i*) trophic interactions can be inferred between vertebrate species, and (*ii*) the resultant trophic network-model topologies differ between low- and high-elevation vertebrate communities. It is hypothesised that, because the highland vertebrate community has greater species richness (Chapter 2), highland communities will have a higher network complexity, compared to the lowland (Dunne et al., 2002a) in terms of connectance; highland communities will, therefore, have longer trophic distances between basal resource and consumer species. As prey diversity drives predator diversity in terrestrial ecosystems (Sandom et al., 2013), it is predicted that highland communities will have a higher richness of predator species compared to lowland communities (measured by degree centrality). Finally, because endothermic species eat fewer species at higher elevations (Zvereva & Kozlov, 2022), it is predicted that highland species eat fewer species, while lowland predators prey on more species (measured by diet breadth).

Methods

Building trophic interactions datasets

To use the random forest machine-learning algorithm to infer species trophic interactions, I collected and formatted different vertebrate interaction data. Using R v4.1.3 (R Core Team, 2022) and the `rGloBI` (v0.2.27) R package, I extracted 9,076 predator-prey trophic interactions between amphibians, mammals, birds, and reptiles from the *Global Biotic Interactions* database (GloBI) (globalbioticinteractions.org). I kept unique source (predator) and target (prey) species with binomial scientific names only, providing 3,229 interacting pairs. I collected more interaction data on Australian Wet Tropics species from an online survey (approved by Human Research Ethics Committee #2862) sent to five experts with specialist vertebrate knowledge from the Wet Tropics bioregion (see Appendix Table 2), providing 20 additional observations. Additionally, a systematic search of peer-reviewed journal articles explicitly pertaining to species interaction records, gut content, histology, and isotope analysis on each species found in low and highland communities revealed another 85 records. I also collected 171 records using the citizen-science platform *iNaturalist* through a custom open collection project (inaturalist.org/projects/pci-project). Identifying only 17 interactions that observed species found in either community as strictly predator and prey, I subsetted these as validation data for inferred trophic interactions between species. I then generated pseudo-non-interactions by making each possible species pair from all the species in the interaction data and removing those combinations observed in the interaction dataset. I subtracted all instances where species were recorded as interacting from the pseudo non-interaction dataset, resulting in a combined dataset of 418,861 interactions.

I also made pseudo-non-interaction combinations for predator species identified in each community in which detailed diet data already existed in the interaction dataset. Specifically, I added 1,016 pseudo-non-interactions for six predator species identified. Out of these pseudo-non-interactions, I randomly sampled 17 interactions used as validation data for inferring trophic interactions between species found in low and highland communities.

Calculating phylogenetic distances

I extracted phylogenetic data from the *Vertlife* database (vertlife.org) for all 3,371 species in the interaction/non-interaction datasets. Specifically, I took 100 sample trees from a chosen pseudo-posterior distribution of 10,000 trees for each major taxonomic group (including amphibians, birds, mammals, and squamates). I used the species most closely related to the species found in each community in the phylogeny for the species that were not included in those phylogenies. These included phylogenetic data from (*i*) *Trichoglossus flavoviridis* substituting *T. mollucanus*, (*ii*) *Pogonomys fergussoniensis* substituting *P. mollipilosus*, (*iii*) *Lophorina superba* substituting *L. victoriae*, (*iv*) *Cyclodomorphus branchialis* substituting *C. gerrardii*, (*v*) *Coracina incerta* substituting *Edolisoma tenuirostre* (same family), (*vi*) *Monarcha castus* substituting *Carternornis leucotis* (same family), (*vii*) *Monarcha axillaris* substituting *Symposiachrus trivirgatus* (same family), and (*viii*) *Sphenomorphus maculatus* substituting *Gnypetoscincus queenslandiae* (same family). I removed all other species from the interaction dataset without associated phylogenetic data, leaving 1,235 unique species.

Using *FigTree* (v1.4.4), I spliced each phylogenetic Class into one phylogenetic tree by adding branches to common ancestors. I combined each phylogeny by subtracting the root node age (in millions of years) of each taxonomic class to eight decimal places to the next closest taxonomic class. I repeated this process five times, using a different tree for each taxonomic group. I then did a principal coordinates analysis on all species with phylogenetic data to calculate the phylogenetic distance between all species using each phylogenetic tree, keeping only the first 100 eigenvectors. I then combined all species' phylogenetic distance data with all other associated interaction data.

Inferring trophic interactions and network construction

To infer trophic interactions between species in low and highland communities, I used the random forest machine-learning algorithm in the `Ranger` (v0.14.1) (Wright & Ziegler, 2015) R package. Specifically, I randomly sampled 50 interactions and 50 non-interactions to make a testing dataset from the aforementioned trophic interaction and non-interaction dataset I constructed. I used all other interaction data and an equal number of randomly sampled non-interaction data (1,259 instances) to make the training dataset and train the random forest algorithm. I repeated this entire process 100 times (on 100 resampled training and testing datasets), providing a probability of interaction (> 0.49 = interaction, ≤ 0.49 = non-interaction). I calculated the true skill statistic and a contingency table for each iteration using the randomly sampled testing dataset to evaluate the number of correctly inferred interactions and pseudo-non-interactions based on the predicted probability of interaction. The true skill statistic provides a value between 1 (completely accurate prediction) and -1 (completely inaccurate prediction), and accounts for both sensitivity (the proportion of true interactions correctly predicted) and specificity (the proportion of true non-interactions correctly predicted) (Allouche et al., 2006). From the contingency tables, I also derived interaction accuracy (proportion of known interactions correctly inferred as positive) and non-interaction accuracy (proportion of known non-interactions correctly inferred as negative) values. I then used the mean true skill statistic, interaction accuracy, and non-interaction accuracy calculated across iterations to evaluate model performance and to optimise the random forest parameters, including the total number of decision trees, maximum tree depth, number of variables considered at each split, variable importance, and splitting rule.

Using all interaction and randomly sampled non-interaction data as a training set to retrain the random forest algorithm, I then inferred trophic interactions for all possible predator-prey interactions between species in both low and highland vertebrate communities. In this application, I only inferred prey for predatory species based on broad diet data collated from previously published datasets (Meiri, 2018; Oliveira et al., 2017; Williams et al., 2010). However, where I could not find general diet data for amphibians, I used interaction data collected from *GloBI* to find the body size of the smallest amphibian recorded to prey on another vertebrate. I assumed that amphibians above this size could feed on other vertebrates while those below the threshold could not feed on vertebrates. After applying the diet restrictions to both low- and highland species, the total number of possible predator-prey interactions between study species was 6,765, including 41 predator and 165 prey species. I again calculated mean true skill statistics and contingency tables using the inferred results of each of the 100 iterations to evaluate model performance. Using the mean probability of interaction over the 100 interactions, I then converted the finalised interaction output into a graph adjacency matrix to produce one directed network model for both low and highland species separately, in which every row/column of the matrix is a species, and the value at row i and column j is a measure of the trophic interaction between i and j species.

These evaluation procedures allowed me to assess the reliability of the inferred interactions and the predictive performance of the random forest model. I interpreted the combination of true skill statistic, interaction accuracy, and non-interaction accuracy as a comprehensive measure of classifier performance. By repeating the resampling process across multiple iterations, I generated distributions of these metrics to evaluate model stability and reduce the risk of overfitting. This approach provided confidence that the final network structures represent plausible trophic architectures based on model generalisation rather than artefacts of a particular training subset.

Assessing ecological network structures

To compare community-mean descriptors of network topology for low and highland communities, I calculated different network metrics using the `Cheddar` (v0.1-636) (Hudson et al., 2013) and (Csardi & Nepusz, 2006) `iGraph` (v1.3.4) packages in R. These included the total number of species (v) (both prey and predator species and their ratios), total number of interactions between species (L), and the mean number of interactions per species (L/v), further grouped by taxonomic class as a mean value. The food-web connectance (*C*, which measures the fraction of interactions present (realised) across the network relative to all possible interactions) was then evaluated, and grouped by taxonomic class by assessing associated species and number of interactions:

$$C = Lv^{-2}$$

To evaluate network structures in more detail, I used different centrality metrics to highlight the relative importance of each species to the connectivity of low- and high-elevation communities. These metrics included degree centrality (C_D) (Freeman, 1977) to calculate the total number of interactions (deg) connected to a given species:

$$C_D(v) = \deg(v)$$

This metric required calculating both in-degree (total number of interactions going to a species) and out-degree (total number of interactions going out from a species). I also calculated betweenness centrality (C_B) to assess the number of shortest (geodesic) paths that go through a given species:

$$C_B(v) = \sum_{i,j:i\neq j,i\neq v,j\neq v} \frac{g_{ij(v)}}{g_{i,j}}$$

where $g_{ij(v)}$ is the number of shortest paths (geodesics) between species i and j that pass through species v, and g_{ij} is the total number of shortest paths between i and j. I also calculated closeness centrality (C_C) (Bavelas, 1950), which is the inverse of the sum of distances to all reachable species in the network:

$$C_c(v) = \frac{1}{\Sigma_{i\neq v}\, d_{v,i}}$$

To assess variability in diet breadth (generality) between networks, as well as across taxonomic classes as mean values, I also calculated the number of prey species per predator, including isolated vertices (G_v):

$$G_v = \frac{1}{L/v} \sum_{j=1}^{v} a_{i,j}$$

where $a_{i,j}$ are the values of the adjacency matrix α food web. Similarly, I also calculated the vulnerability of species in each network by assessing the number of predators that prey on each species ($G_{i,v}$), also as a mean by taxonomic class:

$$G_{i,v} = \frac{1}{L/v} \sum_{j=1}^{v} a_{i,j}$$

I evaluated the trophic positioning by measuring the trophic levels (i.e., trophic height) (Jonsson et al., 2005) (TL) of each species (i). These included chain-averaged, $\frac{\Sigma(TL_i)}{N} + 1$, shortest, $\min(TL_i) + 1$, and longest, $\max(TL_i) - \min(TL_i) + 1$, trophic lengths from node to basal species (Williams & Martinez, 2004) in each network, further grouped by taxonomic class as a mean. To provide measurements for only connected predator and prey species, I completed all analyses without consideration of isolated vertices within the networks. To test for differences among networks, I implemented randomisation tests for each metric by using 10,000 randomised versions of each network. Specifically, in each randomised iteration, I rewired the edges within the network while preserving the overall network structure (also allowing for cannibalistic links as per the original networks) using the `iGraph` (v1.3.4) (Csardi & Nepusz, 2006) R package, and assessed the proportion of randomised metric values that were ≥ the observed metric values for each network.

Results

Random forests model performance

Models trained and tested on partial *GloBI* and other miscellaneous interaction data predicted best (mean true skill statistic = 0.606 against the testing dataset). Specifically, inferred interactions had a mean accuracy of 64%, while inferred non-interactions had an accuracy of 96%. For inferring interactions for species in low- and high-elevation communities, models trained on *GloBI* (including all testing data used in previous models) and other miscellaneous interaction data displayed moderate predictive performance (true skill statistic = 0.45 against known interaction and non-interaction data of Australian Wet Tropic species). Interactions inferred by these models had an accuracy of 88.2%, while inferred non-interactions had an accuracy of 41.2% against the validation dataset.

Low- and high-elevation network structures

In the lowland network comprising 117 vertebrate species, I inferred 511 interactions, while the highland network, with 128 vertebrate species, had 629 such interactions (Table 1, Figure 1). When examining consumer-resource composition, the highland network featured 34 predators and 122 prey species, compared to the lowland network's 28 predators and 111 prey species. Both networks exhibited a comparable predator-to-prey ratio, with 0.27:1 in the highland network and 0.25:1 in the lowland network (Table 1).

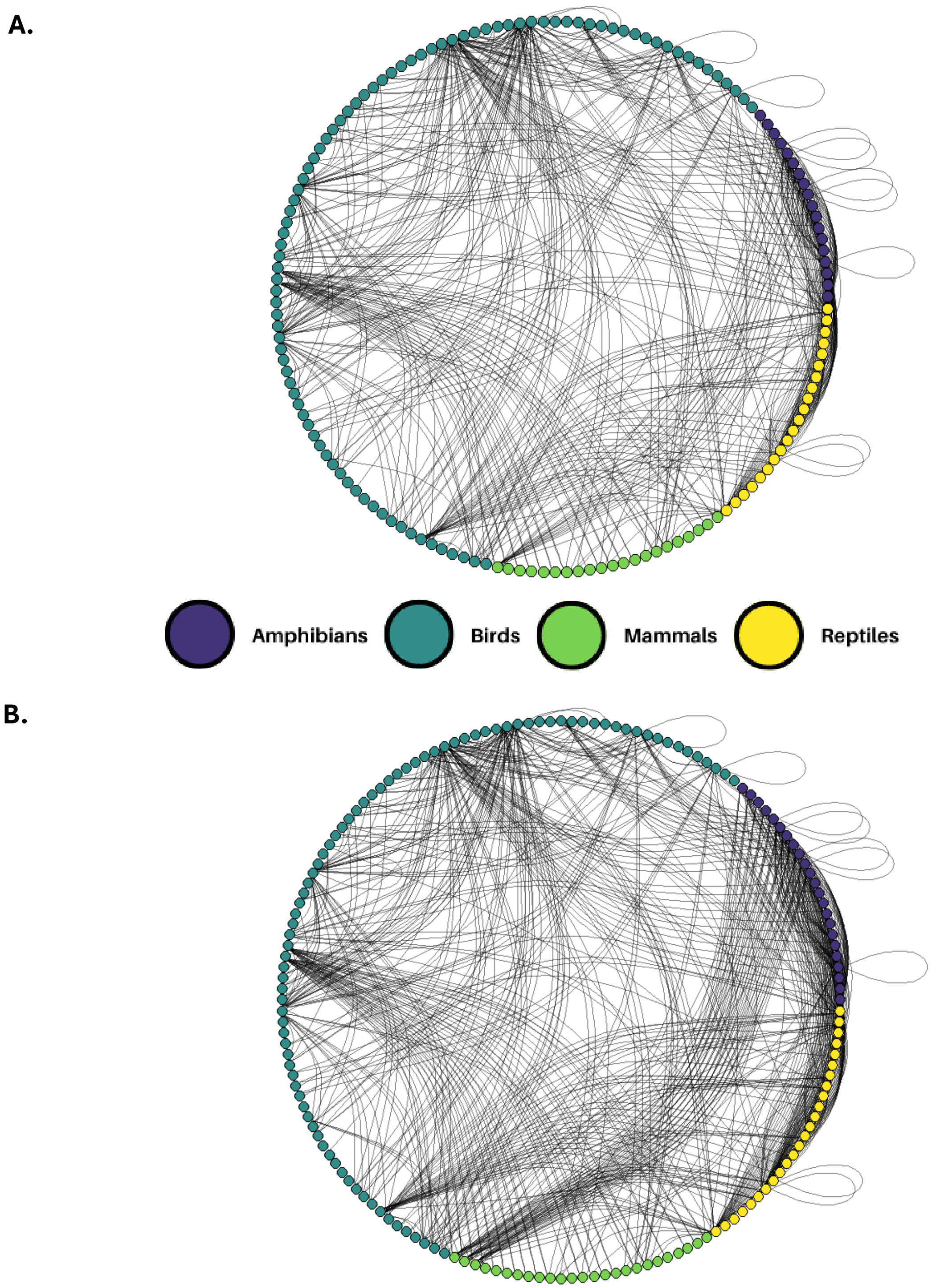

Figure 1. Two-dimensional ecological network models depicting predator-prey interactions (black lines – loops represent cannibalistic interactions) between vertebrate species (coloured circles) in the Australian Wet Tropics lowland (A, i.e., < 450 m elevation) and highland (B, i.e., > 850 m elevation) communities.

Table 1. Network properties, including possible and inferred trophic interactions for low- and high-elevation vertebrate communities.

network	possible interactions $(\boldsymbol{P} \times \boldsymbol{Q})$	inferred interactions $(\boldsymbol{L})$	possible predators $(\boldsymbol{P})$	inferred predators	possible prey $(\boldsymbol{Q})$	inferred prey	no. species $(\boldsymbol{v})$	predator-prey ratio
highland	6519	629	41	34	128	122	128	0.27:1
lowland	5215	511	35	28	117	111	117	0.25:1

The lowland network had a lower average number of interactions per species (L/v = 4.37) compared to the highland network (L/v = 4.94) ($p < 0.001$), although mammals showed a slightly higher mean number of interactions in the lowland network (L/v = 3.05) compared to the highland network (L/v = 2.86) (Figure 2). Lowland and highland networks showed similar food-web connectance (C = 0.037 and 0.039 for lowland and highland, respectively), with most taxonomic classes showing higher connectance than the mean for their entire lowland (C = 0.271 ± 0.22) and highland network (C = 0.243 ± 0.177). Specifically, birds exhibited lower connectance (C_{birds} = 0.03 and 0.033 for low- and high-elevation networks, respectively), while amphibians and mammals had higher connectance in the lowland network ($C_{\mathrm{amphibians}}$ = 0.582 and C_{mammals} = 0.138) compared to the highland network ($C_{\mathrm{amphibians}}$ = 0.494 and C_{mammals} = 0.11) ($p < 0.001$) (Figure 3).

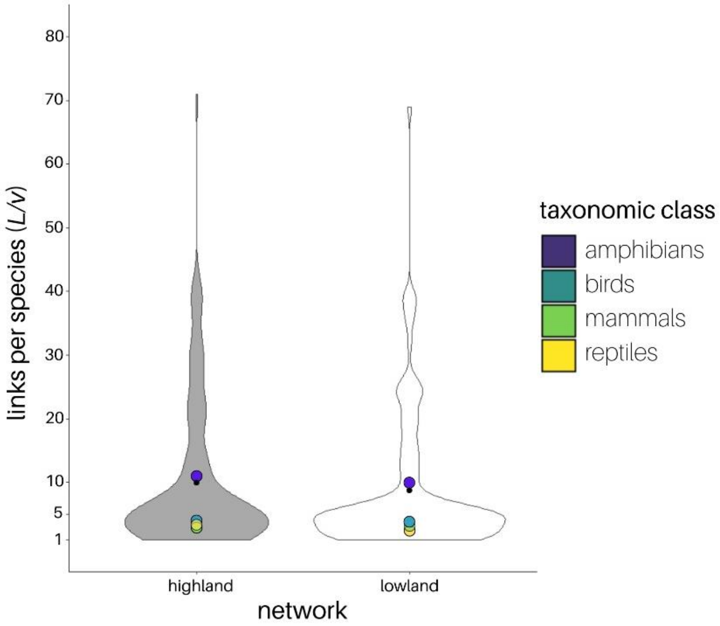

Figure 2. Links per species (L/v) for low- (white) and high-elevation (grey) networks. Black circles denote mean values, while coloured circles denote mean values for taxonomic classes.

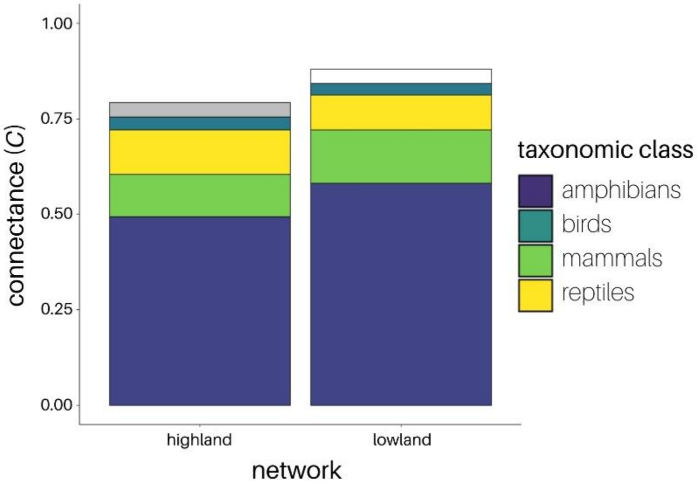

Figure 3. Food-web connectance (C) for lowland (white bar) and highland (grey bar) networks, divided into taxonomic classes (coloured bars).

Mean closeness centrality was also similarly low among highland (C_C = 0.0030 ± 0.0005) and lowland (C_C = 0.0032 ± 0.0005) networks (p < 0.001), showing *Dicrurus bracteatus* (spangled drongo) with the highest values in both networks (0.005 and 0.0044 for low- and high-elevation networks, respectively), with the only difference in species composition being the inclusion of *Austrochaperina robusta* (robust frog) (0.0039) in the lowland network, and *Zoothera lunulate* (bassian thrush) (0.0041) in the highland network (Figure 4). No mammal species had high closeness centrality in lowland or highland networks. Mean betweenness centrality was also similar in lowland (C_B = 3.03 ± 15.42) and highland (C_B = 3.74 ± 16.59) networks ($p < 0.001$), again with *Dicrurus bracteatus* having the highest value (144.75 and 156.75 for low- and high-elevation networks, respectively). However, this highlights that more mammal species, including *Antechinus godmani* (Atherton antechinus) and *Antechinus adustus* (tropical antechinus) (both 26.67), had higher importance than measured by the closeness centrality in the highland network (Figure 5). Further, high betweenness centrality for *Pachycephala simplex* (grey whistler) (0.75) and *Austrochaperina robusta* (robust frog) (0.71) was only observed in the lowland network and not in the highland network. In contrast, the rest of the species with degree centrality were the same in both networks, with *Antechinus flavipes* (yellow-footed antechinus) being the only mammal species represented in the lowland network (64) (Figure 5).

Mean degree centrality was also similar in both the highland (C_D = 9.88 ± 11.77, 34 species > 0 in-degree & 121 species > 0 out-degree) and lowland (C_D = 8.74 ± 10.93, 28 species > 0 in-degree & 111 species > 0 out-degree) networks ($p < 0.001$), with mostly the same species scoring highly in this metric. However, there were some differences in the composition of species with high degree centrality. For example, *Antechinus godmani* (Atherton antechinus) and *A. adustus* exhibited high degree centrality in the highland network but not in the lowland network, a pattern also reflected in their betweenness centrality. Similarly, *Aviceda subcristata* (Pacific baza) and *Stegonotus cucullatus* (Slaty-grey snake) were the only species with high degree centrality in the lowland network (21 and 18) but not in the highland network, although with even higher degree values of 22 and 20, respectively (Figure 6). Overall, 48 species in the lowland network (32.2%) and 44 species in the highland network (27.7%) had a degree of ≤ 1.

D. bracteatus had the highest degree centrality in both networks (69 and 71 for low- and high-elevation networks, respectively), with *A. flavipes* the only mammal species with high degree centrality in the lowland network (20) (Figure 5). Further analysis of degree centrality for in-degree edges showed that *D. bracteatus* was consistently the most influential predator species, with 64 predator species in the lowland network and 66 in the highland network. However, when comparing out-degree centrality, *Litoria infrafrenata* (white-lipped tree frog) was the most common prey item, with 17 predator species in the lowland network and 22 in the highland network (see Appendix Tables 5 & 6 for detailed centrality metrics for all low- and high-elevation species).

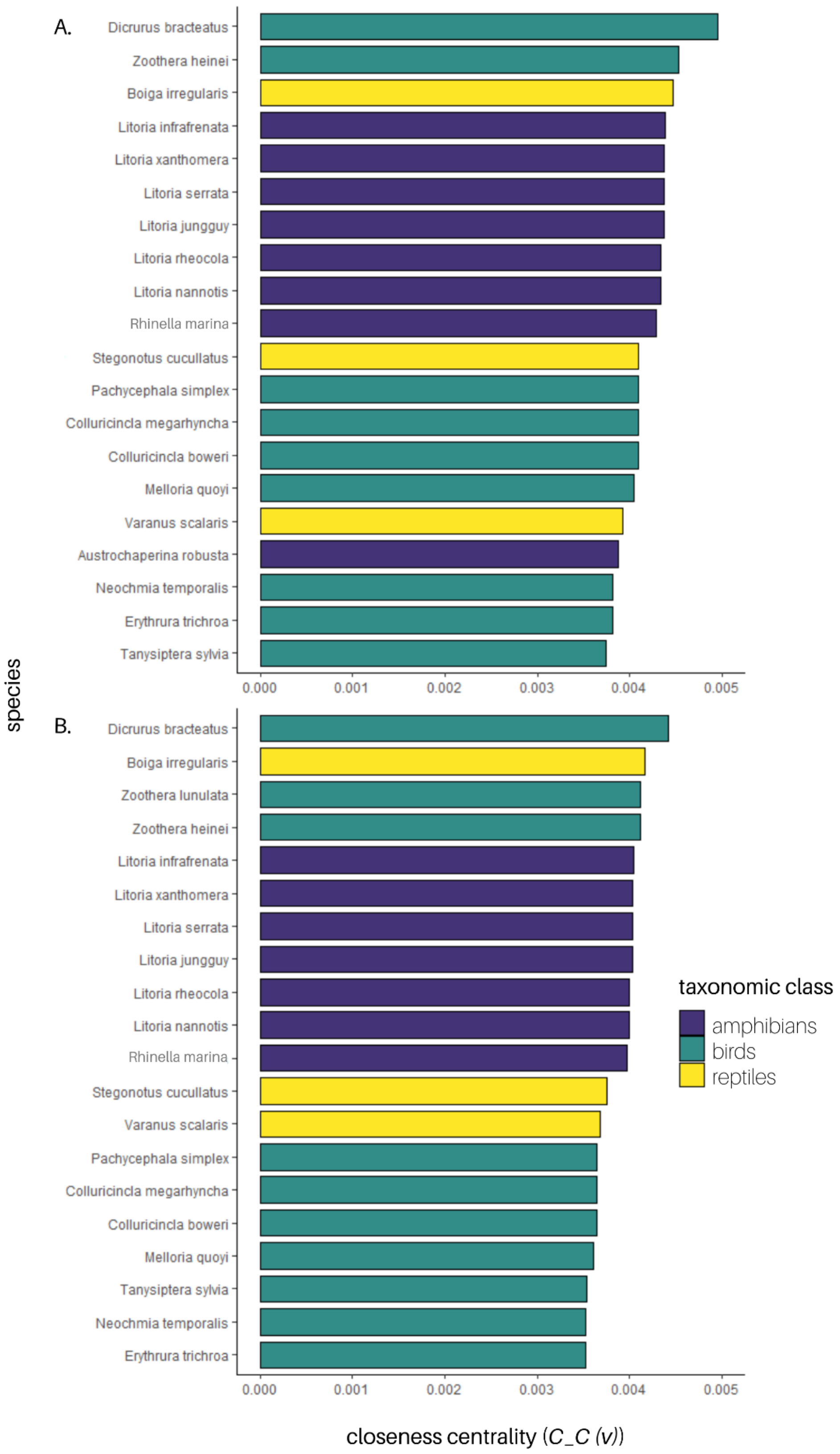

Figure 4. Top 20 species with the highest closeness centrality (C_c) values in highland (A) and lowland (B) networks. Coloured bars denote taxonomic class for individual species.

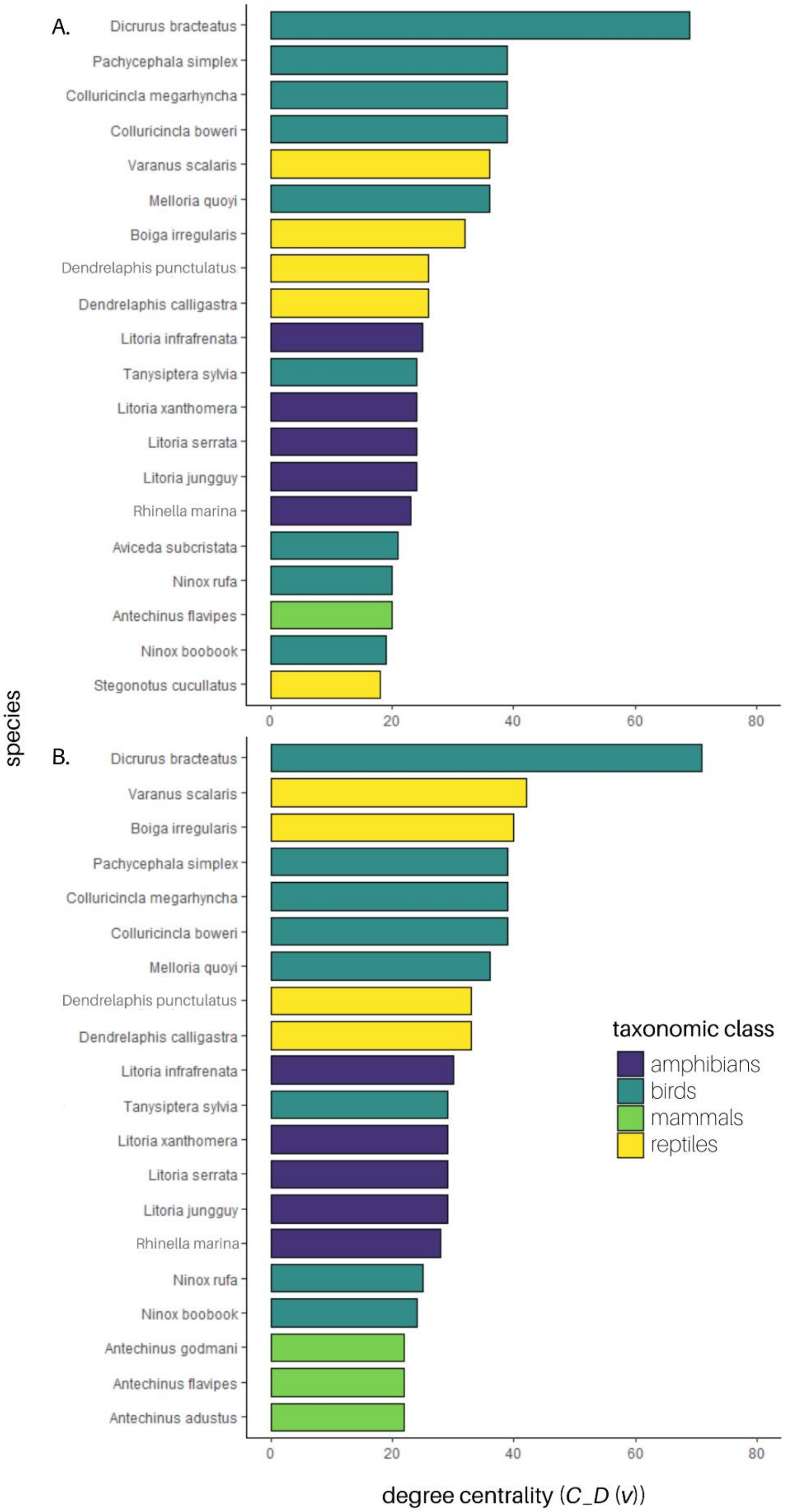

Figure 5. Top 20 species with the highest degree centrality (C_D) values in highland (A) and lowland (B) networks. Coloured bars denote taxonomic class for individual species.

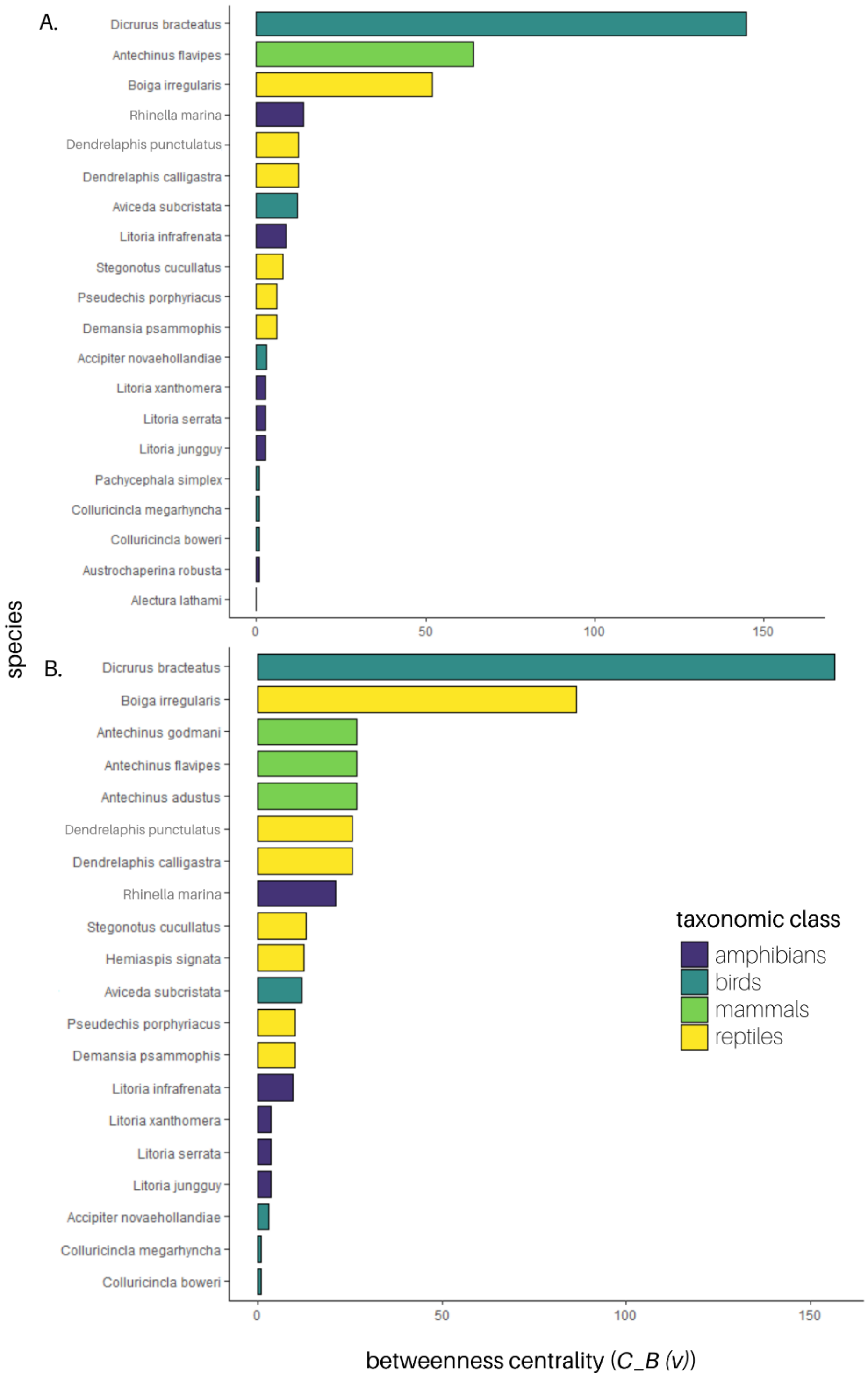

Figure 6. Top 20 species with the highest betweenness centrality (C_B) values in highland (A) and lowland (B) networks. Coloured bars denote taxonomic class for individual species.

Mean diet breadths (generality) indicated more prey species per predator in the highland (G_v = 3.96 ± 4.76) compared to the lowland network (G_v = 3.43 ± 3.90) ($p < 0.001$) across all taxonomic classes except for mammals that had marginally more prey species in the lowland (2.76) compared to the highland network (2.64). In contrast, amphibians were the most common prey species in both networks (9.89 and 10.87 in low- and high-elevation networks, respectively; Figure 7). Vulnerability differed marginally between networks, with species in the highland network tending to have more predators ($G_{i,v}$ = 3.96 ± 9.96) than those in the lowland network ($G_{i,v}$ = 3.43 ± 9.33) ($p < 0.001$) across all taxonomic classes, with mammals having the largest difference between lowland (0.86) and highland (2.4) networks (Figure 7). However, reptiles had the highest mean number of predators in both networks (6.86 and 7.44 in low- and high-elevation networks, respectively), driven by several species of snake (15.14 ± 8.77 and 19.14 ± 9.86 predators in low- and high-elevation networks, respectively), and one lizard, *Varanus scalaris* (spotted tree monitor), with 41 predator species in both networks (Figure 7).

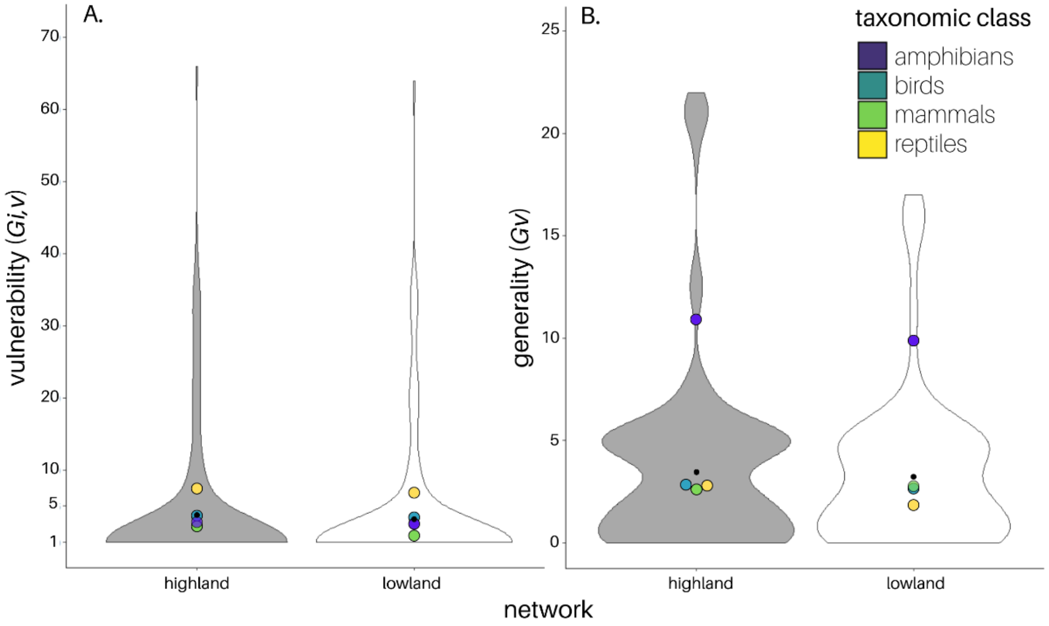

Figure 7. Vulnerability (A) and generality (B) for low- (white) and high-elevation (white) networks. Black circles denote mean values, while coloured circles denote mean values for different taxonomic classes.

The mean chain-averaged trophic level was similar for lowland (TL = 2.25 ± 2.45) and highland networks (TL = 2.43 ± 2.60) networks ($p < 0.001$). However, the highland network had a marginally higher maximum averaged trophic level (9.61) compared to the lowland network (9.30) across all taxonomic classes, with mammals having the largest difference (2.23 *versus* 1.5 for low- and high-elevation networks, respectively) (Figure 8). Mean longest chain length was also marginally higher in the highland network (TL_l = 2.89 ± 3.43) compared to the lowland network (TL_l = 2.71 ± 3.35) ($p < 0.001$), with reptiles showing the highest longest chain lengths (4 in both low- and high-elevation networks), while mammals had the lowest longest chain lengths (TL_s = 2.23 and 1.5 in low- and high-elevation networks, respectively) (Figure 8). Species in both low- and high-elevation networks had different chain-averaged trophic level (highland: 0.19 ± 0.12 longer chain lengths than the lowland network). Across both chain-averaged and longest trophic levels, the same four mid-sized birds (*Colluricincla boweri* – bowers shrikethrush –, *Colluricincla megarhyncha* – Arafura shrikethrush –, *Melloria quoyi* – black butcherbird –, and *Pachycephala simplex* – grey whistler) all shared the highest chain distances (13) in both low- and high-elevation networks (see Appendix Tables 5 & 6 for values by individual species in each network). As observed across longest chain lengths, mean shortest chain length in the highland network was also marginally higher (TL_s = 1.28 ± 0.5) than the lowland network (TL_s = 1.26 ± 0.48) ($p < 0.001$) across all taxonomic classes, with reptiles again with the highest chain lengths (1.7 in both low- and high-elevation networks) and mammals with the lowest chain lengths (1.14 and 1.06 in low- and high-elevation networks, respectively; Figure 8). Across networks, 59.1% of species in the highland and 59.7% of species (89) in the lowland network had a chain-averaged trophic level equal to 1 (Figure 8, also see Appendix Tables 3 & 4 for values by species level in both networks).

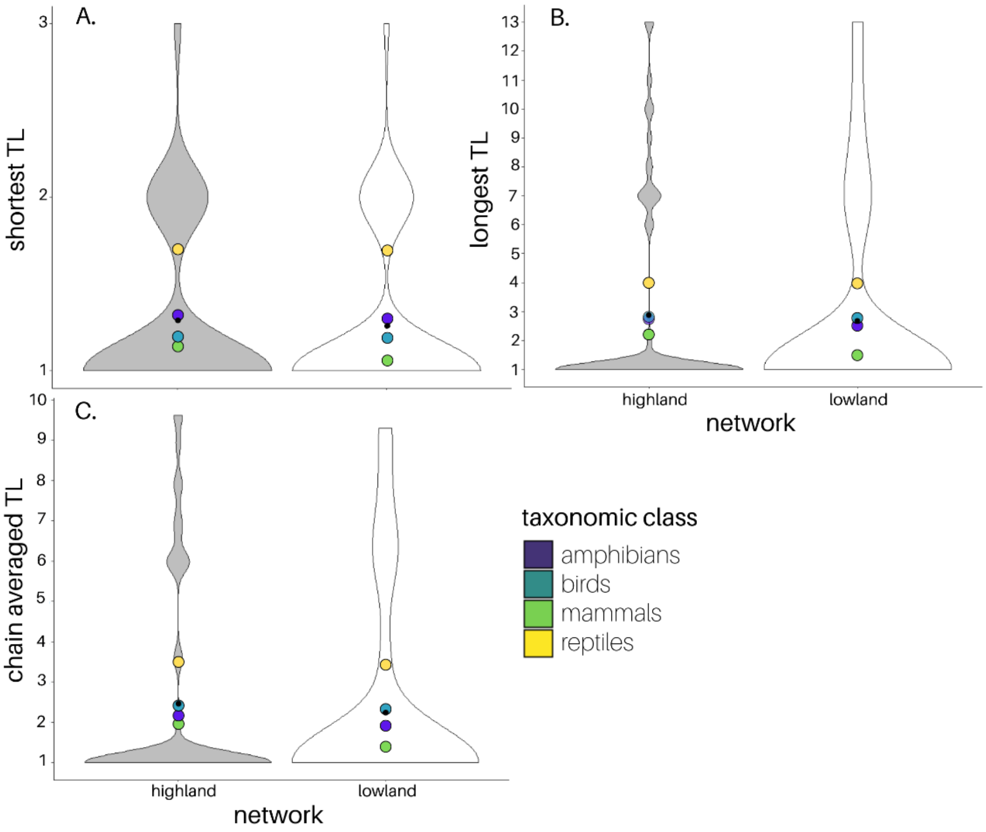

Figure 8. Shortest (A), longest (B), and chain-averaged trophic level (C) in low- (white) and high-elevation (white) networks. Black dots denote mean values.

Discussion

Low- and high-elevation vertebrate trophic network structures

Using defined low- and high-elevation vertebrate communities in the Australian Wet Tropics bioregion outlined in Chapter 2 as a case study, I used random forest to infer trophic relationships between species and construct network models of these communities. The resultant constructed networks show that low- and high-elevation vertebrate communities in the Wet Tropics appear to share similarities and differences regarding their food-web structure, as indicated by comparing various topological properties of their networks. These results support the hypothesis that the highland community has greater network complexity than the lowland community. While results show that predator-prey ratios were similar between both networks, no support for the hypothesis that highland species prey on fewer species than predators in the lowland network was found. However, the hypothesis that highland communities have more predator species than lowland communities was supported.

Low- and high-elevation communities differ in predator diversity, vulnerability, and the role of specific taxa as important nodes in their trophic structures. The higher diversity of predators in the highland network, corroborated by their higher vulnerability, is driven primarily by the higher diversity of mammals in the highland community. Almost no mammals in both networks, however, were inferred to have predators, except for *Antechinus flavipes* (yellow-footed antechinus), which was predicted to have 18 predators in the low- and high-elevation networks, respectively. Likewise, *Antechinus adastus* (tropical antechinus) and *Antechinus godmani* (atherton antechinus) were each predicted to have 18 predator species in the highland network. This higher number of vertebrate predators is not unexpected given that *Antechinus* spp. are known prey items for many predator species in different locations across Australia (Triggs et al., 1984; Wallis & Brunner, 1987). These results, combined with their high degree centrality, suggest that *Antechnus* spp. in both networks are important prey and play a central role in connecting species that might not otherwise be connected directly in each network. However, mammals have a slightly lower mean number of interactions in the highland compared to the lowland network, highlighting the potential importance of mammals to the trophic structure of the lowland vertebrate community. Though predator-prey diversity is higher in the highland community, predator-prey interactions are likely to be several times fewer than in the lowland community at lower elevations because predators at higher trophic levels tend to have a higher metabolic rate and more active foraging behaviours; traits primarily shaped by various abiotic factors (Zvereva & Kozlov, 2022). While the highland network exhibited greater predator species diversity, driven partly by a more diverse mammal assemblage, the intricacies of predator-prey interactions and trophic structures suggest important differences between the low- and high-elevation communities.

Food-web connectance and trophic interactions also differed between low- and high-elevation vertebrate communities. Food-web connectance was low for both low- and high-elevation networks, suggesting simplistic trophic structures supported by a low averaged number of trophic interactions per species. While previous research on trophic relationships between reptiles, amphibians, birds, and various invertebrates in a Puerto Rican tropical rain forest, found food-web connectance was also low (0.063), the rain forest had a higher average number of interactions per species (9.74) (Reagan & Waide, 1996) compared to our analysis in the Wet Tropics calculated here. This low connectance implies that the vertebrate communities examined might be less resilient to perturbations (Dunne et al., 2002a; Dunne et al., 2002b; Vieira & Almeida-Neto, 2015). One reason for this increased risk is that low-connectance communities are more likely to lose species due to successful invasive species incursions than highly connected communities (Romanuk et al., 2017). Low connectance and trophic levels indicate less-intricate and less-complex interaction pathways, despite the assumption that species in tropical rain forests have a high potential for inter-trophic level interactions (Dyer, 2007), leading to complex trophic pathways (Rosenzweig & MacArthur, 1963). However, the real-world connectance for both the communities examined here is likely higher because the networks constructed excluded invertebrates and plants. Low trophic levels also indicate that fewer vertebrates function at higher trophic levels in both networks, a pattern observed in other tropical rain forest vertebrate communities (Kupfer et al., 2006). Comparing connectance, the average number of links per species, and predator-prey ratios in modelled communities with those found in comparatively different sub-Mediterranean and boreal-alpine environments, such has those found in the southeastern slopes of the Pyrenees (Galiana et al., 2014), results further support that ecosystems with higher species diversity like the Wet Tropics, typically exhibit more complex interaction networks than in less diverse systems.

Results further suggest disparities in species vulnerability and trophic interactions in both networks. Why models inferred that snakes have many predators in both networks could be explained by their high incidence of oviparity (80% of all species across both networks), presumably leaving their eggs vulnerable to many potential predators (Laurance & Grant, 1994), such as predatory birds. The finding, however, that reptiles generally have more predators than other taxa in both networks highlights a potential limitation of using biotic interaction data gathered from *GloBI*. The life stages for both predator and prey species specified in the training datasets were seldom known, so trophic interactions inferred by random forest do not clarify whether reptile species can only interact when at specific stages. This ambiguity in the training data is likely the case for *Varanus scalaris* (spotted tree monitor) because they are also oviparous and leave their offspring exposed to many potential predators; however, as adults, they are unlikely to be eaten by most predators due to their large body size (25.3 cm snout-vent length) (Williams et al., 2010). Such life-history complexity, where individuals shift between being vulnerable prey and higher-level predators, can increase trophic diversity and contribute to the stability and modularity of food webs.

In contrast, the mean number of inferred prey species for each inferred predator in all the vertebrate taxonomic classes (except for amphibians) being low could indicate that most vertebrates in the Australian Wet Tropics feed primarily on invertebrates and plants (Parsons et al., 2007; Williams et al., 2010). Therefore, vertebrates are, in general, less commonly chosen as prey. Compared to other tropical rain forest communities in Africa (Ray & Sunquist, 2001) and South America (Bianchi et al., 2011), where carnivorous vertebrates tend to eat few other vertebrate species, the Australian Wet Tropics is not an anomaly.

Most species in both networks occupied basal trophic levels, suggesting that species at these levels are key drivers of predator-prey dynamics within each community. This observation aligns with the finding that mammals, which have the shortest and longest trophic lengths among all taxonomic classes in both networks, predominantly occupy low trophic positions in the Wet Tropics, including, for example, the herbivorous green ringtail possum, *Pseudochirops* *archeri,* (Jones et al., 2006) and spectacled flying fox, *Pteropus conspicillatus* (Parsons et al., 2007).

Models inferred that amphibians preyed on the most species in both networks, likely reflecting biases in the *GloBI* training datasets. Only 15.9% of the interactions derived from the *GloBI* database included anuran predators, while 24.5%, 26.3%, and 28.5% of the predators in the dataset came from birds, reptiles, and mammals, respectively. This proportionally smaller number of interactions in the interaction dataset were mainly from temperate regions for frog and toad species (e.g., cosmopolitan and generalist species from North America such as the western toad *Anaxyrus boreas* and Cuban tree frog *Osteopilus septentrionalis*). In contrast, many microhylid frog species in the Wet Tropics (e.g., tapping nursery frog *Cophixalus aenigma*) are smaller-bodied and regionally endemic rain forest specialists (Hoskin & Hero, 2008; Williams & Hero, 1998). These differences give rise to the lower probabilities of pairwise interactions inferred for amphibians, an expectation considering that the performance of random forest and other binary classifiers trained on taxonomically biased datasets predict sub-optimally when projecting to species absent in the training set (Strydom et al., 2022). Future research should, therefore, avoid biases in interaction data collected from global repositories such as *GloBI,* by training on interaction and non-interaction data specific to target taxonomic classes to increase the accuracy of inferred interactions. Although some vertebrates might be able to prey on such species like *Rhinella marina* (cane toad), a known invasive of both low- and high-elevation communities, many predators avoid this putative species due to its toxicity (Greenlees et al., 2010; Llewelyn et al., 2010). The disparities in inferred trophic interactions across taxonomic classes appear to highlight more of the limitations of using global databases like *GloBI*, especially when examining regionally endemic or ecologically specialised species.

Degree, closeness, and betweenness centrality were broadly similar between low- and high-elevation networks. Findings suggest that the highland community had more predator species than the lowland community, with few species having many vertebrate predator or prey species, as found in other communities (Dunne et al., 2002a). The degree of links, however, shows few species with many trophic interactions in both networks and most species with few interactions, a phenomenon observed in most real-world ecological networks

(Ghalmane et al., 2020). Birds have shown more influence in lowland than in highland communities, suggesting their important role as connectors across trophic levels, and as potentially targeted species for biodiversity recovery following community collapses (Bhatia et al., 2023). This structural prominence likely reflects their generalist foraging behaviour, which enables them to interact across multiple trophic levels. However, their influence appears more concentrated within modules rather than between them, limiting their role as cross-network integrators. There was also a higher proportion of 'generalists' than 'specialists' in both low- and high-elevation communities, which could be related to the expansion and contraction of rain forest refugia combined with non-random species extinction throughout the Wet Tropics bioregion (Williams & Pearson, 1997). This prevalence of generalists suggests a community-wide shift toward flexible resource use and broader trophic roles, which can influence redundancy and robustness in food-web structure. More generalist species in the highland network lend support to this conclusion; their presence might increase redundancy across modules and buffer against localised extinctions, although not all generalists necessarily function as structural hubs. However, it is also important to note that species in networks classified as 'specialists' are often opportunistic omnivores, while true resource specialists tend to be network 'generalists' because resources are only one trophic component of a community (Dehling, 2018). This illustrates the complexity in linking ecological roles with structural metrics. Dietary breadth might not always align with network position, especially if a specialist consumes a widely shared prey or occupies a unique trophic link. While birds in the lowland network (black butcherbird *Melloria quoyi* and Australian boobook *Ninox boobook* in particular) both had high degree centrality (≥ lowest top 20 values) and low betweenness centrality (≤ lowest top 20 values) and high connectivity, they do not play an important connecting role with other species in their network (Delmas et al., 2019). This pattern suggests that although these birds interact with many species (high degree), they do so primarily within a subset of the network, limiting their bridging capacity and structural influence. As such, these birds exemplify how some generalists can have locally dense but globally peripheral network positions. Instead, they likely have more direct, localised interactions in both networks. Other bird species, including *Ninox rufa* (rufous owl) in the lowland network and *Tanysiptera sylvia* (white-tailed kingfisher) and *V. scalaris* in the highland network, also had similar network importance.

The centrality measures alone do not unveil the shared characteristics of 'important' species or their potential influence on others. For instance, while *L. infrafrenata* emerged as the most frequent predator, its prevalence might not necessarily reflect its commonality because this species is mainly found < 400 m above mean sea level in the Australian Wet Tropics (Hoskin & Hero, 2008). Like mammals, the high degree of centrality of reptiles and their many inferred predators indicates their importance as prey species in both networks. Their particularly high betweenness centrality also suggests they are important connectors, a finding corroborated by their highest shortest and longest trophic levels compared to all other taxonomic classes. Further, high closeness centrality in birds and amphibians in both networks also indicates that these groups tend to have a higher efficiency in influencing their networks if, for example, a perturbation affects one of these species (Estrada & Bodin, 2008). In contrast, mammals in both networks have a lower efficiency to affect other species within their respective networks. These results, when viewed together, illustrate how species from different taxonomic groups can contribute differently to network topology, whether through high connectivity, bridging modules, or occupying basal trophic positions, reflecting a spectrum of generalist and specialist roles across vertebrate communities.

At the species level, why *D. bracteatus* emerged as the most influential species in low- and high-elevation communities across all centrality metrics could reflect its ability to adapt to varying ecosystems across northern and eastern Australia (Wood, 2012). In particular, its high centrality might indicate its importance to both low- and high-elevation communities during its latitudinal and altitudinal migrations to northern Queensland in the winter (Sukmantoro et al., 2006); indeed, some migratory bird species in northern Australia are important for sustaining food availability within these communities (Natusch et al., 2016). However, during other times when this species is absent, species like *Boiga irregularis* (brown tree snake) with consistently high centrality might be similarly influential in low- and high-elevation communities. Amphibians also consistently had high centrality, but this might indicate modularity in the network, where species are cannibalistic. Many frogs are, in fact, common predators in anuran communities (Measey et al., 2015). Alternatively, biases in the training data might explain this observation. Together, these findings reinforce how different species may play distinct but complementary roles in shaping network structure, stability, and vulnerability to perturbations.

Limitations

Pairwise interactions inferred from random forest depict theoretically plausible trophic relationships among vertebrate species, but they do not provide insights into the frequency, rarity, or existence of these interactions within the real-world ecological communities they represent. Another limitation is the focus on vertebrates, which ignores many other relationships, including those between plants and their pollinators or parasites and their hosts. While this focus was a deliberate choice to enable network inference based on available data, it is a sub-set of these communities. Caution is therefore warranted in interpreting the results, because excluding these broader interactions might limit the ecological scope of the findings. Understanding how these other relationships structure ecological communities and influence their responses to perturbations is necessary to predict the broader effects of current and future environmental change. Without access to abundance data for each species, I could not weight the interactions between species (e.g., by variation in population size). This limitation potentially restricts the network's ability to account for population dynamics and to evaluate extinction risks within each community (Doherty et al., 2023).

I also assumed that all unobserved interactions were non-interactions. If incorrect, this assumption could cause the random forest to perform poorly on erroneous data. Additionally, the training data I used to infer interactions lacked consistent information on species' life stages. This introduces ecological ambiguity, because the plausibility and directionality of trophic interactions depend on ontogenetic stage. As a result, some inferred interactions might represent relationships that are only possible during particular life stages or are biologically implausible in others. This limitation could influence network structure and the accuracy of derived metrics, potentially overestimating the number or distribution of interactions across the network.

Although uncertainty regarding inferred ecological networks is inherent, the random forest approach I used provides advantages over alternative inference methods (Chapter 1). Inference methods, such as generalised linear models (Desjardins-Proulx et al., 2017), or co-occurrence and joint species distribution models (Momal et al., 2020), often yield low predictive accuracy due to their heavy reliance on simplistic assumptions or the absence of direct trophic data. By contrast, supervised machine-learning methods like random forest use observed interaction and trait data to infer interactions, improving predictive reliability, particularly in complex terrestrial ecosystems characterised by diverse species assemblages (Desjardins-Proulx et al., 2017; Pichler et al., 2020). Consequently, despite inherent limitations and uncertainties, this method is still suitable for identifying general patterns of vulnerability, community structure, and generating ecologically relevant comparative insights. Future research should prioritise collecting detailed empirical interaction and life-stage datasets to validate and refine these inference models.

Additionally, because trophic levels are inferred from the structure of the predicted networks, they might not always represent ecologically realistic positions for individual species. In particular, the absence of invertebrate and plant nodes in the networks likely alters the apparent vertical structure, meaning that species' absolute trophic levels should be interpreted cautiously. Nonetheless, the relative trophic positions of species or groups within and between the low- and high-elevation networks remain informative for comparison and still reflect underlying differences in community organisation.

Future research

Measuring network structure to gauge its stability or resilience to disturbance has many potential applications in conservation. However, validating these inferences is currently impracticable (Tylianakis et al., 2010), particularly in terrestrial ecosystems. This limitation underlines the urgent need for developing robust methodologies that can accurately measure and predict the impact of environmental disturbances on network dynamics, especially in complex terrestrial ecosystems where observational challenges are most pronounced. Determining how direct and indirect interactions between species influence their broader distribution might also be important for understanding broader-scale patterns in biodiversity. Other network characteristics, such as modularity, allow for measuring the density of links within communities compared to those between communities (Pringle & Hutchinson, 2020), might give further insight into the organisation and stability of network structures (Garay-Narváez et al., 2014; Takemoto & Kajihara, 2016).

Improving and validating network models will require more data (e.g., life history and morphological traits), such as more observed interactions and validated non-interactions. Random forest outputs can differ because of the way the algorithm classifies pairwise interactions among species, so generating several iterations of each network could provide a better estimate of predictive uncertainty.

Conclusions

Ecological network modelling can elucidate trophic structures in highly complex terrestrial communities through the application of machine learning-based inference and network metrics, with important implications for understanding extinction risks and community dynamics. These findings enrich our understanding of the potential trophic dynamics by quantifying the differential impact of elevation on highland versus lowland communities in the Wet Tropics, highlighting that communities might differ in their resilience to environmental perturbations, with certain species groups playing different trophic roles. However, the ability to measure network structure for assessing ecosystem stability and resilience highlights the necessity for robust methodologies that can accurately predict environmental impacts on biodiversity, specifically in complex terrestrial ecosystems. Enhancing and validating these network models necessitates additional data and multiple iterations to refine predictions and manage the inherent variability in modelling techniques like random forest. Together, this research provides both a resource that other researchers and natural resource managers can use to predict and manage threats to biodiversity in this bioregion, as well as serves as a foundation for other research to model analogous terrestrial ecosystems.

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Appendix

Collecting interaction data from experts

A form was designed and sent out to expert individuals from James Cook University to collect data on any terrestrial species interaction (e.g., plant-pollinator, host-parasite, and predator-prey) between any two species within the Australian Wet Tropics bioregion. Experts were defined and selected as any scientist or researcher with specialist knowledge of vertebrate species in the Australian Wet Tropics bioregion. Responses were collected using a Google Forms questionnaire, which included multiple short and long answer questions (Table 2). Responses collected were initially filtered by species relevant to defined low- and high-elevation communities, and then by responses only with verifiable evidence (photo, video, or audio recording).

Table 2. Questionnaire form used by experts to record any terrestrial species interaction (e.g., plant-pollinator, host-parasite, and predator-prey interactions) between any two species within the Australian Wet Tropics bioregion.

Question 1. (mandatory)
Q: Email address
A: (Short answer text)
Q: Full name
A: (Short answer text)

Question 2.
Q: Is the interaction between a plant and a pollinator?
A: (Yes/No)

Question 3.
Q; Pollinator (scientific name)
A: (Short answer text)
Q: Plant (scientific name)
A: (Short answer text)

Question 4.
Q: Is the interaction between a producer and consumer (trophic interaction)?
A: (Yes/No)

Question 5.

Q: Consumer (scientific name)
A: (Short answer text)
Q: Producer (scientific name)
A: (Short answer text)

Question 6.
Q: What was the interaction relationship?
A: Predator/Prey, Herbivore/Plant, Pathogen/Host, Parasite/Host, Other.

Question 7:
Q: Evidence of observation: Please provide evidence of interaction if possible (photo, sound recording or video).
A: (Upload media).

Table 3. Longest chain, shortest chain, and chain-averaged trophic level for each vertebrate species in the highland network.

Species	Longest chain trophic level	Shortest chain trophic level	Chain-averaged trophic level
Accipiter novaehollandiae	8	2	6.860999
Alectura lathami	1	1	1
Alisterus scapularis	1	1	1
Antechinus adustus	10	2	7.896155
Antechinus flavipes	10	2	7.896155
Antechinus godmani	10	2	7.896155
Aplonis metallica	1	1	1
Arses kaupi	1	1	1
Artamus leucorynchus	1	1	1
Austrochaperina fryi	1	1	1
Austrochaperina pluvialis	1	1	1
Austrochaperina robusta	7	2	6.002191
Aviceda subcristata	7	2	5.890688
Boiga irregularis	8	2	6.722177
Rhinella marina	6	2	3.764356
Cacatua galerita	1	1	1
Cacomantis flabelliformis	1	1	1
Cacomantis variolosus	1	1	1
Carlia rubrigularis	1	1	1
Carternornis leucotis	1	1	1
Cercartetus caudatus	1	1	1
Chalcites lucidus	1	1	1
Chrysococcyx minutillus	1	1	1

Coeranoscincus frontalis	1	1	1
Colluricincla boweri	13	2	9.61186
Colluricincla megarhyncha	13	2	9.61186
Columba leucomela	1	1	1
Cophixalus aenigma	1	1	1
Cophixalus australis	7	2	6.002191
Cophixalus concinnus	1	1	1
Cophixalus hosmeri	1	1	1
Cophixalus infacetus	1	1	1
Cophixalus monticola	1	1	1
Cophixalus neglectus	1	1	1
Cophixalus ornatus	1	1	1
Coracina lineata	1	1	1
Cyclodomorphus gerrardii	1	1	1
Cyclopsitta diophthalma	1	1	1
Dactylopsila trivirgata	1	1	1
Demansia psammophis	7	2	5.860215
Dendrelaphis calligastra	9	2	7.068395
Dendrelaphis punctulatus	9	2	7.068395
Dendrolagus bennettianus	1	1	1
Dendrolagus lumholtzi	1	1	1
Dicaeum hirundinaceum	1	1	1
Dicrurus bracteatus	9	2	7.159218
Edolisoma tenuirostre	1	1	1
Erythrura trichroa	1	1	1
Eudynamys scolopacea	1	1	1
Eulamprus quoyii	7	3	6.030928
Glaphyromorphus fuscicaudis	7	3	6.030928
Glaphyromorphus mjobergi	7	3	6.030928
Gnypetoscincus queenslandiae	1	1	1
Hemiaspis signata	7	2	5.950481
Hemibelideus lemuroides	1	1	1
Heteromyias albispecularis	1	1	1
Hirundapus caudacutus	1	1	1
Hypsiprymnodon moschatus	1	1	1
Lalage leucomela	1	1	1
Lampropholis coggeri	1	1	1
Lampropholis robertsi	1	1	1
Limnodynastes peronii	1	1	1
Litoria infrafrenata	6	2	3.596598

Litoria jungguy	6	2	3.588283
Litoria nannotis	1	1	1
Litoria rheocola	1	1	1
Litoria serrata	6	2	3.588283
Litoria xanthomera	6	2	3.588283
Lopholaimus antarcticus	1	1	1
Lophorina victoriae	1	1	1
Machaerirhynchus flaviventer	1	1	1
Macropygia amboinensis	1	1	1
Macropygia phasianella	1	1	1
Megapodius reinwardt	1	1	1
Melloria quoyi	13	2	9.61286
Melomys cervinipes	1	1	1
Mixophyes carbinensis	1	1	1
Mixophyes coggeri	1	1	1
Mixophyes schevilli	1	1	1
Monarcha melanopsis	1	1	1
Neochmia temporalis	1	1	1
Nyctimene robinsoni	1	1	1
Oriolus flavocinctus	1	1	1
Orthonyx spaldingii	1	1	1
Pachycephala pectoralis	1	1	1
Pachycephala simplex	13	2	9.61186
Perameles pallescens	1	1	1
Platycercus elegans	1	1	1
Pogonomys mollipilosus	1	1	1
Pseudechis porphyriacus	2	2	2
Pseudochirops archeri	1	1	1
Pseudochirulus cinereus	1	1	1
Pseudochirulus herbertensis	1	1	1
Psophodes olivaceus	1	1	1
Pteropus conspicillatus	1	1	1
Ptilinopus magnificus	1	1	1
Ptilinopus regina	1	1	1
Ptilinopus superbus	1	1	1
Rallina tricolor	1	1	1
Rattus fuscipes	1	1	1
Rattus leucopus	1	1	1
Rhipidura fuliginosa	1	1	1
Rhipidura rufifrons	1	1	1
Saproscincus basiliscus	1	1	1

Saproscincus czechurai	1	1	1
Saproscincus tetradactylus	1	1	1
Scythrops novaehollandiae	1	1	1
Sminthopsis leucopus	1	1	1
Sphecotheres vieilloti	1	1	1
Stegonotus cucullatus	7	2	5.971739
Strepera graculina	1	1	1
Symposiachrus trivirgatus	1	1	1
Taudactylus rheophilus	7	2	6.006579
Thylogale stigmatica	1	1	1
Tregellasia capito	1	1	1
Trichoglossus chlorolepidotus	1	1	1
Trichoglossus moluccanus	1	1	1
Trichosurus vulpecula	1	1	1
Uromys caudimaculatus	1	1	1
Zoothera heinei	1	1	1
Zoothera lunulata	1	1	1
Zosterops lateralis	1	1	1
Ninox rufa	11	2	8.893858
Ninox boobook	11	2	8.893962
Varanus scalaris	8	2	6.713199
Morelia amethistina	2	2	2
Tanysiptera sylvia	10	2	7.908445
Ceyx azureus	7	2	5.961379

Table 4. Longest chain, shortest chain, and chain-averaged trophic level for each vertebrate species in the lowland network.

Species	**Longest chain trophic level**	**Shortest chain trophic level**	**Chain-averaged trophic level**
Accipiter novaehollandiae	8	2	6.872801
Alectura lathami	1	1	1
Alisterus scapularis	1	1	1
Antechinus flavipes	10	2	7.624599
Aplonis metallica	1	1	1
Arses kaupi	1	1	1
Artamus leucorynchus	1	1	1
Austrochaperina fryi	1	1	1
Austrochaperina pluvialis	1	1	1
Austrochaperina robusta	7	2	6.002191

Aviceda subcristata	7	2	5.899865
Boiga irregularis	8	2	6.453413
Rhinella marina	6	2	3.769998
Cacatua galerita	1	1	1
Cacomantis castaneiventris	1	1	1
Cacomantis flabelliformis	1	1	1
Cacomantis variolosus	1	1	1
Carlia rubrigularis	1	1	1
Carternornis leucotis	1	1	1
Cercartetus caudatus	1	1	1
Chalcites lucidus	1	1	1
Chrysococcyx minutillus	1	1	1
Coeranoscincus frontalis	1	1	1
Colluricincla boweri	13	2	9.294761
Colluricincla megarhyncha	13	2	9.294761
Columba leucomela	1	1	1
Cophixalus aenigma	1	1	1
Cophixalus exiguus	1	1	1
Cophixalus infacetus	1	1	1
Cophixalus ornatus	1	1	1
Coracina lineata	1	1	1
Cyclodomorphus gerrardii	1	1	1
Cyclopsitta diophthalma	1	1	1
Dactylopsila trivirgata	1	1	1
Demansia psammophis	7	2	5.902174
Dendrelaphis calligastra	9	2	6.808565
Dendrelaphis punctulatus	9	2	6.808565
Dendrolagus bennettianus	1	1	1
Dendrolagus lumholtzi	1	1	1
Dicaeum hirundinaceum	1	1	1
Dicrurus bracteatus	9	2	6.869451
Edolisoma tenuirostre	1	1	1
Erythrura trichroa	1	1	1
Eudynamys scolopacea	1	1	1
Eulamprus quoyii	7	3	6.030928
Glaphyromorphus fuscicaudis	7	3	6.030928
Gnypetoscincus queenslandiae	1	1	1
Heteromyias albispecularis	1	1	1
Hirundapus caudacutus	1	1	1
Hypsiprymnodon moschatus	1	1	1

Lalage leucomela	1	1	1
Lampropholis coggeri	1	1	1
Limnodynastes peronii	1	1	1
Litoria infrafrenata	6	2	3.595031
Litoria jungguy	6	2	3.586926
Litoria nannotis	1	1	1
Litoria rheocola	1	1	1
Litoria serrata	6	2	3.586926
Litoria xanthomera	6	2	3.586926
Lopholaimus antarcticus	1	1	1
Lophorina victoriae	1	1	1
Machaerirhynchus flaviventer	1	1	1
Macropygia amboinensis	1	1	1
Macropygia phasianella	1	1	1
Malurus amabilis	1	1	1
Megapodius reinwardt	1	1	1
Melloria quoyi	13	2	9.296339
Melomys cervinipes	1	1	1
Mixophyes carbinensis	1	1	1
Mixophyes coggeri	1	1	1
Mixophyes schevilli	1	1	1
Monarcha melanopsis	1	1	1
Neochmia temporalis	1	1	1
Nyctimene robinsoni	1	1	1
Oriolus flavocinctus	1	1	1
Orthonyx spaldingii	1	1	1
Pachycephala pectoralis	1	1	1
Pachycephala simplex	13	2	9.294761
Perameles pallescens	1	1	1
Platycercus elegans	1	1	1
Poecilodryas superciliosa	1	1	1
Pogonomys mollipilosus	1	1	1
Pseudechis porphyriacus	2	2	2
Pseudochirops archeri	1	1	1
Pseudochirulus cinereus	1	1	1
Pseudochirulus herbertensis	1	1	1
Psophodes olivaceus	1	1	1
Pteropus conspicillatus	1	1	1
Ptilinopus magnificus	1	1	1
Ptilinopus regina	1	1	1
Ptilinopus superbus	1	1	1

Rallina tricolor	1	1	1
Rattus fuscipes	1	1	1
Rattus leucopus	1	1	1
Rhipidura fuliginosa	1	1	1
Rhipidura rufifrons	1	1	1
Saproscincus basiliscus	1	1	1
Saproscincus tetradactylus	1	1	1
Scythrops novaehollandiae	1	1	1
Sphecotheres vieilloti	1	1	1
Stegonotus cucullatus	7	2	5.971739
Strepera graculina	1	1	1
Symposiachrus trivirgatus	1	1	1
Thylogale stigmatica	1	1	1
Tregellasia capito	1	1	1
Trichoglossus chlorolepidotus	1	1	1
Trichoglossus moluccanus	1	1	1
Trichosurus vulpecula	1	1	1
Uromys caudimaculatus	1	1	1
Zoothera heinei	1	1	1
Zosterops lateralis	1	1	1
Ninox rufa	11	2	8.6134
Ninox boobook	11	2	8.613988
Varanus scalaris	8	2	6.436589
Morelia amethistina	2	2	2
Tanysiptera sylvia	10	2	7.602825
Ceyx azureus	7	2	5.972337

Table 5. Degree (including in and out), closeness, and betweenness centrality for each vertebrate species in the lowland network.

Species	**Degree centrality**	**In-degree**	**Out-degree**	**Closeness centrality**	**Betweenness centrality**
Accipiter novaehollandiae	14	12	2	0.003268	3
Alectura lathami	4	0	4	0.00346	0
Alisterus scapularis	2	0	2	0.002732	0
Antechinus flavipes	20	18	2	0.003704	64
Aplonis metallica	7	0	7	0.003597	0
Arses kaupi	5	0	5	0.003195	0
Artamus leucorynchus	5	0	5	0.003195	0
Austrochaperina fryi	5	0	5	0.003663	0
Austrochaperina pluvialis	5	0	5	0.003663	0

Austrochaperina robusta	13	8	5	0.003876	0.714286
Aviceda subcristata	21	19	2	0.00346	12
Boiga irregularis	32	29	3	0.004464	52.04762
Rhinella marina	23	7	16	0.004292	14
Cacatua galerita	1	0	1	0.002278	0
Cacomantis castaneiventris	1	0	1	0.003155	0
Cacomantis flabelliformis	1	0	1	0.003155	0
Cacomantis variolosus	1	0	1	0.003155	0
Carlia rubrigularis	4	0	4	0.00266	0
Carternornis leucotis	5	0	5	0.003195	0
Cercartetus caudatus	2	0	2	0.002551	0
Ceyx azureus	11	11	0	0.003049	0
Chalcites lucidus	1	0	1	0.003155	0
Chrysococcyx minutillus	1	0	1	0.003155	0
Coeranoscincus frontalis	1	0	1	0.002618	0
Colluricincla boweri	39	34	5	0.004098	0.75
Colluricincla megarhyncha	39	34	5	0.004098	0.75
Columba leucomela	3	0	3	0.002793	0
Cophixalus aenigma	5	0	5	0.003663	0
Cophixalus exiguus	5	0	5	0.003663	0
Cophixalus infacetus	5	0	5	0.003663	0
Cophixalus ornatus	5	0	5	0.003663	0
Coracina lineata	5	0	5	0.003195	0
Cyclodomorphus gerrardii	1	0	1	0.002618	0
Cyclopsitta diophthalma	2	0	2	0.002732	0
Dactylopsila trivirgata	2	0	2	0.002551	0
Demansia psammophis	8	6	2	0.003268	6
Dendrelaphis calligastra	26	22	4	0.003584	12.33333
Dendrelaphis punctulatus	26	22	4	0.003584	12.33333
Dendrolagus bennettianus	2	0	2	0.002551	0
Dendrolagus lumholtzi	2	0	2	0.002551	0
Dicaeum hirundinaceum	7	0	7	0.003731	0
Dicrurus bracteatus	69	64	5	0.00495	144.75
Edolisoma tenuirostre	5	0	5	0.003195	0
Erythrura trichroa	11	0	11	0.003817	0
Eudynamys scolopacea	1	0	1	0.003155	0
Eulamprus quoyii	2	1	1	0.003012	0
Glaphyromorphus fuscicaudis	2	1	1	0.003012	0
Gnypetoscincus queenslandiae	1	0	1	0.002618	0
Heteromyias albispecularis	5	0	5	0.003195	0

Hirundapus caudacutus	1	0	1	0.003155	0
Hypsiprymnodon moschatus	2	0	2	0.002551	0
Lalage leucomela	5	0	5	0.003195	0
Lampropholis coggeri	4	0	4	0.00266	0
Limnodynastes peronii	15	0	15	0.00369	0
Litoria infrafrenata	25	8	17	0.004386	8.714286
Litoria jungguy	24	8	16	0.004367	2.714286
Litoria nannotis	16	0	16	0.004329	0
Litoria rheocola	16	0	16	0.004329	0
Litoria serrata	24	8	16	0.004367	2.714286
Litoria xanthomera	24	8	16	0.004367	2.714286
Lopholaimus antarcticus	1	0	1	0.002375	0
Lophorina victoriae	5	0	5	0.003195	0
Machaerirhynchus flaviventer	5	0	5	0.003195	0
Macropygia amboinensis	3	0	3	0.002793	0
Macropygia phasianella	3	0	3	0.002793	0
Malurus amabilis	1	0	1	0.003155	0
Megapodius reinwardt	4	0	4	0.00346	0
Melloria quoyi	36	31	5	0.004049	0
Melomys cervinipes	5	0	5	0.003676	0
Mixophyes carbinensis	5	0	5	0.003413	0
Mixophyes coggeri	5	0	5	0.003413	0
Mixophyes schevilli	5	0	5	0.003413	0
Monarcha melanopsis	5	0	5	0.003195	0
Morelia amethistina	7	7	0	0.003086	0
Neochmia temporalis	11	0	11	0.003817	0
Ninox boobook	19	19	0	0.003559	0
Ninox rufa	20	20	0	0.003584	0
Nyctimene robinsoni	2	0	2	0.003333	0
Oriolus flavocinctus	5	0	5	0.003195	0
Orthonyx spaldingii	5	0	5	0.003195	0
Pachycephala pectoralis	5	0	5	0.003195	0
Pachycephala simplex	39	34	5	0.004098	0.75
Perameles pallescens	1	0	1	0.002538	0
Platycercus elegans	2	0	2	0.002732	0
Poecilodryas superciliosa	5	0	5	0.003195	0
Pogonomys mollipilosus	5	0	5	0.003676	0
Pseudechis porphyriacus	7	5	2	0.002924	6
Pseudochirops archeri	2	0	2	0.002551	0
Pseudochirulus cinereus	2	0	2	0.002551	0
Pseudochirulus herbertensis	2	0	2	0.002551	0

Psophodes olivaceus	5	0	5	0.003195	0
Pteropus conspicillatus	2	0	2	0.003333	0
Ptilinopus magnificus	2	0	2	0.0025	0
Ptilinopus regina	3	0	3	0.002793	0
Ptilinopus superbus	3	0	3	0.002793	0
Rallina tricolor	1	0	1	0.002597	0
Rattus fuscipes	8	0	8	0.003717	0
Rattus leucopus	8	0	8	0.003717	0
Rhipidura fuliginosa	5	0	5	0.003195	0
Rhipidura rufifrons	5	0	5	0.003195	0
Saproscincus basiliscus	4	0	4	0.00266	0
Saproscincus tetradactylus	4	0	4	0.00266	0
Scythrops novaehollandiae	1	0	1	0.003155	0
Sphecotheres vieilloti	5	0	5	0.003195	0
Stegonotus cucullatus	18	15	3	0.004098	7.714286
Strepera graculina	5	0	5	0.003195	0
Symposiachrus trivirgatus	5	0	5	0.003195	0
Tanysiptera sylvia	24	24	0	0.003745	0
Thylogale stigmatica	2	0	2	0.002551	0
Tregellasia capito	5	0	5	0.003195	0
Trichoglossus chlorolepidotus	2	0	2	0.002732	0
Trichoglossus moluccanus	2	0	2	0.002732	0
Trichosurus vulpecula	2	0	2	0.002551	0
Uromys caudimaculatus	5	0	5	0.003676	0
Varanus scalaris	36	36	0	0.003922	0
Zoothera heinei	13	0	13	0.004525	0
Zosterops lateralis	6	0	6	0.003521	0

Table 6. Degree (including in and out), closeness, and betweenness centrality for each vertebrate species in the highland network.

Species	**Degree centrality**	**In-Degree**	**Out-degree**	**Closeness centrality**	**Betweenness centrality**
Accipiter novaehollandiae	15	13	2	0.002967	3
Alectura lathami	4	0	4	0.003205	0
Alisterus scapularis	2	0	2	0.002538	0
Antechinus adustus	22	20	2	0.003484	26.66667
Antechinus flavipes	22	20	2	0.003484	26.66667
Antechinus godmani	22	20	2	0.003484	26.66667
Aplonis metallica	7	0	7	0.003205	0
Arses kaupi	5	0	5	0.002874	0

Artamus leucorynchus	5	0	5	0.002874	0
Austrochaperina fryi	5	0	5	0.0033	0
Austrochaperina pluvialis	5	0	5	0.0033	0
Austrochaperina robusta	13	8	5	0.003497	0.625
Aviceda subcristata	22	20	2	0.003175	12
Boiga irregularis	40	35	5	0.004167	86.35833
Rhinella marina	28	7	21	0.003968	21
Cacatua galerita	1	0	1	0.002079	0
Cacomantis flabelliformis	1	0	1	0.002841	0
Cacomantis variolosus	1	0	1	0.002841	0
Carlia rubrigularis	5	0	5	0.002513	0
Carternornis leucotis	5	0	5	0.002874	0
Cercartetus caudatus	2	0	2	0.002358	0
Ceyx azureus	13	13	0	0.002825	0
Chalcites lucidus	1	0	1	0.002841	0
Chrysococcyx minutillus	1	0	1	0.002841	0
Coeranoscincus frontalis	1	0	1	0.002445	0
Colluricincla boweri	39	34	5	0.00365	0.75
Colluricincla megarhyncha	39	34	5	0.00365	0.75
Columba leucomela	3	0	3	0.002591	0
Cophixalus aenigma	5	0	5	0.0033	0
Cophixalus australis	13	8	5	0.003497	0.625
Cophixalus concinnus	5	0	5	0.0033	0
Cophixalus hosmeri	5	0	5	0.0033	0
Cophixalus infacetus	5	0	5	0.0033	0
Cophixalus monticola	5	0	5	0.0033	0
Cophixalus neglectus	5	0	5	0.0033	0
Cophixalus ornatus	5	0	5	0.0033	0
Coracina lineata	5	0	5	0.002874	0
Cyclodomorphus gerrardii	1	0	1	0.002445	0
Cyclopsitta diophthalma	2	0	2	0.002538	0
Dactylopsila trivirgata	2	0	2	0.002358	0
Demansia psammophis	12	8	4	0.003067	10
Dendrelaphis calligastra	33	27	6	0.003413	25.73333
Dendrelaphis punctulatus	33	27	6	0.003413	25.73333
Dendrolagus bennettianus	2	0	2	0.002358	0
Dendrolagus lumholtzi	2	0	2	0.002358	0
Dicaeum hirundinaceum	7	0	7	0.003356	0
Dicrurus bracteatus	71	66	5	0.004425	156.75
Edolisoma tenuirostre	5	0	5	0.002874	0
Erythrura trichroa	12	0	12	0.003521	0
Eudynamys scolopacea	1	0	1	0.002841	0

Eulamprus quoyii	2	1	1	0.002793	0
Glaphyromorphus fuscicaudis	2	1	1	0.002793	0
Glaphyromorphus mjobergi	2	1	1	0.002793	0
Gnypetoscincus queenslandiae	1	0	1	0.002445	0
Hemiaspis signata	19	15	4	0.003195	12.4
Hemibelideus lemuroides	2	0	2	0.002358	0
Heteromyias albispecularis	5	0	5	0.002874	0
Hirundapus caudacutus	1	0	1	0.002841	0
Hypsiprymnodon moschatus	2	0	2	0.002358	0
Lalage leucomela	5	0	5	0.002874	0
Lampropholis coggeri	5	0	5	0.002513	0
Lampropholis robertsi	5	0	5	0.002513	0
Limnodynastes peronii	19	0	19	0.003472	0
Litoria infrafrenata	30	8	22	0.004049	9.375
Litoria jungguy	29	8	21	0.004032	3.375
Litoria nannotis	21	0	21	0.004	0
Litoria rheocola	21	0	21	0.004	0
Litoria serrata	29	8	21	0.004032	3.375
Litoria xanthomera	29	8	21	0.004032	3.375
Lopholaimus antarcticus	1	0	1	0.00216	0
Lophorina victoriae	5	0	5	0.002874	0
Machaerirhynchus flaviventer	5	0	5	0.002874	0
Macropygia amboinensis	3	0	3	0.002591	0
Macropygia phasianella	3	0	3	0.002591	0
Megapodius reinwardt	4	0	4	0.003205	0
Melloria quoyi	36	31	5	0.00361	0
Melomys cervinipes	5	0	5	0.003356	0
Mixophyes carbinensis	7	0	7	0.003175	0
Mixophyes coggeri	7	0	7	0.003175	0
Mixophyes schevilli	7	0	7	0.003175	0
Monarcha melanopsis	5	0	5	0.002874	0
Morelia amethistina	8	8	0	0.002817	0
Neochmia temporalis	12	0	12	0.003521	0
Ninox boobook	24	24	0	0.003311	0
Ninox rufa	25	25	0	0.003333	0
Nyctimene robinsoni	2	0	2	0.002985	0
Oriolus flavocinctus	5	0	5	0.002874	0
Orthonyx spaldingii	5	0	5	0.002874	0
Pachycephala pectoralis	5	0	5	0.002874	0

Pachycephala simplex	39	34	5	0.00365	0.75
Perameles pallescens	1	0	1	0.002347	0
Platycercus elegans	2	0	2	0.002538	0
Pogonomys mollipilosus	5	0	5	0.003356	0
Pseudechis porphyriacus	11	7	4	0.002786	10
Pseudochirops archeri	2	0	2	0.002358	0
Pseudochirulus cinereus	2	0	2	0.002358	0
Pseudochirulus herbertensis	2	0	2	0.002358	0
Psophodes olivaceus	5	0	5	0.002874	0
Pteropus conspicillatus	2	0	2	0.002985	0
Ptilinopus magnificus	2	0	2	0.002288	0
Ptilinopus regina	3	0	3	0.002591	0
Ptilinopus superbus	3	0	3	0.002591	0
Rallina tricolor	3	0	3	0.002445	0
Rattus fuscipes	8	0	8	0.00339	0
Rattus leucopus	8	0	8	0.00339	0
Rhipidura fuliginosa	5	0	5	0.002874	0
Rhipidura rufifrons	5	0	5	0.002874	0
Saproscincus basiliscus	5	0	5	0.002513	0
Saproscincus czechurai	5	0	5	0.002513	0
Saproscincus tetradactylus	5	0	5	0.002513	0
Scythrops novaehollandiae	1	0	1	0.002841	0
Sminthopsis leucopus	2	0	2	0.002358	0
Sphecotheres vieilloti	5	0	5	0.002874	0
Stegonotus cucullatus	20	15	5	0.003759	13.025
Strepera graculina	5	0	5	0.002874	0
Symposiachrus trivirgatus	5	0	5	0.002874	0
Tanysiptera sylvia	29	29	0	0.003534	0
Taudactylus rheophilus	14	7	7	0.003311	0
Thylogale stigmatica	2	0	2	0.002358	0
Tregellasia capito	5	0	5	0.002874	0
Trichoglossus chlorolepidotus	2	0	2	0.002538	0
Trichoglossus moluccanus	2	0	2	0.002538	0
Trichosurus vulpecula	2	0	2	0.002358	0
Uromys caudimaculatus	5	0	5	0.003356	0
Varanus scalaris	42	42	0	0.003676	0
Zoothera heinei	13	0	13	0.004115	0
Zoothera lunulata	13	0	13	0.004115	0
Zosterops lateralis	6	0	6	0.003145	0

Chapter 4

Evaluating vertebrate extinction risks from bottom-up cascades

Abstract

Humans have driven most extinctions over the past century and remain a primary threat to biodiversity. While the direct impacts of threats including climate change and habitat loss have been well-studied, the cascading effects of extinctions derived from these threats on ecological communities, particularly bottom-up trophic cascades, are less understood. This knowledge gap highlights a need for more research on these complex interactions and their implications for biodiversity management in terrestrial ecosystems. Capturing and modelling cascades is essential for predicting extinction risks in the Wet Tropics vertebrate communities. To quantify the mechanisms of bottom-up cascades and how they can affect the extinction vulnerability of terrestrial communities, this study used low- and high-elevation vertebrate network models constructed in Chapter 3 for the Australian Wet Tropics, combined with estimates for plants and invertebrates as basal resources. Using these models to assess the impact of primary and secondary extinctions across different extinction scenarios simulated over varying background extinction rates, the results reveal increased vertebrate extinctions with the removal of basal resources, particularly in the highland network. This increase is associated with a higher proportion of secondary extinctions, with magnitude of the effect contingent on assumed coextinction thresholds assumed per species and number of basal resources removed. The resilience of vertebrate communities to extinctions differed between low- and high-elevation communities, with different taxonomic classes showing disparate vulnerabilities to primary and secondary extinctions. This study highlights the important role bottom-up trophic cascades can play in influencing the extinction dynamics in complex terrestrial ecosystems, underscoring the importance of incorporating basal resource interactions in trophic network models when evaluating extinction risks and their essential role in modulating community resilience. This study also underlines the importance of identifying basal resource loss to mitigate possible extinction tipping points within communities, particularly as future environmental conditions

become more extreme. This study also emphasises the need to evaluate how interdependencies with basal species potentially affect extinction risk in threat assessments.

Introduction

Humans have been responsible for most vertebrate extinctions over the past century (e.g., Ceballos et al., 2015) and remain the greatest threat to biodiversity today (Shukla et al., 2019). To reveal and quantify both the mechanisms for and vulnerability to extinction, research has often focused on the direct impacts of humans and human-caused environmental change, such as inferring species vulnerability (*i*) to climate change by comparing species' thermal tolerance limits to predicted shifts in temperature (Khaliq et al., 2014; Yuan et al., 2016) and/or (*ii*) to habitat loss by examining the minimum area of suitable habitat a species requires (Ducatez & Shine, 2017; Gonçalves-Souza et al., 2020). These direct impacts can lead to broader consequences within ecological communities, potentially triggering coextinctions or extinction cascades. However, we know very little about species' coextinction risk (Strona, 2022).

Although the proportion of extinctions attributable to cascading effects remains uncertain, many past and future extinctions result from such cascades (Kehoe et al., 2021; Ripple & Van Valkenburgh, 2010). Coextinctions arise from ecological dependencies, meaning that when a species loses others on which it depends, it too can go extinct. Such dependencies include plants and their pollinators, plants and their seed dispersers, and predators and their prey relationships. Of these, trophic dependencies appear to be one of the primary mechanisms, having been implicated in ancient extinction events (e.g., Llewelyn et al., 2022; Pires et al., 2015; Pires et al., 2020). Trophic extinction cascades can be 'bottom-up', where the loss of lower-trophic levels triggers extinctions in higher tropic levels (Hunter & Price, 1992). Or, they can be 'top-down', where the loss of a predator alters competition and survival in lower trophic levels (Feit et al., 2020). Irrespective of the pathways, extinction cascades can alter the composition and structure of entire communities (Culot et al., 2013), making it necessary to prevent such cascades to preserve biodiversity. Unfortunately, identifying how extinction cascades unfold is challenging because of the complexity inherent in the webs of dependencies through which they operate.

Because the web of species dependencies within ecological communities is complex, it is also challenging to elucidate what species have the highest risk of extinction. For terrestrial vertebrates, species have diverse ecological characteristics and evolutionary backgrounds, and so are likely to have different risks of extinction. For instance, diet-breadth and type predict extinction risk in vertebrates, with species in higher trophic levels (Cardillo et al., 2004; Purvis, Gittleman, et al., 2000) or with lower trophic flexibility (Purvis, Jones, et al., 2000) tending to be more vulnerable to extinction. Moreover, different vertebrate taxonomic classes vary in their susceptibility to extinction across drivers (Chichorro et al., 2019). However, primary extinction risk is not likely to reflect risk to secondary extinction. Risk-assessment systems like the IUCN Red List use criteria such as geographic range, population size, and trends (IUCN, 2023), and relate risk to direct effects without explicitly considering their indirect effects. As such, it remains unclear how well such risk assessments highlight direct and indirect determinants of extinction risk.

To understand and predict extinction cascades and their effects on extinction risks, ecological network models can be informative (Schleuning et al., 2016). Although the underlying mechanism of coextinctions posits that resource scarcity culminates in the extinction of dependent consumer species (Colwell et al., 2012; Strona & Bradshaw, 2018; Strona & Bradshaw, 2022), few empirically based ecological network models have evaluated the effects of bottom-up cascades on extinction risks in terrestrial ecosystems (Dorresteijn et al., 2015; Kagata et al., 2005; Scherber et al., 2010). Trophic models evaluating extinction risks in terrestrial communities have instead focused on primary predator extinctions (Cardillo et al., 2005; Fritz et al., 2009) and top-down effects (Borrvall et al., 2000; Ebenman et al., 2004). This research bias could stem from the disproportionate impact of humans on larger body-sized, top predators (Ripple et al., 2017), among other factors (see Chapter 1). This dearth of research examining bottom-up effects limits our understanding and capacity to manage biodiversity (Nicholson et al., 2012). However, it is possible to research these mechanisms by constructing network models based on real-world communities (see Chapters 2 & 3) to investigate risks associated with both primary and secondary mechanisms.

Basal resources such as plants and invertebrates are often excluded in trophic models, obscuring how bottom-up cascades operate in these ecosystems (Roopnarine et al., 2007) (see Chapter 1 for details). The main reason for omitting basal resources is likely due to a lack of data, with research traditionally focussing more on vertebrates (Di Marco et al., 2017).

Research in Australia exemplifies this bias, where researchers assume that approximately 30.8% of invertebrates and 91.7% of plants have been described, compared to 95.5% of all tetrapods (Chapman, 2009).

This limited understanding of how basal resources in terrestrial ecosystems interact trophically, and their influences on extinction risk, also holds true for the tropical rain forest communities of the Australian Wet Tropics bioregion. For example, despite intensive field surveys over the last few decades across some subregions in this area (Yeates & Monteith, 2008) showing high diversity and spatial variation of mainly insects (Connolly et al., 2008; Pearson et al., 2015; Staunton et al., 2016; Wilson et al., 2007), few data exist describing complete invertebrate assemblages. Similarly, there is comparatively little data on the plant communities in the bioregion. While there are 16 main rain forest vegetation types (e.g., mesophyll vine forest) that vary spatially (Webb, 1978), and documenting thousands of endemic and invasive plant species (avh.chah.org.au), there is still no comprehensive list of plant species in this bioregion. These gaps mean how these food resources affect vertebrate communities remains largely unknown (Metcalfe & Ford, 2008).

Many vertebrates in the Wet Tropics are also mainly invertivores, with some dependence on plants (Williams et al., 2010). The loss of such basal resources can destabilise entire ecosystems through trophic cascades and coextinctions (e.g., Eklöf & Ebenman, 2006). For example, when primary producers go extinct, species at higher trophic levels lose their food sources, and this can increase extinction rates (Estes et al., 2011). However, the resilience of communities to trophic cascades can depend on the specificity and sensitivity of species to the loss of their prey (e.g., Bellingeri et al., 2013). The dependence of vertebrates at lower trophic levels on these basal resources in the Wet Tropics could mean that the communities there are sensitive to changes in food availability (e.g., Llewelyn et al., 2022). With mounting global declines in invertebrate populations, we need better insights into their role in stabilising ecosystems (Van Klink et al., 2020).

In this chapter, I attribute plant and invertebrate basal trophic links to both low- and high-elevation vertebrate networks constructed in Chapter 3 and evaluate the role of bottom-up cascades in how they can affect extinction risks in these communities. I aim to determine if including basal resources is warranted when evaluating the extinction risk of vertebrate communities in this region. Specifically, I address three main questions: (*i*) How does coextinction threshold and number of basal resources removed in simulations affect the number of total primary and secondary vertebrate extinctions? (*ii*) How does the coextinction threshold and number of basal resources removed in simulations affect the number of total primary and secondary vertebrate extinctions? (*iii*) And, what vertebrates are the most and the least vulnerable to extinction across each scenario simulated?

I hypothesise that the lower the coextinction threshold and the greater the removal rate of basal resources, the more secondary extinctions will occur compared to primary extinctions. I also hypothesise that I can identify vertebrate communities' collapse, influenced by basal resource assumptions (i.e., the probability each vertebrate community reaches an extinction tipping point and collapses, escalating as more basal resources become extinct). I further hypothesise that different vertebrate taxonomic classes have different vulnerabilities to secondary extinction across scenarios. I moreover identify which threatened species are more prone to primary than secondary extinction.

Methods

I built trophic network models of low- and high-elevation communities in the Wet Tropics and assessed their resilience to extinction cascades by running *in silico* extinction simulations. The network vertebrate models are based on the ones in Chapter 3, but also included inferred plant and invertebrate assemblages. Adding these basal components help capturing secondary extinctions (defined by vertebrates that went coextinct due to loss of food resources) triggered by primary extinctions (defined by vertebrates that went extinct from background rates) among basal resources and the vertebrate communities.

To assess the vulnerability of both communities to secondary extinctions, I did various *in silico* simulations using the *DeepThought* High Performance Computing facility (Flinders University, 2021). I considered three extinction scenarios based on conservative or highly conservative background extinction rates for vertebrates, plants, and invertebrates for pre-Anthropocene, modern, and predicted future periods. I also divided each scenario into four sub-scenarios, where I removed 0%, 25%, 50%, or 75% of basal resource nodes consumed by vertebrates in each network. I also evaluated varying coextinction thresholds (≥ the percentage of resources extinct before a consumer goes coextinct). Including plants and invertebrates and simulating different extinction scenarios allows for a comprehensive assessment of how the loss of these resources triggers more extinctions among vertebrates. This approach determines whether assumptions about basal resources influence the likelihood of vertebrate community collapse, how different coextinction thresholds affect extinction risk, and its effect on the extinction risk of different vertebrate species.

Estimating invertebrate and plant species diversity

I used global diversity estimates of vertebrates, terrestrial and freshwater invertebrates, and terrestrial and freshwater plants (Grosberg et al. 2012) to calculate the relative species diversity of these groups (mean = 281 terrestrial invertebrate species, 4.91 freshwater invertebrates, 0.12 freshwater plants, and 11.2 terrestrial plants per vertebrate species). Based on these ratios, I estimated invertebrate and plant diversity for the low- and high-elevation vertebrate networks built in Chapter 3 (lowland network: 149 vertebrates and ~ 732 freshwater invertebrates, 41,869 terrestrial invertebrates, 18 freshwater plants, and 1,669 terrestrial plants; highland network: 159 vertebrates and ~ 781 freshwater invertebrates, 44,679 terrestrial invertebrates, 19 freshwater plants, and 1,781 terrestrial plants).

Estimating diet breadths and adding links to invertebrates and plants

To identify which Wet Tropics vertebrates consumed plants and invertebrates, and therefore, which species needed trophic links to these components, I compiled a comprehensive list of dietary information from two primary sources: (1) Australian Wet Tropic vertebrate trait database (Williams et al., 2010) and (2) the Elton traits database (V1.0, Wilman et al., 2014). These sources indicated the approximate proportion of each species' diet composed of plants and invertebrates, but did not indicate diet breadths (i.e., number of trophic links). I obtained additional data on the diet breadth of a diverse range of vertebrate species found in various regions, including herbivores, insectivores, and omnivores, from peer-reviewed journal articles (e.g., Llewelyn et al., 2022) (see Appendix Tables 1 and 2).

I then used the diet breadth data to calculate kernel density estimates for each diet type (herbivore, invertivore, and omnivore) using the `kdensity` R package (Moss & Tveten, 2018). I assigned these diet breadths to invertebrate and plant-consuming vertebrates in the networks by sampling from these distributions, limiting the sampled breadths to a realistic range: from 1 to the maximum diet breadth (+ 10%) to account for the possibility of some species having diet breadths not captured or underrepresented in the dataset. I repeated this process separately for invertivore, herbivore, and omnivore vertebrates. To avoid overestimating diet breadths, I adjusted the assigned diet breadths of omnivores because they feed from multiple food groups. Here, I assigned the omnivore diet breadth data into proportions using the percentage of their diet consisting of plant, invertebrate, and vertebrate resources, and multiplied by the respective diet breadth by that proportion. For example, if a species diet was 10% plants and 90% invertebrates, its assigned plant diet breadth was multiplied by 0.1 and its assigned invertebrate diet breadth by 0.9. This process accounted for the proportion of vertebrates eaten by other vertebrates as omnivores or carnivores to prevent overestimating diet breadth for these species. Guided by these assigned diet breadths, I added trophic links between vertebrates and random nodes to the pool of plants and invertebrates estimated for each network. I added plants and invertebrates to the networks as individual species nodes because this was more ecologically realistic and did not alter network structure compared to other methods (e.g., as single ‘super’ nodes; see Appendix Figure A1 and associated methods for more detail). As for carnivores, using random forest to assign trophic links in Chapter 3 did not change the number of links compared to what sampling from the diet breadth distribution would have assigned for this group (see Appendix Figure A2). I then converted the resulting pairwise trophic interactions into adjacency matrices (one for low- and high-elevation networks) and combined them with the vertebrate predator-prey trophic interactions identified in Chapter 3 for each community (Figures 1 and 2).

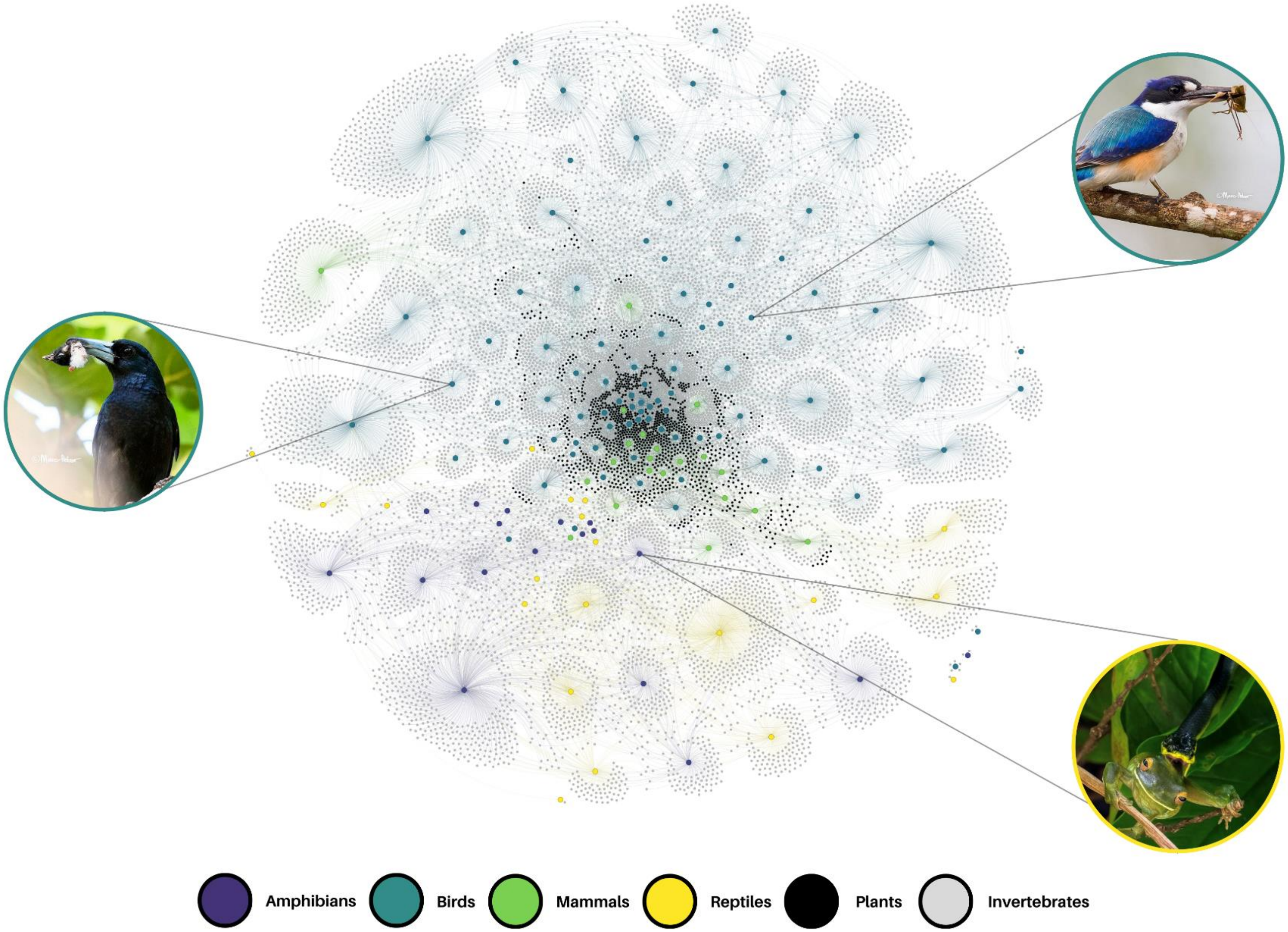

Figure 1. A two-dimensional depiction of the lowland network, illustrating directed trophic interactions (coloured lines) between vertebrates, plants, and invertebrates (coloured circles).

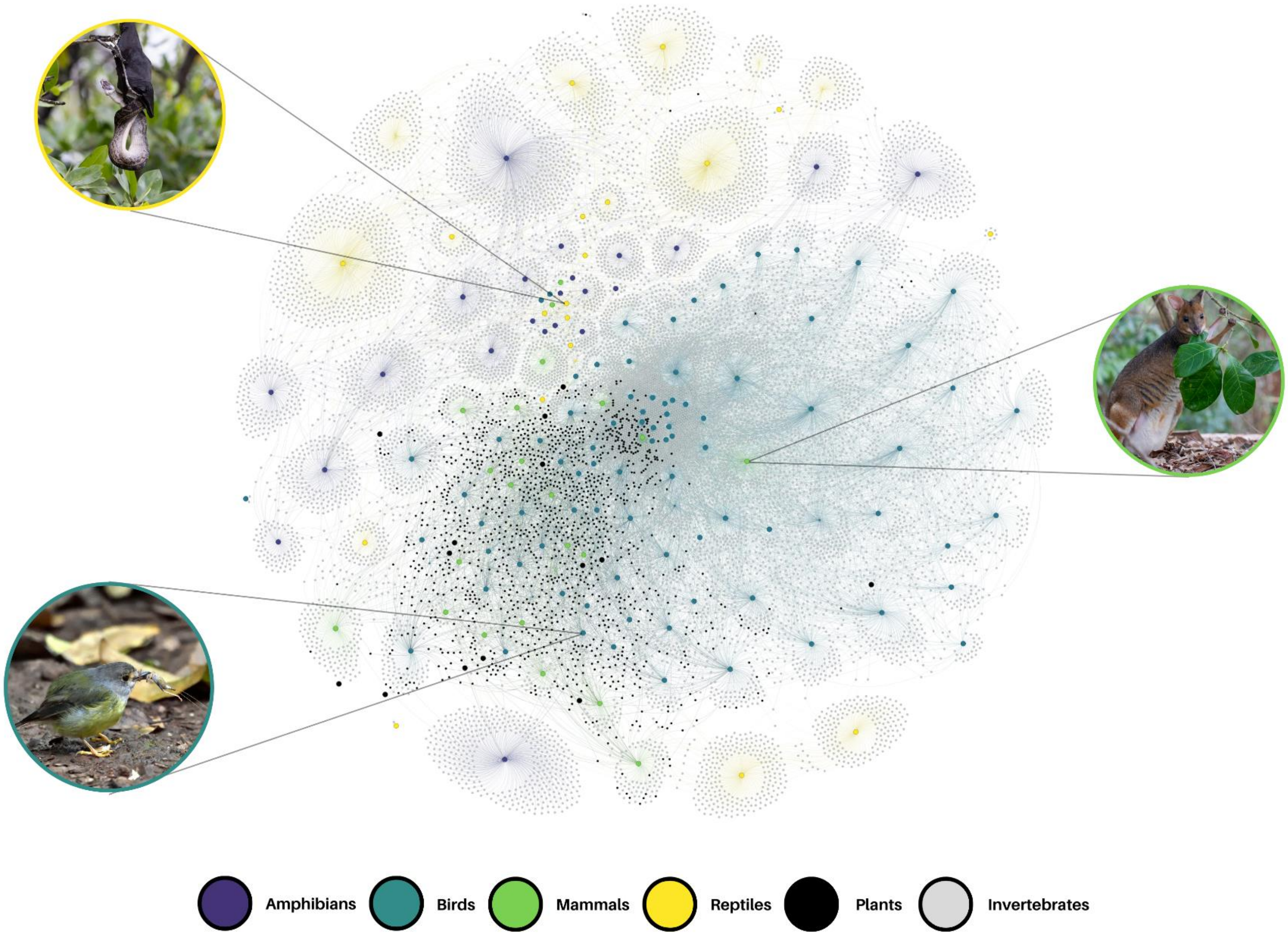

Figure 2. A two-dimensional depiction of the highland network, illustrating directed trophic interactions (coloured lines) between vertebrates, plants, and invertebrates (coloured circles).

Extinction simulations: network resilience to basal resource removal

To test the vulnerability of the low- and high-elevation communities to secondary extinctions, I ran different *in silico* extinction simulations to represent various extinction scenarios. To achieve this, three main simulations were assigned, whereby I set the background extinction rate for vertebrates, plants, and invertebrates according to either a conservative or highly conservative (1) pre-Anthropocene, (2) modern, and (3) predicted future extinction rate, which quantifies species primary and secondary extinctions (E) per 10,000 species per 100 years (MSY) (E/MSY).

For non-mammalian vertebrates, plants, and invertebrates, I set the pre-Anthropocene extinction rates between 0.1–1 $\mathrm{E/MSY}$ (extinctions per million species years) (Ceballos et al., 2015) due to a lack of data available to treat each taxonomic group's extinction risk differently, while I assigned mammals a pre-Anthropocene extinction rate of 2 $\mathrm{E/MSY}$ (Barnosky et al., 2011) in this scenario. For each iteration of the simulation, I sampled values randomly from this $\mathrm{E/MSY}$ range using a uniform distribution for species belonging to these groups, respectively. I applied these pre-Anthropocene extinction rates to the same contemporary communities used in all simulations; I did not add or reconstruct extinct species. Thus, the extinction rates define a lower-extinction baseline for the extant species pool, rather than a reconstruction of past communities. For modern extinction rates, I sampled amphibian rates randomly between 10 $\mathrm{E/MSY}$ and 107 $\mathrm{E/MSY}$ following lower (McCallum, 2007) and upper rates (Pimm et al., 2014) published, while I sampled mammal and bird rates from 72–243 $\mathrm{E/MSY}$ and 49-132 $\mathrm{E/MSY}$, respectively (Pimm et al., 2014). Due to a lack of available information on reptile extinction rates, I used a rate of 16–200 $\mathrm{E/MSY}$ (Ceballos et al., 2015), which encompasses those of the other tetrapod classes. For plants, I sampled the extinction rates from 60–171 $\mathrm{E/MSY}$ (Humphreys et al., 2019), and from 150–260 $\mathrm{E/MSY}$ for invertebrates (Cowie et al., 2022). I based future extinction rates on the aforementioned extinction rates for each vertebrate group, plus 42%: the highest expected mean diversity loss (primary extinctions only) for Australasia projected to the year 2100 under the worst-case climate change scenario (SSP5-8.5) (Strona & Bradshaw, 2022). I also used this future extinction rate for invertebrates (modern rate + 42%), because there was not enough distribution or population trend data for this group to infer future extinction rates under varying future climate-projected scenarios. The high extinction rate for invertebrates was justified based on the growing evidence of invertebrate populations declining globally (Cardoso et al., 2020; Van Klink et al., 2020). As for plants, I randomly sampled future extinction rates between 290 and 589 $\mathrm{E/MSY}$ following the lower and upper global estimates quantified under varying climate-change projections (van Vuuren et al., 2006).

For each extinction scenario (pre-Anthropocene, modern, and future), I further divided the simulations into four scenarios, removing either 0%, 25%, 50%, or 75% of basal resource nodes linked to (i.e., eaten by) vertebrate nodes. The number of basal resources removed reflects extreme scenarios to help observe apparent differences in vertebrate extinction rates beyond the background extinction rate when comparing each tested scenario. In the null scenario where I removed 0% of basal resources, I evaluated how removing basal nodes affects the extinction rates of the vertebrates in each network beyond that of the specific simulated background extinction rate. I also evaluated the effect of varying the coextinction threshold in each scenario (1% to 100% at 1% increments for each vertebrate species).

I used a simulation time and removal period of 50,000 years, tested across 10,000 replicates for each coextinction threshold. I assumed this time scale was an appropriate balance between computation efficiency and the ability to ensure that the background extinction rates were neither too small to quantify nor too uncertain to provide meaningful ranges for the outcomes. In each iteration, the model simulated the expected number of extinctions under this rate for all species over the specified time using a Poisson distribution separately for vertebrate species, and then for all plant and invertebrate species combined, with a mean equal to the expected number of extinctions based on the assumed background extinction rate simulated. I attributed the vulnerability of vertebrates to primary extinction randomly across nodes according to the expected number of extinctions calculated for vertebrates. I also made plant and invertebrate nodes go randomly extinct based on the expected number of extinctions from the background extinction rate with the same parameters.

In each network model and at each time step, I removed basal resources. This process included removing nodes according to simulated natural extinction rates, in addition to a manual percentage of nodes removed. Following these removals, I calculated the percentage of outgoing trophic links (i.e., links to food resources) for each vertebrate node. If a species lost more food resources than the predetermined coextinction threshold (i.e., the maximum number of food links that species could lose before triggering coextinction), I categorised it as extinct. I then calculated the sum of vertebrate nodes lost in each scenario as the percentage of vertebrates made extinct in each iteration.

Across all scenarios simulated, I analysed the proportion of primary extinctions versus secondary extinctions for each coextinction threshold. Next, I further identified vertebrate taxonomic classes vulnerable to both primary and secondary extinctions across all scenarios of basal resource removal and background extinction rates combined for low- and high-elevation networks separately. I then combined species' conservation status (IUCN, 2023) with data from the Queensland Nature Conservation Act 1992 and its Nature Conservation (Wildlife) Regulation 2006 (last updated 7 March 2023) (accessed 26 October 2023) by the Queensland Government (apps.des.qld.gov.au/data-sets/wildlife/wildnet/species.*csv*) to compare species' simulated extinction vulnerability with currently classified threat status.

Results

Vertebrate extinctions

Pre-Anthropocene extinction rate

In simulations with a pre-Anthropocene extinction rate across all basal resource removal scenarios, mean estimated vertebrate extinction rates varied between 0.04% and 99.3% in the lowland network, and 0.03% and 99.5% in the highland network. Specifically, in simulations with 0% basal resource removal, vertebrate extinction rates remained at a mean of 0.04% (95% confidence interval: 0–0.7%) in the lowland network, and 0.03% (0–0.7%) in the highland network, peaking at 0.8% (3.4–3.4%) and 0.8% (3.02–3.15%) at a 1% coextinction threshold, respectively (Figure 3a). The proportion of secondary extinctions increased rapidly from < 0.01 to 0.95 at a 1% coextinction threshold in both networks (Figure 4a & 5a).

Removing 25% of all basal resources, extinction rates started at 0.6% (0–1.7%) in the lowland network and 0.7% (0–1.6%) in the highland network, increasing to 92.5% (89.9–95.3%) and 90.2% (87.8–93.4%) at a 1% coextinction threshold, respectively (Figure 3d). Concurrently, the proportion of secondary extinctions in the lowland network increased from 0.91 to 0.99 at a 42% coextinction threshold (Figure 4d), and in the highland network from 0.9 to 0.99 at a higher coextinction threshold of 60% (Figure 5d). With 50% resource removal, both networks had increased vertebrate extinctions, starting at 1.2% (0–2.7%) in the lowland network and 1.3% (0–2.5%) in the highland network, increasing to 98.0% (96.0–99.3%) and 97.6% (95.5–99.2%) at a 1% coextinction threshold, respectively (Figure 3g). The proportion of secondary extinctions were similar, starting from 0.97 in both networks, increasing to 0.98 in the lowland network (Figure 4g) and 0.99 in the highland network at a coextinction threshold of 84% (Figure 5g). At 75% resource removal, both networks had near-total extinction of all vertebrates, with rates of 99.3% (98.0–100%) in the lowland and 99.5% (98.1–100%) in the highland network at a 1% coextinction threshold (Figure 3j), with the proportion of secondary extinctions consistently at 0.99 across all thresholds tested (Figure 4j & 5j).

Modern extinction rate

In simulations with a modern extinction rate across all basal resource removal scenarios, compared with pre-Anthropocene results, mean minimum estimated vertebrate extinction rates increased to 5.0% in both low- and high-elevation networks, with only marginal increases in maximum mean rates (99.6% and 99.7%, respectively). Specifically, for 0% basal resource removal, the lowland network began with an extinction rate of 5.0% (1.3–9.4%), increasing to 92.5% (86.6–97.3%) at a 1% coextinction threshold (Figure 3b). The highland network had a similar trend, starting at 5.0% (1.9–9.4%) and reaching a marginally lower rate at 91.8% (85.5–96.2%) at the same 1% coextinction threshold (Figure 3b). The proportion of secondary extinctions in the lowland network started at 0.02 and peaked at 0.95 at a 1% coextinction threshold (Figure 4b), while the highland network began at 0.01, also reaching 0.95 at the same coextinction threshold (Figure 5b). With 25% basal resource removal, vertebrate extinctions began at 5.4% (2.0–10.1%) in the lowland network and 5.4% (1.9–9.4%) in the highland network at a 100% coextinction threshold, escalating to 97.8% (95.3–100%) and 97.82% (95.5–100%) at a 1% coextinction threshold, respectively (Figure 3e). Secondary extinctions in both networks followed a similar pattern, starting at 0.1 in the lowland network (Figure 4e) and 0.08 in the highland network (Figure 5e), both at 0.95, although at a lower coextinction threshold in the highland network (16%) than in the lowland network (23%).

This extinction trend became even more pronounced with 50% resource removal, where the lowland network experienced extinction rates starting at 6.2% (2.7–10.7%) and reaching a maximum of 99.1% (97.3–100%) at a 1% threshold (Figure 3h). Concurrently, the proportion of secondary extinctions began at 0.21 and peaked at 0.95 at a 40% threshold (Figure 4h). In the highland network, extinction rates started at 6.3% (2.5–10.7%), increasing to 99.1% (97.5–100%) at a 1% threshold, with the proportion of secondary extinctions starting higher at 0.3 and reaching a maximum of 0.95 at a lower coextinction threshold of 24% (Figure 5h).

With 75% basal resource removal, the lowland network saw extinction rates begin at 7.4% (3.4–11.4%) and escalate to 99.7% (98.7–100%) at a 1% threshold (Figure 3k). The proportion of secondary extinctions started at 0.33 and reached a maximum of 0.95 at a 50% coextinction threshold (Figure 4k). The highland network showed a slightly higher trend, with vertebrate extinctions beginning at 7.8% (4.4–12.0%) and reaching 99.7% (98.7–100%) at a 1% threshold (Figure 3k). The proportion of secondary extinctions started higher at 0.36, reaching the same peak of 0.95 but at a lower threshold of 31% (Figure 5k).

Future extinction rate

In simulations with a future extinction rate across all basal resource-removal scenarios, mean minimum estimated vertebrate extinction rates increased to 7.1% in the lowland highland networks, with only marginal increases in maximum mean rates (99.8% in both networks). Specifically with 0% resource removal, the lowland network started at an extinction rate of 7.1% (2.7–12.8%), increasing to a maximum of 95.5% (90.6–98.7%) at a coextinction threshold of 1% (Figure 3c). The highland network had a similar increase from 7.1% (3.1–12.0%) to 95.1% (90.6–98.1%) at the same coextinction threshold (Figure 3c). The proportion of secondary extinctions in both networks mirrored this trend, starting from 0.02 in the lowland network (Figure 4c) and 0.01 in the highland network (Figure 5c), and reaching peaks of 0.92 at a 2% coextinction threshold and 0.93 at a threshold of 4%, respectively. The trend of increasing primary and secondary extinctions continued after removing 25%, 50%, and 75% of basal resources. At 25% resource removal, extinction rates in the lowland network increased to 98.4% (96.0–100%), while in the highland network, mean extinction rates were slightly lower at 98.3% (96.2–100%) at the same 1% coextinction threshold (Figure 3f). The proportion of secondary extinctions in the lowland network increased from 0.08 to 0.93 at a coextinction threshold of 18% (Figure 4f). In the highland network, the proportion of secondary extinctions started at 0.07 and peaked at 0.93 at a lower coextinction threshold of 12% (Figure 5f).

With 50% basal resource removal under the future extinction rate, the lowland network had an increase in vertebrate extinction rates, starting at 8.3% (4.0–13.4%) and reaching a maximum of 99.3% (98.0–100%) at a 1% coextinction threshold (Figure 3i). Secondary extinctions followed this increase, beginning at 0.16 and peaking at 0.93 at a 29% coextinction threshold (Figure 4i). In the highland network, extinction rates started marginally higher at 8.4% (3.8–13.8%) and reached 99.3% (98.1–100%) at a 1% coextinction threshold (Figure 3i). Secondary extinctions in the highland network followed a similar trend, starting at 0.2 and reaching a peak of 0.93 but at a lower coextinction threshold of 18% (Figure 5i).

The most extreme scenario of 75% resource removal in the future extinction rate resulted in near-total extinction in both networks. The lowland network began with extinction rates at 9.4% (5.4–14.8%) at a coextinction of 100%, scaling to 99.8% (98.7–100%) at a 1% coextinction threshold (Figure 3l). Concurrently, secondary extinctions started at 0.26, increasing to 0.93 at a 34% coextinction threshold (Figure 4l). The highland network had a marginally higher trend in vertebrate extinctions, starting at 9.8% (5.7–15.1%) at a coextinction of 100%, also reaching 99.8% (98.7–100%) at a 1% coextinction threshold (Figure 3l). Secondary extinctions in the highland network mirrored this, beginning at 0.29 and peaking at 0.93, although at a lower coextinction threshold of 24% (Figure 5l).

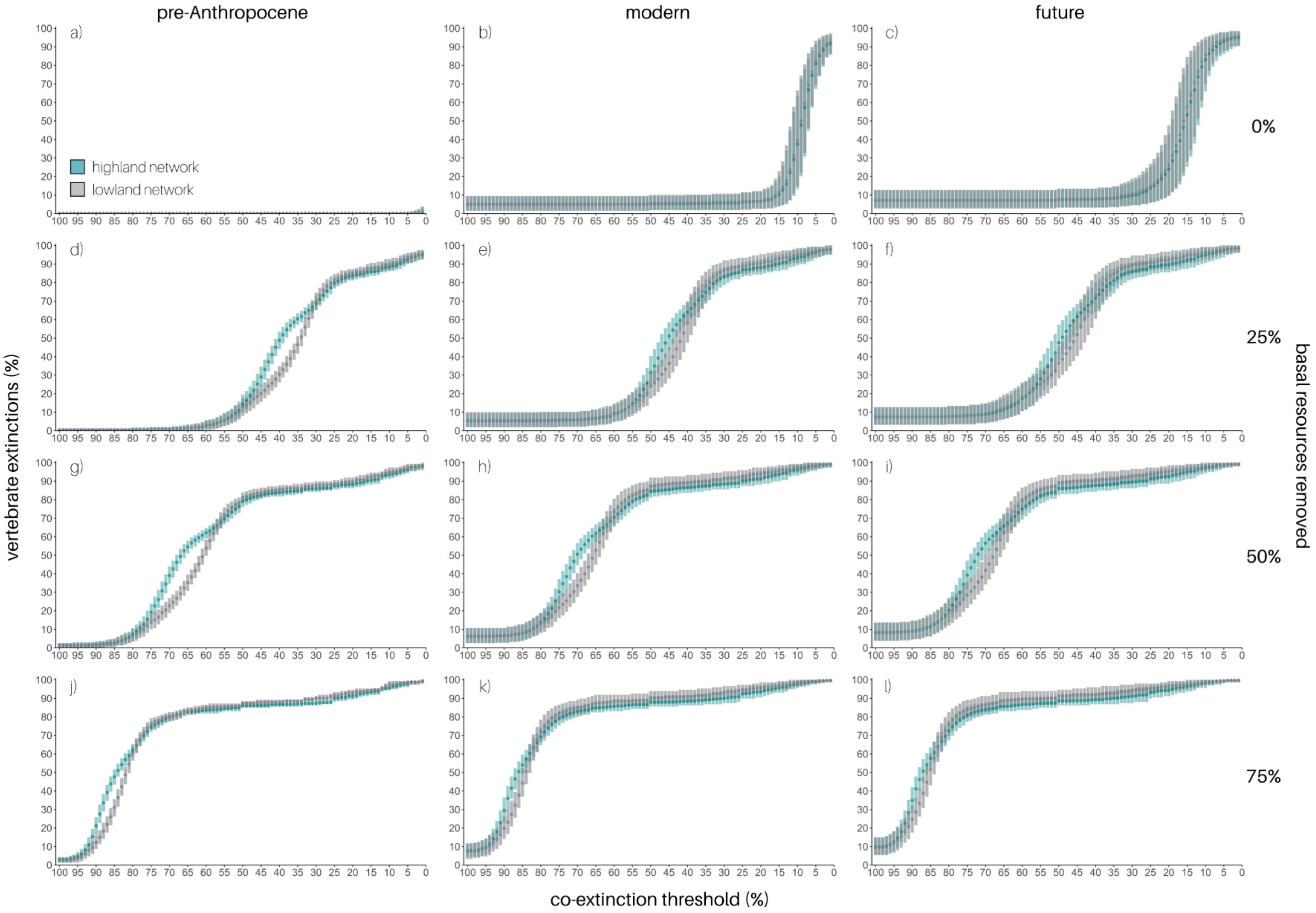

Figure 3. Vertebrate extinctions in lowland (blue) and highland (grey) networks across different simulated background extinction rates (pre-Anthropocene, modern, and future extinctions) and scenarios of basal resources extinction (0%, 25%, 50% and 75% basal resource removal), assessed across different coextinction thresholds from 100–1% in 1% increments. Points denote mean values, and lines denote 95% CI for each increment.

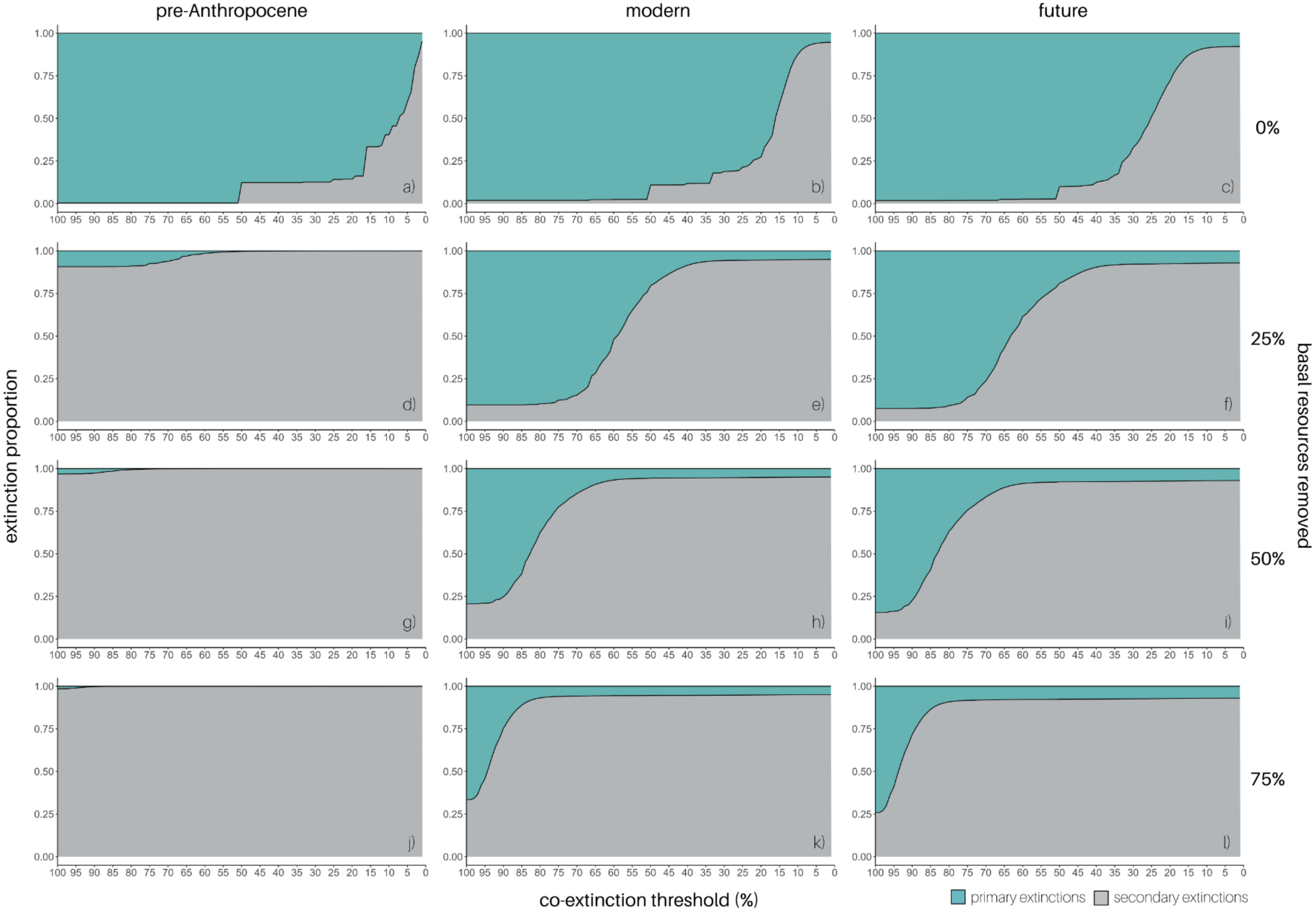

Figure 4. The proportion of primary (blue) and secondary (grey) vertebrate extinctions in the lowland network across different simulated background extinction rates (pre-Anthropocene, modern, and future extinctions) and scenarios of basal resources extinction (0%, 25%, 50%, and 75% basal resource removal), assessed across different coextinction thresholds from 100–1% in 1% increments.

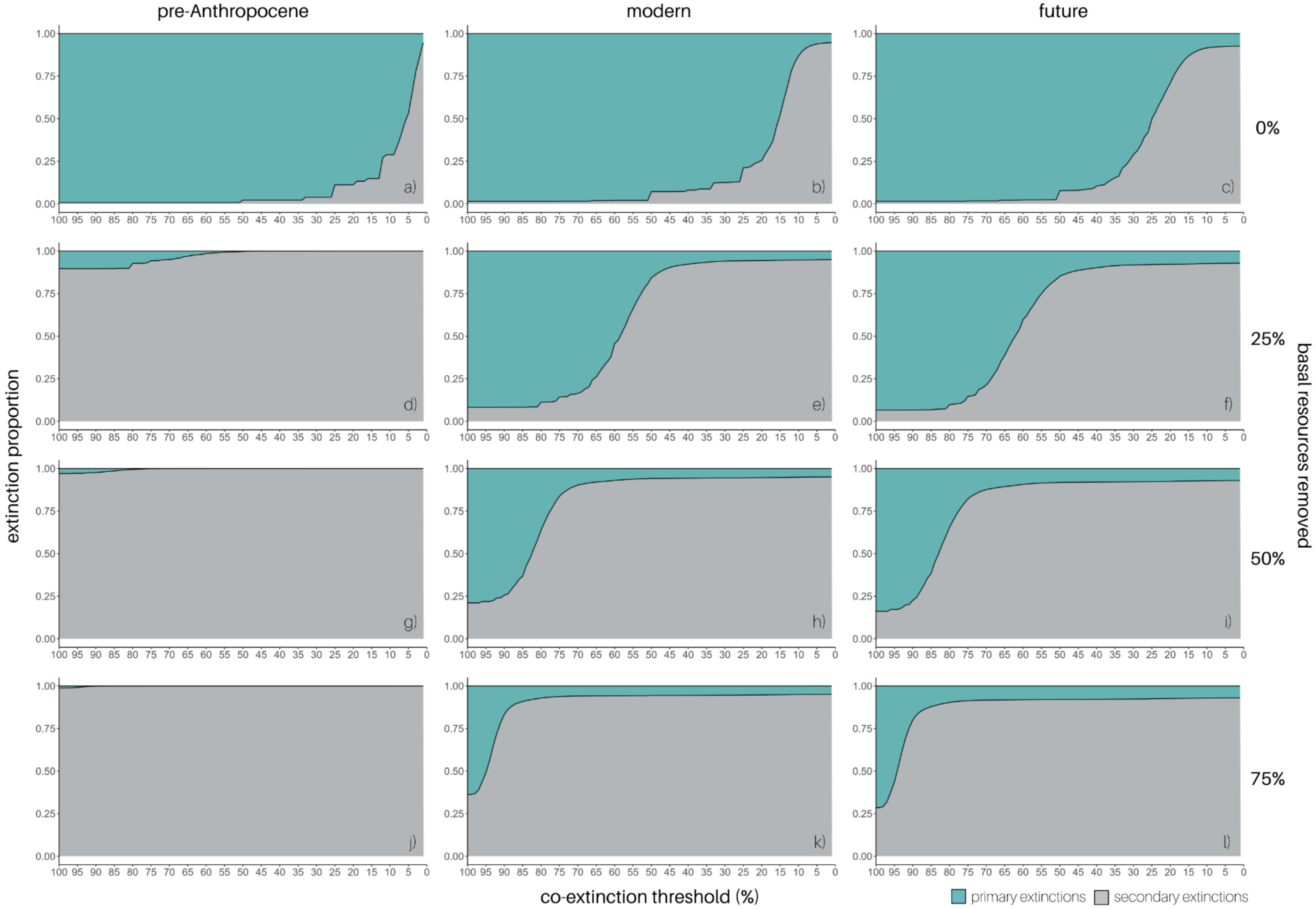

Figure 5. The proportion of primary (blue) and secondary (grey) vertebrate extinctions in the highland network across different simulated background extinction rates (pre-Anthropocene, modern, and future extinctions) and scenarios of basal resources extinction (0%, 25%, 50%, and 75% basal resource removal), assessed across different coextinction thresholds from 100–1% in 1% increments.

Vertebrate vulnerability to primary and secondary extinctions

Primary extinctions

Vulnerability to primary extinctions was low in both low- and high-elevation networks, with median estimated extinction rates across all classes ranging between 4.3% and 4.6% in the highland network, and 3.4% and 4.5% in the lowland network. Specifically in the highland network, all classes had low vulnerability to primary extinctions, with the highest median (interquartile range) being 4.6% (0.04–6.5%) for amphibians, followed by birds at 4.5% (0.04–6.4%), reptiles at 4.4% (0.1–6.5%), and mammals at 4.3% (0.1–6.0%) (Figure 6). Species across all classes with a conservation status > Least Concern also had marginally higher vulnerability to primary extinctions, with a median of 4.6% (0.04-6.6%) compared to those classified as Least Concern with a median rate of 4.5% (0.1–6.4%) (Figure 7).

As for the lowland network, all classes had low vulnerability to primary extinctions. Amphibians had the highest median of 4.5% (0.02–6.6%), followed by birds at 4.4% (0.03–6.3%), reptiles at 4.2% (0.03–6.2%), and mammals at 3.4% (0.03–6.1%) (Figure 6). As for the highland network, species across all classes with a conservation status > Least Concern had similar vulnerability to primary extinctions, with a median of 4.3% (0.02–6.1%) compared to those classified as Least Concern with a median of 4.3% (0.03–6.4%%) (Figure 7).

Secondary extinctions

Vulnerability to secondary extinctions was much higher than primary extinctions, with median estimated extinction rates across all classes ranging from 28.7% to 50.8% in the highland network, and 33.3% and 55.8% in the lowland network. Specifically in the highland network, mammals with a median (interquartile range) of 50.8% (16.7–73.3%) and birds at 50.2% (16.03–74.86%) had the highest vulnerability to secondary extinction (Figure 6). Conversely, amphibians had a much lower median rate of 32.5% (12.8–55.8%), while reptiles had the lowest at 28.7% (9.2–54.8%) (Figure 6). Species across all classes with a conservation status > Least Concern had higher vulnerability to secondary extinctions, with a median of 51.2% (24.5–72.8%) compared to those classified as Least Concern at 45.8% (13.0–71.3%) (Figure 7).

In the lowland network, mammals had the highest vulnerability to secondary extinctions, with a median of 55.8% (18.6–75.7%) (Figure 6). Birds had the second-highest median of 47.8% (15.2–71.4%), followed by amphibians and reptiles at 33.6% (13.37–59.42%) and 33.3% (9.4–61.0%), respectively (Figure 6). Species across all classes with a conservation status > Least Concern again had higher vulnerability to secondary extinctions, with a median of 52.8% (26.8–74.3%) compared to those classified as Least Concern at 43.6% (13.4–69.6%) (Figure 7).

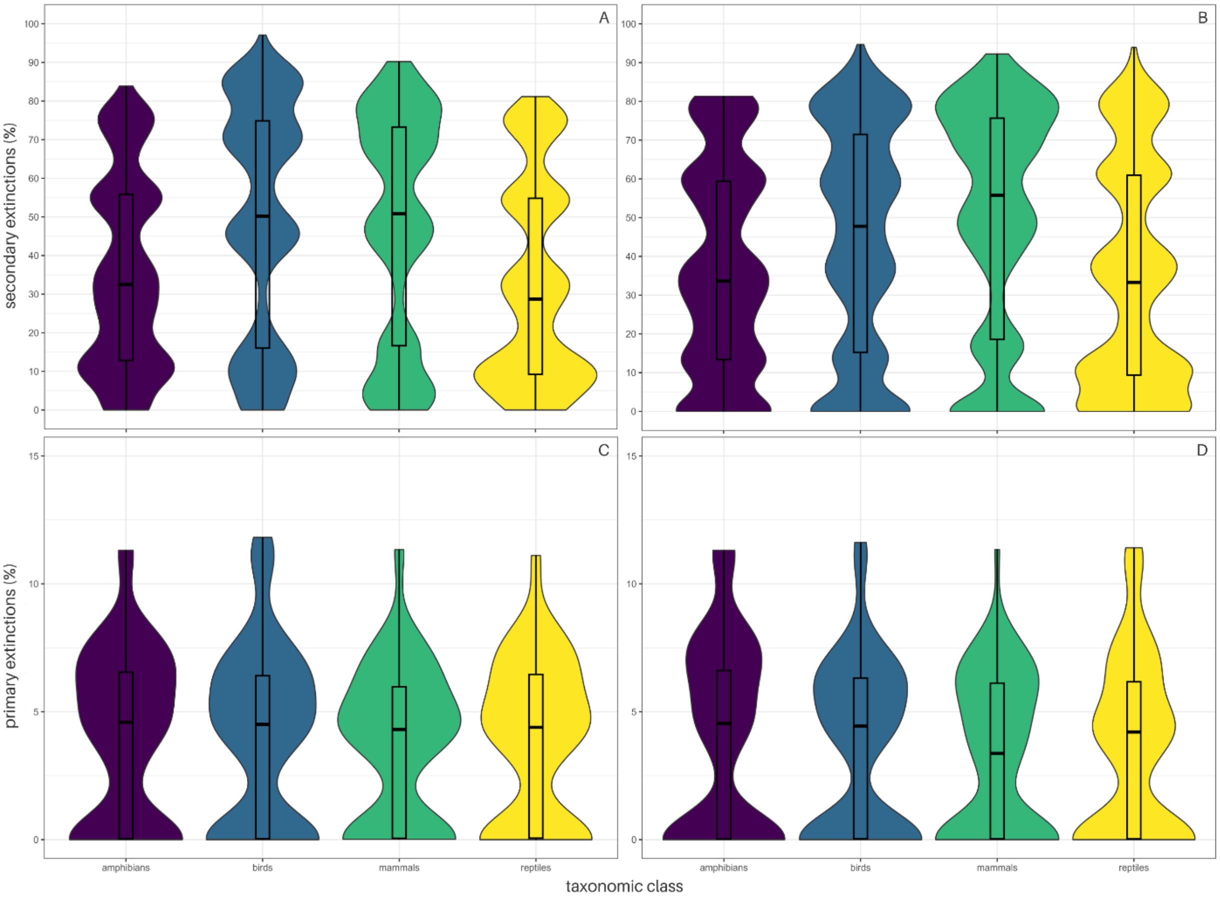

Figure 6. Frequency of vertebrate secondary extinctions (A = highland network and B = lowland network) and primary extinctions (C = highland network and D = lowland network) for each taxonomic class across all simulated background extinction rates (pre-Anthropocene, modern, and future extinctions), scenarios of basal resource removal (0%, 25%, 50%, and 75%), and extinction thresholds assessed (100-1%). The boxplot displays the distribution of vertebrate secondary extinctions, indicating median (central line), interquartile range (box edges representing the 25th and 75th percentiles), and total range (whiskers extending to the minimum and maximum values) of frequency. Colours denote the different taxonomic classes (purple = amphibians, blue = birds, green = mammals, and yellow = reptiles).

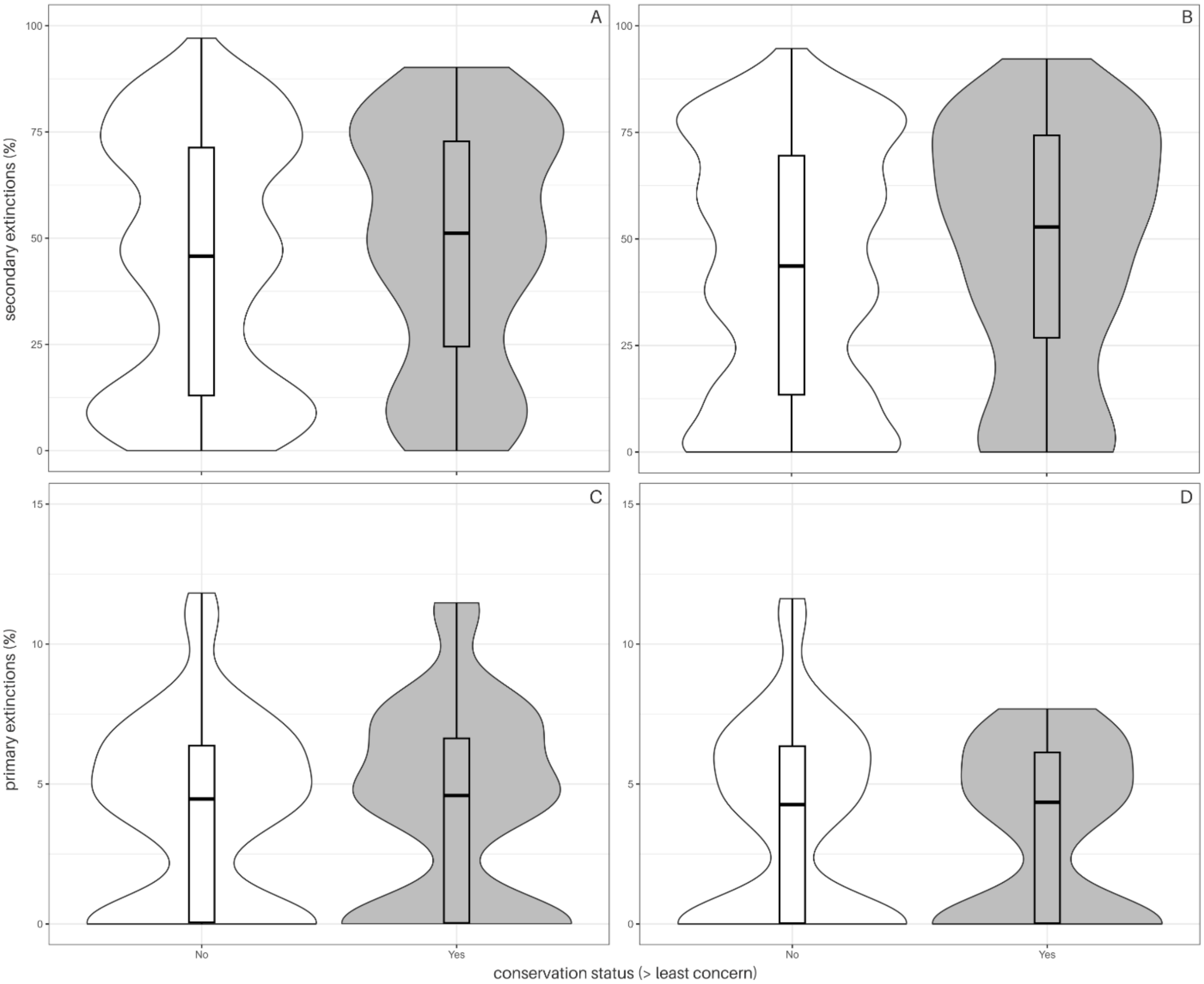

Figure 7. Frequency of vertebrate secondary extinctions (A = highland network and B = lowland network) and primary extinctions (C = highland network and D = lowland network) for species categorised as either having a conservation status > Least Concern as classified by Queensland Nature Conservation Act (1992) or IUCN Red List (2024), under all simulated background extinction rates (pre-Anthropocene, modern, and future extinctions), scenarios of basal resource removal (0%, 25%, 50%, and 75%), and extinction thresholds assessed (100-1%). The boxplot displays the distribution of vertebrate secondary extinctions, indicating median (central line), interquartile range (box edges representing the 25th and 75th percentiles), and total range (whiskers extending to the minimum and maximum values) of frequency. Colours denote species conservation status as either classified as Least Concern (white) or higher than Least Concern (e.g., Endangered) (grey).

Discussion

Vertebrate extinction risks from bottom-up cascades

Compared to simulations where I did not remove basal resources, vertebrate extinctions increased from a minimum of 0.6% in the lowland network and 0.7% in the highland network. These results illustrate a concerning trend where the extinction rate of vertebrates in both networks increases with an increasing number of basal resources removed. This pattern correlates positively with a proportionately higher increase in secondary extinctions than primary extinctions, with this effect increasing with a decreasing coextinction threshold. These results support the hypothesis that lower coextinction thresholds and greater basal resource removal lead to more secondary than primary extinctions, and thus suggest a pervasive vulnerability to bottom-up effects via the loss of basal resources, highlighting their importance in maintaining community stability (e.g., Pimm & Raven, 2000; Sole & Montoya, 2001).

While both low- and high-elevation networks had a high proportion of secondary extinctions under various increments of basal resource removal, the highland network tended a relatively higher proportion of secondary extinctions at different coextinction thresholds compared to the low-elevation network. This trend is consistent across the pre-Anthropocene, modern, and future extinction scenarios I tested, suggesting that the highland network — while more susceptible to primary extinction (de la Fuente et al., 2022; de la Fuente & Williams, 2023; Williams et al., 2003; Williams & de la Fuente, 2021b) — might also be more susceptible to secondary extinctions via bottom-up effects compared to the lowland network under the same conditions. This result contrasts with other research suggesting that networks with higher connectance, like the highland network (Chapter 3), should raise the threshold at which the removal of highly connected species can have large impacts on food web structures (Eklöf & Ebenman, 2006) and reduce risk to secondary extinctions (Dunne et al., 2002a; Dunne et al., 2002b). This discrepancy between networks suggests that factors other than network complexity might decrease community resilience to secondary extinctions via bottom-up effects. This effect could occur, for example, in species that are both highly susceptible to primary extinction and are highly connected, leading to more coextinctions thereafter. Alternatively, while increased network complexity can buffer coextinction risks, losing species within lower trophic levels can undermine the resilience that one would expect it to provide (e.g., Borrvall et al., 2000).

Bottom-up effects and extinction tipping points

My results also support the hypothesis that while I can identify extinction tipping points in communities, the timing of collapse from bottom-up effects depends on the assumed coextinction threshold and the number of basal resources disappearing. In both networks, extinction tipping points occurred when I applied different basal resource loss and species coextinction thresholds, showing the extent to which variation in the underlying parameters influence relative extinction risks. These findings are consistent with other simulation studies demonstrating the impact of variation in parameters like coextinction threshold (e.g., Strona & Bradshaw, 2018; Valiente-Banuet & Verdú, 2013). However, I also found that extinction tipping points in both networks shifted towards lower coextinction thresholds, changing from pre-Anthropocene to future extinction rates and from increasing basal resource removal (0% to 75%). More extreme future scenarios might, therefore, lower the coextinction threshold needed to trigger extinction tipping points in both networks. The differences in extinction risks between the two networks lessen as the number of basal resources going extinct declines, suggesting a potential convergence in their responses to escalating future anthropogenic pressures despite topological differences. Thus, my results underline the importance of identifying species-specific coextinction thresholds and the rate of basal resource loss that terrestrial communities might face. These data are required to determine possible community extinction tipping points and implement effective management strategies.

Assuming species cannot adapt to changes in their prey availability, such as broadening their diet breadth (dietary plasticity) (Evans & Moustakas, 2018) or changing prey type (diet specialisation), could over-estimate extinction risk based on projections of reduced food resources. While it is clear that the removal of basal resources can negatively affect the relative extinction risk of vertebrate species, such extinction tipping points for each species would likely vary. Not knowing the explicit extinction rates across different types or groups of plants and invertebrates could bias estimates of extinction risk. For invertebrates, differences in extinction risk across species are likely because invertebrate diversity can vary substantially both across elevation and strata (e.g., forest floor, sub-canopy, and canopy) (Hill & Cermak, 1997; Yeates & Monteith, 2008). For example, the spatial distribution and population density of the Dipteran sub-order Schizophora in the Carbine subregion of the Wet Tropics indicated that high-elevation assemblages are at higher risk of extinction under as little as 2°C of warming (Wilson et al., 2007). In plants, different growth forms in tropical rain forests vary in their vulnerability to extinction, particularly across different extinction drivers (Tng et al., 2022). However, because there is a lack of detailed taxonomic data for most of these assemblages across this bioregion (and even globally), there is no way to predict how extinction risks might vary due to differences in biological characteristics. Future research should focus on developing more robust methodologies to model trophic and non-trophic interactions, enhancing understanding of how changes in basal resource availability affect ecological communities more broadly in terrestrial ecosystems. Investigating the variability in extinction risk across different taxa and environments and the role of climatic changes will be necessary. Detailed taxonomic studies, particularly in under-researched terrestrial ecosystems, could help provide the granularity needed to predict and mitigate the cascading effects of species loss.

Vulnerability to bottom-up cascades across vertebrate groups

Mammals and birds in both low- and high-elevation networks had the highest vulnerability to coextinction from bottom-up processes, highlighting the potential for cascading trophic and non-trophic effects within these communities. Herbivorous mammals in both networks were the most vulnerable, indicating their lower diet breadths and higher dependence on plants than other classes. Indeed, losses in the diversity of primary producers like plants can disproportionally impact herbivores in terrestrial ecosystems (e.g., Kagata et al., 2005; Scherber et al., 2010). Trophic separation can mitigate these cascading effects on higher trophic levels, and lower trophic positions of herbivorous mammals might further support this (Chapter 3). Conversely, amphibians and reptiles were more resilient to such extinctions, thus helping to support the hypothesis that different vertebrate taxonomic classes exhibit different vulnerabilities to secondary extinction across scenarios.

I found that birds (mostly omnivorous) in the highland network were vulnerable to secondary extinction from bottom-up effects. Their higher vulnerability is likely due to their greater reliance on invertebrates, combined with their strong dependency on plant species and their high degree and closeness centrality (Chapter 3). While omnivory is often assumed to confer dietary flexibility, in this context it could reflect a broader set of dependencies rather than true functional generalism. This broader dependence could expose these species to more indirect effects, particularly if essential resources or trophic links are lost. Consequently, the higher risk of losing such herbivorous and omnivorous species could have even worse implications for their associated communities. For example, by also affecting plant diversity in tropical rain forests, secondary impacts might cause even more wide-spread trophic and non-trophic effects within communities (Camargo-Sanabria et al., 2015), particularly for plants that heavily rely on animals for successful seed dispersal (e.g., *Casuarius casuarius*) (Stocker & Irvine, 1983). For insectivorous vertebrate species, their increased risk of decline or extinction could also increase the consumption of tree seedlings by herbivores and modify nutrient cycles as invertebrate populations increase (Dunham, 2008). Indeed, there is evidence for higher vulnerability to coextinctions from vertebrate population declines in the Wet Tropics. For example, ringtail possums (*Hemibelideus lemuroides*, *Pseudochirops archeri*, *Pseudochirulus herbertensis* and *Pseudochirulus cinereus*) have declined and are projected to continue declining from changes in mean annual temperature and frequency of heatwaves (de la Fuente & Williams, 2023). Similarly, several bird populations by up to 50% over the last decade, particularly specialised and regionally endemic species in highland areas (Williams & de la Fuente, 2021a). The increased extinction risk in these groups could stem from their heightened vulnerability to bottom-up trophic cascades caused by the decline and loss of basal resources in their communities (Braby et al., 2021; Van Klink et al., 2020).

In contrast, amphibians and reptiles were less vulnerable to secondary extinctions in both networks. This result could be due not only to the high connectedness of amphibians with invertebrates, but also to their high modularity (intraspecific predation), a feeding trait that could buffer amphibians from trophic cascades in other parts of the network (Chapter 3). While reptiles tend to occupy higher trophic and more vulnerable positions in both networks (Chapter

3), they do not interact trophically with plants and depend much less on invertebrates. No reliance on plants could protect reptiles from the direct loss of basal resources, which could partly explain the higher endangerment of amphibians in the Wet Tropics (Fordham et al., 2016; Geyle et al., 2021; Hero et al., 2015; McKnight et al., 2017) (Geyle et al., 2020; Tingley et al., 2019) and globally (Wake & Vredenburg, 2008). While ectotherms like reptiles and amphibians appear more vulnerable to the direct impacts of climate change, their trophic positioning and connectance could offer some resilience against indirect, bottom-up cascades triggered by these same changes. Given the global decline of basal species (Van Klink et al., 2020; Wagner, 2020), management strategies must prioritise conserving these resources.

Threatened species also showed an increased vulnerability to primary and secondary extinctions compared to species of Least Concern. This result does not support the hypothesis that threatened species are more prone to primary than secondary extinction, implying that current threat assessments could already encapsulate the increased risk of secondary extinction for such species. While stressors like chytrid fungus are often attributed as the primary cause for amphibian decline, their trophic position and dependence on basal resources could also be exacerbating this risk (e.g., Llewelyn et al., 2022). Although higher threat status might already reflect an increased vulnerability to secondary extinction, high vulnerability across all categories signals that even species deemed Least Concern might not be entirely immune to the effects of bottom-up cascades. Indeed, threat assessments like the IUCN Red List cannot capture the full extent of extinction risk (Schmidt et al., 2023). By implication, threat assessments probably do not capture the gamut of increasing threats across entire communities. This limitation emphasises the need for conservation strategies to consider the broader ecological interactions and the potential cascading effects within communities beyond immediate threats (Peng et al., 2023). Incorporating these consumer-resource relationships into threat assessments and policies could enhance their accuracy (Moir & Brennan, 2020).

Conclusions

As the biodiversity crisis amplifies, bottom-up trophic cascades have a major role in shaping extinction dynamics within terrestrial ecosystems. The differential resilience I observed between low- and high-elevation networks and variable vulnerabilities across species and taxonomic groups highlights the need to incorporate basal resource interactions in trophic network models to evaluate extinction risks more realistically. My results highlight the imperative of conserving basal resources and understanding individual species' coextinction thresholds to mitigate potential extinction tipping points, especially as environmental conditions intensify. Understanding and managing these interdependencies will be essential for more effective biodiversity conservation and threat assessment amid ongoing environmental change in terrestrial ecosystems.

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Appendix

To compare how including or excluding basal resources affect network structure, and therefore, their properties, I also compared low- and high-elevation vertebrate network models to two other model variants that included variable basal resources (plants and invertebrates) using different network metrics (Figure A1). The first model variant included invertebrates and plants as one 'super' node where edges depended on whether vertebrates eat invertebrates, and the second variant included invertebrates and plants as individual nodes, with the number of nodes and links determined by diet breadth estimates for omnivorous, herbivorous, and insectivorous vertebrates.

To compare differences between these model variants from the perspective of the vertebrates in each model, I also compared connectance (C) (fraction of links from vertebrates to all associated plant and invertebrate resources, relative to all possible links between these groups), chain-averaged trophic length (TL) (average number of interactions between top predator vertebrates and basal invertebrate prey and plants in each network – which uses the `Cheddar` R package (v0.1-636) (Woodward et al., 2012), and generality (G_v) (average number of invertebrate prey and plants per vertebrate predator) to evaluate network properties. I completed this process after removing the top $G'_{10\%}$, $G'_{20\%}$, and $G'_{50\%}$ of the highest connected vertebrate nodes in each network to highlight potential differences between model variants. The results indicate differences between low- and high-elevation network types and similar trends in percentages of node removal.

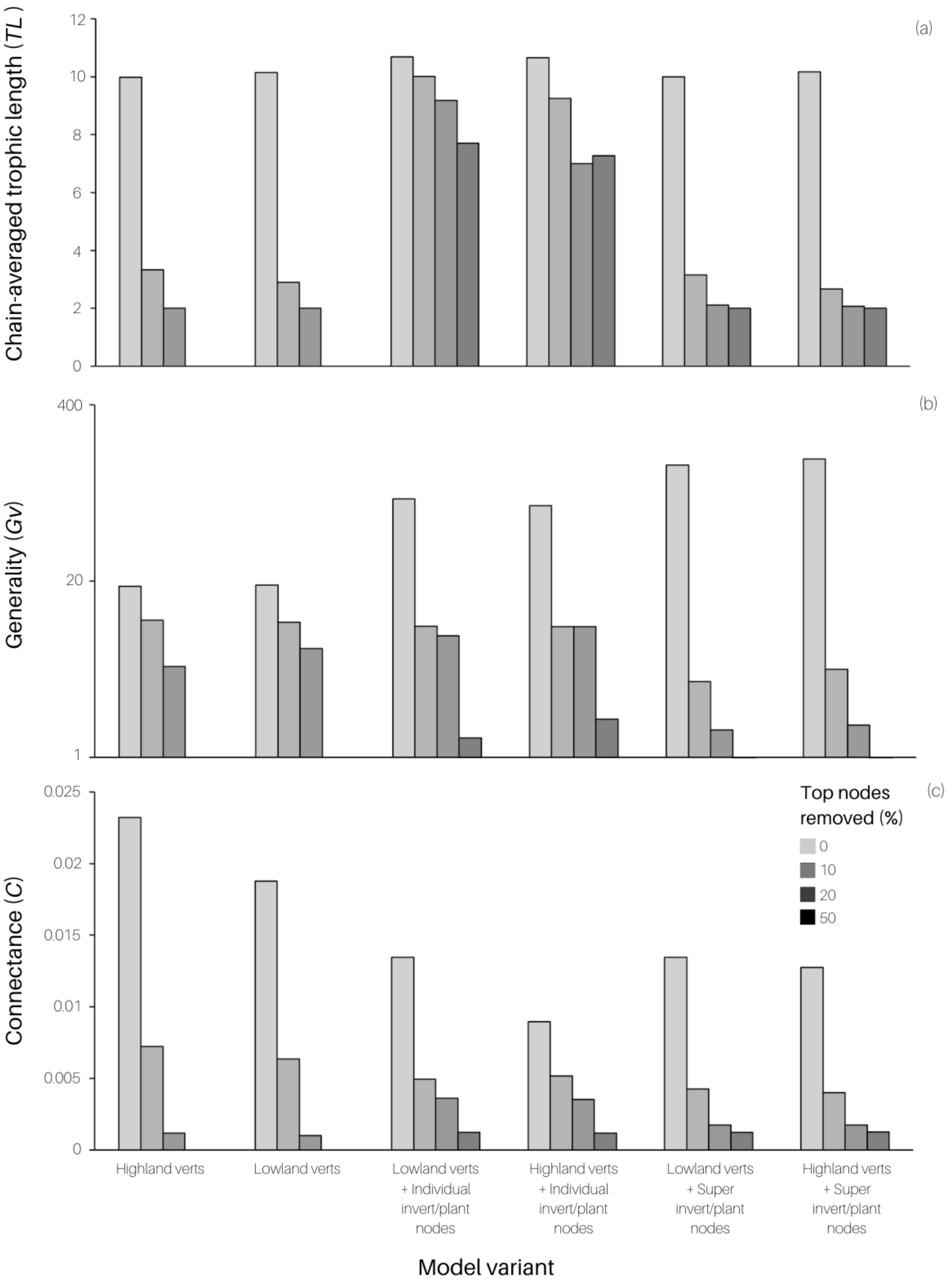

Figure A1. Model variants for including and excluding basal resource nodes (invertebrates and plants) in low- and high-elevation vertebrate networks. The top nodes removed represent the percentage of vertebrate species removed with the highest degree in each model variant. Chain-averaged trophic length (mean) ($\boldsymbol{TL}$) (a), generality ($\boldsymbol{G_v}$) (b), and connectance ($\boldsymbol{C}$) (c) represent network property metrics. Note that values missing for model variants with the top 50% nodes removed result from no edges existing between remaining nodes. Generality y-scale is *Log*20 transformed with a minimum value of 1

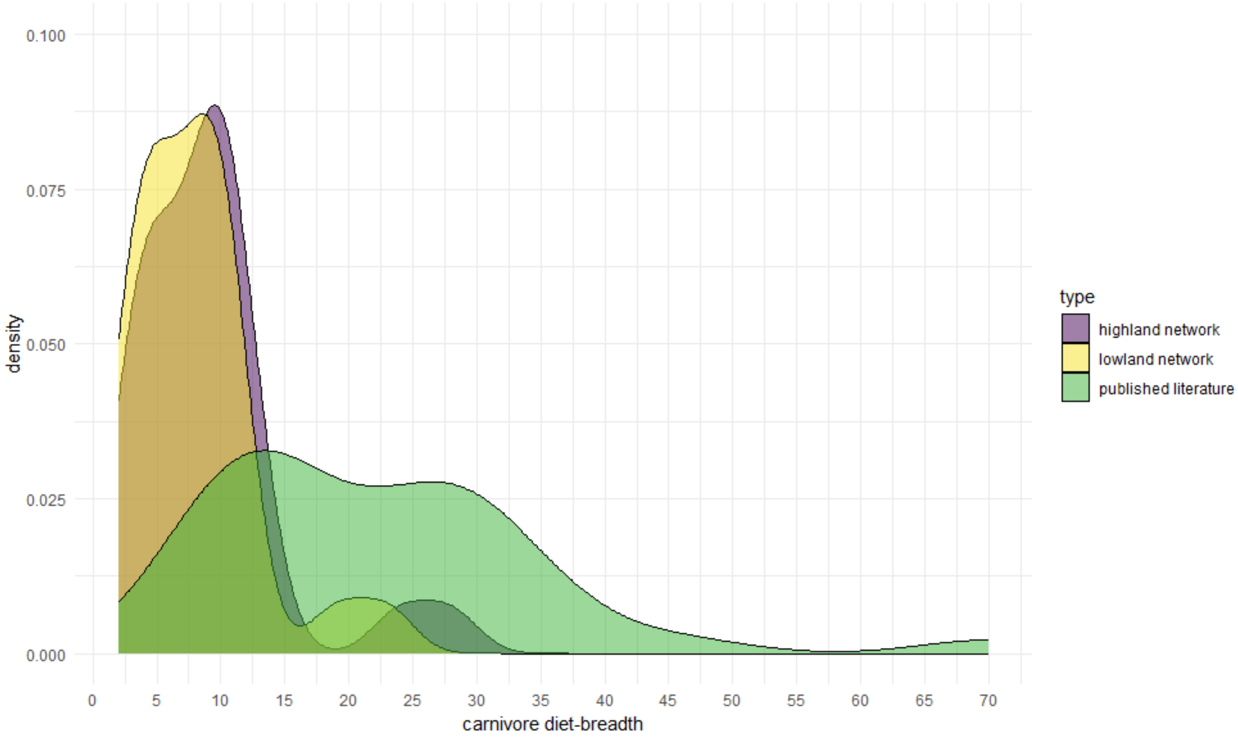

Figure A2. Distribution of carnivore diet-breadths for low- and high-elevation networks compared against diet-breadth data collected from published literature by Llewelyn et al. (2022).

Table 1. Diet breadth, classified into plant, invertebrate, and vertebrate trophic links, and trophic guild classification, for all lowland network vertebrate species.

Species	**Plant links**	**Invertebrate links**	**Vertebrate links**	**Trophic guild**
Ailuroedus melanotis	54	19	1	omnivore
Alectura lathami	63	2	5	omnivore
Alisterus scapularis	24	8	3	omnivore
Aplonis metallica	54	97	8	omnivore
Bolemoreus frenatus	68	17	1	omnivore
Cacatua galerita	56	156	2	omnivore
Casuarius casuarius	87	94	1	omnivore
Cercartetus caudatus	59	96	3	omnivore
Chalcophaps indica	57	154	1	omnivore
Columba leucomela	63	7	4	omnivore
Coracina lineata	64	172	6	omnivore
Cyclopsitta diophthalma	69	166	3	omnivore
Dactylopsila trivirgata	33	20	3	omnivore
Dicaeum hirundinaceum	47	50	8	omnivore

Species	**Plant links**	**Invertebrate links**	**Vertebrate links**	**Trophic guild**
Erythrura trichroa	38	175	11	omnivore
Eudynamys scolopacea	59	174	1	omnivore
Hypsiprymnodon moschatus	35	14	3	omnivore
Lalage leucomela	34	2	6	omnivore
Lopholaimus antarcticus	23	19	2	omnivore
Macropygia amboinensis	57	16	4	omnivore
Macropygia phasianella	81	34	4	omnivore
Megapodius reinwardt	62	164	5	omnivore
Meliphaga lewinii	54	176	1	omnivore
Meliphaga notata	37	37	1	omnivore
Microptilotis gracilis	32	172	1	omnivore
Myzomela obscura	28	5	1	omnivore
Myzomela sanguinolenta	66	5	1	omnivore
Neochmia temporalis	62	4	11	omnivore
Nyctimene robinsoni	52	187	3	omnivore
Oriolus flavocinctus	87	1	6	omnivore
Perameles pallescens	53	85	1	omnivore
Philemon buceroides	57	37	1	omnivore
Platycercus elegans	83	8	3	omnivore
Pogonomys mollipilosus	67	1	6	omnivore
Pteropus conspicillatus	66	167	3	omnivore
Ptilinopus magnificus	21	55	3	omnivore
Ptilinopus regina	37	45	4	omnivore
Ptilinopus superbus	31	17	4	omnivore
Ptilonorhynchus violaceus	30	14	1	omnivore
Rattus fuscipes	61	26	9	omnivore
Rattus leucopus	63	42	9	omnivore
Scenopoeetes dentirostris	35	96	1	omnivore
Scythrops novaehollandiae	33	93	2	omnivore
Sphecotheres vieilloti	70	35	6	omnivore
Strepera graculina	83	35	6	omnivore
Sus scrofa	21	162	1	omnivore
Trichoglossus chlorolepidotus	33	169	3	omnivore
Uromys caudimaculatus	33	2	6	omnivore
Xanthotis macleayanus	69	90	1	omnivore
Zosterops lateralis	32	173	7	omnivore
Acanthorhynchus tenuirostris	0	5	1	carnivore
Accipiter novaehollandiae	0	2	2	carnivore
Antechinus flavipes	0	8	3	carnivore
Aviceda subcristata	0	9	2	carnivore

Species	**Plant links**	**Invertebrate links**	**Vertebrate links**	**Trophic guild**
Boiga irregularis	0	4	4	carnivore
Rhinella marina	0	2	1	carnivore
Carphodactylus laevis	0	3	1	carnivore
Ceyx azureus	0	3	1	carnivore
Demansia psammophis	0	1	3	carnivore
Dendrelaphis calligastra	0	8	3	carnivore
Dendrelaphis punctulatus	0	2	1	carnivore
Dicrurus bracteatus	0	1	5	carnivore
Eulamprus quoyii	0	8	2	carnivore
Gnypetoscincus queenslandiae	0	5	2	carnivore
Intellagama lesueurii	0	1	1	carnivore
Litoria infrafrenata	0	8	15	carnivore
Litoria serrata	0	5	14	carnivore
Melloria quoyi	0	5	5	carnivore
Mixophyes carbinensis	0	6	5	carnivore
Mixophyes coggeri	0	2	5	carnivore
Mixophyes schevilli	0	2	5	carnivore
Morelia amethistina	0	7	1	carnivore
Ninox rufa	0	8	1	carnivore
Pseudechis porphyriacus	0	6	3	carnivore
Rallina tricolor	0	1	2	carnivore
Stegonotus cucullatus	0	2	4	carnivore
Varanus scalaris	0	4	1	carnivore
Acanthiza katherina	0	104	1	invertivore
Arses kaupi	0	149	6	invertivore
Artamus leucorynchus	0	178	6	invertivore
Austrochaperina fryi	0	97	5	invertivore
Austrochaperina pluvialis	0	179	5	invertivore
Austrochaperina robusta	0	62	5	invertivore
Cacomantis castaneiventris	0	79	2	invertivore
Cacomantis flabelliformis	0	123	2	invertivore
Cacomantis variolosus	0	155	2	invertivore
Carlia rubrigularis	0	222	5	invertivore
Carternornis leucotis	0	187	6	invertivore
Chalcites lucidus	0	236	2	invertivore
Chrysococcyx minutillus	0	76	2	invertivore
Coeranoscincus frontalis	0	80	2	invertivore
Colluricincla boweri	0	229	5	invertivore
Colluricincla megarhyncha	0	130	5	invertivore

Species	**Plant links**	**Invertebrate links**	**Vertebrate links**	**Trophic guild**
Cophixalus aenigma	0	278	5	invertivore
Cophixalus exiguus	0	558	5	invertivore
Cophixalus infacetus	0	248	5	invertivore
Cophixalus ornatus	0	144	5	invertivore
Cormobates leucophaea	0	216	1	invertivore
Cyclodomorphus gerrardii	0	100	2	invertivore
Edolisoma tenuirostre	0	4	1	invertivore
Gerygone magnirostris	0	60	1	invertivore
Gerygone mouki	0	293	1	invertivore
Gerygone palpebrosa	0	147	1	invertivore
Glaphyromorphus fuscicaudis	0	541	2	invertivore
Heteromyias albispecularis	0	142	6	invertivore
Hirundapus caudacutus	0	122	2	invertivore
Hypsilurus boydii	0	247	1	invertivore
Lampropholis coggeri	0	271	5	invertivore
Limnodynastes peronii	0	108	15	invertivore
Litoria jungguy	0	62	14	invertivore
Litoria nannotis	0	187	15	invertivore
Litoria rheocola	0	47	15	invertivore
Litoria xanthomera	0	209	14	invertivore
Lophorina victoriae	0	83	6	invertivore
Machaerirhynchus flaviventer	0	68	6	invertivore
Malurus amabilis	0	319	2	invertivore
Merops ornatus	0	359	1	invertivore
Monarcha melanopsis	0	13	6	invertivore
Ninox boobook	0	229	1	invertivore
Oreoscopus gutturalis	0	55	1	invertivore
Orthonyx spaldingii	0	161	6	invertivore
Pachycephala pectoralis	0	43	6	invertivore
Pachycephala simplex	0	499	5	invertivore
Pitta versicolor	0	71	1	invertivore
Podargus papuensis	0	59	1	invertivore
Poecilodryas superciliosa	0	20	6	invertivore
Psophodes olivaceus	0	130	6	invertivore
Rhinolophus megaphyllus	0	358	1	invertivore
Rhipidura fuliginosa	0	112	6	invertivore
Rhipidura rufifrons	0	29	6	invertivore
Saltuarius cornutus	0	204	1	invertivore
Saproscincus basiliscus	0	185	5	invertivore
Saproscincus tetradactylus	0	129	5	invertivore

Species	**Plant links**	**Invertebrate links**	**Vertebrate links**	**Trophic guild**
Sericornis citreogularis	0	567	1	invertivore
Sericornis keri	0	286	1	invertivore
Sericornis magnirostra	0	186	1	invertivore
Symposiachrus trivirgatus	0	84	1	invertivore
Tanysiptera sylvia	0	526	1	invertivore
Tregellasia capito	0	261	6	invertivore
Zoothera heinei	0	101	14	invertivore
Dendrolagus bennettianus	23	0	3	herbivore
Dendrolagus lumholtzi	57	0	3	herbivore
Melomys cervinipes	53	0	6	herbivore
Pseudochirops archeri	38	0	3	herbivore
Pseudochirulus cinereus	37	0	3	herbivore
Pseudochirulus herbivoreertensis	31	0	3	herbivore
Thylogale stigmatica	28	0	3	herbivore
Trichoglossus moluccanus	25	0	1	herbivore
Trichosurus vulpecula	26	0	3	herbivore

Table 2. Diet breadth, classified into plant, invertebrate, and vertebrate trophic links, and trophic guild classification, for all highland network vertebrate species.

Species	Plant links	Invertebrate links	Vertebrate links	Trophic guild
Ailuroedus melanotis	54	19	1	omnivore
Alectura lathami	63	2	5	omnivore
Alisterus scapularis	24	8	3	omnivore
Amblyornis newtonianus	63	164	1	omnivore
Aplonis metallica	54	97	8	omnivore
Bolemoreus frenatus	68	17	1	omnivore
Cacatua galerita	56	156	2	omnivore
Casuarius casuarius	87	94	1	omnivore
Cercartetus caudatus	59	96	3	omnivore
Chalcophaps indica	57	154	1	omnivore
Columba leucomela	63	7	4	omnivore
Coracina lineata	64	172	6	omnivore
Cyclopsitta diophthalma	69	166	3	omnivore
Dactylopsila trivirgata	33	20	3	omnivore
Dicaeum hirundinaceum	47	50	8	omnivore
Erythrura trichroa	38	175	12	omnivore
Eudynamys scolopacea	59	174	1	omnivore
Hypsiprymnodon moschatus	35	14	3	omnivore
Lalage leucomela	34	2	6	omnivore
Lopholaimus antarcticus	23	19	2	omnivore
Macropygia phasianella	81	34	4	omnivore
Megapodius reinwardt	62	164	5	omnivore
Meliphaga lewinii	54	176	1	omnivore
Meliphaga notata	37	37	1	omnivore
Microptilotis gracilis	32	172	1	omnivore
Myzomela obscura	28	5	1	omnivore
Myzomela sanguinolenta	66	5	1	omnivore
Neochmia temporalis	62	4	12	omnivore
Nyctimene robinsoni	52	187	3	omnivore
Oriolus flavocinctus	87	1	6	omnivore
Perameles pallescens	53	85	1	omnivore
Philemon buceroides	57	37	1	omnivore
Platycercus elegans	83	8	3	omnivore
Pogonomys mollipilosus	67	1	6	omnivore
Pteropus conspicillatus	66	167	3	omnivore
Ptilinopus magnificus	21	55	3	omnivore
Ptilinopus regina	37	45	4	omnivore

Species	**Plant links**	**Invertebrate links**	**Vertebrate links**	**Trophic guild**
Ptilinopus superbus	31	17	4	omnivore
Ptilonorhynchus violaceus	30	14	1	omnivore
Rattus fuscipes	61	26	9	omnivore
Rattus leucopus	63	42	9	omnivore
Scenopoeetes dentirostris	35	96	1	omnivore
Scythrops novaehollandiae	33	93	2	omnivore
Sminthopsis leucopus	55	48	3	omnivore
Sphecotheres vieilloti	70	35	6	omnivore
Strepera graculina	83	35	6	omnivore
Sus scrofa	21	162	1	omnivore
Trichoglossus chlorolepidotus	33	169	3	omnivore
Uromys caudimaculatus	33	2	6	omnivore
Xanthotis macleayanus	69	90	1	omnivore
Zosterops lateralis	32	173	7	omnivore
Acanthorhynchus tenuirostris	0	5	1	carnivore
Accipiter novaehollandiae	0	2	2	carnivore
Antechinus flavipes	0	8	3	carnivore
Antechinus godmani	0	1	3	carnivore
Aviceda subcristata	0	9	2	carnivore
Boiga irregularis	0	4	6	carnivore
Rhinella marina	0	2	1	carnivore
Carphodactylus laevis	0	3	1	carnivore
Ceyx azureus	0	3	1	carnivore
Demansia psammophis	0	1	5	carnivore
Dendrelaphis calligastra	0	8	5	carnivore
Dendrelaphis punctulatus	0	2	1	carnivore
Dicrurus bracteatus	0	1	5	carnivore
Eulamprus quoyii	0	8	2	carnivore
Gnypetoscincus queenslandiae	0	5	2	carnivore
Hemiaspis signata	0	6	5	carnivore
Intellagama lesueurii	0	1	1	carnivore
Litoria infrafrenata	0	8	20	carnivore
Litoria serrata	0	5	19	carnivore
Melloria quoyi	0	5	5	carnivore
Mixophyes carbinensis	0	6	7	carnivore
Mixophyes coggeri	0	2	7	carnivore
Mixophyes schevilli	0	2	7	carnivore
Morelia amethistina	0	7	1	carnivore
Ninox rufa	0	8	1	carnivore

Species	**Plant links**	**Invertebrate links**	**Vertebrate links**	**Trophic guild**
Pseudechis porphyriacus	0	6	5	carnivore
Rallina tricolor	0	1	4	carnivore
Stegonotus cucullatus	0	2	6	carnivore
Varanus scalaris	0	4	1	carnivore
Acanthiza katherina	0	104	1	invertivore
Antechinus adustus	0	160	3	invertivore
Arses kaupi	0	149	6	invertivore
Artamus leucorynchus	0	178	6	invertivore
Austrochaperina fryi	0	97	5	invertivore
Austrochaperina pluvialis	0	179	5	invertivore
Austrochaperina robusta	0	62	5	invertivore
Cacomantis flabelliformis	0	123	2	invertivore
Cacomantis variolosus	0	155	2	invertivore
Carlia rubrigularis	0	222	6	invertivore
Carternornis leucotis	0	187	6	invertivore
Chalcites lucidus	0	236	2	invertivore
Chrysococcyx minutillus	0	76	2	invertivore
Coeranoscincus frontalis	0	80	2	invertivore
Colluricincla boweri	0	229	5	invertivore
Colluricincla megarhyncha	0	130	5	invertivore
Cophixalus aenigma	0	278	5	invertivore
Cophixalus australis	0	199	5	invertivore
Cophixalus concinnus	0	185	5	invertivore
Cophixalus hosmeri	0	139	5	invertivore
Cophixalus infacetus	0	248	5	invertivore
Cophixalus monticola	0	579	5	invertivore
Cophixalus neglectus	0	12	5	invertivore
Cophixalus ornatus	0	144	5	invertivore
Cormobates leucophaea	0	216	1	invertivore
Cyclodomorphus gerrardii	0	100	2	invertivore
Edolisoma tenuirostre	0	4	1	invertivore
Gerygone mouki	0	293	1	invertivore
Gerygone palpebrosa	0	147	1	invertivore
Glaphyromorphus fuscicaudis	0	541	2	invertivore
Glaphyromorphus mjobergi	0	90	2	invertivore
Heteromyias albispecularis	0	142	6	invertivore
Hirundapus caudacutus	0	122	2	invertivore
Hypsilurus boydii	0	247	1	invertivore
Lampropholis coggeri	0	271	6	invertivore
Lampropholis robertsi	0	513	6	invertivore

Species	Plant links	Invertebrate links	Vertebrate links	Trophic guild
Limnodynastes peronii	0	108	19	invertivore
Litoria jungguy	0	62	19	invertivore
Litoria nannotis	0	187	20	invertivore
Litoria rheocola	0	47	20	invertivore
Litoria xanthomera	0	209	19	invertivore
Lophorina victoriae	0	83	6	invertivore
Machaerirhynchus flaviventer	0	68	6	invertivore
Merops ornatus	0	359	1	invertivore
Monarcha melanopsis	0	13	6	invertivore
Ninox boobook	0	229	1	invertivore
Oreoscopus gutturalis	0	55	1	invertivore
Orthonyx spaldingii	0	161	6	invertivore
Pachycephala pectoralis	0	43	6	invertivore
Pachycephala simplex	0	499	5	invertivore
Pitta versicolor	0	71	1	invertivore
Podargus papuensis	0	59	1	invertivore
Psophodes olivaceus	0	130	6	invertivore
Rhinolophus megaphyllus	0	358	1	invertivore
Rhipidura fuliginosa	0	112	6	invertivore
Rhipidura rufifrons	0	29	6	invertivore
Saltuarius cornutus	0	204	1	invertivore
Saproscincus basiliscus	0	185	6	invertivore
Saproscincus czechurai	0	73	6	invertivore
Saproscincus tetradactylus	0	129	6	invertivore
Sericornis citreogularis	0	567	1	invertivore
Sericornis keri	0	286	1	invertivore
Sericornis magnirostra	0	186	1	invertivore
Symposiachrus trivirgatus	0	84	1	invertivore
Tanysiptera sylvia	0	526	1	invertivore
Taudactylus rheophilus	0	387	7	invertivore
Tregellasia capito	0	261	6	invertivore
Zoothera heinei	0	101	14	invertivore
Zoothera lunulata	0	95	14	invertivore
Dendrolagus bennettianus	23	0	3	herbivore
Dendrolagus lumholtzi	57	0	3	herbivore
Hemibelideus lemuroides	27	0	3	herbivore
Melomys cervinipes	53	0	6	herbivore
Pseudochirops archeri	38	0	3	herbivore
Pseudochirulus cinereus	37	0	3	herbivore

Species	**Plant links**	**Invertebrate links**	**Vertebrate links**	**Trophic guild**
Pseudochirulus herbivoreertensis	31	0	3	herbivore
Thylogale stigmatica	28	0	3	herbivore
Trichoglossus moluccanus	25	0	1	herbivore
Trichosurus vulpecula	26	0	3	herbivore

Chapter 5

Quantifying coextinction risk of vertebrates in the Australian Wet Tropics under future climate change

Abstract

Climate change will directly impact biodiversity, with coextinctions potentially exacerbating these losses. However, the indirect effects of climate-induced coextinctions remain underexplored, particularly at finer spatio-temporal scales needed to manage terrestrial ecosystems. Using trophic network models of vertebrate communities in the Wet Tropics of Australia, I evaluated potential climate-induced coextinctions through extinction/coextinction simulations. These simulations tested coextinction rates under four climate-projection scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, SSP5-8.5) by 2100, examining how species' abilities to rewire trophic interactions, shift elevational ranges, and withstand resource loss affected extinction risk. Results suggest that temperature increases will cause as many or more primary extinctions as coextinctions, with coextinction contributing ≤ 24% and ≤ 50% in low- and high-elevation communities, respectively. The adaptive abilities of a species influence their extinction vulnerabilities; in the lowland network, the ability to shift elevational range reduced risks more, while trophic rewiring was more important for species in the highland network to reduce risks due to spatial constraints. These adaptions, when combined, provided more defences against coextinction, especially for species in the lowland network; however, the inherent vulnerability of species from the highland network suggested an overall elevated and sustained extinction risk. Vertebrates at higher trophic levels, despite lower susceptibility to primary extinction, had greater vulnerability to coextinctions, especially in ectothermic taxa. Some species in lower-medium-trophic levels also had high coextinction risks, potentially destabilising communities, although they were largely negligible compared to coextinctions caused by loss of basal resources. These patterns were consistent across different simulations, suggesting that the food-web topology of communities influences coextinction dynamics more

than the adaptive abilities of specific species. Conservation efforts should therefore focus on critical species groups and the maintenance of basal resources to maintain ecological stability and preserve these vulnerable communities under future climate change. In this chapter, I advocate for multifaceted conservation strategies addressing primary and coextinction risks to preserve biodiversity in the Wet Tropics. I also highlight the need to apply this approach to identify potentially hidden extinction pathways in other similarly complex terrestrial communities. The chapter also accentuates how future research should continue refining extinction risk predictions by incorporating multiple threats and enhancing the ecological realism of network models to evaluate coextinction risks.

Introduction

How global warming will directly affect species by challenging their thermal tolerances is a well-established research area (Dressler et al., 2023; Hickling et al., 2006; Sunday et al., 2012). Recent estimates of the direct effects forecast extinction rates of between 3 million and 6 million species in the next 50 years globally (Wiens & Zelinka, 2024). Yet, our understanding of how climate change influences the risk of extinction in vertebrate species through indirect mechanisms — such as trophic cascades — remains inadequately explored, particularly at fine spatio-temporal scales (e.g., regional or local areas over shorter seasonal, annual, or decadal ecologically relevant timeframes) to monitor and manage ecological communities (Doherty et al., 2023). The dearth of such studies is in part due to the difficulty of describing community boundaries (Fraser et al., 2019), documenting and quantifying trophic interactions (e.g., cryptic relationships) (Pringle & Hutchinson, 2020), and simulating the processes of ecological cascades realistically (Strona, 2022b; Chapter 1).

Coextinctions — defined as extinctions triggered by other extinctions (extinction cascades) — are a major contributor to the current decline of biodiversity globally (Kehoe et al., 2021). Not considering or underestimating coextinctions caused by climate change or other anthropogenic threats can give inaccurate predictions of how biodiversity will respond. Indeed, trophic cascades and coextinctions magnify the impact of primary extinctions (Colwell et al., 2012; Strona & Bradshaw, 2018) because extinction risks substantially increase when coextinctions are considered (Chapter 4). For instance, Strona and Bradshaw (2022) quantified coextinction risks of terrestrial vertebrate food webs to future climate and land-use changes at a global scale and found that coextinctions substantially increase extinction risks, and that this effect was most prominent under intermediate-severity projection scenarios. Conversely, coextinctions were a smaller proportion of the simulated total extinctions in the worst-case projection scenarios because the direct effects of increasing temperatures exceeded most species' thermal tolerances and led to more primary extinctions. These findings highlight the important role coextinctions could play in escalating biodiversity loss in the coming decades. If we are to develop management actions aimed at minimising extinction rates, we need to consider both primary extinctions and coextinctions.

Nevertheless, our understanding of which species, or types of species, are most susceptible to coextinction remains limited. Some research supports the prediction that species with a wider diet-breadth can rewire lost trophic interactions more easily than those with a narrower diet-breadth, making the former less sensitive to the loss of trophic resources (Appel et al., 2018; Brzęk et al., 2010). Trophic rewiring can also enhance network persistence (Kondoh, 2003) by reducing trophic cascading effects (Maia et al., 2021; Ramos-Jiliberto et al., 2012; Valdovinos et al., 2010), increasing the number of trophic links that a species has within its community buffering against these effects (Kagata et al., 2005; Scherber et al., 2010), and suggesting that species less able to rewire should have higher risks of coextinction (Schleuning et al., 2016).

The ability of species in terrestrial ecosystems to occupy or move across altitudes can also be inversely related to their extinction vulnerability (White & Bennett, 2015), contributing to the high vulnerability predicted for narrow-range endemic species that have restricted distributions and often a limited capacity to reach cooler refugia (Wheatley et al., 2023). For example, arboreal vertebrates in the Australian Wet Tropics can exploit climatically uncertain areas (i.e., can migrate across both lower and higher elevational ranges), a capability that has served them well through natural climate fluctuations in the past and could help them in the future as temperatures rise (Scheffers et al., 2017). Trophic level can also influence a species' vulnerability, but this is contextual — there is evidence that species from high-trophic levels are particularly vulnerable to coextinction (Duffy, 2003; Purvis et al., 2000), but countervailing data suggesting that species from lower trophic levels are most vulnerable (Llewelyn et al., 2022; Scherber et al., 2010).

Species also differ in terms of their importance for causing coextinctions, with species that play a disproportionate role within their community (e.g., with many links or high betweenness centrality) tending to trigger larger extinction cascades (Eklöf & Ebenman, 2006; Lai et al., 2012). This 'keystone' species concept, originally defined by Paine (1969), posits that a single species can modify the composition or semblance of an ecosystem. From a network perspective, keystone species are those that exert large influence over the structure and function of ecosystems through processes like trophic cascades. Such effects are largely realised by large-bodied, high-trophic level terrestrial carnivores (Ripple et al., 2014), such as wolves (*Canis lupus*) preying on moose (*Alces alces*) that can subsequently affect the growth of balsam fir (*Abies balsamea*) (McLaren & Peterson, 1994). However, other recent analyses suggest that many smaller-bodied, low-trophic level species are more commonly classified as keystone species (Shukla et al., 2023). If confirmed, the extinction of low trophic-level species might elicit more coextinctions than their higher trophic-level counterparts.

Understanding coextinction dynamics is necessary in tropical montane rain forests such as the Wet Tropics because they are global biodiversity hotspots (Peters et al., 2019; Polato et al., 2018) and characterised by substantial endemism (Hamilton et al., 2012). Yet, they are also among the most sensitive ecosystems to global change, being vulnerable to climate change-induced extinctions (Karger et al., 2021) and threatened by other human activities such as deforestation (Cazalis et al., 2021). Projections indicate that ongoing anthropogenic changes will have progressively worse and irreversible consequences for these ecosystems (Jan et al., 2023). Although the Australian Federal and Queensland State governments have jointly established a world-leading management system for the Wet Tropics (e.g., by banning logging and hunting) (Stork et al., 2011), several detrimental processes continue to affect the region's biota. These include invasive species, emerging diseases, habitat fragmentation, vehicle collisions, and changes in hydrological and fire regimes (Goosem, 2009; Laurance & Goosem, 2008; Pearson & Stork, 2008).

Several species endemic to the Wet Tropics have already gone extinct due to these pressures in recent years, including both the sharp-snouted day frog (*Taudactylus acutirostris*) and the mountain mist frog (*Litoria nyakalensis*) (IUCN, 2021; Schloegel et al., 2006), with many more extinctions likely this century (Fordham et al., 2016; Torkkola et al., 2022). While these threats will erode biodiversity, climate change is currently recognised as the greatest threat to the biota of the Wet Tropics in the coming decades (Dyez et al., 2024). Indeed, Williams et al. (2003) predicted large altitudinal range shifts and population declines in response to climate change in the Wet Tropics later this century, and several studies have recently confirmed the initiation of such responses (de la Fuente et al., 2022; de la Fuente & Williams, 2023; Williams & de la Fuente, 2021). Recent data also show that temperatures on certain mountain peaks have reached record highs years ahead of predictions (Queensland Parks and Wildlife Service, unpublished, 2023). Climate-change-induced loss of suitable habitats could lead to many extinctions, especially if temperature increases by > 2 °C this century (Williams et al., 2003). Although some have investigated the primary (direct) effects of climate change on biodiversity in the Wet Tropics using species distribution modelling (Williams et al., 2003) and abundance estimates (S. E. Williams et al., 2010), global extinction/coextinction studies suggest these approaches might underestimate the true impact of climate change on biodiversity because many species will likely go extinct as a result of further indirect effects (Strona & Bradshaw, 2018).

In this chapter, I built on the trophic network models for low- and high-elevation communities from the Wet Tropics constructed in Chapters 3 and 4 and subjected them to extinction/coextinction simulations. In Chapter 4 simulations, I assigned primary extinction at random, adjusting the rate to reflect the estimated baseline, current, or future extinction rates for the different taxonomic groups. In this chapter, I assigned primary extinction rates according to the vulnerability of each species to increases in ambient temperature (under different climate-projection scenarios). I also tested how the ability of species to rewire trophic interactions, shift elevational ranges, and withstand the loss of trophic resources influenced the overall number of extinctions (including primary extinctions and coextinctions). Thus, this chapter aims to evaluate climate change-linked extinction risks of vertebrates in the Wet Tropics bioregion, considering both direct and indirect effects. I ran simulations using different, empirically based climate-projection scenarios (to 2100), with the objective of quantifying the extinction risk of vertebrate species. I address four main questions: (*i*) How important are coextinction cascades to future vertebrate species extinction risk in the Wet Tropics?; (*ii*) Are some vertebrate trophic levels and taxonomic classes more vulnerable to climate change-induced cascades than others?; (*iii*) Are some vertebrate trophic levels and taxonomic classes disproportionally important for maintaining ecosystem stability?; and (*iv*) Is the importance (in terms of the number of extinctions) of climate change-induced cascades influenced by the capacity of species to shift their elevational range and rewire their trophic interactions?

Answering these questions requires testing the following five hypotheses: (1) Under intermediate future climate-projection scenarios (SSP2-4.5 and SSP3-7.0), coextinction will affect species extinction risk disproportionately among species. This effect will be more pronounced than under the worst-case climate-projection scenario (SSP5-8.5) because of initially eliciting some species to go extinct primarily but for others to survive long enough for trophic cascades to occur. In contrast, the direct effects of climate change will proportionally contribute more to vertebrate extinctions due to exceeding more thermal tolerance limits under the worst climate-projection scenario and vice versa (contribute less) for the best-case climate-projection scenario (SSP1-2.6). (2) Coextinction rates under different climate-projection scenarios will increase with trophic level due to the cumulative effects of decreased prey availability across lower trophic levels, leading to increased coextinction risk. (3) Species from lower trophic levels will be more important for triggering coextinctions than species from higher trophic levels. (4) Under most climate-projection scenarios (SSP1-2.6 to SSP3-7.0), communities with species unable to shift their elevational range to track their climate space will experience higher extinction rates compared to communities whose species can adjust their elevational range. However, under the most extreme future climate-projection scenario (SSP5-8.5), I posit that species' ability to shift elevational range will not affect overall extinction much, meaning that extinction rates will be similar for both low- and high-elevation communities as species displaced to the summits of mountain areas eventually run out of suitable climate space and become extinct. (5) Communities, including species with no or limited ability to rewire trophic interactions after losing food resources, will have a higher rate of coextinction than communities consisting of species that can rewire their trophic interactions.

Methods

To assess the vulnerability of low- and high-elevation Wet Tropics communities to climate change-induced primary and coextinctions, I investigated how simulated extinction rates were affected by (*i*) different climate change scenarios, (*ii*) the capacity of species to adjust through trophic rewiring and shifting their elevational range, and (*iii*) differences in sensitivity to the loss of trophic resources (coextinction threshold).

Simulating extinctions

To assess future primary and coextinctions in low- and high-elevation communities, I built network models of each community (defined in Chapter 2; Chapters 3 and 4 detail how I built the networks) and applied four simulation types (Figure 1). These simulations aimed to model networks with different capacities to adjust to climate, forecasting species extinctions assuming: (*i*) no species can shift elevational range or rewire lost trophic interactions when resource nodes go extinct, (*ii*) some selected (dispersive) species can shift elevational range, but no species can rewire lost trophic interactions when resources go extinct, (*iii*) no species can shift elevational range, but they have the ability to rewire a proportion of lost trophic interactions when associated resources go extinct, and (*iv*) some selected species have the ability to shift elevational range, and all species can rewire a proportion of their lost trophic interactions when associated resources go extinct.

For each of the four simulation types, I also varied the coextinction threshold to assess how a species' capacity to withstand the loss of trophic resources influenced extinction rates. These coextinction thresholds are the proportion of trophic resources that can go extinct before a consumer goes coextinct. I tested coextinction thresholds of 25% (worst-case), 50% (intermediate-case), and 100% (best-case). In addition to varying the coextinction threshold and the capacity of species to adjust, I tested outcomes under four climate-projection scenarios (from best-case to worst-case) represented as different Shared Socioeconomic Pathways (SSPs), which are standardised scenarios that simulate the impacts of different socioeconomic trends on future climate change and its consequences. These included SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. I ran one thousand replicate simulations for each combination of the variables (i.e., adaptability, coextinction threshold, and climate-change scenario) using a high-performance computer (DeepThought HPC) (Flinders University, 2021) (Figure 1).

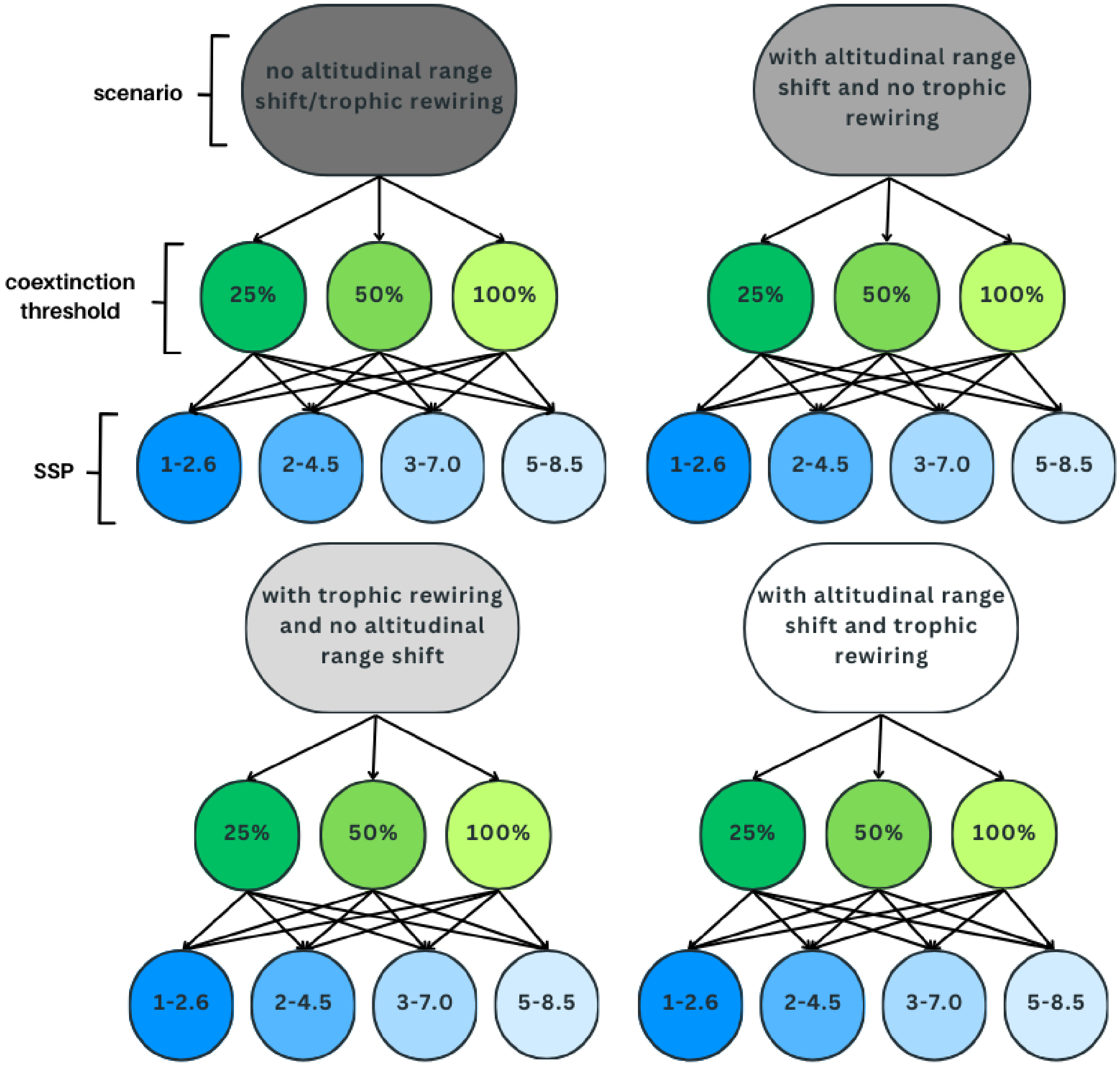

Figure 1. Variable combinations used in the four types of extinction/coextinction simulation. I varied: (*i*) species' capacity to shift elevation, (*ii*) species' capacity to rewire their interactions, (*iii*) the coextinction threshold that triggered coextinctions, and (*iv*) climate change-projection scenarios (SPPs). I ran extinction/coextinction simulations 1,000 times for each of the 48 unique combinations of variables (i.e. species adaptability, coextinction threshold, and climate-change scenario) to assess the impacts of varying parameters and climatic conditions on species extinction risk.

Calculating vertebrate species' upper thermal limit

To estimate each vertebrate species' upper thermal limit (i.e., the hottest environments in which a species can survive and reproduce), I used 3,055,261 species occurrence records gathered by Stephen Williams and colleagues (James Cook University) during standardised field transect surveys through the Australian Wet Tropics bioregion between 1997 and 2008. I combined the occurrence records with historical climate data collected from 1970–2000 at a spatial resolution of 30 seconds (~ 1 km^2) from *WorldClim* (v 2.1). I extracted the maximum values for the bioclimatic variable 'Max Temperature of the Warmest Month' for each species' occurrence records to represent the hottest ambient conditions/environments in which the species can survive and reproduce. This procedure is correlated with species' physiological thermal tolerances in the Wet Tropics (de la Fuente et al., 2022; S. Williams et al., 2010), so that I used these estimates to predict responses to projected future climates. I discarded alternative approaches, such as the use of physiological limits (e.g., critical thermal maxima), because upper thermal physiological limits are not correlated with ambient thermal conditions in many species and might instead reflect thermoregulatory behaviour (Clusella-Trullas et al., 2011; Muñoz et al., 2016). For example, lizards in cold, high-elevation sites can have higher critical thermal maximums than skinks in hotter, low-elevation sites (Carilo Filho et al., 2022). There is also a dearth of physiological data available for species in the Wet Tropics (Bennett et al., 2018). Rather than using physiological data as a measure of the hottest place in which a species is most likely to live, I instead used the hottest known place a species lives.

Calculating vertebrate species' ability to shift elevational range

Depending on the Shared Socioeconomic Pathways realised, the Wet Tropics will likely warm by between 0.4 and 3.9 °C by 2100. For some species, areas that are currently inhabited will become too warm, while other areas that are too cold now (i.e., high-elevation sites) could become suitable refugia. The ability of species to move to higher, cooler elevations is, therefore, likely to increase persistence probability (i.e., avoiding primary extinction) and will also have implications for other species that interact directly or indirectly with them (Hrubá et al., 2023). I therefore tested the effect of elevational migration on primary and coextinctions in my simulations. However, it is not known whether vertebrate species can shift their elevational range from low- to high-elevation areas because only some species might be able to shift. I therefore inferred the capacity for elevational shifts based on each species' potential for long-distance dispersal, as quantified by S. Williams et al. (2010). This measure is a reliable predictor for dispersal success (de la Fuente et al., 2022). For species where the potential for long-distance dispersal was unknown, I used elevation distribution data to infer capacity for elevational shifts (IUCN, 2023). In these cases, if a species occurs at higher elevations (> 850 m above mean sea level; see Chapter 2) in different regions, I assumed they had the ability to migrate to higher elevations in the Wet Tropics. I did not resolve/assign plant and invertebrate species' nodes because few data exist on these assemblages in the Wet Tropics; instead, I based the number of these nodes on relative diversity estimates (see Chapter 4 for methods). Thus, I assumed that species with unknown attributes were not able to shift elevational range. Furthermore, due to the current lack of sufficient data, it was not possible to make informed assumptions about how many plant and invertebrate species might migrate to highland areas and integrate into associated communities under likely future climate change in the Wet Tropics, or make assumptions based on similar communities.

Calculating vertebrate species' ability to rewire trophic interactions

To investigate how the potential for species to rewire their trophic interactions could affect (*i*) their vulnerability to coextinctions and (*ii*) the stability of their associated ecological network, I ran simulations with and without allowing species to establish new trophic interactions following the extinction of their resource nodes.

To calculate species' capacity to rewire trophic interactions, I compiled and $\log_{10}$-transformed species estimated diet-breadths — representing the number of trophic links each vertebrate species had to plants, invertebrates, and vertebrates in each network —to normalise the data. I then re-scaled the diet-breadth data (from 0 to 1) by dividing each species' diet-breadth in the three resource categories (plants, invertebrates, and vertebrates) by the maximum diet-breadth observed for that resource category separately in their respective network. I then used this scaled diet-breadth to infer a species' capacity to rewire links to each resource category (i.e., higher values = a greater capacity to rewire), ensuring comparability and proportionality between species that fed on the different groups of resources. I estimated the number of recovered trophic links by multiplying each species' diet-breadth by the respective fractions of trophic links attributed to invertebrates and plants. I calculated this separately for plant and invertebrate trophic links to reflect the specific proportions of each resource type in the diet (based on the number of links), ensuring that the potential for establishing new trophic interactions was in line with their existing dietary patterns. I further constrained the number of potential new trophic interactions not to exceed the species' original diet-breadth in each resource category to avoid overestimating capacity for dietary plasticity, which I did separately for both low- and high-elevation networks.

Based on the number of possible rewired trophic interactions calculated for each vertebrate species, if any invertebrate or plant nodes that a species preyed upon became lost due to primary or coextinction, the vertebrate species could randomly rewire to any available plant or invertebrate nodes in the network, provided they did not already have an existing trophic link with that node. For example, if a species that initially had 23 plant and 50 invertebrate trophic links and a rewiring capacity of 0.43 and 0.4 for plants and invertebrates, respectively (e.g., the species could rewire up to 40% of its original trophic links, calculated as 50/100 = 0.5, resulting in a maximum of 20 new links by multiplying 0.50 by 40), lost 10 plant links and 33 invertebrate links due to extinction of those resources, it could rewire to 10 new plant nodes and 20 invertebrate nodes. If there were fewer nodes available in the network than the predicted number of rewired trophic links for a species, I limited the number of rewired links realised by the number of remaining available nodes. I also considered plant and invertebrate nodes that were not originally connected to the vertebrate network but were presumed to exist based on the diversity estimates from Chapter 4 when rewiring. I randomly assigned the new trophic links to any available plant or invertebrate nodes in the network. However, if a species' number of trophic links was below the pre-defined coextinction threshold (defined as a proportion — either 25%, 50% or 100% — of the number of links the species originally had) after rewiring, that species could still become coextinct.

Initially, I did not consider rewiring for vertebrate-vertebrate links, because trophic interactions already represent all probable trophic links in their network (Chapter 3). However, in simulations where vertebrate species were able to shift their elevational range from low- to high-elevation areas and subsequently encounter new species, I permitted rewiring between these species if the probability of a trophic link determined by the random forest model was ≥ 50% (consistent with methods in Chapter 3). Additionally, lowland vertebrates that shifted their elevational range to that of the highland network could rewire to all available plant and invertebrate nodes within that network.

Simulating future climate scenarios and calculating species' primary and coextinctions

To forecast the climate low- and high-elevation networks might encounter between 2081–2100, I gathered downscaled, monthly, 30-second (~ 1 km^2) spatial resolution climate forecast data for the Wet Tropics bioregion from the Coupled Model Intercomparison Project (Phase 6) sourced from the *WorldClim* database (v 2.1). I obtained these climate data for each of the 14 general circulation models projecting each SSP (i.e., four scenarios: SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) each year from 2081–2100 to simulate projected climate change to the end of the current century. I stacked each general circulation model into a mean ensemble model for each SSP. I then extracted the 'Maximum Temperature of the Warmest Month' (the same bioclimatic variable used to quantify a species' maximum thermal range) from each ensemble model to examine the hottest temperature projection for each SSP for the Wet Tropics. I averaged this value for both lowland (0–450 m above mean sea level) and highland areas (> 850 m above mean sea level), defined by the elevational range of low- and high-elevation communities (Chapter 2). Overlaying these digital elevation models with the calculated ensemble models for each SSP and linking this to species' distributional data and thermal tolerance, I identified which vertebrate species would go extinct due to the direct effects of temperature increases (i.e., primary extinctions) in low- and high-elevation areas, and the sequence in which they would go extinct. Specifically, the calculation assumed that if ≥ 90% of the identified low- or high-elevation areas exceeded the species' estimated maximum thermal tolerance, it would not survive at that elevation. However, in simulations where species from the low-elevation network could shift their elevational range to that of the high-elevation network, I did not consider them primarily extinct for the low-elevation network.

Because I could not resolve plant and invertebrate nodes to real species, this affected how I could simulate extinctions in these components of the networks. For example, I could not model the primary extinctions triggered by temperature increases in plants and invertebrates in the same way I did for vertebrates because plant and invertebrate nodes did not have associated distributional information and thermal limits. Because I did not include trophic interactions between plants and invertebrates, and between invertebrates, in the networks, I could not model coextinctions in these groups as I did for the vertebrate component of the networks. To overcome these limitations, I used published estimates of extinction rates (including primary and coextinctions) for plants and invertebrates for each SSP projection. For SSPs 2-4.5 and SSP5-8.5, I based plant and invertebrate primary and coextinction rates on estimates by Strona and Bradshaw (2022). However, for SSP1-2.6 and SSP3-7.0, where Strona and Bradshaw (2022) did not estimate extinction rates, I estimated these rates based on an extrapolation of SSPs 2-4.5 and an interpolation of SSP5-8.5, respectively using a linear regression model. For each SSP, I then used these extinction rates to calculate the number of species expected to go extinct among the total estimated number of plants and invertebrates in each network and randomly selected which specific plant and invertebrate nodes went extinct.

After removing extinct plant and invertebrate nodes and vertebrate nodes lost to primary extinction, I simulated the trophic cascades caused by these extinctions. I assumed a vertebrate species went secondarily extinct if it lost a proportion of its resources ≥ the pre-defined coextinction threshold. I designed this process to continue iteratively, so each time a coextinction occurred, I recalculated the number/proportion of resources lost for each remaining species, and any of these species that lost too many resources also went coextinct. This method meant that vertebrate species could also become coextinct first in a given replicate of a simulation due to the primary or coextinction of another vertebrate, plant or invertebrate resource before it could become primarily extinct (as a result of temperatures exceeding its maximum thermal range).

I calculated how many primary and coextinctions occurred under the different simulation scenarios — which varied according to climate-projection scenario and the capacity of species for rewiring and migration — to assess the potential importance of primary and coextinctions in these networks. Here, I pooled the results across coextinction thresholds to analyse overall patterns regarding the total number of estimated extinctions. I also calculated the average proportion of primary versus secondary vertebrate extinctions for the different simulation scenarios and coextinction thresholds tested based on the species initially found in each community.

I calculated vulnerability to both primary and coextinction separately for each network, for each taxonomic class, and trophic level by evaluating the mean percentage a vertebrate species became either coextinct or primarily extinct across all simulation types, coextinction thresholds (25%, 50%, and 100%), and climate-projection scenarios evaluated. In the appendix, I also separated by simulation type and different coextinction thresholds tested, and combined across all climate-projection scenarios assessed. I calculated the trophic level and the propensity to go extinct from primary and coextinctions separately for each species in the different simulations (see Figure 1 for simulation types). Because low- and high-elevation networks do not reliably indicate realistic trophic levels for each species (Chapter 3), I defined trophic levels based on each species' diet type. I classified trophic level = 1 (low) as all herbivores whose diet comprises ≥ 70% plants. I classified trophic level = 1–2 (low–medium) as all omnivores that consume both plants and invertebrates, as well as invertivores. Within these levels, I defined omnivores as having a diet with > 0% but < 70% invertebrates, > 0% but < 70% plants, and no vertebrates. I defined invertivores as species whose diet consists of ≥ 70% invertebrates. I classified trophic level = 2–3 (medium–high) as omnivores that consume plants, invertebrates, and vertebrates. In these levels, I defined omnivores as having a diet with > 0% but < 70% invertebrates, > 0% but < 70% plants, and > 0% vertebrates. Lastly, I defined trophic level = > 3 (high) as vertivores whose diet comprises ≥ 70% of other vertebrates, ignoring cannibalistic links.

Lastly, I also calculated the mean percentage of vertebrate coextinctions caused by primary vertebrate extinctions separately in each network for each trophic level and taxonomic class across all simulation types, coextinction thresholds (25%, 50%, and 100%), and climate-projection scenario evaluated. In the appendix, I separated this further into simulation type and different coextinction thresholds tested, combined across all climate-projection scenarios assessed.

Results

Total primary and coextinctions

The mean proportion of extinctions (primary and coextinctions combined) increased with the severity of climate-projection scenarios across simulations, from 9.5% under the best-case scenario (SSP1-2.6) to 87.7% under the worst-case scenario (SSP5-8.5) in the highland network, and from 5.4% to 100% in the lowland network (Figure 2). Across both elevation networks, the highest mean extinction rates occurred in simulations where species could neither rewire trophic interactions nor shift their elevational range. In the lowland network, extinction rates varied from 43.4% (SD ± 1.1%) under SSP1-2.6 and escalated to 100% (no error) under SSP5-8.5 (Figure 2a). In the highland network, extinctions were lower at 9.5% (± 3.1%) under SSP1-2.6 and 87.6% (± 6.5%) under SSP5-8.5 (Figure 2a).

Allowing species to shift their elevational range but not rewire their trophic interactions had the largest effect in the lowland network, reducing mean estimated extinctions by as much as 37.9% compared to negligible differences in the highland network. Here, mean extinctions dropped to 5.5% (± 1.1%) under SSP1-2.6 in the lowland network, but remained high at 9.5% (± 3.2%) in the highland network (Figure 2b). Under SSP5-8.5, extinction rates still peaked at 86.8% (± 6.9%) in the lowland network and 87.7% (± 6.5%) in the highland network, indicating no detectable reduction in extinction rates in the latter (Figure 2b).

In simulations where species could only rewire trophic interactions but could not shift their elevational range, mean extinction rates were similar to those when species had no adaptive capacities. There were negligible differences in the lowland network, but the mean extinction rates declined by 4.1% in the highland network. The lowland network maintained elevated extinction rates at 43.4% (± 1.1%) under SSP1-2.6, and increased up to 100% under SSP5-8.5, while the highland network had lower extinctions rates at 9.5% (± 3.0%) under SSP1-2.6 and 83.5% (± 0.8%) under SSP5-8.5 (Figure 2c).

When allowing species to rewire trophic interactions and shift their elevational range, extinction rates were the lowest across all climate-projection scenarios, with mean extinction rates reduced by as much as 37.96% in the lowland network and 4.1% in the highland network. In the lowland network, extinction declined to 5.4% (± 1.1%) under SSP1-2.6, but increased to 82.4% (± 0.8%) under SSP5-8.5. In the highland network, extinction rates remained low at 9.5% (± 3.0%) under SSP1-2.6 and increased to 83.5% (± 0.8%) under SSP5-8.5 (Figure 2d).

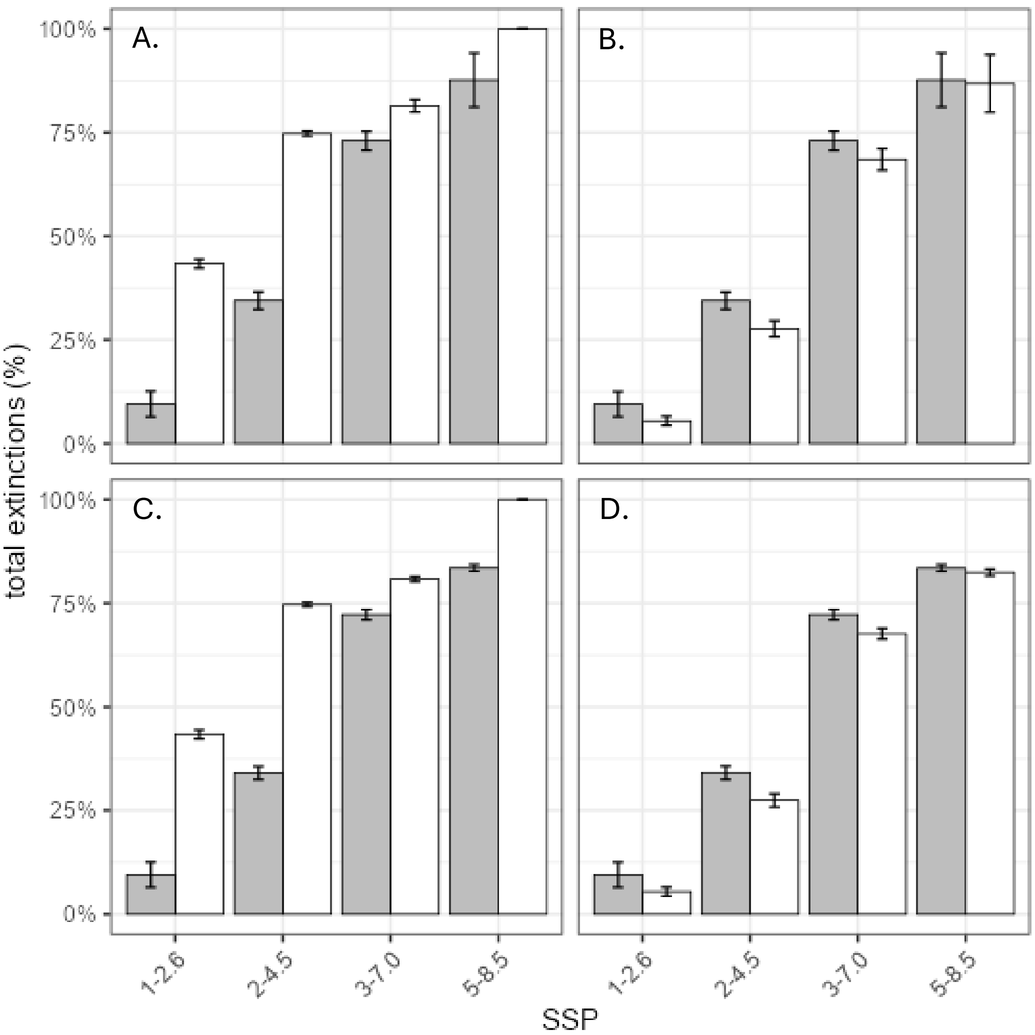

Figure 2. Estimated mean proportion of species that were estimated to go extinct (primary and coextinctions combined = total extinction in %) in both the lowland network (white bars) and highland network (grey bars) under four climate change-projection scenarios (shared socioeconomic pathways; SSPs) and four types of extinction simulation. The four types of simulation compared include: A. species cannot rewire interactions or shift elevational range, B. species can shift elevational range, C. species can rewire trophic interactions, and D. species can shift elevational range and rewire trophic links. Simulation results for all coextinction thresholds modelled (25%, 50%, and 100%) were also incorporated and combined for each SSP.

Proportion of primary versus coextinctions

The proportion of total vertebrate extinctions that were coextinctions varied widely across climate-projection scenarios and simulations, generally decreasing with increasing coextinction threshold. In the lowland network, the proportion of coextinctions ranged from 0.01 to 0.83, while in the highland network, they ranged from 0 to 0.86. For simulations where vertebrate species could neither shift their elevational range nor rewire trophic interactions, the proportion of coextinctions in the lowland network under a 25% coextinction threshold ranged from 0.12 to 0.83 across climate-projection scenarios, peaking under SSP5-8.5 (Figure 3a). This trend of fewer coextinctions persisted across higher thresholds, with SSP5-8.5 yielding low proportions (0.04 to 0.06 at 50% and < 0.01 at 100%; Figure 3a). In the highland network under the same 25% threshold, the proportion of coextinctions ranged from 0.22 to 0.85, again the highest under SSP5-8.5 (Figure 4a). This trend of reduced proportion of coextinctions at higher thresholds persisted, although highland coextinctions remained consistently higher than those in the lowland network (0.08–0.09 at 50% and 0.00–0.02 at 100%; Figure 3a & 4a).

In simulations where species could only shift their elevational range, the proportion of coextinctions in the lowland network followed a similar decreasing pattern with increasing threshold, but remained somewhat higher in most climate-projection scenarios (SSP1-2.6: 0.30, SSP2-4.5: 0.25, SSP3-7.0: 0.23), but highest under SSP5-8.5 at a 25% threshold (0.83; Figure 3b). In the highland network, coextinctions proportionally dominated again under SSP5-8.5 at a 25% threshold (0.86), with generally higher proportions across all climate-projection scenarios compared to the lowland network (e.g., SSP1-2.6: 0.42, SSP2-4.5: 0.29, SSP3-7.0: 0.31; Figure 3b & 4b). For simulations where species could only rewire trophic interactions, the proportion of coextinctions in the lowland network declined across all climate-projection scenarios as coextinction thresholds increased (e.g., SSP1-2.6: 0.12–0.02, SSP2-4.5: 0.12–0.01, SSP3-7.0: 0.14–0.02, SSP5-8.5: 0.16–0.01; Figure 3c). In the highland network, proportions were marginally lower than in simulations where species could only shift their elevational range at a 25% threshold (SSP2-4.5: 0.21, SSP3-7.0: 0.16, SSP5-8.5: 0.21), but remained high under SSP1-2.6 where coextinctions proportionally accounted for nearly half of all extinctions (0.48); again the same trend of greater decreases with increasing coextinction threshold (25% to 100%;

Figure 4c). Generally, the highland network had higher coextinction proportions than the lowland network across climate-projection scenarios and thresholds (Figure 3c & 4c).

When species could shift their elevational range and rewire trophic interactions in the lowland network, coextinction patterns were similar to those when species could only rewire trophic interactions (Figure 3c & d), except for some climate-projection scenarios (SSP1-2.6 and SSP2-4.5) with marginally higher or a comparable proportion of coextinctions at a 25% threshold (0.50 and 0.24, respectively; Figure 3d). For higher thresholds (50% and 100%), specific climate-projection scenarios (SSP1-2.6, SSP2-4.5, and SSP3-7.0) had no observed coextinctions (Figure 3d). In the highland network, these simulations reflected similar trends, but with generally higher coextinction proportions across climate-projection scenarios and thresholds (e.g., SSP1-2.6: 0.50–0.00, SSP2-4.5: 0.25–0.02, SSP3-7.0: 0.19–0.00, SSP5-8.5: 0.17–0.00), consistently exceeding those observed in the lowland network (Figure 4d).

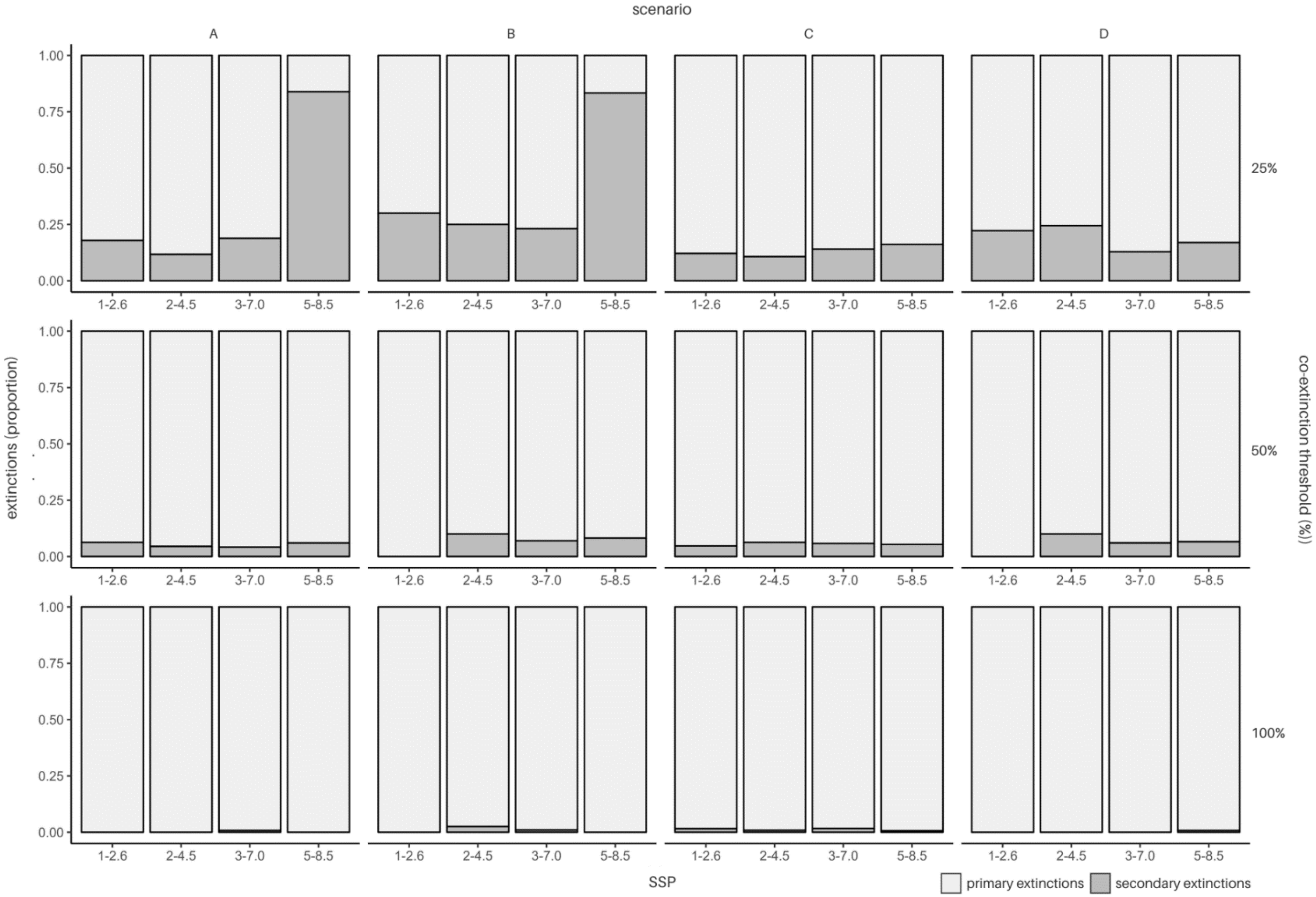

Figure 3. Proportion of primary versus secondary vertebrate extinctions in the lowland network across different coextinction thresholds (in %), Shared Socioeconomic Pathways (SSPs), and simulation types (varying in whether species could rewire trophic links and shift their elevational range). Four distinct simulations are compared (columns: A) species cannot rewire trophic links or shift their elevation range, B) species can shift elevational range, C) species can rewire trophic interactions, and D) species can shift elevational range and rewire trophic interactions. Each simulation type also applies across different coextinction thresholds (rows; 25%, 50%, and 100%) and SSPs (bars; SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5).

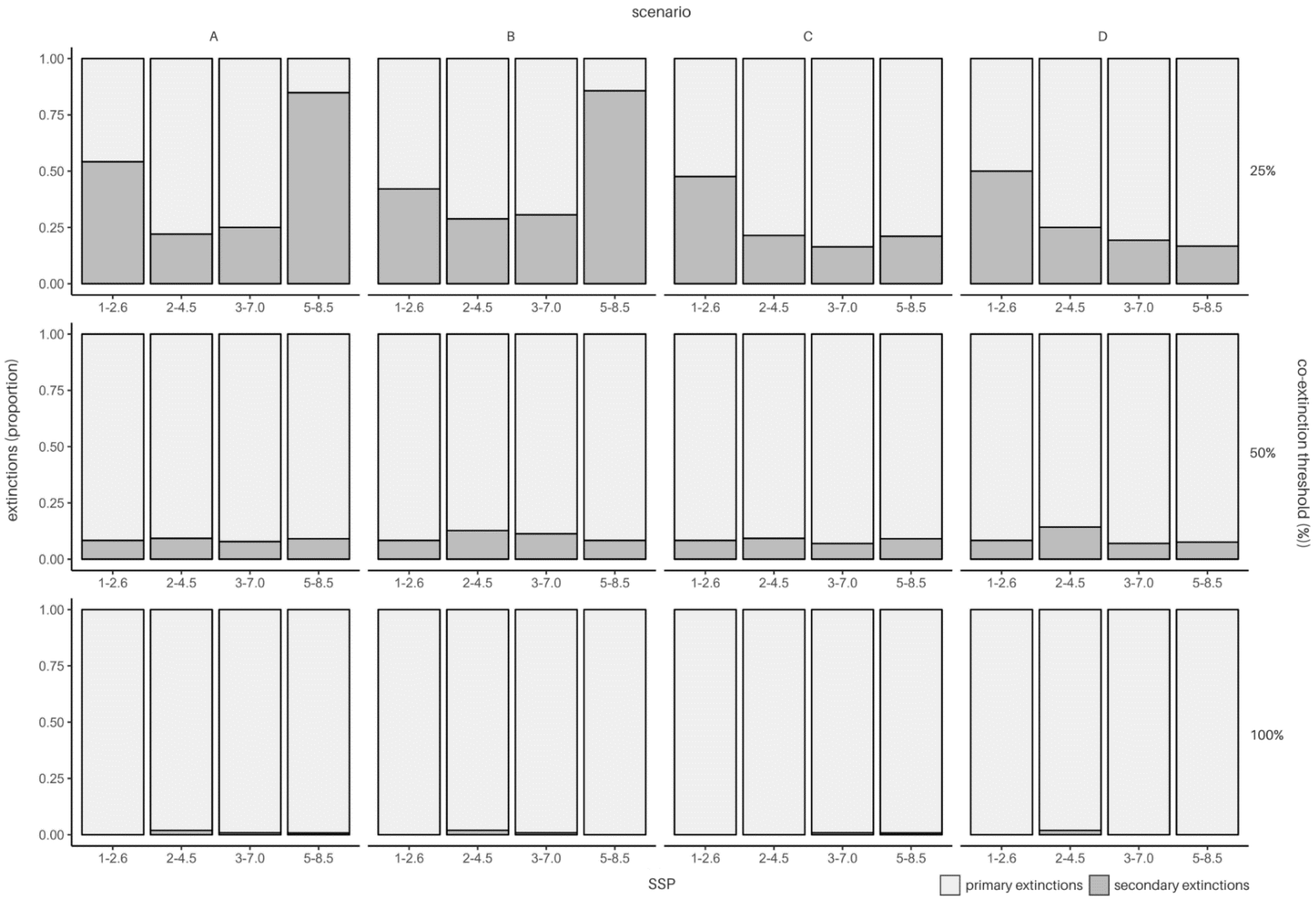

Figure 4. Proportion of primary versus secondary vertebrate extinctions in the highland network across different coextinction thresholds (in %), Shared Socioeconomic Pathways (SSPs), and simulation types (varying in whether species could rewire trophic links and shift their elevational range). Four distinct simulations are compared (columns: A) species cannot rewire trophic links or shift their elevation range, B) species can shift elevational range, C) species can rewire trophic interactions, and D) species can shift elevational range and rewire trophic interactions. Each simulation type also applies across different coextinction thresholds (rows; 25%, 50%, and 100%) and SSPs (bars; SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5).

Vertebrate trophic levels, taxonomic classes, and vulnerability to coextinction

Across all simulation types, coextinction thresholds, and climate-projection scenarios tested in low- and high-elevation networks, the estimated vulnerability to coextinction was consistently highest at trophic levels > 3 (high) and mainly in reptiles. In the highland network, the median (interquartile range) vulnerability was 20.3% (23.9–16.8%), with some species reaching up to 23% and 64.4% in trophic levels 1–2 (low–medium) and 2–3 (medium–high), respectively (Figure 5a). In the lowland network, the median vulnerability was 46.1% (59.4–38.7%), with some species reaching 56.1% in trophic levels 2–3 (medium–high) (Figure 5c). Reptiles had the highest vulnerability to coextinction in both networks, with a median of 9.0% (13.7–3.6%) in the highland network (Figure 5b) and 7.0% (21.3–3.8%) in the lowland network (Figure 5d). However, other taxonomic groups also had species with higher vulnerability, particularly birds, where some species reached 64.4% in the highland network (Figure 5a) and 71.5% in the lowland network (Figure 5c). However, these trends did not emerge across any of the simulation types with a 100% coextinction threshold because these estimated that the overall number of coextinctions was negligible in both networks (see Appendix for Figures A1–A48, and A73–A96).

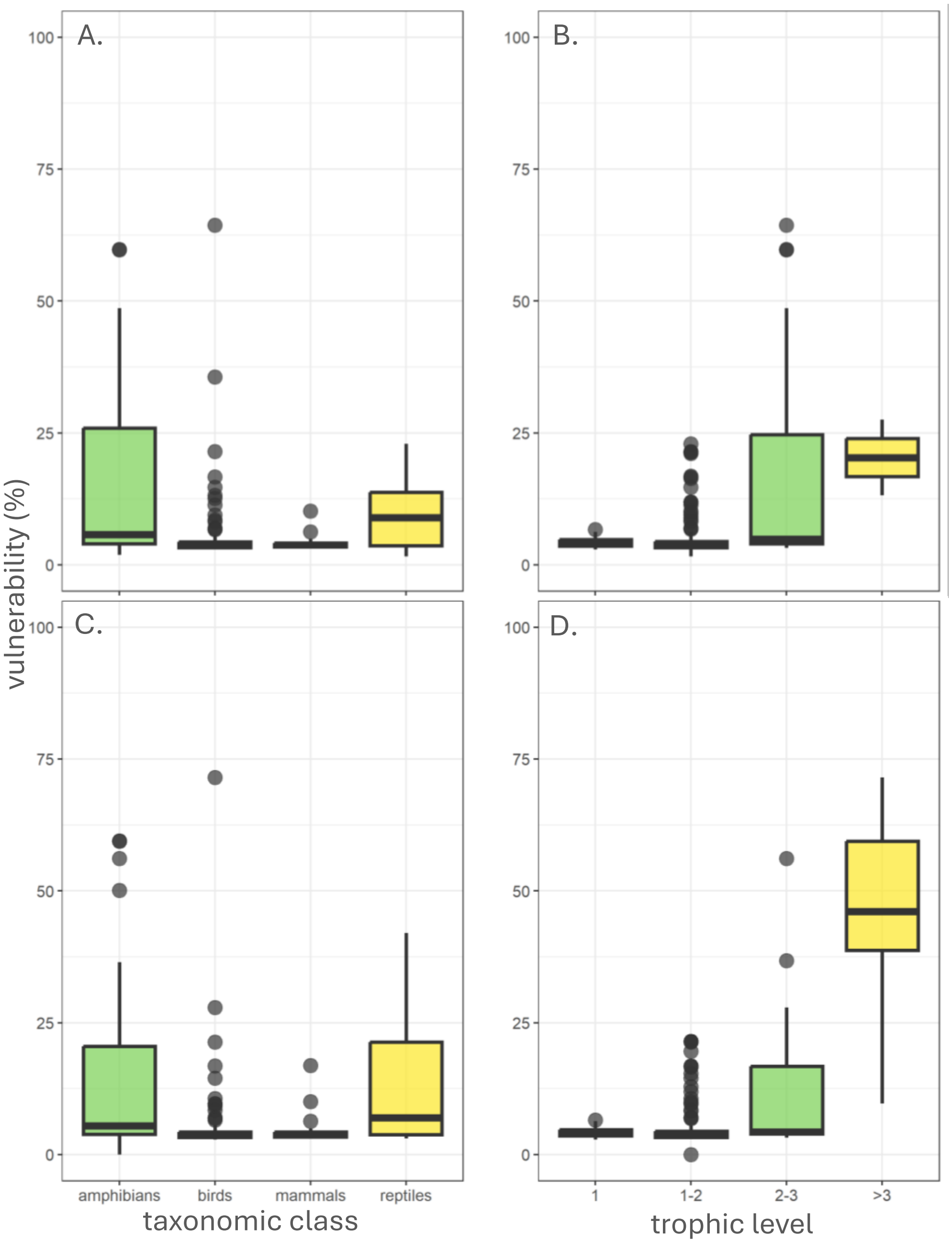

Figure 5. Mean vulnerability to coextinction for each vertebrate species in the highland network (A and B) and the lowland network (C and D) grouped by trophic level and taxonomic class across all simulation types, coextinction thresholds (25%, 50%, and 100%), and climate-projection scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) tested.

Vertebrate trophic levels, taxonomic classes, and vulnerability to primary extinction

Across all simulation types, coextinction thresholds, and climate-projection scenarios tested in low- and high-elevation networks, the estimated vulnerability to primary extinction was consistently highest in trophic levels 1–2 (low–medium) and mainly mammals. In the highland network, the median (interquartile range) primary extinction vulnerability was 59% (71.6–43.5%; Figure 6a) (see Figures A61–A72 for breakdown by each combination of simulation type and coextinction threshold), while in the lowland network, primary extinction vulnerability was 46.3% (59.1–21.9%; Figure 6c). In both networks, mammals were the most vulnerable to primary extinction, with a median of 83.5% (84.3–71.1%) in the highland network (Figure 6b; see also Figures A49–A60 for breakdown by each combination of simulation type and coextinction threshold) and 71.2% (83.1–46.6%) in the lowland network (Figure 6d). However, other taxonomic classes also had more vulnerable species, with reptiles in the highland network and amphibians in the lowland network including species with estimated vulnerability of 98.4% and 100%, respectively (Figures 6b & 6d) (see also Figures A133–A144 for the lowland network and Figures A121–A132 for the highland network for breakdown by each combination of simulation type and coextinction threshold).

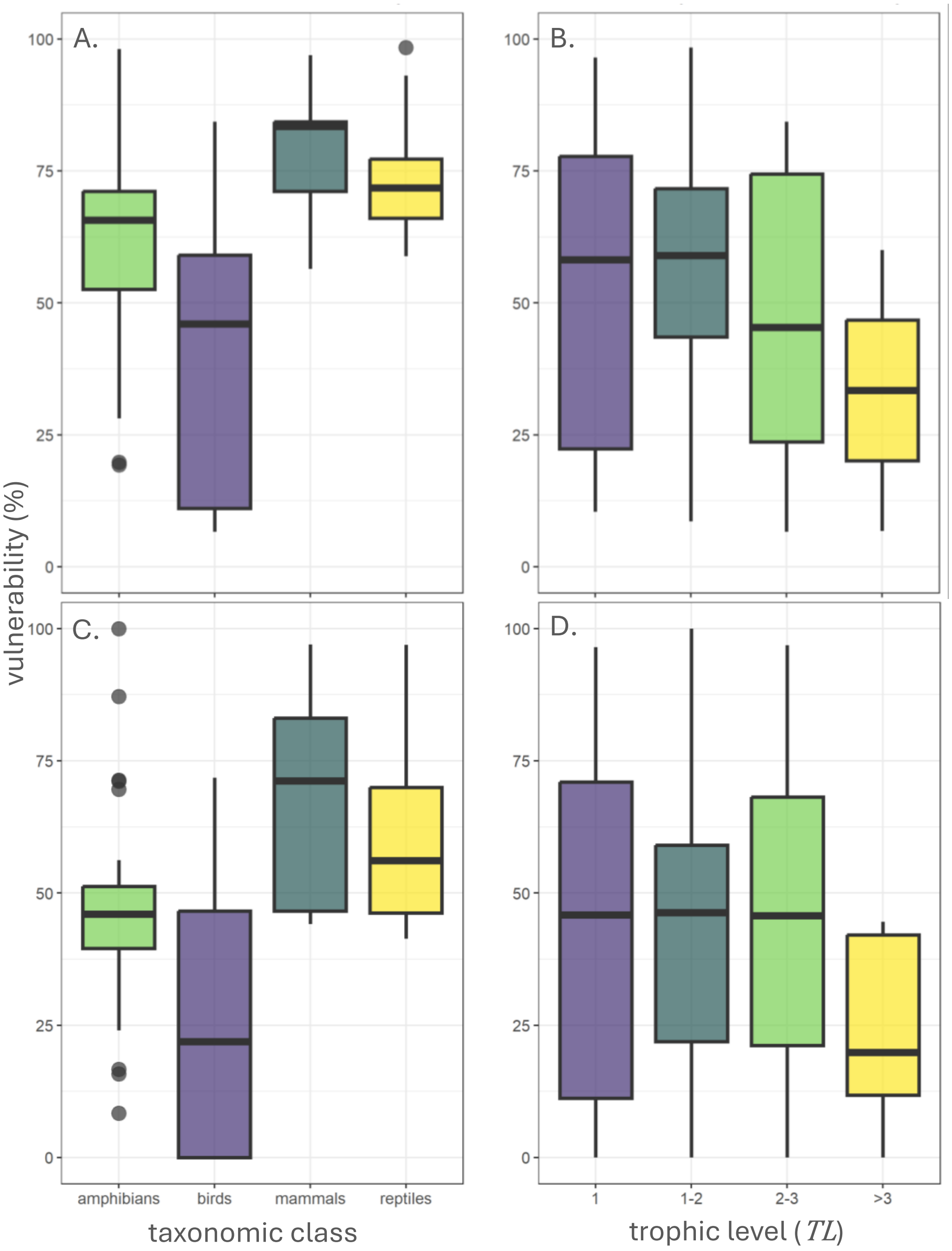

Figure 6. Mean vulnerability to primary extinction for each vertebrate species in the highland network (A and B) and lowland network (C and D) grouped by trophic level and taxonomic class across all simulation types, coextinction thresholds (25%, 50%, and 100%), and climate-projection scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) tested.

Vertebrate primary extinctions of trophic levels and taxonomic classes that elicited vertebrate coextinctions

Across all simulation types, coextinction thresholds, and climate-projection scenarios in both low- and high-elevation networks, the median percentage of vertebrate coextinction(s) from trophic cascades following their primary extinctions was ≤ 0.01%. In the lowland network, prevalence of coextinction was highest for trophic levels > 3 (high) at 0.01% (no error; Figure 7d). However, trophic levels 1–2 (low–medium) and 2–3 (medium–high) had some species with higher coextinctions with a median of 2.7% and 0.2%, respectively (Figure 7d). As for the highland network, such coextinctions were also 0.01% across all trophic levels (Figure 7b), although with trophic levels 1–2 (low–medium), 2–3 (medium–high), and > 3 (high) also including some species with comparatively higher coextinctions at 5.6%, 0.4% and 0.03%, respectively (Figure 7b). Comparing taxonomic classes, the estimated median coextinction(s) was also 0.01% in low- and high-elevation networks (Figure 7a & 7c). In the lowland network, all taxonomic classes included species that exceeded this coextinction rate, with the primary extinction of reptiles and amphibians resulting in the most coextinctions (2.7%; Figure 7c). As for the highland network, all taxonomic classes also included species with a higher coextinction rate, with the primary extinction of amphibian species resulting in the most coextinctions (5.6%; Figure 7a) (see also Figures A109-A120 and A97–A108 for the lowland network, and Figures A37–A48 and A25–A36 for breakdown by each combination of simulation type and coextinction threshold).

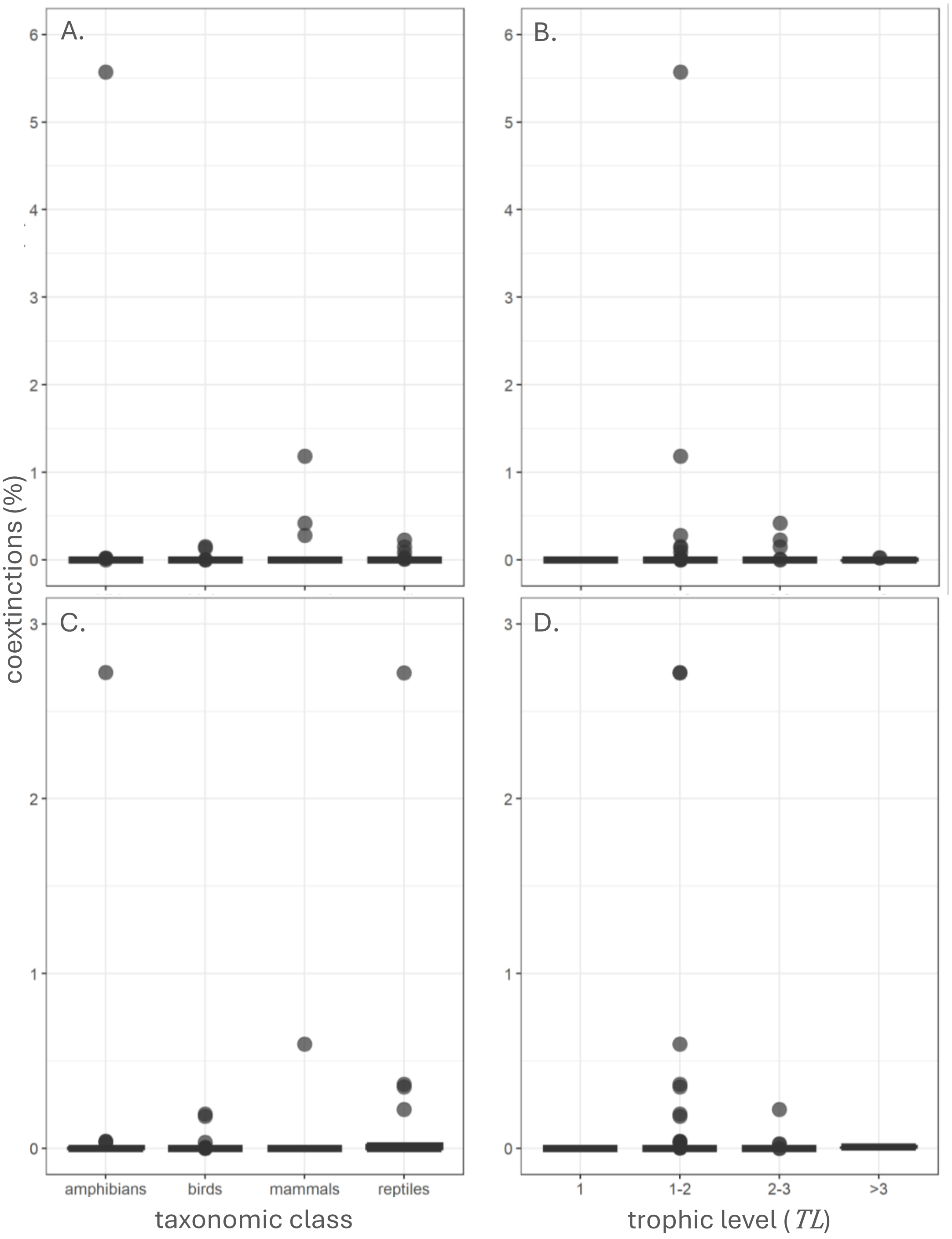

Figure 7. Mean percentage of vertebrate coextinctions caused by primary vertebrate extinctions in the highland network (A and B) and lowland network (C and D) grouped by trophic level *TL* and taxonomic class across all simulation types, coextinction thresholds (25%, 50%, and 100%), and climate-projection scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) tested.

Discussion

Future extinction risk for vertebrates in the Wet Tropics

My simulations revealed that most extinctions in the Australian Wet Tropics caused by temperature increases in the coming decades will be due to the direct effects of these changes (primary extinctions), with a smaller proportion arising from coextinctions. These results therefore do not support the hypothesis that primary extinctions resulting directly from temperature increase contribute proportionally less to vertebrate extinctions under the best-case climate-projection scenario (SSP1-2.6). In the most ecologically realistic simulations where select species can shift their elevational range and rewire trophic interactions across all climate-projection scenarios, the estimated proportions of total extinctions that were coextinctions were ≤ 24% and ≤ 50% in low- and high-elevation communities, respectively. Although a negative correlation existed between these coextinction rates and increasing coextinction threshold, they became negligible or non-existent at higher thresholds (50% and 100%). My findings suggest that the intermediate-severity climate-projection scenarios (SSP2-4.5 and SSP3-7.0) may destabilise ecological networks more than the best- and worst-case scenarios as a result of a particular balance of primary extinctions under these conditions, leading to a relatively higher proportion of coextinctions. This finding aligns with findings by Strona and Bradshaw (2022), who suggest that such intermediate scenarios may produce ecological conditions that amplify coextinction risks. However, because primary extinctions still dominate proportionally under these scenarios (SSP2-4.5 and SSP3-7.0), there is no support for the hypothesis that coextinction disproportionately affects extinction risk under intermediate-severity scenarios. In contrast, these results support the hypothesis that primary extinctions contribute proportionally more to vertebrate extinctions than coextinctions under the most extreme scenario in both networks. Earlier studies focused on the direct effects of future climate change in the Wet Tropics (Williams et al. (2003) have, therefore, probably already identified most species at risk.

For all scenarios I tested, high-elevation communities were more vulnerable than low-elevation communities to climate change-induced extinctions (both total extinctions and coextinctions). This finding confirms that projected climate change this century will cause species in high-elevation areas, particularly highly specialised, endemic, and narrow climate-niche species, to be more at risk (Knight, 2022; Shoo et al., 2005; Williams et al., 2003). My models also corroborate how simulated elevational shift in vertebrate communities will lead to the extinction of populations in high-elevational bands in the Wet Tropics (de la Fuente et al., 2022), as well as in other tropical regions such as the Peruvian mountains where recent warming has already extirpated many high-elevational bird populations (Freeman et al., 2018). The similarity in overall extinction vulnerability across both networks under the worst-case climate-change scenario supports the 'escalator to extinction' effect that occurs when warming compromises organisms to find suitable habitats as cool-adapted species shift their ranges upslope, and where some species encounter thermal or physical barries to moving higher or finding cooler refugia (Marris, 2007; Urban, 2018). These results support the notion that vertebrate communities, particularly highland species, in the Wet Tropics are likely to experience high extinction risk this century due to climate change (de la Fuente et al., 2022; Hilbert et al., 2001; Shoo et al., 2005; Williams et al., 2003; Williams & de la Fuente, 2021).

The true extinction risk of these communities remains underestimated. We are currently on track for a 2.5–2.9°C temperature rise above pre-industrial averages this century (Hausfather & Peters, 2020; UNEP, 2023), making SSP1-2.6 and SSP2-4.5 (currently) the most plausible of the climate-projection scenarios I tested. This trend implies that the proportion of total extinctions that are coextinctions peaks in intermediate-severity conditions (e.g., Figures 3 & 4; Strona & Bradshaw, 2022)**,** and this is before even considering that the synergistic effects of multiple extinction drivers (e.g., habitat loss and invasive species incursions) (Loope & Krushelnycky, 2007; Stork et al., 2011) will amplify these risks (Brook et al., 2008). The overall impact on network structure will likely increase vulnerability in these communities.

Although some combinations of simulation parameters (e.g., under SSP5-8.5 with species coextinction threshold = 100%) showed no detectable or negligible differences in vertebrate extinctions, or in the proportions of primary *versus* coextinctions, the networks still lost thousands of trophic links and basal resource nodes. This depletion affects trophic complexity and connectance (Dunne et al., 2002), likely making communities more vulnerable to other future environmental perturbations, such as deforestation (Sanders et al., 2018). This effect on extinction vulnerability would likely be more prominent under severe climate change because more species and links are lost (Figure 2; Strona & Bradshaw, 2022). For example, severe climate and land-use changes are predicted to make terrestrial food webs more compact and densely interconnected, and reduce predator generality and diversity in various trophic groups (Yan et al., 2024). This observation suggests that terrestrial vertebrate communities impacted by climate change will be more vulnerable to the propagation of extinctions. For terrestrial communities, like those found in the Wet Tropics, conservation interventions should, therefore, continue to focus on mitigating primary extinctions elicited by climate change, for example, by implementing assisted adaptation measures and managing invasive species (WTMA, 2023), but also on further preventing the additional but far-reaching coextinction effects in communities.

Effects of rewiring and shifting elevational range on extinction risk

A species' ability to adapt by shifting elevational ranges and rewiring trophic interactions is likely to influence vulnerability to climate change. Trophic rewiring was more important for highland species, whereas lowland species relied more on elevational range shifts. However, both rewiring and shifting elevational range provide the most protection against extinction risk, supporting the hypothesis that species with these abilities will have a lower rate of coextinction than communities consisting of species with no or limited ability to rewire trophic interactions after losing food resources. Species have higher extinction vulnerabilities when unable to track optimal conditions along an elevational gradient under most climate-projection scenarios. However, under the most extreme climate-change projection, extinction risk becomes similarly high across low- and high-elevation communities. While adaptive capacity offers some resilience, its effectiveness at lowering extinction risk diminishes under more severe climate change.

For highland network species, the ability to rewire trophic interactions is generally more effective than elevational range shifts in reducing coextinctions, especially under more severe climate change, as species become altitudinally constrained. With more intense climate change, both metrics indicate an increase in extinction risk, suggesting that while adaptive capacity can reduce coextinction risk for species in the highland network, total extinctions remain consistently high. In other words, adaptive capacity reduces the risk of coextinction but does not strongly affect the total number of extinctions arising mainly from exceeding thermal tolerances. In contrast, shifting elevational range was more important for reducing coextinctions and the total number of extinctions under milder climate change. However, effectiveness decreases when climate change is severe.

Trophic rewiring was effective across all scenarios, often surpassing the effect of elevational range shifts in maintaining community stability. The number of species extinctions from the lowland network varied across different simulations, indicating that adaptive abilities have an important effect on overall extinction rates. When species can rewire trophic interactions and shift their elevational range, they reduce primary and coextinctions, resulting in fewer extinctions overall. When species can adapt by shifting their elevational range, extinctions at low elevations are reduced, even in intermediate and severe climate change. Conversely, when only trophic rewiring occurs, extinction remains high, suggesting that the ability to shift elevational range is essential for lowland species to persist under changing climatic conditions. However, the combined effect of these adaptive capacities often provides the most robust defence against coextinctions, with species from the lowland networks having greater reductions due to their capacity to move into higher areas (Scheffers & Williams, 2018). In contrast, high-elevation communities are more susceptible to extinction because they are spatially constrained (e.g., Williams et al., 2003), but some species will be able to persist by rewiring their trophic interactions (e.g., Kaiser-Bunbury et al., 2010; Sanders et al., 2018).

But rewiring trophic interactions is a double-edged sword, because although it provides short-term advantages to predators by decreasing their coextinction risk, it also potentially harms long-term community persistence. For example, increasing predation pressure on the remaining prey species within the network could lead to overexploitation of food resources (Gilljam et al., 2015), a mechanism I could consider in my models. Shifts in predator behaviour could also regulate other prey species, especially if the latter release from competition and/or have migrated from lower elevations. Although a species' ability to shift elevational range influences extinction risk, such shifts could also change the remaining lowland community, potentially eroding network interactions. For example, the movement of species from low to high-elevation communities could pose a threat to many of the specialised, endemic, highland species via increased competition with generalists (Williams & de la Fuente, 2021).

Environmental and conservational management should ideally aim to enhance the resilience of communities by facilitating the capacity to shift elevational range. This outcome could be achieved by increasing and maintaining habitat connectivity across elevational gradients (Heller & Zavaleta, 2009), or by assisting small-scale range expansions by translocating individuals (Butt et al., 2021), helping to maintain or facilitate novel trophic interactions between predator and prey species. Interventions like these will be necessary for sustaining biodiversity to minimise coextinctions, although future directions for conserving highland communities beyond lowering global greenhouse-gas emissions are unclear. Alternatively, one could consider ex-situ conservation strategies (e.g., establishment of a captive breeding program in multiple zoos), but as outlined by the management authority of the Wet Tropics (WTMA, 2023), these approaches can be costly, raise ethical concerns, and might not be effective in ultimately preventing species extinction.

Trophic levels, taxonomic classes, and vulnerabilities to coextinction risks

My model predictions support the hypothesis that vulnerability to coextinction will increase with trophic level as temperatures increase. Species occupying high-trophic levels and their lower estimated vulnerability to primary extinction under the same conditions explain this result. Estimated vulnerability to coextinction varies between low- and high-elevation networks in terms of their most vulnerable taxonomic classes and trophic levels, and this could be due to the same types of species found in both communities occupying similar positions within their respective networks.

Reptiles and amphibians were the most vulnerable groups in both networks to coextinction. Frogs, in particular, are highly at risk from climate change and other disturbances both in the Wet Tropics (Fordham et al., 2016; Geyle et al., 2021; Hero et al., 2015; McKnight et al., 2017; Wake & Vredenburg, 2008) and globally (Stuart et al., 2004), as are reptiles (e.g., Geyle et al., 2020; Li et al., 2024). However, some species in other taxonomic classes like birds might also have a high risk of coextinction, highlighting the complexity of predicting extinction risk to climate change. I found consistent patterns of vulnerability across trophic levels and taxonomic classes, regardless of species adaptive abilities or coextinction thresholds, indicating that while most vertebrates are resilient to coextinction in both low- and high-elevation networks, reptiles, amphibians, and species in high trophic levels, as well as some birds and lower trophic-level species, will be susceptible to coextinction in a warming world. A species' capacity to shift elevational range or rewire trophic interactions might therefore not entirely mitigate vulnerability to coextinction, with vulnerability instead influenced more by trophic level and connection type within the network (e.g., Duffy, 2003; Jonsson et al., 2006; Purvis et al., 2000).

Trophic levels, taxonomic classes, and influences on ecosystem stability

Primary extinctions of vertebrates will not uniformly lead to widespread cascading effects in either the low or high-elevation networks. However, some species, especially those in low–medium and medium trophic levels, might still trigger coextinctions. Therefore, there is partial support for the hypothesis that some species in lower trophic levels could be more important in influencing coextinction risk than higher trophic levels (e.g., Binzer et al., 2011; Shukla et al., 2023). However, it is still unclear whether lower or higher trophic levels are more important for influencing these ecological processes in networks at different elevations.

Higher trophic levels were generally associated with increased coextinction risk in the lowland network. However, some species in lower trophic levels might still also cause coextinctions. In the highland network, the lower coextinction rates reflect a mostly similar, but possibly more resilient, ecological structure that arises from differences in species composition or interactions compared to the lowland network, even if certain species at various trophic levels still demonstrated the potential to cause coextinctions. Disruptions to various points in these food webs have the potential to propagate through communities, leading to unexpected coextinction outcomes. Amphibians were particularly influential in both low- and high-elevation networks among reptiles in the lowland network, suggesting their possible importance in modulating stability, even if negligible, in these communities. This influence could be related to their position as both predator and prey, modulating the stability of these communities by linking across multiple trophic levels (Hocking & Babbitt, 2014).

The trophic levels and taxonomic classes most important for maintaining ecosystem stability are not artefacts of adaptive capacities, but rather represent fundamental characteristics of both low- and high-elevation networks. Specifically, similar patterns emerged whether I restricted species from adapting, indicating that these coextinction dynamics are insensitive to the various scenarios of adaptive capacity. This consistency suggests that the structural and functional properties of food webs, particularly species' positions within trophic levels and their taxonomic classes, are likely more important for determining coextinction outcomes (e.g., Staniczenko et al., 2010) than the species-specific adaptive responses to climate change.

Although the primary extinction of different trophic levels in both networks contributed to some coextinctions of other vertebrate species, the number of vertebrate extinctions overall in each network was low relative to the total number of vertebrate extinctions simulated in each climate-projection scenario. This low contribution might therefore indicate that the largest modulator of vertebrate coextinction risk will not be from vertebrates themselves, but rather from the loss of basal resources (Chapter 4). The declines of many highland vertebrate species in the Wet Tropics related to temperature increases (de la Fuente & Williams, 2023; Williams & de la Fuente, 2021) and invertebrate species globally (e.g., Van Klink et al., 2020; Wagner, 2020) already demonstrate this increased risk and sensitivity. Environmental management should therefore focus on conserving species that occupy lower and medium-trophic levels, including amphibians and some reptiles, for maintaining ecological stability under changing conditions in the Wet Tropics. Conserving these groups could be necessary for increasing the overall resilience of vertebrate communities to trophic cascades and coextinctions. Conservation priorities should also be considered for invertebrates and plants as basal resources, because they will likely be even more essential for protecting communities from trophic cascades and coextinctions.

Limitations

Coextinction thresholds are likely to vary among species, and so applying single threshold values could be underestimating species' vulnerability to coextinction. Better empirical measures of coextinction thresholds and randomly varying them in models will inevitably provide more insight (Chapter 4; Strona & Bradshaw, 2018). Varying resource availability rather than only considering total resource depletion as a threshold could also be applied, because even slight reductions in basal resources can cause extinctions (Strona, 2022a). Investigating how varying coextinction thresholds relate to body size and thermoregulation (endothermic versus ectothermic) would also modify conclusions about vulnerability to coextinction. Larger-bodied species tend to be more prone to extinctions (Cardillo et al., 2005), perhaps indicating their lower threshold to environmental change. Conversely, ectothermic species might exhibit higher thresholds if their populations are less constrained by food resources.

Assuming that all generalist vertebrate species can compensate for lost interactions more effectively than specialist species is also a simplification of real-world dynamics (Robinson et al., 2019). This assumption could be biasing predictions of coextinction risk. Combining different species traits (e.g., life history, morphological, behavioural) in models to predict observed changes in trophic interactions could identify species-specific trophic flexibility. Based on empirical data describing species' interactions before and after environmental changes could reveal how some species adjust their feeding behaviour and interactions in response.

By not allowing vertebrates to rewire lost trophic interactions with other vertebrates in their networks in some simulations, I assumed that carnivores (and some omnivores) had the same rewiring capacity in all vertebrate-to-vertebrate links (> 0.49; see Chapter 3 methods). However, the capacity of herbivores and invertivores to rewire trophic interactions differs between those simulations. Thus, if the ability to rewire influences vulnerability to coextinction, not varying rewiring capacity for carnivores and some omnivores might have underestimated vulnerability when trophic rewiring did not occur, or overestimated vulnerability when trophic rewiring was allowed. Calculating a vertebrate species' diet breadth from empirical diet data could alleviate these potential biases.

Conclusions

This chapter presents a framework for identifying species at high risk of coextinction and those that could trigger extinction cascades, guiding environmental policies and biodiversity management. Although coextinctions may be less pronounced than primary extinctions, they remain important elements of overall extinction dynamics in complex ecosystems such as the Australian Wet Tropics. This study underlines the need for multifaceted management strategies focused on whole-community conservation under future climate-projection scenarios, providing a model that can be applied to similarly complex terrestrial ecosystems globally. In future, research should refine predictions of extinction risk by considering multiple environmental variables (e.g., temperature, precipitation, and habitat type) on species distributions and the possible synergistic effects of multiple extinction drivers (e.g., invasive species and habitat loss). Research should also focus on refining the ecological realism of network models by including more attributes/detail for basal nodes (which often appear pooled or undifferentiated), trophic and non-trophic interactions, and individual node responses to changing environmental conditions. Investigating varying simulation parameters (e.g., coextinction thresholds) will also be necessary for further enhancing the realism of methods used to evaluate impacts on species coextinction risks.

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Appendix

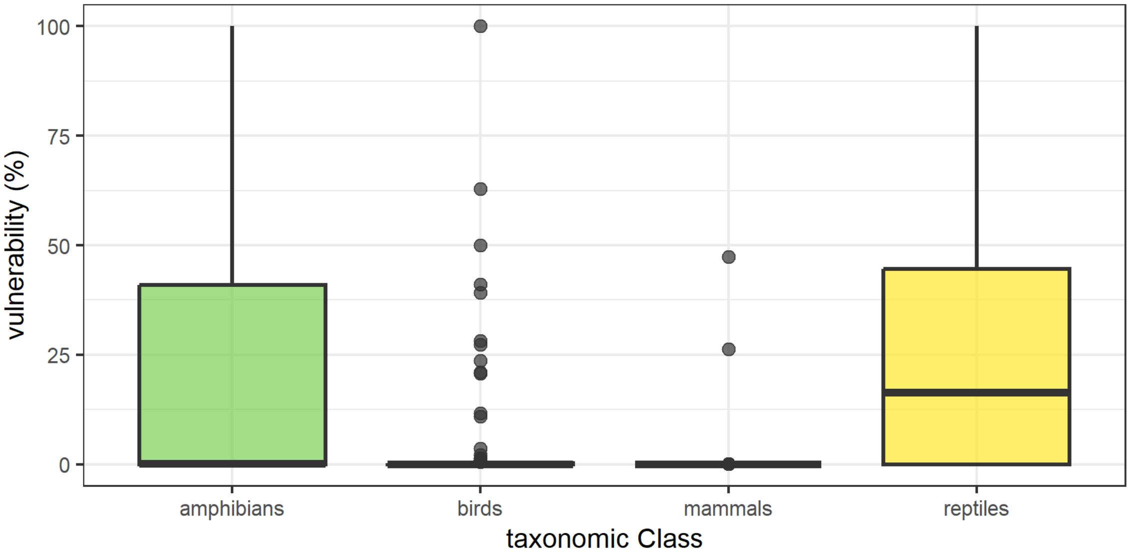

Figure A1. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

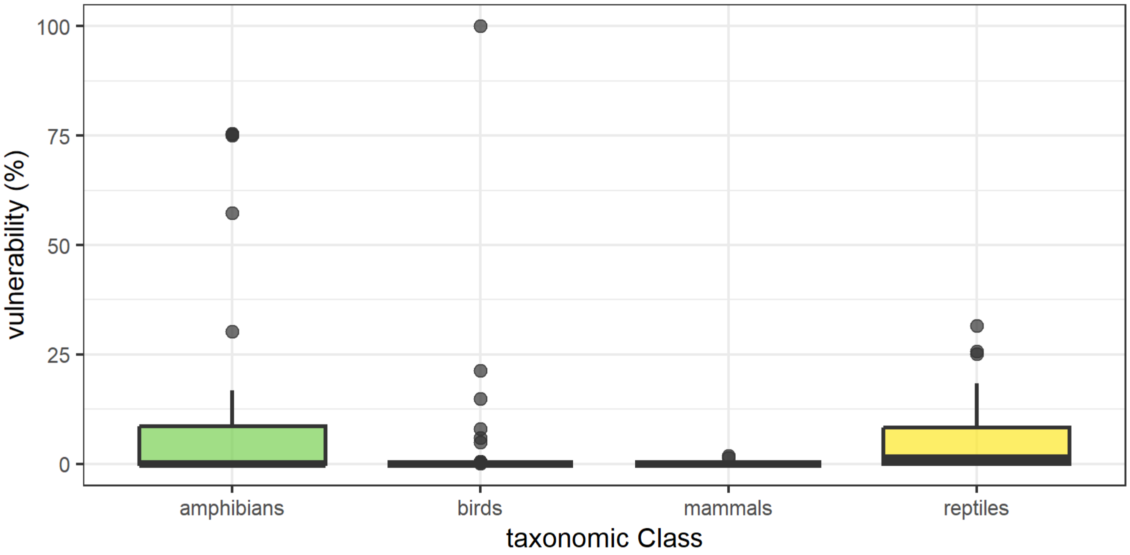

Figure A2. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

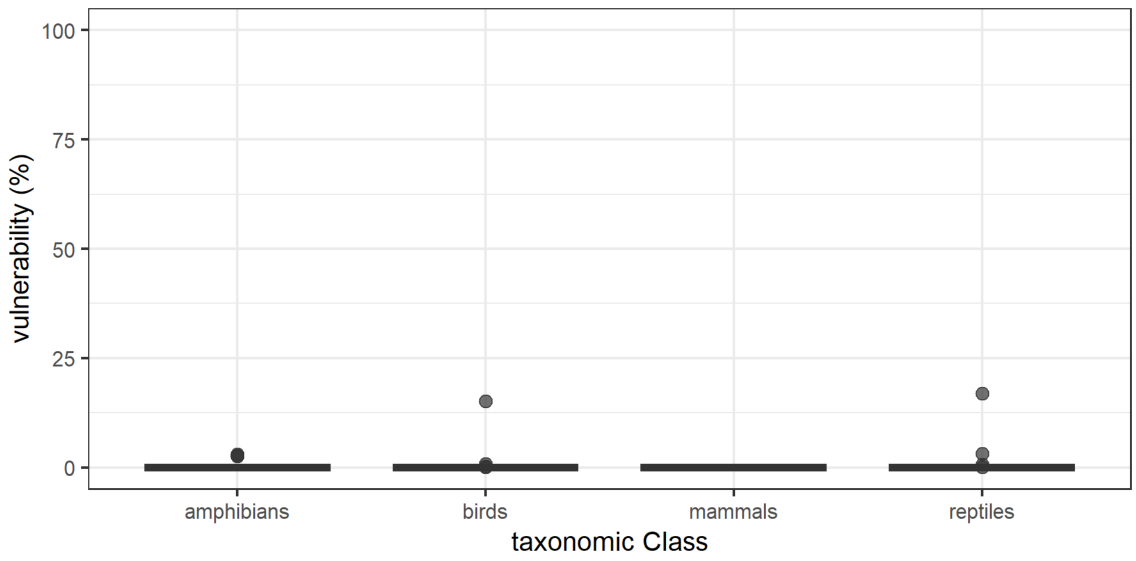

Figure A3. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

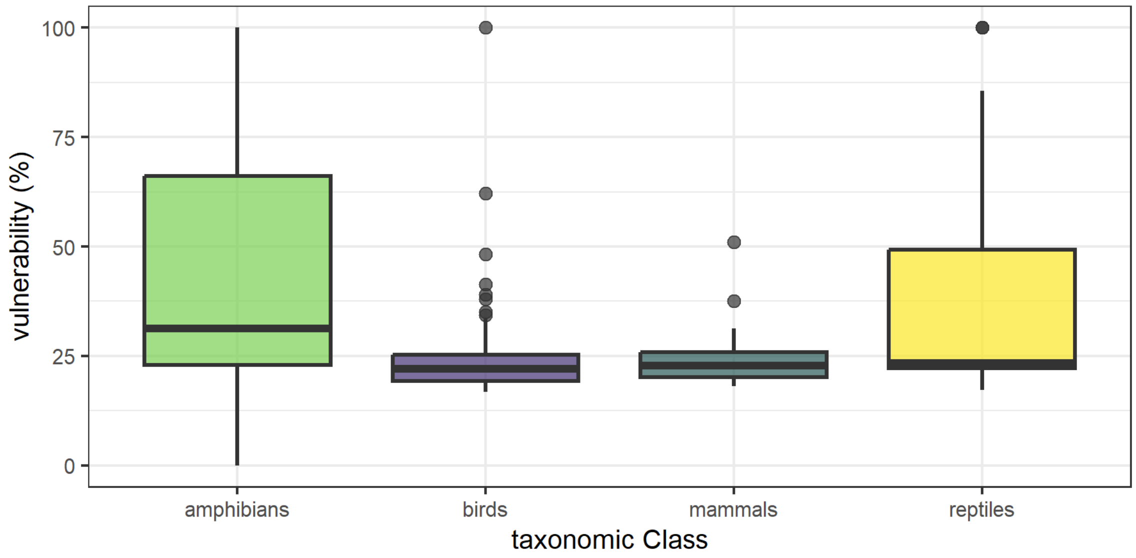

Figure A4. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

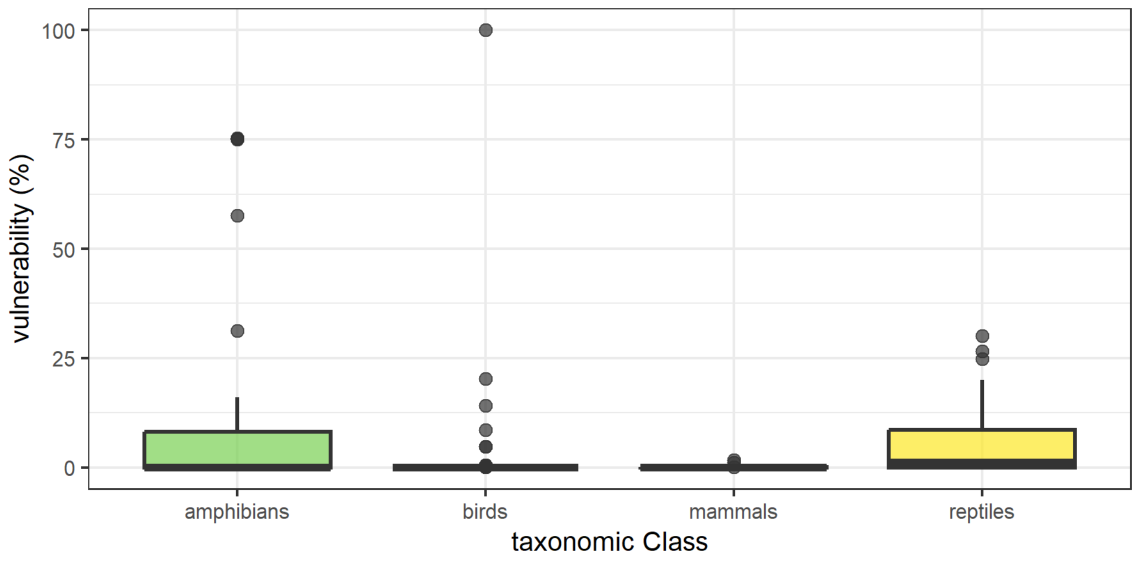

Figure A5. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

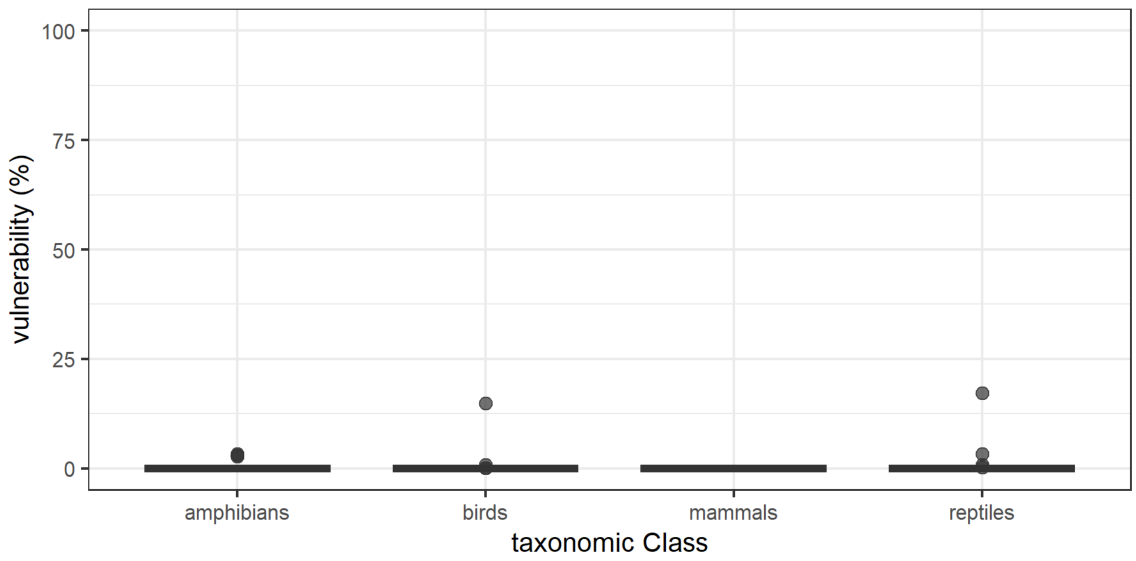

Figure A6. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

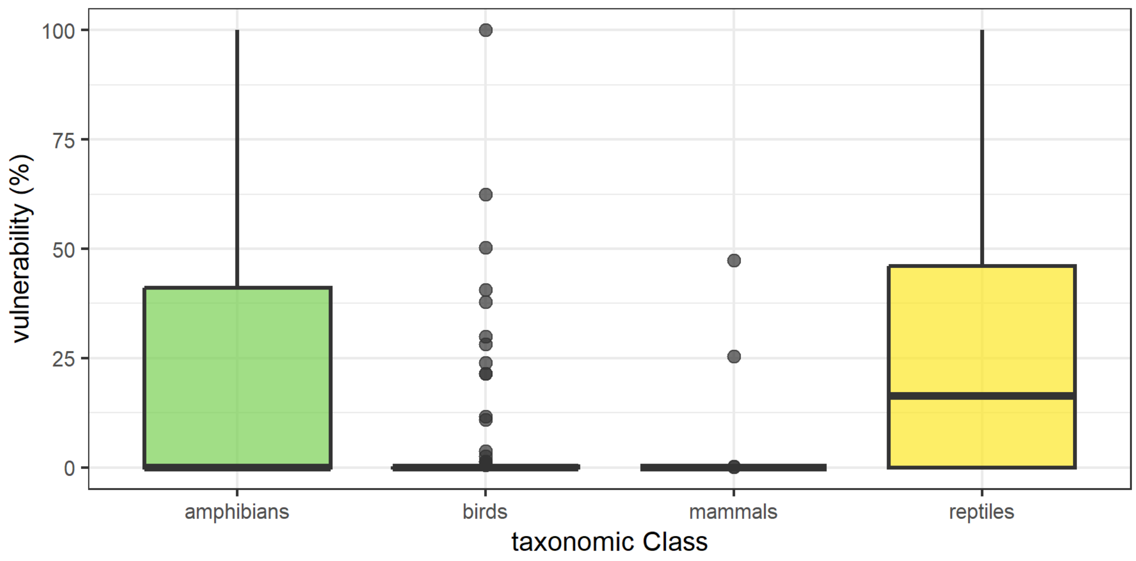

Figure A7. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

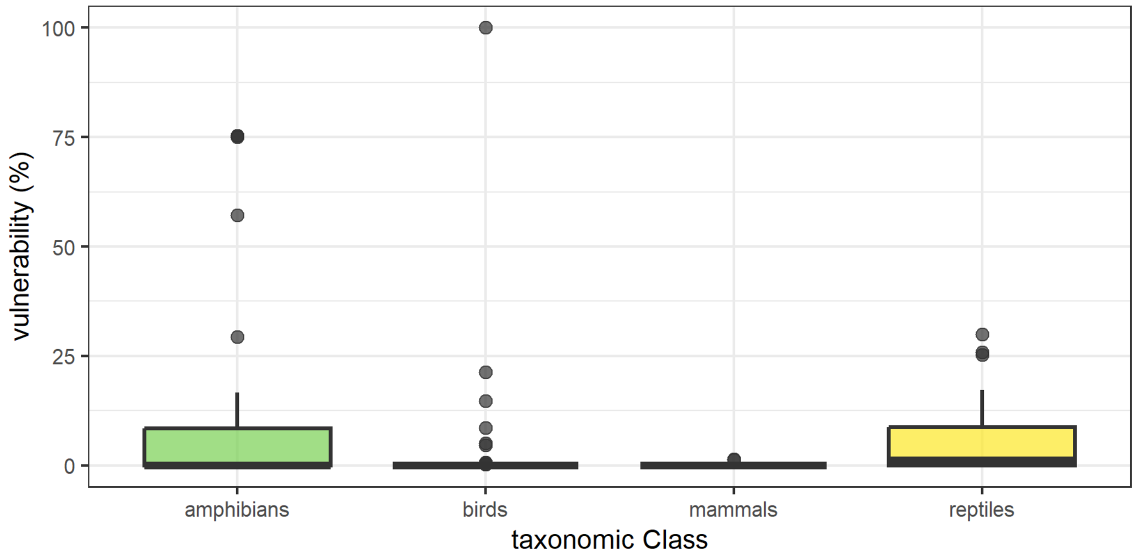

Figure A8. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

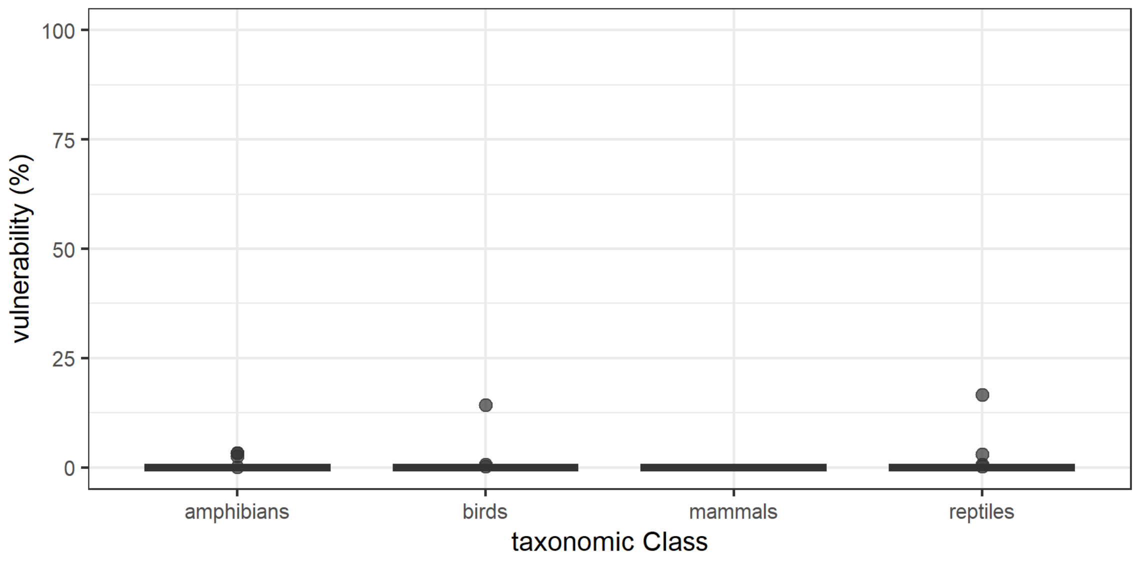

Figure A9. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

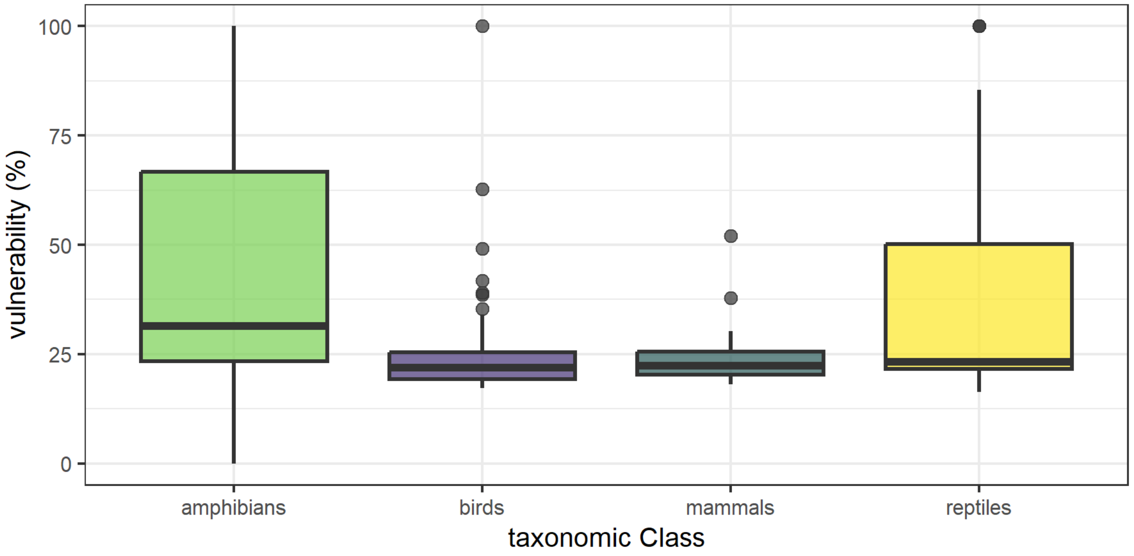

Figure A10. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

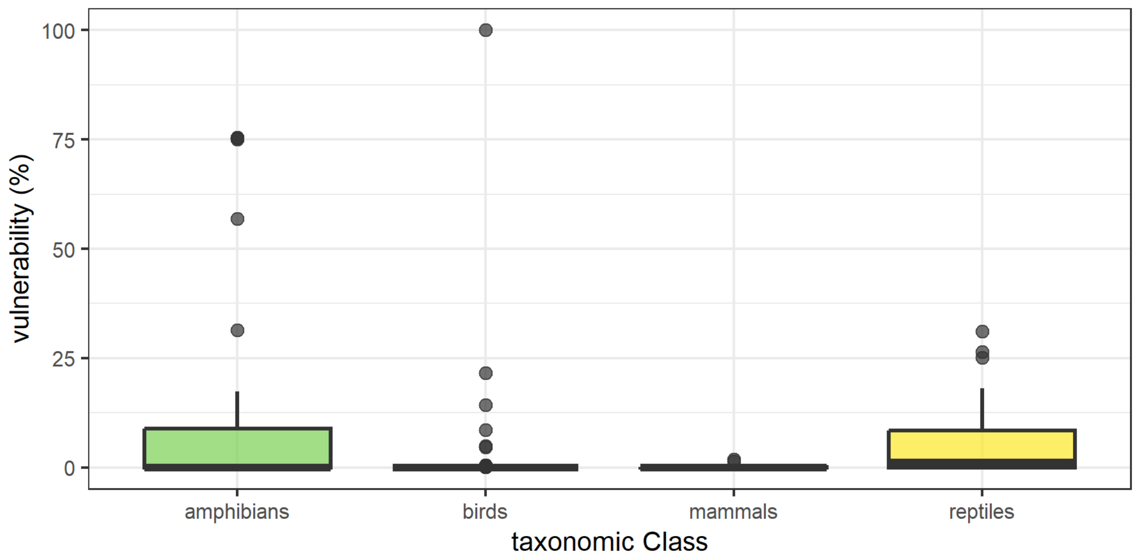

Figure A11. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

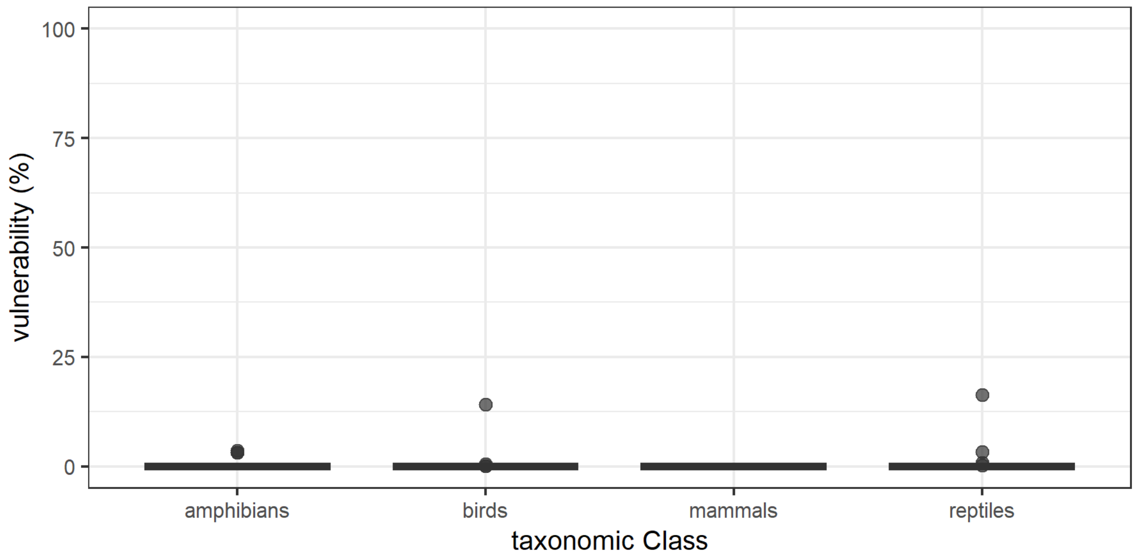

Figure A12. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

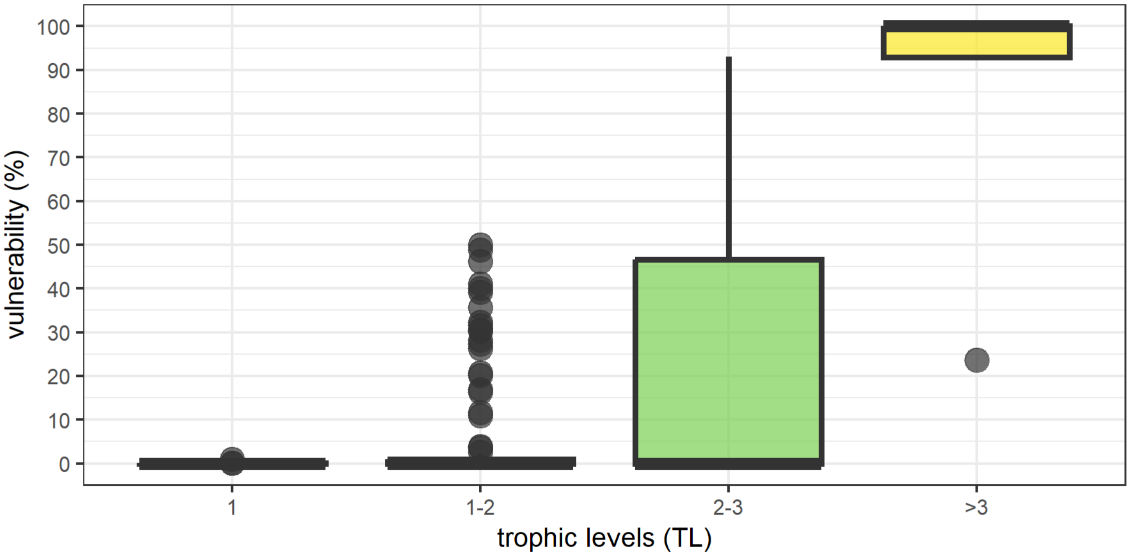

Figure A13. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

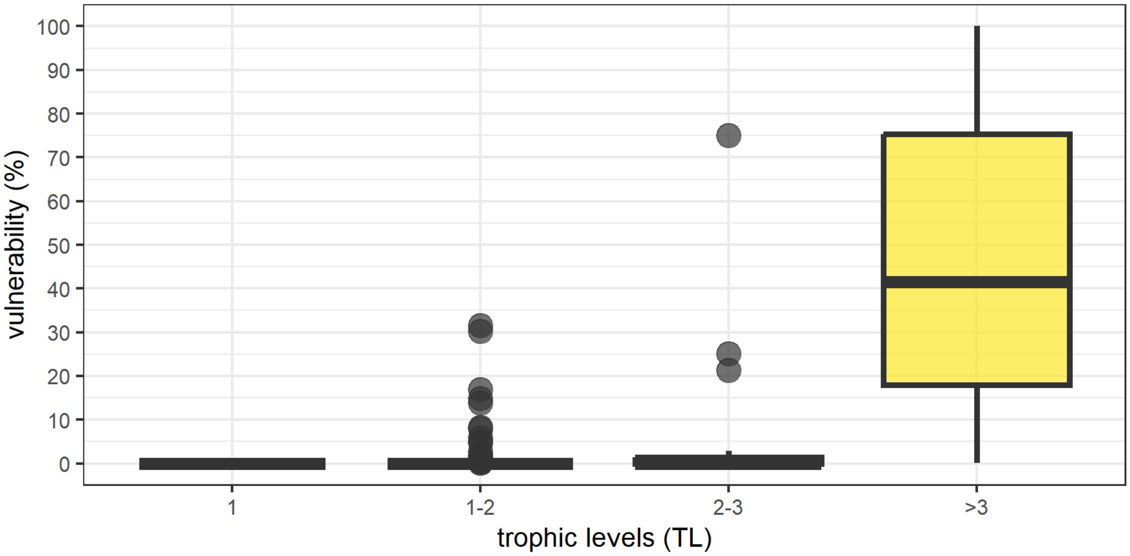

Figure A14. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

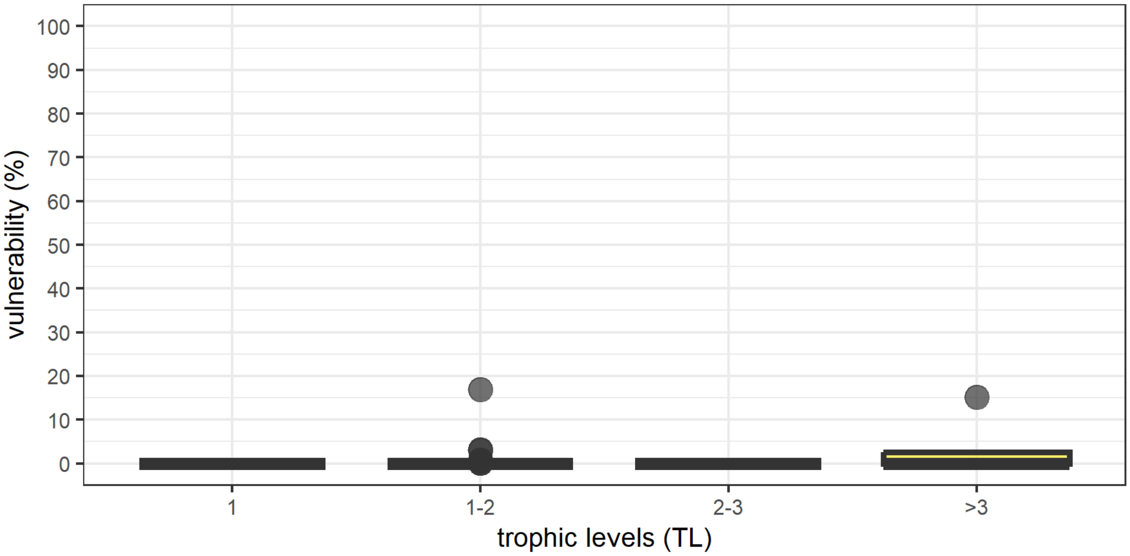

Figure A15. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

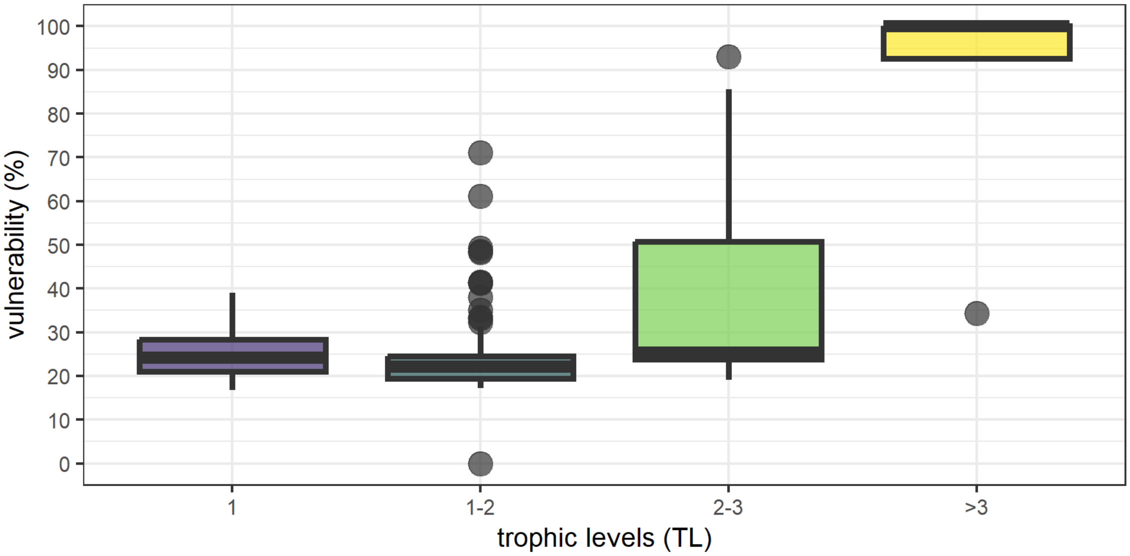

Figure A16. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

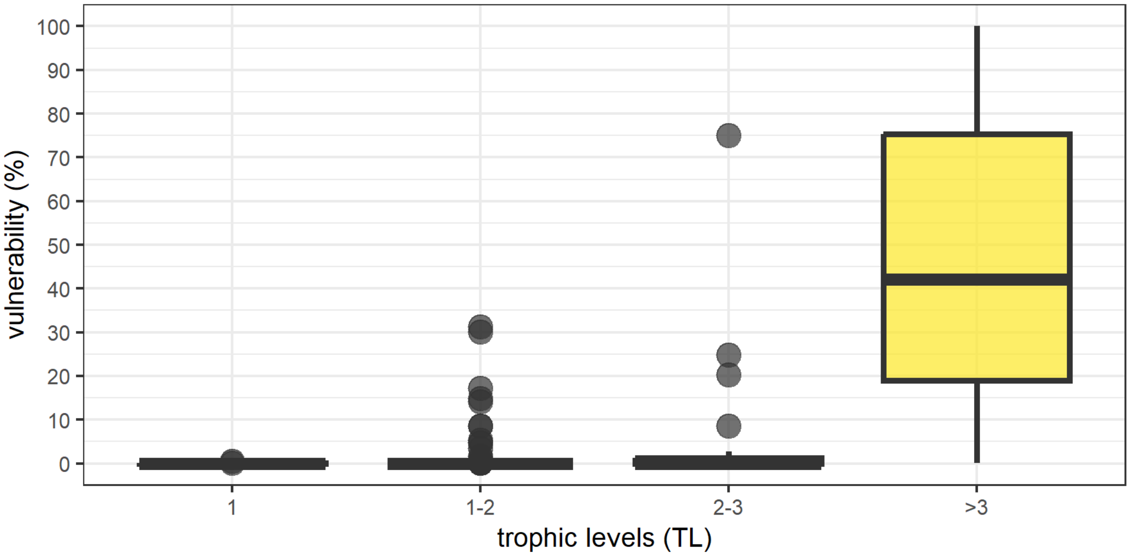

Figure A17. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

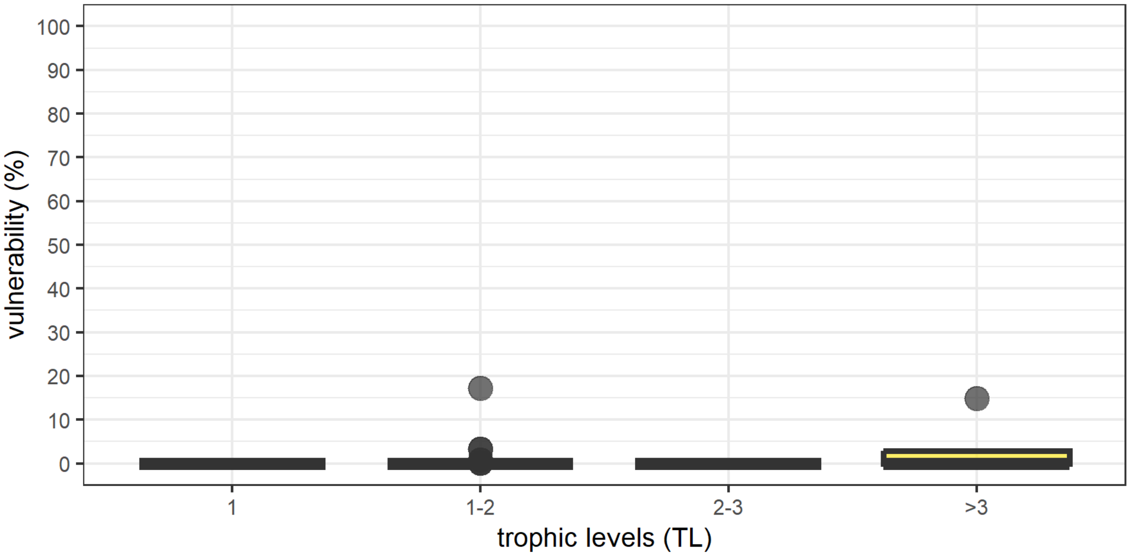

Figure A18. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

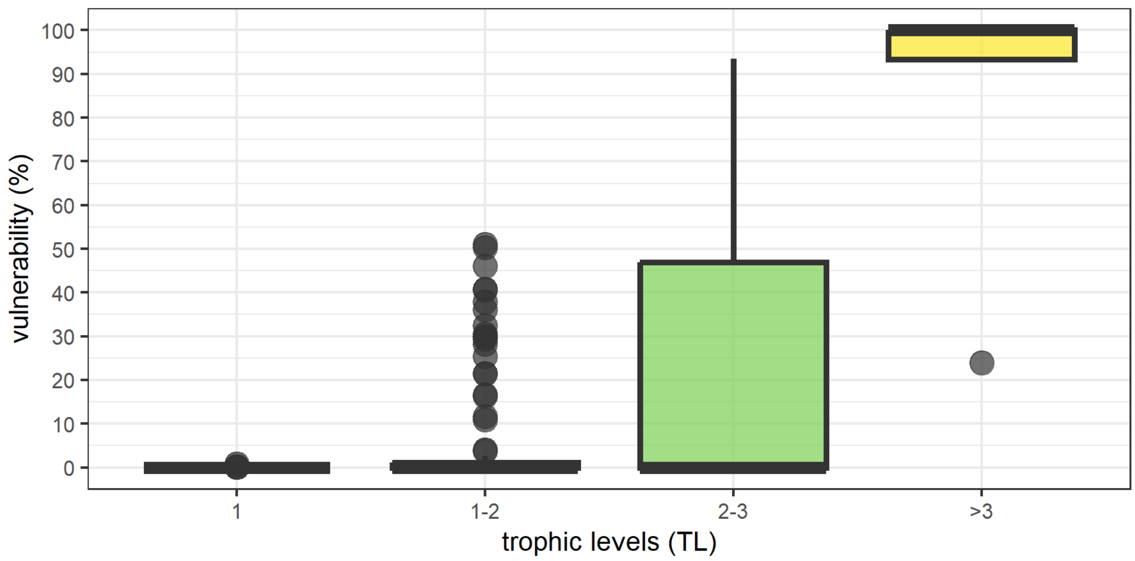

Figure A19. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

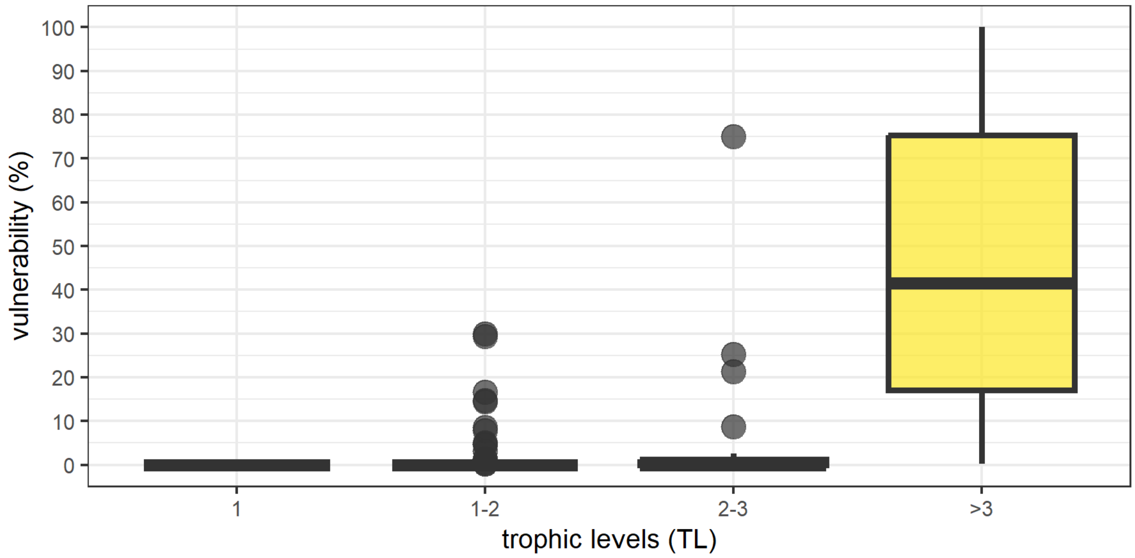

Figure A20. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

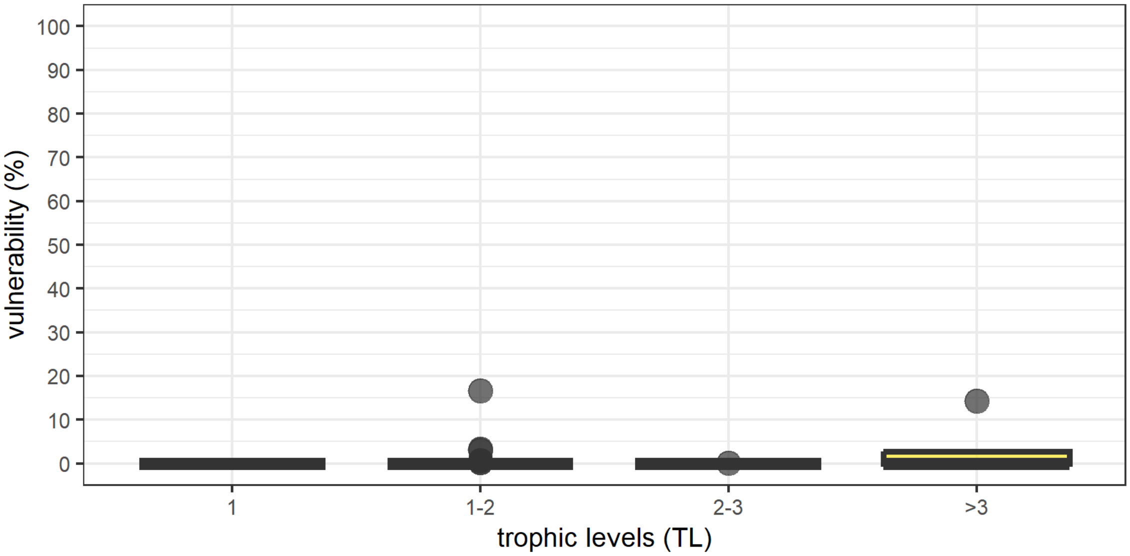

Figure A21. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

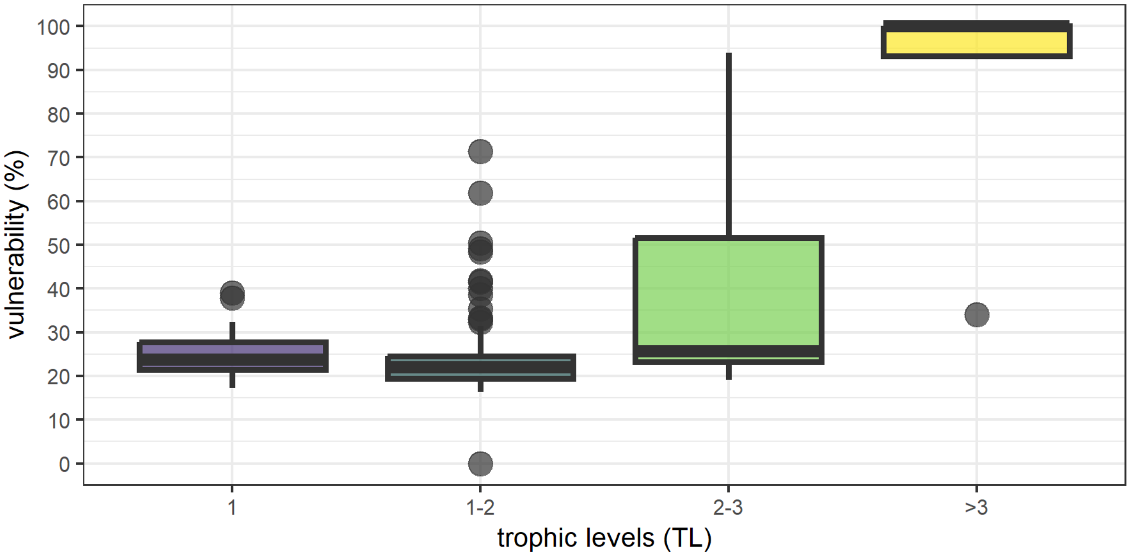

Figure A22. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

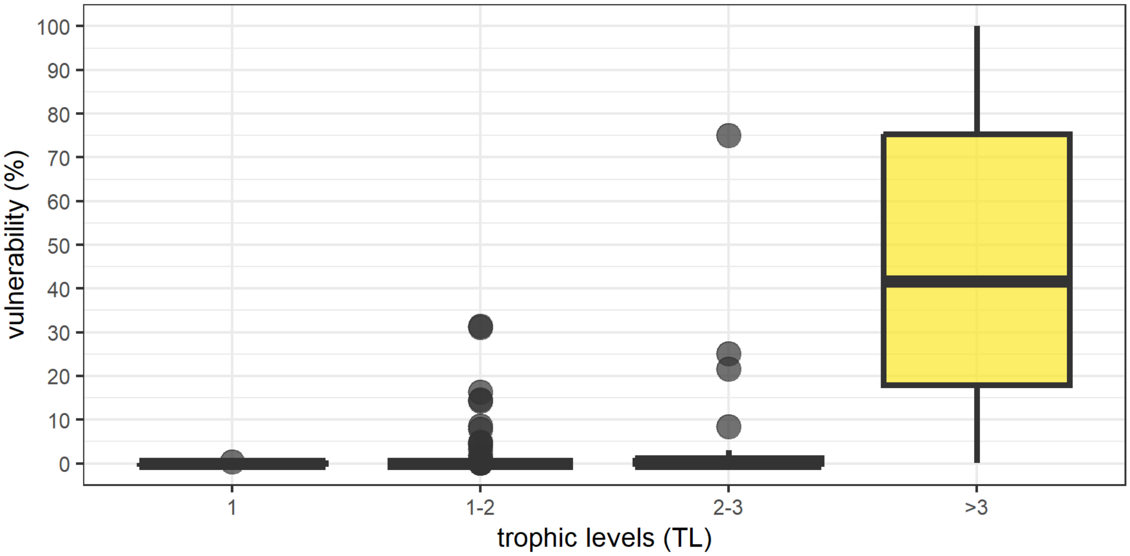

Figure A23. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

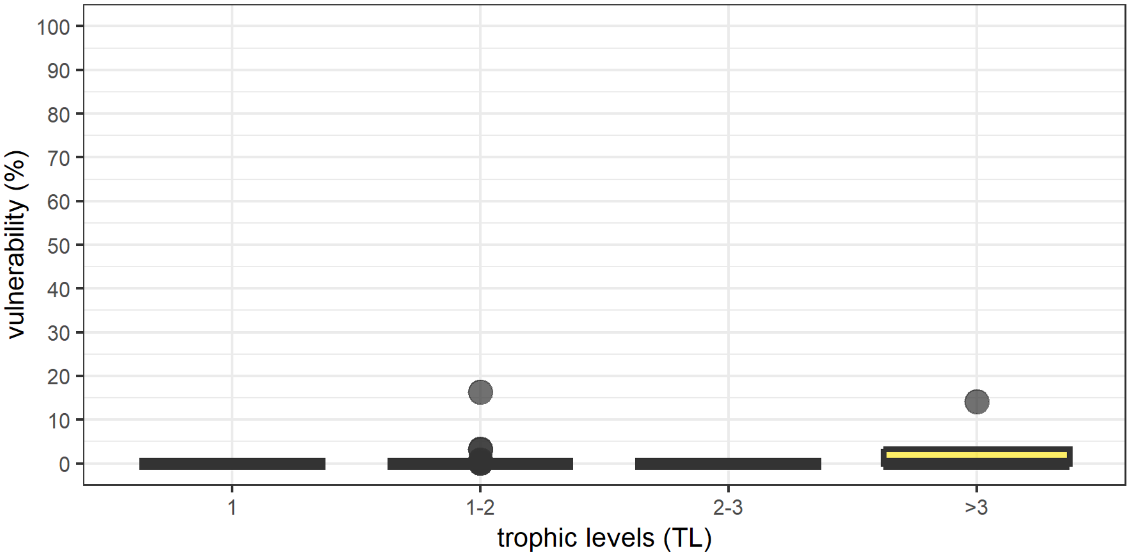

Figure A24. Mean vulnerability to coextinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

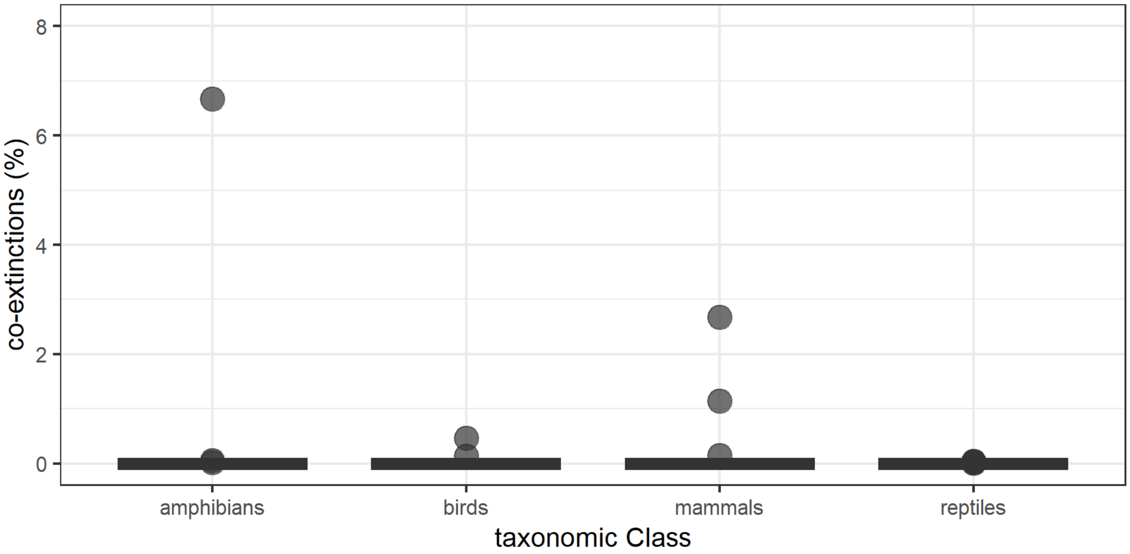

Figure A25. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

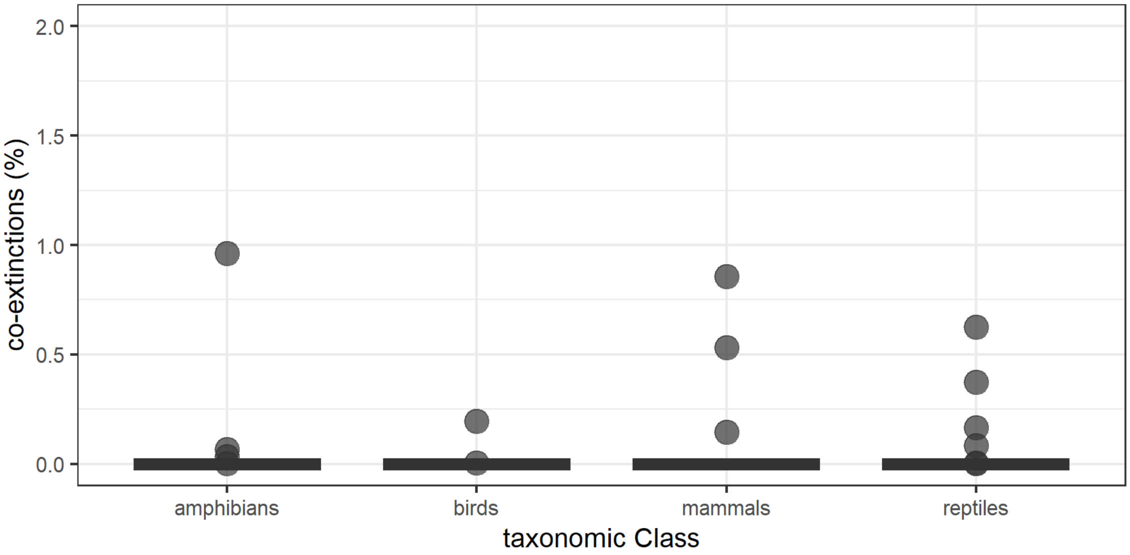

Figure A26. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

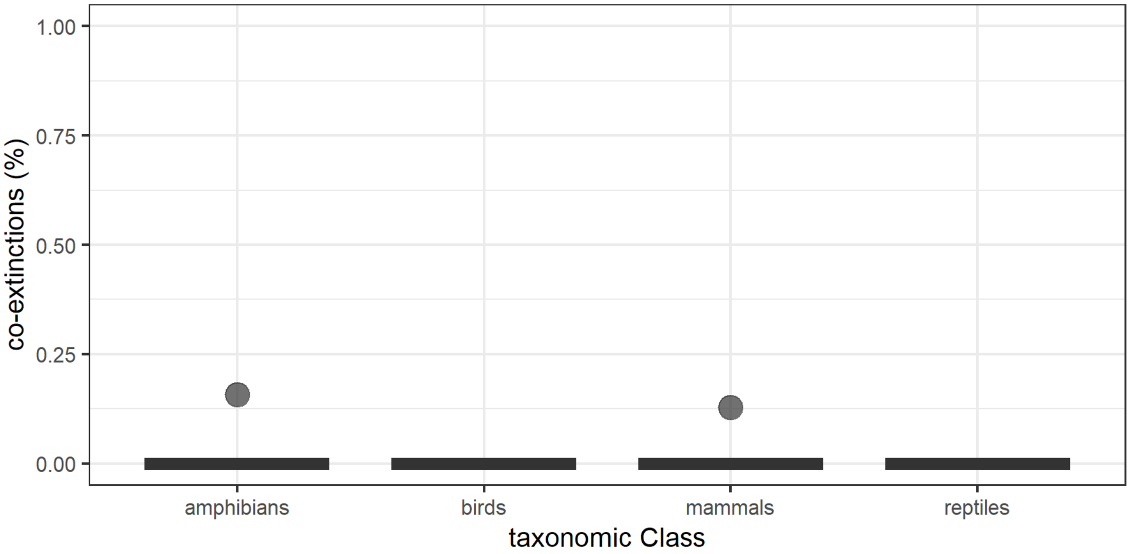

Figure A27. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

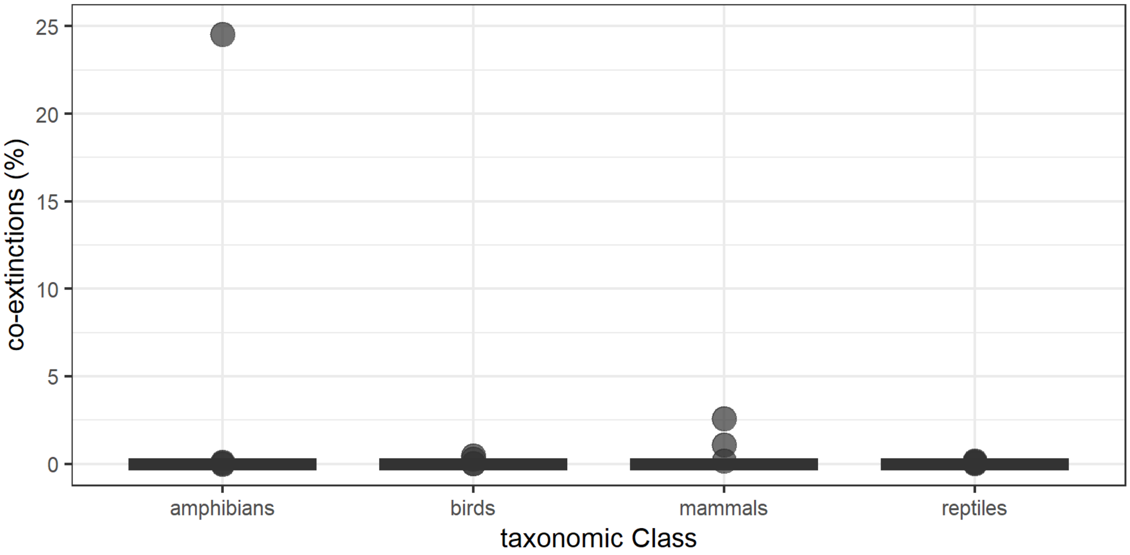

Figure A28. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

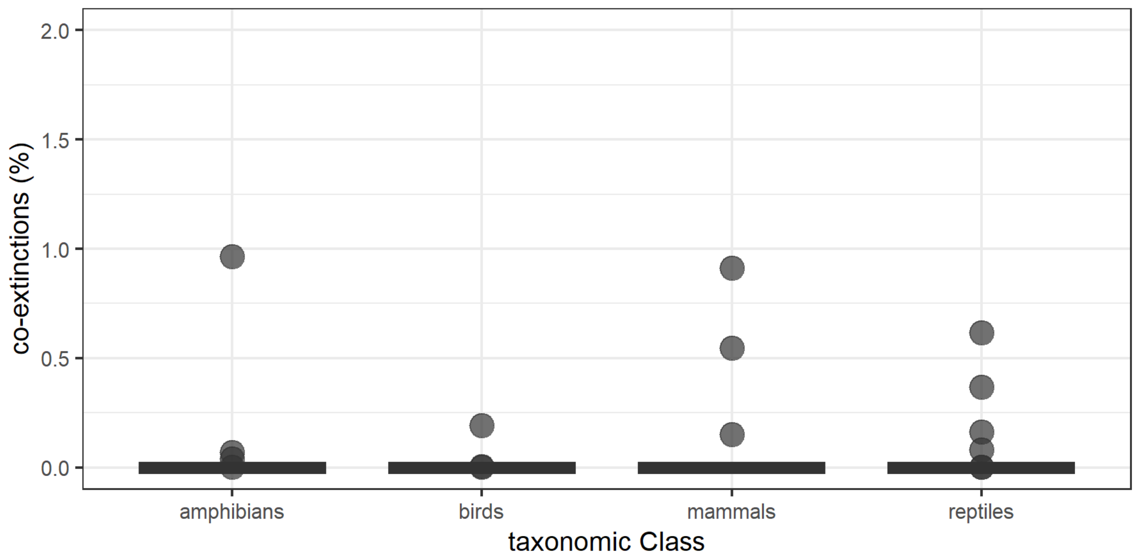

Figure A29. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

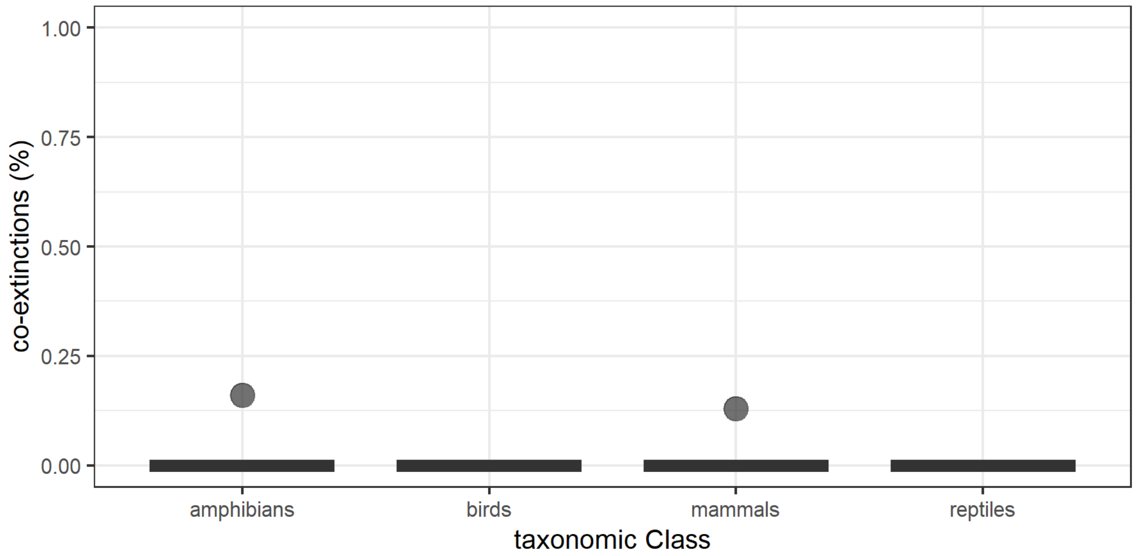

Figure A30. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

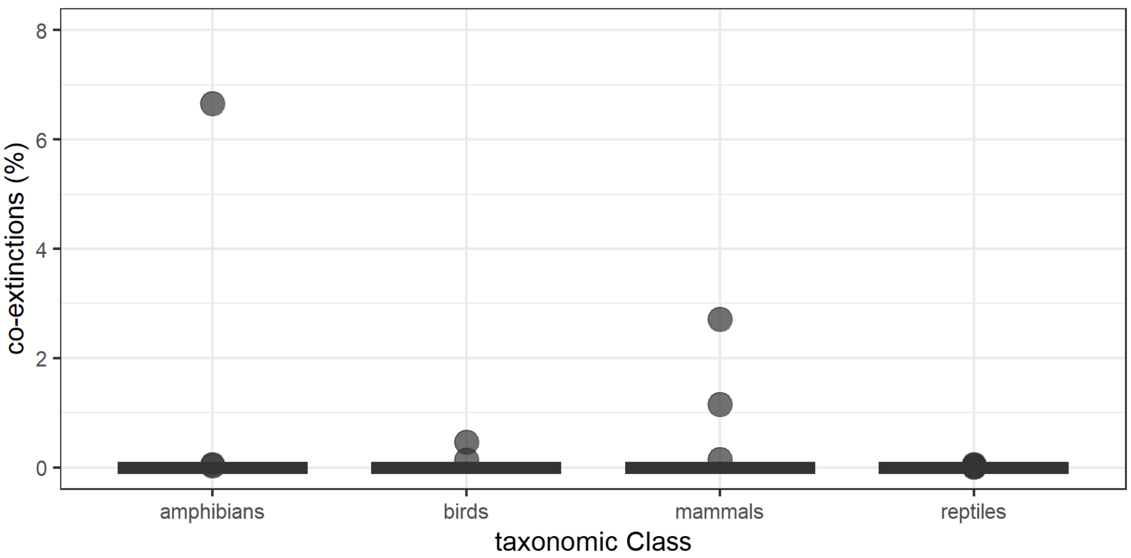

Figure A31. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

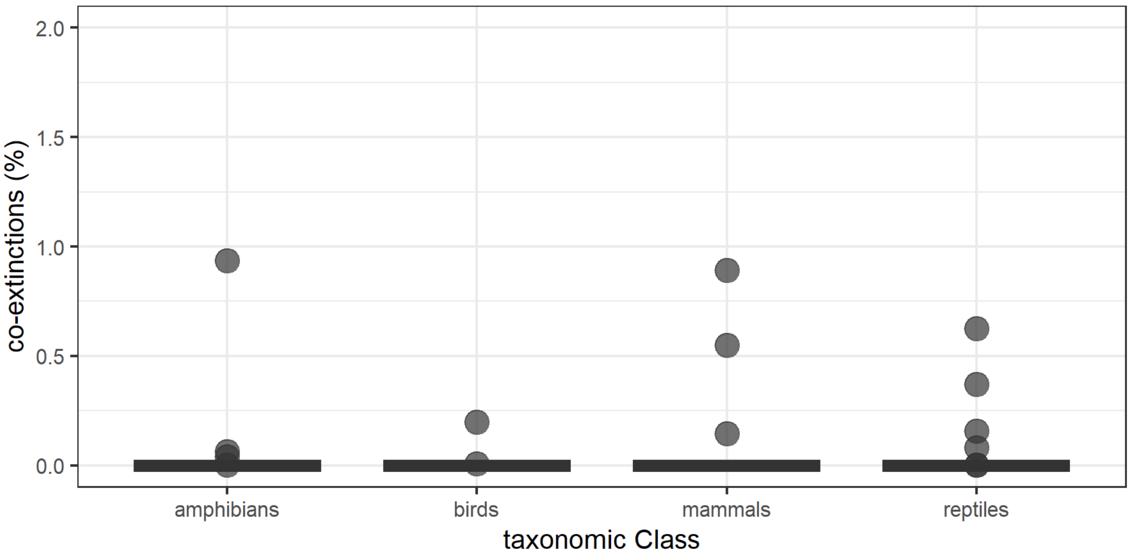

Figure A32. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

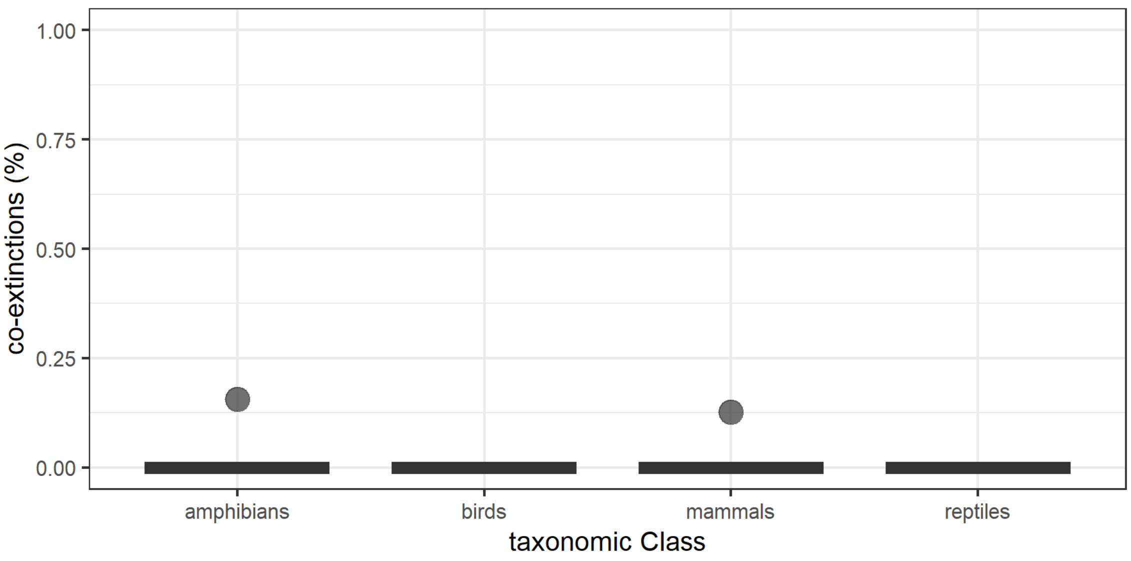

Figure A33. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

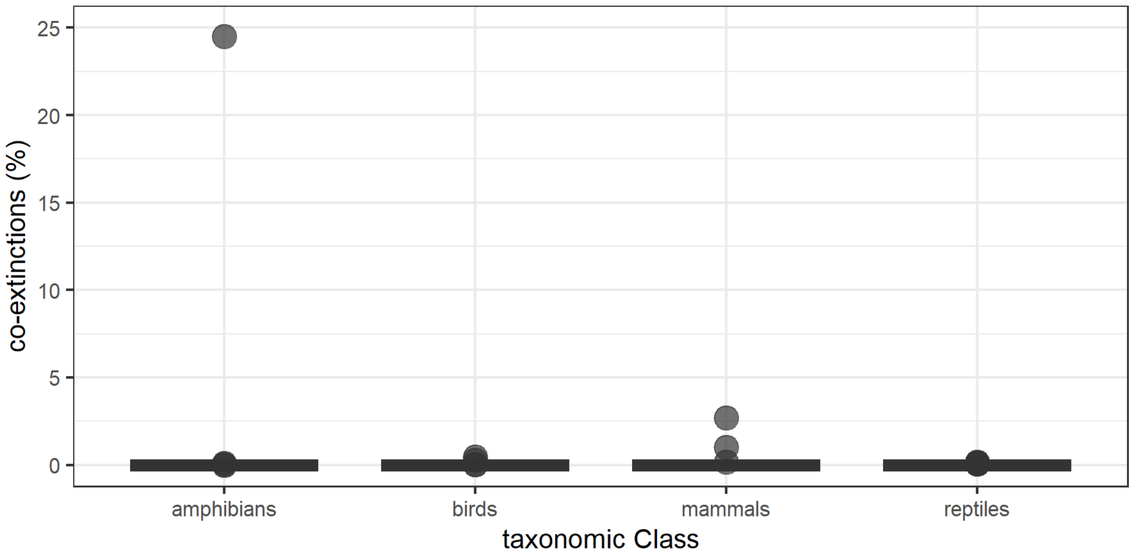

Figure A34. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

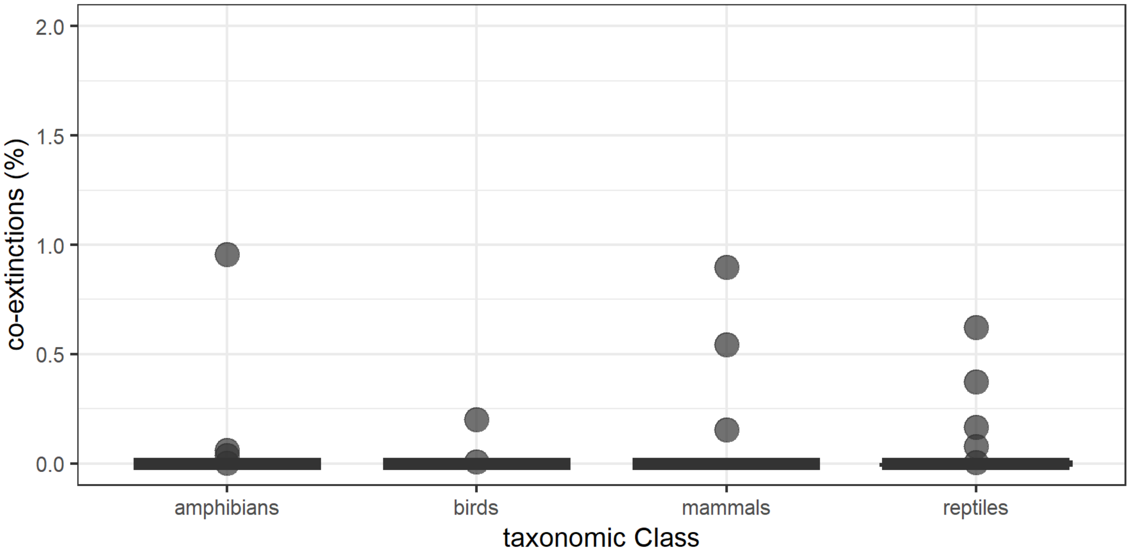

Figure A35. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

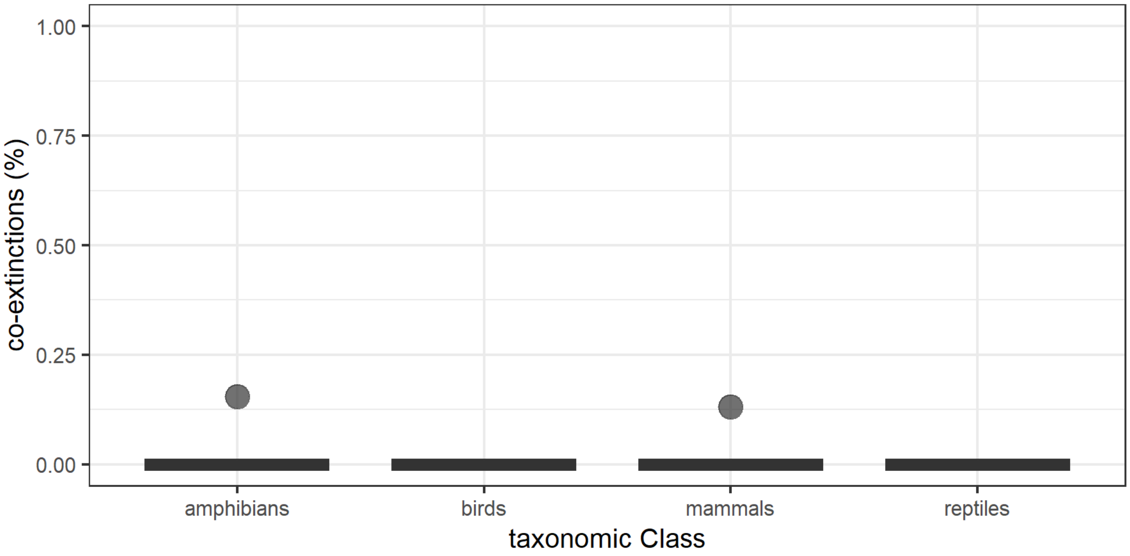

Figure A36. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

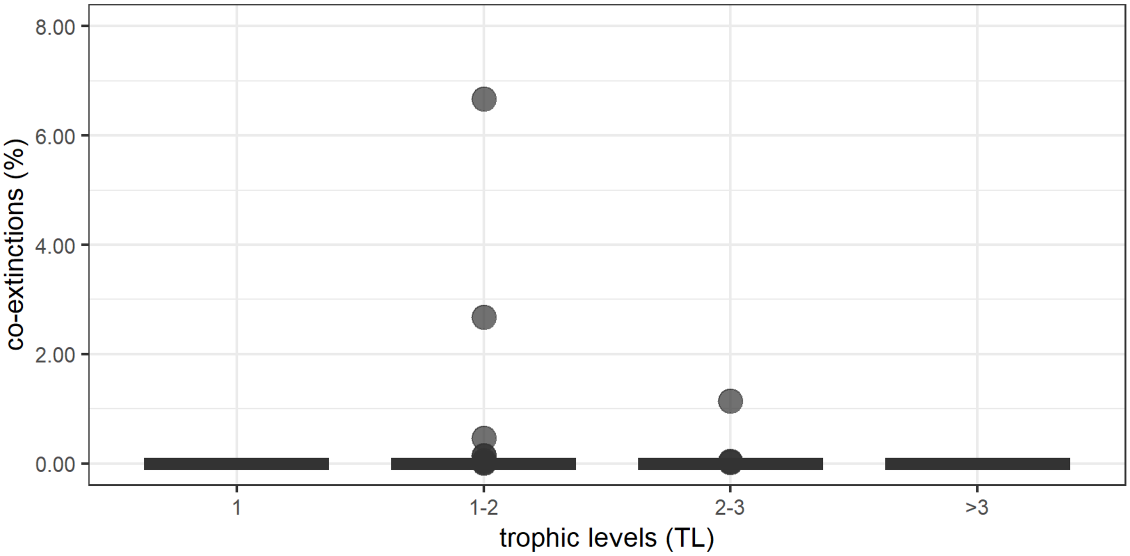

Figure A37. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

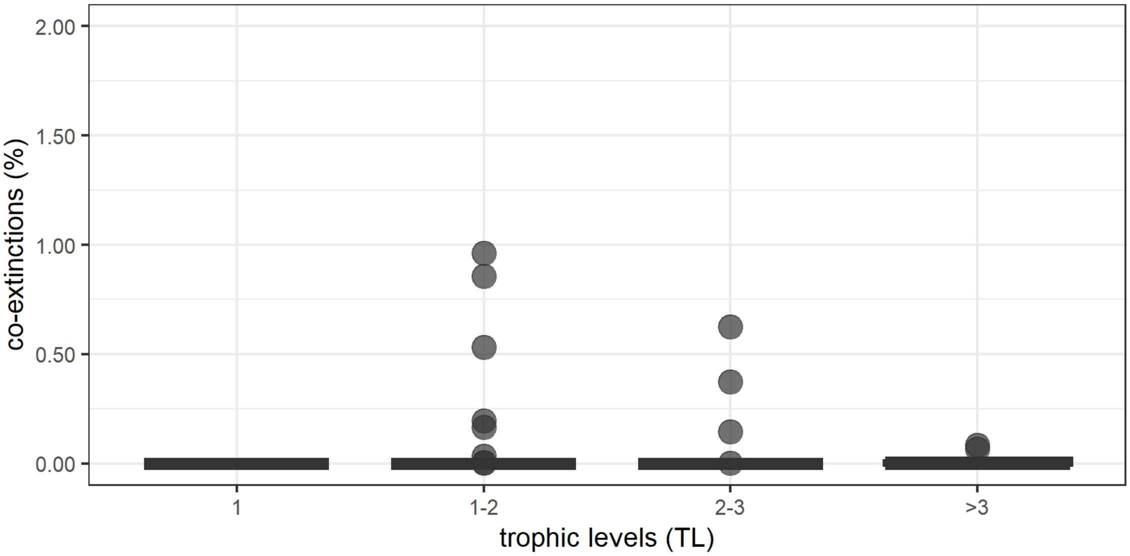

Figure A38. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

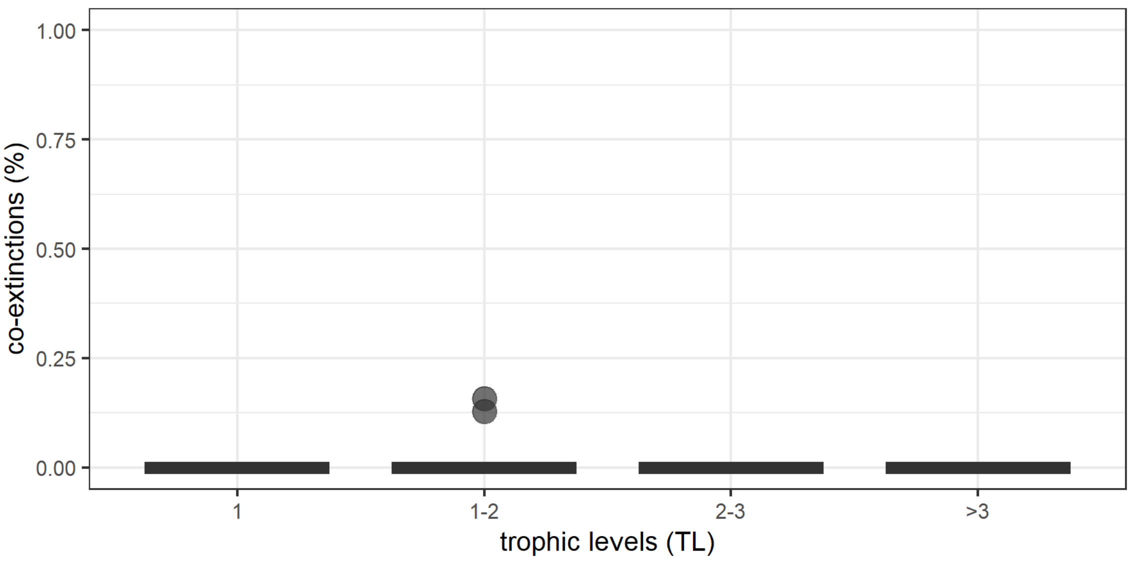

Figure A39. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

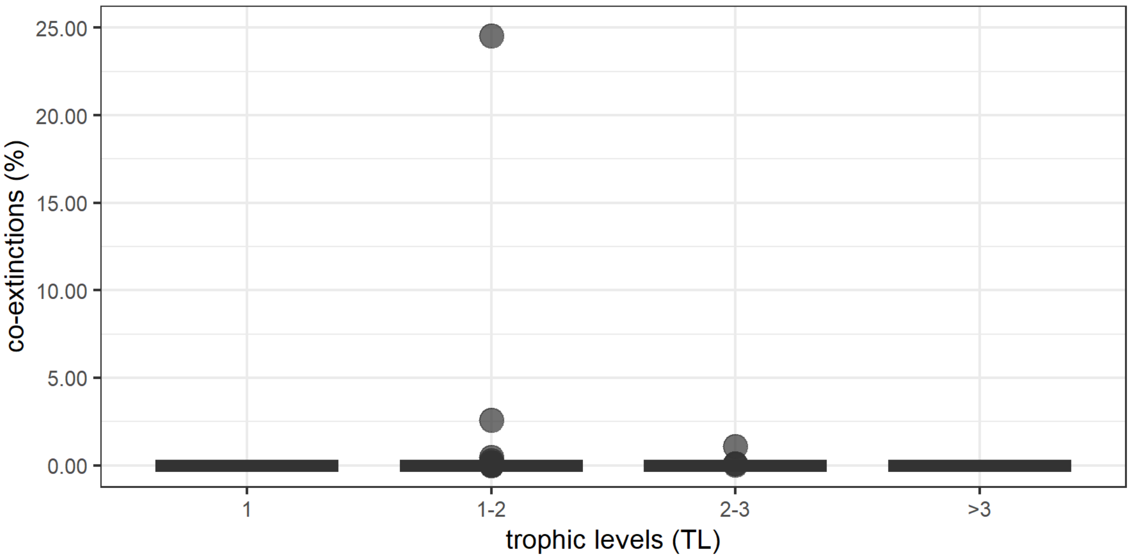

Figure A40. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

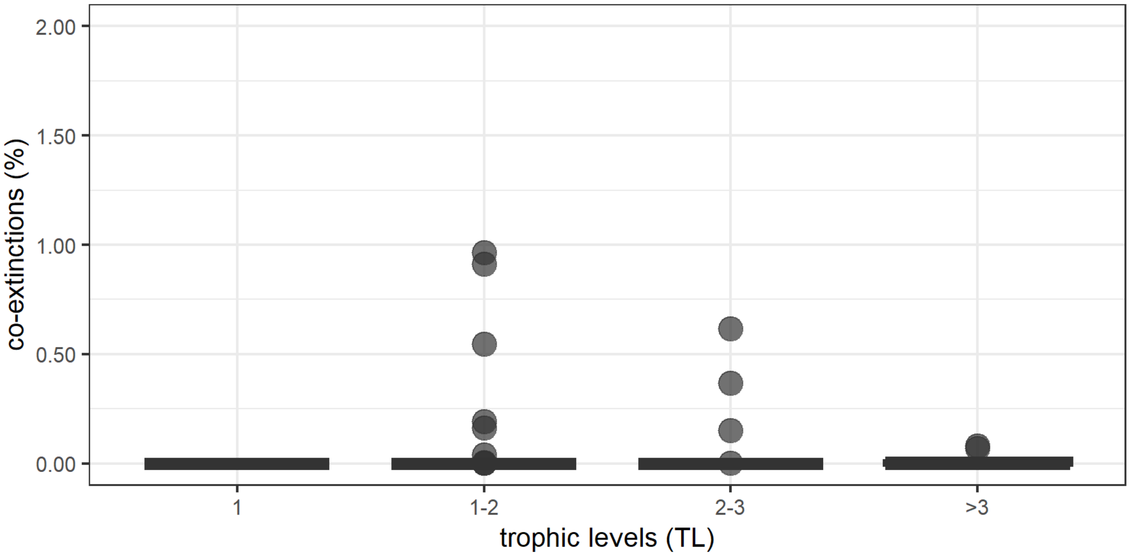

Figure A41. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

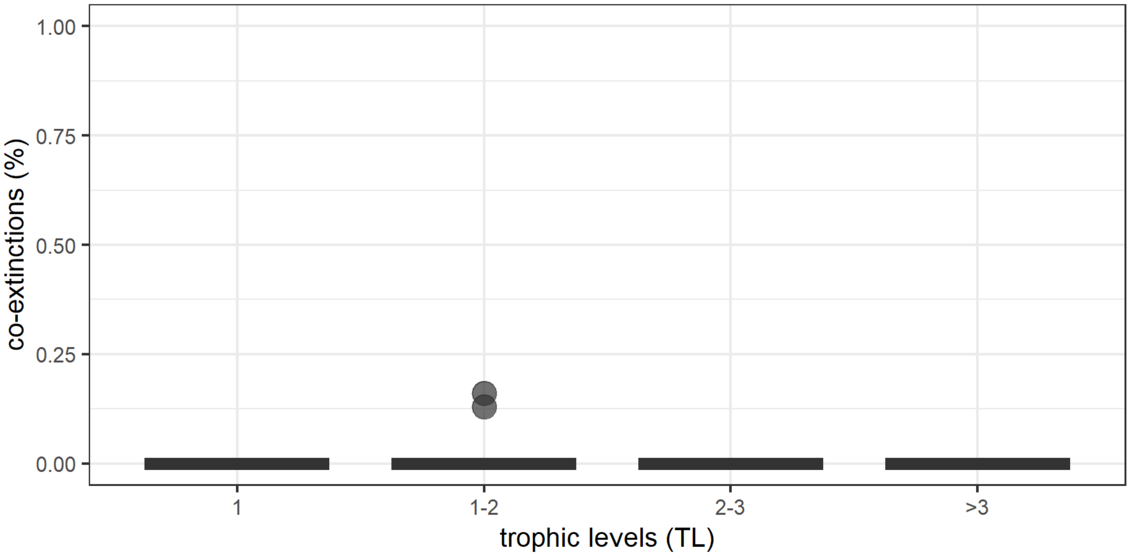

Figure A42. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

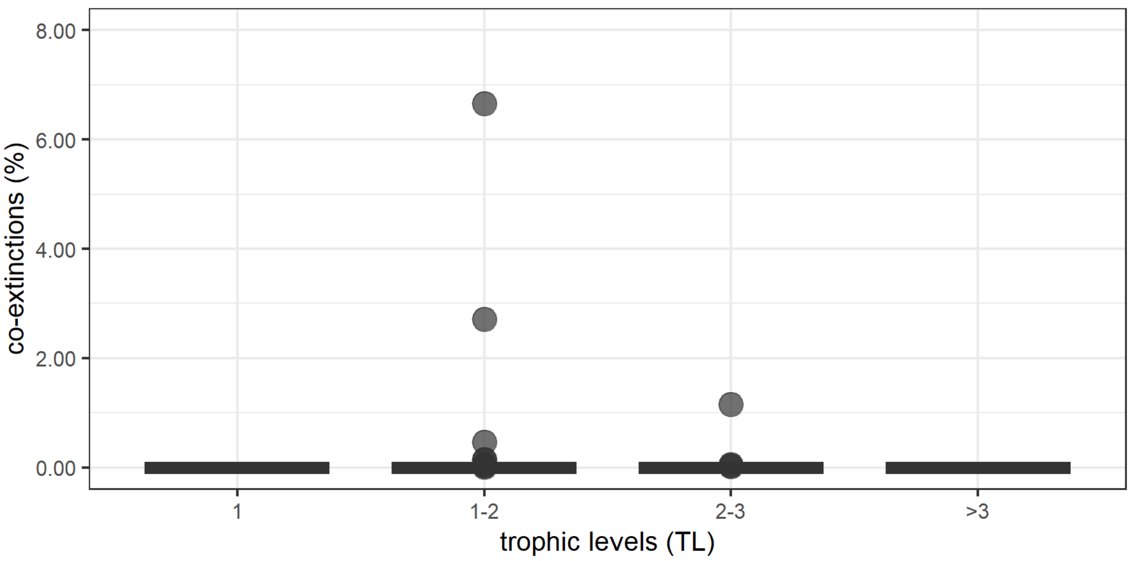

Figure A43. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

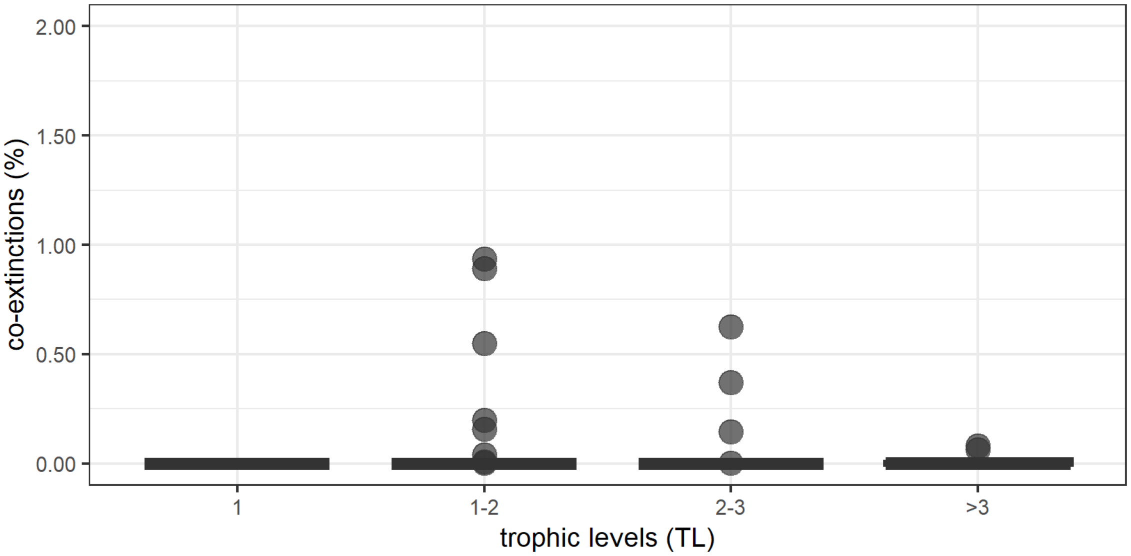

Figure A44. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

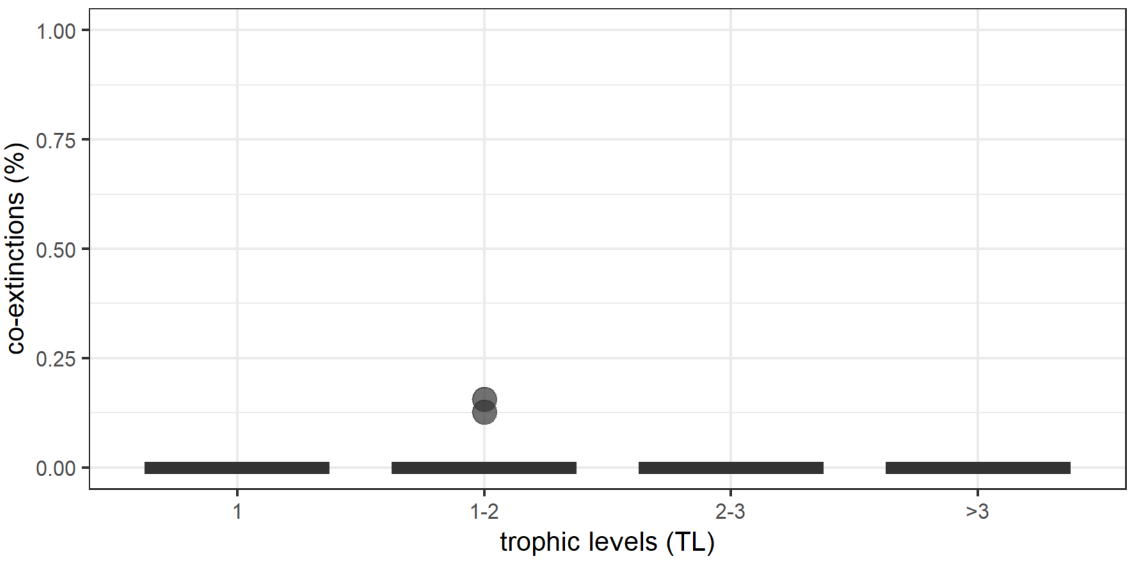

Figure A45. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

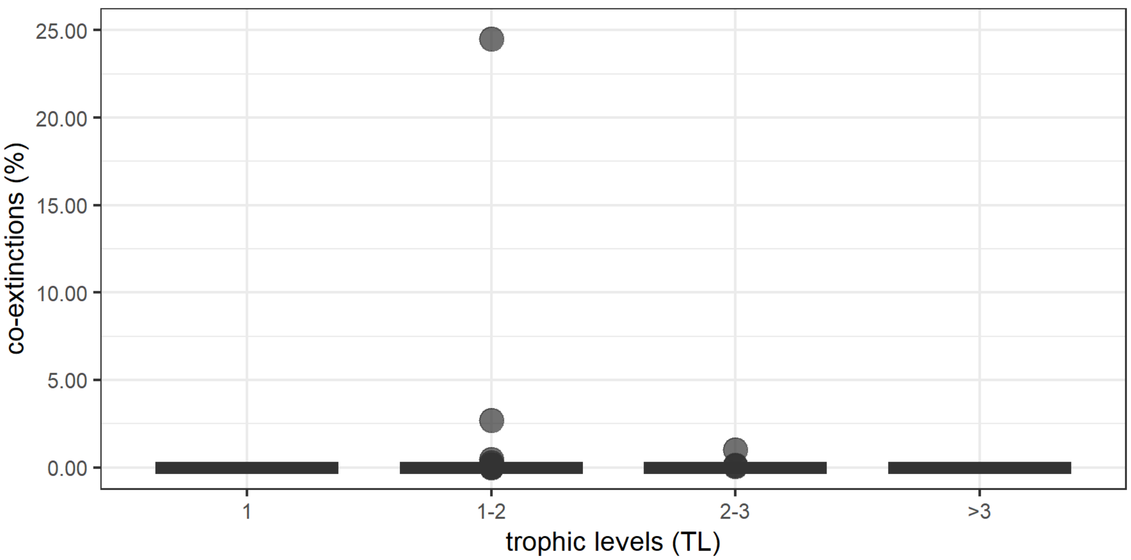

Figure A46. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

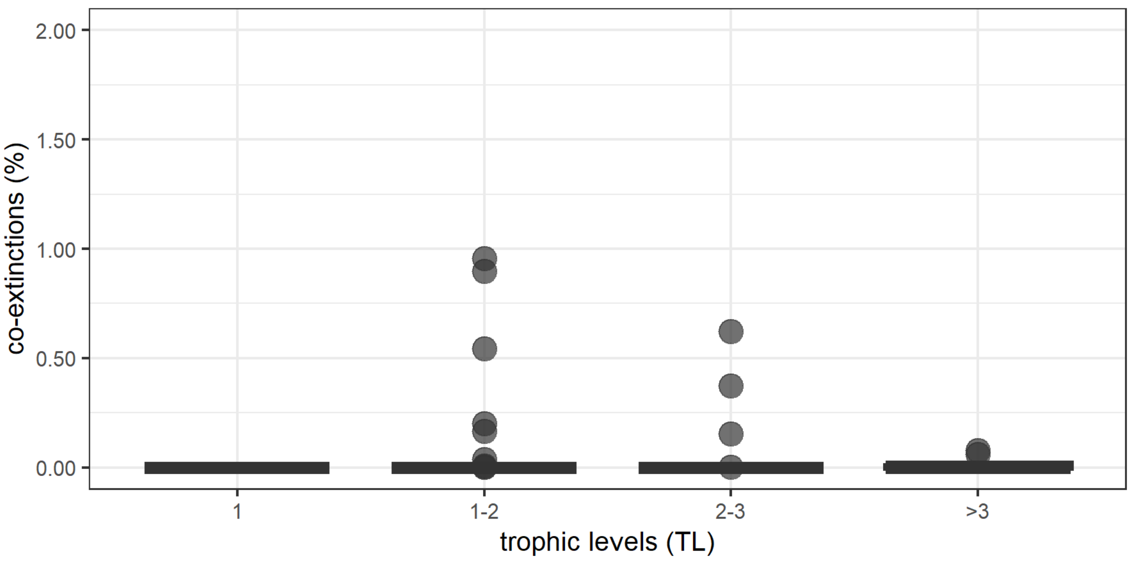

Figure A47. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

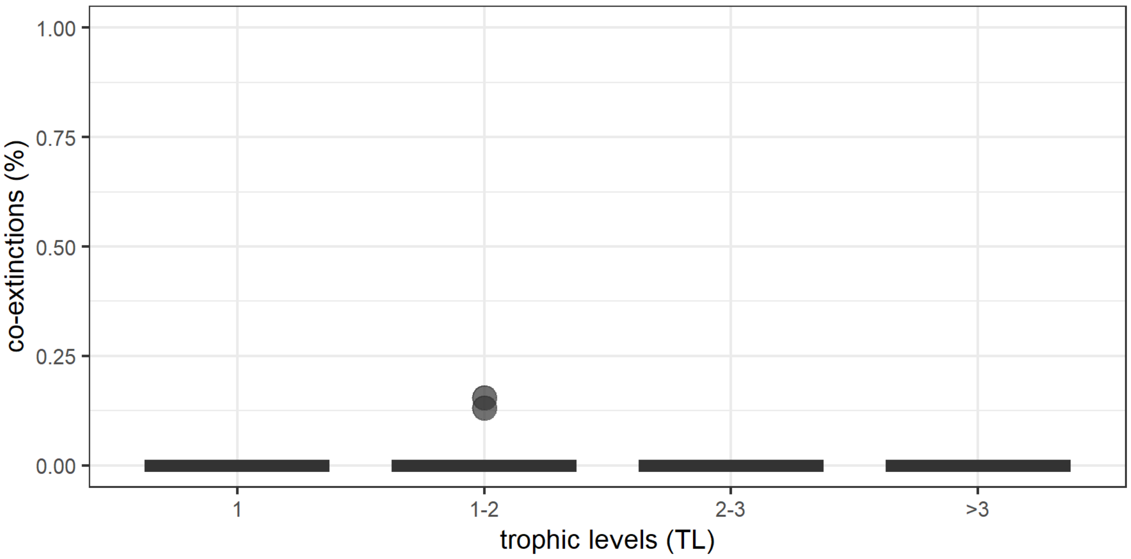

Figure A48. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the highland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

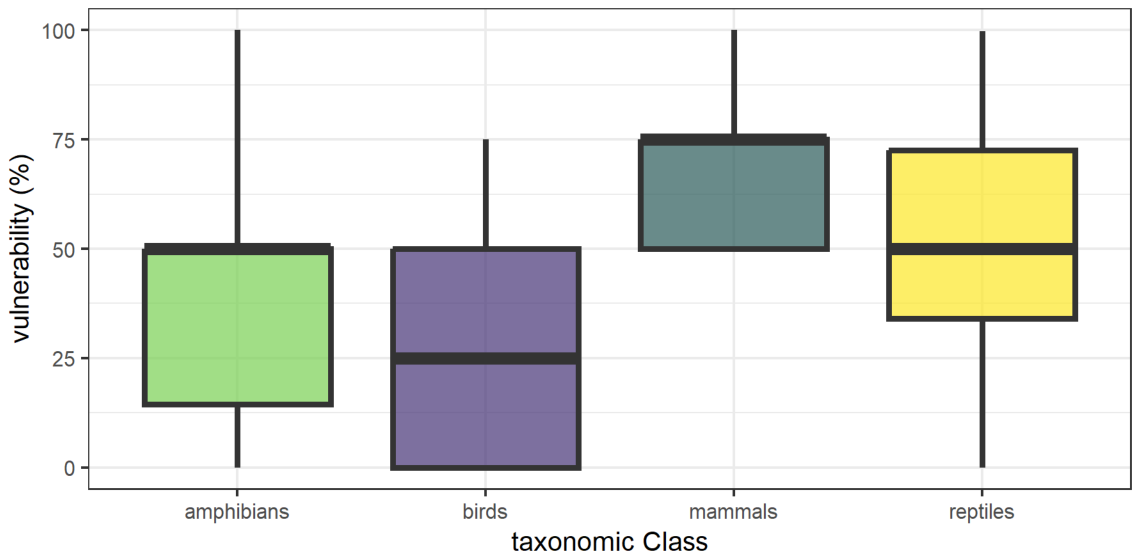

Figure A49. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

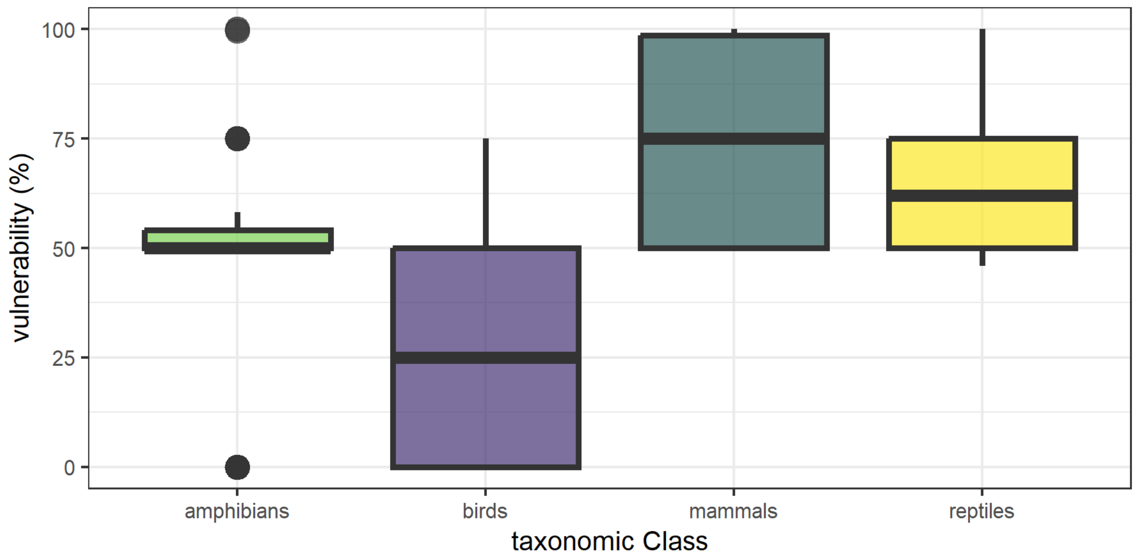

Figure A50. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

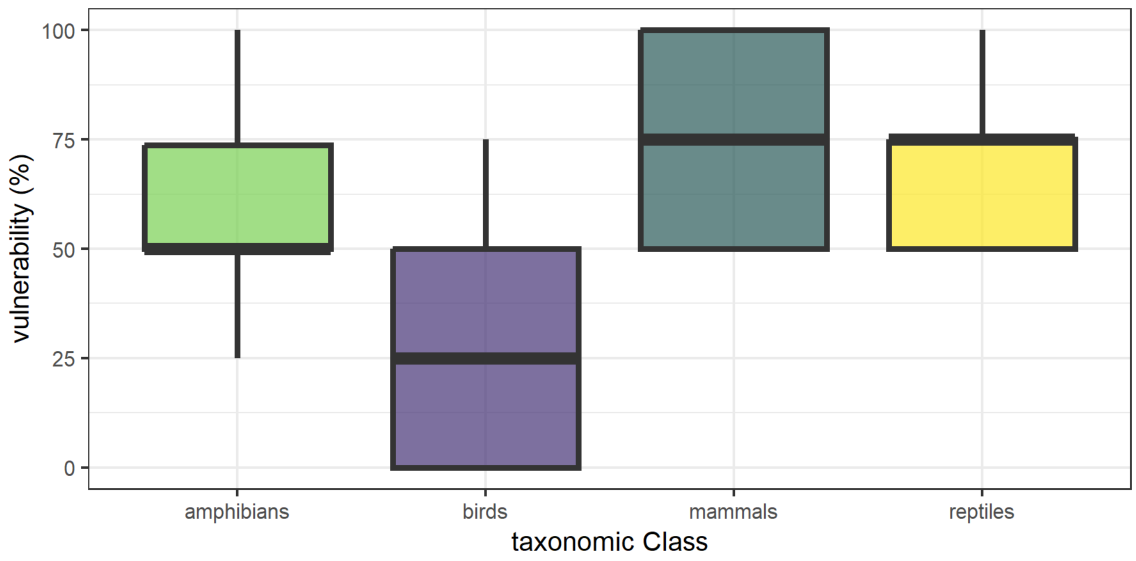

Figure A51. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

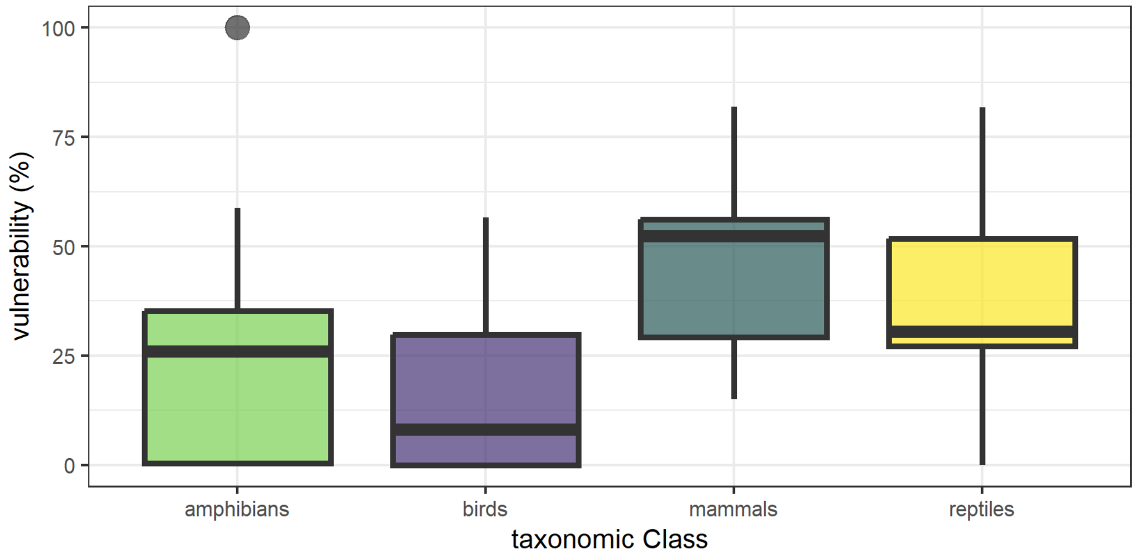

Figure A52. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

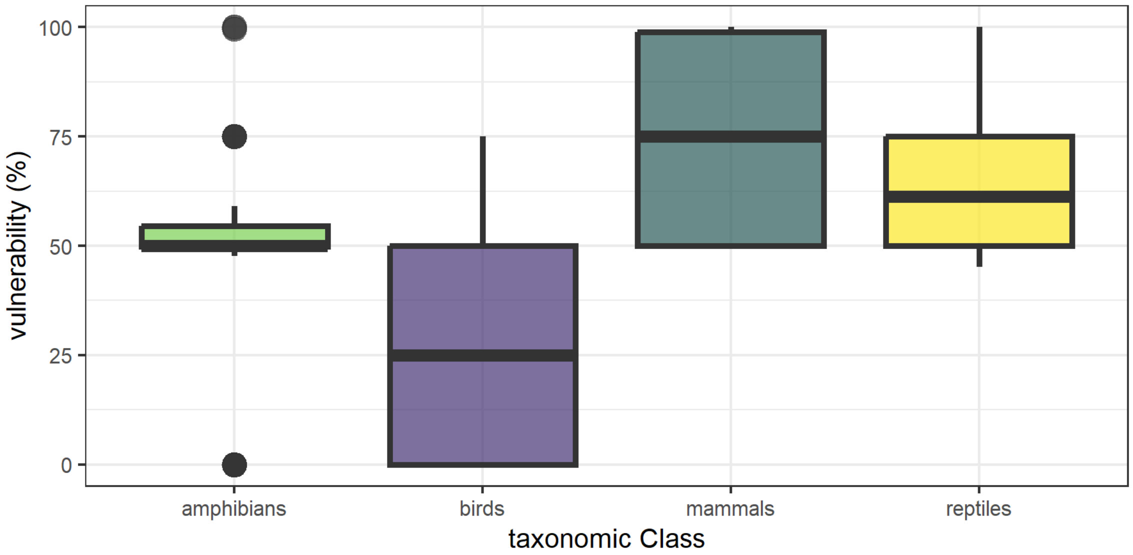

Figure A53. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

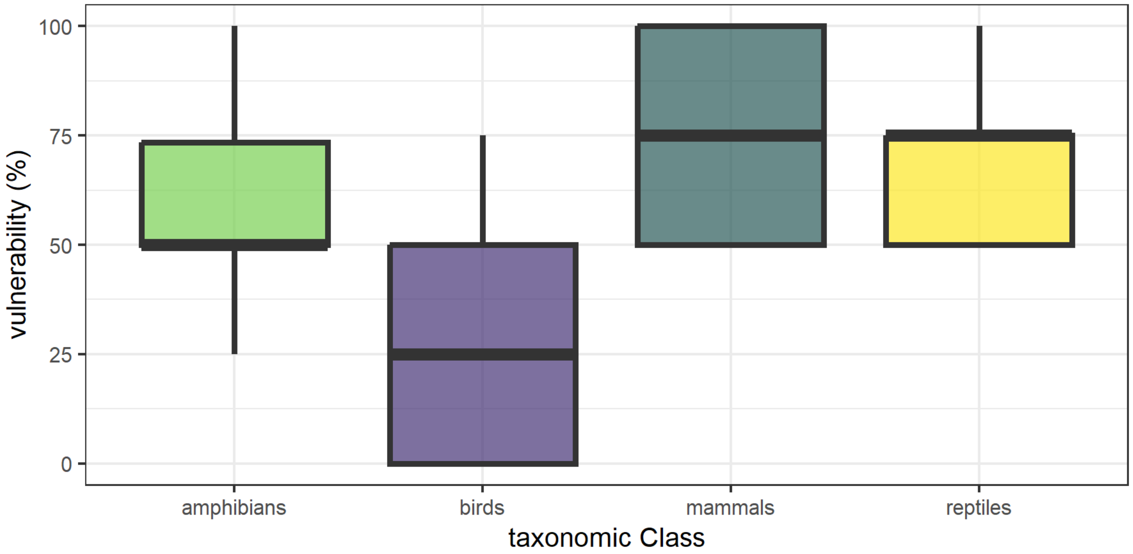

Figure A54. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

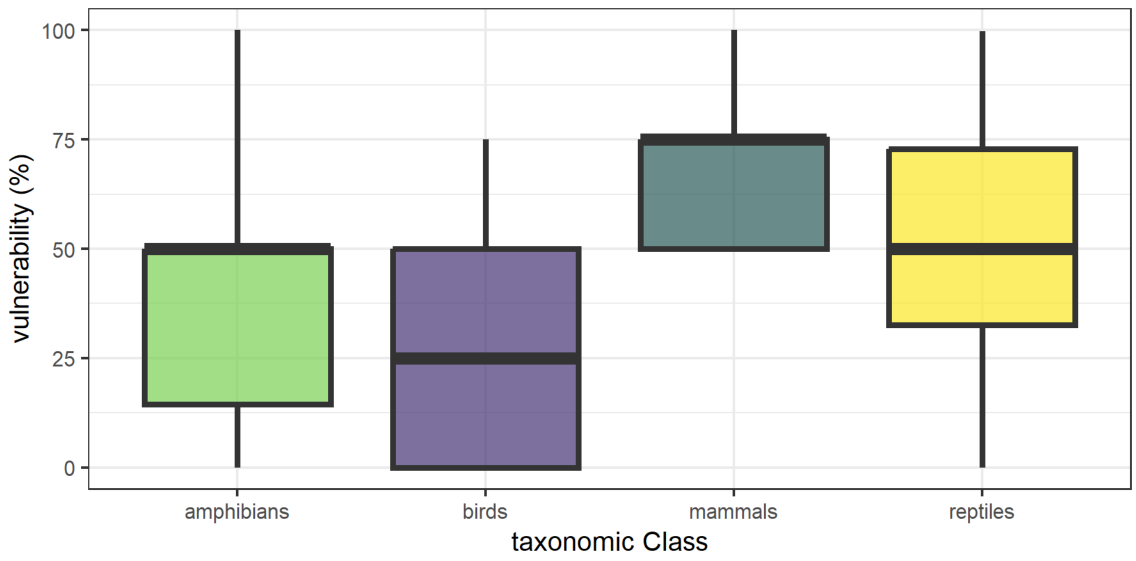

Figure A55. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

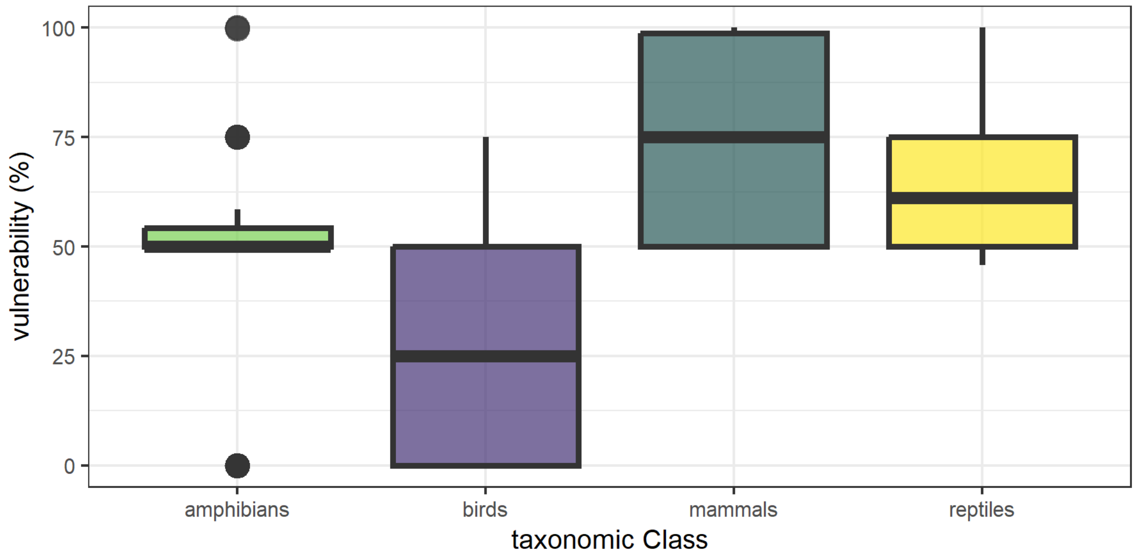

Figure A56. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

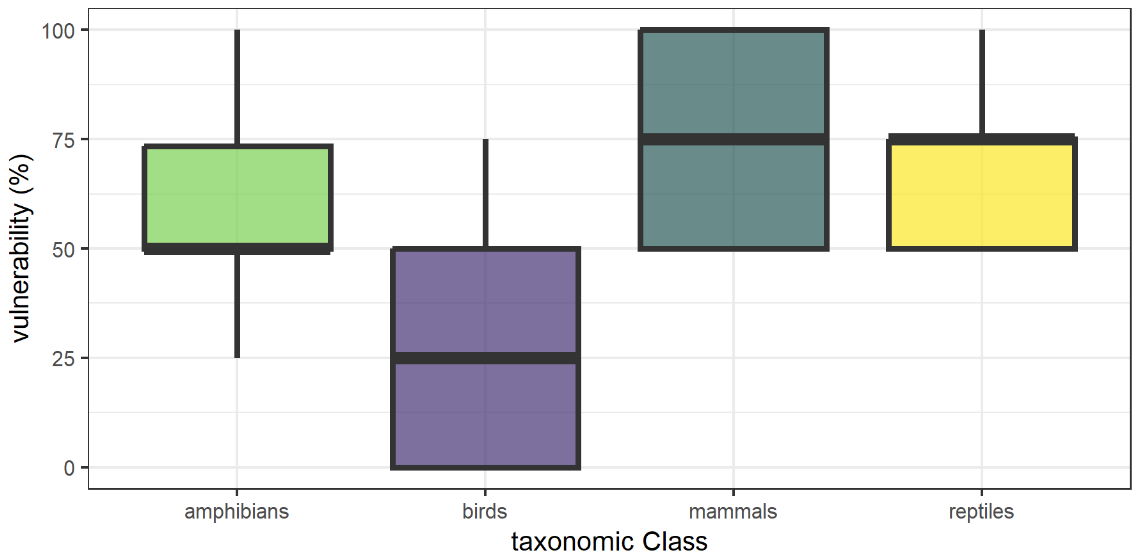

Figure A57. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

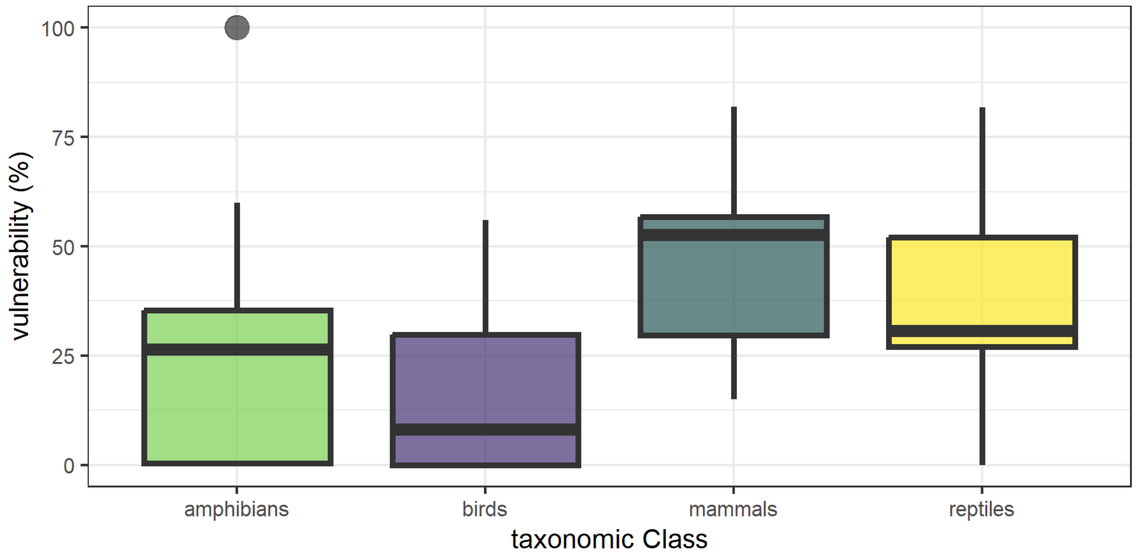

Figure A58. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

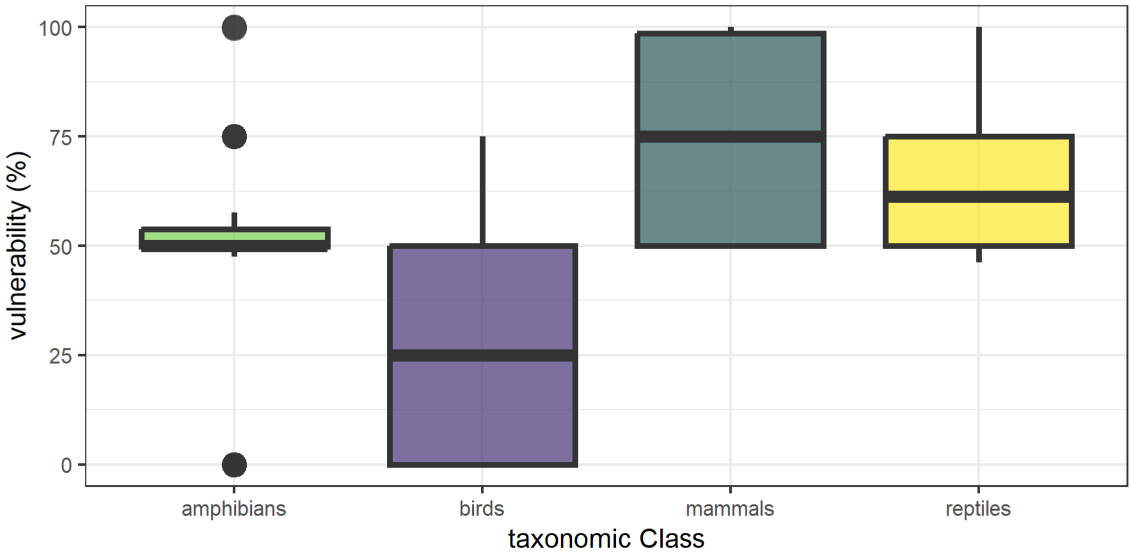

Figure A59. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

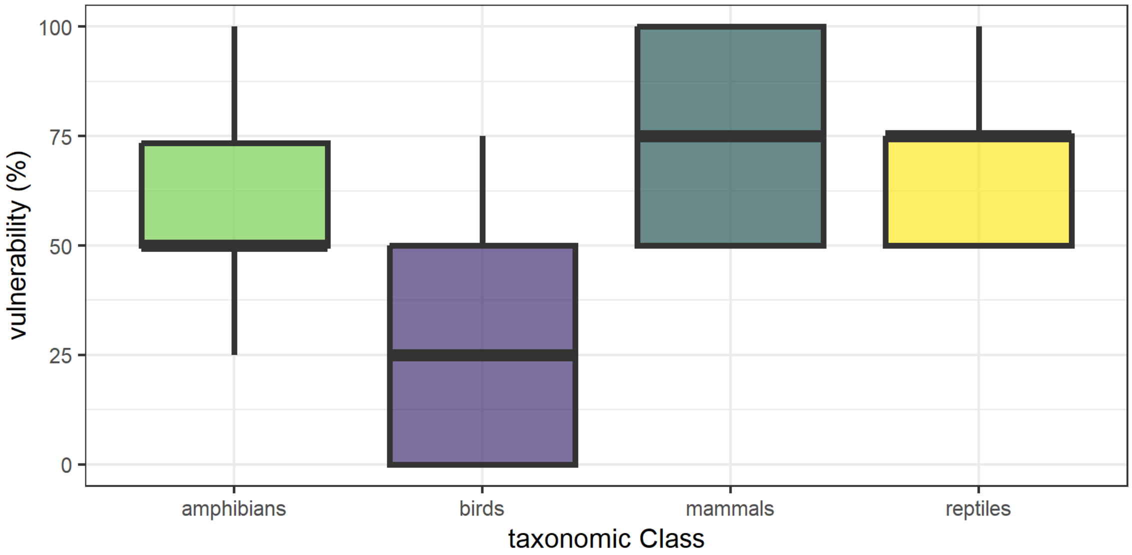

Figure A60. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

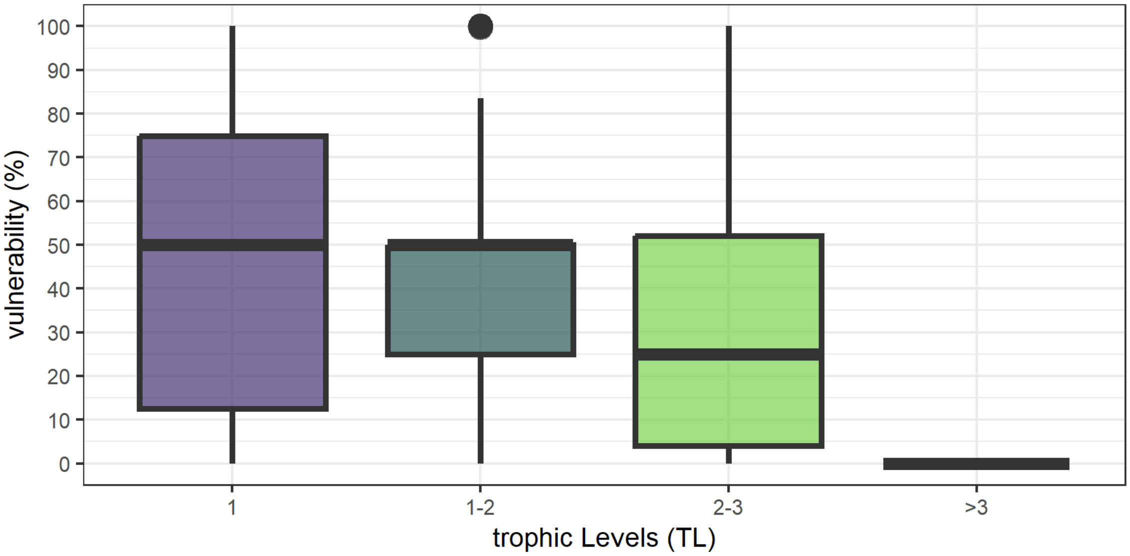

Figure A61. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

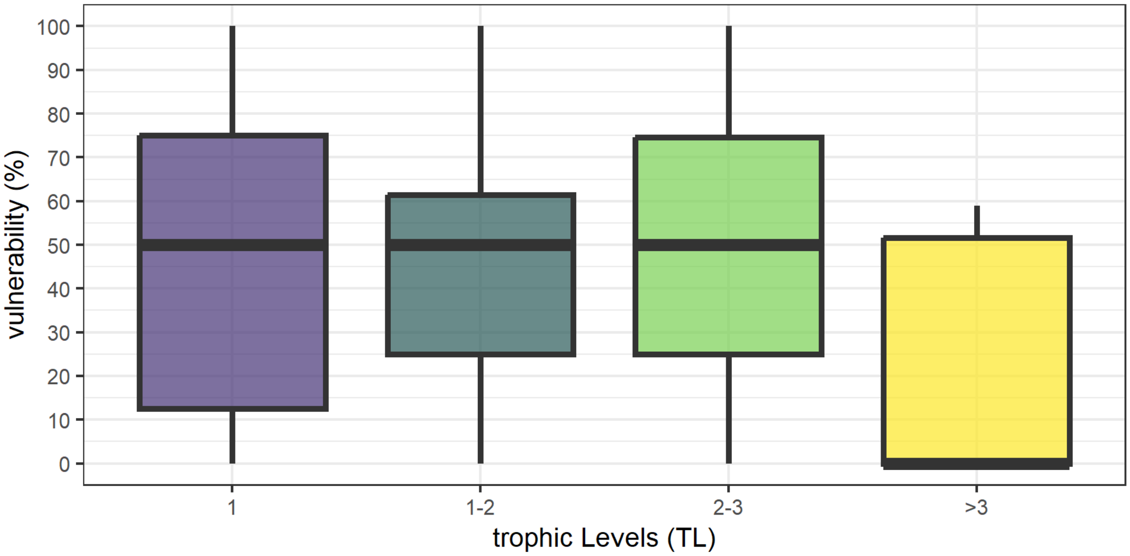

Figure A62. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

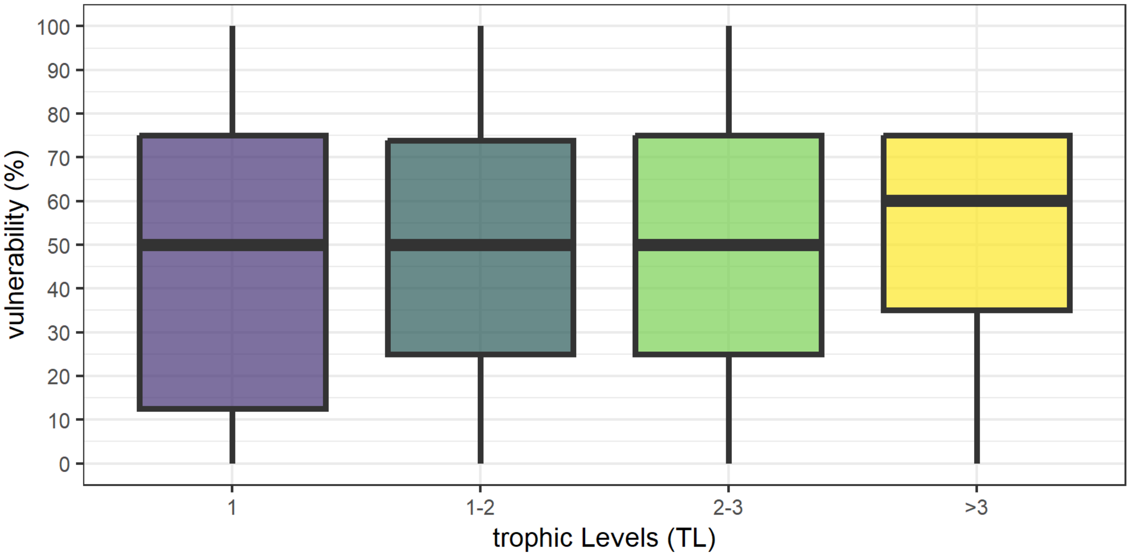

Figure A63. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

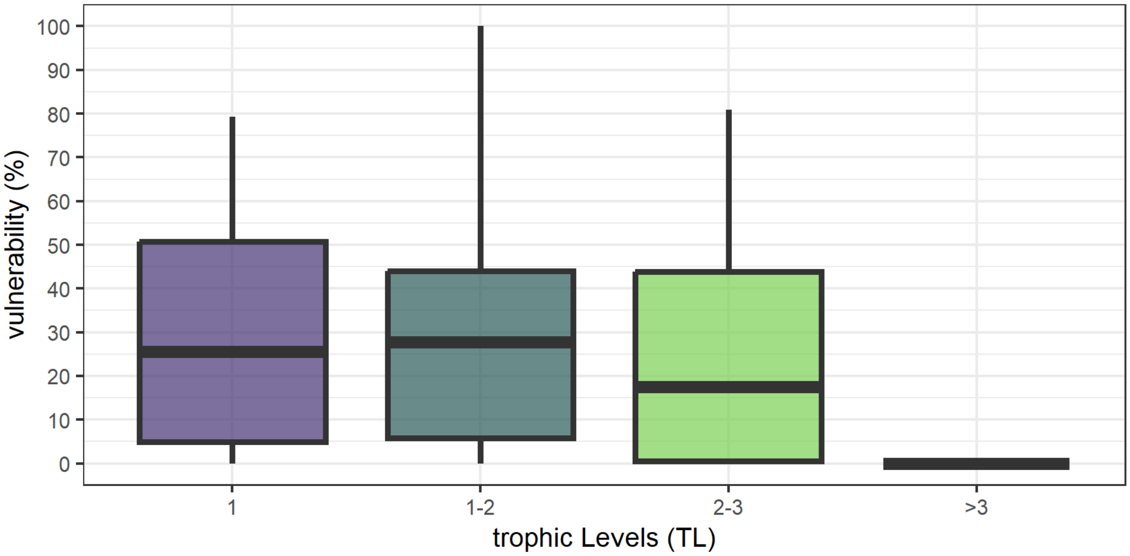

Figure A64. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

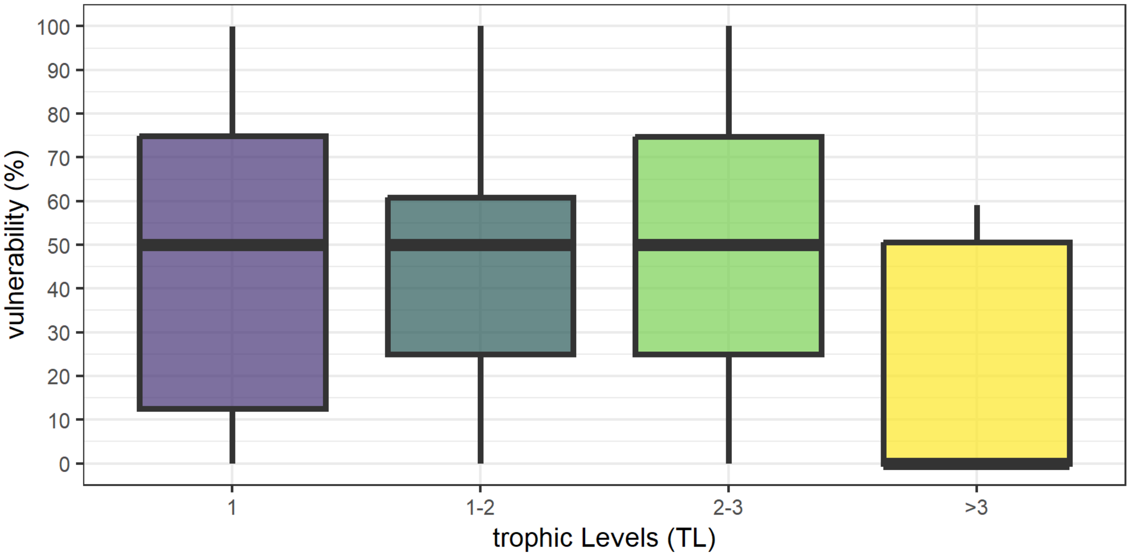

Figure A65. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

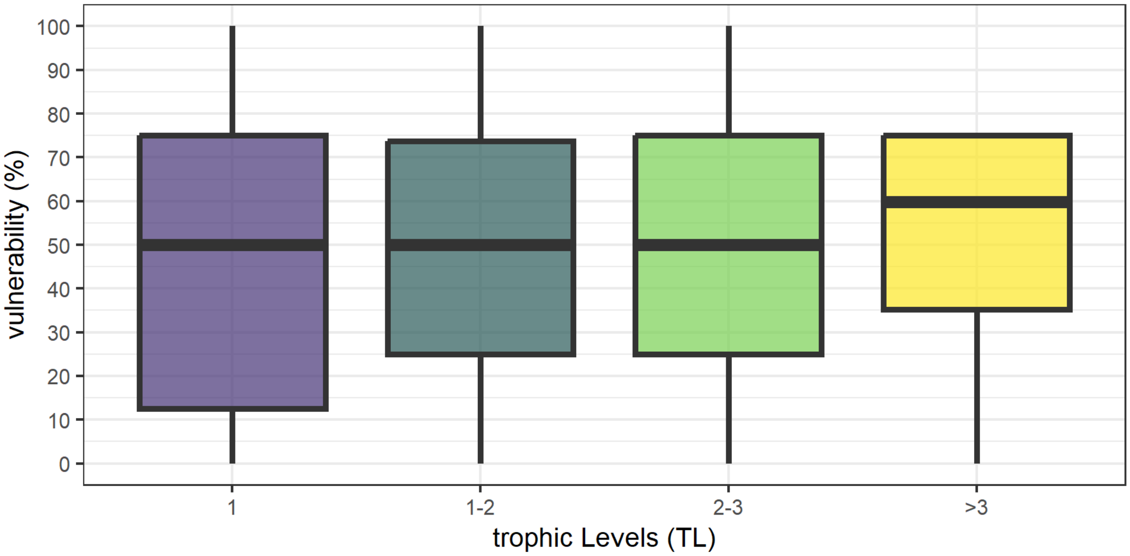

Figure A66. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

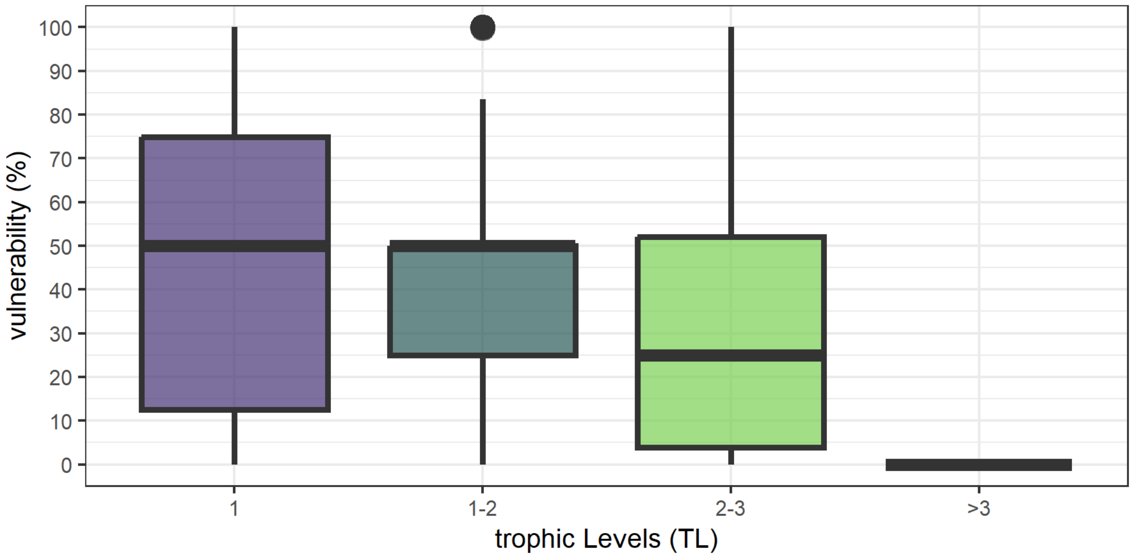

Figure A67. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

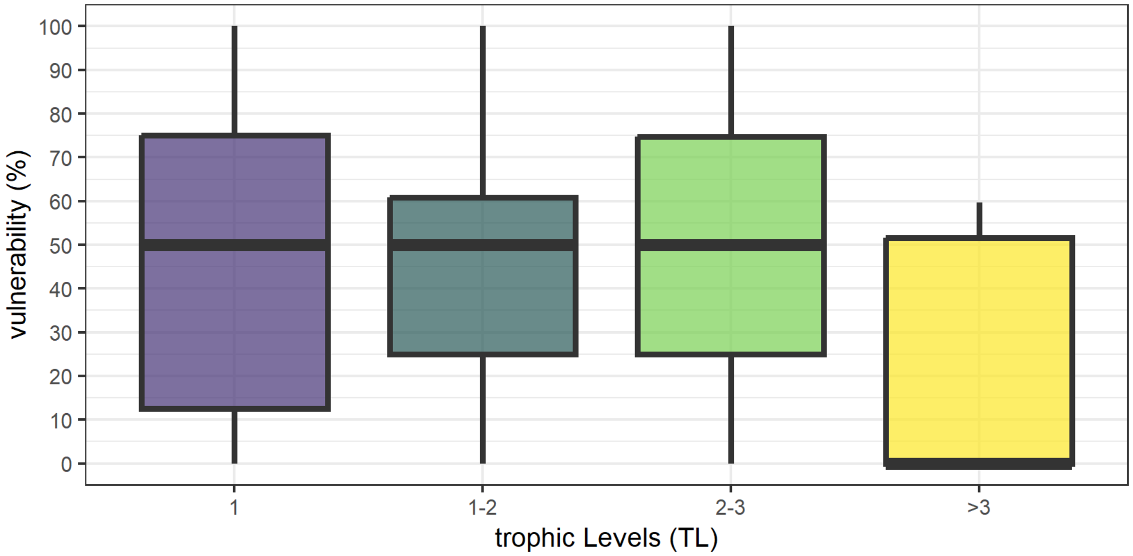

Figure A68. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

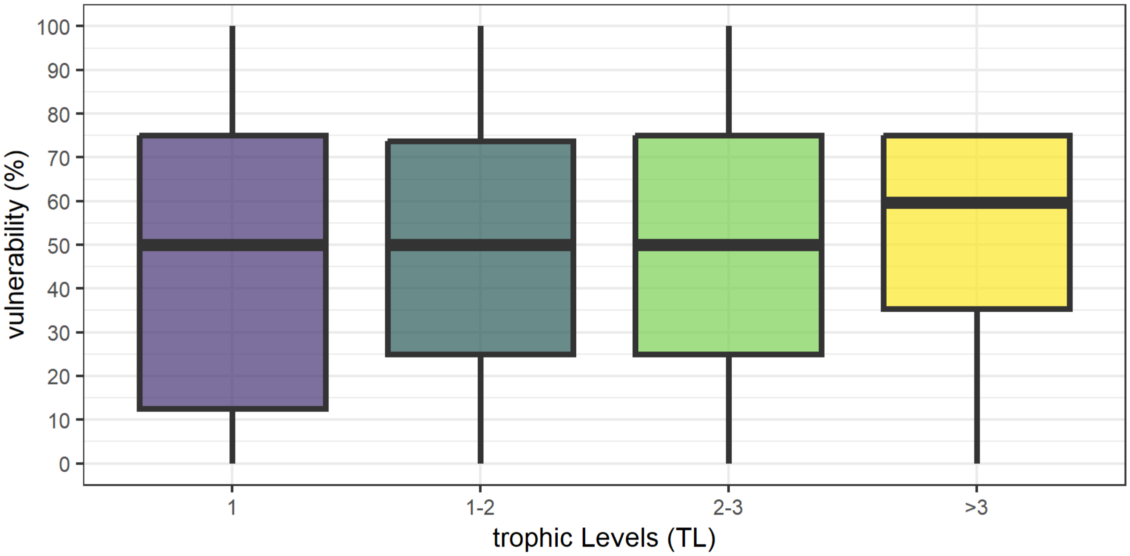

Figure A69. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

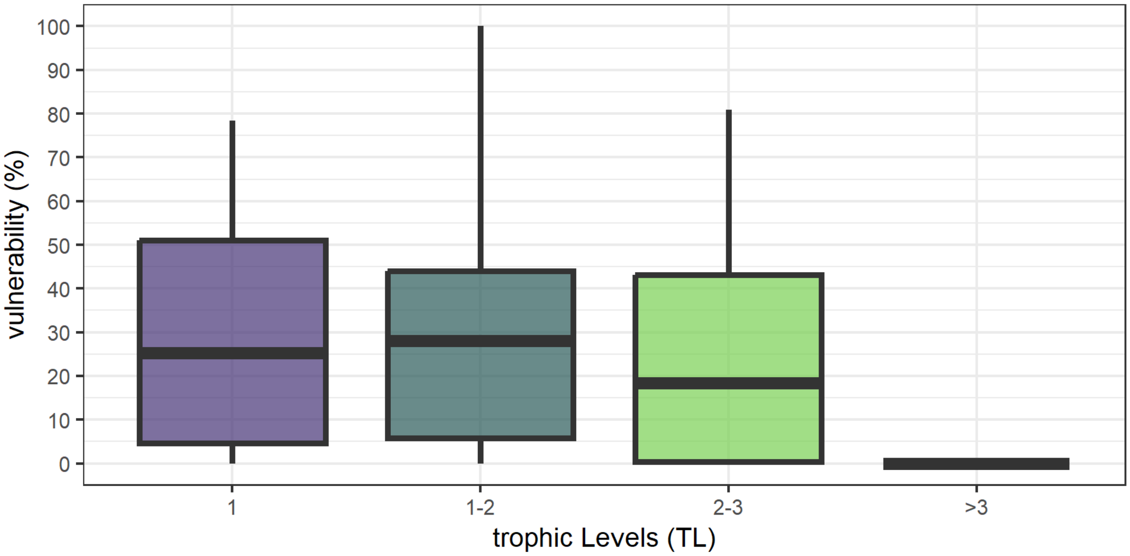

Figure A70. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

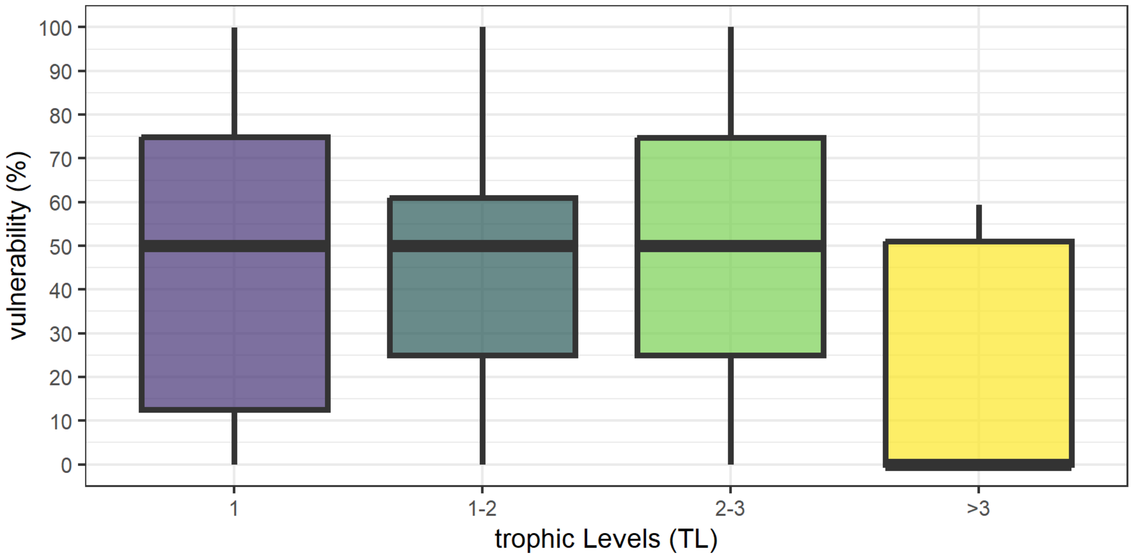

Figure A71. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

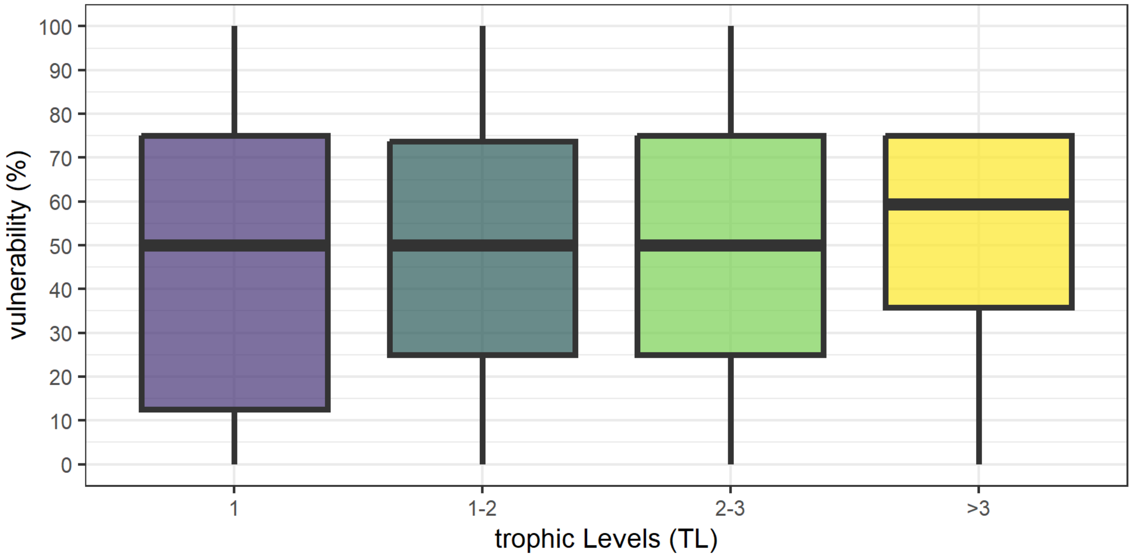

Figure A72. Mean vulnerability to primary extinction for each vertebrate species in the highland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

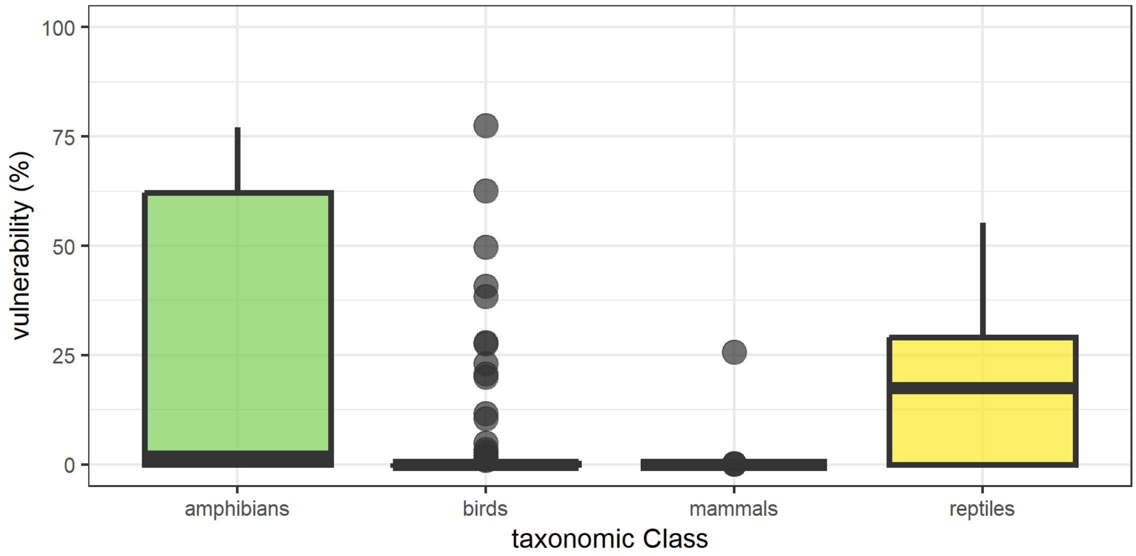

Figure A73. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

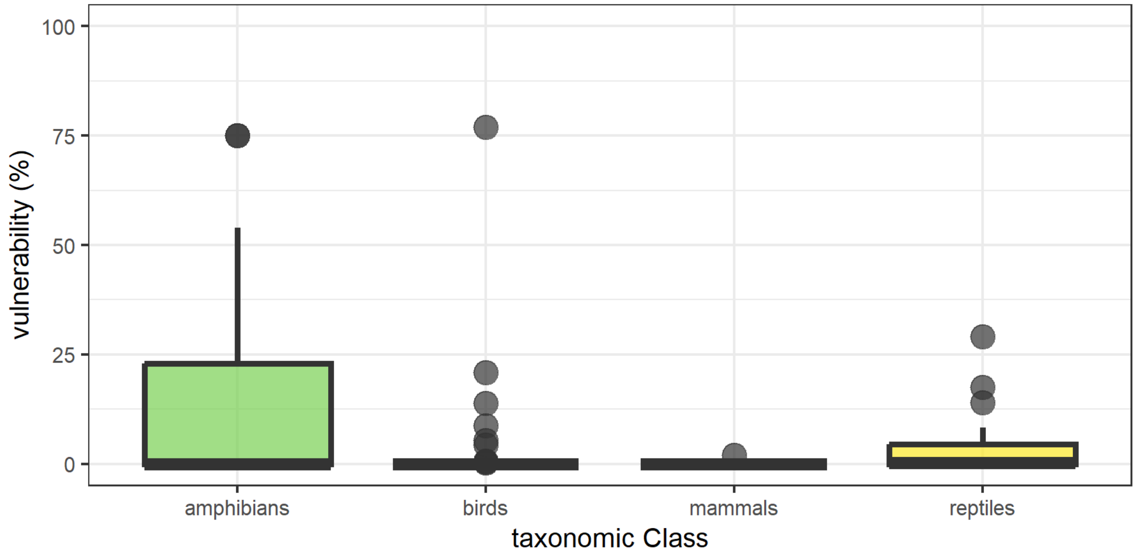

Figure A74. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

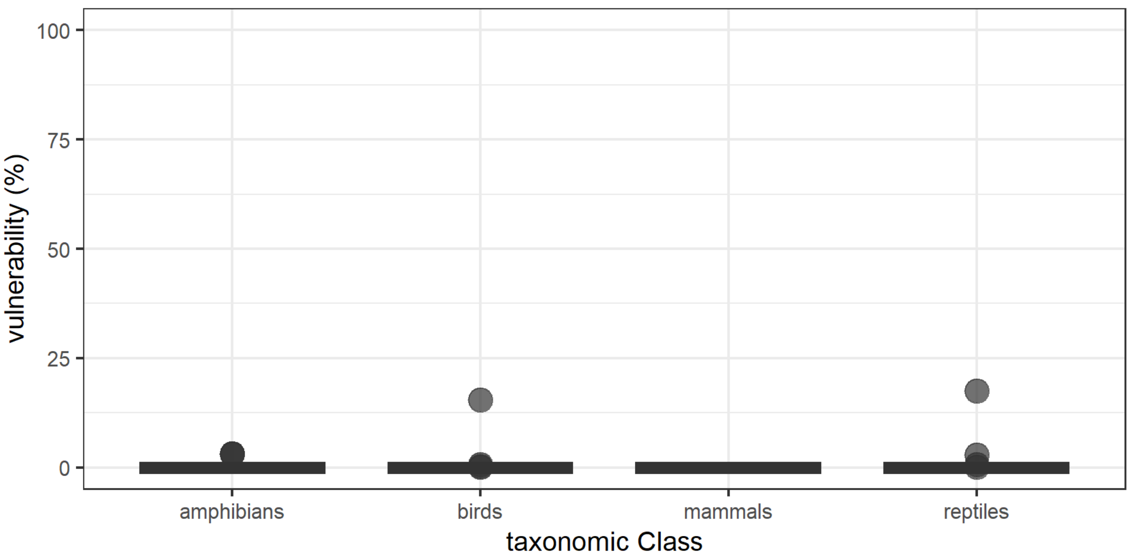

Figure A75. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

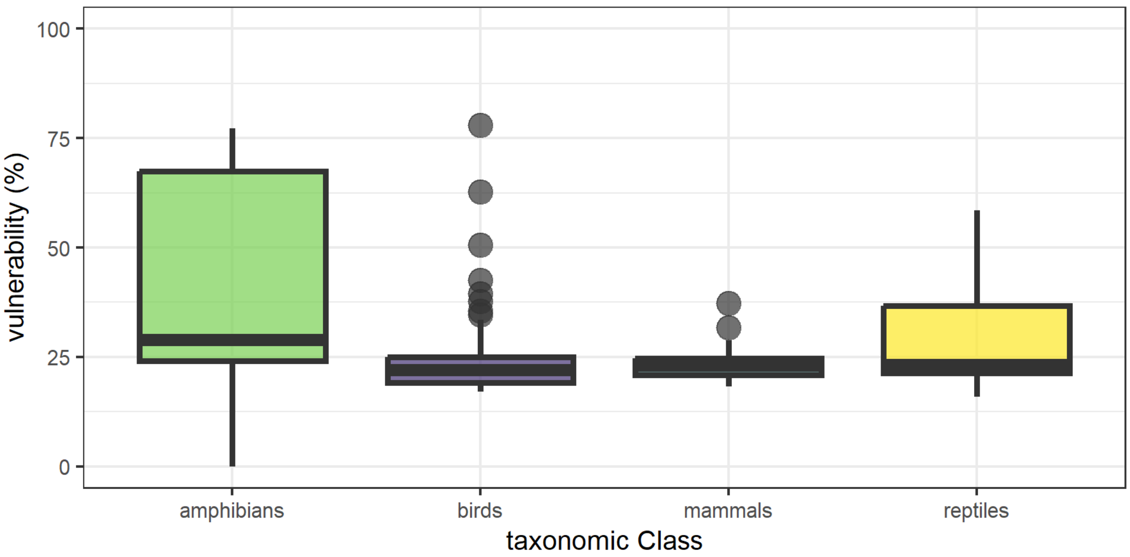

Figure A76. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

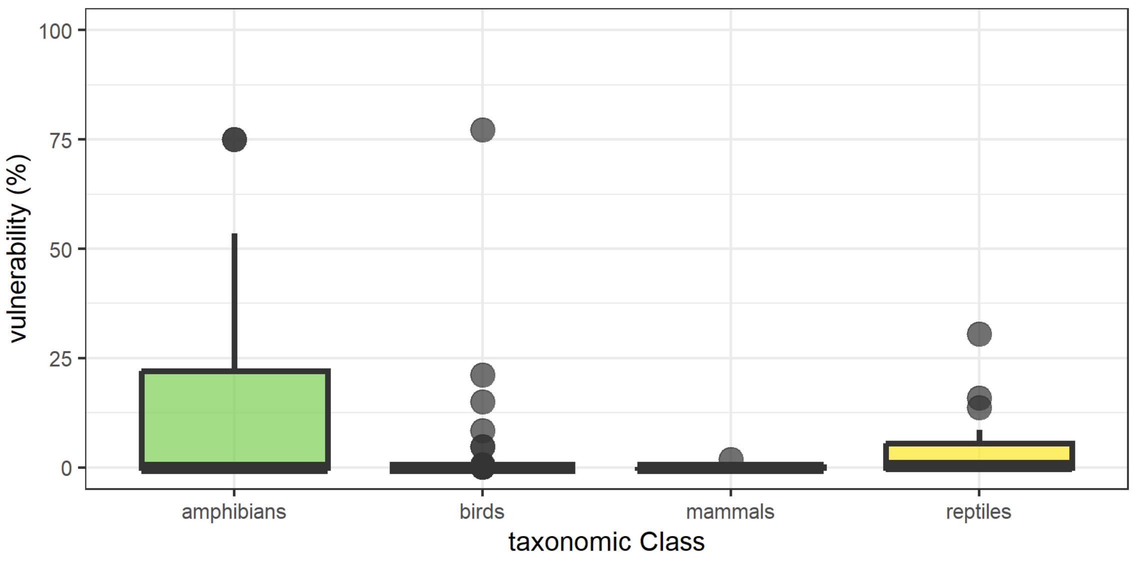

Figure A77. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

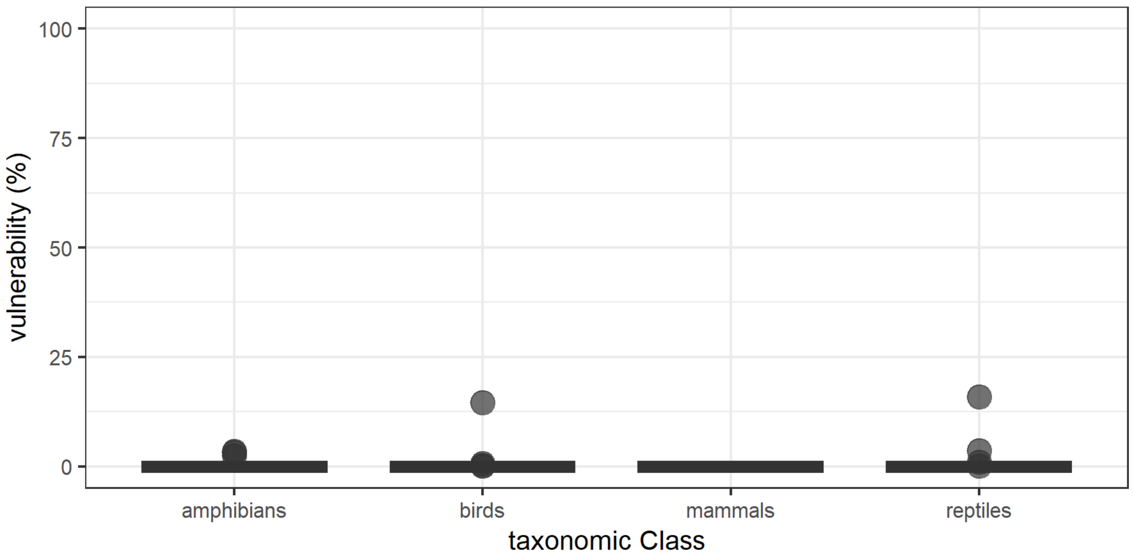

Figure A78. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

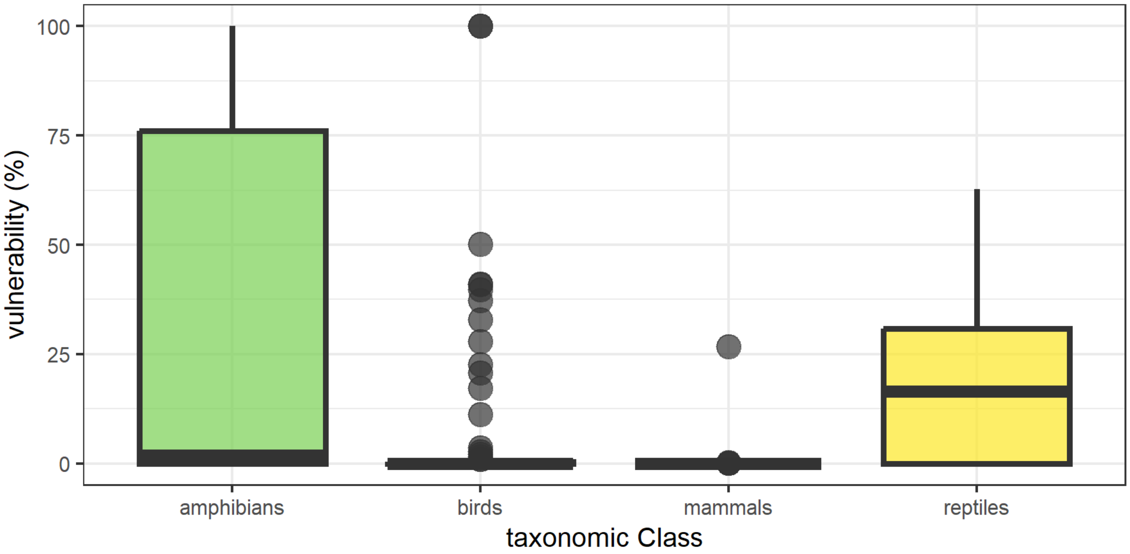

Figure A79. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

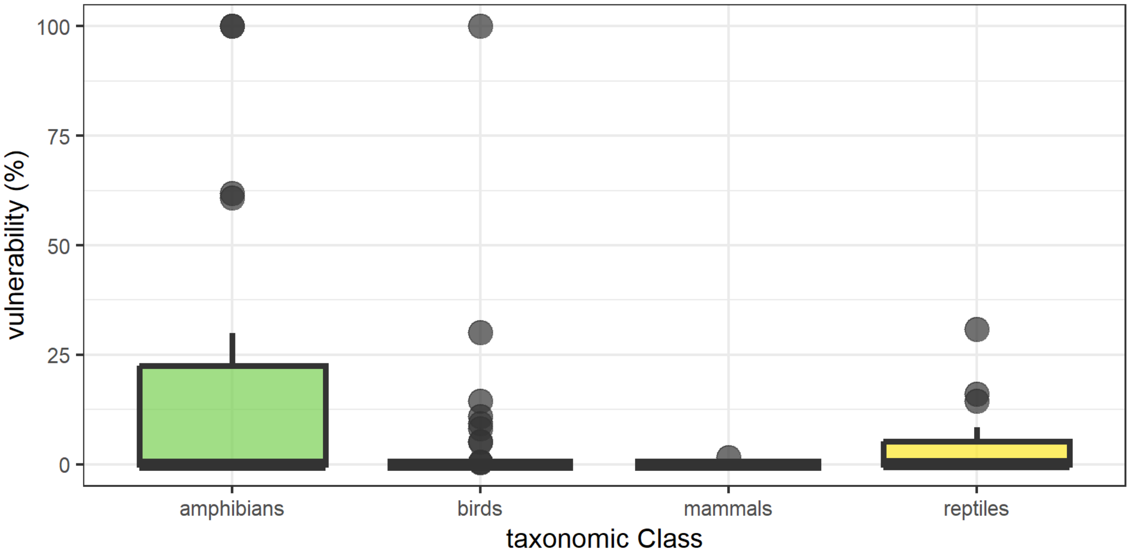

Figure A80. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

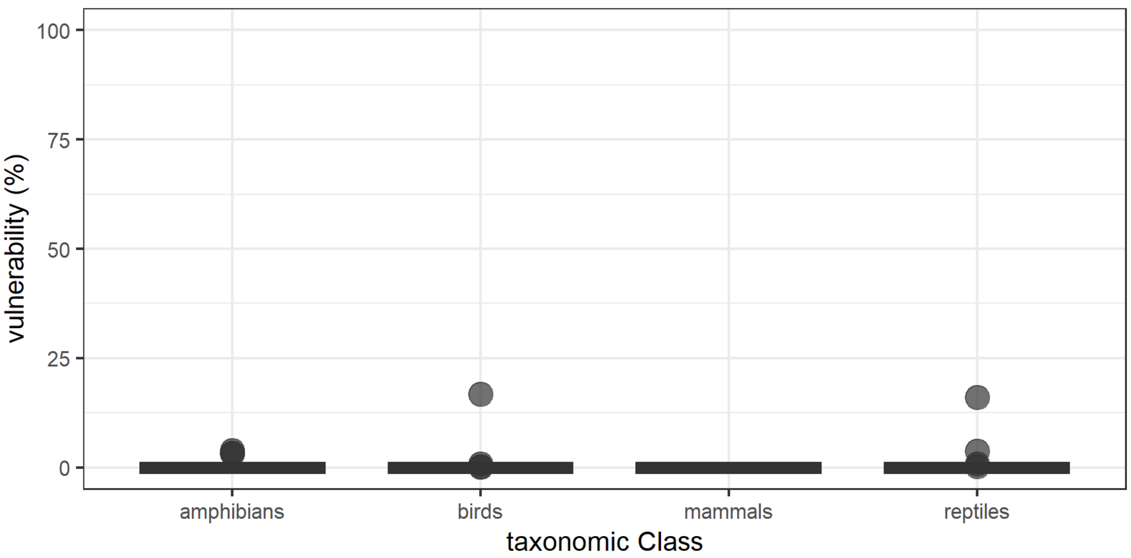

Figure A81. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

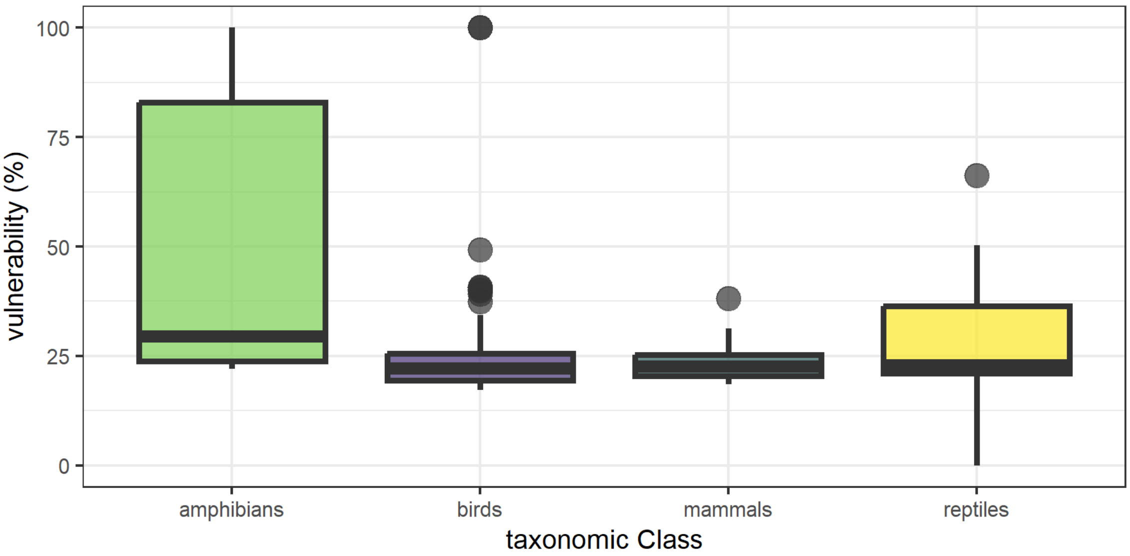

Figure A82. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

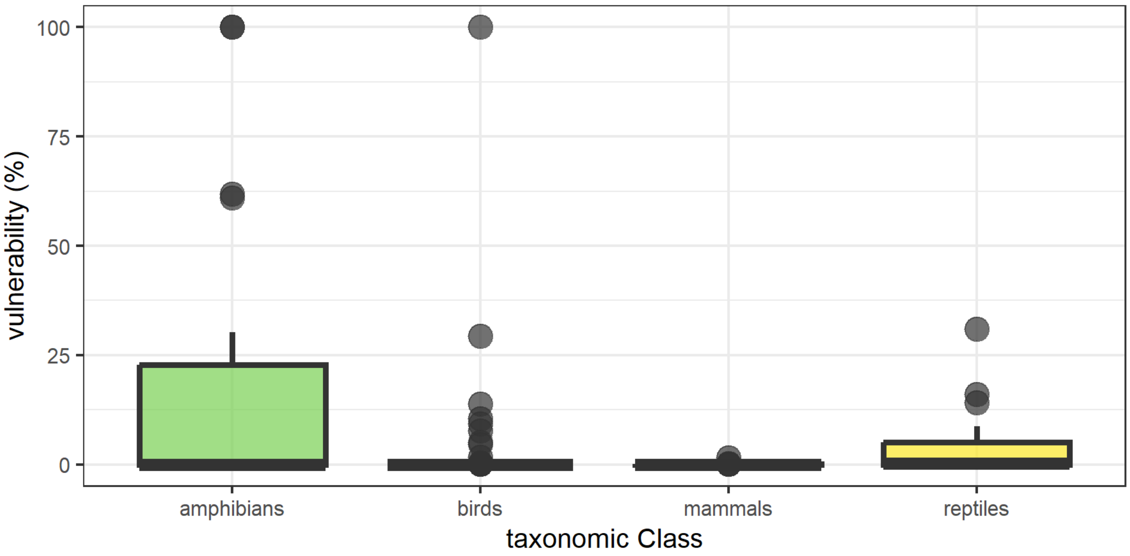

Figure A83. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

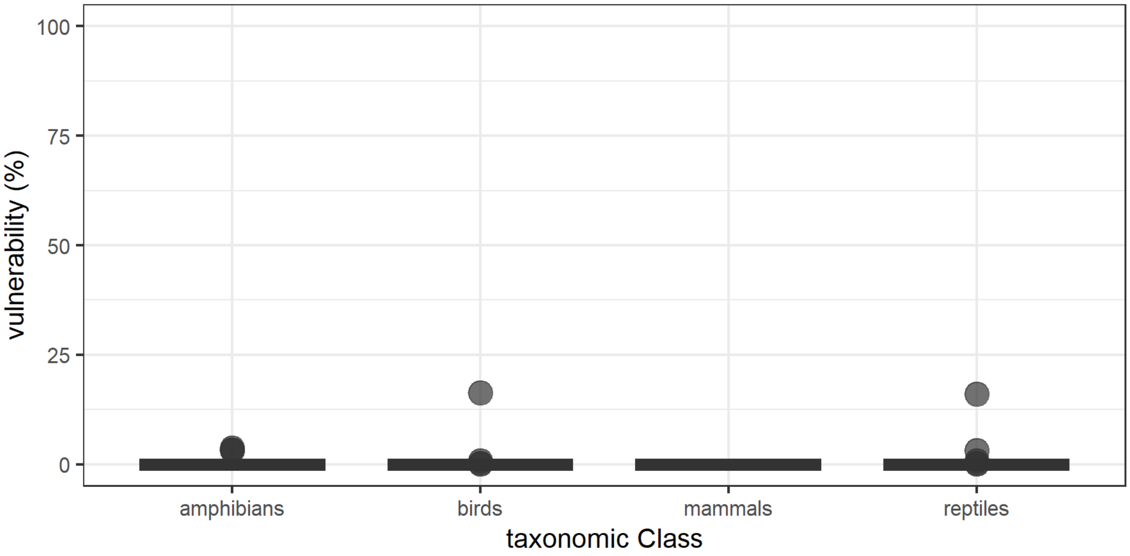

Figure A84. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

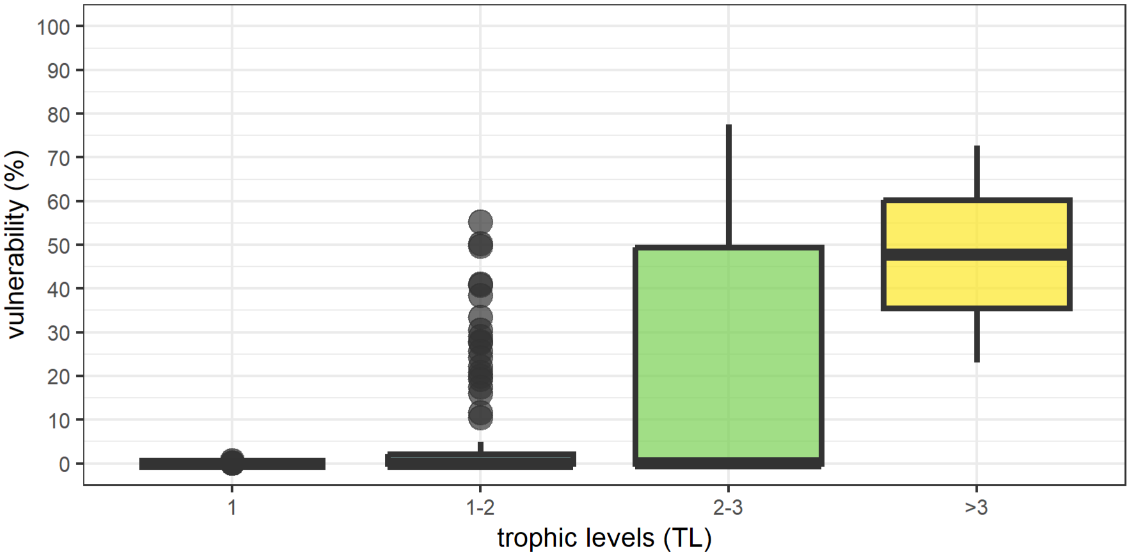

Figure A85. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

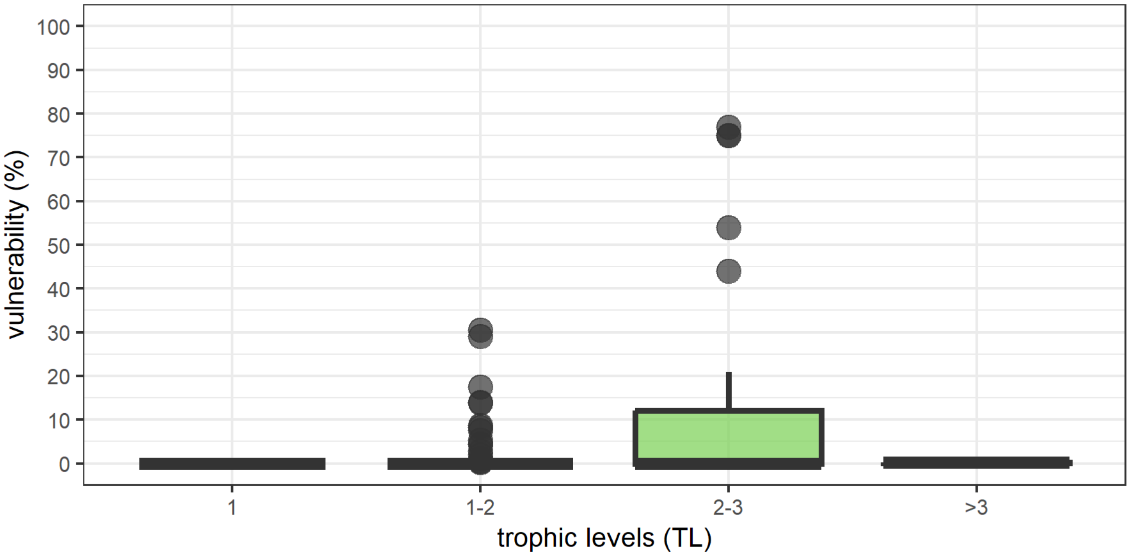

Figure A86. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

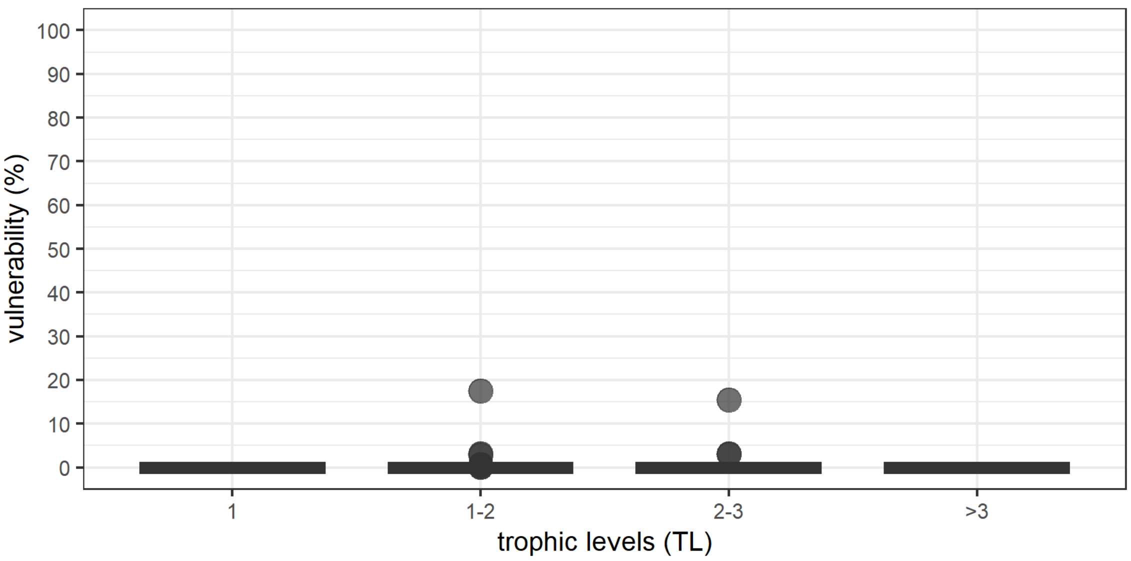

Figure A87. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

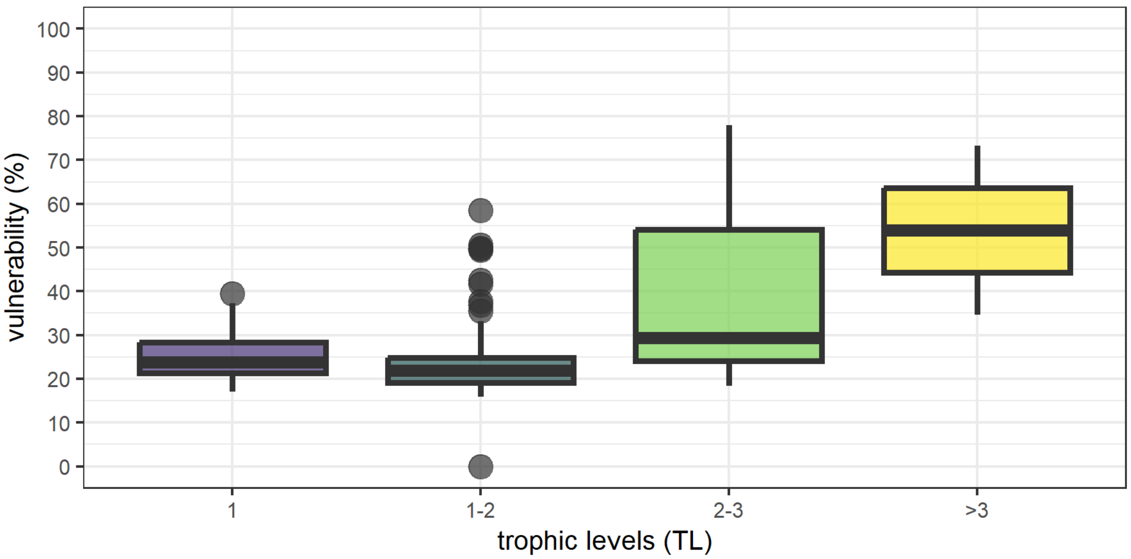

Figure A88. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

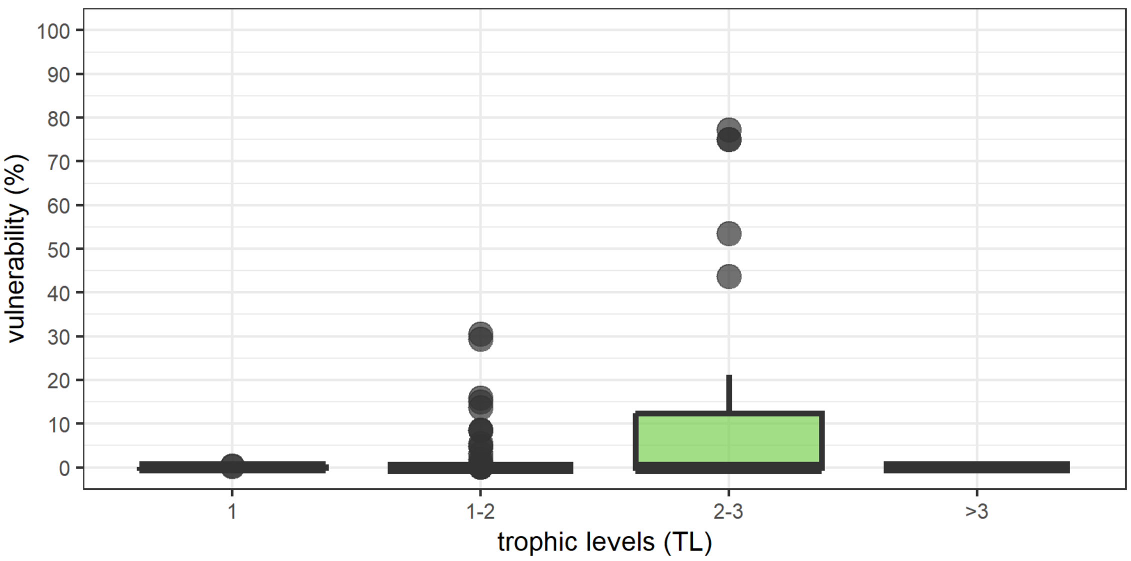

Figure A89. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

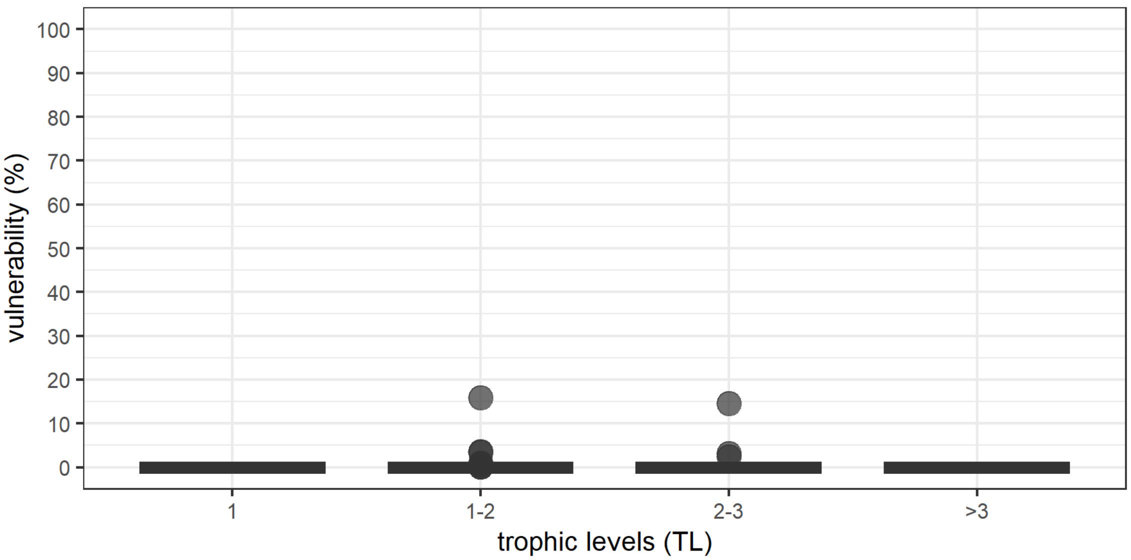

Figure A90. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

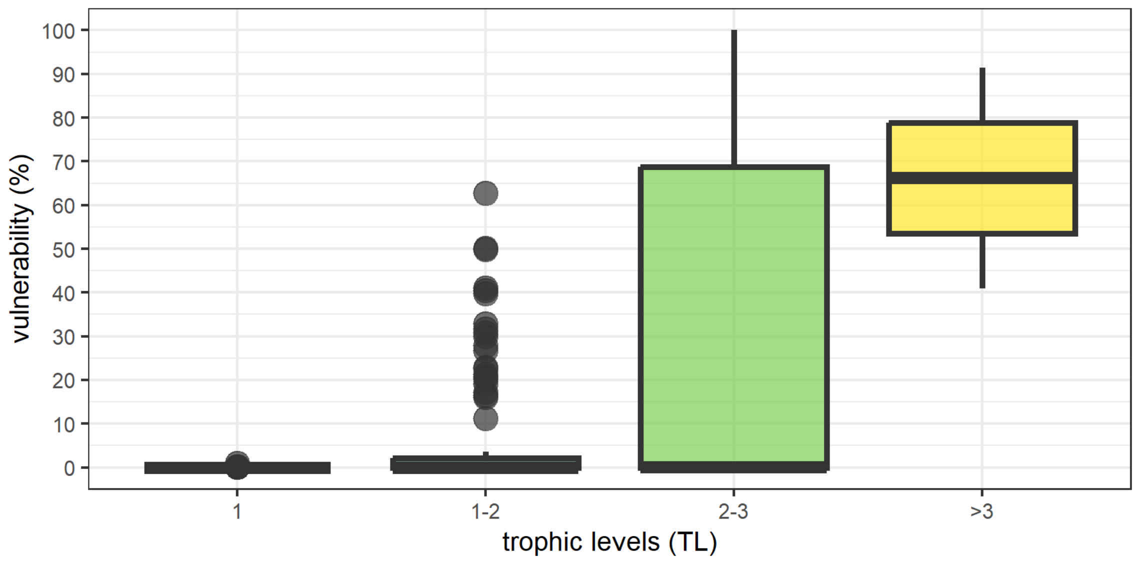

Figure A91. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

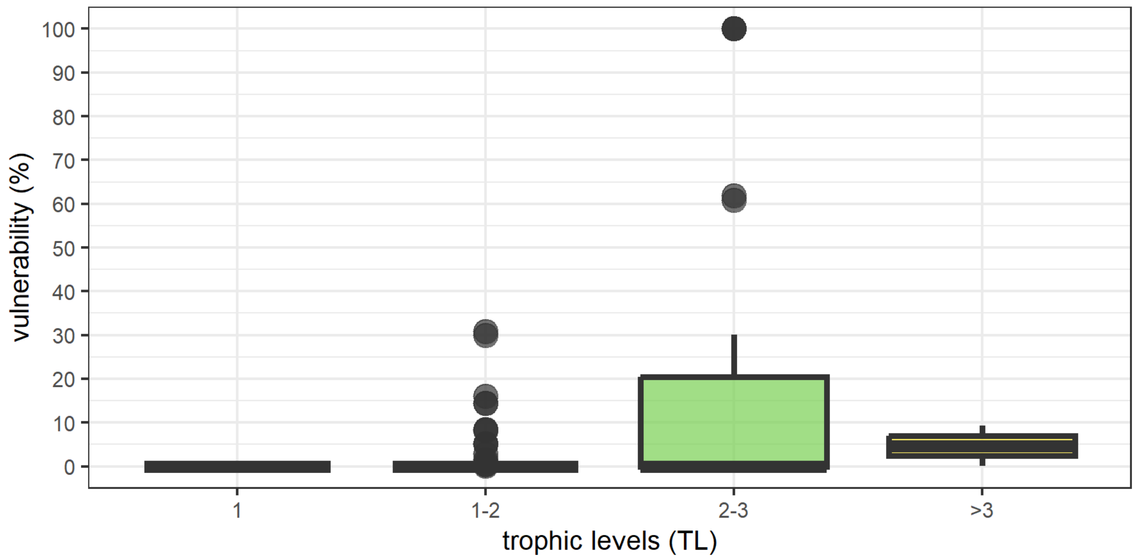

Figure A92. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

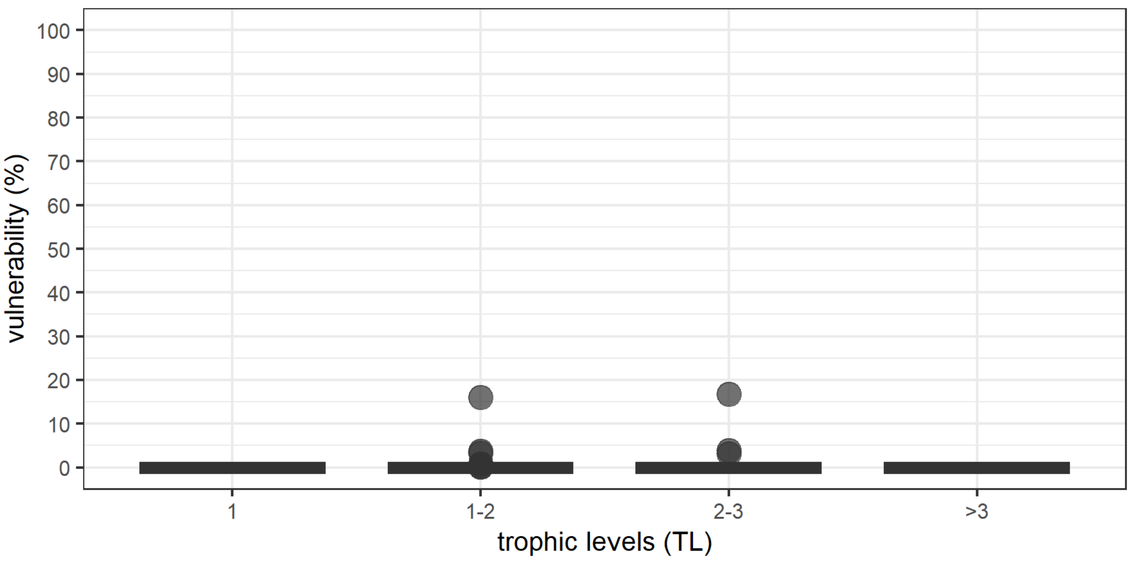

Figure A93. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

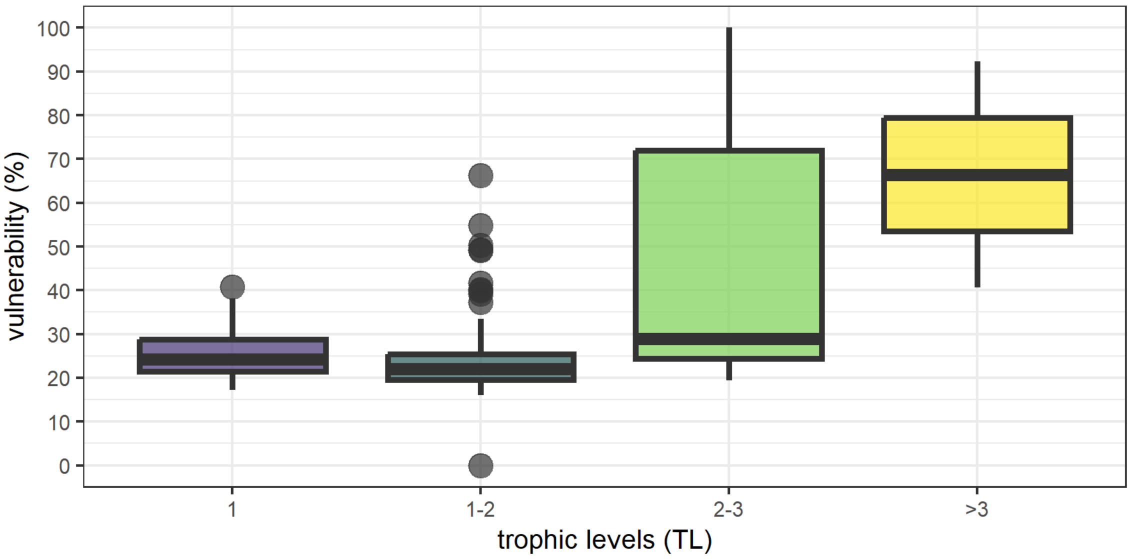

Figure A94. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

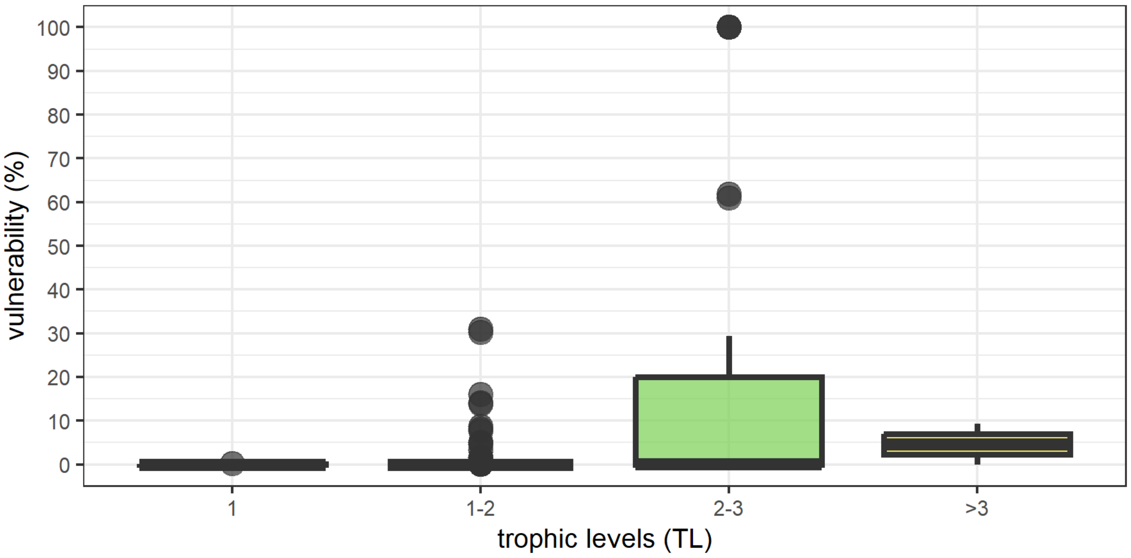

Figure A95. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

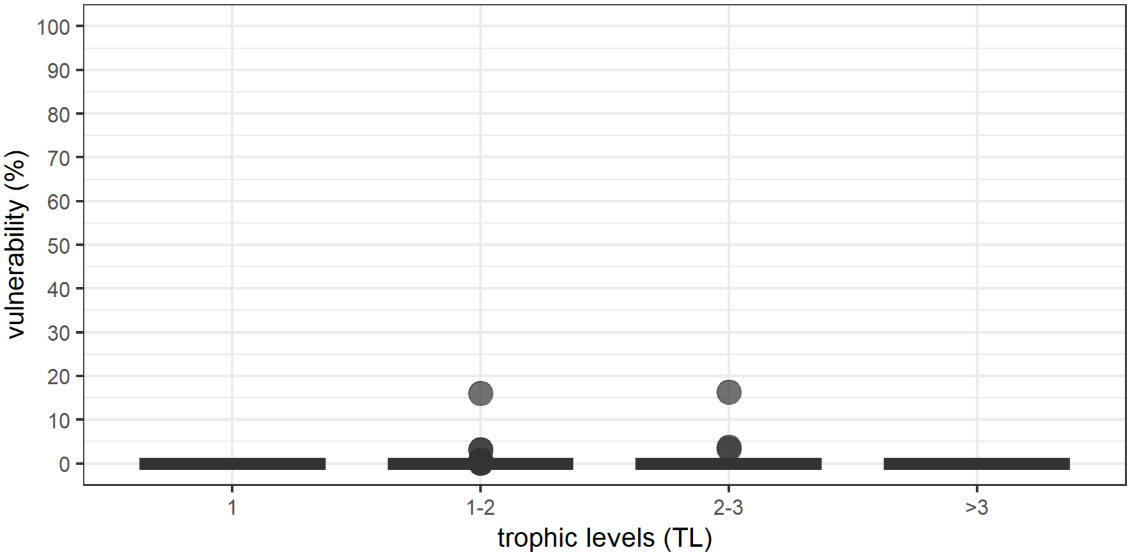

Figure A96. Mean vulnerability to coextinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

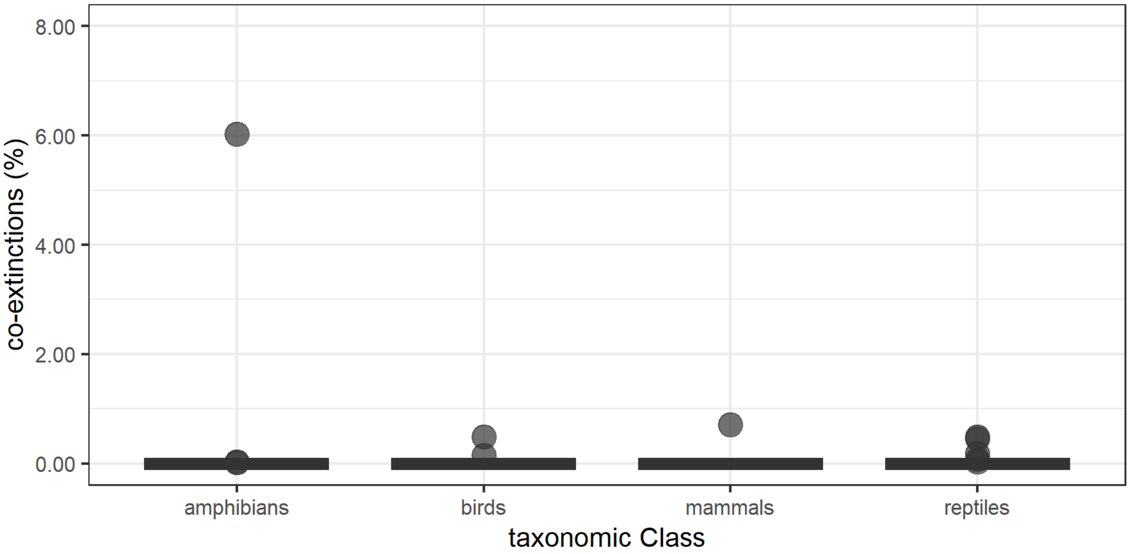

Figure A97. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

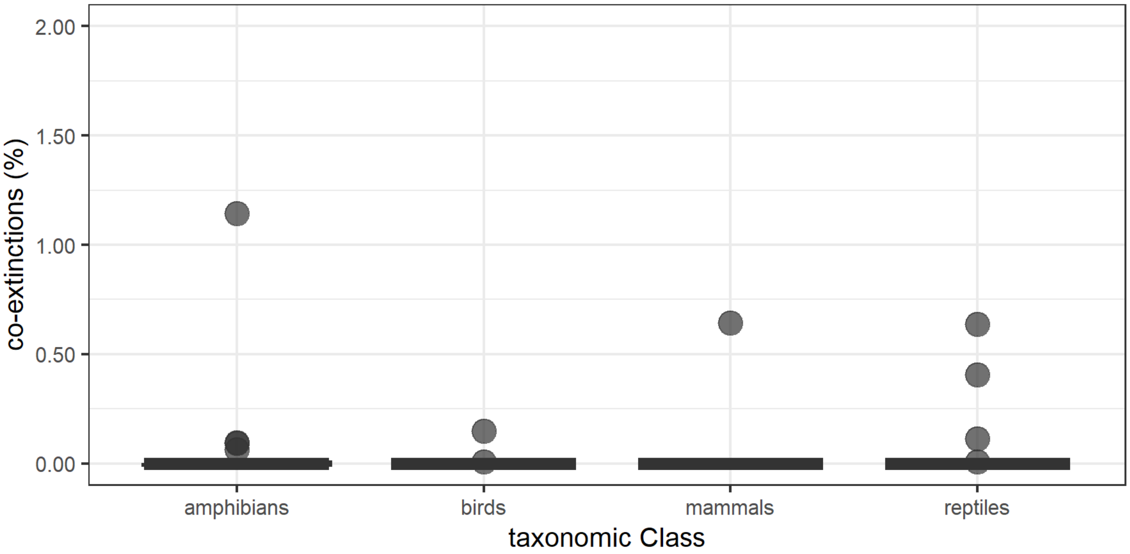

Figure A98. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

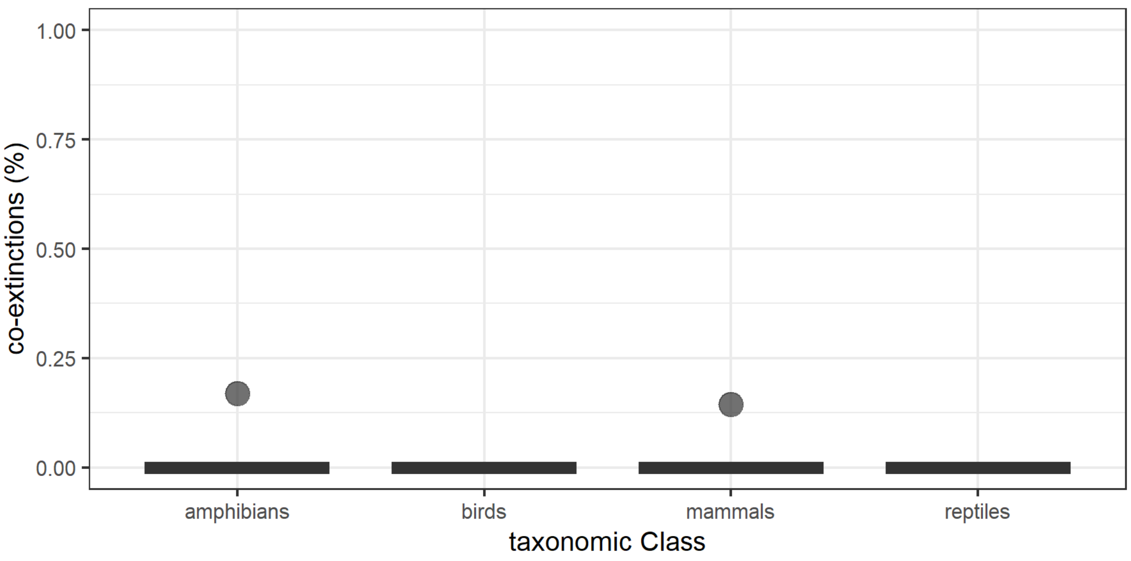

Figure A99. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

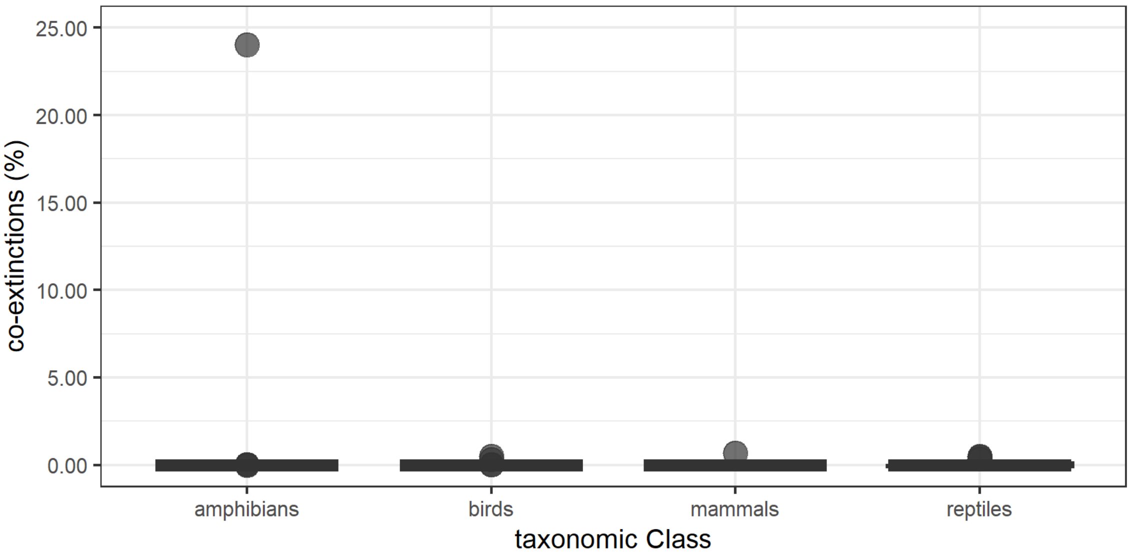

Figure A100. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

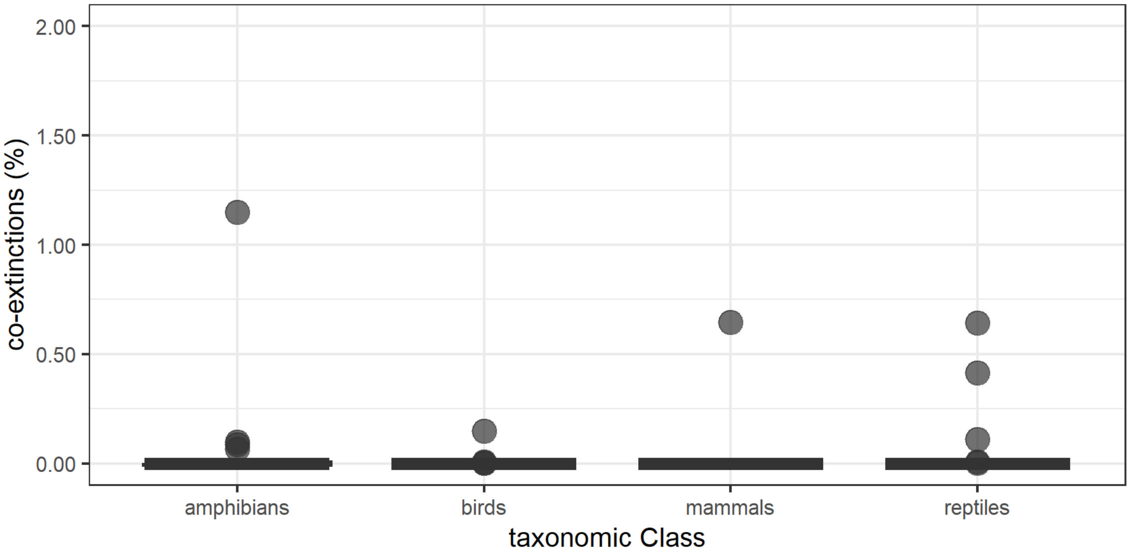

Figure A101. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

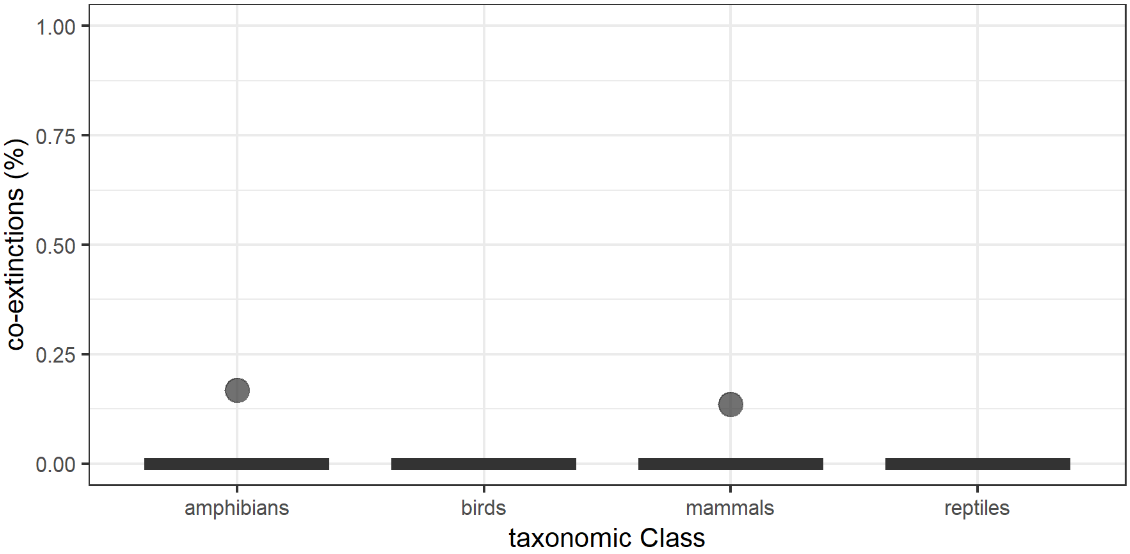

Figure A102. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

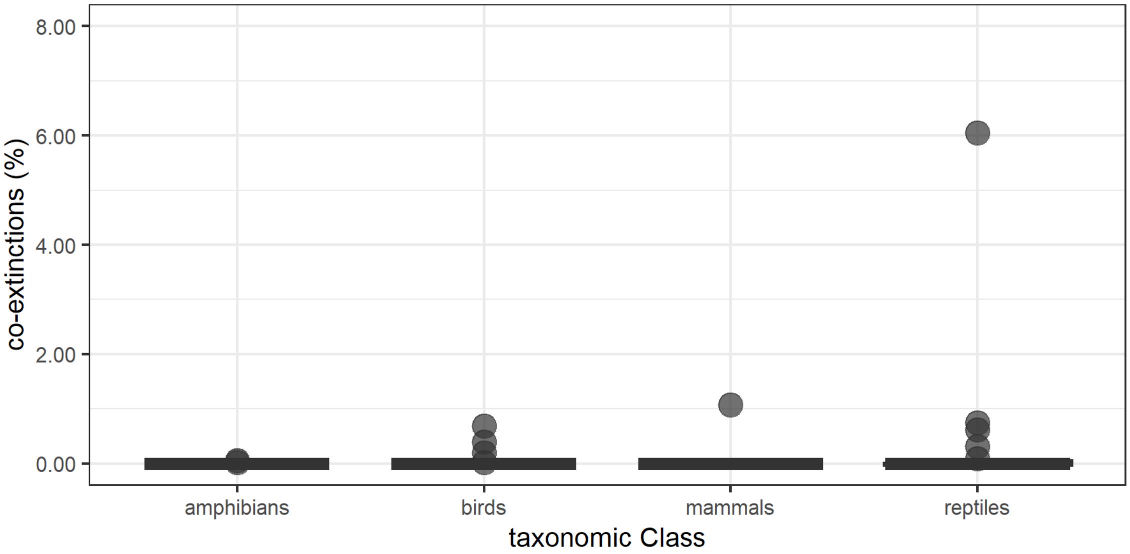

Figure A103. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

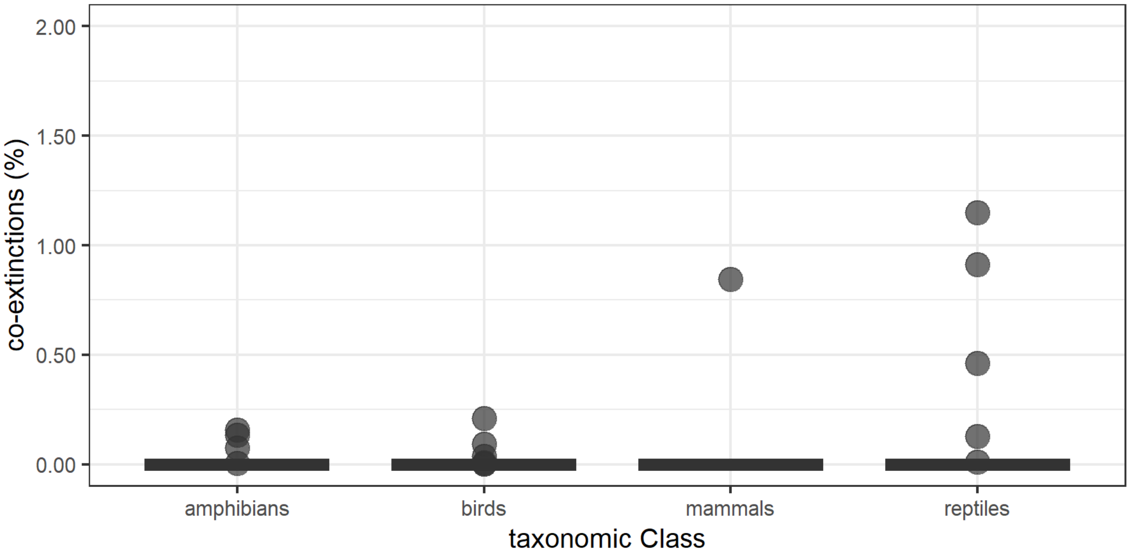

Figure A104. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

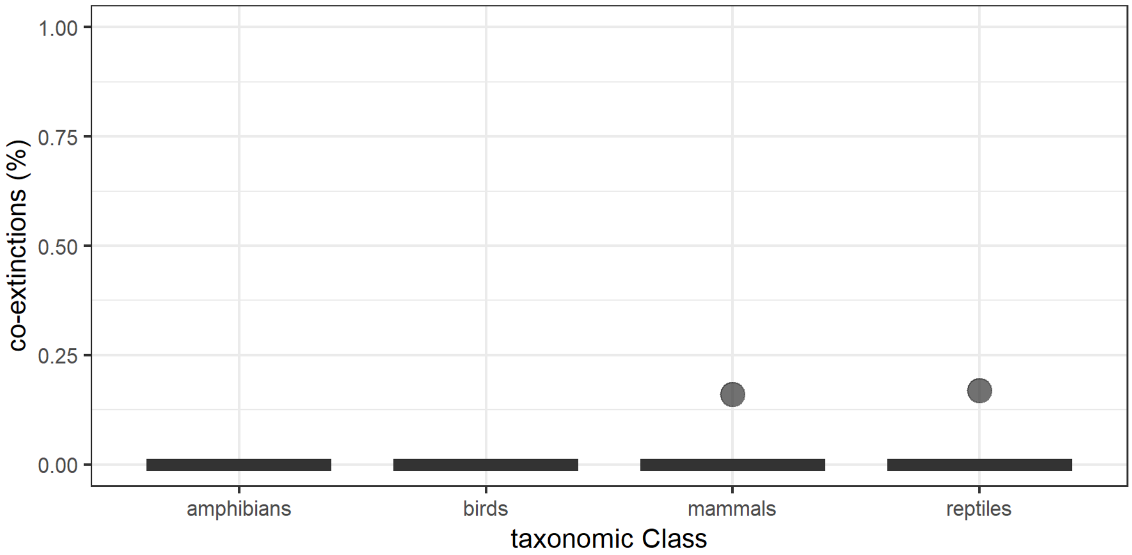

Figure A105. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

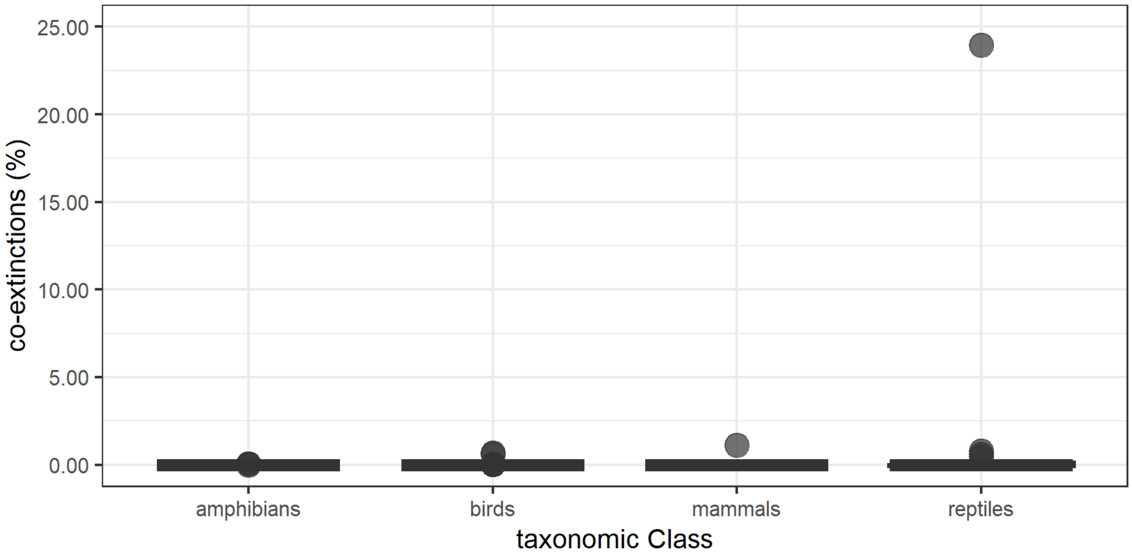

Figure A106. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

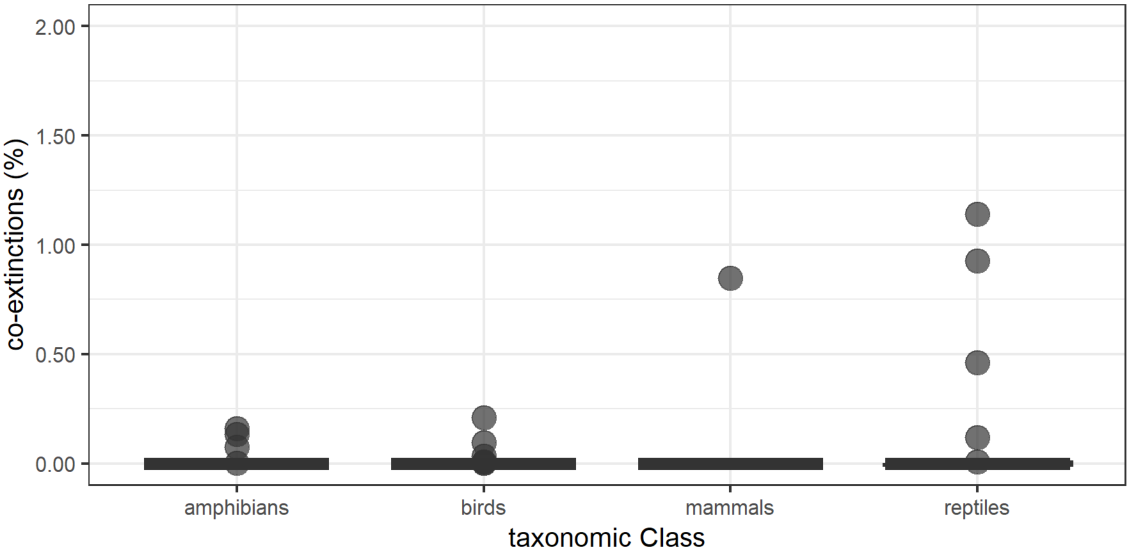

Figure A107. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

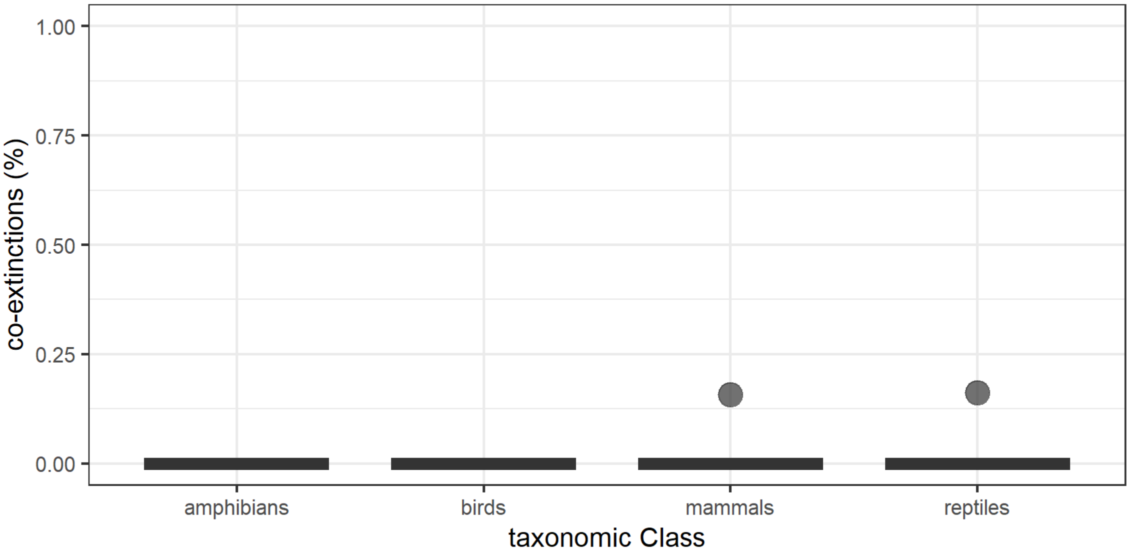

Figure A108. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

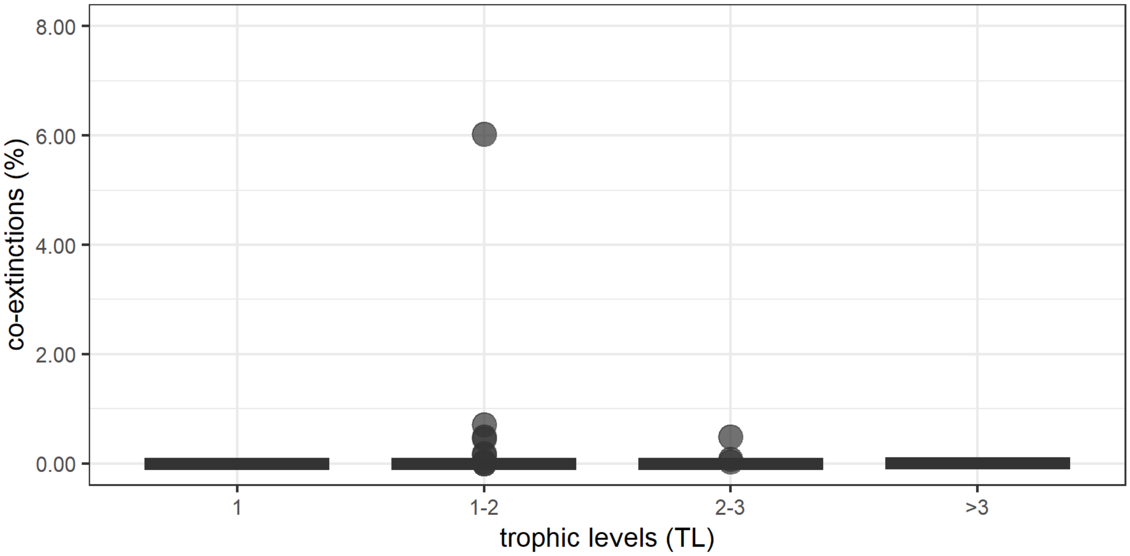

Figure A109. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

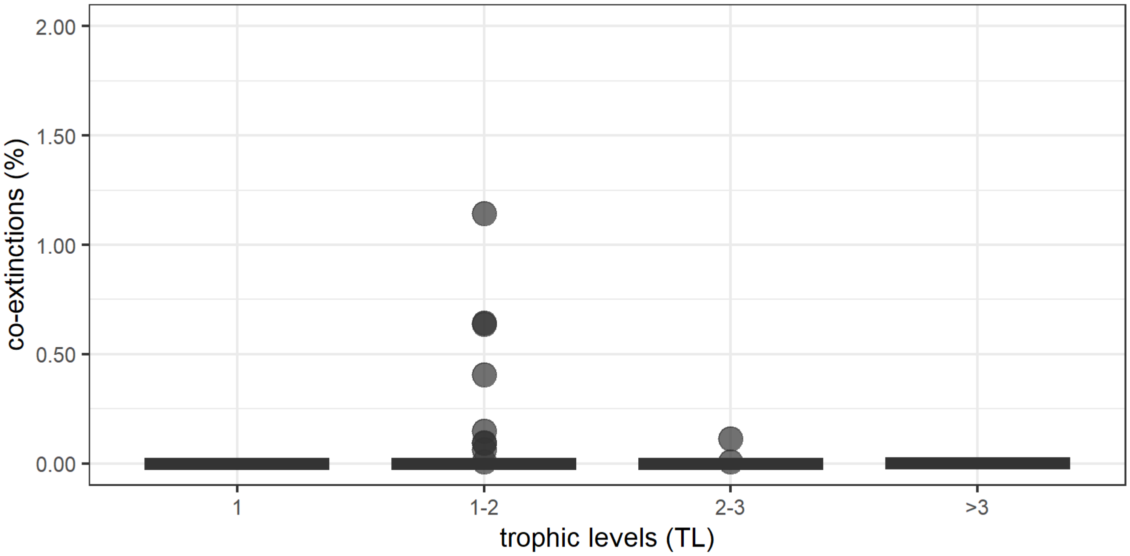

Figure A110. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

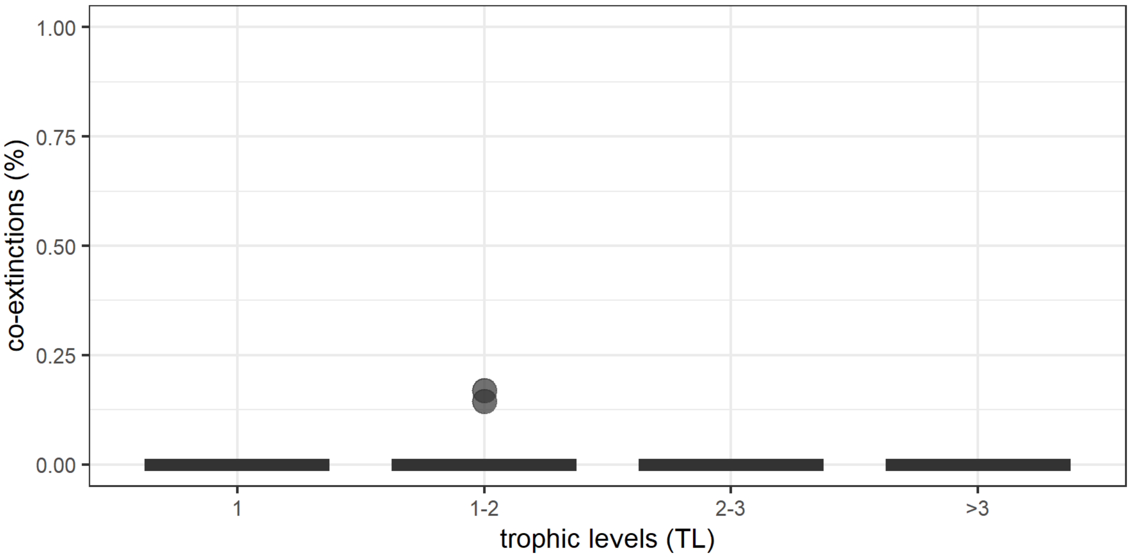

Figure A111. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

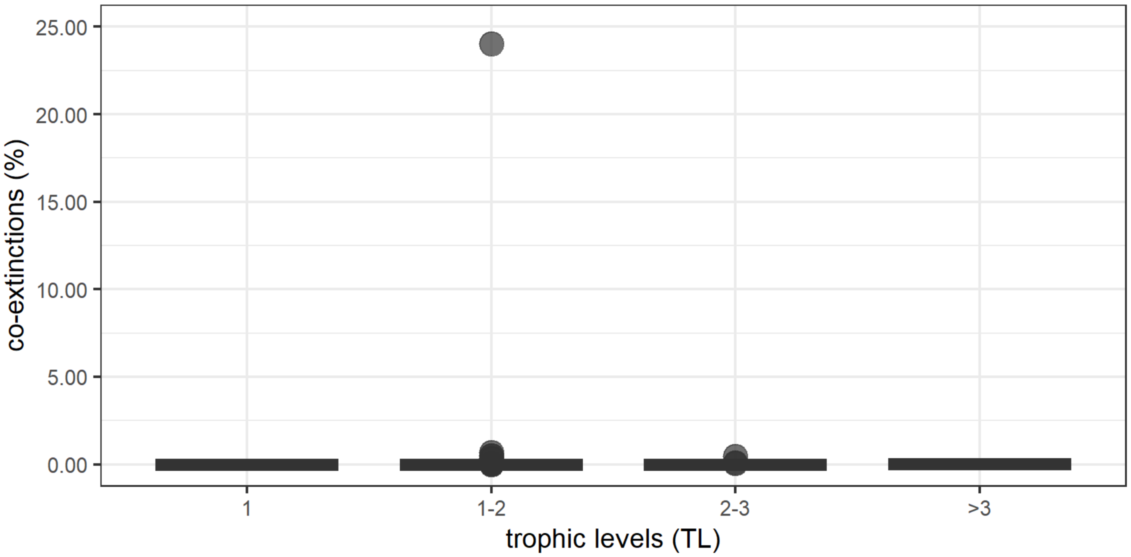

Figure A112. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

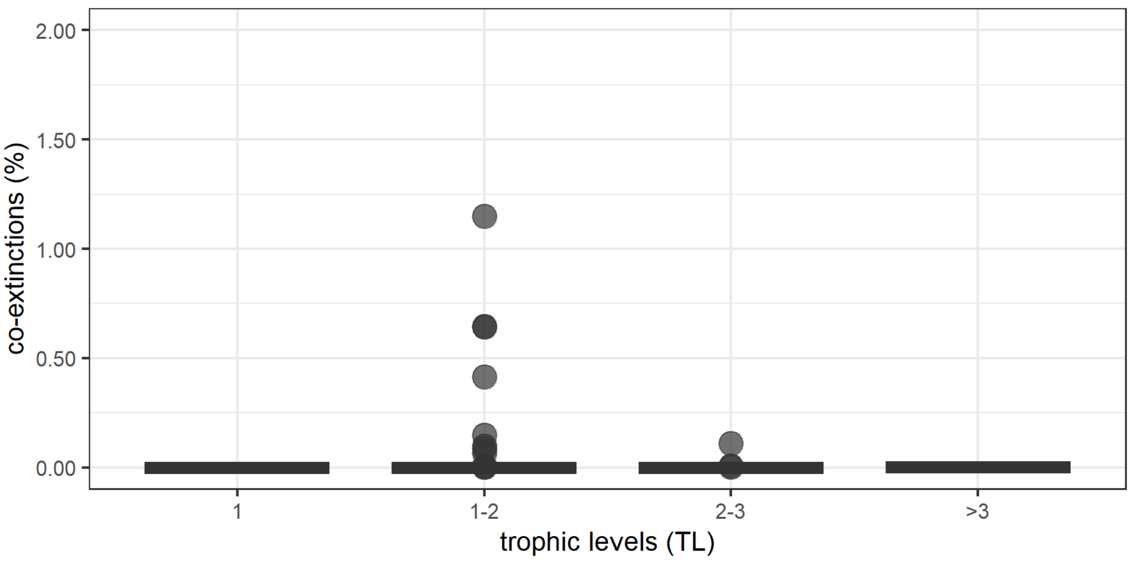

Figure A113. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

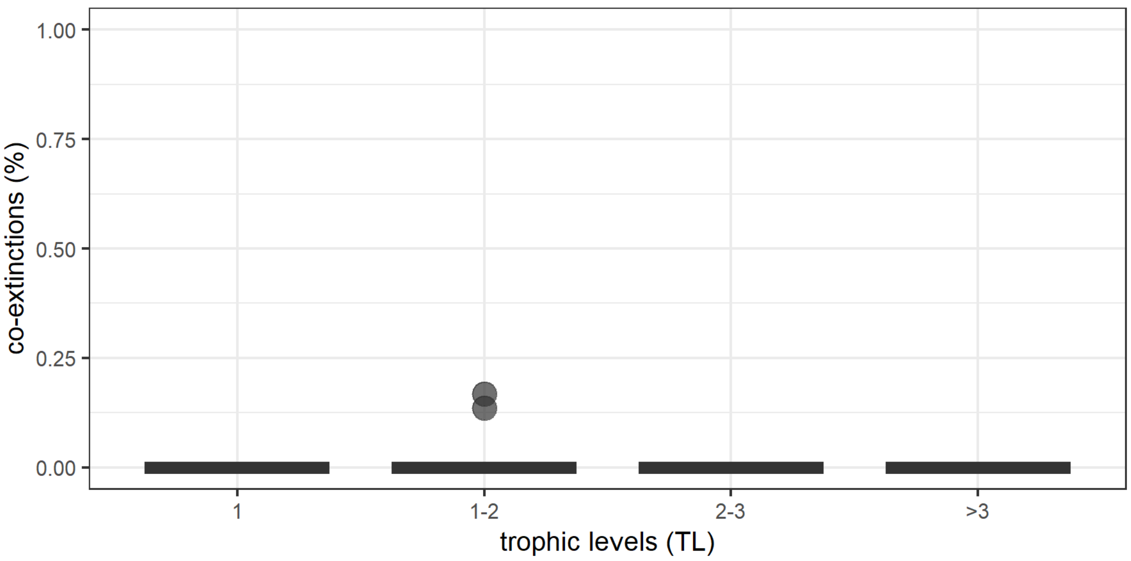

Figure A114. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

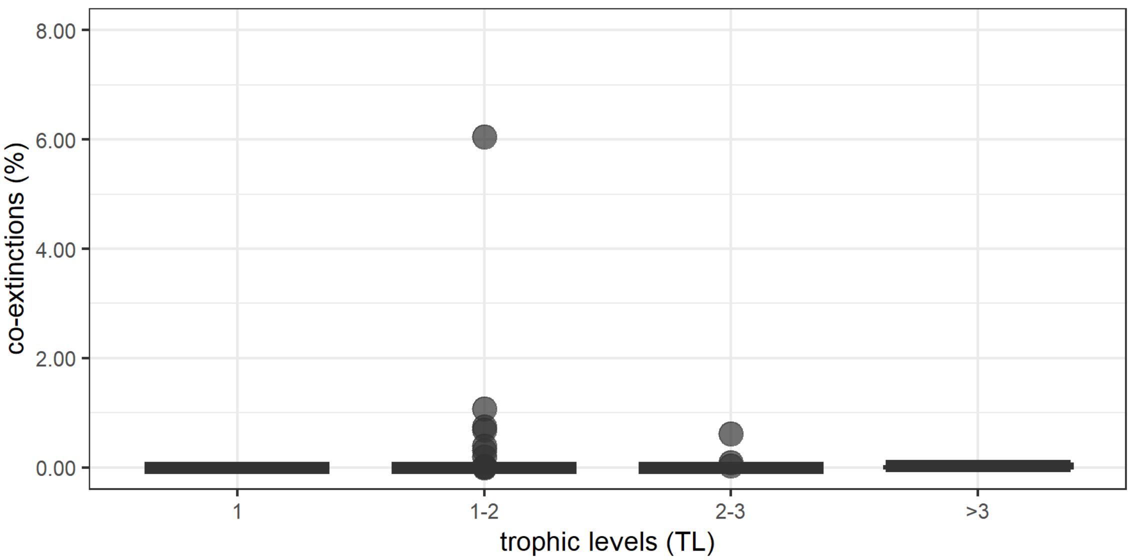

Figure A115. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

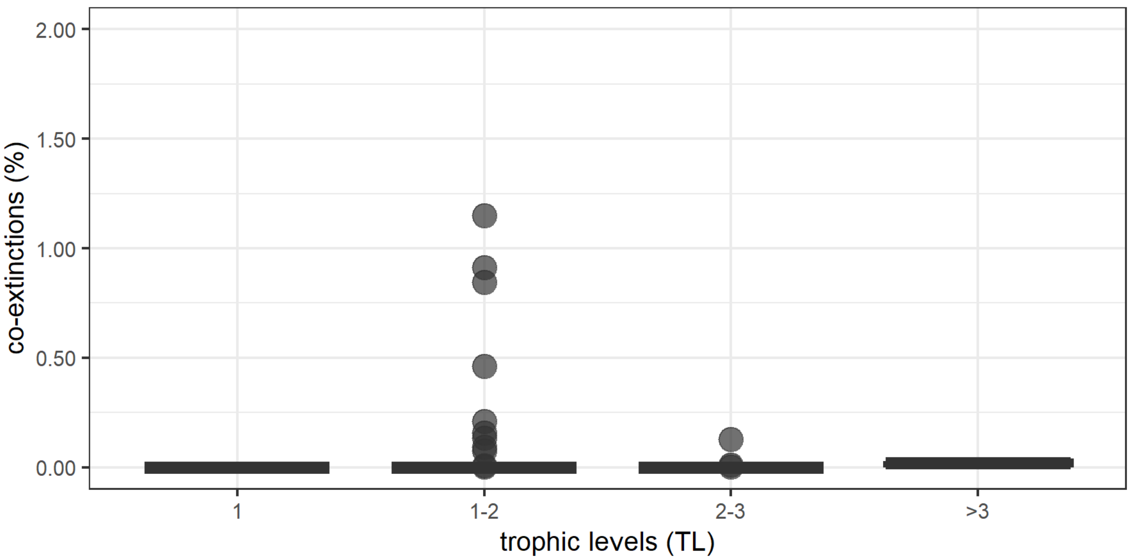

Figure A116. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

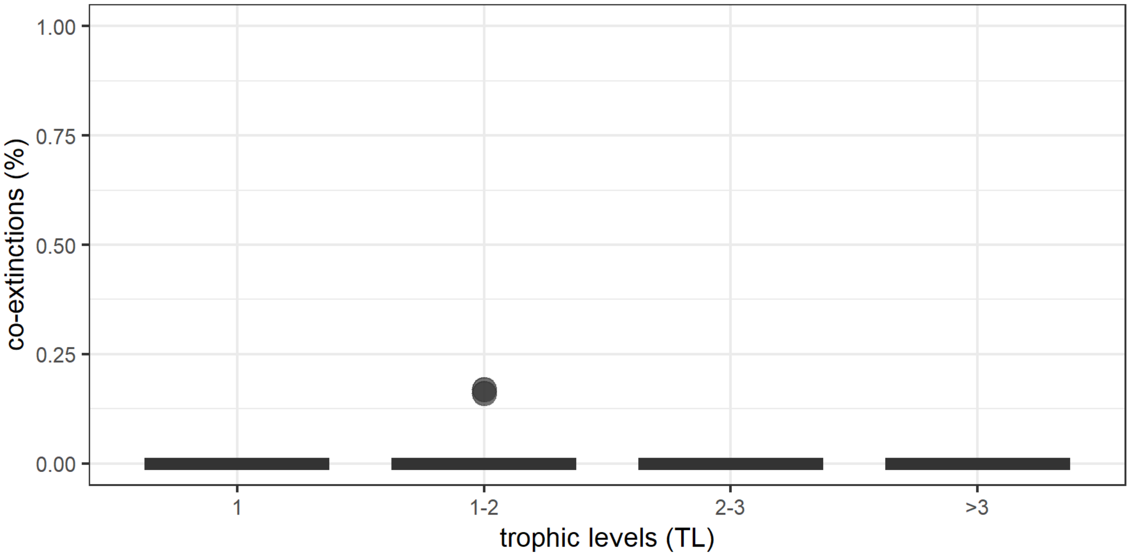

Figure A117. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

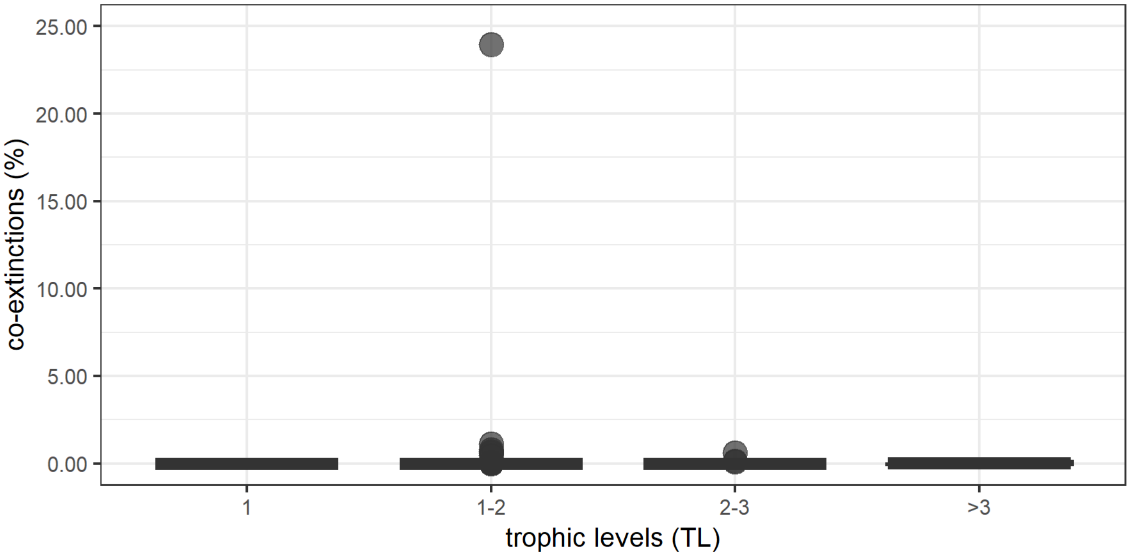

Figure A118. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

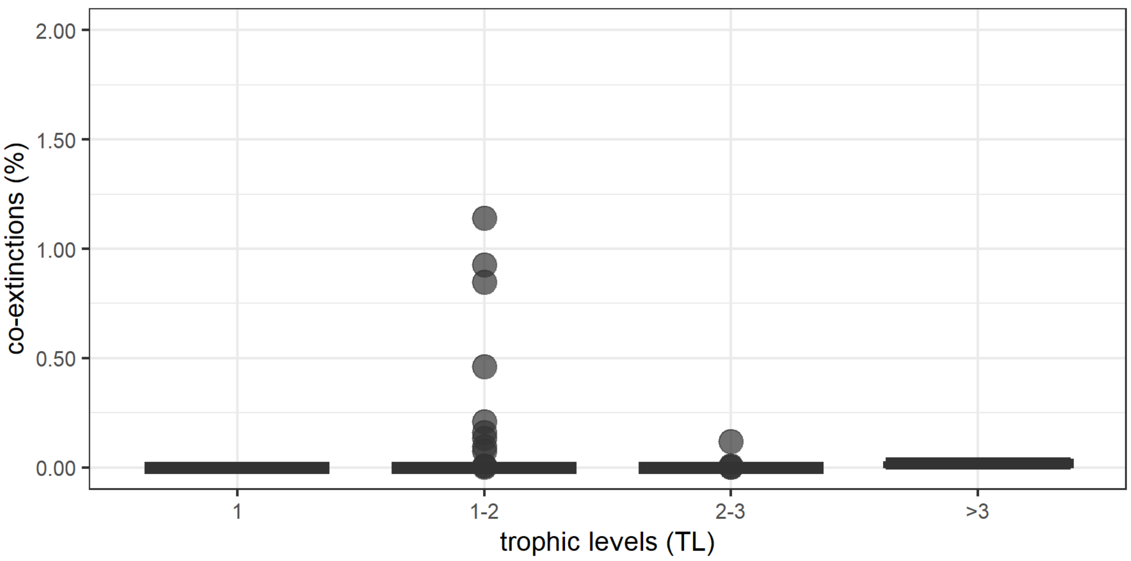

Figure A119. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

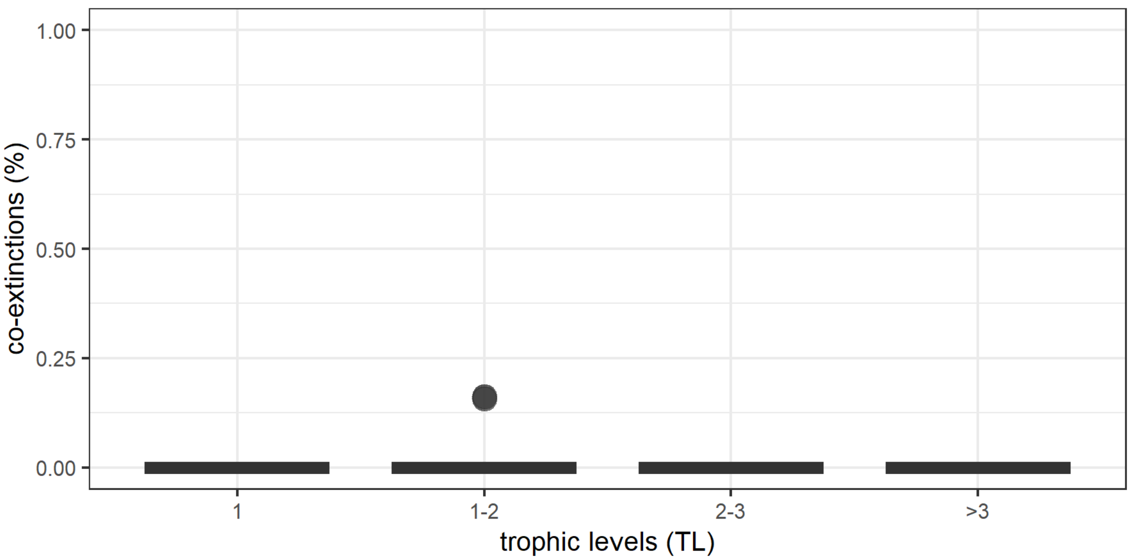

Figure A120. Mean percentage of vertebrate secondary extinctions caused by primary vertebrate extinctions in the lowland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

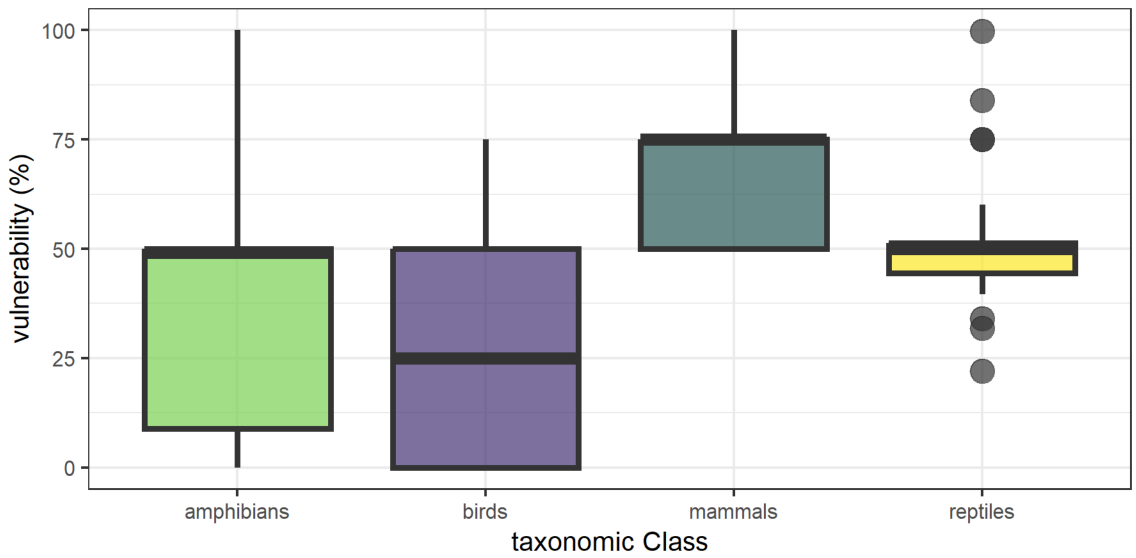

Figure A121. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

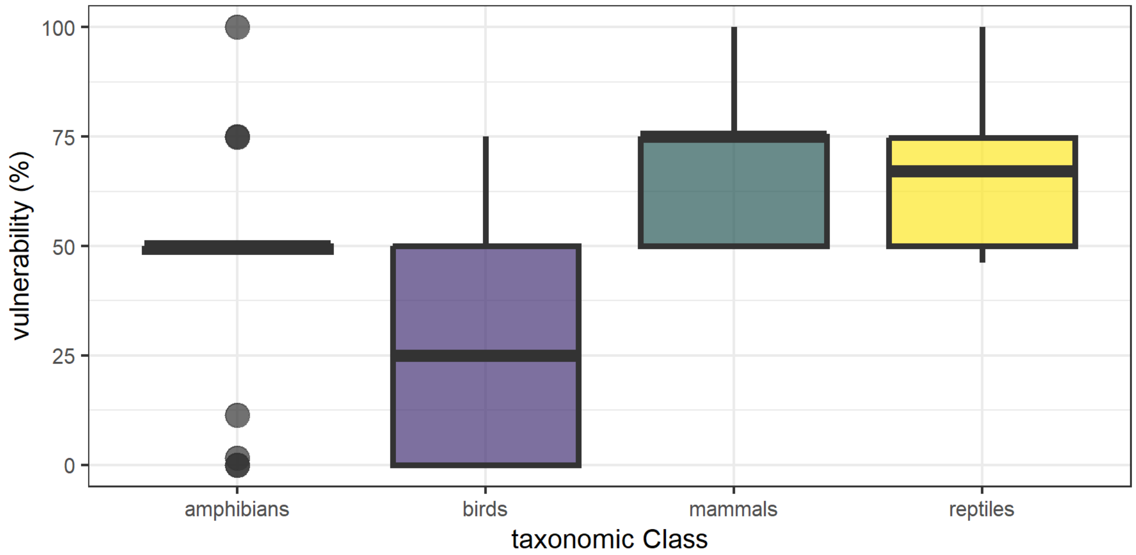

Figure A122. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

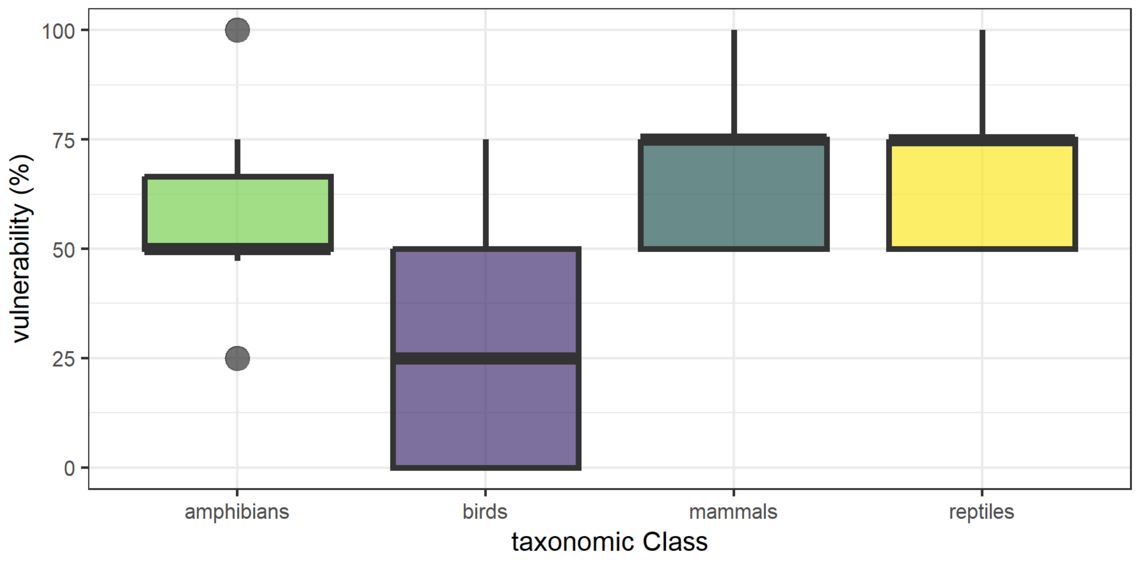

Figure A123. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

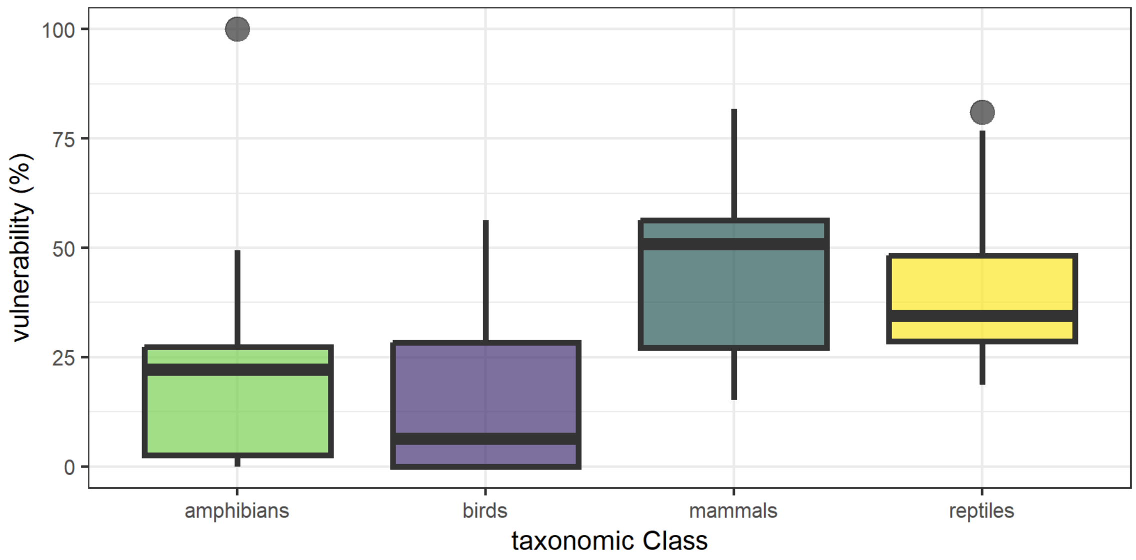

Figure A124. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

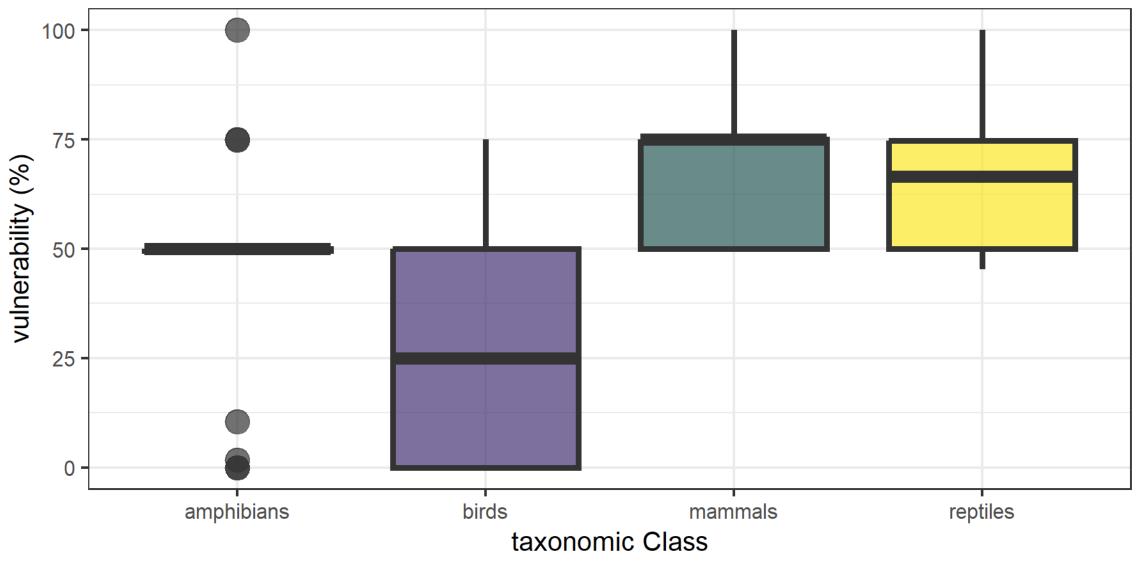

Figure A125. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

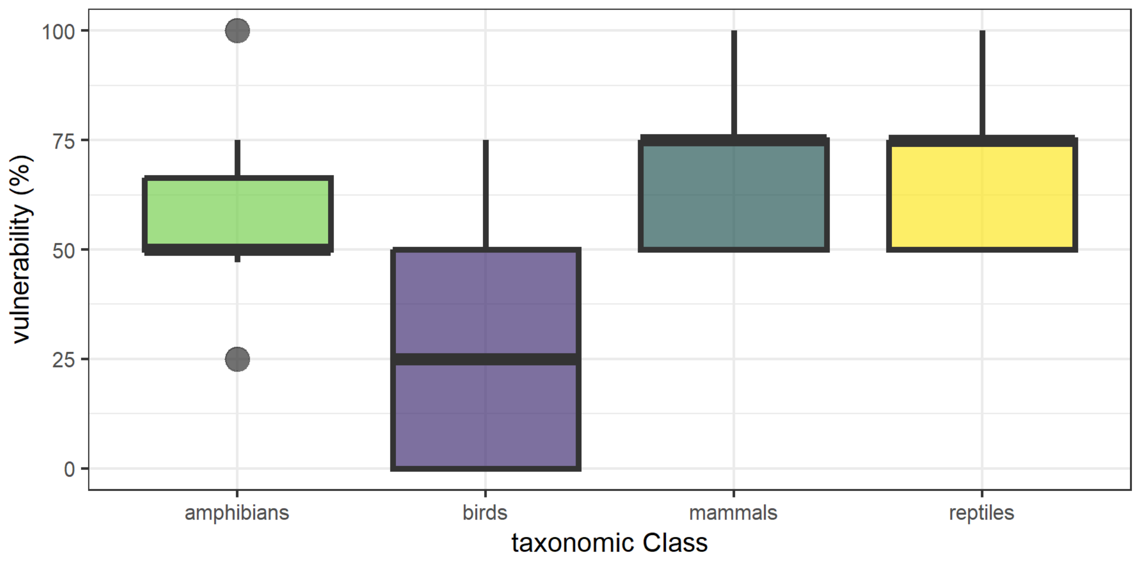

Figure A126. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

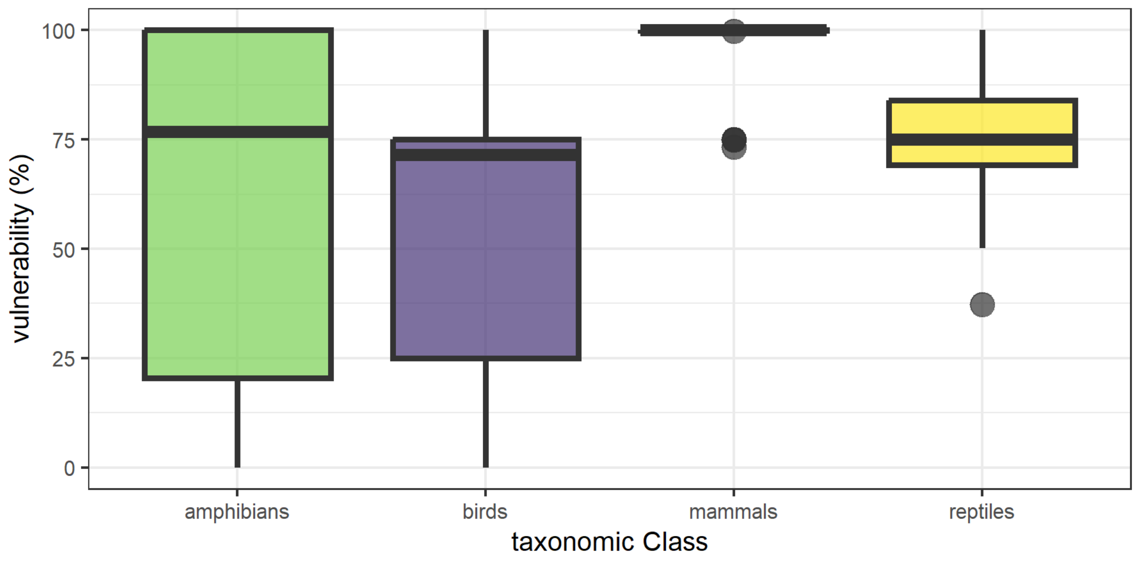

Figure A127. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

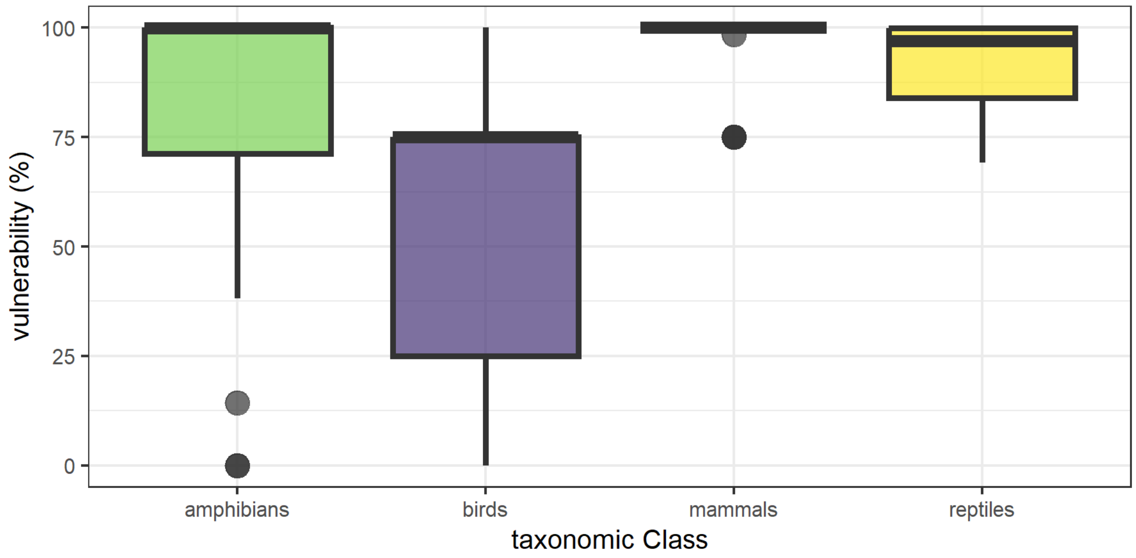

Figure A128. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

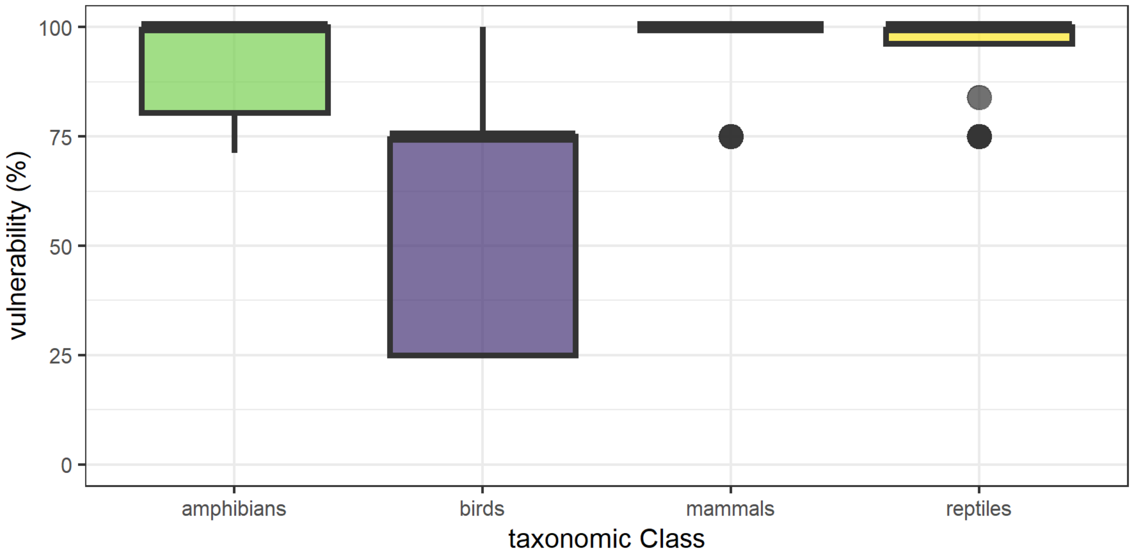

Figure A129. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

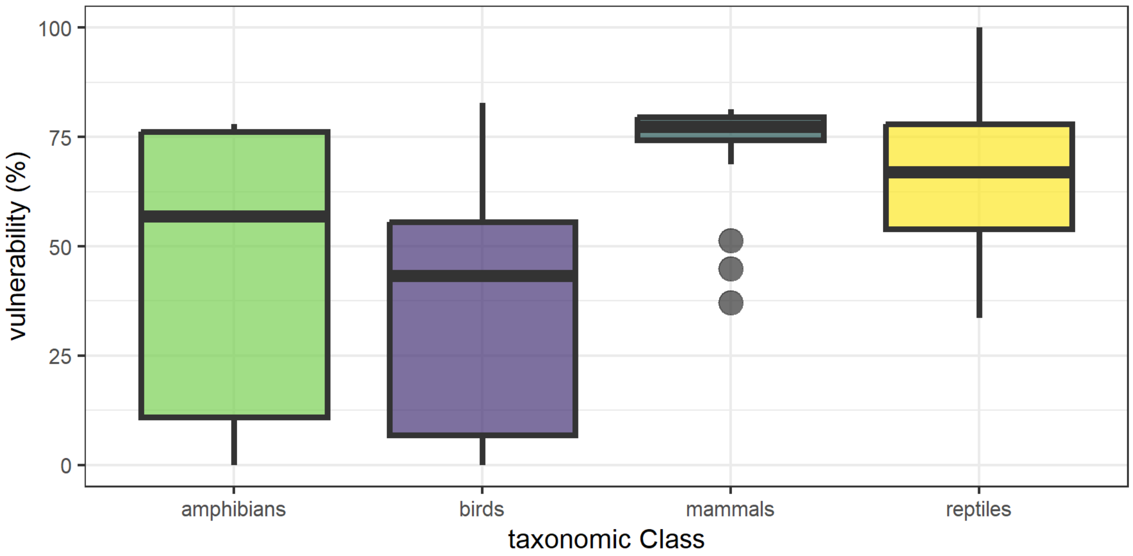

Figure A130. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

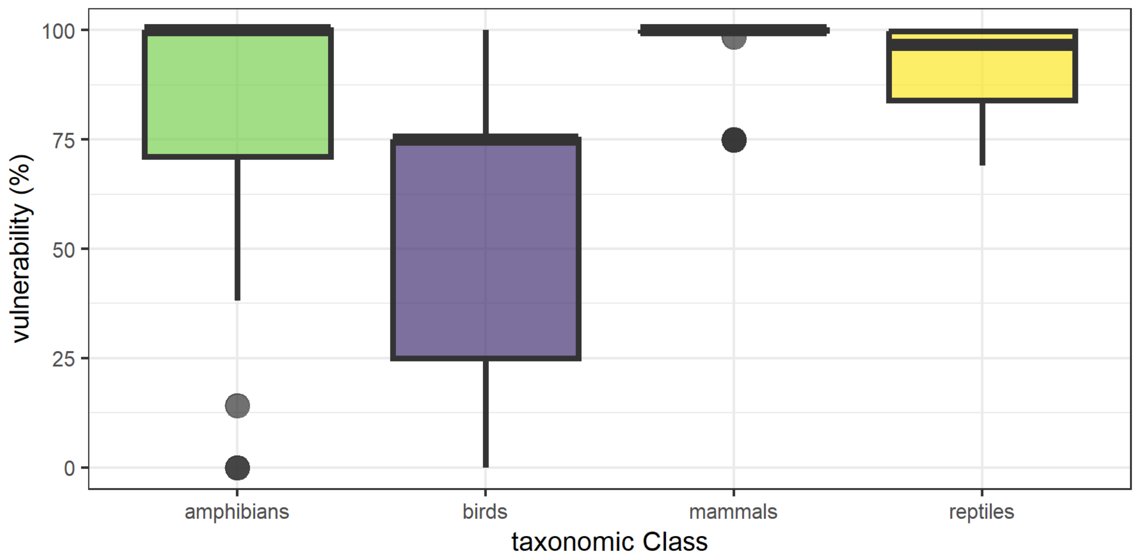

Figure A131. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

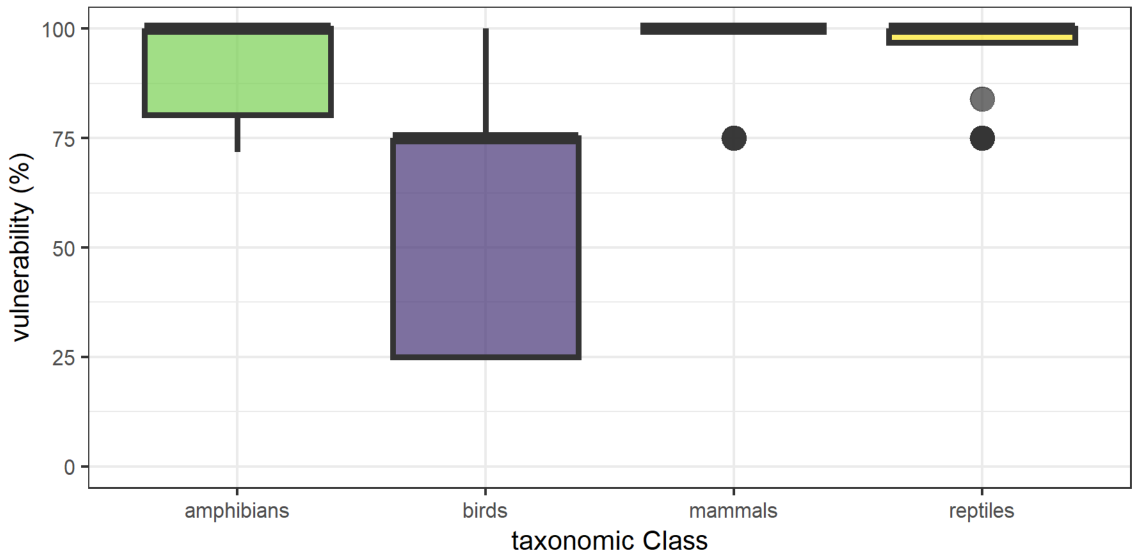

Figure A132. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by taxonomic class in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

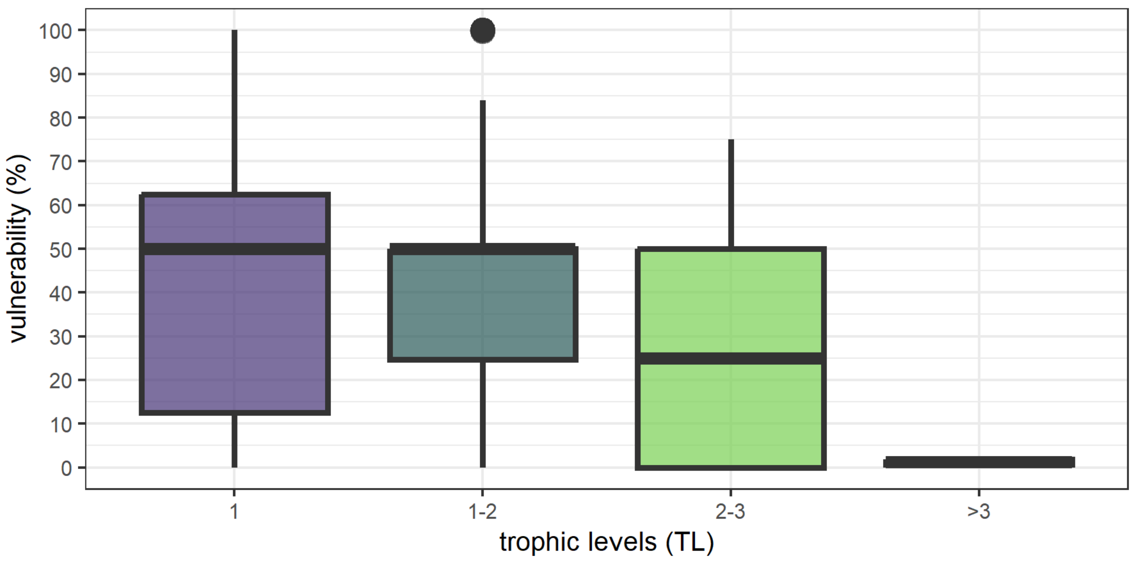

Figure A133. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

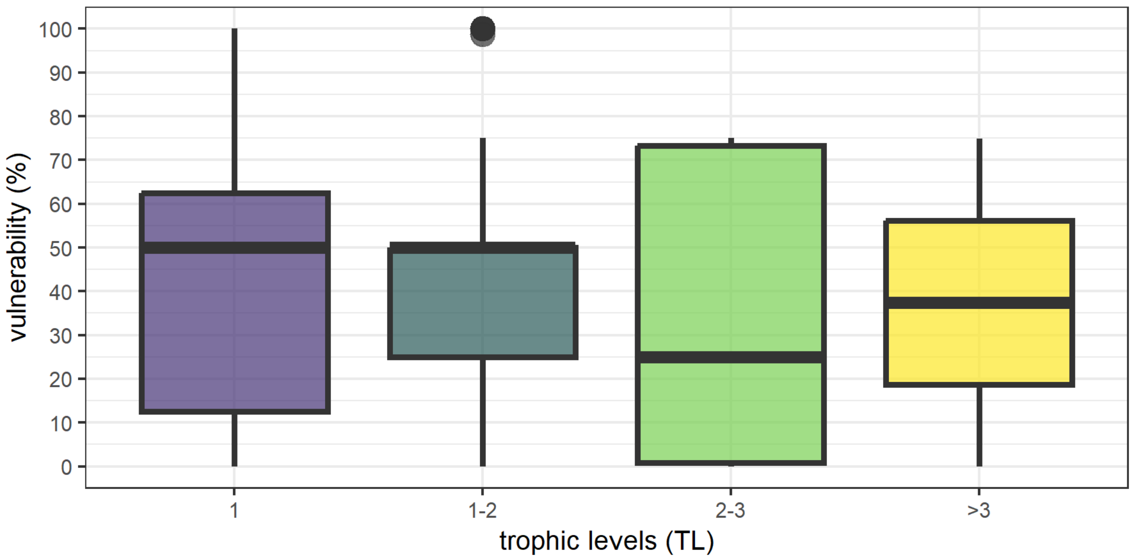

Figure A134. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

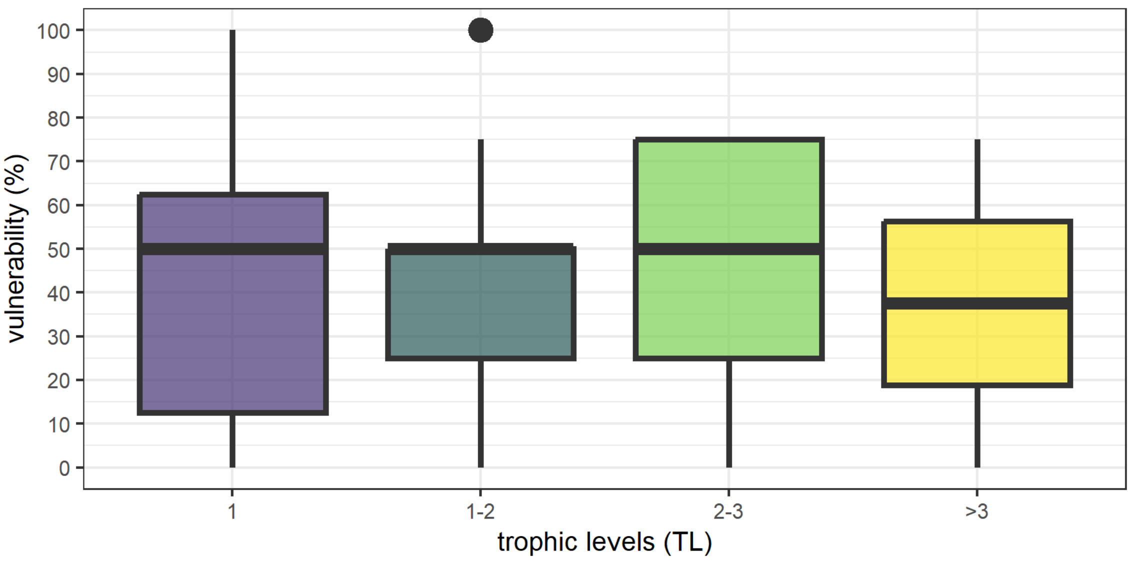

Figure A135. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could both rewire trophic interactions and shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

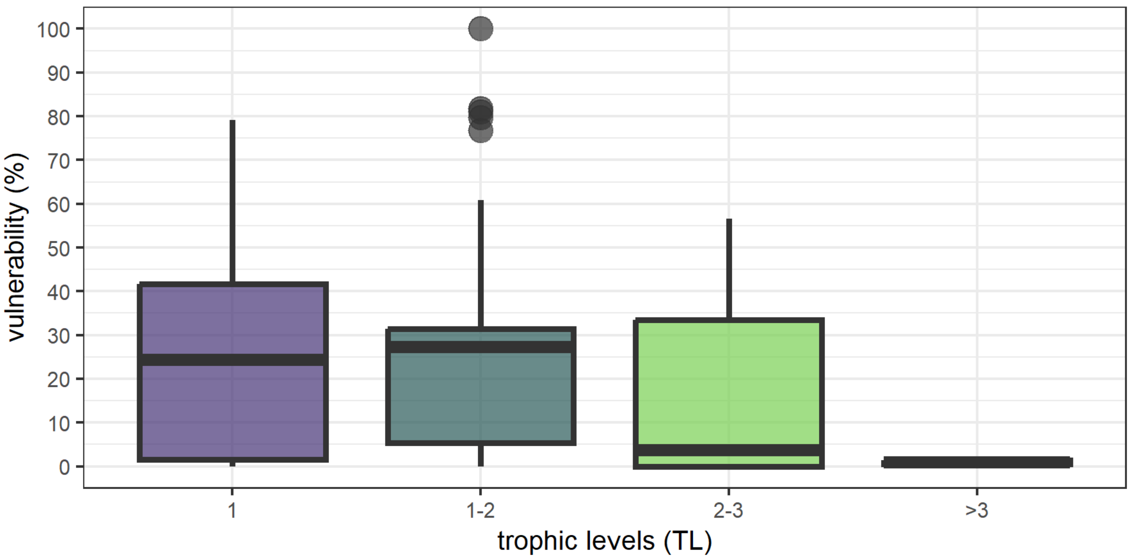

Figure A136. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 25% coextinction threshold across all climate-projection scenarios tested.

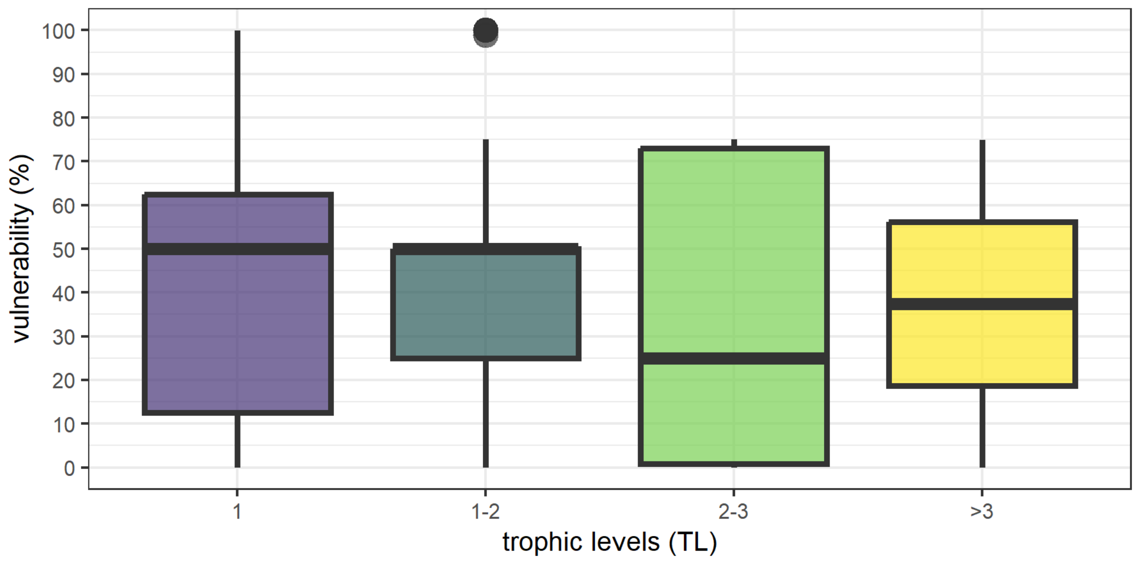

Figure A137. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 50% coextinction threshold across all climate-projection scenarios tested.

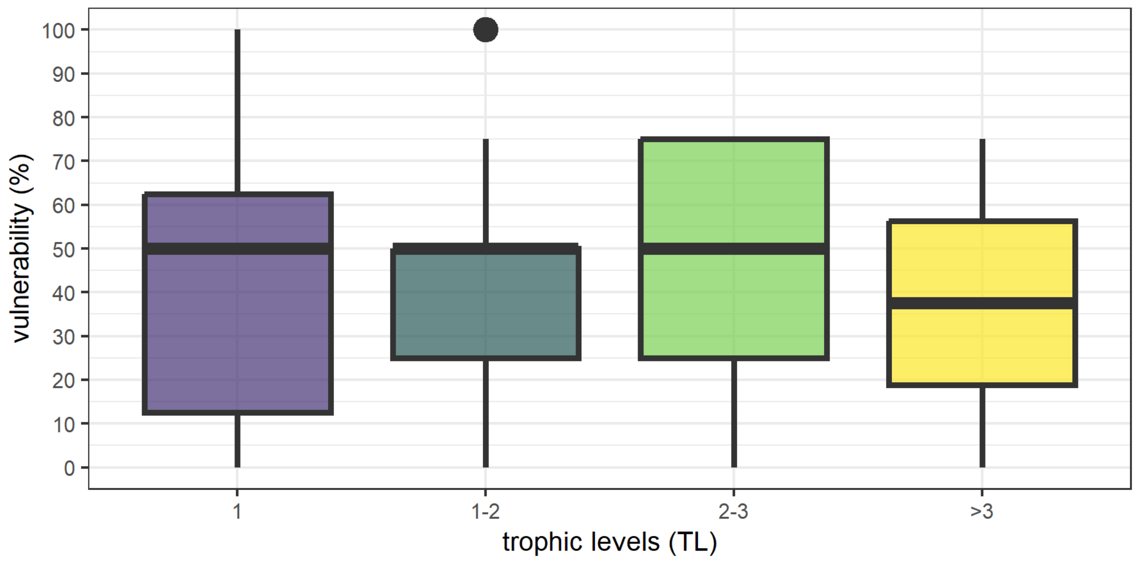

Figure A138. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only shift elevational range but could not rewire trophic interactions at a 100% coextinction threshold across all climate-projection scenarios tested.

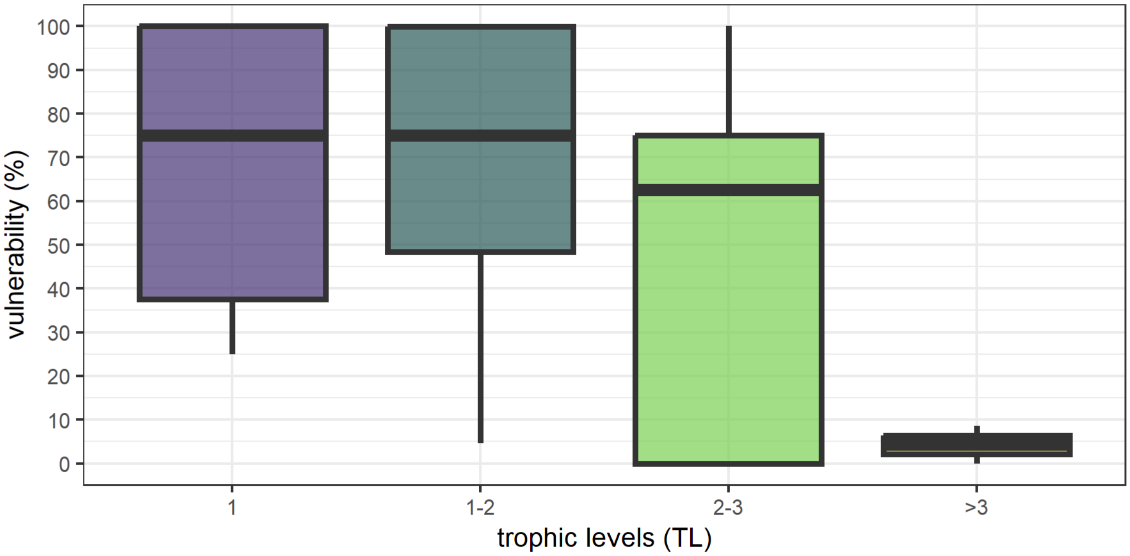

Figure A139. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

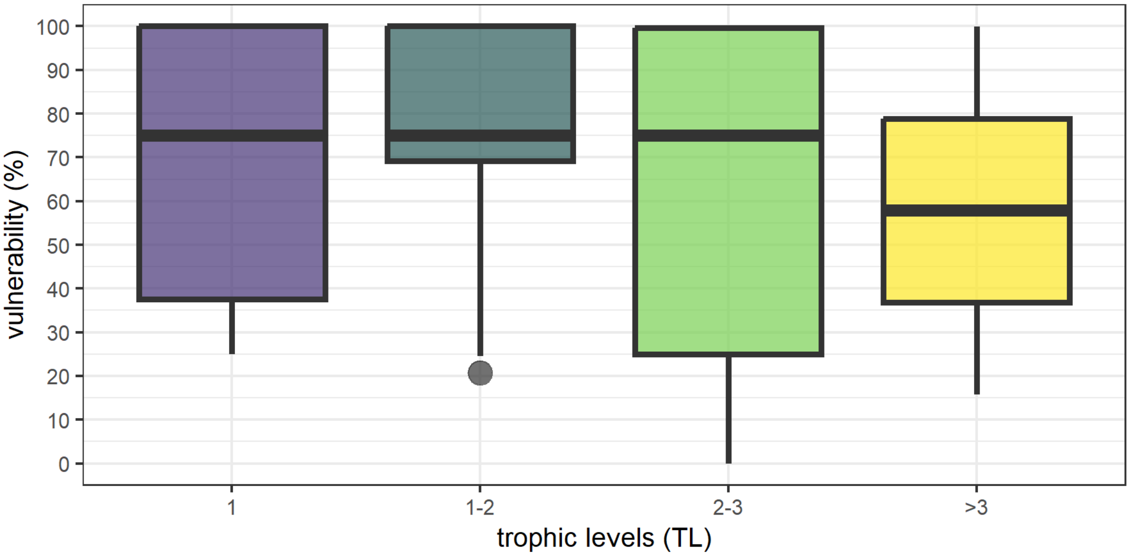

Figure A140. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could only rewire trophic interactions but could not shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

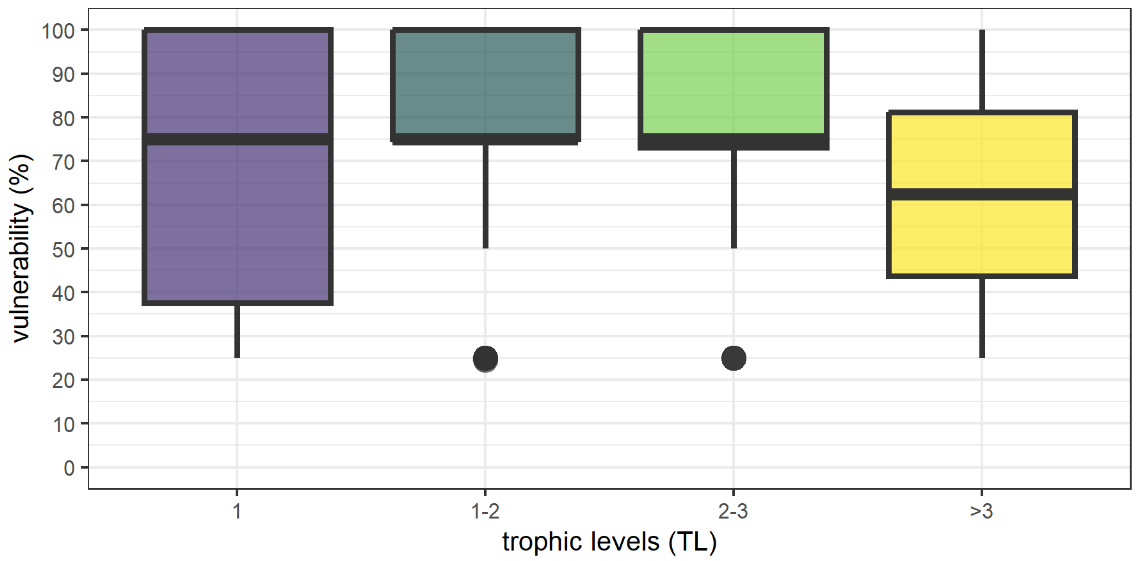

Figure A141. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species only rewire trophic interactions but could not shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

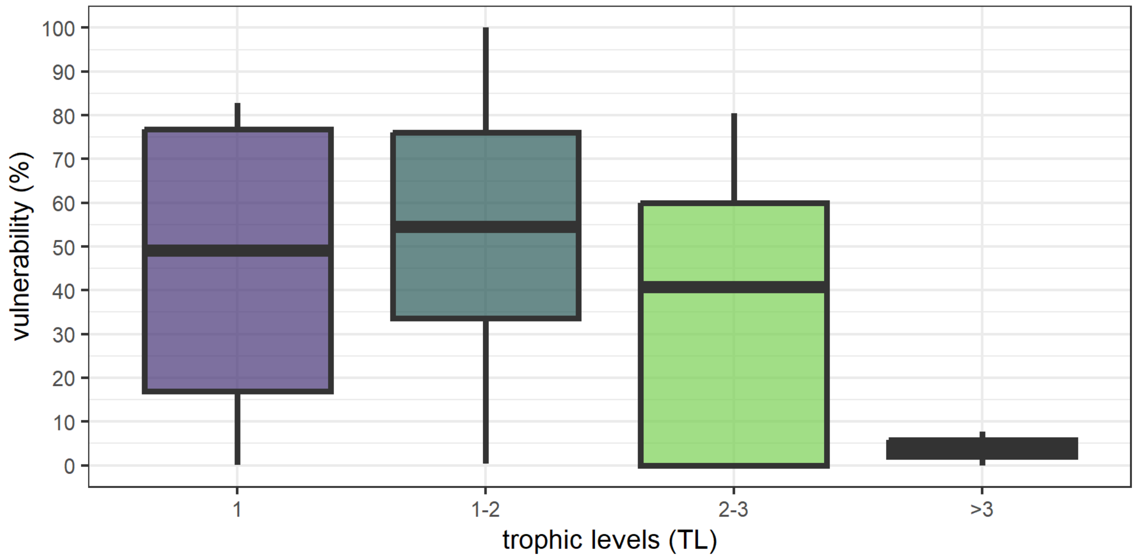

Figure A142. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 25% coextinction threshold across all climate-projection scenarios tested.

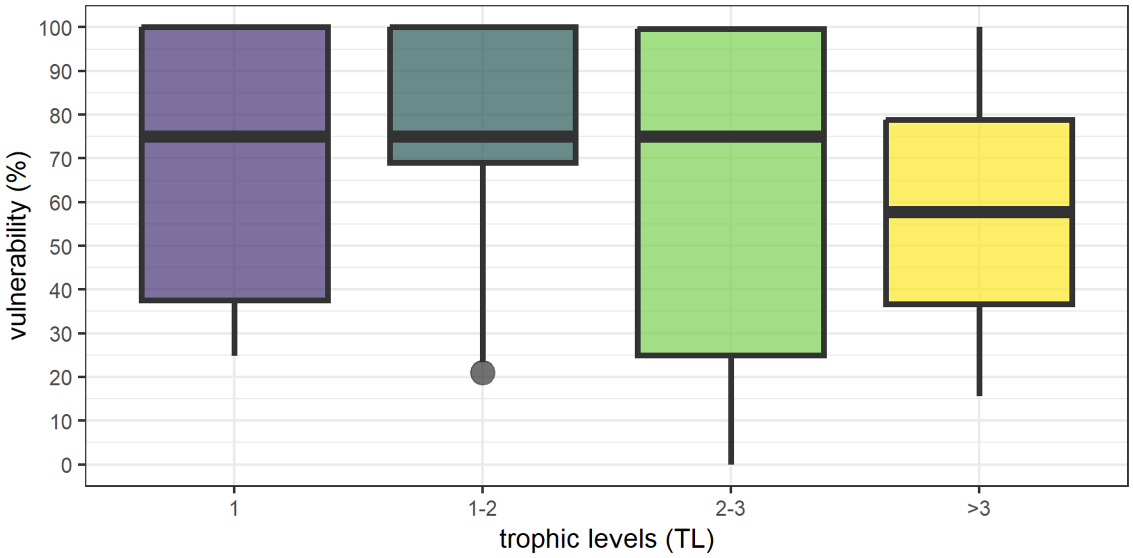

Figure A143. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 50% coextinction threshold across all climate-projection scenarios tested.

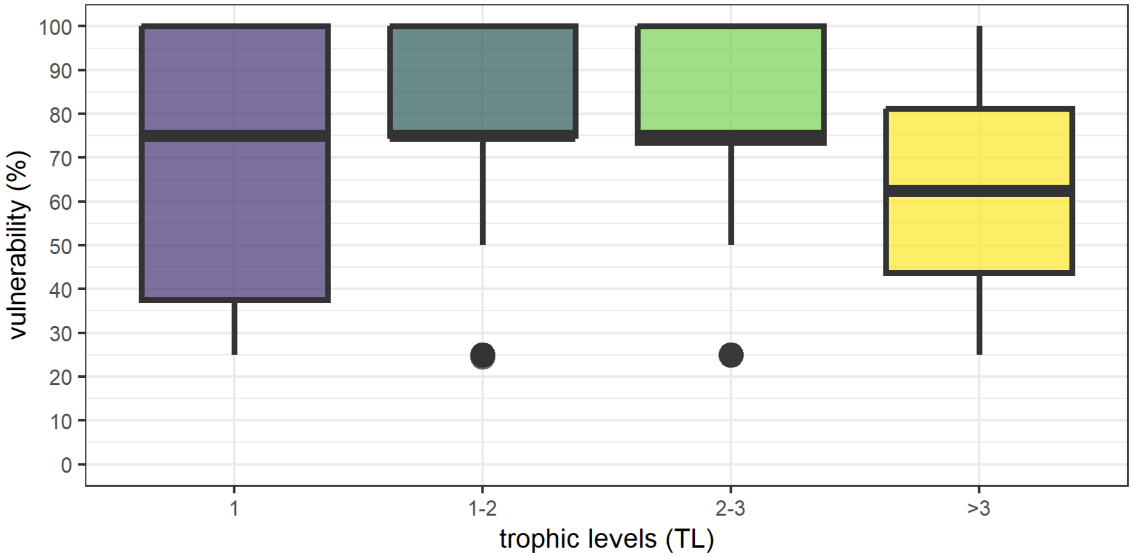

Figure A144. Mean vulnerability to primary extinction for each vertebrate species in the lowland network grouped by *TL* in simulations where species could not rewire trophic interactions or shift elevational range at a 100% coextinction threshold across all climate-projection scenarios tested.

Thesis discussion

Predicting how trophic cascades and coextinction influence extinction risk in ecological communities has steadily gained traction over the last few decades, particularly in freshwater and marine ecosystems (Batten et al., 2018; Jones et al., 2017). Terrestrial ecosystems have comparatively received less attention given both the complexity and dearth of data (e.g., Golubski et al., 2016; Momal et al., 2020) needed to create network models. This is despite global studies indicating that trophic cascades and coextinctions are likely to play increasingly important roles under changing environmental conditions (Strona & Bradshaw, 2018; Strona & Bradshaw, 2022). Thus, predicting how cascades and coextinctions affect the extinction risk of species in terrestrial ecosystems at fine spatio-temporal scales using empirical data is required, particularly if we are to mitigate such threats. The research I present in this thesis evaluated such extinction dynamics in some of the most well-studied, terrestrial ecological communities in Australia. In the following section I surmise my findings, including their implications for both the associated ecological communities and other terrestrial ecosystems globally. Finally, I discuss the limitations of my findings and propose ways forward regarding new questions, hypotheses, and discussions.

Summary

I set out to answer how climate change could shape extinction risk among vertebrate species in the Australian Wet Tropics, focusing on the indirect mechanisms of trophic cascades and coextinctions. I proposed a novel framework that can represent terrestrial food webs more realistically and simulate trophic cascades influenced by probable future perturbations (Chapter 1). Building on this foundation, I operationalised this framework using the Wet Tropics as a case study to provide a holistic view of extinction risk in real terrestrial communities.

A major outcome of this research is the recognition that defining ‘ecological communities’ fundamentally affects how we detect, model, and ultimately predict extinction dynamics. I showed that vertebrate communities across the Wet Tropics are generally similar in their functional trait space but differ more across elevation than latitude space (Chapter 2). This result underpins subsequent analyses by confirming that while each sub-region across this bioregion has compositional idiosyncrasies, they can still be considered cohesive networks distinguished only across elevational space when assessing cross-scale extinction drivers. From there, I constructed empirically based trophic network models for defined low- and high-elevation vertebrate communities (Chapter 3). These network models revealed that the structuring of predator-prey relationships can influence the resilience of different vertebrate species groups to environmental perturbations, and how certain species groups can play different roles from a trophic-centric view.

Through modelling bottom-up cascades, I highlighted the critical role basal resources play in sustaining vertebrate communities. The loss of basal resources due to climate change can trigger bottom-up cascades, and the severity of these cascades can vary across elevational gradients (Chapter 4). At the same time, coextinction events appear to compound overall extinction risk, although the magnitude of coextinctions varies with the severity of climate projection assumed (Chapter 5). These findings support the notion that climate change can indirectly exacerbate biodiversity loss by destabilising the trophic links that underlie vertebrate communities in terrestrial ecosystems. By simulating multiple future climate-projection scenarios and testing the potential for species to adjust (through trophic rewiring or shifting elevational range), I also found that the direct effects of climate change have the potential to cause as many or more primary extinctions as coextinctions in the Wet Tropics. Nevertheless, the compounding influence of coextinctions and trophic cascades becomes more pronounced when climate stress pushes communities closer to ecological ‘tipping points’, and that extinction vulnerability varies according to species trophic level, taxonomic class, and elevation. These integrated findings emphasise that the overall impact of climate change cannot be accurately predicted by focusing on direct physiological impacts alone, and that indirect effects mediated by trophic cascades and coextinctions are likely to exacerbate the extinction of vertebrate species under future warming.

Implications for the Wet Tropics and other terrestrial ecosystems globally

Given that many, if not most, past and future extinctions can be attributed at least in part to trophic cascades (Kehoe et al., 2021; Ripple & Van Valkenburgh, 2010), the need to estimate coextinction risks in terrestrial ecosystems is growing. Gaining a holistic ecological perspective on the impacts of environmental disturbances will enhance the understanding of ecosystem responses to climate change and other stressors, ultimately informing more effective environmental policies and conservation strategies to mitigate the expected losses.

The Wet Tropics symbolise the global struggle to preserve biodiversity in the face of multiple contemporary threats. Its very own management authority since 1993 has continuously strived to manage and protect this region (WTMA, 2024b). As part of this duty, the Wet Tropics Management Authority has pledged a Wet Tropics Climate Adaptation Plan for the region for 2020–2030, which effectively compiles 27 different action guides from all relevant Commonwealth, state, and region programs, plans, and policies, including the *Wet Tropics Plant for People & Country* initiative by Terrain NRM, *Queensland Climate Adaptation Strategy 2017–2030*, and the *Australian Environmental Restoration Fund* (WTMA, 2020). The Queensland Government has since supplemented this plan by launching a Threatened Species Program from 2020–2040 (DESI, 2020), aimed at coordinating efforts in identifying, protecting, and recovering threatened species while mitigating threats to their habitats; these combine with a national government pledge to protect 30% of all land in Australia by 2030 to mitigate species declines and extinctions (Plibersek, 2023). In addition, a national 2022–2032 *Threatened Species Action Plan* pledges “zero new extinctions” that specifically include the Wet Tropics as one of just 20 priority regions across Australia, including some of its inhabitants like the mountain top nursery frog (*Cophixalus monticola*) (DCCEEW, 2022a). A *Nature Positive Plan* (DCCEEW, 2022b) has also been promised to strengthen environmental legislation for the ongoing protection and restoration of areas like the Wet Tropics.

Despite the exhaustive list of these large and ambitious plans that mainly consist of conventional environmental management approaches, my work indicates an important shortfall: by not considering ecological cascades and coextinction, environmental managers, policymakers, and researchers ignore an important pathway to extinction (e.g. Strona &

Bradshaw, 2022; Chapter 4 & 5). Without appreciating this aspect, we are doomed to more extinctions if we keep to the same official strategies of *ad hoc* responses and single-species management. The major component not explicitly considered in the existing environmental legislation, management, and conservation strategies is coextinctions. My findings, combined with existing research on the Wet Tropics (de la Fuente et al., 2022; de la Fuente & Williams, 2023; Williams et al., 2003; Williams & de la Fuente, 2021), demonstrate that despite high coverage of protected areas in the region, its ecological communities still face extensive threats via coextinctions under continued warming (Lee et al., 2023; Chapter 5). To be effective, conservation strategies must address not only the direct impacts of threats on individual species, but also their indirect effects on the associated communities to minimise the overall extinction rate.

Building on the foundation of the existing research done in the Wet Tropics, my findings also carry important implications for estimating and managing coextinction threats in terrestrial ecosystems globally (Chapters 1-5). My research provides an unprecedented case study for how ecological communities can be defined to estimate coextinction risks in terrestrial ecosystems. Specifically, striking a balance between functional and species composition is important for delineating communities, and this balance should consider meaningful spatial and temporal scales (Chapter 2). I also highlight that we need to consider other factors potentially influencing how a community can be protected (e.g., meeting the criteria of local environmental protection legislation; Chapter 2). However, how a community is defined also depends on a study's specific objectives and data availability. By developing robust network models, I have demonstrated how one can apply mathematical approaches and machine learning to infer predator-prey relationships across multiple taxa in highly diverse vertebrate communities.

My research further highlights how bottom-up trophic cascades can influence extinction dynamics within complex terrestrial communities, and how incorporating basal resource interactions can alter estimates of extinction risk (Chapter 4). Broadly, my findings emphasise the need to quantify and prevent resource losses, calculate species-specific coextinction thresholds, and quantify the ability of different species to rewire their trophic interactions when community composition changes (Chapters 4 & 5). My work has also emphasised the importance of multifaceted conservation strategies that address not only direct extinction risk, but also the indirect effects of extinction cascades (Chapters 4 & 5). These insights are relevant for policymakers aiming to develop holistic environmental policies that aim to reduce primary and secondary extinction risks, ensuring more effective biodiversity conservation outcomes.

My findings come with certain limitations that primarily relate to the accuracy of inferred predator-prey interactions needed to develop trophic network models (e.g., biases in interaction training data and assumption of unobserved interactions as non-interactions; see Chapter 3) and some ecological complexities (e.g., assumed coextinction thresholds and predator-prey interactions with basal resources; Chapters 4 & 5) that I could not determine easily.

Looking forward

There are many avenues to advance our understanding of how trophic cascades and coextinctions influence the extinction risks in terrestrial ecosystems. Future research should focus on testing multiple versions of constructed network models that rely on ensemble-learning algorithms. The random forest algorithm (Chapter 3) constructs multiple decision trees during the training phase, each using a randomly sampled subset of the training data and features ('bootstrap aggregating'). During the construction of each tree, a random subset of features determines the selection of splitting attributes at each node (Breiman, 2001). When these trees collectively contribute to the final decision tree via a majority-voting mechanism, the ensemble prediction might vary marginally with each run of the model, providing different probabilities of inferred pairwise interactions between predators and prey. The implication is that the approach could cause measurable topological changes to subsequent ecological models. Because of topological variation, relative extinction risks of particular vertebrate groups (e.g., carnivores) or whole communities (e.g., via increased or decreased connectance) might also vary. Determining how the variability introduced by such algorithms like random forest for constructing trophic network models affects predicted extinction risk has yet to be determined. For example, studies show that network connectance relates to the robustness of food webs to environmental changes (e.g., Dunne et al., 2002), so changes in the complexity of models theoretically have implications for vulnerability to these changes. Addressing this question will elucidate the possible consequences of model variability on inferred extinction risks.

Future research should also determine how alterations in the intricacies of network models and coextinction simulations (e.g., intraspecific variation, heterogeneity of coextinction threshold) impact the occurrence of trophic cascades and coextinctions. Recognising all potential trophic interactions among species within an ecosystem is often overlooked in coextinction models, which typically eliminate species sequentially without considering how species may adapt their interactions when other species are lost or introduced into the community. Additionally, basal resources like invertebrates and plants are often ignored or grouped together (pooled nodes) due to insufficient data, simplifying the representation of the community in a way that can affect coextinction simulation outcomes (Start & Gilbert, 2017; Chapter 4). Consequently, incorporating greater detail in network models and coextinction simulations will likely improve the accuracy of extinction/coextinction predictions.

Temperature is not the only variable shifting in the Wet Tropics due to climate change (Chapter 5). The frequency and severity of tropical cyclones are also expected to change: the total number of cyclones is expected to decrease, while high-intensity cyclones are expected to become more frequent (Watterson et al., 2015). The impact of these changes must be considered because changes in storm activity might affect plants and other components of ecological communities, potentially triggering ecological cascades. For example, cyclones in the Wet Tropics can substantially affect the composition of plant communities (AKA ‘cyclone scrub’; Metcalfe & Ford, 2008). In addition, non-native or non-endemic plants, such as vines, or trees like *Miconia calvescens*, threaten biological communities in this region (Weber et al., 2021), and they have a high potential to invade bare patches following large storms or cyclones. This change in vegetation structure and composition could lead to substantial changes in invertebrate and vertebrate communities and the availability of habitat and food resources. Indeed, the southern cassowary (*Casuarius casuarius*) that normally favours fallen fruit, also consumes small vertebrates, among other resources (Bradford et al., 2008), especially following cyclones when fruit availability is limited (WTMA, 2024a). Therefore, determining how changes in cyclone patterns and other climate-change-linked factors (e.g., seasonality of precipitation) affect the composition of plant and invertebrate communities in the Wet Tropics is a key area for future research.

A palaeontological review of the Wet Tropics bioregion during the Last Glacial Maximum could provide important contextual data for the results arising from Chapter 5. Hindcasting each of the network models for the Wet Tropics back to that period could simulate distributional changes across elevational gradients, and then cross-validated with known range shifts of species, using for example genetic datasets (Schneider & Moritz, 1999), to assess the accuracy of simulation models. The ensuing results could shed light on how ecological communities respond to future environmental perturbations, focusing on ideas of stability-diversity hypotheses, which posits that more diverse ecosystems are more stable (McCann, 2000), and refugia (i.e. geographic areas that have consistently provided stable environmental conditions over extended periods, communities to survive despite broader habitat changes (Laffan et al., 2010; Rossetto & Kooyman, 2021)).

Investigating multiple and possibly synergistic effects of different extinction drivers could also complement my research. For instance, identifying the direct and indirect impacts of species that have begun to or are likely to invade these communities, such as feral cats (*Felis catus*) (Rowland et al., 2020), or yellow crazy ants (*Anoplolepis gracilipes*) (Lach & Hoskin, 2015), could also be simulated in these network models. Multiple environmental stressors can bypass ecological buffers, further increasing coextinction risk (Brodie et al., 2014), so future research could test how invasive incursions affect trophic dynamics and extinction risks. Future research could also test how the loss of functional niches from trophic cascades impacts risk, focussing on whether functional redundancy remains sufficient to ensure trophic stability.

I developed trophic network models that did not change dynamically (Chapters 3 & 4), but species composition, abundance, and traits can change across time (e.g., migratory birds, ontogenetic stages). Such seasonal variation could either exacerbate coextinction risk or provide mechanisms of resistance. For example, some lowland species in the Wet Tropics have already increased in abundance by 190% at higher elevations, while some highland species have declined by 50% in recent years (Williams & de la Fuente, 2021). Future research could examine how abundance trends alter predictions of trophic interactions (Lotka, 1910; Pringle et al., 2019; Rosenzweig & MacArthur, 1963) by weighting edges in networks according to relative abundance. Incorporating such dynamics could also allow for the simulation of processes such as extinction lags (Cornford et al., 2023).

Advancements in artificial intelligence and machine learning have already begun transforming nearly every scientific field (Jordan & Mitchell, 2015). One contemporary application of artificial intelligence that shows its promising future is its application to construct plant-pollinator networks based on species traits (Pichler et al., 2020). This technological capability showcases how artificial intelligence can enhance our understanding of complex ecological interactions and, consequently, coextinction risks. I foresee a future where artificial intelligence could provide avenues for real-time classification of both trophic and non-trophic interactions *in situ* via enhanced computer vision models and modified camera-trap devices, combined with other technology (e.g., bioacoustic sensors) that feed into remote, cloud databases.

Artificial intelligence could also provide a solution for developing dynamical multiplex networks where not only trophic interactions are considered, but also non-trophic interactions (e.g. mutualistic plant-pollinator networks). The inevitable emergence of artificial general intelligence, as the hotly debated next evolution of AI (Mitchell, 2024), could also transform our approach to ecological research in unforeseen ways. Artificial general intelligence has the potential to process vast amounts of data and identify patterns beyond human capability. This development could lead to unprecedented insights into not just how species interact within ecosystems, but also the potential patterns and complex processes in terms of community assembly, species dispersal, and evolution that mediate these relationships. This development could translate into more accurate predictions of coextinction risks and better strategies for biodiversity conservation work.

General conclusions

In this thesis, I aimed to predict how anthropogenic threats affect the extinction risk of communities through trophic cascades and coextinctions in terrestrial ecosystems. My research emphasises the importance of trophic cascades and coextinction risks and provides a robust framework for predicting (and therefore potentially mitigating) these threats. By demonstrating that coextinction risks are important by constructing the first trophic network models of tropical, terrestrial vertebrate communities, I have demonstrated the need to quantify localised, indirect impacts of environmental threats. My research showcases the development of a novel framework to assess coextinction risks, investigates methods to define ecological communities accurately, and constructs and analyses ecological network models to understand the structure and dynamics of species trophic interactions. My work also evaluates the potential impact of bottom-up trophic cascades on vertebrate extinction risks and assesses coextinction risks under various future climate change-projection scenarios, highlighting the influence of different species' adaptive capacities.

My results collectively emphasise the need for comprehensive, multifaceted approaches to biodiversity conservation that consider both direct and indirect effects of environmental change. By demonstrating the role of ecological interactions and the potential cascading effects of future environmental changes, my research adds to the call for more comprehensive and adaptive management to preserve biodiversity amidst accelerating global change. Moving away from single-species management frameworks and towards integrated strategies that consider the influence of biotic interactions are essential. Future research should continue to refine the use of tools like network modelling to capture the dynamic nature of communities and explore new technologies to enhance our understanding and mitigation of extinction risks. As Janzen (1971) once noted, "The most insidious sort of extinction, the extinction of ecological interactions" could not be more prescient. However, an insidious world does not have to be our reality if we choose to act. Embracing these advancements and continuing to understand coextinction risks offers a promising pathway to preserving the web of life and ensuring the resilience of ecosystems in the face of ongoing environmental change.

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