Understanding how local climatic changes modify the response of biodiversity to land-use changes

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I, Jessica Jacqueline Williams, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

Anthropogenic changes to Earth's ecosystems are putting global biodiversity under ever-increasing pressure. Land-use and climate change are two of the biggest pressures facing terrestrial species. These environmental changes, however, are not occurring in isolation and, consequently, may interact. One route by which these two pressures could interact is through the local-scale climatic changes that occur due to land-use change. Human-altered land uses are often hotter and drier than natural habitats, which may lead to these land uses (such as agricultural areas) favouring certain species. Moreover, environmental changes do not impact species uniformly across their distributions. Populations' climatic positions (i.e., how close the environmental climatic conditions populations experience are to their species' climatic tolerance limits) have been found to influence populations' responses to global climate change, but whether they impact responses to land-use change remains unknown. By using three of the most comprehensive assemblage databases to date (the PREDICTS, Living Planet and BioTIME databases), this thesis investigates the impact of local climatic changes on vertebrate responses to land-use changes. I find that human-altered land uses are reshaping communities by favouring species affiliated with more extreme climatic conditions, especially at tropical latitudes. Further, responses differ across species ranges, with populations' climatic positions influencing abundances within human-altered land uses. In particular, those populations experiencing temperatures closer to their thermal limits are filtered out of human-altered land uses. In addition, population trends were influenced by interactions between land use, habitat loss, climatic position, and climate change. These results are likely, at least in part, due to the local climatic changes ensuing land-use change. Overall, accounting for these local climatic differences between land uses is essential if we are to fully understand the impacts of environmental changes on biodiversity, set up suitable conservation and management plans to mitigate their effects, and minimise future biodiversity loss.

Impact statement

The Earth's ecosystems provide a wealth of goods and services to humans, from food and building materials, to pest regulation and soil formation. Beyond these provisioning, regulating, and supporting services, nature also provides cultural benefits. For example, during the SARS-CoV-2 pandemic, the positive impact of nature on mental and physical well-being has been repeatedly highlighted. However, with ongoing anthropogenic changes, particularly to Earth's terrestrial surface and climate, biodiversity is being placed under ever-increasing pressure. Subsequently, many vertebrate populations are declining, and the benefits humans receive from nature are threatened. To reduce further biodiversity loss, major and urgent efforts to conserve greater areas of land, restore degraded land, and practise landscape-level conservation planning are needed. To make these efforts effective, it is critical that information is available on how species respond to land-use changes (both habitat loss and restoration), how this differs spatially, and how responses may be impacted by ongoing global climate changes.

This thesis provides novel insights into the impacts of land-use change on vertebrate species around the world, how these impacts may differ geographically, and the interactive effects between land-use and climate change. Chapter 2 reviews the current understanding of how land-use changes impact biodiversity, focusing on the effect of the local changes in temperature and precipitation that follow habitat change, and highlights key knowledge gaps. This work was published in 2019 in *Diversity and Distributions* (it was one of the most downloaded papers in 2018-2019), and was cited in the WWF Living Planet Report (2020). Chapters 3-5 fill many of the knowledge gaps highlighted in Chapter 2, significantly contributing to our understanding of the impacts of land-use change on biodiversity. Chapter 3 identifies that, globally, human-altered land uses (e.g., agricultural areas) are favouring vertebrate species affiliated with certain climates, and was published in 2019 in *Ecography*. Chapter 4 builds on this by looking at variation across species' ranges in responses to human land uses and highlights the importance of accounting for the position of a population with regard to their climatic tolerance limits (i.e., their climatic position). This work was published in 2021 in *Diversity and Distributions*. Further, interactions between anthropogenic pressures have been identified as one of the biggest uncertainties in biodiversity change predictions, potentially hindering our ability to produce effective policy and management decisions. Chapter 5 investigates such interactions, finding that land-use and climate change interact to impact vertebrate population trends, with surrounding land-cover type and populations’ climatic positions also playing important roles in these interactions. These findings can be taken forward by the field, for example, by combining climatic position into trait-environment interactions to gain a clearer picture of the mechanisms underlying land-use change responses. The results presented in this thesis, which have been presented at major international conferences, further our understanding of the impact of anthropogenic pressures on biodiversity and add to the information available for conservationists, land-use planners, and policy makers, so that we can work towards altering the current trajectory of biodiversity loss and preserve the benefits humans receive from nature.

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Second, I would like to thank all those who contributed to or helped with the mammoth task of assembling the three key databases used in this thesis, the PREDICTS, Living Planet and BioTIME databases.

A huge thank you also goes to the members of the Global Biodiversity Change Group, my other colleagues within CBER, and collaborators/friends from around the world (Jeremy Kerr, Peter Soroye, Amanda E. Bates, Conor Waldock, Robin Freeman, to name a few). I feel extremely lucky to have met so many fantastic scientists and made so many good friends throughout my PhD. Their help and advice have made this a better thesis, and their friendship and trips to the pub have added so much fun to the last four years.

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Thesis outline of contents and collaborators

Chapter 1

Introduction

In this chapter, I introduce the main concepts underlying this thesis, highlight the knowledge gaps regarding the impact of local climatic changes following land-use change that I aim to fill, and set out the thesis' overarching hypotheses.

Chapter 2

Local climatic changes affect biodiversity responses to land use: a review

In this chapter, I review the current understanding of the impact of local climatic changes on biodiversity responses the land-use change and the potential underlying mechanisms. I also critically discuss the methods used to explore this topic and identify key knowledge gaps within our understanding. This work was conducted in collaboration with Tim Newbold. I developed the ideas with input from TN. I led the writing of the manuscript, with feedback from TN. A version of this chapter was published in October 2019 in the journal *Diversity and Distributions*, under the same title, and was among the top 10% most downloaded papers from the journal during the 2018-2019 period.

Chapter 3

Human-dominated land uses favour species affiliated with more extreme climates, especially in the tropics

In this chapter, I investigate whether human-dominated land uses systematically favour species with distinctive climatic niches, and whether this differs between tropical and temperate latitudes. This work was carried out in collaboration with Amanda E. Bates and Tim Newbold. This work was conceived by myself and TN, with input from AEB. I carried out the analyses and wrote the paper, with feedback from all co-authors. A version of this chapter was published in November 2019 in *Ecography*, under the same title. I presented this work at the Student Conference on Conservation Science (poster, 2018), the British Ecological Society Macroecology Special Interest Group meeting (talk, 2018) and the International Biogeography Society Biennial Conference (talk, 2019). Additional thanks to R. Pearson, K. Jones, and J.-Y. Barnagaud for feedback on early versions of this paper, to C. Waldock for his help with creating indices using GBIF data, to A. Etard for the use of the habitat specialisation index, and to S. Butchart for use of the BirdLife data.

Chapter 4

Vertebrate responses to human land use are influenced by their proximity to climatic tolerance limits

In this chapter, I explore whether a population's climatic position (the difference between the species' thermal and precipitation tolerance limits and the environmental conditions a population experiences) influences their relative abundance across land-use types. This work was carried out in collaboration with Tim Newbold; we jointly conceived the idea, I carried out the analyses and led the writing of the manuscript, with feedback from TN. A version of this chapter was published in May 2021 in *Diversity and Distributions*, under the same title. I presented this work at the British Ecological Society Annual Meeting (talk, 2019) and the Ecological Society of America Annual Meeting (virtual talk, 2020). Thanks also to R. Pearson, K. Jones, J. Kerr, and P. Soroye for useful discussions during the production of this manuscript, and to S. Butchart for use of the BirdLife data.

Chapter 5

Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change

In this chapter, I explore whether the local climatic changes ensuing land-use change may be leading to interactions between land-use and climate change by investigating the impacts of these variables on vertebrate population trends. This work was carried out in collaboration with Robin Freeman, Fiona Spooner, and Tim Newbold. I conceived the idea for this chapter, with input from TN and RF. I carried out the analyses, with input from FS. The chapter was written by myself, with feedback from all co-authors. A version of this chapter is currently under review at a scientific journal. I presented this work at the British Ecological Society Annual Meeting (virtual talk, 2020). Additional thanks to L. McRae for her help with the Living Planet database, S. Butchart for use of the BirdLife data, and G. Griffiths, S.A. Manzoor and C. Howard for useful discussion regarding the ESA CCI land-cover data.

Chapter 6

Discussion and synthesis

In this chapter, I evaluate the key findings presented in this thesis with regard to their contribution to broader knowledge. I also reflect on some of the challenges of global models in relation to the research within this thesis and outline outstanding questions and directions of future work.

Appendices

Appendix 1

Supplementary materials for Chapter 3.

Appendix 2

Supplementary materials for Chapter 4.

Appendix 3

Supplementary materials for Chapter 5.

Appendix 4

Further publications. In this appendix, I provide details of two other published papers on which I am co-author and which I contributed to by using the expertise and knowledge acquired over the course of my PhD.

List of main text figures and tables

Figures

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Supplementary figures and tables for all chapters are included in Appendices 1-3.

Chapter 1:

Introduction

Anthropogenic changes to the Earth's ecosystems are putting global biodiversity under ever-increasing pressure (Steffen, Crutzen, & McNeill, 2007; Tilman et al., 2017). Over the last 50 years, human modifications of the world's terrestrial surfaces have accelerated, reshaping animal and plant communities globally (Meyer & Turner, 1992; Millennium Ecosystem Assessment, 2005; Pereira, Navarro, & Martins, 2012; Steffen, Richardson, et al., 2015). Biodiversity provides multiple goods and services on which humans rely, from pollinating our crops and providing medicinal resources, to regulating diseases, water, and air quality (Haines-Young & Potschin, 2010; WWF, 2018). As such, the loss of biodiversity can negatively impact the provision of ecosystem services and, subsequently, human well-being (Carpenter et al., 2009; Díaz, Fargione, Chapin, & Tilman, 2006; Millennium Ecosystem Assessment, 2005; Newbold, Hudson, Arnell, et al., 2016; TEEB, 2010).

Currently, the conversion of land for human use is considered the main driver of change for terrestrial biodiversity, affecting almost 90% of threatened bird, amphibian, and mammal species (Baillie et al., 2004; WWF, 2020). The extensive impacts of land-use change are set to continue and increase as the world's human population rises and demands for resources, such as food and wood, escalate (Haddad et al., 2015; Newbold et al., 2015; Newbold, Hudson, Hill, et al., 2016; van Vuuren et al., 2012). It is predicted, however, that over the next few decades, climate change could surpass land-use change to become the greatest global threat to biodiversity (Leadley et al., 2010; Newbold, 2018). Climate change is expected to affect every level of biodiversity, from that of the biome down to the organism (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Parmesan, 2006). To minimise future species loss and sustain the benefits human derive from ecosystems, it is critical that we understand how species are, and will be impacted by these global drivers of change.

1.1 Land-use change

Land-use change is driving substantial modifications to the world's ecosystems (Millennium Ecosystem Assessment, 2005; Pereira et al., 2012). Changes in land use encompass changes to landscape composition, configuration and the intensity of human use (Andrén, 1994; de Chazal & Rounsevell, 2009; Seppelt et al., 2016). Landscape composition is the number and expanse of different habitat types across a landscape, and changes to this result from the conversion of natural habitats (such as primary forest or grassland with no history of human disturbance) to human-altered land uses (such as agriculture or urban sites), or from the restoration of these human-altered land uses back to forest or grassland (de Chazal & Rounsevell, 2009; Seppelt et al., 2016). Changes to landscape configuration are often due to habitat fragmentation, where continuous habitat is subdivided into smaller patches (Andrén, 1994). Finally, land-use intensity can be altered by varying management practices, the use of fertilisers or labour input, for example (Hudson et al., 2014; Seppelt et al., 2016).

Many studies have explored the impacts of land-use changes on biodiversity. For instance, marked reductions have been found in species richness along gradients of natural to human-altered land uses, increasing human-use intensity, and increasing forest fragment isolation (Haddad et al., 2015; Newbold et al., 2015; Newbold, Scharlemann, et al., 2014; Pfeifer et al., 2017). Further, conversion of natural habitat to human-altered land uses leads to shifts in ecological assemblages, towards wide-ranging species and away from certain dietary guilds for example, which can lead to biotic and functional homogenisation, respectively, and subsequent deterioration in ecosystem functioning (Clavel, Julliard, & Devictor, 2011; Newbold et al., 2018; Newbold, Scharlemann, et al., 2014). However, in recent years, focus has shifted away from concentrating on the effects of single stressors such as land-use change alone, to looking at how drivers of change interact to affect biodiversity (Brook, Sodhi, & Bradshaw, 2008; Mantyka-Pringle, Martin, & Rhodes, 2012; Sala et al., 2000). In particular, there have been calls to investigate how land-use changes interact with climatic changes to impact biodiversity (de Chazal & Rounsevell, 2009; Mantyka-Pringle et al., 2012; Oliver & Morecroft, 2014).

1.2 Climate change

Climatic changes are occurring at the global and local level. Definitions of climate change can vary slightly depending on whether the changes are attributed solely to human activity; here, I use the term climate change to refer to any changes in climatic variables (precipitation, temperature, or wind, for example), including those that are a result of human actions or natural variability (this is the definition also used by the Intergovernmental Panel on Climate Change; de Chazal & Rounsevell, 2009; Parry, Canziani, Palutikof, van der Linden, & Hansen, 2007). Climate change encompasses both changes in the mean of climatic variables, and changes in their variability (such as extreme events and changes in variance and/or distribution; Reyer et al., 2013; Rummukainen, 2012). Current patterns of global climate change are leading to warmer temperatures, increasing frequency of hot extremes, and growing contrasts in precipitation between wet and dry regions, and wet and dry seasons (Collins et al., 2013). Species are responding to these global climatic changes by shifting their ranges and/or habitats, adjusting the timing of phenological events such as fledging or seasonal migrations, and adapting through physiological or behavioural changes (Bellard et al., 2012; Davies, Wilson, Coles, & Thomas, 2006). However, species are not always successful in keeping pace with the climatic changes (e.g., Lindström, Green, Paulson, Smith, & Devictor, 2013), and even when they do, the changes can have negative impacts on communities and ecosystem services through the disruption of species' interactions (Post & Forchhammer, 2008; Reyer et al., 2013). In conjunction with these global climatic changes that many studies focus on, changes in climate also occur at the local level. In particular, local changes to temperature and precipitation regimes occur following land-use change (Jiang, Fu, & Weng, 2015; Nowakowski, Watling, et al., 2017; Senior, Hill, González del Pliego, Goode, & Edwards, 2017). However, these local climatic changes mediated by changes in land use are often overlooked, especially when (1) investigating how species are impacted by habitat changes and (2) exploring mechanisms that could lead to interactions between land-use change and global climate change. These knowledge gaps will be the focus of this thesis.

1.3 The impact of the local climatic changes following land-use change on species' responses to habitat change

Species' responses to land-use changes may be being impacted by the associated local climatic changes. Human-altered land uses are, on average, hotter and drier than natural habitats, and also often experience greater extremes of temperature (Britter & Hanna, 2003; De Frenne et al., 2019; Ewers & Banks-Leite, 2013; Frishkoff et al., 2016; Senior, Hill, González del Pliego, et al., 2017). This is driven, at least in part, by the differences in vegetation between land uses, such as the presence or absence of a canopy layer (discussed in more detail in Chapter 2; Frishkoff et al., 2016; Jiang et al., 2015; Senior, Hill, González del Pliego, et al., 2017; De Frenne et al., 2021). These altered climatic conditions have been suggested to lead to human-altered land uses favouring certain species, specifically those that can tolerate the new temperature and precipitation regimes (Frishkoff, Hadly, & Daily, 2015; Frishkoff et al., 2016; Nowakowski, Frishkoff, Agha, Todd, & Scheffers, 2018; Nowakowski, Watling, et al., 2017). Indeed, at a local scale, for both vertebrates and invertebrates, species situated in agricultural or urban areas have been found to be able to tolerate, or be affiliated with, hotter and drier climates on average, compared to species in forested habitats (Barnagaud, Barbaro, Hampe, Jiguet, & Archaux, 2013; Frishkoff et al., 2015; Frishkoff et al., 2016; Frishkoff, Ke, Martins, Olimpi, & Karp, 2019; Menke et al., 2011; Nowakowski, Watling, et al., 2017; Piano et al., 2017; discussed further in Chapter 2). For example, within bird and herpetofauna communities in Europe and the Neotropics, respectively, warmer-adapted species were found to be favoured in human-altered areas compared to more natural, forested sites (Barnagaud et al., 2013; Frishkoff, Gabot, Sandler, Marte, & Mahler, 2019; Frishkoff et al., 2015). For terrestrial invertebrate species, these patterns have also been observed at the global level, with species' climatic affiliations (particularly preferences for warmer thermal maxima and lower precipitation minima) predicting occurrence within forested or agricultural land uses (Waldock, De Palma, Borges, & Purvis, 2020). However, for terrestrial vertebrates, whether human-altered land uses are favouring species affiliated with certain temperatures or precipitation regimes has yet to be explored globally or for a wide range of taxa. Investigating whether the local scale shifts in vertebrate community composition towards species with certain climatic affiliations are widespread (geographically and taxonomically), will enhance our understanding of the impact human-altered land uses have on vertebrates, enabling us to anticipate the effects of future land-use changes and identify species at risk.

Populations, however, do not respond consistently to environmental changes across species' ranges (Orme et al., 2019; Soroye, Newbold, & Kerr, 2020), and the local climatic changes following land-use change may lead to intraspecific variation in the impact of this pressure. Within the global climate change literature, it has been recognised that a population's climatic position (i.e., how close the environmental climatic (temperature or precipitation) conditions a population experiences are to their species' climatic tolerance limits) influences their responses to global warming (Kingsolver, Diamond, & Buckley, 2013; Soroye et al., 2020). For instance, populations experiencing temperatures closer to their upper thermal limit have been found, or are predicted, to be more negatively impacted (e.g., lower probability of occurrence or greater fitness decline) by warming temperatures (Kingsolver et al., 2013; Soroye et al., 2020). However, whether a population's climatic position leads to differences across species' ranges in responses to land-use change has yet to be investigated.

The closest land-use change research has come to explore an effect of climatic position is to look at how populations differ in their occurrence within different land uses across regional climatic gradients (e.g., precipitation or temperature gradients, or seasonal vs. aseasonal regions; Frishkoff et al., 2016; Murray, Nowakowski, & Frishkoff, 2021; Srinivasan, Elsen, & Wilcove, 2019). Species have been found to shift their habitat use along climatic gradients, with agricultural land more likely to be occupied by species in wetter or more seasonal (greater annual temperate variation) regions, and forests preferred by the same species in drier or more aseasonal regions (Frishkoff et al., 2016; Srinivasan et al., 2019). I predict that this is, at least in part, due to an interaction between populations' climatic positions and the differences in local climate between land uses. This is because, similar to responses to global climate change, populations already experiencing temperature and precipitation conditions close to their tolerance limits may be pushed beyond these limits by local changes in climate following land-use change, leading to population declines (Deutsch et al., 2008; Mitchell et al., 2018; Nowakowski, Frishkoff, Agha, et al., 2018; Nowakowski, Watling, et al., 2018). Conversely, populations with greater thermal or precipitation buffers (greater differences between their tolerance limits and the ambient climate), may be able to tolerate local climatic changes, which may even lead to more favourable temperatures or precipitation conditions (Deutsch et al., 2008; Nowakowski, Watling, et al., 2018). Consequently, to be able to produce suitable conservation and management plans, which account for intraspecific variation in responses to environmental changes, the influence of populations' climatic positions on responses to land use needs to be explored, both at a global scale and across time as well as space.

1.4 The impact of local climatic changes on land-use and climate change interactions

There is a pressing need to understand whether, and if so how, global drivers of change are interacting with one another (Mantyka-Pringle et al., 2012; Sala et al., 2000; Titeux et al., 2017). Where two or more pressures occur concurrently, their effects may combine additively or interact (Oliver & Morecroft, 2014). Interactions can be synergistic, whereby the impact of changes in both pressures is greater than the impact from their additive combination, or they can be antagonistic, whereby the impact of changes is lower than their combined additive effect (Oliver & Morecroft, 2014). It is the possibility of synergistic interactions that pose the greatest concern and risk to global biodiversity (Brook, Sodhi, & Bradshaw, 2008; Northrup, Rivers, Yang, & Betts, 2019). Land-use changes are occurring alongside global climatic changes (Collins et al., 2013), which leads to the potential for these two pressures to interact (Oliver & Morecroft, 2014). Land-use and global climate change can directly influence each other, with changes in land use (such as deforestation and urbanisation) affecting global climatic conditions, and changes in climatic variables able to drastically affect land systems (Kalnay & Cai, 2003; Longobardi, Montenegro, Beltrami, & Eby, 2016; Titeux et al., 2016b). Even though there have been calls to integrate research on these two drivers of change, many studies still only focus on either land-use change or climate change (e.g., Antão et al., 2020; Daskalova et al., 2020), and studies looking at the interaction between them remain rare (but see Mantyka-Pringle et al., 2012; Sirami et al., 2017; Spooner, Pearson, & Freeman, 2018). However, the few studies that have investigated interactions have found that these two variables can interact synergistically (Brodie, 2016; Spooner et al., 2018). For example, rapid changes in both climate and land-use can lead to synergistic interactions: Spooner et al. (2018) found that, for mammals, population declines were greatest in areas that have experienced both high rates of habitat conversion (from natural to agricultural land uses) and warming. Further, human-altered land uses can impact the ability of species to shift their ranges in response to climate change (Oliver & Morecroft, 2014; Travis, 2003), with range expansion rates found to be slower in landscapes with less suitable habitats (Hill et al., 2001). Synergistic interactions can also result from the expansion of human-altered land uses being greater due to shifting climate regimes. For instance, the extent of oil-palm expansion impacting on the ranges of Southeast Asian mammal species has been predicted to be up to four times worse if climatic changes are accounted for (Brodie, 2016).

The local climatic changes that ensue land-use change may be another mechanism leading to interactions between land-use and climate change. For example, the higher hot thermal extremes resulting from the conversion of natural to human-altered land uses (De Frenne et al., 2019) are acting on top of global warming and the increased frequency of heat waves resulting from global climate change (Collins et al., 2013). Consequently, this could lead to a higher number of species being pushed beyond their upper thermal limits than if the two drivers of change were acting independently. Again though, the local climatic changes accompanying land-use change have not been considered in interaction studies (discussed further in Chapter 2). In particular, how interactions between land-use and global climate change may impact populations differently due to their climatic position has not been explored. This limits our ability to both predict those populations most at risk from these drivers of change and identify areas that would most benefit from conservation action (such as habitat restoration). Understanding how interactions between environmental pressures are affecting biodiversity, and how these effects vary across species' ranges, is vital if we are to mitigate the impacts of anthropogenic changes on biodiversity around the world (Sala et al., 2000). Indeed, interactions have been identified as one of the largest uncertainties when it comes to predicting future biodiversity change (Sala et al., 2000).

1.5 Local climatic changes following land-use change as a source of geographic variation in responses to environmental change

Geographic variation is key to take into account when studying the impacts of global drivers of change in order to be able to prioritise conservation efforts (Powers & Jetz, 2019). Due to differences between ecological communities at tropical and temperate latitudes, the impact of local climatic changes following land-use change may vary, leading to geographic variation in biodiversity responses. Such differences between communities could include the factors influencing species' geographical ranges, which have been suggested to differ latitudinally: abiotic factors (such as climate) are thought to dominate at temperate latitudes, and biotic factors (such as interspecific interactions) are thought to be the main influence at tropical latitudes

(Khaliq, Böhning-Gaese, Prinzinger, Pfenninger, & Hof, 2017; MacArthur, 1972; Wiens & Donoghue, 2004). However, species at lower latitudes are thought to be particularly vulnerable to environmental changes, with the tropics often being highlighted as an area of conservation concern (Brook et al., 2008; Newbold et al., 2018; Newbold, Oppenheimer, Etard, & Williams, 2020; Newbold et al., 2013; Pacifici et al., 2017; Sunday et al., 2014; Thuiller, Lavorel, & Araújo, 2005). Reasons for this, which could also lead to the local climatic changes being a source of geographic variation, include the lower seasonality and historically relatively stable climate at tropical latitudes (Janzen, 1967; Pacifici et al., 2017), and the fact that tropical species experience temperatures that are often closer to their upper thermal limits compared to their temperate counterparts (Deutsch et al., 2008; Sunday et al., 2014; discussed further in Chapter 2). On top of this, there are a larger number of tropical than temperate species (particularly endemic and/or threatened species; Barlow et al., 2018; Kearney, Shine, & Porter, 2009), and on average, these species also have smaller range sizes (Newbold, Hudson, Hill, et al., 2016; Stevens, 1989). Currently, due to the lack of large-scale studies looking at how the local climatic changes mediated by land-use change impact species or populations, whether this pressure leads to geographical variation in responses to habitat changes remains unknown. With the rates of current and future climate changes (relative to historical conditions) and land-use changes expected to be greater at tropical compared to temperate latitudes (Hurtt et al., 2011; Mora et al., 2013; Pacifici et al., 2017), understanding where and why species may be more negatively affected by anthropogenic pressures is critical if we are to instigate species conservation and land-management plans that are tailored towards the taxa and/or areas of concern, and that have the greatest chance of being effective.

1.6 Aims and hypotheses

To reduce future terrestrial biodiversity loss, recent work has called for major and urgent efforts towards conserving larger areas of natural habitat, restoring degraded land, and increasing land-use planning at the landscape-level (Leclère et al., 2020). In order to make these efforts effective, it is critical we understand the interspecific and spatial variation in responses to land-use change (both loss of natural habitat and habitat restoration). Furthermore, with land-use changes occurring concurrently to climate change, as mentioned above, a major goal within ecology is to enhance our understanding of how these global pressures interact to influence biodiversity (Mantyka-Pringle et al., 2012; Oliver & Morecroft, 2014; Sala et al., 2000; Titeux et al., 2017). The objective of this thesis is to investigate, globally and across both across space and time, whether human-altered land uses are systematically favouring certain species depending on their climatic affiliations, whether this varies across species' ranges due to populations' climatic positions, and whether local climatic changes may be leading to interactions between land-use and climate change. I start by reviewing the current understanding of how local climatic changes are affecting biodiversity responses to land use, as well as critically discussing the methods used to explore this topic and identifying key knowledge gaps within the field (Chapter 2). Following this, I use three of the most comprehensive compilations of vertebrate assemblage records to date to analyse (1) whether human-altered land uses are favouring species affiliated with certain climatic regimes, and whether this differs between tropical and temperate latitudes (Chapter 3), (2) whether populations' climatic positions influence their relative abundances across land-use types (Chapter 4), and (3) whether a population's climatic position interacts with land use, habitat loss, and climate change to affect population trends over time (Chapter 5). My three overarching hypotheses are:

(1) At the community-level, human-altered land uses will favour species affiliated with hotter and colder extremes of temperature and drier climates, with stronger effects observed at tropical compared to temperate latitudes (Chapter 3).
(2) At the species-level, a population's climatic position will influence their abundance within human-altered land uses. I hypothesise that populations experiencing temperatures closer to their hot or cold thermal tolerance limits, or precipitation conditions closer to their dry tolerance limit, will be filtered out of human-altered land uses to a greater extent than populations experiencing climatic conditions further from their tolerance limits (Chapter 4).
(3) I hypothesise that a population's climatic position will interact with land-use type, land-use change, and climate change to influence population trends over time (Chapter 5).

Overall, I aim to fill the knowledge gaps highlighted above and make a critical contribution towards enhancing our understanding of how vertebrate species are responding to land-use and climate change. As the human population continues to grow, and our demands lead to continuing land-use change and accelerating global climate change, it is essential that we understand how biodiversity across the globe is impacted by these anthropogenic pressures in order to preserve the variety of life on Earth and the multiple ecosystem services it provides.

Chapter 2:

Local climatic changes affect biodiversity responses to land use: a review

2.1 Abstract

Climate and land-use change, the greatest pressures on biodiversity, can directly influence each other. One key case is the impact land-use change has on local climatic conditions: human-altered areas are often warmer and drier than natural habitats. This can have multiple impacts on biodiversity and is a rapidly developing field of research. Here, I summarise the current state of understanding on the impact that local climatic changes have on biodiversity responses to land-use change, in particular looking at whether human-altered land uses favour species with certain climatic niches. To do so, I review studies that have identified links between species' climatic niches and the habitats/land-use types they inhabit. I also critically discuss the methods used to explore this topic (such as the estimation of fundamental vs. realised climatic niches), identify key knowledge gaps by reference to related macroecological literature, and make suggestions for further work. I find that assemblages of vertebrate and invertebrate species in numerous human-dominated land uses have been found to have higher proportions of individuals affiliated with higher temperatures and lower precipitation levels than assemblages within natural habitats. However, uncertainty surrounds the mechanisms that underlie these observed differences between communities across land-use types, and it remains unexplored as to whether these trends differ geographically or taxonomically. Overall, shifts are being observed within human-altered land uses to communities with, on average, warmer and drier climatic niches. A better understanding of the effects of local climatic changes associated with land-use change will enhance our ability to predict future impacts on biodiversity, identify the species most at risk from interactions between climate and land-use change and set up suitable management and conservation plans.

2.2 Introduction

Rapid human population growth has resulted in increasing exploitation of the environment and conversion of land for human use (Foley et al., 2005; Laurance, Sayer, & Cassman, 2014; Meyer & Turner, 1992). Understanding the impact of these changes on biodiversity has become a widely researched topic (Newbold et al., 2015). However, we are still learning about the extensive effects that land-use change has on the local environment, and the subsequent impacts on biodiversity (De Frenne et al., 2019). A rapidly developing field of research, with studies emerging from around the world, is the impact that land-use change has on local climatic systems, and its knock-on effects for biodiversity (e.g., Frishkoff et al., 2015; Menke et al., 2011; Piano et al., 2017; Senior, Hill, González del Pliego, et al., 2017). Conversion of primary (natural, undisturbed) habitats to human-dominated land uses (such as agriculture and urban areas) causes changes to land cover and vegetation structure, which can directly impact local climatic conditions (Sampaio et al., 2007; Senior, Hill, González del Pliego, et al., 2017). Often, areas of land converted for human use are warmer and drier than natural habitats (Britter & Hanna, 2003; Frishkoff et al., 2016). With the importance of integrating thermal biology into landscape ecology recently being highlighted (Nowakowski, Watling, et al., 2018), and the effects of local precipitation changes also beginning to be acknowledged (Frishkoff et al., 2016), it is crucial that these changes in local climatic systems are incorporated into studies aiming to understand species' responses to land-use change.

The climatic changes caused by land-use change can affect local biodiversity, either directly through changes in temperature, precipitation or moisture levels, or indirectly through changes in vegetation structure or resource availability (Barnagaud, et al., 2013; Frishkoff et al., 2016). As a result, this can lead to alterations in community composition (Frishkoff et al., 2016). The studies that have investigated the impacts on biodiversity caused by these climatic changes so far have primarily focused on exploring differences in species' climatic affiliations between habitats/land uses. With land conversions set to continue (Foley et al., 2005), understanding their influence on local climatic conditions and the subsequent effects on biodiversity is both timely and vital in order to predict future biodiversity changes and set up suitable management and conservation plans (Oliver & Morecroft, 2014; Tomimatsu et al., 2013).

I aim to enhance understanding of how local climatic changes (mediated by land-use change) influence species' responses to land use. In order to do this, I briefly review how land-use change impacts the local climate (along with how this varies spatially), and then present a recap of key terms commonly used when studying the effect of such climatic changes on biodiversity. Following this I arrive at the main focus of this review, where I synthesise patterns and identify disparities between studies, discuss the potential mechanisms underlying these trends and compare the methods currently used to explore this topic. Finally, I highlight knowledge gaps within the current literature and suggest directions for future work (some of which will be explored later in this thesis).

2.2.1 The impact of land-use changes on local climatic conditions

Changes in land use result in modifications to landscape composition (i.e., the total amount of different habitat types), landscape configuration (e.g., habitat fragmentation, which is the subdivision of continuous habitat into smaller plots) and/or in changes to land-use intensity (Andrén, 1994; de Chazal & Rounsevell, 2009; Seppelt et al., 2016). Differences in how intensively humans use the land (i.e., 'land-use intensity'), result from variation in management practices and level of external input (e.g., use of chemicals/fertilisers and extent of labour; de Chazal & Rounsevell, 2009; Seppelt et al., 2016). Taking land used for growing crops as an example, more intensive management practices can include larger fields, monocultures (rather than mixed crops or crop rotation), application of *inorganic* fertiliser, use of irrigation systems, and high (relative) annual plant biomass removal (Hudson et al., 2014; Peters et al., 2019). Conversion of natural to human-dominated land uses (such as cultivated or urban land), and from human-dominated land uses back to forest or grasslands (creating secondary vegetation; de Chazal & Rounsevell, 2009) both result in changes to landscape composition.

The extent and type of vegetation cover significantly affect a site's surface temperature, precipitation level and moisture availability (Frishkoff et al., 2016; Hong, Leach, & Raman, 1995; Jiang et al., 2015; Senior, Hill, González del Pliego, et al., 2017). Removal of vegetation, through deforestation for example, can lead to decreases in evapotranspiration and surface roughness (deviation from a flat surface), and rises in surface sensible heat flux (heat transfer from the surface into the atmosphere), which lead to less water entering the atmosphere (a reduction in moisture feedback), decreases in precipitation, and increases in surface temperatures (Alkama & Cescatti, 2016; Sampaio et al., 2007; Savenije, 1995). Consequently, numerous areas transformed for human use are warmer and drier than primary habitats (Britter & Hanna, 2003; Frishkoff et al., 2016; Senior, Hill, González del Pliego, et al., 2017). Land-use type and precipitation are also linked with variation in moisture level; however, their relationship is complex due to the multitude of factors (such as topography, soil properties, and age or species of vegetation present) that also affect moisture levels (Deng, Yan, Zhang, & Shangguan, 2016; Fu, Wang, Chen, & Qiu, 2003).

Within forests, tree canopies buffer temperature extremes, resulting in cooler maximum and warmer minimum temperatures compared to cleared land, such as pastures (De Frenne et al., 2019; Ewers & Banks-Leite, 2013). Accordingly, increases in maximum (hot extremes) and mean temperatures, and decreases in minimum (cold extremes) temperatures occur post-deforestation (Alkama & Cescatti, 2016; Findell et al., 2017; Medvigy, Walko, & Avissar, 2012). For example, during the day, urban and agricultural areas have been recorded to be around 13°C warmer than nearby vegetated or forested sites, respectively (Oke, 1973; Senior, Hill, González del Pliego, et al., 2017). Fewer studies have focused on night time temperatures, but minimum temperatures been recorded to be slightly colder (by around 1°C) in non-forested (e.g., pastures) or deforested areas compared to below forest canopies (Daily & Ehrlich, 1996; De Frenne et al., 2019). Colder minima occur due to a greater amount of radiation released back to the atmosphere in land uses without a canopy cover (Suggitt et al., 2011).

There is great variation in the magnitude of local climatic changes following land-use change (Senior, Hill, González del Pliego, et al., 2017). Temperature changes following conversion from primary vegetation depend on the extent of vegetation change (i.e., the ultimate land-use type), with croplands and pastures increasing more in local temperatures than tree plantations when compared to intact primary forest (Senior, Hill, González del Pliego, et al., 2017). Surface runoff levels also differ between land-use types, and less moisture recycling and lower rainfall are linked with greater surface runoff (Savenije, 1995). Accordingly, highly urbanised areas show the greatest decrease in surface moisture when compared to forested areas in comparison to cultivated sites (Jiang et al., 2015). Due to the lack of canopy cover in naturally non-forested areas (such as grasslands), which reduces buffering of temperature extremes (Jarzyna, Zuckerberg, Finley, & Porter, 2016; Villegas, Breshears, Zou, & Royer, 2010), conversions from grasslands to human-dominated land-use types may not result in as large local climatic changes compared to conversion from primary forests. Another source of variation is latitude; boreal habitats experience smaller changes in mean air temperature following forest clearing than temperate or tropical regions, probably due to the effects of snow albedo (Alkama & Cescatti, 2016; Findell et al., 2017).

2.2.2 Key terminology

I summarise here a few terms that are key to this subject area (many are also used in related fields). Further on in this review I critically discuss the advantages and limitations of the methods introduced below (table 2.1).

Researchers investigating the effects of climate and its interaction with land-use change on biodiversity often use the term '*climatic niche'* (e.g., Castro-Insua, Gomez-Rodriguez, Svenning, & Baselga, 2018; Dallas, Decker, & Hastings, 2017; Sapes, Serra-Diaz, & Lloret, 2017; Sunday, Bates, & Dulvy, 2012), which aims to reflect the climatic elements of a species' multidimensional niche *sensu* Hutchinson (Hutchinson, 1957; Sapes et al., 2017). Within a species' *fundamental* niche (Hutchinson, 1957), the climatic elements encompass the species' physiological climatic tolerances, which are often estimated through laboratory tests (Frishkoff et al., 2015; Peterson et al., 2011). However, the portions of climatic space that a species actually inhabits, it's *realised* climatic niche, is also influenced by dispersal barriers and biotic interactions (HilleRisLambers, Harsch, Ettinger, Ford, & Theobald, 2013; Peterson et al., 2011).

To produce estimates of species' fundamental climatic niches, studies often approximate thermal tolerances using laboratory experiments and frequently calculate *critical thermal limits* (e.g., Frishkoff et al., 2015; Nowakowski, Watling, et al., 2017). These limits are the upper (*critical thermal maxima*) and lower (*critical thermal minima*) temperatures at which an individual is no longer able to accomplish essential behaviours, movement or righting responses, for example (Nowakowski, Watling, et al., 2017; Tuff, Tuff, & Davies, 2016). These limits are then used to estimate species' *thermal safety margins*, which are the differences between the species' critical thermal maxima or minima and the maximum or minimum body temperatures experienced within an environment, respectively (Nowakowski, Watling, et al., 2017; Sunday et al., 2014). These thermal safety margins, based on species' fundamental climatic niches, are then used to explore vulnerability to climate change and the role of physiology versus behaviour by species to avoid temperature extremes (Sunday et al., 2014).

Species' realised climatic niches can be inferred from their observed spatial distribution (e.g., Barnagaud et al., 2013). Studies focusing on realised niches regularly use species or community temperature indices within their analyses (Barnagaud et al., 2013; Devictor, Julliard, Couvet, & Jiguet, 2008). A *species temperature index* is an approximation of the long-term mean temperature experienced by a species throughout all or part of its range (e.g., its breeding range; Devictor, Julliard, & Jiguet, 2008; Pacifici et al., 2017). Species with higher species temperature indices (warmer-dwelling species) are those that live in areas with, on average, warmer temperatures than species with lower species temperature indices. At the community level, a *community temperature index* is the mean (usually weighted by species abundance) of each species' temperature index in an assemblage (Devictor, Julliard, Couvet, et al., 2008; Jiguet, Brotons, & Devictor, 2011). Consequently, assemblages with higher community temperature indices indicate assemblages composed of greater proportions of individuals of warmer-dwelling species, compared to assemblages with lower community temperature indices (Jiguet et al., 2011).

Finally, *climatic niche breadth* describes the breadth of thermal, precipitation or moisture conditions species can tolerate (fundamental niche) or live within (realised niche; Barnagaud et al., 2012; Frishkoff et al., 2016; Khaliq et al., 2017). Using physiological data, previous studies have used estimates of species' *thermal neutral zones* as approximations of thermal niche breadths in endotherms (e.g., Khaliq et al., 2017). The thermal neutral zone is commonly defined as the set of temperatures at which an endothermic species is able to maintain their body temperature without raising their metabolic rate (Khaliq et al., 2017). When calculating realised climatic niche breadths, different methods have been used in the literature; consequently, care has to be taken when comparing these niche breadth results between studies. For example, estimates of climatic niche breadth have been produced from the standard deviation of a climatic variable (e.g., mean annual temperature) over a species range (Frishkoff et al., 2016), as well as from the difference between the average temperature in the hottest and coldest 5% grid cells in which a species is present (Barnagaud et al., 2012).

2.3 Differences in species- and community-level climatic affiliations between natural and human-altered land uses

2.3.1 Temperature affiliations

Previous research points towards local temperature as an important ecological filter, affecting which species are able to survive within human-dominated land uses (Frishkoff et al., 2015; Piano et al., 2017). Across a range of amphibian, reptile and bird communities, species within human-altered land-use types, such as pastures, have been found to be affiliated with (realised climatic niche), or able to tolerate (fundamental climatic niche), higher temperatures (i.e., higher species temperature index or critical thermal maxima, respectively) than species within forested primary habitats (Barnagaud et al., 2012; Clavero, Villero, & Brotons, 2011; Frishkoff et al., 2015; Nowakowski, Watling, et al., 2017). For ectotherms in particular, low heat tolerances and narrower thermal safety margins (in relation to critical thermal maxima) have been linked with greater sensitivity to land-use change (Nowakowski, Watling, et al., 2018). This pattern is not limited to vertebrate assemblages; within invertebrate communities (such as assemblages of carabid beetles and ants), urbanised and agricultural areas contained, on average, warmer-dwelling species (assemblages had higher community thermal indices) in comparison to primary habitats (Menke et al., 2011; Piano et al., 2017). At the individual level, ants from within urban areas were also found to tolerate high temperature extremes for longer compared to rural-living ants (Angilletta et al., 2007). Changes in community composition with regard to average thermal niche have also been detected across gradients of land-use change: the community temperature index of French bird communities was found to increase (indicating increases in the proportion of individuals of warmer-dwelling species) along a gradient of decreasing forest cover and increasing fragmentation (Barnagaud et al., 2013). This link between warmer-affiliated species and human-altered habitats also leads to interactions between land-use change and elevation: through thermal niche tracking, lowland tropical forest species have been found to be able to colonise agricultural areas at higher elevations, leading to large differences in community composition between natural and human-altered habitats at higher altitudes (Frishkoff, Gabot, et al., 2019). Taken together, these findings suggest that human-altered habitats are favouring species with warmer thermal niches. Accordingly, the ability to predict species' occurrence in human-altered sites from species' realised thermal niches (using species temperature indices) has also been found to perform better than or as well as other frequently used traits to predict occurrence, such as body size (Frishkoff et al., 2015).

Surprisingly, despite the lack of ability of some human-altered land uses to buffer minimum temperatures (Suggitt et al., 2011), the few studies comparing estimates of invertebrate cold tolerances found no differences between assemblages in urban and rural habitats (Angilletta et al., 2007; Piano et al., 2017). As the studies investigating differences in minimum thermal tolerance have focused on urban areas as the human-impacted land-use type, this result may be a consequence of the urban heat island effect (Oke, 1973), which may lead to warmer minimum temperatures compared to other human-dominated land uses. In fact, urban areas are often warmer at night than rural, agricultural areas, because the heat absorbed during the day by streets and buildings is released (Kalnay & Cai, 2003; Runnalls & Oke, 2000). Another reason for not finding differences between assemblages in cold tolerances may be because the relative magnitude of difference in cool temperatures between natural and human-altered land uses is much less than the difference in warm temperatures; indeed, the buffering effect of forest canopies has a larger influence on maximum compared to minimum temperatures (De Frenne et al., 2019; Ewers & Banks-Leite, 2013).

2.3.2 Precipitation and moisture affiliations

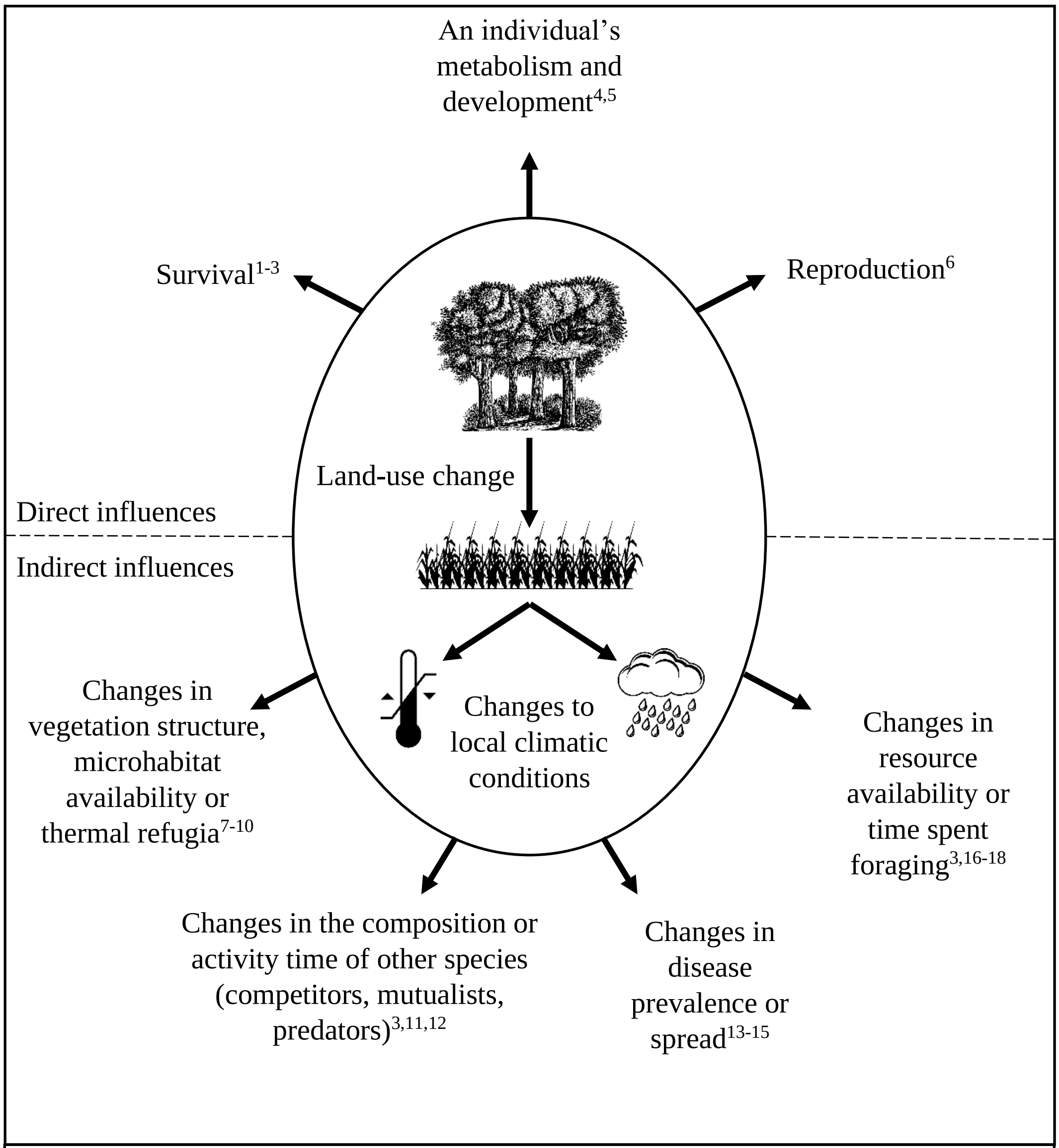
Precipitation niches are also related to association with certain land-use types (Frishkoff et al., 2016). Precipitation (and not temperature) niches were correlated with habitat use in neotropical bird communities; specifically, agricultural land uses were favoured by species associated with drier climates, while those associated with wetter climates favoured forests (Frishkoff et al., 2016). Similarly, invertebrate species usually inhabiting drier climates were found to a greater extent within agricultural and urban assemblages compared with forest assemblages (Menke et al., 2011). These results suggest that human-altered land uses are driving shifts towards communities composed of species that can tolerate drier local climates. However, for some neotropical reptiles and amphibians, realised precipitation niches were not predictive of habitat choices (in this case forested or deforested areas; Frishkoff et al., 2015). This is surprising for amphibians, which are dependent on water availability, and may be because these ectothermic species can find refugia within their tropical habitats (e.g., riparian corridors or remnant trees) and thus persist after changes in local precipitation regimes (Frishkoff et al., 2015). Climate refugia were also found to be important for anole species in pastures, which were areas of low thermal quality where anole body temperatures were often outside preferred thermal ranges (Thompson, Halstead, & Donnelly, 2018). Unfortunately, studies are yet to investigate differences in species' tolerances to moisture availability across land uses, potentially owing to difficulties in acquiring estimates of moisture tolerances (discussed further below) and the complex links between precipitation levels, vegetation cover, soil depth and moisture availability (Deng et al., 2016; Fu et al., 2003).

2.3.3 Climatic niche breadths

Climatic niche breadth also varies between land-use types (Piano et al., 2017). For example, beetle assemblages within more urbanised areas had, on average, wider thermal niches, arising from community-averaged thermal preferences for higher maximum temperatures but similar minimum temperatures, compared to less-urbanised assemblages (Piano et al., 2017). Climatic niche breadth could also be correlated with traits that allow species to be more resilient to environmental change. For instance, thermal and habitat niche breadth were positively correlated for birds within France; in particular, six of the eight species that had the widest thermal niches (classed as climatic generalists) were also those most tightly associated with urban areas (Barnagaud et al., 2012).

2.4 Potential underlying mechanisms

The mechanisms underlying these associations between species' thermal or precipitation affiliations and land-use type are not well known. However, by reference to literature exploring biodiversity responses to global climate change, I can identify several potential ways in which local climatic changes could affect community composition (fig. 2.1).



[1]Mitchell et al., 2018; [2]Deutsch et al., 2008; [3]Porter et al., 2000; [4]Merckx et al., 2018; [5]Russell et al., 2002; [6]Manning & Bronson, 1990; [7]Hannah et al., 2014; [8]Kearney et al., 2009; [9]Karp et al., 2017; [10]Betts et al., 2018; [11]Post et al., 1999; [12]Schweiger et al., 2012; [13]Pounds et al., 2006; [14]Harvell et al., 2002; [15]Becker & Zamudio, 2011; [16]Bolger et al., 2005; [17]Ockendon et al., 2014; [18]Sinervo et al., 2010

Figure 2.1: Direct and indirect influences of local climatic changes. Examples of the impacts local climatic changes mediated by land-use change (for instance, the conversion of a natural habitat to human-dominated land use) may have on biodiversity, which could have knock-on effects for local community composition and/or biotic interactions. The impacts are split into direct influences (where changes in temperature, precipitation or moisture availability affect individuals) and indirect

influences (where the climatic changes affect another aspect of an individual's environment, including interacting species, which in turn influences the individual). Local climatic changes include changes to temperature, precipitation, and/or moisture availability. Many of these potential impacts of local climatic changes originate from studies focused on the consequences of global climate change.

2.4.1 Direct influences of local climatic changes

Climatic changes can impact individuals directly, with unfavourable body temperatures reducing fitness, compromising body functions or causing death (Frishkoff et al., 2016; Lovegrove et al., 2014; Mitchell et al., 2018; Porter, Budaraju, Stewart, & Ramankutty, 2000; Welbergen, Klose, Markus, & Eby, 2008). For example, temperature changes can hinder development and reproduction, with colder temperatures leading to greater overnight weight loss in meerkat pups (Russell et al., 2002), and suppressed ovulation in female mice (Manning & Bronson, 1990). Climatic changes can be especially problematic for sessile species and ectothermic species, whose movement, reproduction, and development are strongly influenced by ambient local temperatures and humidity (Cahill et al., 2012; Deutsch et al., 2008; Walther et al., 2002). For instance, higher temperatures, which lead to increased metabolic costs, are generally expected to drive shifts towards smaller body sizes in ectotherms (Merckx et al., 2018; Sheridan & Bickford, 2011). Conversely, some species may benefit from warmer temperatures; for some ectothermic species, slight warming may actually increase the length of time that they can spend at optimal core temperatures, which would increase the length of time available for activities such as foraging and reproduction (Kearney et al., 2009). The direct responses of individuals to climatic changes may lead to changes in the local abundance of certain species, subsequently causing shifts in community composition (Oliver et al., 2017; Porter et al., 2000).

Changes in precipitation and temperature may also have interactive direct effects on individuals. For example, for species within currently arid or semi-arid habitats, further drying may lead to less available drinking water, which can compromise thermoregulation abilities and increase the risks from heat stress (Mitchell et al., 2018). Thus, differences in community composition may result from declines in species that are unable to tolerate the higher temperatures or lower precipitation levels in human-dominated lands, and increases in species that benefit from the climatic changes.

2.4.2 Indirect influences of local climatic changes

Local climatic changes may also influence which species can inhabit an area indirectly (fig. 2.1; Frishkoff et al., 2016). In human-altered land uses, the vegetation structure may be analogous to natural vegetation in drier and hotter regions, thus favouring species from more arid habitats through bottom-up regulation (Frishkoff et al., 2016; Karp et al., 2017). These sites may also be lower quality habitats with fewer thermal refugia, consequently compromising individuals' abilities to cope with local climatic changes (Betts, Phalan, Frey, Rousseau, & Yang, 2018; Senior, Hill, González del Pliego, et al., 2017). Further, changes in climate may affect food availability (its absolute quantity or seasonal availability), foraging costs, or willingness of individuals to forage (Levy, Dayan, Porter, & Kronfeld-Schor, 2016; Porter et al., 2000), which in turn can affect individuals' survivorship or reproductive output. For instance, reproductive failure in birds during extreme dry conditions has been attributed to lack of available food (Bolger, Patten, & Bostock, 2005). As well as prey, climatic changes could indirectly impact species through influences on the demographics of other species within the community, such as mutualists, hosts or competitors (Oliver & Morecroft, 2014; Post, Peterson, Stenseth, & Mclaren, 1999; Walther et al., 2002). For instance, if host species decline due to the site's climate no longer being suitable, then species dependent on those hosts may also decline; such mismatches are predicted to occur between host-plant-limited butterfly species under future global climate and land-use change (Schweiger et al., 2012). Again, these impacts can affect each species' abundance within a community, subsequently changing community structure (Porter et al., 2000).

Changes in disease prevalence due to local climatic changes in human-altered land uses may also impact community composition (Pounds et al., 2006). In mammals, a higher prevalence of fungal diseases is hypothesised to occur due to increasing global temperatures (Garcia-Solache & Casadevall, 2010). Conversely, for tropical assemblages of amphibians, changes in local climate following habitat loss has been suggested to be one mechanism underlying the lower occurrence and prevalence of the chytrid fungus in human-altered compared to natural habitats (Becker & Zamudio, 2011). Subsequently, this will affect the composition of amphibian communities in these altered land uses. It is likely that similar local-scale changes in temperature, precipitation or moisture availability, as a result of land-use change, may also impact the prevalence of other diseases through pathogen growth or survival (Harvell et al., 2002).

After covering several ways biodiversity may be impacted by local climatic changes following land-use change, it is also important to acknowledge that some differences in species' climatic tolerances/affiliations across land uses may not be solely linked to climatic change, but instead (at least to some extent) result from habitat associations (Barnagaud et al., 2012). The past and present location, and thus climatic distribution, of species' preferred habitats may in part determine their realised climatic niches (Barnagaud et al., 2013, 2012). Species' thermal niche breadths have also been found to be positively correlated with their habitat niche breadth, whereby bird species classed as habitat specialists were also those who experienced less temperature variation across their range (Barnagaud et al., 2012). Consequently, the decline of species with narrow and cool-adapted climatic niches within human-dominated land uses may be due to the negative influence of land-use changes on habitat specialists (Devictor, Julliard, & Jiguet, 2008), rather than directly a result of local climatic changes. The difficulty in separating and identifying underlying mechanisms lies partly in the methods used to establish these patterns (see below; Oliver et al., 2017), and the lack of longitudinal data focusing on changes in community composition following land-use change (leading to a reliance on space-for-time studies).

2.5 Common methods – advantages and limitations

The above studies exploring differences in species' climatic affiliations across land-use types analysed either fundamental or realised climatic tolerance estimates, which both have their advantages and limitations (table 2.1). Physiological temperature tests, which are used to provide estimates of species' fundamental thermal niches, allow researchers to calculate thermal tolerances under controlled conditions (Frishkoff et al., 2015; Nowakowski, Watling, et al., 2017). However, there are several potential problems, which can lead to uncertainty regarding how closely the estimated tolerance limits correspond to a species' fundamental niche. First, the measurement protocols used to calculate thermal tolerances often differ between studies, rendering the metrics produced incomparable (Araújo et al., 2013). For example, the rate of temperature increase or decrease within experiments can influence species' thermal tolerances and survival rates, and hence the estimates of fundamental niche generated (Addo-Bediako, Chown, & Gaston, 2000; Hoffmann, Chown, & Clusella-Trullas, 2013). The measure of performance analysed during the temperature changes (e.g., movement or oxygen consumption) also affects the thermal tolerance measures produced (Nowakowski, Frishkoff, Agha, et al., 2018). Additionally, using temperature limits to describe thermal tolerances has been criticised due to survival probability depending on the duration of exposure *and* the intensity of stress (Rezende, Castañeda, & Santos, 2014). Consequently, some researchers suggest using thermal tolerance landscapes instead, which plot the probability of survival as a function of both the duration of exposure and intensity of thermal stress, thus incorporating both aspects influencing thermal tolerance ranges (Rezende et al., 2014). Second, critical temperatures are dependent on other factors that may not be taken into account during experiments, such as water supply (Araújo et al., 2013; Mitchell et al., 2018). Third, calculating thermal tolerances is only possible/desirable for a small number of species, with experiments being time-consuming and expensive (Araújo et al., 2013; Rezende et al., 2014). These tests are far from ideal for threatened species, or species with strict habitat requirements (Hoffmann et al., 2013). Fourth, although widely used to calculate thermal tolerances (e.g., Frishkoff et al., 2015; Nowakowski, Watling, et al., 2017), using physiological tests to quantify precipitation or moisture tolerances is rare (Sunday et al., 2012). Finally, using a species' thermal neutral zone as an estimate of thermal niche breadth has also be criticised because animals are able to survive outside of this zone and, as such, using this measure may overestimate risk from temperature changes (Mitchell et al., 2018).

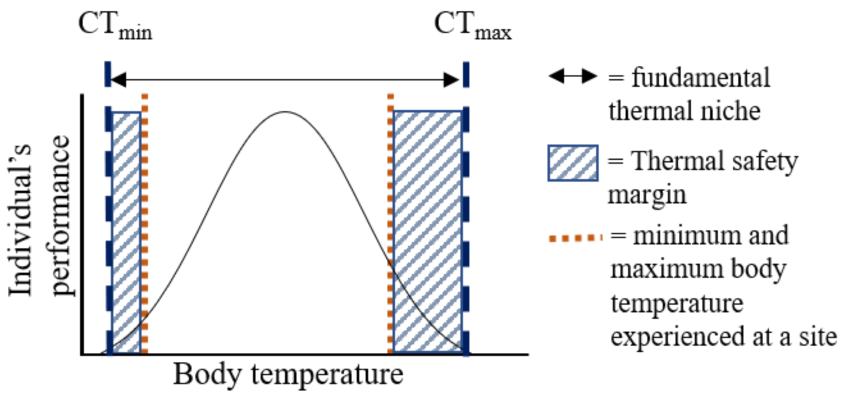
To estimate realised climatic niches, climatic tolerances are extracted by overlaying climate databases, such as WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), on species' distribution maps (Barnagaud et al., 2012; Menke et al., 2011), a method that has a set of advantages and limitations. The first advantage is that this method is often the only feasible way to estimate climatic niches for the majority of species (Oliver et al., 2017). This method can also be readily used to produce estimates of precipitation niches (e.g., Frishkoff et al., 2016). However, extracting realised tolerances has several limitations. First, due to the observed conservatism of upper thermal limits across lineages, extracting heat tolerances from distribution maps may underestimate values for species inhabiting higher latitudes or elevations (Araújo et al., 2013). Second, species' realised niches may be constrained by dispersal limitations, biotic interactions such as competition or mutualism, and/or the distribution of resources (Araújo et al., 2013; HilleRisLambers et al., 2013; Peterson et al., 2011), meaning that realised tolerances may not accurately reflect species' actual climatic tolerances (Araújo et al., 2013). Although, some studies have developed methods to remove the issue of dispersal when calculating realised niches, for example by focusing on species' responses along regional climatic and land-use gradients (where other variables, such as elevation and temperature, are held constant), then using correlative approaches or differences in species abundances to calculate climatic affinities or niche centres and breadths (Frishkoff & Karp, 2019; Karp et al., 2017). Another biological trait that needs accounting for is migration; species may use migration to avoid severe physical conditions in certain areas (Robinson et al., 2009), so using their entire distribution may provide inaccurate climatic tolerance estimates. Besides these ecological issues, the distribution maps used may have inaccuracies. For example, maps drawn up following the precautionary principle have a tendency to underestimate species' geographical ranges (e.g., maps produced by the International Union for Conservation of Nature; Herkt, Skidmore, & Fahr, 2017), exacerbated because some biodiversity occurrence data sources lack records for large expanses of land (e.g., the Global Biodiversity Information Facility; Meyer, Kreft, Guralnick, & Jetz, 2015). Yet again, expert-drawn range maps can also overestimate species ranges if they include unoccupied/unsuitable areas between locations where a species exists (Graham & Hijmans, 2006). These limitations may impact the reliability of the climatic tolerances extracted.

Community temperature indices provide a simple index and are a common and powerful method to study changes in average realised climatic niche across or within communities (Bowler & Böhning-Gaese, 2017; Frishkoff et al., 2016; Oliver et al., 2017), but they too have a set of limitations. This practical index allows researchers to study these changes in the absence of standardised surveys of species occurrence, abundance or population sizes across land-use types and spanning climatic gradients (which are rare). However, a drawback of the community temperature index is that, because it is a community-level index, the mechanisms underlying differences in this metric cannot be identified and it can disguise qualitatively different trends between taxa (Barnagaud et al., 2013; Oliver et al., 2017). Further, species' identities and occurrence are not accounted for when calculating community temperature indices, which may result in the presence or absence of an outlier species (which may/may not occur for reasons unrelated to the focal environmental factor) unduly influencing community temperature index results (Bowler & Böhning-Gaese, 2017). Considering which climate variables are used to produce community temperature indices is also important; for example, the choice between using mean or extreme temperatures within a species' range will depend on which is more biologically relevant to the study taxon and question (Parmesan, Root, & Willig, 2000; Sunday et al., 2014). This could cause issues when producing community temperature indices for assemblages, which are composed of a variety of species. Similarly, the spatial scale at which temperature is measured (i.e., landscape vs. microhabitat), and at which the focal taxon perceives the environment also need to be considered (Nowakowski, Frishkoff, Agha, et al., 2018). Even though there are limitations to these methods of estimating climatic tolerances, they have been used extensively when studying responses to local and global climatic changes, and are able to capture differences in species- and community-level climatic niches across land-use types and over time (Frishkoff et al., 2015; Oliver et al., 2017).

Table 2.1: A summary of the key terms. A summary of the key terms and metrics used in this review, the data sources underlying them, and the main advantages and limitations of the metrics calculated. Superscripts refer to the references at the bottom of the table.

Key term	Metrics calculated	Data sources	Main advantages	Main limitations
Fundamental climatic niche	Critical thermal limits - Critical thermal maxima (CT_{max}) - Critical thermal minima (CT_{min}) (these limits are used to calculate thermal safety margins)	Physiological tests in the laboratory	• Calculated under controlled conditions	• Metrics produced are often incomparable across studies due to different measurement protocols[1] • Critical thermal limits are dependent on other factors as well as temperature (e.g., exposure duration, water supply), which may not be taken into account[1,2] • Laboratory tests are only possible for a small number of species[1,2] • Rarely used to calculate precipitation or moisture tolerance limits[3]

Example illustration



Realised climatic niche	Species temperature indices (which are used to calculate community temperature indices)	Overlaying climatic variables on species' spatial distributions (range maps or occurrence data)	• Can be calculated for the majority of species[4] • Can be easily used to produce estimates of precipitation niches[5] • The indices produced are relatively easy to understand[4]	• Estimates of climatic limits may be inaccurate due to influence of dispersal barriers, biotic interactions, and resource distribution on species' distributions[1,6,7] • May underestimate the upper thermal tolerance limits of species found at high latitudes and/or elevations[1] • Relies on accurate species' distribution maps, which are not available for many species[8]. • The mechanisms underlying differences or changes in these metrics can be difficult to identify[4] • The scale of the climatic data used may influence results[9]
Climatic niche breadth (fundamental)	Thermal neutral zone	Physiological tests in the laboratory	• Calculated under controlled conditions	• Can lead to overestimates of the risk posed by climatic changes[10] • Laboratory tests are only possible for a small number of species[1,2]
Climatic niche breadth (realised)	Standard deviation of a climatic variable across a species' distribution[5] OR The difference between the hottest and coldest grid cells in a species' distribution[11]	Overlaying climatic variables onto a species' spatial distribution or from climatic measurements taken throughout a species' range	• Relatively easy to produce for a wide range of species	• Metrics produced are often incomparable across studies due to different proxies for climatic niche breadth used • Species' distribution maps may contain inaccuracies[8] • The scale of the climatic data used may influence results[9]

[1]Araújo et al., 2013; [2]Rezende et al., 2014; [3]Sunday et al., 2012; [4]Oliver et al., 2017; [5]Frishkoff et al., 2016; [6]HilleRisLambers et al., 2013; [7]Peterson et al., 2011; [8]Herkt et al., 2017; [9]Nowakowski, Frishkoff, Agha, et al., 2018; [10]Mitchell et al., 2018; [11]Barnagaud et al., 2012

2.6 Gaps within the literature

Studying how local climatic changes mediated by land-use change affect local communities is a developing research area. By drawing on principles from related macroecological literature, in particular that on global climate change and factors influencing species’ distributions, I highlight below four important knowledge gaps, presenting testable hypotheses where possible (table 2.2). Identifying the mechanisms underlying differences in species’ climatic niches between land uses is one of the greatest areas of uncertainty and warrants more exploration, but as I have already covered this above, it is not included in this section.

Table 2.2: Key knowledge gaps. The key knowledge gaps in our understanding of how the local climatic changes resulting from land-use change impact communities, along with the conceptual underpinnings for each gap and my hypotheses arising from these. Identifying the mechanisms underlying the responses of animals to local climatic changes is also an area of great uncertainty, but this is not mentioned below because potential impacts/mechanisms are highlighted in figure 2.1. Superscripts refer to the references at the bottom of the table.

Gap in the literature	**Conceptual underpinning**	**Hypotheses**
Geographic variation	*Tropical vs. temperate regions* • The factors influencing species' distribution limits are suggested to differ between tropical and temperate latitudes[1,2] • Tropical species are suggested to be more sensitive to temperature changes and live closer to maximum temperature tolerance limits than temperate species[3-5] • Temperature differences are greater between open and closed-canopy areas in tropical compared to temperate regions[6,7]	Increases in temperature due to land-use change from natural to human-altered sites will have greater negative impacts on tropical than temperate species
	Differences between land uses • The magnitude of change in local climate resulting from land-use change depends on both the starting natural vegetation (e.g., forest vs. grassland) and the final land-use type (e.g., pasture, cropland, or urban site)[8,9]	There will be greater community-level shifts towards species with warmer and drier climatic niches following land-use changes that result in greater local climatic changes (e.g., forested natural habitat to cropland)
Taxonomic and trait-based variation	*Endotherms vs. ectotherms* • Endotherms can thermoregulate through metabolic control, whereas ectotherms principally rely on behavioural thermoregulation[7,10] • Temperature and precipitation change directly affect the development, movement, reproduction and biotic interactions of ectotherms[3,11] • Ectotherms frequently operate when their body temperatures are close to their maximum temperature tolerance limits[12]	Temperature and precipitation changes following land-use change from natural to human-altered land uses will have greater impacts on ectothermic than endothermic species

	Other trait-based variation • Traits such as daily activity pattern (e.g., diurnal/nocturnal/crepuscular) and reproductive strategy (e.g., viviparous vs. oviparous species) have been linked to temperature tolerances and may also be linked to precipitation tolerances[13]	Species with traits associated with higher temperature and/or lower precipitation tolerance limits will be less negatively impacted by the local climatic changes ensuing change from natural to human-altered land uses
Focal climatic variables	• Studying differences across land uses in species' precipitation or moisture niches is rare (but see [14]) • The ability of individuals to cope with thermal stress is dependent on water availability[12,13,15] • It is rare for studies to compare species' cold tolerances across different land-use types (but see [16,17]) • Human-altered land uses are often drier and (apart from urban areas) experience colder minimum temperatures compared to natural vegetation[14,18,19]	Communities within human-altered sites will, on average, consist of species tolerant of drier climates and (apart from urban areas) colder minimum temperatures
Proximity to climatic tolerance limits	• The importance of the proximity of populations to their climatic tolerance limits with regard to the potential risk posed by global climate change has been highlighted[3] • Climatic changes are suggested to have greater impacts on populations with narrower safety margins[3,7,20] • This has rarely been considered in the context of land-use change	Populations living in environments where they experience temperature or precipitation conditions that are closer to their maximum thermal or minimum precipitation tolerance limits, respectively, will be more negatively impacted by land-use changes from natural to human-altered land uses
Interaction with global climate change	• Land-use change is occurring alongside global climate change[21] • Global climate change is resulting in, or predicted to generate, hotter temperatures, more extreme heatwaves and greater differences between wet and dry seasons in precipitation[22] • How drivers of change such as global climate change and land-use change will interact poses great uncertainties[23]	Local climatic changes ensuing land-use change has the potential to interact synergistically with global climate change; for example, with both pressures leading to increased temperatures, I predict that ambient temperatures will be pushed above critical thermal limits for a larger number of species than if the two pressures were acting independently

[1]Khaliq et al., 2017; [2]MacArthur 1972; [3]Deutsch et al., 2008; [4]Janzen 1967; [5]Freeman & Freeman, 2014; [6]Kearney et al., 2014; [7]Nowakowski, Frishkoff, Agha, et al., 2018; [8]Senior, Hill, González del Pliego, et al., 2017; [9]Jarzyna et al., 2016; [10]Sunday et al., 2014; [11]Walther et al., 2002; [12]Kearney et al., 2009; [13]Clusella-Trullas et al., 2011; [14]Friskoff et al., 2016; [15]Khaliq et al., 2014; [16]Angilletta et al., 2007; [17]Piano et al., 2017; [18]De Frenne et al., 2019; [19]Kalnay & Cai, 2003; [20]Nowakowski, Watling, et al., 2017; [21]IPCC, 2019; [22]Collins et al., 2013; [23]Oliver & Morecroft, 2014

2.6.1 Geographic variation

The influence of local climatic changes following land-use change may differ in strength across space, such as between tropical and temperate latitudes, but this is yet to be explored. I hypothesise such latitudinal variation will occur owing to the fact that the factors impacting species' range limits are thought to differ geographically (Khaliq et al., 2017; MacArthur 1972). In temperate latitudes, abiotic factors (e.g., climate) are thought to be the primary influence on distribution limits, whereas in the tropics, biotic factors (interactions with other species) are suggested to prevail (Khaliq et al., 2017; MacArthur 1972; Wiens & Donoghue, 2004). For instance, for birds and mammals, minimum temperature tolerances appear to limit distributions across temperate latitudes while, in the tropics, climatic conditions do not have the same influence (Khaliq et al., 2017). On the other hand, due to the current and historic stability of the tropical climate, species within this region are suggested to have a higher sensitivity to temperature changes (Bonebrake & Deutsch, 2012; Cadena et al., 2012; Deutsch et al., 2008; Janzen, 1967). For instance, tropical species are living closer to their maximum thermal physiological tolerances, with small increases in temperature thought to push these species closer to their upper thermal tolerance limit proportionally faster than in temperate realms (Deutsch et al., 2008). Elevational shifts in tropical montane bird species have also been observed to more closely match increases in temperatures compared to those of temperate montane species, supporting suggestions that tropical species have a higher sensitivity to warming temperatures (Freeman & Freeman, 2014). Conversely, for temperate ectotherms, moderate temperature increases following land-use change may be advantageous, increasing the time they can spend within their optimal temperature limits (Kearney et al., 2009). Temperatures also tend to differ more between closed-canopy and open areas at tropical compared to temperate latitudes (although there is seasonal variation; Kearney, Isaac, & Porter, 2014; Nowakowski, Frishkoff, Agha, et al., 2018). Consequently, due to the higher sensitivity to climatic changes in the tropics, I hypothesise that increases in temperatures due to land-use change from natural to human-dominated sites will lead to greater negative impacts on species at tropical compared to temperate latitudes (investigated in Chapters 3 and 4).

The magnitude of local climatic change differs depending on both the starting primary vegetation (e.g., forest vs. grassland) and ultimate land-use type (Jarzyna et al., 2016; Senior, Hill, González del Pliego, et al., 2017). Consequently, grouping together human-altered land uses or only studying a few land uses (such as the focus on natural and urban habitats when comparing cold tolerances) may lead to important differences being missed. There is also currently little research comparing climatic affiliations between communities in non-forested primary habitats and human-dominated land uses (but see Piano et al., 2017). I hypothesise that there will be greater community-level shifts towards species with warmer and drier climatic niches where there are larger changes to local climatic conditions following land-use change from natural habitats (explored in Chapters 3-5). For example, I hypothesise there will be greater shifts following deforestation to create cropland in comparison to conversion of grasslands to pastures. Overall, past research points to several mechanisms by which the impact of local climatic changes ensuing land-use change could affect species differently depending on geographic location. It is vital that these differences are understood in order to produce suitable, spatially explicit conservation and management plans and identify species at risk from land-use change within different regions.

2.6.2 Taxonomic and trait-based variation

Species are affected differently by climatic changes (e.g., Oliver et al., 2017; Warren et al., 2013), which may lead to species-specific differences in the impact of land-use change. Endothermic and ectothermic species, for example, are influenced differently by changes in ambient climatic conditions (Jezkova & Wiens, 2016; Rolland et al., 2018), thus their responses to these changes following land-use change also likely differ. Ectotherms are thought to be more sensitive to climatic changes, a result of the direct effect that shifts in temperature and precipitation have on their development, movement, biotic interactions, and reproduction (Deutsch et al., 2008; Walther et al., 2002). Ectotherms have also been found frequently to operate at body temperatures near their maximum temperature tolerance limits (Kearney et al., 2009). Further, the removal of natural habitat, which can provide thermal refugia, may also impact these species differently. For example, ectotherms predominantly rely on behavioural thermoregulation and the presence of microhabitats that can act as thermal refugia, whereas endotherms can thermoregulate through metabolic control (Nowakowski, Frishkoff, Agha, et al., 2018; Sunday et al., 2014). Thus, I hypothesise that changes in temperature and precipitation following natural to human-dominated land-use changes will have greater impacts on ectothermic than endothermic species (explored in Chapter 3).

Even within endotherms and ectotherms, the strategies used for coping with environmental changes may vary (Khaliq et al., 2017; Khaliq, Hof, Prinzinger, Böhning-Gaese, & Pfenninger, 2014). For instance, to cope with stressful thermal conditions, birds are suggested to use physiological adaptations as their main strategy whereas, in mammals, behavioural strategies are more common (Khaliq et al., 2014). Further, the differences in structure of porous insulation (fur or feathers) between and within mammals and birds will also affect their methods of coping with climatic change (Porter et al., 2000). For example, feathers allow birds to seal off air flow from their skin, a quality that is rarely found in fur (Porter et al., 2000), and may consequently impact how animals respond to cold stress. Moreover, wet- and dry-skinned vertebrate ectotherms may differ in strategies to avoid extreme high temperatures, due to the use of evaporative cooling by wet-skinned amphibians that can offset heat gain via solar radiation (though this is likely dependent on moisture availability; Sunday et al., 2014). Insects also are suggested to differ again in their use of behaviour to prevent overheating (Sunday et al., 2014). Consequently, taxonomic groups likely respond differently to local climatic changes following land-use change, but studies rarely explore how differences in species' climatic niches across land-use types vary between taxa. Importantly, to my knowledge, no studies have yet looked at how the *climatic* niches of mammal communities differ across land uses. Further to this, these differences in how species cope with climatic changes may also lead to taxonomic differences in the predominant mechanisms underlying the impact of local changes in climate. For instance, the loss of thermal refugia may have larger impacts on taxa that are not as mobile and rely heavily on refugia to avoid thermal stress. These research areas are in need of attention.

Species' traits such as daily activity pattern, body mass and reproductive strategy may also influence the impact of local climatic changes. Species active during the day are more likely to be exposed to stress-inducing high temperatures compared to nocturnal species, who instead may face extremes of cold (Kearney & Porter, 2004;

Kearney et al., 2009; Navas, 1997). This is reflected in their heat tolerances and preferred body temperatures, which are generally higher in diurnal than nocturnal species (see Clusella-Trullas, Blackburn, & Chown, 2011). Further, if local climatic conditions are more similar between natural and human-altered sites at night than day, nocturnal species may be more likely able to survive within human-altered sites compared to diurnal taxa (Daily & Ehrlich, 1996). Body mass, which has both direct and indirect associations with physiological processes (Gates 1980; Gillooly, Brown, West, Savage, & Charnov, 2001), is also related to preferred body temperature, although this relationship may vary with precipitation (Clusella-Trullas et al., 2011). In terms of reproductive strategy, oviparous squamate species have been found to be able to tolerate higher temperatures, on average, than viviparous species (Clusella-Trullas et al., 2011). Therefore, these traits likely influence how species react to temperature and precipitation changes, and thus to climatic alterations after land conversion. I hypothesise that species with traits associated with the ability to tolerate higher temperatures and/or lower precipitation will be less negatively affected by the local climatic changes ensuing land-use change from natural to human-dominated sites.

2.6.3 Focal climatic variables and proximity to climatic tolerances

When comparing climatic niches across land uses, there has been a tendency to focus on temperature, in particular mean and maximum temperatures (e.g., Barnagaud et al., 2012; Clavero et al., 2011; Piano et al., 2017), with other climatic variables often neglected. However, precipitation niches are important on their own (Frishkoff et al., 2016) and, in addition, water availability affects the ability of endotherms and ectotherms to cope with thermal stress (Clusella-Trullas et al., 2011; Kearney et al., 2009; Khaliq et al., 2014). For example, amphibians' thermal safety margins are contingent on their hydration status (Sunday et al., 2014). Similarly, studies rarely consider moisture availability (but see Frishkoff et al., 2015), or species' tolerances to this when studying community composition across land-use types. Local moisture availability and precipitation are linked (Savenije, 1995), and certain species are dependent on moisture availability (Frishkoff et al., 2015). So, due to human-dominated land uses generally being hotter *and* drier than natural habitats (Frishkoff et al., 2016), if interactions are occurring between thermal and desiccation stress, there may be greater effects on biodiversity after land conversion than expected just from temperature changes (Clusella-Trullas et al., 2011). Consequently, there should be a greater focus on precipitation and moisture availability alongside temperature. Furthermore, due to land-cover type also influencing minimum temperatures (Suggitt et al., 2011), and species' cold tolerances being closely related to the poleward limits of their distributions at temperate latitudes (Khaliq et al., 2017), changes in minimum temperatures (e.g., winter or night-time temperatures) could have a marked influence on species, but relatively little work has explored this possibility (but see Latimer & Zuckerberg, 2017; Piano et al., 2017). Without canopies to buffer minimum temperatures (De Frenne et al., 2019), I hypothesise that, in comparison to natural forested habitats, communities within human-altered land uses will, on average, be able to tolerate lower minimum temperatures (with the exception of urban areas, due to the urban heat island effect; investigated in Chapter 3).

Another potentially important source of variation in responses to land-use change is a population's proximity to their climatic tolerance limits, a variable highlighted in the global climate warming literature (Deutsch et al., 2008; Soroye et al., 2020). For example, slight local warming or cooling may have greater impacts on the performance of populations that already experience temperatures closer to their hot or cold thermal limits (as they will have narrower thermal safety margins) compared to those populations with larger safety margins (Deutsch et al., 2008; Nowakowski, Frishkoff, Agha, et al., 2018). Very few studies have explored this in the context of land-use change (but see Nowakowski, Watling, et al., 2018). I hypothesise that those populations in environments with ambient climatic conditions closer to their maximum thermal or minimum precipitation tolerance limits will be more negatively impacted following natural to human-dominated land-use changes, because of the shift towards hotter and drier local conditions following this land-use conversion (investigated in Chapters 4 and 5). Identifying whether these potential sources of variation lead to differences in responses to land-use change will also help identify the mechanisms underlying observed trends.

Intraspecific variation in responses to land-use change across a species' distribution could also result from the impacts of local climatic changes differing between tropical and temperate latitudes, particularly for species with large latitudinal range sizes. Calculating realised climatic niches at the species-level using distribution maps may lead to these intraspecific differences being overlooked. This again highlights the importance of looking at differences between populations in their responses to land-use change.

2.6.4 Interaction with global climate change and future projections

Local climatic changes mediated by land-use change are occurring alongside global climate change (Sala et al., 2000), potentially leading to interactions (likely synergistic, investigated in Chapter 5; Frishkoff et al., 2015; Guo, Lenoir, & Bonebrake, 2018; Kearney et al., 2009). Global climate change is resulting in hotter mean temperatures and more extreme hot events (Collins et al., 2013), so rises in local temperatures due to land-use change will further increase the temperatures to which organisms are exposed (Frishkoff et al., 2016). This may push ambient temperatures above critical thermal limits for a greater number of species than if global climate change was acting independently. Further, species' responses to multiple stressors may be correlated (Vinebrooke et al., 2004). Early theories looking at the impacts of correlated sensitivities to multiple stressors assumed that species were only either adversely impacted, or unimpacted (i.e., never benefited) from environmental pressures (Vinebrooke et al., 2004). These theories predicted that if species' sensitivities to the stressors were negatively correlated, biodiversity would be severely reduced, but positive correlations would lead to smaller overall impacts on community biodiversity (Vinebrooke et al., 2004). However, more recent work has taken into account that species can benefit from environmental change and that the effects of pressures can combine (Frishkoff, Echeverri, Chan, & Karp, 2018). This work has shown that when pressures act simultaneously the outcome for biodiversity is much more complex; for example, positive correlations between sensitivities can lead to either greater *or* fewer numbers of species lost compared to if the stressors acted independently (Frishkoff et al., 2018). Nonetheless, if climate and land-use change favour the same species, such as those that can tolerate higher temperatures or lower precipitation levels, this may lead to biotic homogenisation, which could have detrimental effects for ecosystem functioning (García, Bestion, Warfield, & Yvon-Durocher, 2018; Karp et al., 2017; Mori, Isbell, & Seidl, 2018). Previous work has also indicated that human land conversion can lead to phylogenetic homogenisation, by favouring clades that are more tolerant to land-use change (Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018), which could also be exacerbated by global climate changes. The uncertainty surrounding how community biodiversity will be affected when environmental pressures act simultaneously further highlights the need to understand the mechanisms underlying how these pressures affect different species.

Finally, a crucial area yet to be investigated is the *future* impact of land-use change, its effect on local climatic conditions and the interaction with global climate change. Some papers have made predictions regarding the impact of land-use and climate change on biodiversity (Mantyka-Pringle et al., 2015; Newbold, 2018; Segan, Murray, & Watson, 2016), but haven't accounted for local climatic changes resulting from habitat disturbances. Unfortunately, current predictions of species vulnerability are likely unreliable, due to the limitations in current methods (Sunday et al., 2014), the lack of understanding of the mechanisms underlying differences in climatic niches across land uses (Barnagaud et al., 2013) and the likely geographic and taxonomic variation. Furthermore, disentangling the effects of global climatic changes, local climate changes due to land-use change and the other effects of land-use change can be challenging (Oliver & Morecroft, 2014), which adds extra complications when trying to understand responses. However, with ongoing exploration into these topics, being able to predict how these drivers of change will impact biodiversity will form an essential part of conservation planning.

2.7 Conclusions

Local climatic conditions are affected by land use, with human-dominated land uses often found to have hotter and drier local climates compared to areas of primary vegetation (Britter & Hanna, 2003; Frishkoff et al., 2016). Reflecting this, studies from around the globe have demonstrated that communities of vertebrates and invertebrates within human-dominated land uses are composed of warmer- and drier-dwelling species in comparison to communities within natural, undisturbed habitats (Frishkoff et al., 2015, 2016; Menke et al., 2011). However, further work is needed to understand the mechanisms underlying these community differences, such as the relative strength of direct versus indirect influences of temperature and precipitation changes. As well as the underlying mechanisms being a major gap in our current knowledge, I also highlighted other key areas in need of attention, several of which I investigate later in this thesis, such as how trends may differ geographically and between populations. Additionally, species within human-altered land uses are facing other pressures, such as global climate change, which may lead to complex synergistic interactions and is another area requiring further research (Collins et al., 2013; Frishkoff et al., 2016; Sala et al., 2000). Overall, this is a rapidly developing field with exciting research being carried out that will help us to identify which species or populations may be at risk from land-use change, ways to minimise these negative impacts, and thus aid future conservation planning.

Chapter 3:

Human-dominated land uses favour species affiliated with more extreme climates, especially in the tropics

3.1 Abstract

Rapid human population growth has driven conversion of land for uses such as agriculture, transportation, and buildings. The removal of natural vegetation changes local climate, with human-dominated land uses often warmer and drier than natural habitats. Yet, it remains an open question whether land-use changes influence the composition of ecological assemblages in a direction consistent with the mechanism of local climatic change. Here, I used a global database of terrestrial vertebrates (mammals, birds, reptiles, and amphibians) to test whether human-dominated land uses systematically favour species with distinctive realised climatic niches. I (1) explored the responses of community-average temperature and precipitation niches to different types of land use, (2) quantified the abundances of species with distinctive climatic niches across land uses, and (3) tested for differences in emergent patterns in communities from tropical versus temperate latitudes. I found that, in comparison to species from undisturbed natural habitats, the average animal found in human-altered habitats lives in areas with higher maximum and lower minimum temperatures and higher maximum and lower minimum precipitation levels. Further, I found that tropical assemblages diverged more strongly than temperate assemblages between natural and human-altered habitats, possibly because tropical species are more sensitive to climatic conditions. My findings strongly implicate the role of land-use change in favouring species affiliated with more extreme climatic conditions, thus systematically reshaping the composition of terrestrial biological assemblages. These findings have the potential to inform species' vulnerability assessments and highlight the importance of preserving local climate refugia.

3.2 Introduction

Human modification of the Earth's land surface has accelerated over the last half century, leading to rapid ecosystem change over increasingly large spatial extents (Meyer & Turner 1992; Millennium Ecosystem Assessment 2005; Steffen, Broadgate, Deutsch, Gaffney, & Ludwig 2015). It is well recognised that land-use change is reshaping biodiversity (Millennium Ecosystem Assessment, 2005; Pereira et al., 2012). Identifying the key mechanisms linking land-use change to shifts in biological assemblages will support predictions of species loss and the impacts of future land conversions, and ultimately the development of more sustainable benefits to humans from ecosystems (Foley et al., 2005; Haines-Young, 2009; Titeux et al., 2017; van Vuuren et al., 2012).

While land-use change directly alters the available habitat for species (Millennium Ecosystem Assessment, 2005), removing primary vegetation can also lead to local climatic changes (Chapter 2; Frishkoff et al., 2016). The temperature regimes of croplands, pastures and (to a lesser extent) plantation forests differ from primary forests, with increases in temperature often reported (Senior, Hill, González del Pliego, et al., 2017). Forest canopies can also buffer temperature extremes (Ewers & Banks-Leite, 2013), with both increases in maximum temperatures (hot extremes) and slight decreases in minimum temperatures (cold extremes) recorded in non-forested human-disturbed habitats, such as agricultural areas (Alkama & Cescatti, 2016; De Frenne et al., 2019). Along with a local warming effect, the variability in temperature extremes differs between land uses; for example, day-to-day maximum temperatures are more variable and thus less predictable in pastures compared to forested habitats (Frishkoff et al., 2015). Further, disturbed habitats may offer fewer microhabitat refugia compared to primary vegetation (González del Pliego et al., 2016). Water regimes may also differ among land uses, with the removal of vegetation reducing precipitation levels and moisture feedback into the atmosphere (Sampaio et al., 2007; Savenije, 1995). Overall, human-altered habitats tend to be hotter and drier than natural, more vegetated habitats (Britter & Hanna, 2003; Frishkoff et al., 2016; Senior, Hill, González del Pliego, et al., 2017). These localised climatic changes are expected to shift the types of species that can colonise and survive under altered environmental conditions (Chapter 2; Frishkoff et al., 2016; Nowakowski, Watling, et al., 2018).

Tracking climate-related change for entire biological assemblages has been achieved by quantifying shifts in the climatic niches of species found in particular locations (Barnagaud et al., 2013; Devictor, Julliard, Couvet, et al., 2008; Frishkoff et al., 2015). Here, climatic niches are referring to the climatic dimensions of a species' classic niche *sensu* Hutchinson (Hutchinson, 1957). Species' physiological tolerance limits (fundamental climatic niches) have typically been measured using physiological tolerance assays in the laboratory (e.g., Frishkoff et al., 2015). Such tolerance assays provide estimates of climatic tolerance limits in the absence of other environmental factors – although only for species that can survive in artificial laboratory conditions – and return thresholds that may be decoupled from population shifts in nature (Chapter 2; Mitchell et al., 2018). By contrast, realised climatic limits and niches (the range of environmental conditions occupied in nature; HilleRisLambers et al., 2013) are estimated from observed species' distributions (e.g., Barnagaud et al., 2013). Realised niches are also influenced by non-abiotic factors and, consequently, may not capture species' true (physiological) climatic limits (Araújo et al., 2013; HilleRisLambers et al., 2013). For example, species' realised climatic niches may also partially be a product of the spatial (and thus climatic) distribution of their critical habitats (Barnagaud et al., 2013, 2012). However, realised niches are often the only feasible measures of climatic tolerances for the majority of species. The combination of realised climatic niche estimates with species assemblage data has emerged as a key tool to quantify the effects of climatic changes on the composition of whole assemblages (Chapter 2; Oliver et al., 2017).

A few studies have started to explore whether local changes in environmental conditions are driving systematic changes in ecological assemblage composition. Lower forest cover and deforestation of primary forest to non-forest land uses have been shown to favour vertebrate species inhabiting (realised niche) or tolerant of (fundamental niche) warmer conditions (when comparing both average and maximum temperatures; e.g., French birds, Barnagaud et al., 2013; Costa Rican and Columbian ectothermic vertebrates, Frishkoff et al., 2015; Nowakowski, Watling, et al., 2018). Vegetation removal can also select species relatively tolerant of drier climates, and thus with drier realised precipitation niches (e.g., Costa Rican birds, Frishkoff et al., 2016; insects, Menke et al., 2011; Piano et al., 2017). Animals in human-altered sites may also have to be tolerant of greater climatic variation, due to changes in vegetation structure, subsequent potential loss of climate-buffering microhabitats, and greater variation in temperatures in some human-disturbed land uses compared to natural habitats (Frishkoff et al., 2015; González del Pliego et al., 2016). Indeed, the average breadth of climatic niches within species assemblages has been found to be wider in urban compared to non-urban (rural or forest) assemblages (Barnagaud et al., 2012; Piano et al., 2017). Very few studies have considered how both maximum and minimum extremes of climatic conditions, and variability in exposure to extremes, may impact assemblages in disturbed habitats.

One key question is whether tropical and temperate assemblages will display similar responses to the altered climatic conditions in disturbed habitats (Chapter 2). Evidence from a wide range of studies indicate that tropical species are more sensitive to climate and land-use change than their temperate counterparts, possibly because they have evolved in a climate that has been relatively stable since the Holocene (Corlett 2011; Janzen 1967; Newbold, Hudson, Hill et al., 2016; Pacifici et al., 2017). Many species in the tropics are also exposed to temperatures that are closer to their upper thermal tolerance limits, leading to the expectation that tropical species will be relatively sensitive to warming and the removal of thermal refugia (Deutsch et al., 2008; Khaliq et al., 2014; Sunday et al., 2014). Whether the effects of land use on the climatic niche properties of assemblages differ geographically has not previously been tested. I predict that there will be larger effects of land use on the climatic properties of assemblages at tropical compared to temperate latitudes.

In this chapter, I test whether the local climatic changes associated with human-altered land uses lead to predictable changes in the structure of entire ecological assemblages. I take advantage of the global scope of the data to test the prediction that effects will be stronger at tropical compared to temperate latitudes. I also predict that human-altered habitats will host species able to tolerate a wider range of climatic conditions. Further, to attribute assemblage-level changes to the contributions of different species, I investigate whether the abundances of species with different climatic niches vary systematically with land use. I predict that species affiliated with warmer-than-average temperatures, drier-than-average precipitation levels and greater-than-average range-wide variation in both temperature and precipitation conditions will be the least negatively affected by human-altered habitats.

3.3 Methods

3.3.1 Abundance and land-use data

Data representing the assemblage composition of terrestrial vertebrates in different land uses were acquired from the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) Project database (Hudson et al., 2016, 2017). The PREDICTS database combines data from studies worldwide that compared ecological assemblages under different levels of land use (Hudson et al., 2014). I focus on terrestrial vertebrates because there is reasonably comprehensive species distribution information available for these taxa, which makes the estimation of their realised climatic niches possible. The subset of PREDICTS data that have abundance records for vertebrate assemblages are from 146 studies (6,948 assemblages), representing 4,147 species (527 mammals, 2,941 birds, 317 reptiles and 362 amphibians). The PREDICTS Project database is hierarchically structured: it consists of data from original *Source* publications, each containing one or more *Studies* (studies within a single source are divided if sampling methods differ), which may themselves be split into *Spatial blocks* of individual sampled *Sites* (publication > study > block > site; Hudson et al., 2014).

The PREDICTS Project team assigned a predominant land-use category to each site within each study, based on the description of the habitat given in the original source publication, classified against a detailed set of criteria (Hudson et al., 2014; Appendix 1, Section 1, table S3.1). Land-use categories considered in the present study were: (1) primary vegetation (natural vegetation, no evidence of past destruction), secondary vegetation (natural vegetation recovering from destruction), split into two groups - (2) young secondary vegetation (sites that have not had long to recover) and (3) advanced secondary vegetation (included intermediate and mature secondary vegetation from the PREDICTS Project database, i.e., sites that have been recovering for longer), (4) plantations (e.g., timber/fruit/coffee/oil-palm or rubber plantations), (5) croplands (areas used to cultivate herbaceous crops, including for animal feed) and (6) pastures (land on which livestock are grazed). Even though the land-use classification is coarse and somewhat subjective, a repeatability study showed classifications to be reasonably consistent (reported in Hudson et al., 2014).

3.3.2 Distribution data

Species' distributions (extent-of-occurrence maps) were used to estimate species' realised climatic niches (from here referred to as 'climatic niches'). The extent-of-occurrence maps for terrestrial mammals, amphibians, and reptiles were acquired from the International Union for Conservation of Nature (IUCN 2016a) and for birds from BirdLife International (2012). Since I was interested in the full extent of species' natural ranges, I included all parts of the geographic range where the species occurrence status was considered to be extant, probably extant, possibly extinct or extinct (post 1500); and I included areas where the species is thought to be resident or present in the breeding or non-breeding seasons. Specifically, I excluded areas where the species is possibly extant, its presence is uncertain or is vagrant, and areas that are used for relatively short periods of the year as passages during migration or if the seasonal occurrence is uncertain. The range maps for birds followed the same coding scheme as those provided by IUCN. The original polygon maps were rasterised to an equal-area grid (500 m × 500 m per pixel; Behrmann projection). I selected this resolution as a compromise between the computational limitations of small spatial grains and the need to include as many very-narrow-ranged species as possible. For species with known elevational limits (number of species with only upper limit known = 2,264, lower limit known = 9, both limits known = 694; IUCN 2016a, BirdLife International 2018), distribution maps were cut by these limits (which is standard practice when estimating species' extent-of-occurrence; e.g., Jetz, Wilcove, & Dobson 2007).

I required data for a wide range of species over the global terrestrial area, for which no better maps exist (Herkt et al., 2017). My analyses (which did not predict into unsampled space or time) required a quantitative estimate of the relative (across species) means and range-wide variation in climatic conditions with which each species was affiliated. Expert drawn species distribution maps tend to underestimate species' extent-of-occurrence, but overestimate species occupancy (Herkt et al., 2017). Therefore, I tested the robustness of my realised climatic niche estimates by comparing my main results to results using climatic niches derived from occurrence records in the Global Biodiversity Information Facility (GBIF, https://www.gbif.org), which provides information on area of occupancy (see Appendix 1, Section 2 for details on how I acquired realised niche estimates from GBIF data). Since GBIF occurrence records have strong geographic and taxonomic biases (Meyer et al., 2015), I focus on the results using the IUCN and BirdLife International maps in the main text.

3.3.3 Climatic data

I acquired estimates of climate from WorldClim Version 1.4 (Hijmans et al., 2005), at a 30 arc-second resolution (0.86 km^2 at the equator). These estimates represent averages for the period 1960 – 1990. The raw estimates were resampled to a 500 m equal-area projection (Behrmann projection) using bilinear interpolation to match species' distribution data, following previous studies (Khaliq et al., 2017; Newbold, 2018). In my analysis, I focused on four climatic variables: maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), and precipitation of the wettest (Pp_{max}) and driest (Pp_{min}) months. Variables describing climatic extremes are suggested to be more appropriate than averages for explaining species' distribution and responses to environmental pressures (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Mantyka-Pringle et al., 2012; Zimmermann et al., 2009).

3.3.4 Species-level climatic niche

I quantified the extremes and variation across species' distributions of each of the four climatic variables. I did this by overlaying distribution maps onto climate data and calculating the maximum (for T_{max} and Pp_{max}) or minimum (for T_{min} and Pp_{min}) and standard deviation (Frishkoff et al., 2016) of each climatic variable for each species (ArcGIS 10.4; ESRI 2015). I use the term 'range-wide variation' to reflect the breadth of recorded climatic extremes across a species' distribution. Estimates of climatic niche properties were available for 3,606 species (448 mammals, 2,709 birds, 121 reptiles and 328 amphibians), from 6,123 assemblages (140 studies across 47 countries, see Appendix 1, Section 3, fig. S3.4, and table S3.3 for the spatial extent sampled). Consequently, for each species I calculated eight climatic niche properties: their T_{max} maximum value and range-wide variation, T_{min} minimum value and range-wide variation, Pp_{max} maximum value and range-wide variation and Pp_{min} minimum value and range-wide variation.

3.3.5 Community-average climatic niche properties

For each species assemblage, I calculated community weighted means (CWMs) of species-level climatic extremes and range-wide variation for each climatic niche property. CWMs are calculated by finding the average of each species' climatic niche property across all species in an assemblage, weighted by species' abundance (Jiguet et al., 2011; Oliver et al., 2017). As an example, higher CWM values for maximum T_{max} (denoted by CWM(maxT_{max})) signifies communities with higher proportions of individuals of species found in areas with relatively higher maximum temperatures. At the other end of the spectrum, lower CWM values for minimum T_{min} (CWM(minT_{min})) reflects communities with higher proportions of individuals of species affiliated with lower minimum temperatures. I use CWM(maxPp_{max}) and CWM(minPp_{min}) to refer to the community weighted means for maximum Pp_{max} and minimum Pp_{min}, respectively. Similarly, communities with higher CWM T_{max} range-wide variation are composed of higher proportions of individuals of species that occupy areas experiencing a larger range of maximum temperatures. Further, I produced CWMs unweighted by species abundance (i.e., average for a species within a community, Appendix 1, Section 4) to check that weighting by abundance did not affect my results. I also calculated the correlations between the community-average climatic niche properties to see whether changes in these properties across land uses may be linked (Appendix 1, Section 5). In addition, to explore the potential influence of outliers on CWMs, I also (a) produced community weighted medians (i.e., the median value of each species' climatic extreme and variation across all species in an assemblage, weighted by species' abundance), and (b) produced CWMs after excluding the upper and lower 2.5% of species-level climatic extremes and range-wide variation values.

Changes in community-average climatic niche properties allow us to gain an overall impression of changes in the structure of ecological assemblages. However, community change is multi-dimensional, and the same numerical responses can be underpinned by different responses of species with distinctive climatic niches, representing alternative mechanisms of change. For instance, having a greater proportion of individuals from species affiliated with warmer maximum temperatures and/or fewer individuals from species affiliated with colder maximum temperatures could both contribute to higher CWM(maxT_{max}) values (Jiguet et al., 2011). Whether a species has higher or lower abundances in certain land-use types also likely depends on the breadth of climatic conditions they are able to tolerate. Thus, I explored how differences in the abundance of species groups with different climatic niche properties contribute to changes in community-level properties. To do so, I investigated the response to land use of species with different climatic niches (climatic extremes and range-wide variation). For this analysis, due to the prediction that responses to land use will differ between geographic zones, assemblages at tropical and temperate latitudes were analysed separately. Species within each assemblage were split (a) into four groups around the within-study medians of the T_{max} maximum and range-wide variation and then, separately, (b) into four groups based on Pp_{min} minimum and range-wide variation (Appendix 1, Section 6, table S3.5-6). I focused on T_{max} and Pp_{min} for this analysis because the differences in CWMs across land uses were strongest for these climatic variables.

Migratory species can move to avoid certain climatic conditions (Robinson et al., 2009), which may bias my results. Therefore, I also compared community-average realised climatic niche properties with and without the inclusion of migratory birds (migratory status acquired from BirdLife International 2018).

3.3.6 Covariates

I considered three additional covariates that may influence community-average climatic niche properties (Frishkoff et al., 2015). In all models, I considered a site's (1) elevation and (2) climate (matching the variable used to calculate the CWM, e.g., T_{max} for CWM(maxT_{max})). Measures of these two covariates from each site were acquired from WorldClim Version 1.4 (Hijmans et al., 2005). Species' range size influences sensitivity to land use (Newbold et al., 2018), an effect that may be independent of range-wide climatic variation, with which it is often strongly correlated (Appendix 1, Section 7, table S3.7). Therefore, I also considered (3) community-average range size as a potential covariate in models of CWM range-wide climatic variation. The community-average range sizes (community weighted means) were presented in Newbold et al., (2018) and published alongside the paper (DOI: 10.5519/0066354). The estimates were based on the same species' distribution maps as described above. The polygon maps were first projected onto an equal-area grid using the Project_management function, and the area of each polygon calculated using the CalculateAreas_stats function, in ArcGIS 10.4 (ESRI 2015). The areas of the polygons were then summed to estimate the total range area of each species, before a community weighted mean was calculated, weighted by abundance (Newbold et al., 2018). CWM range sizes were unobtainable for 18.7% of assemblages, so these assemblages were excluded in range-wide climatic variation analyses, leaving 4,977 assemblages composed of 3,415 species (394 mammals, 2,649 birds, 74 reptiles and 298 amphibians). Packages in R 3.4.0 (R Core Team 2019) used for data-handling and geospatial operations included ‘plyr’ v.1.8.4 (Wickham 2011), ‘raster’ v.2.5.8 (Hijmans 2016), ‘rredlist’ v.0.5.0 (Chamberlain 2018) and ‘sp’ v.1.2.5 (Bivand et al., 2013; Pebesma & Bivand 2005).

3.3.7 Statistical analyses

I used linear mixed-effects models to test for differences across land uses in (1) community-average climatic extremes, (2) community-average range-wide climatic variation (table 3.1) and (3) abundances of species groups with different climatic niches. Models were produced in R 3.4.0 (R Core Team 2019), using the package ‘lme4’ v.1.1.17 (Bates, Maechler, Bolker & Walker, 2015). Below I explain which fixed effects, random effects and covariates were included in each model (see table 3.2 for further details).

Table 3.1: Spread of vertebrate assemblages across land uses. The number of vertebrate assemblages from the PREDICTS Project database within each land use included in the analyses looking at differences in community-average climatic extremes (and, in parentheses, range-wide variation). For definitions of land-use types, see Appendix 1, Section 1, table S3.1 and Hudson et al., (2014).

Land use	Geographic zone	
	Tropical	Temperate
Primary vegetation	1369 (1123)	774 (587)
Advanced secondary vegetation (ASV)	504 (363)	84 (75)
Young secondary vegetation (YSV)	301 (269)	156 (150)
Plantation	865 (622)	270 (246)
Cropland	439 (355)	485 (458)
Pasture	564 (435)	291 (273)
Total	4042 (3167)	2060 (1789)

Community-average climatic extremes and range-wide variation

To explore how community-average climatic niches differed across land uses, I produced a set of eight models (one model for each climatic niche property: CWM(maxT_{max}), CWM(minT_{min}), CWM(maxPp_{max}), CWM(minPp_{min}), CWM range-wide variation in $T_{max/min}$, $Pp_{max/min}$). I log(x+1) transformed CWM(maxPp_{max}) and CWM(minPp_{min}). I selected fixed effects using backwards stepwise model simplification (with the models fitted using maximum likelihood; Zuur, Ieno, Walker, Saveliev, & Smith 2009). Land use, geographic zone (tropical or temperate), and the interaction of geographic zone with land use were always included as categorical fixed effects. Sites were classified as ‘Tropical’ if located between 23.44°N and 23.44°S, and ‘Temperate’ if located between the tropics and Arctic or Antarctic Circle (thus including boreal habitats between 50 – 60°N, as there were not enough data to classify them separately). The site’s elevation and the value of the climatic variable in question at each site were added as continuous covariates into the backwards stepwise model simplification. I set a threshold for excluding correlated covariates at $|r| > 0.5$ (recommended for mixed-effects models by Harrison et al., (2018)); if the correlation between elevation and the value of the climatic variable in question at each site were above this threshold, the climatic variable was kept preferentially, as it likely had a more direct influence on communities. For CWM range-wide climatic variation, I also included CWM range size (Newbold et al., 2018) as a continuous covariate into the backwards stepwise model simplification. Within all models I also included a nested random-intercept term for study identity (to account for non-random structure in the response data due to study-dependent differences, e.g., sampling methods) and for the spatial ‘blocks’ of sampled sites within studies. I did not include random slopes in my models (i.e., to let the effect of land use vary across studies) due to convergence issues, which were likely caused by the unbalanced sampling of land uses among studies. However, despite the convergence issues, the results for models with random slopes (not shown) were quantitatively very similar. Further, CWMs may be prone to type I errors (Miller, Damschen, & Ives, 2019); so, for each CWM model, I also used a null model approach to further test the significance of my observed results. To produce null models, I randomly shuffled species-level climatic affiliations between species within each study (I randomised within studies because of the hierarchical structure and global spread of the PREDICTS dataset; Cornwell & Ackerly 2010; Yang, Powell, Zhang & Du, 2012). For each CWM model, 999 randomisations were produced. I then compared my observed results to those produced from the null models using the randomised datasets, with results classed as significant if they were outside the lower 2.5th or upper 97.5th percentile of the null model (i.e., a two-tailed test).

Ambient conditions affect endothermic and ectothermic vertebrates differently, due to their distinctive physiologies (Deutsch et al., 2008; Frishkoff et al., 2016; McNab 2012; Senior, Hill, González del Pliego, et al., 2017); therefore, I also produced a separate set of models comparing the response to land use of community-average climatic niche properties for these two groups. The methods, results and a discussion of these analyses can be found in Appendix 1 (Section 8, table S3.8-11, fig. S3.6).

Abundances of species groups with different climatic niches

In the abundance models, I log(x+1) transformed the abundance measures. I chose this transformation because many different types of abundance measure (including non-integer measures) were included in the database, and so values did not conform to a Poisson distribution. Land use (categorical fixed effect), the site’s elevation and the value of the climatic variable in question at each site (continuous fixed effects) were considered in a backwards stepwise model simplification as above (using the same method for excluding highly correlated covariates). As in the previous models, I included a nested random-intercept term for study identity and spatial block. In these models, advanced and young secondary vegetation categories were grouped to become ‘secondary vegetation’ to ensure all land-use categories had data for over 50 assemblages in each model.

For all models, I tested the statistical significance of fixed effects using likelihood ratio tests (Zuur et al., 2009). To test the main effects, I removed all interaction terms. For the models’ final structures, see Appendix 1 (Section 9, table S3.12). I used Moran’s I tests to check for spatial autocorrelation in the residuals of each individual study (Newbold et al., 2015).

Table 3.2: Model structures. The fixed effects, covariates, and random effects considered for each model (denoted by X). The response variables were either community-average (community weighted mean, CWM) climatic extremes (maximum or minimum) or range-wide variation in one of the climatic variables considered (maximum temperature of the warmest month, T_{max}; minimum temperature of the coldest month, T_{min}; precipitation of the wettest month, Pp_{max}; precipitation of the driest month, Pp_{min}), or the abundance of a species’ group. Fixed effects included land-use type (LU; this effect was included in every model), geographic zone (GZ; tropical vs. temperate latitudes) and the interaction between the two (LU×GZ). Covariates included a site’s elevation (though this was excluded from models focused on T_{max}), the value of the climatic variable in question at the site (CV) and community-average range size (Range). The fixed effects and covariates were selected using backwards stepwise model simplification. The random effects included study identity (to account for differences between studies in sampling methods and response variables) and spatial block (to account for the spatial structure of sites sampled within each study).

Model	Response variable	Fixed effects (categorical)			Covariates (continuous)			Random effects (nested)	
		LU	GZ	LU×GZ	Elevation	CV	Range	Study identity	Spatial block
Community-average climatic niche models									
	CWM(maxT_{max})	X	X	X		X		X	X
	CWM(minT_{min})	X	X	X	X	X		X	X
	CWM(maxPp_{max}) or (minPp_{min}) (log(x+1) transformed)	X	X	X	X	X		X	X
	Variation in T_{max}	X	X	X		X	X	X	X
	Variation in T_{min}/ Pp_{max}/Pp_{min}	X	X	X	X	X	X	X	X
Abundance models									
	Abundance of the species' group (log(x+1) transformed)	X			X (although excluded in T_{max} and tropical Pp_{min} models)	X		X	X

3.3.8 Habitat specialisation

Species' climatic niches may also partially be a product of the spatial (and thus climatic) distribution of their critical habitats (Barnagaud et al., 2013, 2012). As a result, any observed differences in niche properties among land uses may simply reflect differences in the occurrence of habitat specialists (forest specialists in particular due to forest canopies buffering climatic extremes; De Frenne et al., 2019). To check whether this was the case, I explored the influence of habitat specialisation on climatic niche differences across land uses. I first compared species-level climatic niche properties with an index of species-level habitat breadth, and then compared species-level climatic niche properties between forest specialists and non forest-specialists (Appendix 1, Section 10). Finally, I ran two sets of models to compare the responses to land use in community-average climatic niche properties when forest specialist species were included and excluded from analyses. See Appendix 1 (Section 10) for further details of these tests.

3.4 Results

3.4.1 Summary of results

Community-average climatic niche properties varied both across land uses and between geographic zones (table 3.3, fig. 3.1). In comparison to primary vegetation, assemblages in human-altered habitats were composed, on average, of species affiliated with higher maximum and lower minimum temperatures and higher maximum and lower minimum precipitation levels, and generally wider range-wide variation in T_{max} (the effect of land use for all climatic niche properties, $p < 0.001$; fig. 3.1). Differences in climatic niche properties of assemblages relative to primary vegetation were generally larger within the tropics (fig. 3.1). These results appear to be driven by human-disturbed land uses having both higher abundances of some species (as predicted, those inhabiting areas with higher maximum temperatures, lower minimum precipitation levels, and a broader range of climatic conditions) and lower abundances of others (those inhabiting areas with lower maximum temperatures, higher minimum precipitation levels, and a narrower range of climatic conditions; fig. 3.2-3).

Table 3.3: Range and means of community weighted means. The range (and mean in parentheses) of community weighted means (CWM) for each climatic niche property across land uses and within each geographic zone. The climatic niche properties included the CWM of the climatic extreme (maximum or minimum) and range-wide variation in maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) and precipitation of the driest month (Pp_{min}). ASV and YSV denote advanced and young secondary vegetation, respectively.

	Community weighted means							
	Max T_{max} (°C)	Min T_{min} (°C)	Max Pp_{max} (mm)	Min Pp_{min} (mm)	T_{max} variation (°C)	T_{min} variation (°C)	Pp_{max} variation (mm)	Pp_{min} variation (mm)
Land-use type								
Primary vegetation	24.7 – 47.3 (38.3)	-57.0 – 18.8 (-5.9)	112 – 2901 (942.4)	0 – 54.8 (1.8)	0.7 - 8.0 (3.1)	0.7 - 16.4 (5.0)	9.6 - 482.4 (88.3)	1.5 - 108.6 (26.5)
ASV	29.0 – 47.4 (36.9)	-49.3 – 15.6 (-1.3)	253 – 2901 (1100.3)	0 – 103.3 (5.2)	0.7 - 6.5 (2.8)	0.9 - 14.0 (4.3)	39.9 - 446.7 (97.5)	1.7 - 90.8 (37.7)
YSV	30.3 – 48.6 (38.7)	-55.0 – 15.1 (-8.4)	170 – 2901 (1030.5)	0 – 49.0 (1.6)	1.1 - 7.2 (3.3)	1.1 - 15.6 (5.4)	9.6 - 188.3 (85.4)	1.0 - 74.0 (21.5)
Planation	24.4 – 48.9 (37.6)	-47.0 – 19.9 (-3.5)	271 – 2901 (999.5)	0 – 53.0 (3.5)	0.6 - 6.9 (3.1)	0.6 - 16.2 (4.8)	13.9 - 212.4 (89.6)	5.2 - 118.9 (31.8)
Cropland	27.7 – 49.0 (40.8)	-57.0 – 15.4 (-16.5)	271 – 2901 (1112.6)	0 – 8.9 (0.3)	1.4 - 6.9 (4.0)	1.5 - 19.0 (7.3)	27.1 - 381.3 (85.7)	4.4 - 95.4 (25.0)
Pasture	26.5 – 48.9 (39.7)	-57.0 – 15.7 (-9.9)	231 – 2901 (981.6)	0 – 10.5 (0.4)	0.8 - 8.3 (3.5)	1.0 - 21.6 (6.0)	28.3 - 177.8 (86.3)	1.0 - 141.9 (24.5)
Geographic zone								
Tropical	24.4 – 46.8 (37.4)	-57.0 – 19.9 (1.5)	170 – 2901 (949.7)	0 – 103.3 (2.8)	0.6 - 6.9 (2.6)	0.6 - 19.0 (3.6)	9.6 - 188.3 (91.9)	1.0 - 141.9 (30.0)
Temperate	25.9 – 49.0 (40.9)	-57.0 – 11.0 (-24.5)	112 – 2901 (1114.5)	0 – 33.0 (0.6)	1.0 - 8.0 (4.5)	1.1 - 16.2 (8.7)	18.5 - 210.5 (82.5)	2.8 - 69.2 (23.1)

My findings were robust to several possible confounding issues. First, very small differences were observed between community-average climatic niche properties produced with and without migratory bird species included (Appendix 1, Section 11, table S3.20; BirdLife International 2018), so migratory species were included in the analyses. Second, using a null model approach provided additional support for my results relating to community-average climatic extreme affiliations, with the majority of observed results found to be significant using a two-tailed test (fig. 3.1). However, fewer observed community-average range-wide climatic variation results were significantly different in comparison to null expectations (fig. 3.1), thus I urge caution when interpreting these results. Third, when using occurrence data from GBIF, the results were generally qualitatively and quantitatively very similar to those presented in the main text (Appendix 1, Section 2, fig. S3.1-3). Fourth, correlations among community-average climatic niche properties were generally low, though a few (e.g., between CWM T_{max} range-wide variation, CWM T_{min} range-wide variation and CWM(minT_{min})) were more highly correlated (Appendix 1, Section 5, table S3.4). Fifth, correlations between species-level climatic niche properties and habitat breadth were all low ($|r| < 0.41$). Although there were some differences observed between species-level climatic niche properties for species classed as forest versus non forest-specialists (Appendix 1, Section 10, fig. S3.7), the results from models including and excluding forest specialists were also qualitatively and quantitatively very similar (Appendix 1, Section 10, fig. S3.8-9). Finally, using community weighted medians or CWMs that excluded the upper and lower 2.5% of species-level climatic affiliations (results not shown) both produced qualitatively and quantitatively very similar results to models produced using CWMs that included all species, from this I am confident that the results are not being driven by outliers.

3.4.2 Community-average climatic niche properties

Overall (with the exception of temperate plantations), CWM(maxT_{max}) was higher in human-disturbed land uses than primary vegetation, with larger differences relative to primary vegetation in tropical croplands and pastures compared to the same habitats at temperate latitudes (for all community-average climatic niche properties, land use by geographic zone interaction effect, $p < 0.015$; fig. 3.1). CWM(minT_{min}) was consistently lower in human-disturbed land uses than primary vegetation.

Differences in land-use responses between tropical and temperate assemblages were smaller than for CWM(maxT_{max}), but the interaction remained significant ($p < 0.001$). Interestingly, the difference between CWM(minT_{min}) in young secondary vegetation compared to primary vegetation was much larger at temperate compared to tropical latitudes. There were inconsistent (although significant) geographic differences in community-average thermal range-wide variation across land uses. It is important to note that CWM(minT_{min}) and CWM(T_{max} range-wide variation) values were relatively highly negatively correlated (Appendix 1, Section 5, table S3.4), which hinders my ability to separate their relative importance.

CWMs were generally higher for maximum Pp_{max} and lower for minimum Pp_{min} in human-altered land uses compared to primary vegetation across both geographic zones. In most cases, differences in CWM(maxPp_{max}) and CWM(minPp_{min}) values relative to primary vegetation were larger at tropical compared to temperate latitudes. Tropical-temperate differences in community-average precipitation range-wide variation between land uses were not consistent, but the pattern was similar for both Pp_{max} and Pp_{min}, with no noticeable general difference between primary vegetation and human-dominated land uses (fig. 3.1).

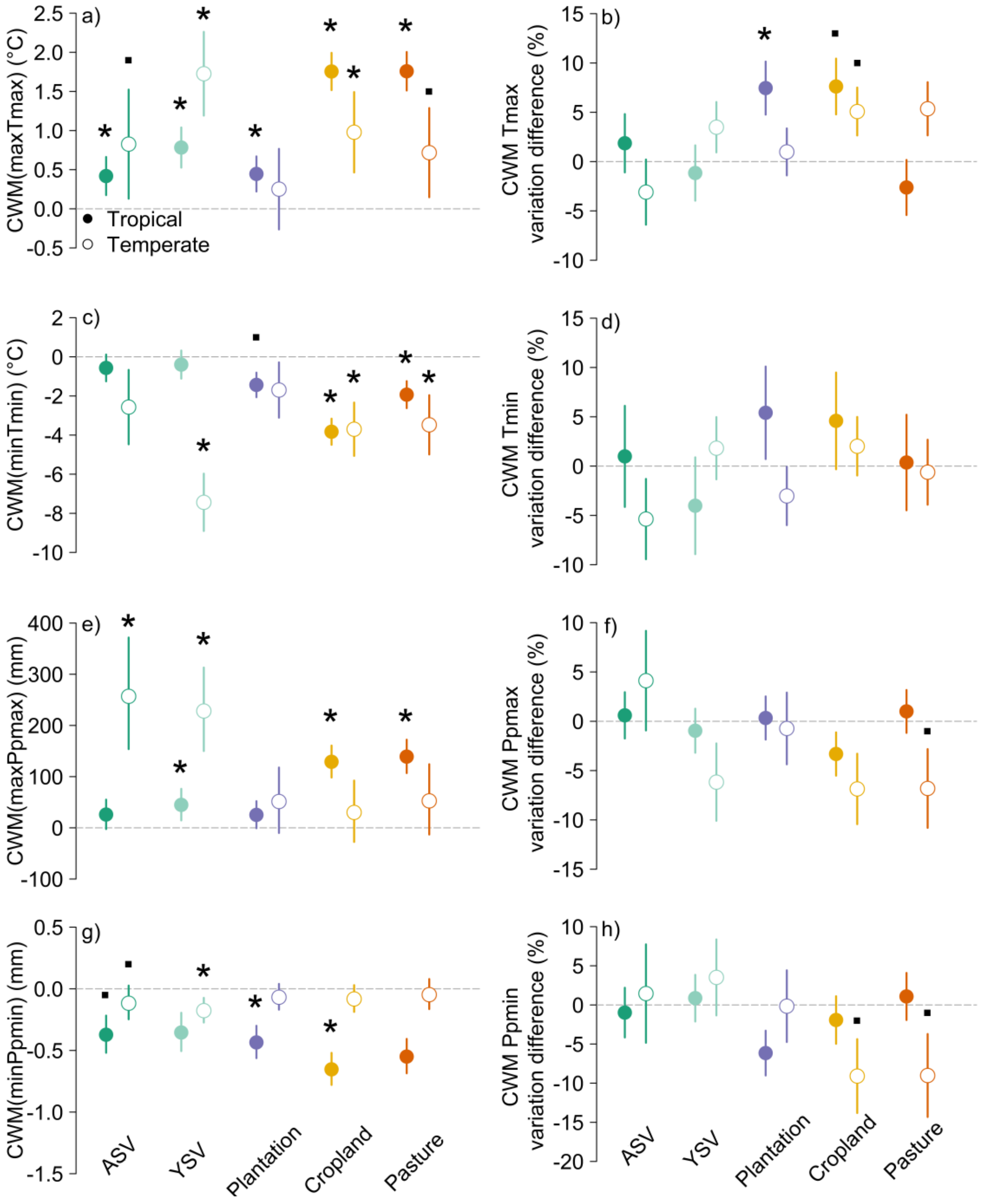


Figure 3.1: Modelled differences in community-average climatic niche properties across land uses. Geographic variation (tropical vs. temperate latitudes) in modelled differences across land uses in community weighted mean (CWM) maximum (max, a, e) or minimum (min, e, g) and range-wide variation (b, d, f, h) in maximum temperature of the warmest month (a, b), minimum temperature of the coldest month (c, d), precipitation of the wettest month (e, f) and precipitation of the driest month (g, h). All values are relative to assemblages within primary vegetation (dotted line). Error bars show 95% confidence intervals. ASV and YSV denote advanced and young

secondary vegetation, respectively. Transformed values were back-transformed from the log-scale used for analysis before plotting. A star (*) or dot (▪) above values indicates that the result was significant when compared against null models in a two-tailed or one-tailed test, respectively.

3.4.3 Abundance models

The abundances of species groups across land uses differed in direction and magnitude depending on the groups' thermal niche properties (fig. 3.2). In the tropics, species with warmer T_{max} maximum values and broader T_{max} range-wide variation had higher abundances relative to primary vegetation across human-altered land uses (fig. 3.2). Generally, other species groups had lower abundances in human-altered land uses. Similar patterns were observed at temperate latitudes, although differences between primary vegetation and human-altered land uses were generally smaller compared to tropical latitudes (fig. 3.2).

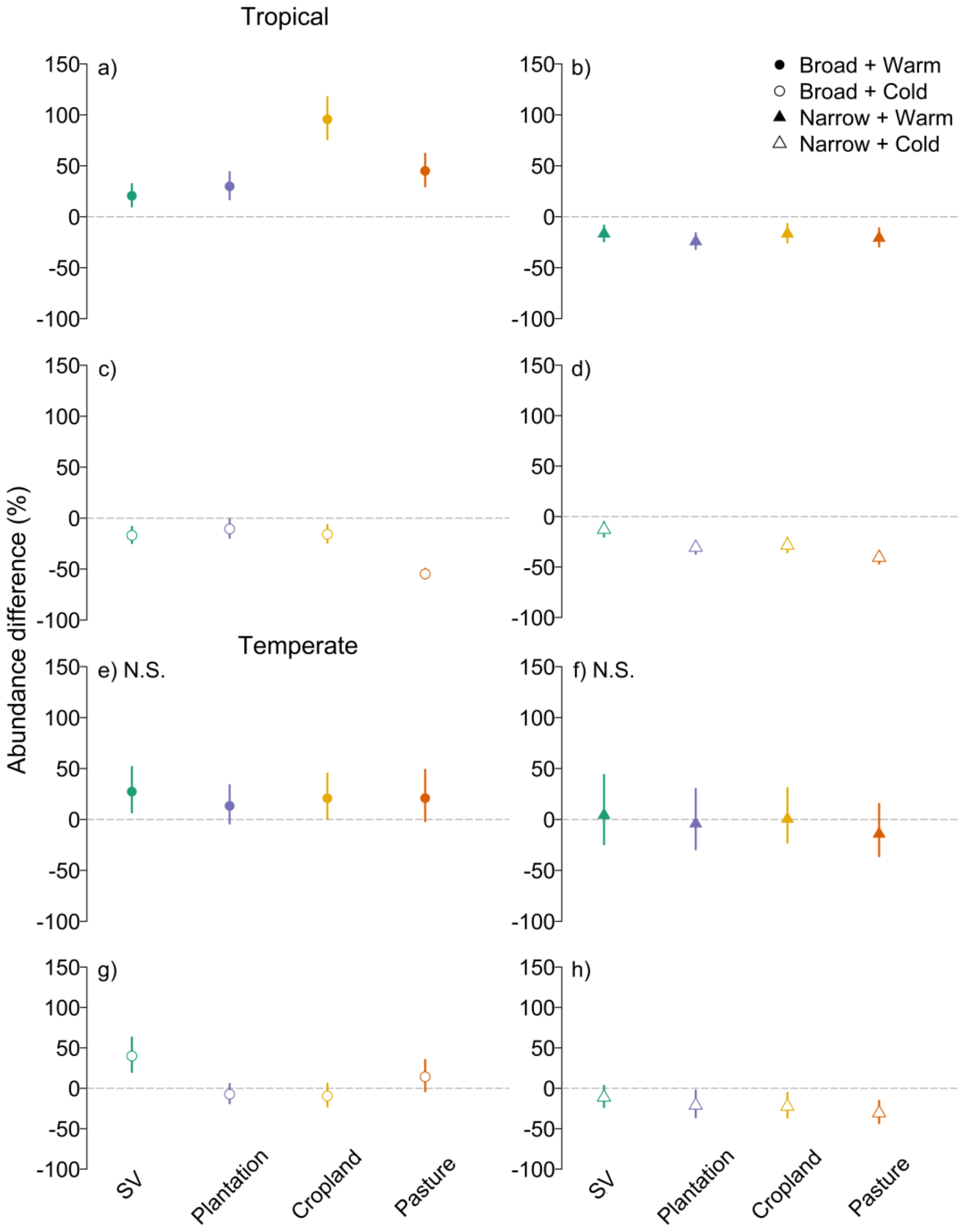


Figure 3.2: Abundance of species with different thermal niches across land uses. The total abundance of species with different thermal (T_{max}) niches at tropical (a-d) and temperate (e-h) latitudes across human-altered land uses, relative to assemblages within primary vegetation (dotted line). Species groups differ in the range-wide variation in thermal (T_{max}) conditions experienced over their range ('broad' vs. 'narrow') and maximum T_{max} value ('warm' vs. 'cold'). Error bars show 95% confidence intervals; SV denotes secondary vegetation (consisting of the young and advanced secondary vegetation land-use categories). Values were back-transformed

from the log-scale used for analysis before plotting. N.S. denotes that the effect of land use was not significant within that species group.

The abundances of species groups across land uses also varied between groups differing in precipitation niches (fig. 3.3). At tropical latitudes, species groups with wetter-than-average minimum Pp_{min} values had the lowest abundances within human-dominated land uses compared to primary vegetation. Species with narrower- and drier-than-average Pp_{min} range-wide variation and minimum values, respectively, were the only group that had higher abundances in some human-disturbed land uses compared to primary vegetation. Differences among species groups were much smaller at temperate latitudes (fig. 3.3).

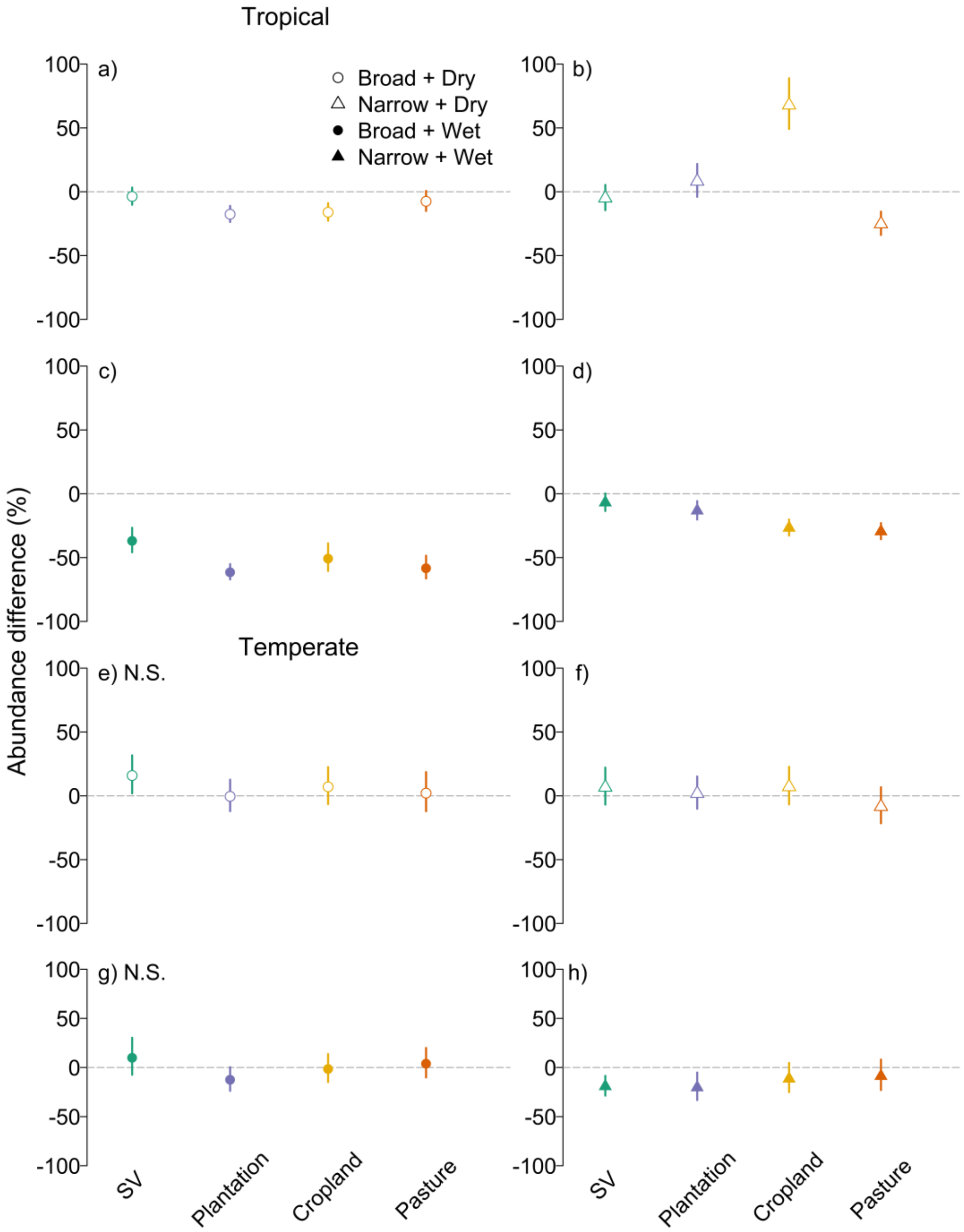


Figure 3.3: Abundance of species with different precipitation niches across land uses. The total abundance of species with different precipitation niches (Pp_{min}) at tropical (a-d) and temperate (e-h) latitudes across human-altered land uses, relative to assemblages within primary vegetation (dotted line). Species groups differ in the range-wide variation in precipitation (Pp_{min}) levels experienced throughout their range ('broad' vs. 'narrow') and minimum P_{min} values ('dry' vs. 'wet'). Error bars show 95% confidence intervals; SV denotes secondary vegetation (consisting of the young and advanced secondary vegetation land-use categories). Values were back-transformed

from the log-scale used for analysis before plotting. N.S. denotes that the effect of land use was not significant within that species group.

For full statistical results, see Appendix 1, Section 9 (table S3.14 and S3.15). The residuals of the community-average climatic niche properties models generally did not show significant spatial autocorrelation for > 5% of studies (as would be expected by chance; Appendix 1, Section 9, table S3.16), but did for the abundance models (range across species groups and climatic variables 0-25%; Appendix 1, Section 9, table S3.17).

3.5 Discussion

Species from assemblages in human-dominated land uses tend to be affiliated with more extreme climates, on average, than species found in primary vegetation, especially within the tropics. This is driven by human-altered land uses having both higher and lower abundances of species with different climatic niches. Specifically, assemblages in human-disturbed land uses were composed of greater proportions of individuals of species affiliated with higher maximum temperature and precipitation and lower minimum temperature and precipitation. These results enhance our understanding of potential interactions between land-use and climate change. Both these major drivers are reshaping communities by selecting for species with affinities for greater extremes in climate (Barnagaud et al., 2012; Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Tayleur et al., 2016), suggesting the likelihood of synergistic interactions. This finding improves our ability to predict how biodiversity will be reshaped by future climatic changes in a world increasingly dominated by human-disturbed land uses.

Local climatic changes are strong ecological filters, influencing which individuals benefit or lose out from land-use change, and ultimately community composition (Chapter 2; Frishkoff et al., 2015). Here, I quantified the effect of species gains and losses on the structure of whole assemblages. A key question is what mechanisms are driving the observed patterns? In addition to changes in average temperatures, land-use change can increase the frequency of heat waves (Mishra, Ganguly, Nijssen & Lettenmaier, 2015) and extreme cold events (Medvigy, Walko and Avissar 2012). Unlike in forests, where the buffering effect of canopies results in warmer minimum and lower maximum temperatures (Ewers & Banks-Leite, 2013), species in human-dominated land uses may not have access to the microhabitats required to avoid extreme heat and cold exposure (McNab 2012; Kearney, Shine and Porter 2009; Sunday et al., 2014). My results highlight that human-dominated land uses may be particularly problematic for cold-affiliated species if they cannot tolerate or avoid the warmer temperatures, and for warm-adapted specialists if they cannot tolerate or avoid extreme cold events.

Human-dominated land uses also favoured species affiliated with greater extremes of precipitation. This effect on community composition may be a consequence of direct and/or indirect effects of local climatic changes resulting from land-use change on biodiversity (Frishkoff et al., 2016; Ogilvie et al., 2017). Directly, changes may favour species that can tolerate the new, drier climate (Frishkoff et al., 2016). Indirectly, the drier climatic conditions may favour vegetation that is characteristic of more arid climates, subsequently favouring species better able to exploit this vegetation (Frishkoff et al., 2016). However, my finding that communities, on average, were affiliated with higher maximum precipitation levels in human-altered land uses was surprising, and the mechanisms underlying this trend warrant further exploration. Such an effect may arise due to differences in moisture levels, which are linked to land-use type and precipitation (Fu et al., 2003), and may impact species' abilities to survive in certain land uses. Although, the links between land use, precipitation, and moisture levels are complex due to the multitude of other factors that can influence moisture availability, such as topography, soil properties (e.g., particle size), and the plant species growing (Fu et al., 2003). Another unexpected result was that species with drier- and *narrower*-than-average Pp_{min} minimum and range-wide variation, respectively, had higher abundances in tropical croplands. It may be that species' experiencing narrower variation in minimum local precipitation levels are better able to cope with drier climates, and thus able to persist and even increase in abundance after land conversion (providing they can tolerate the other changes that occur). Although I am cautious in interpreting this result, as it is only observed in tropical croplands, it highlights the complexities underlying responses to precipitation changes. Nevertheless, my findings implicate a potentially important effect of changes in local precipitation regimes on terrestrial vertebrates.

Biogeographic histories may also have a role in climatic niche differences across land uses, with species' realised niches arising from the spatial and climatic distribution of their habitats (Barnagaud et al., 2013). Consequently, shifts towards species that can tolerate greater extremes of climate in human-altered land uses could be explained by losses of forest specialists, which may coincidentally have climatic niches that do not encompass these extremes (Barnagaud et al., 2013; Ewers & Banks-Leite, 2013). However, my habitat breadth index was not correlated with species' climatic affinities, and similar results were produced when forest specialists were excluded from models (Appendix 1, Section 10). So, although I do not rule out a role of species' biogeographic histories, my results are consistent with local climatic differences between primary and human-dominated land uses playing a strong role in the observed patterns.

Assemblages from tropical locations generally displayed larger differences than temperate assemblages in community-average climatic niche properties relative to primary habitats, particularly in croplands and pastures. There are at least three potential explanations for this result. First, lower seasonality in the tropics and greater historical climate stability may render species more sensitive to environmental changes and the removal of microhabitats (Janzen, 1967; Sunday et al., 2014). Second, the weaker differences across land uses at temperate latitudes may also be because these species are not living as close to their warm tolerance thresholds (Deutsch et al., 2008; Kearney et al., 2009), and so can tolerate (or even benefit from) warmer temperatures (Kearney et al., 2009). Third, the magnitude of temperature increases following conversion of primary vegetation tend to be less pronounced in northern latitudes (partly due to the greater effect of snow albedo in cleared landscapes; Alkama and Cescatti 2016, Findell et al., 2017). Critically, the tropics hold more species, and a greater relative proportion of these species are presently threatened compared to higher latitudes (Brook et al., 2008). Regardless of the mechanism(s), these results add to the growing number of studies highlighting the vulnerability of the tropics to global drivers of change (Brook et al., 2008). This is an important result, given that both land-use and climate change have been projected to occur to the greatest extent and soonest within the tropics (Pacifici et al., 2017; Sala et al., 2000).

Aboveground temperatures in secondary forests are similar or slightly warmer compared with primary forests (Senior, Hill, González del Pliego, et al., 2017); thus, secondary vegetation may provide temporary thermal refugia for migrating species, or those living near their thermal tolerance limits and unable to track climatic changes

(Dent & Wright 2009; Senior, Hill, González del Pliego, et al., 2017). My results partly agree with these expectations, with the smallest differences in community-average climatic niche often observed between primary and advanced secondary vegetation, but not to the degree that other research suggests (particularly within the tropics). Instead, I find that the thermal niches of species within secondary vegetation can be distinguished from species found in primary vegetation, with community-average climatic niches in young secondary vegetation generally differing more than those in plantations when compared to primary vegetation.

Despite a prevalent use of distribution maps to describe species' realised niches and community weighted means (CWMs) to quantify changes in the structure of ecological assemblages (e.g., Allan et al., 2019; Barnagaud et al., 2013; Betts et al., 2017; Khaliq et al., 2017; Merckx & Van Dyck, 2019; Peters et al., 2019), these methods have potential pitfalls. First, if a species is tolerant of human-altered land uses, they may be able to expand their ranges into cooler, previously uninhabitable climates, by switching habitats and colonising the warmer human-altered habitat (e.g., along elevational gradients; Frishkoff, Gabot, et al., 2019). If this has happened historically, before species' ranges were mapped, calculating realised thermal niches from current distributions may lead to a too-low estimate of the minimum temperature that a species can actually tolerate. However, human-altered land uses that are unable to buffer temperatures have colder minima compared to natural vegetation (De Frenne et al., 2019; Ewers & Banks-Leite, 2013), so even if species do expand into new areas by colonising human land uses, they may still face colder extremes. Further work focusing on the propensity of species to switch habitats along climate gradients and the climatic differences populations will experience there is a key future research direction. Second, CWMs have the potential to have inflated type I error rates (Miller et al., 2019). However, I am confident in my observations that human-dominated land uses are favouring species affiliated with more extreme climates based on multiple lines of evidence. (1) The majority of my results are robust based on comparisons to null model expectations and removal of extreme data. (2) I observe consistent patterns in my abundance analyses, where I do not use CWMs, that in human-altered land uses species affiliated with lower maximum temperatures or wetter minimum precipitation levels often have lower abundances in comparison to primary vegetation than warmer- or drier-affiliated species. I urge caution however in interpreting the range-wide variation results, as these were not strongly supported with respect to null model expectations.

Building a complete understanding of how land use and climate change interact to apply similar or contrasting pressures is vital to predict biodiversity change accurately (Oliver & Morecroft, 2014). Key future directions for research include integrating predictions based on fundamental climatic niches (though these are currently not available for the range of species analysed and are also difficult to estimate in a way that reflects real-world conditions; see Mitchell et al., 2018) and the comparison of these predictions with results based on realised tolerances (which may not accurately reflect physiological climatic tolerances; Chapter 2; Araújo et al., 2013; Khaliq et al., 2017; Rolland et al., 2018).

Overall, human-altered habitats favour species affiliated with higher maximum and lower minimum temperatures and higher maximum and lower minimum precipitation levels, leading to shifts in community composition (turnover of species as well as shifts in abundance) between land-use types, especially within the tropics. These results are likely due, at least in part, to local climatic changes mediated by land-use change (either directly or indirectly), which lead to hotter local climates, changes in precipitation regimes (Frishkoff et al., 2015) and greater exposure to temperature extremes (Medvigy et al., 2012). My results demonstrate that land-use and climate change favour similar species, especially in the tropics, which has significant implications for the future impacts of these drivers of change. I show that minimum temperature, an often-neglected climate change variable, appears to have important impacts on community composition. Understanding the effects of land-use change, and how land use influences local climate, is key to anticipate the effects of future environmental change around the globe. This knowledge can also help us to design appropriate and effective management schemes to mitigate shifts in local climatic conditions through restoring and incorporating natural climate refugia into altered landscapes.

3.6 Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c2fqz6149. The original PREDICTS database can be downloaded from https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database. The WorldClim Version 1.4 climatic variable maps can be downloaded from http://www.worldclim.com/version1. Species distribution maps can be downloaded or requested from https://www.iucnredlist.org/resources/spatial-data-download and http://datazone.birdlife.org/species/requestdis, respectively.

Chapter 4:

Vertebrate responses to human land use are influenced by their proximity to climatic tolerance limits

4.1 Abstract

Land-use change leads to local climatic changes, which can induce shifts in community composition. Indeed, human-altered land uses favour species able to tolerate greater temperature and precipitation extremes (Chapter 3). However, environmental changes do not impact species uniformly across their distributions, and most research exploring the impacts of climatic changes driven by land use has not considered potential within-range variation. Here, I used a global dataset of terrestrial vertebrate species to explore whether a population's climatic position (the difference between species' thermal and precipitation tolerance limits and the environmental conditions a population experiences) influences their relative abundance across land-use types. By estimating species' realised climatic tolerance limits, I analysed how the abundance of species within human-altered habitats relative to that in natural habitats varied across different climatic positions (controlling for proximity to geographic range edge). I found that a population's thermal position strongly influenced abundance within human-altered land uses (e.g., agriculture). Where temperature extremes were closer to species' thermal limits, population abundances were lower in human-altered land uses (relative to natural habitat) compared to areas further from these limits. These effects were generally stronger at tropical compared to temperate latitudes. In contrast, the influences of precipitation position were more complex, and often differed between land uses and geographic zones. Mapping the outcome of models revealed strong spatial variation in the potential severity of decline for vertebrate populations following conversion from natural habitat to cropland or pasture, due to their climatic position. Overall, I highlight within-range variation in species' responses to land use, driven (at least partly), by differences in climatic position. Accounting for spatial variation in responses to environmental changes is critical when predicting population vulnerability, producing successful conservation

plans, and exploring how biodiversity may be impacted by future land-use and climate change interactions.

4.2 Introduction

Human impacts on the environment do not affect species uniformly across their distribution (Orme et al., 2019). Accordingly, spatially explicit predictions of risk of population decline are crucial for suitable and successful conservation plans (Wilson et al., 2005). Physiological tolerances to temperature and precipitation, and the proximity of individuals to these tolerance limits (i.e., how close environmental climatic conditions are to an individual's climatic tolerance limits), lead to important differences across species' ranges in responses to environmental change (Deutsch et al., 2008; Gerick, Munshaw, Palen, Combes, & Regan, 2014; Kingsolver et al., 2013; Soroye et al., 2020). By predicting where populations will be pushed beyond their climatic tolerances (thus unlikely able to persist), species bioclimatic envelopes have frequently been used to project how species' ranges may shift under global climate change (Calosi, Bilton, Spicer, Votier, & Atfield, 2010; Pearson & Dawson, 2003). However, climatic changes are not only occurring at the global level. For example, land-use changes also lead to local-scale climatic changes (Chapter 2).

Human-altered land uses (e.g., agricultural areas) are often drier and experience greater extremes of temperature than natural, undisturbed habitats (Chapter 2; De Frenne et al., 2019; Frishkoff et al., 2016). These local climatic changes occur partly due to vegetation changes; for example, evapotranspiration levels are linked to the leaf area and rooting depth of species present (Costa & Foley, 2000), and the canopy layer in naturally forested areas buffers temperature extremes, with these habitats found to have lower maximum and higher minimum (i.e., winter or night-time) temperatures compared to cleared land, such as pastures (Daily & Ehrlich, 1996; De Frenne et al., 2019; Ewers & Banks-Leite, 2013). Studies have recorded average maximum temperatures rising by up to 9°C in croplands, 7°C in pastures and 3°C in plantations compared to primary forests (Nowakowski, Watling, et al., 2017; Senior, Hill, González del Pliego, et al., 2017).

These local climatic differences are associated, directly and indirectly, with shifts in community structure (Chapters 2-3; Frishkoff et al., 2016; Piano et al., 2017).

Human-altered land uses have been found to favour species affiliated with, or able to tolerate, higher maximum and average temperatures, and lower minimum temperatures, compared to natural habitats (Chapters 2-3; Angilletta et al., 2007; Menke et al., 2011; Frishkoff et al., 2015). Affiliations with drier climates have also been linked with a higher probability of occurrence within agricultural land uses (e.g., Neotropical birds; Frishkoff et al., 2016). In addition, in Chapter 3, I found that human land uses were composed of proportionally more individuals of species from regions with wetter maximum precipitation levels. Together, this suggests human-altered land uses favour species able to tolerate greater extremes of precipitation as well as temperature.

Most research however, has not considered potential variation across species' ranges in responses to land use (Chapter 2; but see Srinivasan et al., 2019; Northrup et al., 2019 for regional examples). Consequently, populations at greater risk from land-use change may be overlooked. Here, I extend previous research by asking how populations' proximities to their species-level climatic tolerance limits affect their abundances in human-altered land uses compared to in natural habitat, across terrestrial habitats globally. Due to the local climatic differences, I hypothesise that, relative to abundances in natural habitat, human-altered land uses will filter out populations of species in environments where they experience temperature and precipitation extremes closer to their climatic tolerance limits. I hypothesise that this filtering will be greater at tropical compared to temperate latitudes. The effects of human land use, including community-level differences between natural and human-altered land uses, have previously been shown to be greater in the tropics (Chapter 3; Newbold et al., 2020), potentially due to the past relative stability of the tropical climate, within which many of the taxa present have evolved (Corlett, 2011; Pacifici et al., 2017). This suggests that individuals within this region will be more sensitive to rapid climatic (particularly temperature) changes and extreme conditions (Chapter 2; Corlett, 2011; Janzen, 1967; Pacifici et al., 2017).

The relationship between species' abundance and position within geographical or environmental space forms a lively debate (Santini, Pironon, Maiorano, & Thuiller, 2019; VanDerWal, Shoo, Johnson, & Williams, 2009; Weber, Stevens, Diniz-Filho, & Grelle, 2017). Some studies, for example, report that environmental suitability or distance from the centre of a species' environmental space (environmentally-based centre), can be considered a reasonable proxy for abundance (or at least its upper limit; VanDerWal et al., 2009; Weber et al., 2017), while others find little support for a consistent relationship between species' abundance and environmental suitability or distance from geographically- or environmentally-based centres (Dallas, Decker, & Hastings, 2017; Dallas & Hastings, 2018; Santini et al., 2019). In this chapter, I compare species' abundances within human-altered land uses *relative* to that within primary vegetation in the same part of the species' climatic space, rather than absolute abundances across a species' environmental space. Thus, I do not expect my results to be unduly influenced by the presence or otherwise of abundance variation across environmental space. Nonetheless, a population's distance from its species' range edge can impact behaviour, such as responses to forest loss (Orme et al., 2019) or exploratory behaviour (Liebl & Martin, 2012), so I account for this in my analyses below.

Finally, I extend my results to produce spatially explicit maps of the potential severity of decline of vertebrate populations in human-altered land uses, depending on proximity to climatic tolerance limits. I estimate expected average severity of decline by predicting the difference in abundance between natural and human-altered land uses depending on each population's climatic position and distance to range edge, all else being held equal (as such, actual abundance changes may differ due to other influential factors, which could be included in future work). Meeting the food demands of Earth's growing population is a major challenge and, alongside intensifying current agricultural land, this is leading to the conversion of natural habitat to agriculture (Foley et al., 2011; Millennium Ecosystem Assessment, 2005). It is important to understand how this land-use change will impact biodiversity and whether land-use impacts differ spatially (Molotoks et al., 2018); consequently, I focus on how the severity of decline following land conversion from natural habitats to agriculture (croplands and pastures) may differ across the globe. Being able to estimate how risk differs across species' ranges enhances our ability to produce suitable conservation and management strategies and plan for future land-use changes.

4.3 Methods

4.3.1 Occurrence and abundance data

I acquired occurrence and abundance data for terrestrial vertebrate species from the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) Project database (Hudson et al., 2016, 2017). There are reasonably comprehensive distribution data available for terrestrial vertebrates, thus I focused on this group so I could estimate their realised climatic tolerance limits (see below). The PREDICTS database is a collection of data from studies around the globe that have made spatial comparisons of ecological assemblages across land uses (Hudson et al., 2014). I acquired occurrence data for 4,369 species (3,117 birds, 555 mammals, 377 amphibians and 320 reptiles; of these, 4,150 species also had abundance estimates), from 161 studies across 51 countries. The PREDICTS database is hierarchically structured, whereby data from a published *Source* are divided into *Studies* (split by sampling method), which are further divided into *Spatial blocks*, and then into *Sites* (where the sampling of ecological assemblages takes place; Hudson et al., 2014). Within this chapter, I use the term ‘population’ to refer to groups of individuals of the same species at the same site.

4.3.2 Land-use data

Each site within the PREDICTS database has an assigned land-use type (table 4.1; see Appendix 2, Section 1, table S4.1), allocated by the PREDICTS Project team using a set of criteria and based on the habitat description within the original source or provided by the original study authors (Hudson et al., 2014). Land uses are also split by the intensity with which humans use the land (minimal, light, or intense use), based on factors such as chemical use, crop diversity, and disturbance level (Hudson et al., 2014). I did not include data from minimally-used urban sites (which include extensive green spaces), as assemblages within these areas may not accurately reflect assemblages within more urbanised/human-dominated areas, which were of interest in this chapter.

Table 4.1: Brief definitions of the land-use types considered in this chapter. For complete definitions, see Appendix 2, Section 1, table S4.1 and Hudson et al., (2014).

Land-use type	**Definition**
Primary vegetation	Natural vegetation with no evidence of previous destruction
Mature/Intermediate/Young secondary vegetation	Vegetation that is recovering after removal of the natural vegetation, split into three stages of recovery (mature sites being those that have been recovering for the longest, young sites being those that have started to recover most recently, and intermediate sites in between)
Plantation forest	Agricultural land used for cultivating woody crops, such as oil-palm, rubber, fruit, coffee, or timber
Cropland	Agricultural land used for cultivating herbaceous crops, including fodder for livestock
Pasture	Agricultural land used for livestock grazing
Urban	Areas of human habitation and buildings, from small green spaces, through to villages and cities

4.3.3 Distribution data

Expert-informed species' distribution maps (extent-of-occurrence maps; BirdLife International 2012; IUCN 2016a) were used to estimate species-level realised climatic tolerance limits. I extracted species' native historical ranges (areas where species were resident, or used during breeding or non-breeding seasons, including areas where the species had been reintroduced or introduced). These distribution maps were transformed into equal-area raster files (Behrmann projection, 10 × 10-km pixels; ArcGIS 10.4). Distribution maps were cut by species' elevational limits, if known (2,410 species had known upper limits, 12 had lower limits and 730 had both; BirdLife International 2018; IUCN 2016a). I also removed migratory bird species from my dataset (migratory statuses acquired from BirdLife International 2018), since these species can move between different parts of their ranges to avoid extreme climatic conditions (Robinson et al., 2009), which may lead to biases within my results.

4.3.4 Climatic tolerance limits

I estimated species' *realised* climatic tolerance limits, i.e., the highest and lowest temperature and precipitation a species' experiences within their geographic distribution. To calculate these, I overlaid the species distribution maps onto four climatic variables: precipitation of the wettest month (Pp_{max}), precipitation of the driest month (Pp_{min}), maximum temperature of the warmest month (T_{max}) and minimum temperature of the coldest month (T_{min}; WorldClim Version 1.4; Hijmans et al., 2005). These climatic variable maps contained averaged annual values from 1960 – 1990, at a resolution of 30 arc-seconds, and were resampled (using bilinear interpolation) to 10 km equal-area projection (Behrmann projection) to match the species' distribution data. I extracted the highest Pp_{max} and T_{max} values and lowest Pp_{min} and T_{min} values within each species' distribution (ArcGIS 10.4). These maxima and minima provided my estimates of each species' temperature and precipitation tolerance limits (fig. 4.1).

My analyses required data for a broad range of vertebrates from around the globe, for which the above extent-of-occurrence maps from the IUCN and BirdLife International are currently the best, and most widely used (Allan et al., 2019; Herkt et al., 2017; Khaliq et al., 2017; Shackelford, Steward, German, Sait, & Benton, 2015). Species' extent-of-occurrence tends to be underestimated by expert-informed species distribution maps, whereas area of occupancy is overestimated (Herkt et al., 2017; Hurlbert & Jetz, 2007). Therefore, I tested the robustness of my results by (a) comparing population's climatic positions (see below) produced using the expert-informed distribution maps to those using occurrence records in the Global Biodiversity Information Facility (GBIF, https://www.gbif.org), and (b) running models using the same structure as my final models (see below) using the climatic positions derived from GBIF data (Appendix 2, Section 2). GBIF provides data on species' area of occupancy, but has taxonomic and geographic biases (Meyer et al., 2015).

Biotic interactions and dispersal barriers also influence species' geographic ranges (Chapter 2; HilleRisLambers et al., 2013; Peterson et al., 2011). Therefore, I compared my estimates of climatic position (see below) acquired from distribution maps to those using estimates of thermal tolerances derived from physiological experiments (acquired from GlobTherm; Bennett et al., 2017, 2018). However, physiological thermal tolerance estimates also have issues (see Chapter 2). For example, the tolerance tests often lack real-world context due to being calculated in the absence of other factors and, for many vertebrate species, laboratory tests are not possible (see Mitchell et al., 2018; Rezende et al., 2014). Moreover, the metrics produced (such as critical thermal maxima and lethal maximums) are not comparable across studies (Araújo et al., 2013), limiting the number of species that can be analysed.

4.3.5 Climatic position

I calculated each population's 'climatic position' with respect to their species-level climatic tolerance limits; this index describes the relative position of a site between the lower and upper realised tolerance limits of a species with respect to a given climatic variable. To estimate climatic position, for each study site I extracted climate data for the same four variables as described above (Pp_{max}, Pp_{min}, T_{max}, T_{min}), using climate variable maps resampled (using bilinear interpolation) to 500 m equal-area projection (Behrmann projection) to capture differences between climatic positions for very narrow-ranged species. Then, for each population, I standardised the site-specific climatic data to range between 0 and 1 relative to species' climatic tolerance limits: for thermal tolerance limits, 0 = minimum realised temperature tolerance limit and 1 = maximum realised temperature tolerance limit, and for precipitation tolerance limits, 0 and 1 are the minimum (dry) and maximum (wet) realised monthly precipitation tolerance limits, respectively (fig. 4.1).

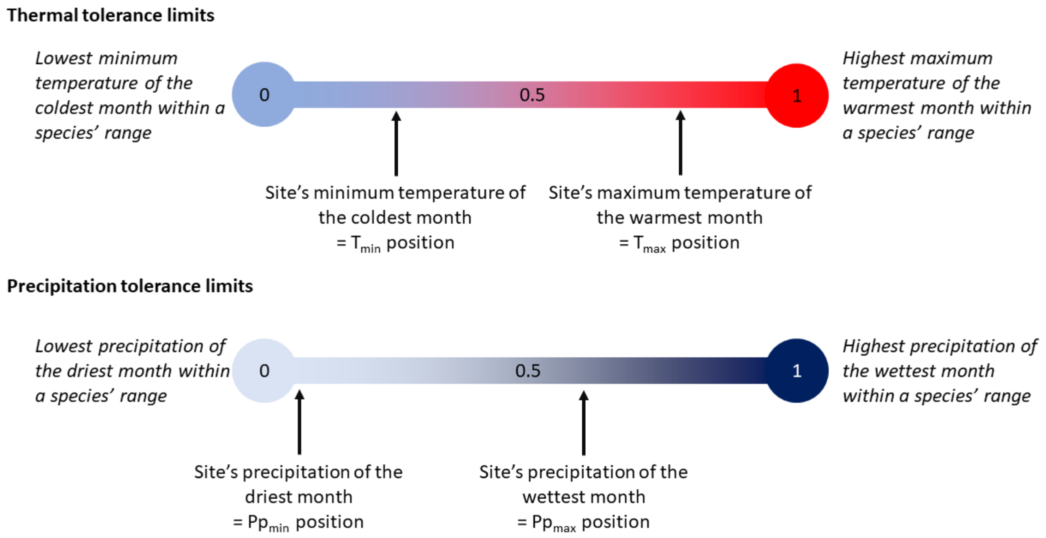


Figure 4.1: Climatic position calculation. A visual example of how the four climatic positions (T_{max}, T_{min}, Pp_{max} and Pp_{min} position) were calculated for each population; 0 and 1 represent the species-level realised thermal or precipitation tolerance limits, extracted from species' distribution maps overlaid on climatic data; the climatic positions were calculated by standardising the population's site-level climate data to range between 0 and 1 relative to the species-level climatic tolerance limits. For example, the closer the maximum temperature of the warmest month at a population's site is to the highest maximum temperature of the warmest month across a species' range, the closer a population's T_{max} position will be to 1. Similarly, the closer the precipitation of the driest month at a population's site is to the lowest precipitation of the driest month across a species' range, the closer a population's Pp_{min} position will be to 0.

A tiny subset of populations (< 0.3%) had climatic position values below 0 or above 1, due to the climatic variable maps capturing slightly greater variation at the 500 m compared to the 10 km scale (Appendix 2, Section 4, table S4.6). I assumed that the very small scale of this discrepancy would mean there was very little influence on my results.

4.3.6 Distance to range edge

To account for variation in population occurrence or abundance due to geographic position within their species' range (Orme et al., 2019), I produced a standardised distance to range edge measure for each population. I first found the shortest distance from each sampled population's location to their species' range edge (populations found outside of their stated distribution were removed from the analysis; BirdLife International 2012; IUCN 2016a). I then found the largest shortest distance from any point in the species' distribution to their range edge (i.e., the furthest distance a population could be from their range edge), by transforming species' distributions maps into a grid of points. Finally, I used this to find the relative position of the sampled population to their range edge (i.e., to account for species' range size), where a measure of 0 refers to populations at their species' range edge, and 1 refers to those nearest the range centre. This was completed in R 3.6.0 (R Core Team 2019) using packages 'raster' v.2.8.19 (Hijmans, 2019), 'rgdal' v.1.4.8 (Bivand, Keitt & Rowlingson, 2019) and 'rgeos' v.0.4.3 (Bivand & Rundel, 2019). As stated above, expert-informed species' distribution maps contain inaccuracies. To ensure that removing populations outside of their distributions did not impact my results, I reran my models (see below) without the distance to range edge measure and compared the results of models including and excluding populations beyond their species' stated distributions (see Appendix 2, Section 3 for more information).

Of the vertebrate species with occurrence data in the PREDICTS database, following the selection of species and land uses as described above, I was able to estimate tolerance limits, climatic positions, and distance from range edge for 88,007 populations, consisting of 2,103 species (384 mammals, 1,491 birds, 92 reptiles, 136 amphibians). Out of these, 81,913 populations (1,954 species) had abundance records (from studies that had sampled abundance, including those that recorded abundances of zero), and within this, 13,321 populations (1,594 species – 334 mammals, 1,087 birds, 87 reptiles, 86 amphibians) had non-zero abundance data. Ideally, I would have comparisons of species' abundance in different land uses across their geographical ranges, but samples do not exist for most species, particularly in the tropics; thus, I rely on collations of data such as the PREDICTS database, in which most of the species included have been recorded in multiple geographic locations and have several climatic position measures (Appendix 2, Section 4, table S4.4).

4.3.7 Statistical analyses

I adopted a two-stage modelling approach (similar to a hurdle model) due to the high number (84%) of abundance records that were zero (Newbold, Hudson, et al., 2014; Potts & Elith, 2006). First, I used generalised linear mixed-effects models (with binomial error distributions) to model the probability of occurrence (assuming detection; P(Occ)) of populations. Second, I used linear mixed-effects models to test for differences in log-transformed abundance (given presence; LogAbund). These models were used to assess whether a terrestrial vertebrate population's climatic position affected their abundance (a combination of a population's probability of occurrence, and relative abundance given presence) across different land uses. Analyses were carried out in R 3.6.0 (R Core Team 2019) using 'lme4' v.1.1.17 (Bates et al., 2015).

For both stages of modelling, I selected main effects and interactions using backwards stepwise variable selection, which uses maximum likelihood estimation to select terms and likelihood-ratio tests to compare the fit of different models (Zuur et al., 2009). Into this model selection I added as potential explanatory variables: (1) land-use type (categorical variable); (2) geographic zone (categorical variable: tropical [between 23.44°S and 23.44°N] or temperate [between 23.44°N/S and 66.56°N/S, respectively]); (3) distance to range edge (continuous variable) and its interaction with land-use type; (4) climatic position with regard to each climatic variable (T_{max}, T_{min}, Pp_{max} and Pp_{min} position; continuous variables fitted as linear terms, I tested for correlations between these; Appendix 2, Section 4, table S4.5); and (5) the 2- and 3-way interactions between land-use type, geographic zone, and each climatic position (e.g., land-use type × geographic zone × T_{max} position). I did not include interactions between climatic positions. A site's elevation was also considered as a continuous covariate due to its potential influence on population abundance (Williams, Shoo, Henriod & Pearson, 2010). For random effects, I included a nested random-intercept term for study (to account for study-dependent variation in methods or measures used) and for sampled site within studies. I also included a random-intercept term for species name, accounting for species-level differences unrelated to land-use type or climatic position. I then ran the final occurrence (assuming detection) and abundance (given presence) models, which included significant fixed effects and interaction terms, and any lower-order, non-significant interaction terms that were nested within significant higher-order interactions.

4.3.8 Robustness checks

I also ran five separate sets of models (using the same structure as the final models above) that (1) only included species of mammals and birds (to ensure my results held for endothermic species, who may be less affected by local climatic changes; Chapter 2), (2) excluded forest specialist species (to ensure my results held for species also found in naturally drier and/or open environments such as grasslands; forest specialist species were defined using species-level habitat preference data (IUCN 2017a); I acknowledge that forest specialism may differ across species' ranges, but unfortunately habitat preference data are currently not available at the population level; Appendix 2, Section 8), (3) fitted climatic positions as quadratic terms (to test for hump-shaped relationships that might occur if populations are sensitive close to any climatic tolerance limit, rather than the specific limits I hypothesised), (4) combined mature and intermediate secondary vegetation land uses (to become an 'advanced secondary' land-use type) and (5) again combined mature and intermediate secondary vegetation land uses but also removed populations within urban sites (to ensure the results were robust with and without the inclusion of land uses with a smaller number of sampled sites). Further, when working with complex datasets, results may potentially differ due to modelling method, so I ran my models using a range of optimisers (allFit function, 'lme4' package; Bates et al., 2015) to check the consistency of my results. I also ran a set of models (again with the same structure as the final models above) using a Bayesian modelling approach (package 'MCMCglmm' v.2.29; Hadfield 2010); these models ran for 60,000 iterations, had a burn-in period of 3,000 iterations and a thinning interval of 10, and I used uninformative priors (the default priors in 'MCMCglmm'), with convergence checked through visual inspection of the MCMC trace plots. Finally, responses to climatic position and land-use type may differ among species, so I ran a set of models including random slopes to account for interspecific differences (i.e., allowing the response of each species to climatic position or land-use type to vary).

4.3.9 Severity of decline following land conversion

To highlight where vertebrate populations may experience more severe declines due to their climatic position and the local climatic changes brought about by land-use change, I produced maps of estimated community-average abundance in cropland and pasture relative to that in primary vegetation, based on the climatic positions of populations within each community. I focused on agricultural land uses because the need to produce enough food to sustain Earth's growing population will likely result in agricultural expansion and intensification (Foley et al., 2011; Millennium Ecosystem Assessment, 2005). To do this, I used the available expert-informed terrestrial vertebrate species' distribution maps (BirdLife International 2012; IUCN 2016a), processed them as described above and removed migratory bird species (BirdLife International 2018). This left me with 22,267 species (5,074 mammals, 8,179 birds, 5,139 amphibians, 3,875 reptiles). For each species, I then produced maps of T_{max}, T_{min}, Pp_{max} and Pp_{min} (WorldClim Version 1.4; Hijmans et al., 2005) across their distribution and standardised them to between 0 and 1 in the same way as above. Then, using the main-effect and interaction estimates (Appendix 2, Section 6, table S4.7) from the final models (described above), I found the model-estimated probability of occurrence and abundance (given presence) of each species across their range, based on their climatic position, in primary vegetation (*PV*), cropland (*Cr*) and pasture (*Pa*). Following this, for each species, I multiplied the probability of occurrence (*P(Occ)*) and the abundance (given presence; *Ab*) results together (separately for each land use), and then expressed this expected abundance in cropland and pasture relative to that in primary vegetation (i.e., relative abundance, *RA*; equation 4.1 and 4.2, for relative abundance within cropland and pasture, respectively):

$$(4.1) \qquad RA_{Cr} = \frac{P(Occ)_{Cr}\ x\ Ab_{Cr}}{P(Occ)_{PV}\ x\ Ab_{PV}}$$

$$(4.2) \qquad RA_{Pa} = \frac{P(Occ)_{Pa}\ x\ Ab_{Pa}}{P(Occ)_{PV}\ x\ Ab_{PV}}$$

I then averaged and plotted the species-level results within each 10 × 10-km grid cell to display expected community-average severity of decline following conversion of primary vegetation to cropland or pasture, where the 'community' included all the populations whose species' range covered that cell. This was completed in ArcGIS 10.4 (ESRI 2015).

To ensure I did not extrapolate beyond the limits of my data, I found the predicted relative abundance within cropland and pasture for each population from the PREDICTS database included in my models (again using the main-effect and interaction estimates from my models). I then averaged these predicted values for populations in cropland or pasture within each PREDICTS site, producing site-level-average (i.e., community-average) relative abundances, and extracted the minimum and maximum site-level-average relative abundances for each land use. Finally, when producing the global maps described above showing the community-average severity of decline, I only plotted values that fell within these limits (only a very small proportion of the Earth's land surface was excluded in this way).

4.4 Results

4.4.1 Summary of results

Overall, the relative abundance of a species across land uses differed depending on the populations' thermal position and Pp_{min} position, with these effects differing between geographic zones (p values from the backwards stepwise selection process for the interaction between land-use type, geographic zone and (a) T_{max} position, $p_{P(Occ)} = 0.012$, $p_{LogAbund} = 0.001$ (b) T_{min} position, $p_{P(Occ)} = 0.008$, $p_{LogAbund} = 0.186$ (the 3-way interaction was not significant, but the 2-way interaction between T_{min} position and land use was, $p_{LogAbund} = 0.002$), (c) Pp_{min} position, $p_{P(Occ)} < 0.001$, $p_{LogAbund} < 0.001$; figs. 4.2-3, table 4.2; for comprehensive plots for each climatic position, see Appendix 2, Section 4, figs. S4.8-11; for coefficients and their 95% confidence intervals, see Appendix 2, Section 9, figs. S4.20-21). The results supported my hypotheses with regard to thermal position, with populations in human-altered sites where temperature extremes were closer to the species' maximum and minimum thermal limits generally having lower abundances relative to primary vegetation compared to populations that experienced temperatures further from these tolerance limits (fig. 4.2). However, the precipitation position results were more mixed across land-use types (fig. 4.3), not always supporting my predictions. Large spatial differences in community-average severity of decline following agricultural conversion, when based on populations' climatic positions, were also apparent in my global maps (fig. 4.4). Most of the observed results were driven by differences in populations' probability of occurrence, rather than by differences in the abundance of persisting species (Appendix 2, Section

5, figs. S4.12-13). Due to the small number of urban sites in the dataset ($n_{tropical} = 41$, $n_{temperate} = 74$, from 2 and 3 studies, respectively), I exclude the results for this land-use type. I also advise caution when interpreting the results within temperate mature and intermediate secondary vegetation, as there were fewer than 50 sites sampled within these groupings (Appendix 2, Section 4, table S4.3).

Table 4.2: Model structure and interaction significance. The final probability of occurrence (P(Occ)) and abundance (given presence; LogAbund) model structures and the significance (*p*-values) of the climatic position × land-use type interaction terms included in the models (i.e., whether the slope of the relationship of probability of occurrence or abundance – given presence – with climatic position for a given land use was significantly different to the slope for primary vegetation). These final models were used to investigate the influence of climatic position with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}) and precipitation of the wettest (Pp_{max}) and driest (Pp_{min}) months, on a population's probability of occurrence, or abundance (given presence) across different land-use types (LU; these included primary vegetation, different stages of secondary vegetation (mature, intermediate and young; MSV, ISV, and YSV respectively), plantations, croplands, pastures, and urban areas) at tropical and temperate latitudes (geographic zone; GZ). Distance to range edge (Dist) was also added as a covariate. In terms of random effects, a nested random-intercept term for study (SS; to account for study-dependent variation in methods or measures used) and for sampled site within studies (SSBS) was included in all models, along with a random-intercept term for species name (Species). Statisticians advise caution when interpreting *p*-values from mixed-effects models (Bates et al 2015; Luke, 2017).

Probability of occurrence model	Abundance (given presence) model
Model structure	
$P(Occ) \sim Intercept + LU + GZ + T_{max} + T_{min} + Pp_{min} + Pp_{max} + Dist + LU{\times}GZ + LU{\times}Dist + LU{\times}T_{max} + LU{\times}T_{min} + LU{\times}Pp_{max} + LU{\times}Pp_{min} + T_{max}{\times}GZ + T_{min}{\times}GZ + Pp_{max}{\times}GZ + Pp_{min}{\times}GZ + LU{\times}T_{max}{\times}GZ + LU{\times}T_{min}{\times}GZ + LU{\times}Pp_{min}{\times}GZ + (1\|SS) + (1\|SSBS) + (1\|Species)$	$LogAbund \sim Intercept + LU + GZ + T_{max} + T_{min} + Pp_{min} + Dist + LU{\times}GZ + LU{\times}T_{max} + LU{\times}T_{min} + LU{\times}Pp_{min} + GZ{\times}T_{max} + GZ{\times}Pp_{min} + LU{\times}T_{max}{\times}GZ + LU{\times}Pp_{min}{\times}GZ + (1\|SS) + (1\|SSBS) + (1\|Species)$

Significance of key terms[+]

Tropical latitudes

Probability of occurrence model

	MSV	ISV	YSV	Plantation	Cropland	Pasture
Tmax		***	*	***	***	***
Tmin		***			***	**
Ppmax		*			*	***
Ppmin		*		**	***	

Abundance (given presence) model

	MSV	ISV	YSV	Plantation	Cropland	Pasture
Tmax						
Tmin			*	*	*	
Ppmax	▨	▨	▨	▨	▨	▨
Ppmin				*		

Temperate latitudes

Probability of occurrence model

	MSV	ISV	YSV	Plantation	Cropland	Pasture
Tmax			*			
Tmin			***			
Ppmax						
Ppmin						

Abundance (given presence) model

	MSV	ISV	YSV	Plantation	Cropland	Pasture
Tmax				*		
Tmin						
Ppmax	▨	▨	▨	▨	▨	▨
Ppmin						

[+] Shaded = interaction term was not included in this model, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

4.4.2 Thermal position

At tropical latitudes, in most human-altered land uses, populations with high T_{max} positions or low T_{min} positions (thus in sites where they experience temperature extremes closer to their maximum or minimum thermal limits, respectively), had much lower abundances relative to those in primary vegetation (by 25-50%), than populations in sites with temperatures further from their thermal limits (fig. 4.2). This filtering out of populations close to their thermal limits was not seen in mature secondary vegetation, where abundances showed little difference relative to primary vegetation. Interestingly, within tropical plantations and croplands, populations further from their thermal limits had higher abundances relative to populations with the same T_{max} or T_{min} position in primary vegetation.

At temperate latitudes, populations with high T_{max} positions again had lower relative abundances in plantations and croplands, and those with low T_{min} positions had lower relative abundances in plantations, croplands, and young secondary vegetation (fig. 4.2), compared to populations further from their thermal limits.

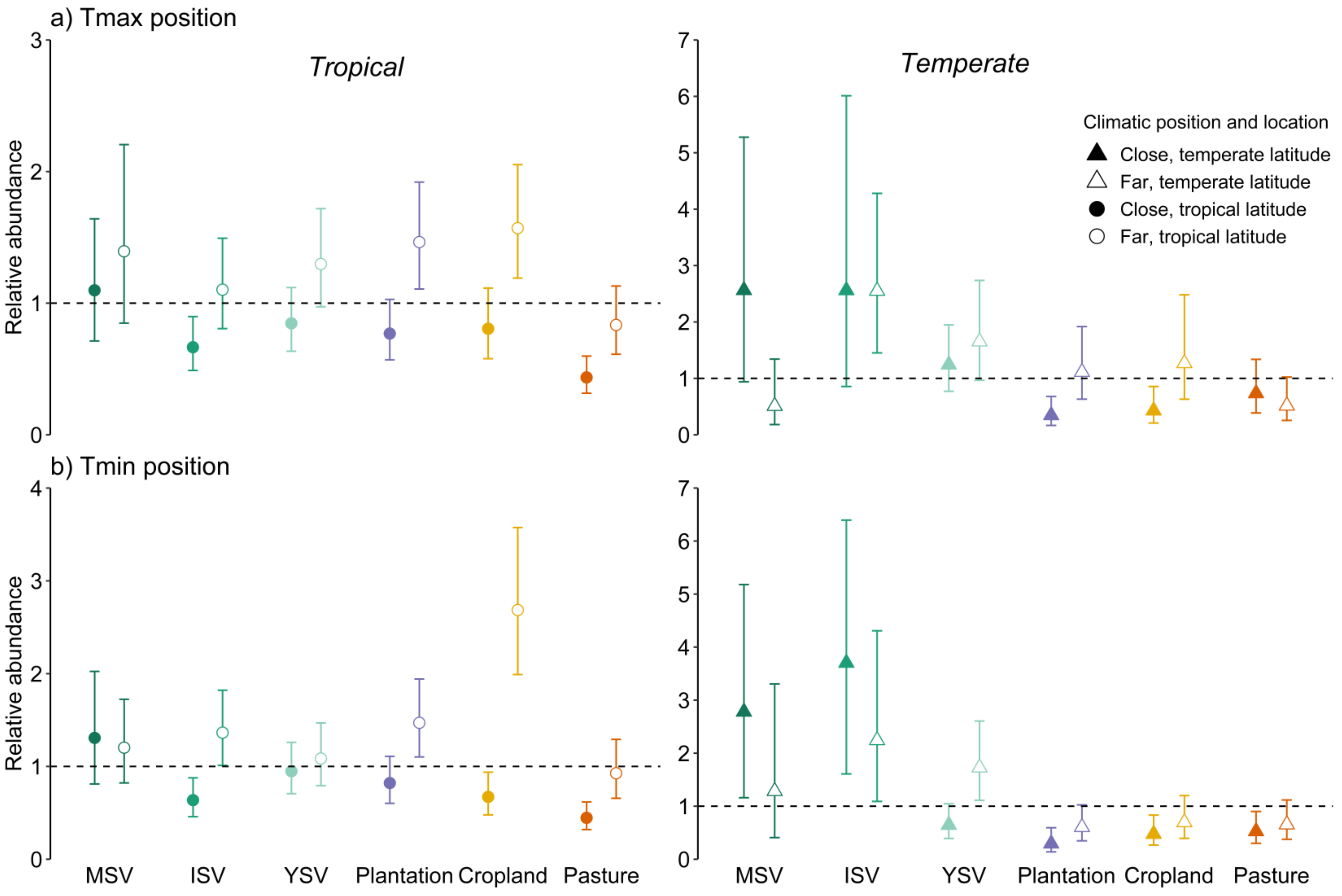

a) Tmax position
Tropical
Temperate
Relative abundance
0
1
2
3
4
5
6
7
Climatic position and location
▲ Close, temperate latitude
△ Far, temperate latitude
● Close, tropical latitude
○ Far, tropical latitude
b) Tmin position
MSV
ISV
YSV
Plantation
Cropland
Pasture

Figure 4.2: The relative abundance of populations across land uses depending on their thermal position. The abundance of species within each land-use type, relative to abundance in primary vegetation (indicated by the dotted line), for populations with T_{max} or T_{min} positions 'close' or 'far' from their thermal tolerance limits at tropical and temperate latitudes. For (a) a population's T_{max} position, 'close' and 'far' refer to a position of 0.9 and 0.7, respectively, for both tropical and temperate latitudes. For (b) a population's T_{min} position, 'close' and 'far' refer to a position of 0.2 and 0.6 at tropical latitudes, and 0.1 and 0.4 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of T_{max} or T_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively.

4.4.3 Precipitation position

A population's Pp_{max} position was not found to influence abundance (given presence), but did effect their probability of occurrence at a site, which also differed across land uses (land-use type × Pp_{max} position, $p_{P(Occ)} < 0.001$, fig. 4.3). Populations experiencing maximum monthly precipitation closer to their maximum precipitation limit (higher Pp_{max} positions) had a lower relative probability of occurrence in croplands and pastures than populations with lower Pp_{max} positions.

Contrary to expectations, in many human-altered land uses, and particularly at tropical latitudes, populations with lower Pp_{min} positions (in sites with minimum monthly precipitation closer to their dry limit), had similar abundances to those in primary vegetation, whereas populations further from their dry limit had lower relative abundances. Different patterns were observed in tropical pastures, where populations with lower Pp_{min} positions were being filtered out (i.e., had lower relative abundances compared to populations with higher Pp_{min} positions). Within temperate plantations and croplands, there was little difference in relative abundances across Pp_{min} positions.

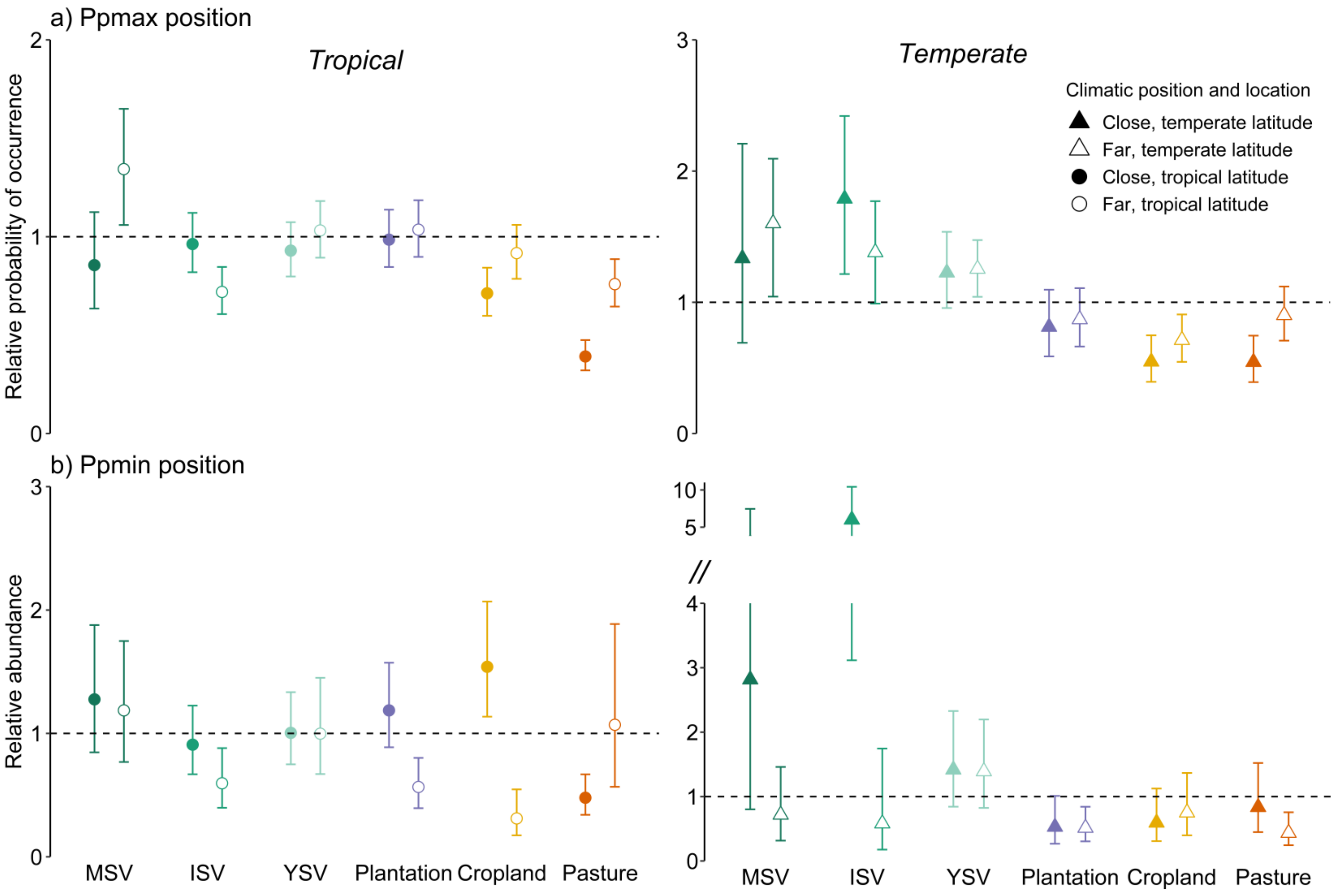

a) Ppmax position
Tropical
Temperate
Relative probability of occurrence
0
1
2
3
Climatic position and location
▲ Close, temperate latitude
△ Far, temperate latitude
● Close, tropical latitude
○ Far, tropical latitude
b) Ppmin position
Relative abundance
0
1
2
3
4
5
10
//
MSV
ISV
YSV
Plantation
Cropland
Pasture

Figure 4.3: The relative probability of occurrence or abundance of populations across land uses depending on their precipitation position. The (a) probability of occurrence or (b) abundance of species within each land-use type, relative to that in primary vegetation (indicated by the dotted line), for populations with (a) Pp_{max} or (b) Pp_{min} positions ‘close’ or ‘far’ from their precipitation tolerance limits at tropical and temperate latitudes. For (a) a population’s Pp_{max} position, ‘close’ and ‘far’ refer to a position of 0.6 and 0.2 at tropical latitudes, and 0.4 and 0.1 at temperate latitudes, respectively. For (b) a population’s Pp_{min} position, ‘close’ and ‘far’ refer to a position of 0 and 0.2 at tropical latitudes, and 0 and 0.1 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of Pp_{max} or Pp_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively. I plot relative probability of occurrence (rather than relative abundance) for Pp_{max} positions because a population’s Pp_{max} position was not found to have a significant effect on abundance, and so was not included in the final abundance (given presence) model. I use a broken y-axis (represented by //) on the plot for Pp_{min} position at temperate latitudes so that the smaller effect sizes can be more easily interpreted.

4.4.4 Robustness checks

I used GBIF data to estimate realised climatic tolerance limits for 1,995 species (84,988 populations) included in my models. The climatic positions produced using these tolerance limits were moderately to strongly positively correlated to those using expert-informed species’ distribution maps ($r > 0.67$; Appendix 2, Section 2, table S4.2). The results of the models run using these climatic positions (rather than those found using species’ distribution maps) were qualitatively identical to the results presented above, but abundances within some land uses (such as mature secondary vegetation, croplands, and pastures) relative to primary vegetation differed slightly (Appendix 2, Section 2, figs. S4.1-2).

Only 76 species included in my models had estimates of physiological thermal tolerance limits within GlobTherm (Bennett et al., 2018). Four of these were estimates of critical thermal maxima and minima, 71 were estimates of thermal neutral zone boundaries, and one was an estimate of the lethal temperatures at which mortality of

50% or 100% of individuals occur. The measures of thermal position calculated using my estimates of realised thermal tolerance limits and using estimates of physiological thermal tolerance limits from GlobTherm were positively correlated (Pearson's correlation coefficient, T_{max} position, $r = 0.62$, T_{min} position, $r = 0.50$).

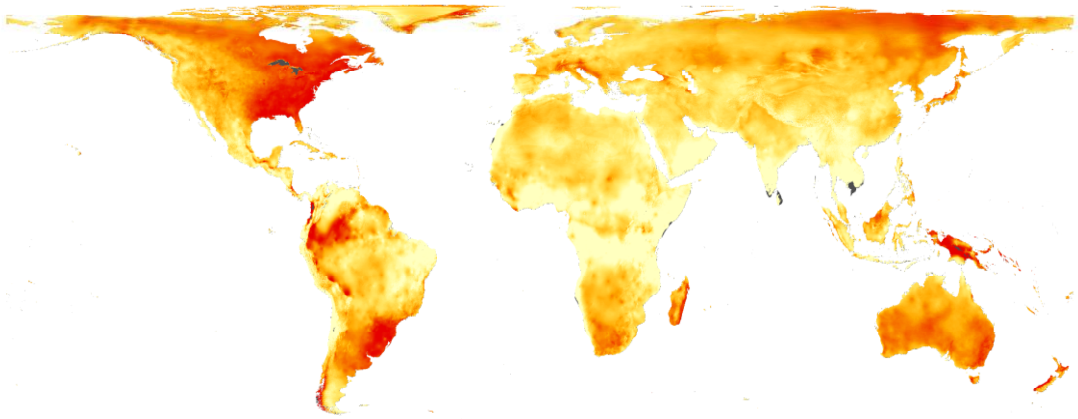
A population's relative abundance differed with their proximity to the species' range edge (Appendix 2, Section 4, fig. S4.7), which further interacted with land use to impact a population's probability of occurrence ($p = 0.003$). When comparing models excluding this distance to range edge measure that included or excluded populations recorded outside of their species' distributions, as stated by the IUCN (2016a) and BirdLife International (2012), the main qualitative results were very similar (Appendix 2, Section 3, figs. S4.3-6). The only exception to the robustness of my results to including and excluding populations outside of their stated range maps was the relationship between Pp_{min} and relative abundance within tropical pastures. In this case, when populations outside of their stated ranges were included, the pattern now matched that seen within cropland and plantations (where populations with higher Pp_{min} positions had lower relative abundances than those with lower Pp_{min} positions). The majority of populations that were recorded outside of their species' distributions were relatively close to their range edges (with a median distance of 16.3 km, and with 75% of populations outside their ranges being within 71 km). Populations recorded furthest from their stated range edges, upon inspection, were found to be populations of species invasive to the recorded location.

The results of models only including endotherms or excluding forest specialists (Appendix 2, Sections 7-8, figs. S4.16-19), were very similar to those presented above. Fitting climatic positions as quadratic terms did not change the pattern of results. Further, including different combinations of land uses, using different optimisers (results not shown), or using Bayesian modelling (Appendix 2, Section 9, figs. S4.20-21) all produced very similar results to those reported above. Finally, models including random-slope terms produced similar results to the models above (Appendix 2, Section 10, figs. S4.22-24); I report the results from the random-intercept model here because of convergence issues with the random-slope models.

4.4.5 Severity of decline following land conversion

Community-average severity of decline following conversion to agricultural land uses, based on populations’ climatic positions, differed greatly across space (fig. 4.4). Communities expected to experience the most severe declines following conversion to cropland, due to the climatic positions of the populations present, appeared in north eastern North America, south eastern South America, Australia, and New Guinea. Conversely, the average severity of decline within communities across equatorial Africa and southeast mainland Asia appeared to be lower, which may be a result of local climatic changes following land-use change producing more favourable conditions (which could lead to population increases). Following conversion to pasture, communities in central North and South America, Australia, western Africa, and northeast Asia may experience the most severe declines, whereas equatorial Africa and parts of Europe were predicted not to experience such severe declines, based on the climatic positions of the populations present. As stated above, these maps are not displaying which areas *will* see abundance decreases or increases following land-use change, but instead present locations where the potential average severity of declines within communities *may* be higher or lower following conversion of natural habitat to agricultural land uses due to how close the local climatic conditions are to the realised climatic tolerance limits of the populations present. These maps can also be viewed as highlighting areas within which habitat restoration may be particularly effective, on the basis of the local populations’ climatic positions.

a) Cropland



b) Pasture

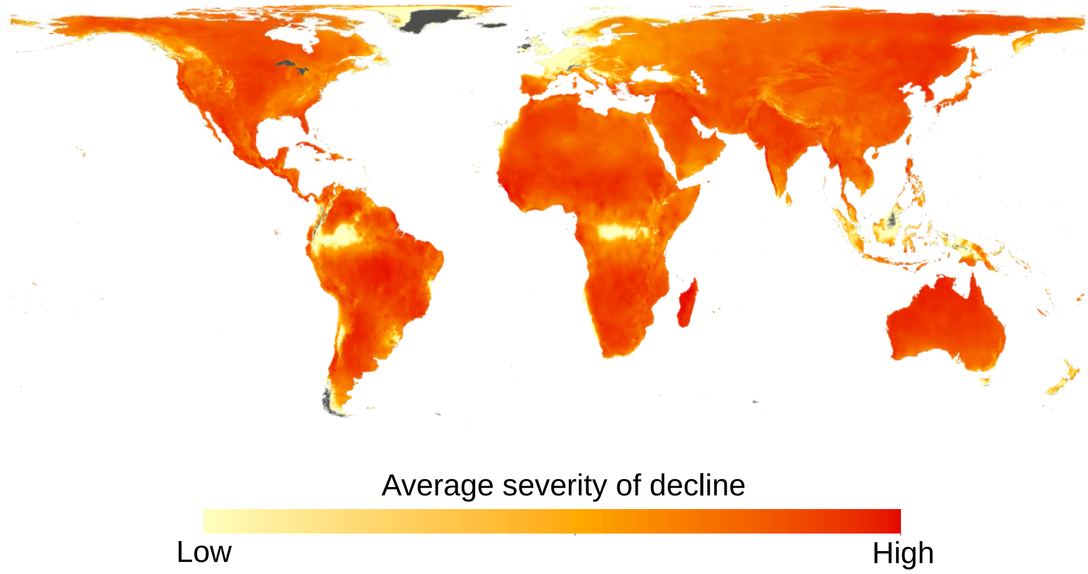


Figure 4.4: The average severity of decline of terrestrial vertebrate communities following conversion of natural habitat to (a) cropland and (b) pasture, based on the climatic positions of populations within each community. I estimated severity of decline by calculating the abundance of populations in (a) croplands and (b) pastures, relative to that in primary vegetation (depending on each population's climatic position) and averaged this within each community (10 × 10-km pixel). I present global maps (Behrmann projection) to demonstrate how the potential severity of decline within communities may differ due to the local climatic changes following land-use change, whilst recognising that land conversion from primary vegetation to

agriculture is not possible, or has already happened, for large parts of the world (although these maps could also be useful in highlighting areas in which habitat restoration may be more beneficial, based on the climatic positions of the local populations). Dark grey areas represent locations that were not covered by any of the species' ranges in my dataset (some of the Great Lakes in North America, for example), or where community-average measures were beyond the limits of my dataset (see methods). The scale of severity is separate for each map, based on the limits of community-average abundances within each land-use type, relative to expected abundances within primary vegetation. For cropland and pasture, respectively, the deepest red (greatest average severity of decline) represents community-average relative abundances of 0.13 and 0.07 (to 2 decimal places), the lightest yellow (lowest average severity of decline) represents community-average relative abundances of above 2 and up to 1.61, and the middle colour of orange represents a community-average relative abundance of 1. Relative probability of occurrence patterns were similar, but for croplands patterns were generally more negative (Appendix 2, Section 6, fig. S4.15). I also produced maps displaying the percentage of populations in each community with abundances in croplands and pastures predicted to be half or less than that in primary vegetation, based on populations' climatic positions (Appendix 2, Section 6, fig. S4.14).

4.5 Discussion

Populations' thermal positions strongly influenced abundance across land-use types, with stronger effects often observed at tropical latitudes. As predicted, human-altered land uses generally appeared to be filtering out populations experiencing temperature extremes close to their maximum or minimum thermal limit. Populations experiencing maximum monthly precipitation closer to their wet limit also had a lower probability of occurrence in human-altered land uses, in line with my predictions. However, the influences of climatic position regarding minimum monthly precipitation were more complex and did not consistently support my hypothesis. I also demonstrate how my results can be used to highlight communities that may experience more severe declines following habitat conversion due to the climatic positions of the populations present. Consequently, this chapter emphasises how species' responses to human-altered land uses can differ significantly across their distributions, which is essential to account for when assessing risk, predicting future changes, and mitigating negative impacts from global drivers of change.

In general, agricultural land (plantations, croplands, and pastures) filtered out populations where maximum temperatures were close to species-level maximum thermal limits and populations at sites with minimum temperatures close to species-level minimum thermal limits. Conversion from a natural to human-altered land use usually leads to hotter and colder local temperature extremes (De Frenne et al., 2019). For populations closer to their thermal limits, these climatic changes may push ambient temperatures beyond species' tolerance limits, directly impacting individuals (Chapter 2; Frishkoff et al., 2016). Heat or cold stress can cause population decline because they can negatively impact processes such as reproduction (Manning & Bronson, 1990) and development (Russell et al., 2002), or lead to death (Welbergen et al., 2008). Temperature changes can also directly impact individual's metabolic rates (through effects on biochemical reaction rates; Gillooly et al., 2001), influencing energy use and, consequently, the demand for food and allocation of energy resources (Barneche, Jahn, & Seebacher, 2019; Dillon, Wang, & Huey, 2010). For species relying on behavioural rather than physiological adaptations to cope with unfavourable temperatures, population declines could result from loss of thermal refugia following land-use change (Betts et al., 2018; Sunday et al., 2014). Populations closer to their thermal limits would be the most negatively impacted if individuals could no longer use refugia to escape thermal extremes. There were also geographical differences in the effect of thermal position on relative abundance within human-altered land uses. For instance, differences in relative abundance between populations with different climatic positions were greater at tropical compared to temperate latitudes; this is consistent with previous work suggesting species at lower latitudes are more sensitive to temperature changes due to the past stability of the tropical climate (Janzen, 1967). Interestingly, in tropical plantations and croplands, populations experiencing thermal extremes further from their thermal limits had higher abundances compared to populations at the same thermal position in primary vegetation. This could be due to the local climatic conditions within these human-altered land uses being more favourable for species found within the region than conditions within primary vegetation. Similar scenarios have been observed along elevational gradients, whereby localised warmer maximum temperatures following deforestation has facilitated the invasion of these areas by species from lower elevations (leading to these populations having higher abundances within human-modified land uses compared to nearby primary vegetation; Frishkoff, Gabot, et al., 2019).

Unexpectedly, populations at sites where minimum monthly precipitation was closer to species-level dry limits often had similar or higher relative abundances than populations further from this limit, particularly in tropical plantations and croplands. For 79% of populations with Pp_{min} position values of 0 (i.e., in sites where they experience the lowest monthly precipitation of anywhere in the species' distribution), the absolute precipitation tolerance limit was zero (i.e., no rainfall in the driest month). Thus, I propose my results may be due to these populations already experiencing very low rainfall levels in their natural habitats, meaning they may have behavioural strategies to cope with droughts. Consequently, these populations that are already tolerant of very dry conditions (compared to those further from their dry limits) may be better at coping with, or less negatively impacted than expected by local climatic changes following conversion from natural to human-altered land uses. Additionally, the magnitude of change in minimum precipitation with land-use change may be smaller in such dry areas, because although drought duration may increase, you cannot get less rainfall in the driest month if the minimum is already zero. However, I acknowledge that my minimum precipitation position measure cannot distinguish between populations that experience a single month versus multiple months of no rain. Therefore, complementary work using temporal data is needed to look at the impacts of land-use change on minimum precipitation in drier areas, and the variation in how local populations react to these changes.

Overall, the influence of a population's precipitation position was complex. As well as the unexpected results regarding Pp_{min} position, a population's Pp_{max} position was found to influence a population's probability of occurrence, but not their abundance if they were present. Previous work has highlighted the complexity of precipitation regime changes on biodiversity, partly due to its complex interactions with other abiotic (e.g., moisture) and biotic (e.g., plant growth) factors in the environment, making detecting the underlying mechanisms difficult (Chapter 2; Brown et al., 2001; Fu et al., 2003). For example, changes in the distribution of precipitation (timing and/or severity) impact soil water content, which can substantially affect plants and their processes (see Zeppel, Wilks, & Lewis, 2014), but whether these effects are positive or negative depends (at least partly) on the initial climatic conditions, such as aridity and the season the changes occur in (Morecroft et al., 2004; Zeppel et al., 2014). These complicated impacts on vegetation likely have knock-on effects for local vertebrates, and may act alongside or interact with the direct impacts of local water or moisture availability changes (Brown et al., 2001). Another complication of investigating the effects of local precipitation changes, is that irrigation systems are often used within human-altered land uses, impacting water vapour concentration (Boucher, Myhre, & Myhre, 2004). These artificial water systems may alter how populations are affected by local climatic changes. Consequently, although my results provide a start to exploring the impact of precipitation position on responses to human-altered land uses, due to the complexity of rainfall regimes, moisture availability and human impact (through land-use change and irrigation), alternative methods using different precipitation measures are needed to explore the influence of precipitation changes, and the mechanisms underlying its impact on vertebrate populations further. Ideally, biologically meaningful measures of moisture availability (at species-specific spatial scales) would be used with site-specific irrigation considered, but data on both are rare.

Secondary vegetation is suggested to be important in biodiversity conservation, potentially providing refugia from certain threats, such as global climatic changes (Dent & Wright, 2009; Senior, Hill, González del Pliego, et al., 2017). Generally, I find only mature secondary vegetation has the potential to provide thermal refugia, particularly at tropical latitudes. The inability of tropical earlier-stage secondary vegetation to provide refugia for populations close to their thermal tolerance limits is concerning, especially as thermal refugia are becoming increasingly important as land-use changes continue alongside global climate change, pushing temperatures even higher (Collins et al., 2013; Frishkoff et al., 2016; Jarzyna et al., 2016).

My results suggest the impacts of land use on vertebrate populations vary spatially, with the effect of temperature and precipitation changes differing with land use and latitude. For example, focusing on plantations, croplands, and pastures, it appears that while T_{max} positions may have large impacts globally on how populations are impacted by these land uses, T_{min} position has a greater impact on variation between populations at tropical compared to temperate latitudes. While I recognise land conversion from natural habitat to agriculture has already occurred or is not possible across large expanses of the Earth's terrestrial surface, I show that the potential severity of decline following land-use change likely differs greatly across space, depending on populations' climatic positions. I also observed that this spatial variation differed between conversion to cropland versus pasture, which may be due to the differences observed in the impact of a population's Pp_{min} position within these two land uses (see fig. 4.3). This variation is critical to account for as we predict how vertebrate populations might react to future land-use changes. Further research is needed into the mechanisms underlying how local climatic changes impact populations with different climatic positions, which will help to refine these maps. Within my model, I had a larger number of sites at tropical compared to temperate latitudes (Appendix 2, Section 4, table S4.3), and gathering more data for sites within temperate latitudes may also help to refine results across this area. My maps display estimates of mean potential severity of decline across the populations present in each cell, due to their climatic position, and do not make predictions of absolute abundance, which would require inclusion of other factors influencing species' responses to land-use change, such as biotic interactions and habitat preferences.

Overlaying climatic data on species' distribution maps to estimate species' realised climatic tolerance limits allowed me to include over 2,000 species within my models and study the impacts of temperature and precipitation positions across geographic zones. Using species' distribution or occurrence data with climatic data to calculate climatic affiliations has been widely used, especially when studying species' responses to land-use or global climate change (e.g., Barnagaud et al., 2013; Barnagaud et al., 2012; Frishkoff et al., 2016; Oliver et al., 2017). Nevertheless, I acknowledge that by using global climate data, I do not account for the microclimates species experience or potential intraspecific variation in climatic tolerances. Furthermore, species' observed distributions are also influenced by biotic interactions and barriers to dispersal (HilleRisLambers et al., 2013; Peterson et al., 2011). Consequently, my approach, which estimates realised climatic tolerance limits, may not precisely reflect species' physiological tolerances. Unfortunately, estimates of physiological thermal limits are only available (or obtainable) for a very small number of vertebrate species (Araújo et al., 2013), and estimates of physiological precipitation or moisture tolerance limits are rare (Sunday et al., 2012). Even if they were available, physiological climatic tolerance limits estimated under laboratory settings also have limitations (see Chapter 2). Therefore, I consider my approach to be the best with the data currently available. Lastly, I acknowledge that my approach is correlative, so there may be other factors underlying the differences in relative abundance across climatic positions between land uses and, as previously mentioned, further work is needed to ascertain the underlying mechanisms.

In conclusion, my results suggest that the proximity of temperature extremes to species-level thermal limits affects the relative abundance of vertebrate populations across human-altered land uses, with populations in sites where temperature extremes are closer to their maximum or minimum thermal limit being filtered out of most human-altered land uses. Proximity to minimum and maximum monthly precipitation extremes was also found to influence species' relative abundance and probability of occurrence, respectively, in human-altered land uses. These results are likely due, at least in part, to the local climatic changes following land-use change directly and/or indirectly impacting vertebrate populations. Overall, I highlight variation in responses to human-altered land uses across a species' range, depending on population's climatic positions. This variation has important implications when assessing risk from land-use pressures, exploring interactions between environmental pressures, and producing conservation or management plans.

4.6 Data availability statement

Data are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.sj3tx964n) and code on a public GitHub repository (https://github.com/JJWilliams24/Vertebrate-responses-to-human-land-use-are-influenced-by-their-proximity-to-climatic-tolerance-limit). The original PREDICTS database can be downloaded from https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database. The WorldClim Version 1.4 climatic variable maps can be downloaded from http://www.worldclim.com/version1. Species distribution maps can be downloaded or requested from https://www.iucnredlist.org/resources/spatial-data-download and http://datazone.birdlife.org/species/requestdis, respectively.

Chapter 5:

Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change

5.1 Abstract

Rapid human-driven environmental changes are impacting animal populations around the world. Currently, land-use and climate change are two of the biggest pressures facing biodiversity. However, studies investigating the impacts of these pressures on population trends often do not consider potential interactions between climate and land-use change. Further, a population's climatic position (how close the ambient temperature and precipitation conditions are to the species' climatic tolerance limits) is known to influence responses to climate change but has yet to be investigated with regard to its influence on land-use change responses over time. Consequently, important variation across species' ranges in responses to environmental changes may be being overlooked. Here, I combine data from the Living Planet and BioTIME databases to carry out a global analysis exploring the impacts of land use, habitat loss, climatic position, climate change, and the interactions between these variables, on vertebrate population trends. By bringing these datasets together, I analyse over 7,000 populations across 42 countries. I find that, as well as significantly impacting population trends on its own, land-use change is interacting with climate change and a population's climatic position to influence rates of population change. Moreover, features of a population's local landscape (such as surrounding land cover) play important roles in these interactions. For example, populations in agricultural land uses where maximum temperatures were closer to their hot thermal limit were found to decline at faster rates when there had also been rapid losses in surrounding semi-natural habitats. The complex interactions between these variables on population trends highlights the importance of taking intraspecific variation and interactions between local and global pressures into account. Understanding how drivers of change are interacting and impacting populations, and how this varies spatially, is critical if

we are to identify populations at risk, predict species' responses to future environmental changes and produce suitable conservation strategies.

5.2 Introduction

Global animal populations are facing rapid human-driven environmental changes (IPBES, 2019). According to the Living Planet Index, average vertebrate population abundance has fallen by two-thirds in the last 50 years (WWF, 2020), with declines being clustered in certain locations around the world (Leung et al., 2020). However, studies of different time-series data, such as the BioTIME database, report little change in abundance over time for the majority of populations (Dornelas et al., 2019). Many reasons have been put forward as to why the conclusions drawn regarding global populations trends differ between the datasets, including selection biases, publication biases, monitoring methods (population- or assemblage-level), extreme clusters within the datasets and geographic biases (Dornelas et al., 2019; Gonzalez et al., 2016; Leung et al., 2020). Whatever the overall trend, we need to understand the drivers underlying population fluctuations. Furthering our understanding as to why, and which, populations are changing or staying constant may help us to identify why we see such differences in trends between time-series datasets.

Recent studies investigating the influence of drivers of change on biodiversity have primarily focused on the impacts of climate and land-use change (Antão et al., 2020; Daskalova et al., 2020; Northrup, Rivers, Yang, & Betts, 2019; Spooner et al., 2018). Using BioTIME assemblage time-series data, Antão et al. (2020) found that the abundance trends of temperate terrestrial biodiversity were not coupled to temperature changes. However, this study did not account for land-use changes, and changes in forest cover have been found to impact population changes, with both declines and increases observed to intensify after forest loss (Daskalova et al., 2020). Neither of these studies accounted for interactions between land-use change and climate change. Drivers of change are not occurring in isolation, and as such interactions between land-use and climate change are critical to take into account when studying how populations are changing (Chapter 2; Mantyka-Pringle et al., 2012; Oliver & Morecroft, 2014; Sirami et al., 2017). Indeed, when interactions are accounted for, a different picture is drawn as to the influence of global drivers on populations. For example, a global-level analysis using the Living Planet database (LPD), not only found that declines in endothermic vertebrate populations were greater at sites where there had been rapid increases in temperature, but also, for mammals, that this effect interacted with land-use change, with declines due to rapid warming amplified in areas with high rates of conversion from natural to agricultural land uses (Spooner et al., 2018). Interestingly though, unlike forest loss (Daskalova et al., 2020), land-use change on its own did not influence population changes (Spooner et al., 2018). At a more local scale, climatic changes (warming and drying) have also been found to interact synergistically with forest loss to influence bird declines in the northwest forests of the United States (Northrup et al., 2019).

One route by which land-use change and climate change could interact to impact how vertebrate populations respond to global drivers of change is through the local-scale climatic changes that occur due to land-use change (Chapters 2-4; De Frenne et al., 2019; Frishkoff et al., 2016). Human-altered land uses (such as agricultural and urban areas) are, on average, hotter and drier than natural habitats (De Frenne et al., 2019; Frishkoff et al., 2016). In addition, the removal of canopy layers, such as through conversion from forest to croplands, leads to greater temperature extremes (De Frenne et al., 2019; Senior, Hill, Benedick, & Edwards, 2017). For example, average maximum daily temperatures in pastures and pineapple farms have been recorded to be around 6°C and 9°C higher than that in forest (Nowakowski, Watling, et al., 2017). These local climatic differences between land uses have been associated with community shifts: at both local- and global-levels, human-altered land uses have been observed to favour species that can tolerate greater hot and cold extremes of temperature, and greater wet and dry extremes of precipitation (Chapter 3; Frishkoff et al., 2015; Nowakowski, Watling, et al., 2017; Waldock et al., 2020). As these local-scale climatic changes are occurring alongside global climatic changes, this has the potential to lead to complex interactions (Chapter 2).

Populations, however, do not respond to environmental changes uniformly across their species' ranges (Orme et al., 2019; Soroye et al., 2020; Spooner et al., 2018). Recent work, such as Srinivasan et al. (2019) and the research presented in Chapter 4, is highlighting that ambient climate and, more specifically, how close the local temperature and precipitation conditions are to a species' climatic tolerance limits (climatic position), may impact how populations respond to land-use change, leading to variation in responses across species' ranges. At a regional level, across the

Himalayas, bird species common to locations across the region were more forest-dependent (using agricultural sites less) in relatively aseasonal compared to highly seasonal locations (Srinivasan et al., 2019). At a global level, in Chapter 4, I found that populations in environments where extreme temperatures were closer to their hot or cold thermal limits were filtered out of human-altered land uses. Further, despite human-altered land uses being drier on average (Frishkoff et al., 2016), I found that populations in locations where minimum precipitation was closer to the species' dry tolerance limit had similar abundances to that in natural habitats. In comparison, populations with a larger buffer between their dry limit and the location's minimum precipitation levels did worse (had lower abundances relative to that in natural habitat; Chapter 4). This variation across species' ranges may be due, at least in part, to the local climatic changes following land-use change. However, climatic position and its interaction with land use has yet to be considered when analysing global population trends.

Here, I combine time-series data from the LPD and BioTIME database, with the aim to investigate whether changes in vertebrate population abundances are influenced by their climatic position, the habitat they are found within, the rates of climate change and changes in surrounding land use and, importantly, interactions between these variables. I make three specific hypotheses:

(1 & 2) Populations experiencing (1) maximum or (2) minimum temperatures closer to their upper or lower thermal tolerance limits, respectively, will decrease more rapidly in human-altered land uses (and in areas that have experienced greater increases in surrounding human-altered land uses), compared to populations in more natural habitats, especially in places where hot maxima and cold minima have got more extreme over time;

(3) Relative to populations in more natural habitats, populations in human-altered land uses (and in areas that have experienced greater increases in surrounding human-altered land uses) that experience minimum precipitation closer to their dry tolerance limit will have a lower rate of decline over time compared to populations experiencing minimum precipitation levels further from their dry limit (following from my results in Chapter 4).

I also look at a population's climatic position with regard to maximum precipitation level. At the community-level, I found that human-altered land uses favoured species affiliated with wetter precipitation extremes (Chapter 3), but at a population-level, a population's maximum precipitation position relative to their species-level precipitation tolerance limits was found to influence probability of occurrence, but not abundance (given presence) within human-altered land uses relative to natural habitats (Chapter 4). Therefore, I do not have a clear hypothesis regarding how populations over time will be influenced by their maximum precipitation position.

By bringing together these two global databases and incorporating previously overlooked variables and interactions, I complete the most comprehensive analysis to date to further our understanding on how vertebrates are being influenced by environmental changes around the world, how drivers of change are interacting, and which populations may be at higher risk from human-induced changes.

5.3 Methods

5.3.1 Population time-series data

I acquired population time-series data for terrestrial vertebrates from the Living Planet database (LPD; Living Planet Index database, January 2020) and the BioTIME database (Dornelas et al., 2018; see Appendix 3, Section 13, for the original data citations), for the period covering 1992 to 2015 (to match the land-cover data, see below). These two databases together contain time-series of population estimates for over 100,000 terrestrial vertebrate populations from around the globe within my timeframe. Here, I use the term 'population' to refer to a group of individuals of the same species at the same location. As in previous chapters, I focused on vertebrates due to the reasonably comprehensive data available on their distributions, which was necessary in order to estimate species' realised climatic tolerance limits (see below).

From both the LPD and BioTIME database, I extracted annual population estimates for non-migratory terrestrial vertebrate populations whose specific locations were known (so that I could assign land-use and environmental data to the site). In the BioTIME database, if there were multiple population estimates per year, I took the mean of these. I further removed any birds or mammals classed as migratory according to data obtained from BirdLife International (2018) and Gnanadesikan, Pearse, & Shaw (2017). From the BioTIME database, I also excluded studies looking at biomass, and populations that were part of treatment studies such as burning, harvesting, or predator exclusion experiments. Finally, I excluded studies that were within the Arctic Circle, spanned less than 6 years, or had 5 or fewer population estimates over the time-series (following Spooner et al., 2018). This left me with a dataset comprised of 9,601 populations, consisting of 423 species (147 mammal, 224 bird, 30 reptile and 22 amphibian species) in 1,669 locations across 48 countries.

For each population I calculated the average logged annual rate of population change ($\overline{\lambda_{\boldsymbol{Y}}}$), following the method used by Spooner et al. (2018). In brief, I first took the log (base 10) of each population estimate (if an estimate was zero, I instead took the log of 1% of the mean estimate from the entire time-series, including the zeros). Second, each time-series was fit with a generalised additive model (GAM), with a smoothing parameter set to the half the number of population estimates in the time-series (Collen et al., 2009). Then, $\overline{\lambda_{\boldsymbol{Y}}}$ was calculated for each time-series following equation 5.1:

$$\text{(5.1)} \quad \overline{\lambda_{\boldsymbol{Y}}} = \frac{1}{\boldsymbol{Y}} \sum_{0}^{n} \left(\log_{10} \left(\frac{n_y}{n_{y-1}} \right) \right)$$

in which *n* is the population estimate for year *y*, and ***Y*** is the number of years from the first to the last estimate for a population. Values for missing annual population estimates were imputed from the GAMs.

5.3.2 Land-cover data

I obtained global land-cover maps from the European Space Agency Climate Change Initiative (ESA CCI; ESA Land Cover CCI project team, Defourny, 2019). These maps are available for the years 1992 to 2015, at a spatial resolution of 300 m and categorise land into 37 land-cover classes (Defourny et al., 2017). I grouped these land-cover classes into the broader categories of agriculture, forest, grassland, wetland, urban and other (I did not include the water or permanent snow and ice categories, so removed populations located in these categories; Appendix 3, Section 1, table S5.1), closely following the groupings used by the Intergovernmental Panel on Climate Change (Defourny et al., 2017). The land-cover category that each population was located in when the population was first recorded within the 1992 to 2015 timescale was recorded as it’s starting land-use type (there were not enough populations starting in urban or wetland land-use types to include in the analysis, so the populations in these categories were removed, leaving forest, grassland, agriculture and other as starting land-use types).

To calculate the rate of change in land cover each population experienced over time, I first extracted the percentage of semi-natural habitat (SNH) within a 1 km radius of the population’s location for each year between its first and last estimate. A radius of 1 km has previously been used when assessing the impact of land-use change on local biodiversity (Le Provost et al., 2020), and due to my focus on the *local* climatic changes brought about by land-use change, concentrating on the changes in SNH within a 1 km radius surrounding a population was appropriate (however, to check the sensitivity of my results, I also calculated percentage change in SNH within a 5-, 10- and 50-km radius). Land-cover categories included as SNH were forest, grassland, wetland and shrubland (Appendix 3, Section 1, table S5.1). I also incorporated a weighting system, in which I used the maximum percentage cover of a specific land use (detailed in the ESA’s land-use categories) to weight each category. For example, the category ‘Tree cover, broadleaved, deciduous, closed to open (>15%)’ was given a weighting of 1, as it could cover 100% of the 300 × 300-m area, whereas the category ‘Tree cover, broadleaved, deciduous, open (15-40%)’ was given a weighting of 0.4, as this could cover a maximum of 40% of the 300 × 300-m area (see Appendix 3, Section 1, table S5.1 for a full listing of the weightings; non-SNH categories were given a weighting of 0). Then, for each location with a population time-series, a linear regression was fit to the percentage of SNH within the surrounding 1 km radius over the length of the population time-series, with the resulting slope extracted to give the average annual rate of change in SNH.

5.3.3 Climatic tolerance limits

I estimated species’ realised climatic tolerance limits, i.e., the maximum and minimum of temperature and monthly precipitation that a species’ experiences across its geographic distribution. I obtained expert-informed species distribution maps (extent-of-occurrence maps) from BirdLife International (2012) and the International Union for Conservation of Nature (IUCN 2016a-b, 2017a-c, 2018a-b, 2019a-c). For each species, I extracted their native historical ranges (where they were resident, or present during breeding or non-breeding seasons) and areas the species had been introduced or reintroduced (i.e., excluding areas where presence or seasonal occurrence is uncertain, species are possibly extant or vagrant, or areas classed as passages, such as areas used for short periods of time during migration). These extracted areas were then rasterised into 500 × 500-m equal-area grids (Behrmann projection). I chose this resolution so that I could include as many species as possible with very narrow ranges. Areas outside of species' elevation limits, if known (BirdLife International 2018; IUCN 2016a-b, 2017a-c, 2018a-b, 2019a-c), were removed from their distribution maps.

I obtained climate maps for average monthly maximum temperature of the warmest month, average monthly minimum temperature of the coldest month, and precipitation of the wettest and driest months from WorldClim Version 1.4 (Hijmans et al., 2005). These maps had a resolution of 30 arc-seconds and encompassed averaged yearly values from 1960 – 1990. I resampled these climate maps using bilinear interpolation to 500 × 500-m equal-area grids (Behrmann projection) to match the projection of the species' distribution maps. I overlaid the species' distribution maps on these four climatic variables and extracted the highest maximum temperature of the warmest month and precipitation of the wettest month, and the lowest minimum temperature of the coldest month and precipitation of the driest month across each species' distribution (ArcGIS 10.4). These values provided my estimates of each species' realised upper and lower temperature and precipitation tolerance limits (fig. 5.1).

5.3.4 Climate change and starting climatic position

Monthly average daily maximum and minimum temperature, and monthly precipitation data were acquired from the gridded (0.5° × 0.5°) Climatic Research Unit (CRU) Time-series data v. 4.03 (Harris & Jones, 2020). From these, I found the highest monthly average daily maximum temperature, lowest monthly average daily minimum temperature, and maximum (wettest) and minimum (driest) monthly precipitation per year at the location of each observed population within my dataset. For each population, values for the four climatic variables were extracted for each year between the first and last population estimate. Linear regressions were fit to each set of climatic variables for each population, with the slopes of these extracted to give the average annual rate of change in maximum temperature of the warmest month, minimum temperature of the coldest month and precipitation of the wettest and driest months over the length of the population time-series.

For each population, I calculated their starting climatic position with regard to maximum temperature of the warmest month (T_{max} position), minimum temperature of the coldest month (T_{min} position), precipitation of the wettest month (Pp_{max} position) and precipitation of the driest month (Pp_{min} position). These positions describe the thermal and precipitation conditions (CRU Time-series data v. 4.03; Harris & Jones, 2020) a population experienced in the first year they were measured at a site, standardised to range between 0 and 1 relative to the lower and upper realised temperature or precipitation tolerance limits of the species (where, for thermal tolerance limits, 0 = minimum realised temperature tolerance limit and 1 = maximum realised temperature tolerance limit, and for precipitation tolerance limits, 0 = minimum (dry) realised precipitation tolerance limit and 1 = maximum (wet) realised precipitation tolerance limit; fig. 5.1). I chose to use the temperature and precipitation conditions a population experienced in the first year of their time-series because I wanted a measure of where each population started in relation to their species-level climatic limits. However, to check the sensitivity of my results, I also calculated starting climatic position using the average maximum and minimum temperature and precipitation conditions (CRU Time-series data v. 4.03; Harris & Jones, 2020) in the three years up to and including the first year of a population's time-series, and ran a model (see below) using this measure (Appendix 3, Section 4).

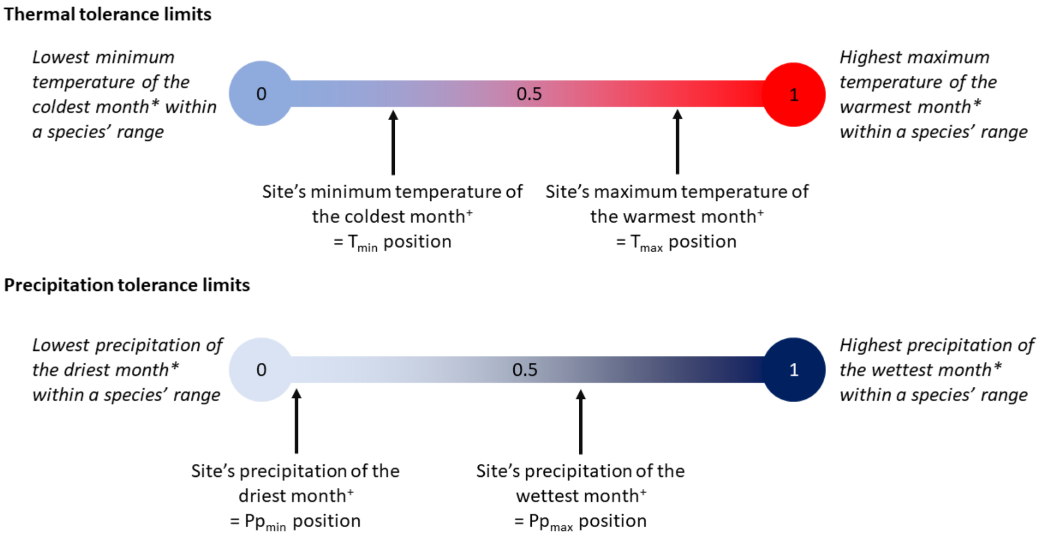


Figure 5.1: Climatic position calculation. A visual example of how the starting climatic positions (T_{max}, T_{min}, Pp_{max} and Pp_{min} position) were calculated for each population. 0 and 1 represent the species-level realised minimum and maximum thermal or precipitation tolerance limits, extracted from species' distribution maps overlaid on climatic data from WorldClim Version 1.4 (denoted by the *; Hijmans et al., 2005). The starting climatic positions were calculated by standardising the population's site-level temperature and precipitation data (obtained from the Climatic Research Unit, denoted by $^+$; Harris & Jones, 2020) in the year that the population was first recorded to range between 0 and 1 relative to the species-level climatic tolerance limits. For example, a T_{max} position closer to 1 means that the maximum temperature of the warmest month experienced by a population was closer to the highest maximum temperature of the warmest month across the species' range. Similarly, a Pp_{min} position closer to 0 describes a population that experienced precipitation levels in their driest month that were closer to the lowest precipitation of the driest month across the species' range.

5.3.5 Distance to range edge

Within my analyses, I also accounted for a population's location relative to their species' range edge. For each population in my dataset, I found the shortest distance from their location to their species' range edge and, to account for range size, divided it by the greatest distance a population of that species could be from their range edge (calculated by transforming species distribution maps into spatial points dataframes). Therefore, each population had a standardised (between 0 and 1) distance to range edge measure, where a value of 0 meant the population was located at the species' range edge, and values closer to 1 meant the population was closer to the range centre. Populations that were recorded outside of their distributions as stated by the distribution maps (BirdLife International 2012; IUCN 2016a-b, 2017a-c, 2018a-b, 2019a-c), were removed.

The final dataset comprised of 7,123 populations, consisting of 341 species (126 mammal, 186 bird, 12 reptile and 17 amphibian species) in 1,151 locations across 42 countries (Appendix 3, Section 2, fig. S5.1).

5.3.6 Statistical analyses

I used linear mixed-effects models to investigate how the rate of population change was affected by land-use type and change, the population's climatic position, and the rate of climate change experienced. I selected which main effects and interactions to include in the final model by using backwards stepwise variable selection. The population's starting land-use type, the rate of change in SNH they experienced, their starting T_{max}, T_{min}, Pp_{max} and Pp_{min} positions and the rate of change in climate experienced (for the four climatic variables detailed above) were all included as fixed effects (table 5.1; correlations between continuous variables were checked, Appendix 3, Section 3, table S5.2). The distance of a population from its species' range edge, and its interaction with starting land-use type, were also added as covariates to account for potential differences in responses due to proximity to range edge (Liebl & Martin, 2012; Orme et al., 2019). I included three 3-way interactions: (1) starting land-use type × rate of change in SNH × starting climatic position, to look at whether populations in human-altered land uses experiencing temperatures and precipitation closer to their climatic limits as well as greater rates of decreases in SNH have larger negative rates of population change, (2) starting land-use type × starting climatic position × rate of change in climate (with the same focal climatic variable as the climatic position, e.g. starting land-use type × starting T_{max} position × rate of change in maximum temperature of the warmest month), to explore whether populations in human-altered land uses experiencing temperatures and precipitation closer to their climatic limits on top of greater increases in climatic extremes have larger negative rates of population change, and (3) starting land-use type × rate of change in SNH × rate of change in climate, to look at whether populations in human-altered land uses experiencing greater decreases in SNH as well as increases in extreme climatic conditions have larger negative rates of population change. The lower-order 2-way interactions between the variables in each 3-way interaction were also included (table 5.1). I included three random intercept terms: species name (to account for interspecific differences in responses), study site (to account for site-specific effects), and database (LPD or BioTIME, to account for differences between datasets; table 5.1). I then ran the final model, with the average logged annual rate of population change ($\overline{\lambda_{Y}}$) as the response variable, and included the selected main effects, interactions (also including any non-significant lower-order interaction terms nested within these) and the random effects stated above. All of the above was completed in ArcGIS 10.4 (ESRI 2015), and R 3.6.0 (R Core Team 2019) using packages 'dplyr' v.0.8.3 (Wickham, François, Henry & Müller, 2019), 'lme4' v.1.1.26 (Bates et al., 2015), 'ncdf4' v.1.17 (Pierce, 2019), 'plyr' v.1.8.6 (Wickham, 2011), 'raster' v.2.8-19 (Hijmans, 2019) and 'tidyr' v.1.0.0 (Wickham & Henry, 2019).

Table 5.1: Parameters included in the backwards stepwise variable selection. Symbols represent variables within the same 2- or 3-way interaction (for example, starting land-use type and rate of change in semi-natural habitat both have a ● symbol, indicating that I included a 2-way interaction between these variables – starting land-use type × rate of change in semi-natural habitat – in the backwards stepwise variable selection). Interactions combining both starting climatic position and rate of change in climate included the same climatic variable (e.g., starting T_{max} position × rate of change in maximum temperature of the warmest month, or starting Pp_{min} position x rate of change in minimum monthly precipitation). Interactions between starting positions with respect to different climate variables, or between rates of change in different climatic variables were not included.

Parameter	**Description**	**Type of effect**	**Included in an interaction?**	
			2-way	3-way
Starting land-use type	The land-use type (forest, grassland, agriculture, or other) the population was within in the first year of its time-series.	Fixed, categorial	●▲ ✚▼	○△ □
Rate of change in semi-natural habitat	The average annual rate of change in the percentage of semi-natural habitat (which included forest, grassland, wetland, and shrubland) within a 1 km radius of the population, over the length of the population time-series.	Fixed, continuous, quadratic	●■ ◆	○△
Starting climatic position	The a) maximum temperature of the warmest month (T_{max}), b) minimum temperature of the coldest month (T_{min}), c) precipitation of the wettest month (Pp_{max}), and d) precipitation of the driest month (Pp_{min}), a population experienced in the first year they were measured, relative to the species-level upper and lower realised thermal (for a and b) or precipitation (for c and d) tolerance limits.	Fixed, continuous, quadratic	▲■ ⧗	○□
Rate of change in climate	The average annual rate of change in a) maximum temperature of the warmest month, b) minimum temperature of the coldest month,	Fixed, continuous, quadratic	✚◆ ⧗	△□

	c) precipitation of the wettest month, and d) precipitation of the driest month, over the length of the population time-series.		
Distance to range edge	The distance of a population from their species’ geographic range edge, standardised to account for overall range size.	Fixed, continuous, linear	▼
Species name	Species binomial, to account for interspecific differences in responses.	Random intercept	
Study site	ID based on the population’s location (latitude and longitude), included to account for site-specific effects.	Random intercept	
Database	The database the population’s time-series data was acquired from (Living Planet database or BioTIME database), to account for differences between the databases (differences in inclusion criteria or sampling method, for example).	Random intercept	

5.3.7 Robustness checks

I compared the ESA land cover maps to recently produced global maps of terrestrial habitat types (Jung et al., 2020), to check the consistency of land use-types across data sources. These latter maps are only available for 2015 – 2019, so for each site in my final dataset (n = 1,151), I compared the land-use types between the 2015 ESA land cover map and Jung et al.'s (2020) global map of terrestrial habitat types for 2015. In particular, I wanted to ensure that there were not a large number of plantations or pastures at sites that I classed as forest or grasslands, respectively, as land-cover maps may miss these land uses.

The IUCN and BirdLife International species' distribution maps (BirdLife International 2012; IUCN 2016a-b, 2017a-c, 2018a-b, 2019a-c) provide data for a wide range of vertebrates from around the world, and as such have been used extensively (Allan et al., 2019; Herkt et al., 2017; Khaliq et al., 2017; Shackelford et al., 2015). However, they do contain inaccuracies as they tend to overestimate area of occupancy and underestimate species' extent-of-occurrence (Herkt et al., 2017; Hurlbert & Jetz, 2007). Therefore, to check the robustness of my climatic position measure, I also calculated species' climatic limits using occurrence records from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org), rather than species' distribution maps (Appendix 3, Section 4). Further, to ensure that my climatic position measures were robust to the climatic data used to estimate climatic limits, I calculated another estimate of a population's climatic position, this time using the CRU Time-series data v. 4.03 (Harris & Jones, 2020), extracting temperature and precipitation data from 1992, to calculate species' climatic limits (rather than using WorldClim data). I compared both the climatic positions themselves, and the results of models run (with the same structure as the final model) using the climatic positions calculated through these different methods of estimating climatic limits (Appendix 3, Section 4).

Further, using the same structure as the final model, I also ran models that (1) included the average annual rate of change in the percentage of forest (instead of SNH) within a 1 km radius of the population's location (calculated in the same way as for SNH, but only including the forest category; Appendix 3, Section 1, table S5.1), to investigate whether it was change in forest specifically, rather than semi-natural habitat, driving differences in population trends (Daskalova et al., 2020); (2) included percentage of SNH within a 1 km radius of the population in the first year they were recorded, rather than starting land-use type, to see if this explained more variance in the data (Appendix 3, Section 5); (3) only included time-series with $R^2 \geq 0.5$ when fit to the GAM, to remove populations with more variable estimates over the years, for which interpolated values may not be as accurate (Appendix 3, Section 8); (4) excluded time-series with $\overline{\lambda_Y}$ above and below the upper and lower 97.5th and 2.5th percentile, respectively, to ensure results were not being influenced by extreme positive or negative rates of population change (following Daskalova et al., (2020) and Spooner et al., (2018), I do not remove extreme values in my main model; Appendix 3, Section 9); (5) excluded birds from the genus *Gyps,* as a previous study using the Living Planet database found that they had a big influence on model estimates (Green et al., 2020; Appendix 3, Section 10); (6) excluded ectotherms, to check these taxa were not driving any observed declines; and (7) included populations that were beyond their species' ranges as stated by BirdLife International (2012) and IUCN (2016a-b, 2017a-c, 2018a-b, 2019a-c), to ensure that removing these did not affect my results (Appendix 3, Section 11). I also carried out cross validation tests to ensure there were no overly influential locations or species in my dataset (Appendix 3, Section 12). I checked to see if I could run models separately for each vertebrate class (Mammalia, Aves, Reptilia and Amphibia), but there were insufficient data.

5.4 Results

5.4.1 Results summary

The 7,123 populations analysed had an average time-series length of 15 years, covered a variety of starting land-use types and climatic positions and, across these populations, there were both increases and decreases experienced in surrounding SNH and all climatic variables (table 5.2).

Table 5.2: Summary statistics for the population time-series analysed, split by the originating database (the Living Planet database or BioTIME database). The average annual rate of change in semi-natural habitat refers to change within a 1 km radius surrounding each population. Fitted values were based on fixed effects only.

	Living Planet database	BioTIME database
Number of populations analysed	367	6756
Average annual rates of population change (% / year)		
Mean of observed (and fitted) values	-2.83 (-0.99)	-0.03 (-1.54)
Median of observed (and fitted) values	-0.53 (-1.33)	0 (-1.51)
Number of populations with a positive (↑) or negative (↓) values	↑ 152 ↓ 215	↑ 3299 ↓ 3319
Mean length of population time-series (years)	13	15
Number of countries from which populations originated	42	4
Average annual rates of change in semi-natural habitat		
Range (% / year)	-7.75 – 3.97	-7.27 – 9.24
Mean (% / year)	-0.17	0.02
Median (% / year)	0	0.03
Number of populations with a positive (↑) or negative (↓) values	↑ 137 ↓ 168	↑ 3882 ↓ 2592
Percentage of populations starting in each starting land-use type (%, to 1 decimal place)		
Forest	58.9	54.2
Grassland	3.5	11.6
Agriculture	17.7	28.3
Other	19.9	5.8

In summary, my results highlight the complexity of the impact that climatic position, land-use type and change, and climate change have on populations over time, with all these variables interacting with each another in complex ways (table 5.3).

Notably, the rate of change in SNH significantly affected the rate of population change (from the backwards stepwise selection process, $p = 0.002$) and, although not significant by itself, starting land-use type appeared to play an important role within interactions, particularly in its influence on how populations were affected by rates of change in climate and their starting climatic position (table 5.4). Neither the distance of populations from their species' range edge, or its interaction with starting land-use type, significantly affected rate of population change. The fixed effects that were included in the final model (table 5.3) explained 7.4% of variation in the rate of population change (marginal pseudo-R^2, *sensu* Nakagawa & Schielzeth, 2013) and together with the random effects, explained 46.1% of the variation (conditional pseudo-R^2).

Table 5.3: The fixed-effects included in the final model. The model included the land-use type the population was within in the first year of recording (LU), the average annual rate of change in semi-natural habitat in a 1 km radius surrounding the population (SNH_rate), a population's starting climatic position with regard to maximum temperature of the warmest month, minimum temperature of the coldest month, and precipitation of the wettest and driest months (referred to as Tmax_pos, Tmin_pos, Ppmax_pos and Ppmin_pos, respectively), and the average annual rate of change in climate with regard to maximum temperature of the warmest month (MaxT_rate), minimum temperature of the coldest month (MinT_rate), and the precipitation of the wettest (MaxP_rate) and driest (MinP_rate) month. Continuous variables in the model were run as second-degree (i.e., quadratic) orthogonal polynomials (denoted by poly(x,2), where x is the continuous variable).

Fixed-effects	Term		
Main effects	LU	poly(Tmax_pos,2)	poly(MaxT_rate,2)
	poly(SNH_rate,2)	poly(Tmin_pos,2)	poly(MinT_rate,2)
		poly(Ppmax_pos,2)	poly(MaxP_rate,2)
		poly(Ppmin_pos,2)	poly(MinP_rate,2)
Two-way interactions	LU × poly(SNH_rate,2)	poly(SNH_rate,2) × poly(Tmax_pos,2)	poly(MaxT_rate,2) × poly(Tmax_pos,2)
	LU × poly(Tmax_pos,2)	poly(SNH_rate,2) × poly(Tmin_pos,2)	poly(MinT_rate,2) × poly(Tmin_pos,2)
	LU × poly(Tmin_pos,2)	poly(SNH_rate,2) × poly(Ppmax_pos,2)	poly(MaxP_rate,2) × poly(Ppmax_pos,2)
	LU × poly(Ppmax_pos,2)	poly(SNH_rate,2) × poly(MaxT_rate,2)	poly(MinP_rate,2) × poly(Ppmin_pos,2)
	LU × poly(Ppmin_pos,2)	poly(SNH_rate,2) × poly(MinT_rate,2)	
	LU × poly(MaxT_rate,2)	poly(SNH_rate,2) × poly(MaxP_rate,2)	
	LU × poly(MinT_rate,2)		
	LU × poly(MaxP_rate,2)		
	LU × poly(MinP_rate,2)		
Three-way interactions	LU × poly(SNH_rate,2) × poly(Tmax_pos,2)	LU × poly(MaxT_rate,2) × poly(Tmax_pos,2)	LU × poly(SNH_rate,2) × poly(MaxT_rate,2)
	LU × poly(SNH_rate,2) × poly(Tmin_pos,2)	LU × poly(MinT_rate,2) × poly(Tmin_pos,2)	LU × poly(SNH_rate,2) × poly(MinT_rate,2)
	LU × poly(SNH_rate,2) × poly(Ppmax_pos,2)	LU × poly(MaxP_rate,2) × poly(Ppmax_pos,2)	LU × poly(SNH_rate,2) × poly(MaxP_rate,2)
		LU × poly(MinP_rate,2) × poly(Ppmin_pos,2)	

Table 5.4: The 10th, 50th, and 90th percentiles of the continuous explanatory variables included in the final dataset. Tmax, Tmin, Ppmax and Ppmin position refer to a population's starting climatic positions with regard to maximum temperature of the warmest month, minimum temperature of the coldest month, and precipitation of the wettest and driest months, respectively.

Continuous explanatory variables	Percentiles		
	10th	50th	90th
Average annual rate of change in semi-natural habitat (% / year)	-1.20	0.02	1.07
Starting climatic position			
Tmax position	0.73	0.82	0.91
Tmin position	0.19	0.32	0.44
Ppmax position	0.09	0.20	0.56
Ppmin position	0.004	0.03	0.08
Average annual rate of change in climate			
Maximum temperature of the warmest month (°C / year)	-0.04	0.04	0.20
Minimum temperature of the coldest month (°C / year)	-0.07	-0.003	0.13
Precipitation of the wettest month (monthly mm / year)	-4.33	-0.59	3.19
Precipitation of the driest month (monthly mm / year)	-1.70	-0.26	0.64
Distance from range edge	0.02	0.17	0.62

Table 5.5: The statistical results from the backwards stepwise selection for the two- and three-way interactions including starting land-use type (categorical variable) that were included in the final model. Variables within these interactions included continuous variables for the average annual rate of change in semi-natural habitat (SNH_rate), a population's starting climatic positions with regard to maximum temperature of the warmest month, minimum temperature of the coldest month, and precipitation of the wettest and driest months (referred to as Tmax_pos, Tmin_pos, Ppmax_pos and Ppmin_pos, respectively), average annual rate of change in climate with regard to maximum temperature of the warmest month (MaxT_rate), minimum temperature of the coldest month (MinT_rate), precipitation of the wettest (MaxP_rate) and driest (MinP_rate) months. Continuous variables in the model were run as second-degree (i.e., quadratic) orthogonal polynomials (denoted by poly(*x*,2), where *x* is the continuous variable).

Term	χ^2	Degrees of freedom	*p*-value	
LU × poly(SNH_rate,2)	6.70	6,245	0.349	
LU × poly(Tmax_pos,2)	23.29	6,217	<0.001	***
LU × poly(Tmin_pos,2)	37.31	6,217	<0.001	***
LU × poly(Ppmax_pos,2)	3.64	6,270	0.726	
LU × poly(Ppmin_pos,2)	18.77	6,217	0.005	**
LU × poly(MaxT_rate,2)	28.85	6,217	<0.001	***
LU × poly(MinT_rate,2)	19.54	6,217	0.003	**
LU × poly(MaxP_rate,2)	6.08	6,239	0.414	
LU × poly(MinP_rate,2)	1.47	6,276	0.962	
LU × poly(SNH_rate,2) × poly(Tmax_pos,2)	35.20	16,217	0.004	**
LU × poly(SNH_rate,2) × poly(Tmin_pos,2)	32.82	16,217	0.008	**
LU × poly(SNH_rate,2) × poly(Ppmax_pos,2)	33.86	16,217	0.006	**
LU × poly(MaxT_rate,2) × poly(Tmax_pos,2)	53.88	16,217	<0.001	***
LU × poly(MinT_rate,2) × poly(Tmin_pos,2)	71.45	16,217	<0.001	***
LU × poly(MaxP_rate,2) × poly(Ppmax_pos,2)	33.73	16,217	0.006	**
LU × poly(MinP_rate,2) × poly(Ppmin_pos,2)	31.73	16,217	0.011	*
LU × poly(SNH_rate,2) × poly(MaxT_rate,2)	40.12	16,217	<0.001	***
LU × poly(SNH_rate,2) × poly(MinT_rate,2)	35.47	16,217	0.003	**
LU × poly(SNH_rate,2) × poly(MaxP_rate,2)	39.10	16,217	0.001	**

* *p*-value < 0.05, ** *p*-value < 0.01, *** *p*-value < 0.001

5.4.2 Detailed results

I found that the rate of change in SNH surrounding a population had a significant effect on their rate of population change ($\chi^2 = 9.66$, df = 1,19, $p = 0.002$). The direction of the effect differed (although not significantly) depending on the land-use type that the population started in ($\chi^2 = 6.70$, df = 6,245, $p = 0.349$; fig. 5.2). While testing the sensitivity of my results, I included the percentage of SNH within a 1 km radius of the population in the first year they were measured (rather than starting land-use type); the results indicated that populations surrounded by a higher percentage of human-altered habitats at the start of recording often had greater negative rates of population change (Appendix 3, Section 5, figs. S5.8-11). This is another very interesting result and I present it in the appendices (due to it being a post-hoc test, as well as having a lower marginal R^2 compared to my main model, and not capturing the difference between populations starting in forest versus grassland). Below I do not plot the results for populations that started in habitats classed as ‘other’ because, following my hypotheses, I want to focus on how the impact of climatic position, land-use, and climate change on the rate of population change differs between those starting in human-altered habitats (agriculture) compared to those in more natural habitats (forest and grasslands).

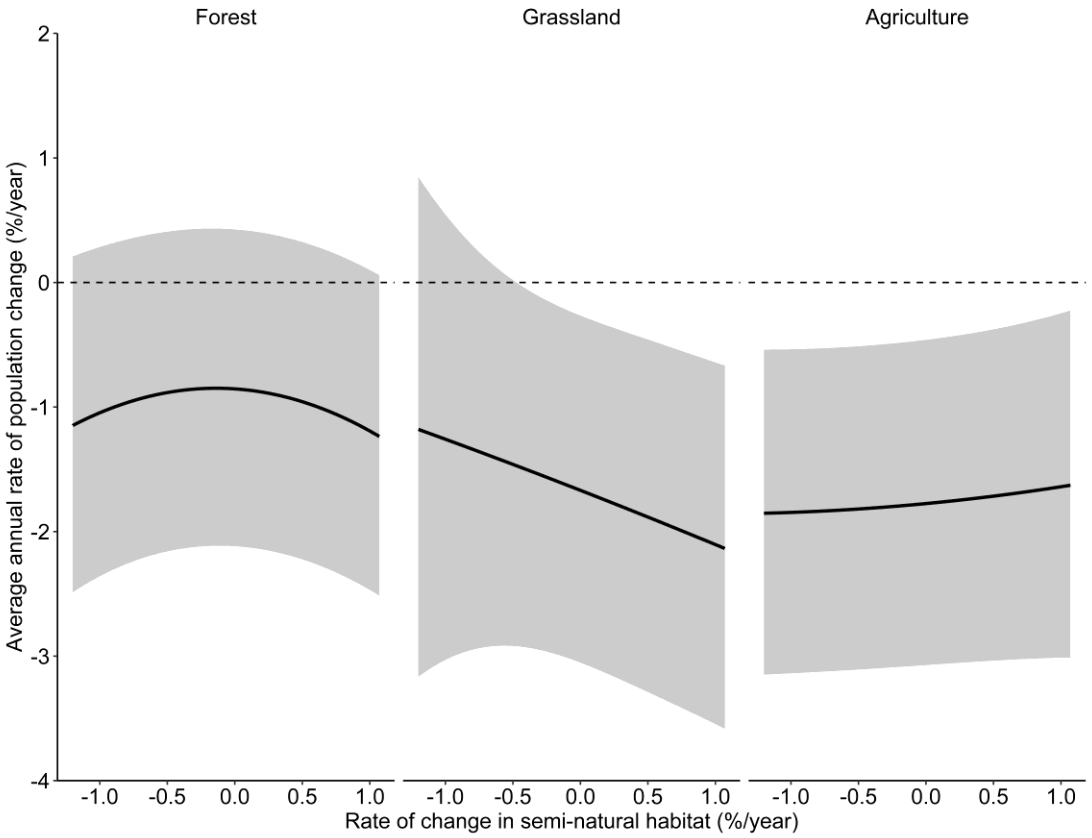


Figure 5.2: The average annual rate of population change depending on the average annual rate of change in semi-natural habitat, split by the land-use type a population was in when the first population measure was recorded. Error margins denote ±1 standard error.

The influence of starting thermal position on a population's rate of change over time differed significantly between starting land-use types, with this effect also depending on the rate of change in SNH (table 5.5). For populations with high starting T_{max} positions (indicating they initially experienced maximum temperatures closer to their hot thermal limit), as predicted, those that started in agricultural areas and experienced more rapid loss in SNH, had more negative rates of population change (fig. 5.3). Interestingly, populations starting in agricultural land uses with lower starting T_{max} positions (indicating they initially experienced maximum temperatures further from their hot thermal limit) also had more negative rates of population change in areas that had experienced more rapid increases in SNH in the surrounding landscape. Further, in line with predictions, for populations with low T_{min} positions (initially in environments where they experienced minimum temperatures closer to their cold thermal limit) in agricultural land uses, those that experienced more rapid increases in SNH had more positive rates of population change (fig. 5.3).

A populations' starting Pp_{max} position also interacted with the rate of change in SNH, with this effect differing between starting land-use types (table 5.5, fig. 5.3). Effects of Pp_{max} positions and rate of change in SNH were stronger for populations starting in grassland sites compared to forest or agriculture. A population's starting Pp_{min} position also impacted rate of population change differently across the starting land uses (table 5.5, fig. 5.3), but this effect did not differ significantly depending on rate of change in SNH that a population experienced. Unexpectedly, for populations starting in agricultural land uses, those experiencing minimum precipitation levels closer to their dry tolerance level (low starting Pp_{min} position), had more negative rates of population change (compared to forested and grassland habitats, and compared to populations with higher Pp_{min} positions).

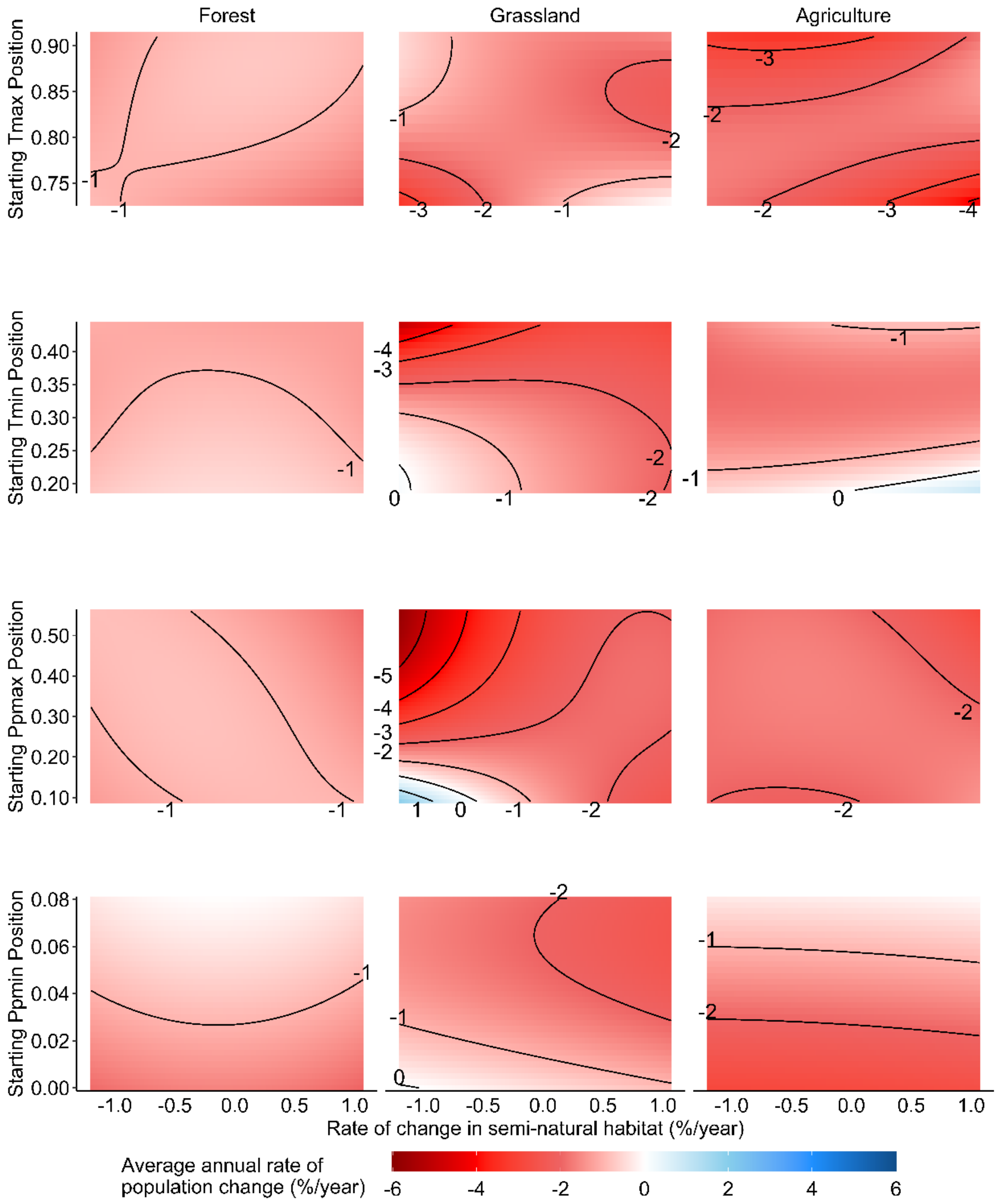


Figure 5.3: The interaction between starting land-use type, rate of land-use change, and climatic position. The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) a population's starting climatic position with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled

values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

The rate of change in climate experienced by a population also influenced their rate of population change, with these effects differing across starting land-use types and further depending on starting climatic position (table 5.5, fig. 5.4). Surprisingly, for populations that experienced greater rates of increase in maximum temperatures, those starting within agriculture and with higher starting T_{max} positions (experiencing maximum temperatures closer to their hot thermal limit), had the most positive rate of population increases. Further, and again against predictions, despite decreases in minimum temperatures, populations in agriculture with lower starting T_{min} positions (experiencing minimum temperatures closer to their cold thermal limit), had less negative rates of population change, compared to populations with higher T_{min} positions. The declines in agriculture of populations with lower Pp_{min} positions (experiencing minimum precipitation levels closer to their dry tolerance level) were stronger in areas that had experienced decreases in precipitation in their driest month.

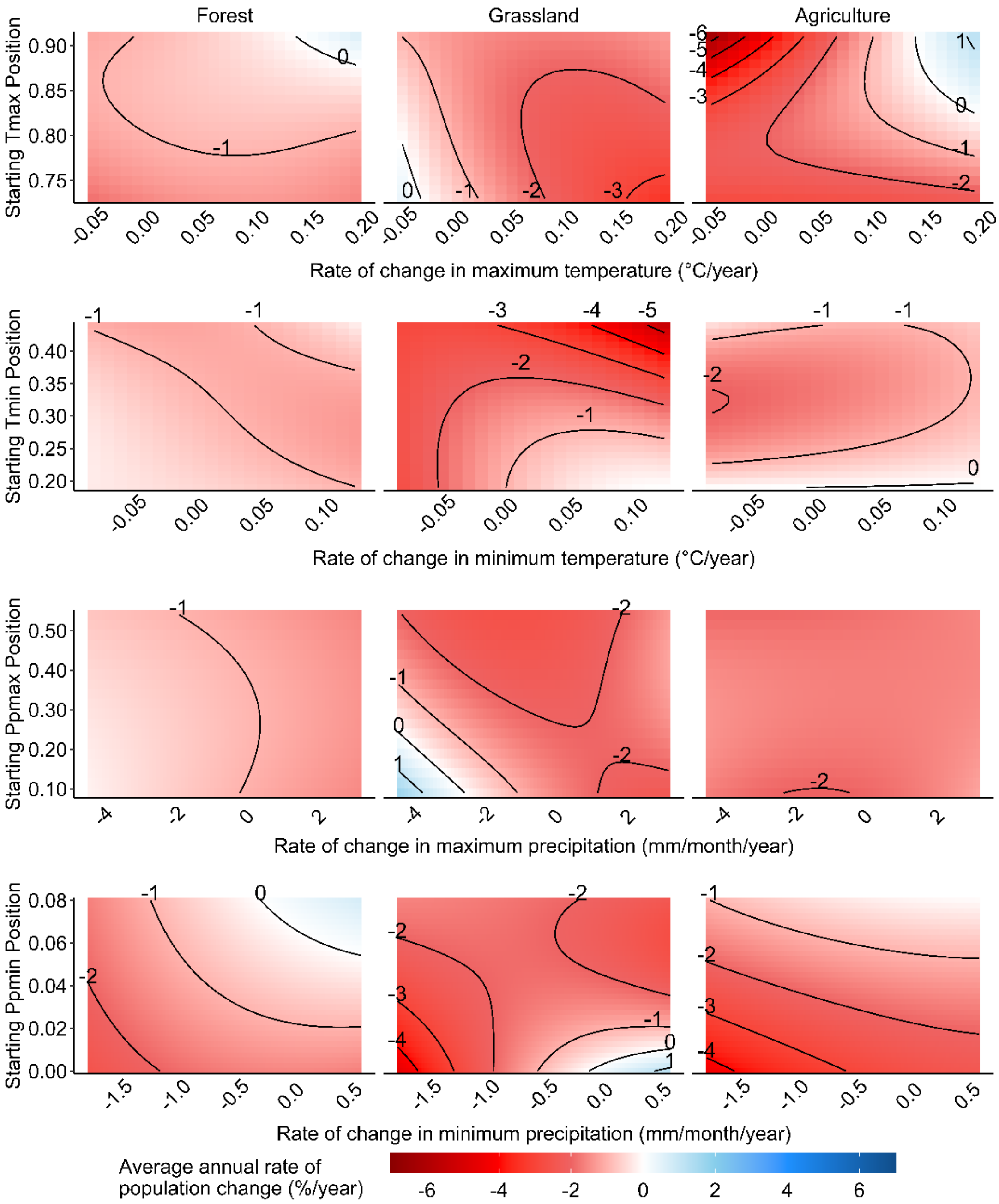


Figure 5.4: The interaction between starting land-use type, rate of climate change, and climatic position. The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in climate; and (ii) a population's starting climatic position. Climatic variables considered in both cases were maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}), and precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of

each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

Finally, three-way interactions were observed between rate of change in SNH, starting land-use type and the rate of change in three climatic variables: maximum temperature of the warmest month, minimum temperature of the coldest month and precipitation of the wettest month (table 5.5, fig. 5.5). Interestingly, as with the other interactions, this highlights how the average annual rate of population change for those starting in forested sites is relatively similar (declining at a rate of around -1%) across populations experiencing different rates of change in SNH and climate. The most variation is seen in populations that started in grasslands, with positive rates of change seen for those populations experiencing more rapid decreases in maximum temperature and SNH, and negative rates of change seen for those populations experiencing faster increases in SNH and decreases in minimum temperature.

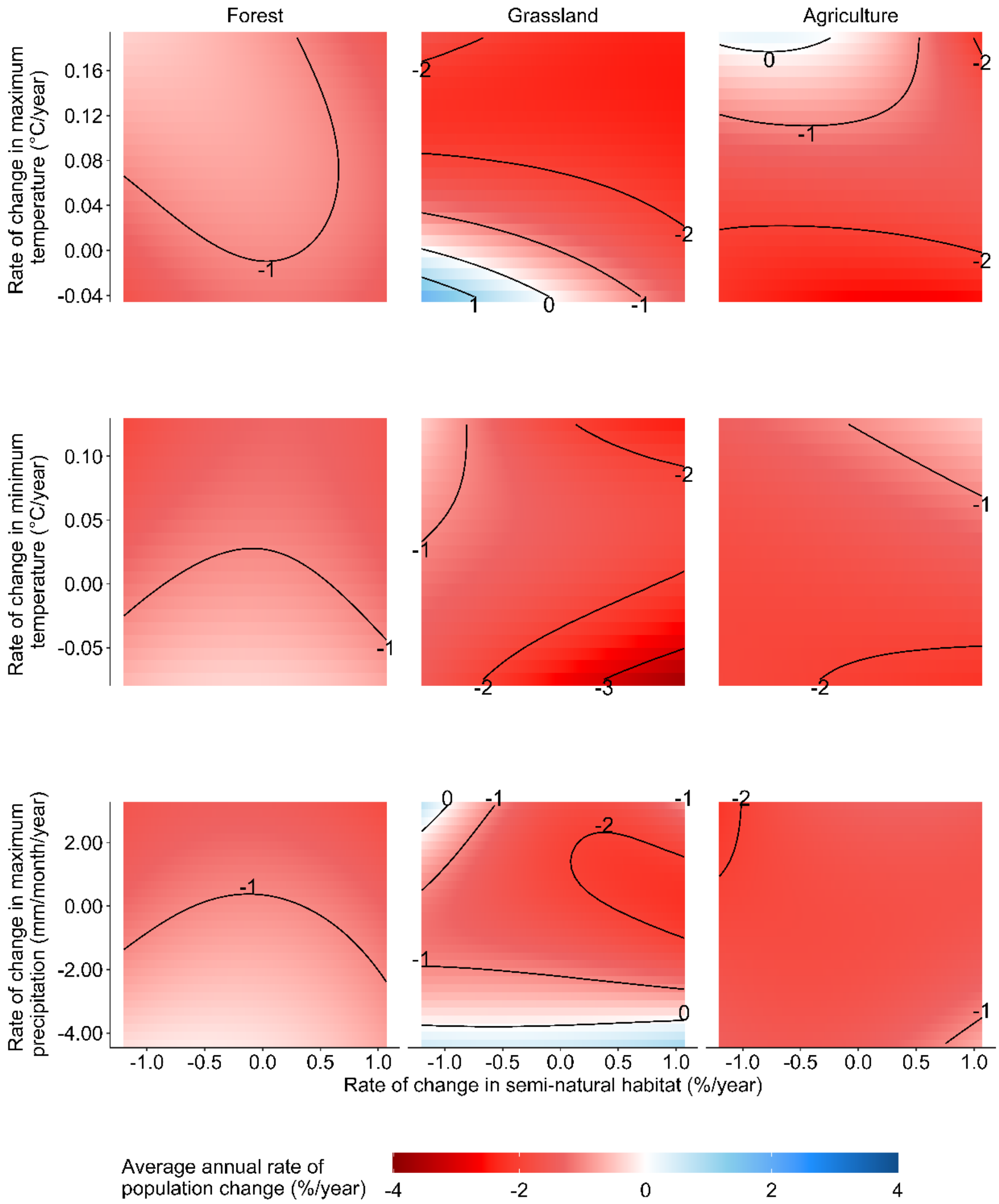


Figure 5.5: The interaction between starting land-use type and the rate of change in climate and land use. The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) average annual rate of change in climate with regard to maximum temperature of the warmest month (°C/year), minimum temperature of the coldest month (°C/year), and precipitation of the wettest month (monthly mm/year). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

5.4.3 Robustness checks

Land-use types extracted from the 2015 ESA land cover map (ESA Land Cover CCI project team, Defourny, 2019) and the 2015 global map of terrestrial habitat types (Jung et al., 2020) were the same for over 70% of sites in my dataset (Appendix 3, Section 6, table S5.4-5). Out of the sites that differed, there were a low number of discrepancies between forest and plantation (n = 24, 2.1% of all sites in the dataset) and between grassland and pasturelands (n = 6, 0.5% of all sites in the dataset). The larger discrepancies between the data sources included (1) sites that were classed as forest by the ESA land cover map but as shrubland by the global map of terrestrial habitat types (n = 58, 5.0% of all sites in the dataset) and (2) sites that were classed as agriculture by the ESA land cover map but as forest by the global map of habitat types (n = 40, 3.5% of all sites in the dataset).

Using the average temperature and precipitation conditions in the three years up to and including the first year of a population's time-series to calculate climatic position (rather than the temperature and precipitation in the first year) explained almost the same amount of variance in rate of population change and produced very similar results to those presented above (Appendix 3, Section 4, figs. S5.2-3). The climatic positions calculated using CRU Time-series data (instead of WorldClim climate maps) to estimate species' climatic limits were strongly correlated to the climatic positions used in the main model ($r > 0.9$), and the results of the models run using these climatic position estimates were very similar to those above (Appendix 3, Section 4, table S5.3, figs. S5.4-5). I was able to calculate climatic positions using GBIF occurrence data (instead of species' distribution maps) for 324 of the species found in my final dataset (6,681 populations), and these were also strongly correlated to the climatic positions reported here ($r > 0.78$; Appendix 3, Section 4, table S5.3). The overall pattern of results using climatic positions derived from GBIF data was similar to the results reported above (Appendix 3, Section 4, figs. S5.6-7).

Including the average annual rate of change in the percentage of SNH within a 1 km radius of each population, as in the model reported above, explained more variance (higher marginal R^2 values) than using rates of change within a 5- or 10-km radius. The model including rate of change in SNH within a 50 km radius explained around the same amount of variance as within a 1 km radius, but as my hypotheses were focused on local climatic changes following land-use change, the 1 km radius was more appropriate. The model that included average annual rate of change in the percentage of forest within a 1 km radius, rather than SNH, explained less variance in rate of population change, but overall patterns in forest and agriculture were similar between the models (Appendix 3, Section 7, figs. S5.12-13).

Excluding populations whose time-series did not have a GAM $R^2 \geq 0.5$ removed around three-quarters of populations. The resulting model had a higher marginal R^2 and predicted more extreme rates of population change (in both the positive and negative direction) than those reported above, but patterns with respect to the environmental variables discussed in the main findings above were very similar (Appendix 3, Section 8, figs. S5.14-16). Excluding time-series with $\overline{\lambda_Y}$ above and below the upper and lower 97.5th and 2.5th percentile, respectively, resulted in a model that did not explain as much variance as the main model, but overall patterns were similar (although the rates of population change were shifted slightly towards less negative values; Appendix 3, Section 9, table S5.6, figs. S5.17-19). Excluding species from the genus *Gyps* produced a model with a slightly higher marginal R^2 value (by 0.007), but very similar results to the model above (although very slight shifts in the rates of population change towards less negative values were observed; Appendix 3, Section 10, figs. S5.20-22). Running models without ectothermic species did not change the results (results not shown). The results of models including populations that were outside of their species' ranges as stated by the BirdLife International (2012) and IUCN (2016a-b, 2017a-c, 2018a-b, 2019a-c) distribution maps were very similar to those presented above (Appendix 3, Section 11, figs. S5.23-25). The majority of populations recorded outside of their species' ranges were relatively close to the range edge (70% were within 82 km), with those further away generally being species invasive to the recorded location. Finally, cross validation tests showed that there were no overly influential locations or species within the dataset (Appendix 3, Section 12, figs. S5.26-29).

5.5 Discussion

Vertebrate populations are not responding uniformly to land-use change across their distributions. Rather, I show that as well as significantly impacting population trends on its own, land-use change is interacting with climate change and a population's climatic position to influence rates of population change. Further, features of a population's local landscape (their starting land-use type and the land cover in the surrounding 1 km) play an important role in these interactions. This is the first time that a population's climatic position has been included in a study investigating the impact of habitat change and observed to have an important influence on the rate of change in populations over time. These results highlight the need to, first, account for populations' climatic positions when investigating the impacts of land-use change (not just climate change) and second, include interactions occurring between drivers of change. These should be incorporated in both big-data global models, such as the one I present here, as well as local scale conservation and management plans – these interactions and differences across species' ranges in responses to environmental changes cannot be overlooked if we are to mitigate the impact of anthropogenic changes on vertebrate populations around the world.

The land-use type a population was within when their population was first measured (starting land-use type: forest, grassland, agriculture, or other), and the percentage of surrounding SNH at the start of recording, played vital roles within interactions. This emphasises that habitat type needs to be accounted for within large-scale models analysing the impacts of drivers of change – otherwise, the weight of any driver's influence may be dampened or obscured due to the buffering effects of natural habitats. For example, I observe that, although populations starting in forests were generally declining by around 1% per year, this rate was similar for populations with different starting climatic positions and experiencing different rates of land-use and climate change. This suggests that forests act as buffers, providing climatic conditions and/or habitat quality (e.g., due to the thermal buffering properties of a canopy layer and the complexity of microhabitats; De Frenne et al., 2019; González del Pliego et al., 2016) that protect populations from surrounding landscape-level (change in SNH) and global-level (climate change) environmental changes. Similarly, those populations surrounded by higher percentages of SNH at the start of recording generally had weaker and less negative population trends, suggesting that surrounding SNH can also help buffer populations from land-use and climatic changes, across different climatic positions.

For the first time, I show that a population's climatic position has an important influence on its rate of change over time, interacting with land-use type and change, as well as climate change. I observed several results consistent with my hypotheses. First, for populations initially in environments where maximum temperatures were closer to the species' hot thermal limit, those that were in agriculture and experienced more rapid losses in surrounding SNH (i.e., high T_{max} position + agriculture + SNH loss, fig. 5.3), had more negative rates of population change compared to populations in forest or grassland. Second, within agriculture, for populations initially in environments with minimum temperatures close to their species' cold thermal limit, those that experienced increases in surrounding SNH (i.e., low T_{min} position + agriculture + SNH gain, fig. 5.3) had positive rates of population change (whereas populations experiencing declines in SNH had negative population trends). However, there were also unexpected results. For example, populations in agriculture, and initially in environments where maximum temperatures were further from the species' hot thermal limit, had more negative rates of population change in areas that had more rapid increases in surrounding SNH (i.e., low T_{max} position + agriculture + SNH gain). This observation may be due to individuals recolonising the surrounding restored areas (Nichols & Grant, 2007), and so moving out of the agricultural sites. Whilst my analyses reveal several very important results, one limitation is that I was not able to determine *how* the focal variables are influencing population trends, whether it is through effects on birth, death, immigration, or emigration rates. The mechanisms underlying how populations are influenced by climatic changes, and how their climatic positions may interact with the local climatic changes following land-use change are complex (Chapter 2). Further work is needed to explore the mechanisms underlying the influence of climatic position and interactions with land-use and climate change on population trends.

These results using population time-series data contrasted in some respects when compared to my space-for-time analysis using data from the PREDICTS Project database in Chapter 4, particularly with regard to minimum precipitation position. The space-for-time analysis in Chapter 4 suggested that agricultural land uses had little impact on population abundance (relative to that in primary vegetation) in environments where precipitation in the driest month was close to the species' dry limit. However, in this chapter, I observe that agricultural populations initially in environments where precipitation in the driest month was closer to the species' dry limit (i.e., low Pp_{min} position + agriculture) had more negative rates of population change relative to populations in more natural habitats. The two types of analysis are capturing different attributes of population abundance (a snapshot in time versus temporal trends), and resulting differences may be due to the influence of temporal lags, an interaction with global climate change, or the locations of populations in the analyses. First, commonly observed lags in responses to environmental changes (Lira, de Souza Leite, & Metzger, 2019) may mean that populations with lower Pp_{min} positions are initially able to tolerate local changes towards drier conditions following land-use change, due to drought adaptations for example, but they may not be able to sustain numbers if the conditions continue. Lagged responses are not captured in most space-for-time analyses (De Palma et al., 2018). Second, ongoing drying trends in the tropics (Lau & Kim, 2015) may interact with precipitation position to lead to more rapid declines for populations with lower Pp_{min} positions (indeed, I observe this trend in my results above, fig. 5.4), a trend which may be hidden if the rate of climate change is not considered. Finally, and perhaps most importantly, most populations in my temporal analysis were found at temperate latitudes, and in Chapter 4's space-for-time analysis, the pattern regarding Pp_{min} position was much stronger for agricultural populations at tropical latitudes. This emphasises the need to collect more time-series data for tropical populations (discussed further below), in order to explore geographic differences. Ultimately, exploring similar questions using both space-for-time and temporal analyses is key, as overall we get a clearer answer to our questions, with the analyses highlighting different results as well as aspects that may be missed by one or other method.

By analysing time-series data from both the LPD and BioTIME database together, not only was I able to analyse over 7,000 vertebrate populations, but I could also highlight some of the differences between the databases, which may contribute to the conflicting results between previous studies analysing these databases separately (e.g., Dornelas et al., 2019; WWF 2020). After filtering, there were roughly the same number of populations from tropical (n = 174) and temperate (n = 193) latitudes from the LPD, whereas all BioTIME populations (n = 6,756) came from temperate latitudes. Even though abiotic factors are suggested to have greater impact on species distributions at higher latitudes (Khaliq et al., 2017; MacArthur, 1972), the tropics have continuously been identified as particularly vulnerable to drivers of change such as land-use and climate change (Brook et al., 2008; Newbold et al., 2020). Further, in

Chapter 3 where I examined the impact of the local climatic changes following land-use change at the community-level, I found greater differences between natural and human-altered land uses in tropical than temperate latitudes. Reasons for this include the relative stability (past and present) of the tropical climate (Janzen, 1967; Pacifici et al., 2017), the smaller average range sizes of species within the tropics (Stevens, 1989; Thuiller et al., 2005), the fact that tropical species are often living closer to their maximum thermal tolerance limits (Deutsch et al., 2008; Sunday et al., 2014), and the larger proportion of specialist species (habitat and dietary specialists) inhabiting the tropics (Forister et al., 2015). Consequently, the skew of BioTIME data towards temperate assemblages may not give an accurate representation of global population trends. Indeed, analyses of vertebrate populations of forest specialists from the LPD found that the average abundance trends were positive in temperate biomes and negative in tropical biomes (Green et al., 2020). Ideally, I would test whether population trends were influenced differently by my focal variables depending on whether the population was at a tropical or temperate latitude. However, there were insufficient tropical data to do so. In my final dataset, the LPD contributed populations from 42 countries, whereas the BioTIME database contributed populations from just 4 countries (United States of America, Canada, South Africa, and Brazil; Appendix 3, Section 2, fig. S5.1). Historical pressures on biodiversity can impact vulnerability to present-day environmental changes (Balmford, 1996). Therefore, analyses based on data from a small number of countries need to take this into account and, in the case of the BioTIME database, the countries contributing data all have long histories of environmental changes (although, in the case of Brazil, this varies spatially within the country; Goldewijk, 2001; Goldewijk, Beusen, Van Drecht, & De Vos, 2011; Nehren, Kirchner, Sattler, Turetta, & Heinrich, 2013). Consequently, this may be another reason for disparities between previous studies using data from the LPD versus BioTIME database.

Using species' distribution maps and climate data from WorldClim to estimate species' realised climatic tolerance limits meant that I was not able to take into account climatic adaptations over time, intraspecific differences in climatic tolerances, or microclimatic conditions. However, at present, the data are not available to include these variables, especially for the large number of species (almost 350) that were included in this analysis. Hopefully it will be possible to account for these variables in the future. Further, I use estimates of realised climatic tolerance limits, which can be influenced by factors other than climate, such as dispersal barriers and biotic interactions (HilleRisLambers et al., 2013; Peterson et al., 2011). Nevertheless, I use these rather than physiological climatic tolerance limits because physiological data are available for very few species, the metrics produced in laboratory tests are often incomparable to one another (due to different measurement procedures), and laboratory tests have been criticised for not being reflective of real-world conditions (Chapter 2; Araújo et al., 2013; Rezende et al., 2014; Sunday et al., 2012).

In conclusion, local land-use changes and global climate changes are interacting to impact vertebrate population trends around the world. Further, these interactions do not impact populations uniformly across species' ranges. Rather, a population's climatic position is key within these interactions. Consequently, I highlight the importance of taking a population's climatic position into account, not just when studying the impacts of climate change (Soroye et al., 2020), but also land-use change. Even though the effects of these interactions are complex, and further work is needed on the mechanisms underlying how these variables influence populations, my results allow us to identify populations that may be at greater risk of decline. In order to prevent further population declines and mitigate the impact of anthropogenic changes, we cannot ignore interactions between drivers of change, and we must account for variation across species' ranges in responses to local and global environmental changes in both local conservation strategies and global models.

5.6 Data availability statement

The Living Planet Index database (apart from the confidential data) can be found at https://livingplanetindex.org/data_portal, and the BioTIME database can be downloaded from http://biotime.st-andrews.ac.uk/downloadArea.php. The European Space Agency Climate Change Initiative land cover maps can be downloaded from https://catalogue.ceda.ac.uk/uuid/b382ebe6679d44b8b0e68ea4ef4b701c. The WorldClim Version 1.4 climatic variable maps can be downloaded from http://www.worldclim.com/version1 and species distribution maps can be downloaded or requested from https://www.iucnredlist.org/resources/spatial-data-download and http://datazone.birdlife.org/species/requestdis, respectively.

Chapter 6:

Discussion and synthesis

Anthropogenic drivers of change are reshaping terrestrial vertebrate communities around the world (Bellard et al., 2012; Newbold et al., 2015; Olivier, Thébault, Elias, Fontaine, & Fontaine, 2020). To minimise future biodiversity losses, and protect the ecosystem services that nature provides, calls have been made to increase the extent of protected areas, restore degraded land and generalise land-use planning at the landscape-level (Leclère et al., 2020; WWF 2018). For these efforts to be successful, it is vital that they account for the variation in responses to land-use change, across both species and space. Moreover, with ongoing global climate change (Collins et al., 2013), the potential for the effects of land-use and climate change to interact cannot be ignored (Mantyka-Pringle et al., 2012; Oliver & Morecroft, 2014; Sala et al., 2000). Furthering our understanding of variation in responses to and interactions between drivers of change will allow conservation and management practitioners to target and prioritise their efforts towards the species, populations, and areas most at risk, giving us a better chance of altering the current trajectory of biodiversity decline (Murray et al., 2021; Powers & Jetz, 2019).

In this thesis, I analysed three of the most comprehensive compilations of vertebrate assemblage records to date, with the aim of enhancing our understanding of how local climatic changes modify the response of biodiversity to land-use changes. To begin, I reviewed the current understanding of how local climatic changes are affecting biodiversity responses to land use and highlighted key knowledge gaps (Chapter 2). Then, I went on to address some of these gaps by investigating, globally and across both space and time, whether human-altered land uses systematically favour certain species depending on their climatic niche properties (Chapter 3), whether this varies across species' ranges due to populations' climatic positions (Chapters 4 and 5), and whether the local climatic changes may be leading to interactions between land-use and climate change (Chapter 5). I found that, at the community-level and particularly at tropical latitudes, human-altered land uses are reshaping vertebrate communities by favouring species affiliated with more extreme climatic conditions (Chapter 3). This provided support for the first overarching hypothesis of this thesis.

However, species' do not respond uniformly across their ranges and, in line with my second overarching hypothesis, a population's climatic position was found to influence abundance within human-altered land uses (Chapter 4). One of the key findings of Chapter 4 was that populations experiencing temperatures closer to their hot or cold thermal tolerance limits were being filtered out of human-altered land uses to a greater extent than populations experiencing temperatures further from their thermal limits. Finally, support was provided for my third overarching hypothesis, with populations' climatic positions found to interact with land-use type, habitat loss, and climate change to influence population trends over time (although these results were complex, and did not always conform to my predictions; Chapter 5). As discussed within each chapter, these findings are likely, at least in part, due to the local climatic changes that occur following land-use change.

In this final chapter, I will discuss how the research presented in this thesis contributes to broader knowledge, reflect on some of the challenges of global models, and highlight outstanding questions. First, I will discuss the contributions of this work to our understanding of how human-altered land uses and land-use change are impacting vertebrate populations globally. In particular, I will focus on the importance of considering local climatic differences and populations' climatic positions when studying the past, present, and future impacts and risks of land-use change. Second, I will discuss the contributions of these studies to our understanding of interactions between drivers of change, specifically land-use and climate change, and I will offer examples of how this work can be used to further other areas of research into global pressures and their interactions. Last, I will compile some of the limitations and challenges of global models in relation to the research presented here, and finish by outlining outstanding questions and directions of future work.

6.1 Contributions to the understanding of how human-altered land uses and land-use changes are impacting global biodiversity

The local climatic changes mediated by land-use change are one likely mechanism by which human-altered land uses filter out certain species (Frishkoff, Gabot, et al., 2019; Frishkoff et al., 2016; Karp et al., 2017). Previous work has highlighted that, at the local scale, vertebrate species within human-altered land uses can often tolerate hotter and drier climates than those in natural habitats (Frishkoff et al., 2015; Frishkoff et al., 2016; Nowakowski, Watling, et al., 2018, 2017). The research presented in this thesis builds on this, demonstrating that these patterns are occurring across the globe, for a much larger number and range of species than previously considered, and are not restricted to affiliations with hot and dry extremes (but also cold and wet extremes; Chapter 3). This adds to the list of ways in which human-altered land uses around the world are driving shifts in community composition (Frishkoff, Gabot, et al., 2019; Newbold et al., 2018). Other ecological and functional traits that can affect how land-use changes impact species include reproductive strategy, dietary guild, longevity, body mass, migratory status, and habitat specialisation (Murray et al., 2021; Newbold et al., 2013; Nowakowski, Thompson, Donnelly, & Todd, 2017). The loss of less tolerant species, due to climatic limits or the aforementioned traits for example, can result in the functional homogenisation of biodiversity and, subsequently, declines in ecosystem functioning (Clavel et al., 2011). With land-use changes set to continue (Powers & Jetz, 2019), it is vital that we are aware of which species are being filtered out of anthropogenically-modified habitats and, importantly, why this is occurring in order to introduce strategies to protect these species, maintain diversity across landscapes, and preserve ecosystem functioning (Frishkoff, Gabot, et al., 2019; Pecl et al., 2017).

Understanding how responses to environmental changes vary spatially is another critical piece of information needed for effective conservation and management plans, and thus a key goal within ecology and conservation (Orme et al., 2019). Recent studies exploring spatial variation in responses to land use have looked at both local-scale variation across species' ranges (the relationship between distance to range edge and sensitivity to deforestation, for example) and global-scale geographic variation (for instance, the impact of human-altered land uses on species' richness across biomes; Newbold et al., 2020; Orme et al., 2019; Srinivasan et al., 2019). The studies presented within this thesis add to this research by providing novel insights into how the local climatic changes following land-use change may be a source of variation in responses to habitat change, both across species' ranges (depending on populations' climatic positions; Chapters 4 and 5) and between tropical and temperate latitudes (Chapters 3 and 4). Geographically, I found that there were often larger differences between communities in community-average climatic affiliation (Chapter 3) or between populations with different climatic positions

(Chapter 4) at tropical compared to temperate latitudes. This extends the growing list of studies drawing attention to the vulnerability of tropical biodiversity to global drivers of change (Brook et al., 2008; Deutsch et al., 2008; Green et al., 2020; Newbold et al., 2020; Sunday et al., 2014). This is a cause for concern among conservationists as 60% of terrestrial biodiversity hotspots are located within the tropics, and they contain a substantially higher number of threatened endemic species compared to non-tropical hotspots (Brook et al., 2008; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Moreover, habitat modification, through conversion to agricultural land uses specifically, is predicted to occur predominantly at tropical latitudes in the coming decades (Hurtt et al., 2011). By further highlighting the sensitivity of tropical biodiversity to land-use changes, and demonstrating the role that local climatic changes following land-use change likely play, this work not only adds to the current understanding of how habitat loss and restoration impact species (which can be used to inform conservation actions), but also adds to calls to act now to preserve tropical biodiversity (Barlow et al., 2018; Brook et al., 2008).

Species' climatic tolerances are regularly considered when analysing the current and future impact of climate change on biodiversity (e.g., Jiguet et al., 2011; Soroye et al., 2020; Trisos, Merow, & Pigot, 2020), but have only recently been considered in research on habitat preferences and land-use change (Frishkoff et al., 2015, 2016; Nowakowski, Frishkoff, Agha, et al., 2018; Waldock et al., 2020). In particular, in Chapter 4, I introduce the variable 'climatic position', which is rarely considered in research on the impact of human land uses. Including a population's climatic position into these analyses helps to capture the influence of the local climatic changes that occur following habitat change. Taking into account these local climatic changes is critical if we are to gain a full picture of the impacts of land-use change (Frishkoff et al., 2015; Nowakowski, Frishkoff, Agha, et al., 2018). Further, as mentioned above, climatic position is linked to variation across a species' range in responses to human-altered land uses and, all else held equal, could lead to big differences in the impact of habitat conversion on communities (Chapter 4, fig. 4.4). This spatial variation is an important element to consider when managing both land-use changes at the landscape-level and species conservation efforts (Allan et al., 2019; Nowakowski, Frishkoff, Agha, et al., 2018). Moreover, with the ongoing calls to restore degraded land (Leclère et al., 2020), taking into account the climatic positions' of the populations present could also be used to identify areas where habitat restoration may be particularly effective. As global climate change continues, the impacts of land-use change will also likely shift due to changes in populations' climatic position (for further discussion on interactions, see below). Consequently, climatic position can no longer be a variable restricted to research on climate change, but should also be incorporated into land-use change research.

Areas of habitat containing vegetation regrowing following removal or damage, known as secondary vegetation, have been suggested to potentially provide refugia from global threats (such as climate change) and be important for biodiversity conservation (Dent & Wright, 2009; Hughes, Edwards, Sayer, Martin, & Thomas, 2020; Jucker et al., 2018; Senior, Hill, González del Pliego, et al., 2017). However, there is a clear distinction between secondary vegetation at an early compared to advanced stage of recovery (González del Pliego et al., 2016; Newbold, Hudson, Hill, et al., 2016; Phillips, Newbold, & Purvis, 2017). Regeneration of secondary vegetation and, crucially, the microhabitat composition of the habitat takes time (González del Pliego et al., 2016). In connection with this, the range of temperatures experienced within secondary vegetation also differs with stage of recovery, becoming more similar to that within primary vegetation over time (González-del-Pliego et al., 2020). As a likely consequence, the composition of species in earlier-stage secondary vegetation is markedly different compared to primary habitats, with the composition becoming more similar in more advanced secondary vegetation (Newbold, Hudson, Hill, et al., 2016; Phillips et al., 2017). Similarly, in Chapters 3 and 4, I found a clear distinction between young- and advanced-stage secondary vegetation, with the younger stages differing more in community-average climatic affiliations relative to that in primary vegetation, which, taking into account previous research, likely means that these habitats are also less able to provide thermal refugia (although, it is possible that this is a coincidental effect of colonisation lags; Watts et al., 2020). Further, it has been found that the recovery of biodiversity within secondary forests is influenced by their proximity to primary forests (Hughes et al., 2020). In Chapter 5, although I did not look at secondary vegetation specifically, I found that the rate of change in surrounding semi-natural habitat influenced rate of population change. This again highlights the need for landscape-level land-use planning (Leclère et al., 2020). Overall, these results suggest that the planning of habitat restoration efforts, and particularly their location, needs careful consideration, and that it will take time for the benefits of restorations to be observed.

6.2 Contributions to the understanding of interactions

There is a pressing need to understand whether, and if so how, global drivers of change are interacting with one another (Mantyka-Pringle et al., 2012; Northrup et al., 2019; Sala et al., 2000; Titeux et al., 2017). How land-use and climate change may interact has received increasing attention, in part due to the large and growing threats that they pose (Leadley et al., 2010; Mantyka-Pringle et al., 2012; Northrup et al., 2019; Oliver & Morecroft, 2014; Pereira et al., 2012). The work presented in this thesis adds to the research on this interaction, by investigating whether the local-scale climatic changes that occur due to land-use change lead to interactions between land-use and climate change (Chapters 3-5). Building on previous research, I highlight that land-use and climate change are indeed interacting with one another, but that the interaction is complex, with interactions differing across land-use types and between populations with different climatic positions. This variation is likely a result, at least in part, of the local climatic changes ensuing land-use change. As a result, this further emphasises that we can no longer focus on single stressors in isolation (Mantyka-Pringle et al., 2012; Northrup et al., 2019; Oliver & Morecroft, 2014). Previous work has also stressed the need for interactions to be taken into account when assessing how biodiversity will fare in the future, particularly when policy decisions are based on such predictions (Mantyka-Pringle et al., 2012; Sala et al., 2000; Titeux et al., 2017). The work presented here highlight the need for local climatic differences across land uses to be incorporated as well to help capture these interactions. For example, predictions have been made on the timings of disruption to ecological assemblages as a result of climate change, but these were based on changes due to global climate change and did not consider local changes due to habitat modification (Trisos et al., 2020). Consequently, for some communities, abrupt ecological disruption may occur earlier than predicted, due to the local climatic changes following land conversion (such as greater temperature extremes; Frishkoff et al., 2015; Senior, Hill, González del Pliego, et al., 2017) acting on top of global climatic changes (Collins et al., 2013). Overall, not considering interactions could impose critical constraints to policy decisions and conservation actions, and potentially lead to them being ineffective (Mantyka-Pringle et al., 2012; Titeux, Henle, Mihoub, & Brotons, 2016a).

Range expansions are one way in which species are responding to global climate change (Bellard et al., 2012; Parmesan, 2006). In order for species to colonise areas with a suitable climate, there also needs to be suitable habitat and a route to this habitat available (Rayfield, Pelletier, Dumitru, Cardille, & Gonzalez, 2016; Schloss, Nunez, & Lawler, 2012; Veech, Small, & Baccus, 2011). Research on species' range expansions have incorporated interactions into their analyses, looking at the interplay between exposure to climate, habitat associations, and the surrounding landscape (Oliver et al., 2017; Opdam & Wascher, 2004; Platts et al., 2019). In particular, attention has been drawn to the importance of managing landscapes to aid the movement of species in response to climatic changes (Oliver et al., 2017; Opdam & Wascher, 2004). However, as well as ensuring the availability of suitable habitat and physical connectivity across landscapes, it is also important to maintain suitable local climatic conditions, both within the new habitat and across landscapes, to enable range expansions (Nowakowski, Frishkoff, Agha, et al., 2018). Due to local differences in climatic conditions between land uses, some landscapes may be impermeable for certain species (Nowakowski, Frishkoff, Agha, et al., 2018; Senior, Hill, González del Pliego, et al., 2017). In addition, I have shown that populations' climatic positions are important in determining land-use responses (Chapters 4 and 5), and as such, may impact the ability of populations to move across landscapes with different local climates. For instance, in a fragmented landscape undergoing global warming, forest-specialist species affiliated with cooler climates may not be able disperse across more open and hotter habitats to other forest patches, leaving certain populations cut off from the rest of their species and unable to track global climatic changes (Nowakowski, Frishkoff, Agha, et al., 2018). It is likely that populations already experiencing temperatures close to their upper thermal tolerance limit will be most at risk of this occurring. In sum, furthering our understanding of the impact on biodiversity of interactions between climate, habitat, and changes in these, can help us maintain connectivity across landscapes for species on the move.

Variation in responses to anthropogenic changes may also stem from species' traits and their interaction with the environment (Murray et al., 2021). However, investigating such trait-environment interactions with regard to their impact on species’ responses to anthropogenic changes remains rare. Although, recently it has been found that reproductive strategy can interact with climatic variables to influence responses to land-use change (Murray et al., 2021). Throughout this thesis I estimated species’ thermal and precipitation tolerances to then either determine species’ climatic affiliations or calculate population-level climatic positions, and looked at how these variables may impact responses to human-altered land uses (Chapters 3-5). It may be however, that there are traits linked with certain climatic affiliations, such as reproductive mode (Nowakowski, Watling, et al., 2018; von May et al., 2019), which may also impact responses to habitat modification (Murray et al., 2021). Consequently, to advance the work presented in this thesis, and that on interactions between traits and environmental variables, it would be interesting to combine climatic affiliation or position (for species- or population-level studies, respectively), into trait-environment interactions. There are likely multiple mechanisms by which species’ are filtered out of human-altered land uses (Chapter 2; Murray et al., 2021; Newbold et al., 2013), and by analysing interactions between the environment and species- or population-specific variables (such as climatic affiliations, arboreality, or reproductive strategy), we may gain a clearer picture of how these elements interact, which variables/interactions are driving responses to anthropogenic change, and how this differs between species or populations.

6.3 Challenges, outstanding questions, and future directions

In this thesis, I used mixed-effects models to explore the differences in community-average climatic niche across human-altered land uses (Chapter 3), the influence of populations' climatic positions on relative abundances across land uses (Chapter 4), and the effect of interactions between climate and land use variables on the rate of change in populations (Chapter 5). As a result of using statistical models, I cannot infer causation, and the mechanisms underlying the associations found require further investigation. I explored potential ways in which local climatic changes could affect community composition in Chapter 2, and then, in Chapters 3 to 5, proposed potential mechanisms underlying the specific associations found within each of these chapters. A consequence of using statistical models is that there may be variables that I have not considered in these analyses correlated with both the response and explanatory variables, which are underlying the observed results. Again, work into the mechanisms underlying how the local climatic changes following land-use change influence species, and how this varies between populations, will help to identify causal pathways.

By overlaying climatic data on maps of species' distributions to estimate species' realised climatic affiliations or tolerances (a commonly used method; e.g., Barnagaud et al., 2013; Frishkoff et al., 2016; Kampichler, van Turnhout, Devictor & van der Jeugd, 2012; Menke et al., 2011; Waldock et al., 2020), I was able to include thousands of species' within my analyses and look at patterns at a global scale. Nevertheless, a limitation of this method is that I was not able to take into account potential intraspecific differences or temporal changes in climatic tolerances. At present, there are not the data or methods available to include these sources of potential variation within estimates of climatic tolerances, especially for the number of species considered in my analyses. Further, the climate maps obtained from WorldClim had a 30 arc-second resolution, which corresponds to roughly 0.86 km^2 at the equator, and is the finest spatial resolution of global climate data currently available (Nadeau, Urban, & Bridle, 2017). However, individuals can make use of microrefugia within their habitat to avoid adverse climatic conditions (Lenoir, Hattab, & Pierre, 2017; Nowakowski, Frishkoff, Agha, et al., 2018). Consequently, the species' physiological climatic tolerances may not span the range of ambient temperatures and precipitations recorded across their ranges. In addition, the microclimates that individuals are exposed to, and particularly the level of microclimatic heterogeneity (across 100 m^2 grid cells or within the canopy of a forest, for example), can influence responses to global climatic changes (Lenoir et al., 2017; Suggitt et al., 2018). As such, the effect of local climatic changes following land-use change on biodiversity may also be influenced by microclimate heterogeneity. Currently, global models are unable to capture this fine-scale microclimatic variability (due to lack of microclimatic data and the computational power required to run microclimatic models). Similarly, in Chapter 5, the global land-cover maps I obtained from the European Space Agency Climate Change Initiative (ESA Land Cover CCI project team, Defourny, 2019) had a spatial resolution of 300 m and, as such, variation in land uses at a finer resolution may be missed. Currently, these land-cover maps are the best available for the purpose of this work, which needed global scale maps that classified land into multiple different land-use classes (rather than only giving a percentage coverage of certain land uses, for example), and that were available on an annual basis over a long enough timeframe for analyses to be viable. By using a land-use weighting system when categorising land-cover classes as semi-natural habitat (Chapter 5), I attempted to capture some of the finer-scale variation; however, ultimately, land-cover data at a finer resolution are needed. Hopefully in time, as more data become available, these sources of potential variation in land uses, climate, and climatic tolerances will be able to be included in analyses such as the ones presented in this thesis.

To estimate precipitation affiliations, tolerances, and positions, I obtained data for precipitation of the wettest and driest month. These are (to my knowledge) currently the best data on precipitation available at the global scale and are widely used (e.g., Frishkoff et al., 2015; Jezkova & Wiens, 2016; Menke et al., 2011; Waldock et al., 2020). Nevertheless, the impacts of changes in precipitation on biodiversity are complex, especially as precipitation interacts with multiple other factors within a habitat, leading to many potential direct and indirect effects (Brown, Whitham, Morgan Ernest, & Gehring, 2001; Fu et al., 2003; Morecroft et al., 2004; Zeppel et al., 2014). For example, precipitation changes influence moisture levels (which itself is linked with topography, soil properties, and local vegetation) and plant growth, both of which may separately impact local vertebrate populations (Brown et al., 2001; Fu et al., 2003). As a result, the precipitation measures used here may not be capturing all the changes that individuals are exposed to when precipitation regimes are altered. In addition, the presence of artificial water sources (such as irrigation systems, ponds, or fountains) may also impact the influence of land-use changes on biodiversity, complicating analyses looking at the impact of the local precipitation changes ensuing land-use changes. Consequently, the results presented in this thesis add to the current literature exploring the effects of local precipitation differences across land-use types and introduce a novel way of looking at this through investigating the impacts of populations' climatic positions. However, further work is needed to explore alternative precipitation measures that take into account moisture availability (ideally at species-specific scales), as well as incorporating data on artificial water sources within habitats. At present, data on these variables are rare, so work on this may have to start with smaller, more localised studies, which could also provide an opportunity to dig into the mechanisms underlying how precipitation changes impact local ecological communities.

Despite using three of the most comprehensive compilations of vertebrate assemblage records to date (the PREDICTS, Living Planet, and BioTIME databases), there were still apparent spatial and taxonomic biases. Across all databases there were more records for mammals and birds than amphibians and reptiles. Due to different thermoregulatory strategies, it may be that the impact of changes in local climate following land-use change varies in strength between endotherms and ectotherms. Indeed, within agricultural land uses, I observed that endothermic and ectothermic assemblages differed in their degree of shift towards species affiliated with greater thermal extremes (relative to assemblages in natural habitats; Appendix 1, Section 8, fig. S3.6). Unfortunately, there were not enough populations of ectothermic species to analyse whether the impact of climatic position differed between the two groups (in Chapters 4 and 5). The rate of temperature increase has also been found to influence birds more strongly than mammals (Spooner et al., 2018). So, there is also likely variation between each terrestrial vertebrate class. In future, as the datasets comparing ecological assemblages across time and space grow, there will hopefully be enough data to explore these potential sources of variation. Spatially, it was apparent in Chapter 5 that there is a bias in time-series data for vertebrate populations towards temperate compared to tropical latitudes. This meant that there were not enough data to explore geographic variation in the time-series model. In my earlier chapters, where there were enough data to explore geographic variation, I found that there were often greater differences in community-average climatic affiliation across land uses (Chapter 3) or between populations with different climatic positions (Chapter 4) at tropical latitudes. Further, as mentioned above, ecological communities at lower latitudes are thought to be particularly vulnerable to changes in their environment (Brook et al., 2008; Newbold, 2018; Newbold et al., 2020; Pacifici et al., 2017; Sunday et al., 2014). Consequently, it may be that the effect of the interactions between climatic position, climate change, land-use type, and habitat loss is stronger at tropical latitudes than observed in Chapter 5. Again, with continuing efforts to add data to the Living Planet and BioTIME databases, hopefully it will be possible to make geographic comparisons in models such as the one presented in Chapter 5 in the future.

6.4 Conclusion

As the Earth's human population continues to grow, the demands for food, raw materials, and land to reside upon will also increase (Godfray et al., 2010; WWF, 2018). This will likely lead to further habitat loss and land-use intensification around the globe (Hurtt et al., 2011; Tilman, Balzer, Hill, & Befort, 2011). Moreover, unless there are drastic shifts in the pattern of energy use and subsequent reductions in greenhouse gas emissions, global mean temperatures will continue to rise, hot extremes will increase in frequency, and the contrast in precipitation between wet and dry regions and seasons will grow (Collins et al., 2013). The work presented in this thesis builds on the understanding of how these pressures are affecting biodiversity, specifically by furthering our knowledge on how local climatic changes are modifying responses of vertebrates to land-use changes, and on the interactions between land-use and climate change. This enhances our insight into the interspecific and spatial variation underlying responses to habitat loss and restoration, information which is vital to account for in protected area designation, the prioritisation of restoration activities, and landscape-level conservation planning, for example. Overall, with the pressures on terrestrial biodiversity mounting, this understanding is critical if we are to establish effective conservation plans, make informed policy decisions, mitigate the impacts of these drivers of change, and ultimately preserve the variety of life on Earth.

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Appendices

Appendix 1: Supplementary materials for Chapter 3

The sections contained in this appendix are:

Section 1: Land-use class definitions

Table S3.1: Classifications of the land-use classes and land-use intensity (reproduced from Hudson et al., 2014). For the analyses in Chapter 3, to ensure all groupings in the analyses reached my target minimum threshold of 50 communities, I combined mature secondary vegetation and intermediate secondary vegetation (to become advanced secondary vegetation).

Level 1 Land Use	**Predominant Land Use**	**Minimal use**	**Light use**	**Intense use**
No evidence of prior destruction of the vegetation	Primary Vegetation	Any disturbances identified are very minor (e.g., a trail or path) or very limited in the scope of their effect (e.g., hunting of a particular species of limited ecological importance).	One or more disturbances of moderate intensity (e.g., selective logging) or breadth of impact (e.g., bushmeat extraction), which are not severe enough to markedly change the nature of the ecosystem. Primary sites in suburban settings are at least Light use.	One or more disturbances that is severe enough to markedly change the nature of the ecosystem; this includes clear-felling of part of the site too recently for much recovery to have occurred. Primary sites in fully urban settings should be classed as Intense use.
Recovering after destruction of the vegetation	Mature Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
Recovering after destruction of the vegetation	Intermediate Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
Recovering after destruction of the vegetation	Young Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use

Human use (agricultural)	Plantation forest	Extensively managed or mixed timber, fruit/coffee, oil-palm or rubber plantations in which native understorey and/or other native tree species are tolerated, which are not treated with pesticide or fertiliser, and which have not been recently (< 20 years) clear-felled.	Monoculture fruit/coffee/rubber plantations with limited pesticide input, or mixed species plantations with significant inputs. Monoculture timber plantations of mixed age with no recent (< 20 years) clear-felling. Monoculture oil-palm plantations with no recent (< 20 years) clear-felling.	Monoculture fruit/coffee/rubber plantations with significant pesticide input. Monoculture timber plantations with similarly aged trees or timber/oil-palm plantations with extensive recent (< 20 years) clear-felling.
Human use (agricultural)	Cropland	Low-intensity farms, typically with small fields, mixed crops, crop rotation, little or no inorganic fertiliser use, little or no pesticide use, little or no ploughing, little or no irrigation, little or no mechanisation.	Medium intensity farming, typically showing some but not many of the following: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, no crop rotation, mechanisation, monoculture crop. Organic farms in developed countries often fall within this category, as may high-intensity farming in developing countries.	High-intensity monoculture farming, typically showing many of the following features: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, mechanisation, no crop rotation.
Human use (agricultural)	Pasture	Pasture with minimal input of fertiliser and pesticide, and with low stock density (*not* high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture either with significant input of fertiliser or pesticide, or with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture with significant input of fertiliser or pesticide, *and* with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).

Section 2: Using species' realised climatic niches based on GBIF data

Occurrence data from the Global Biodiversity Information Facility (GBIF 2015) were extracted for terrestrial vertebrate species in the PREDICTS Project database. For each of these species, data on maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), and precipitation of the wettest (Pp_{max}) and driest (Pp_{min}) months (WorldClim version 1.4; Hijmans, Cameron, Parra, Jones, & Jarvis 2005) were extracted for every recorded location within GBIF. Then, for each species, the extremes (maximum or minimum) and standard deviation of these values were found, to estimate the species realised temperature or precipitation extremes and climatic variation across a species' range, respectively (I was able to do this for 3,432 species). These species-level realised climatic niche properties were then used to calculate community weighted means (CWMs; to test for patterns in the responses to land use of (1) the community-average extreme climatic conditions and (2) mean range-wide climatic variation species are affiliated with), and to split the species into groups depending on their climatic affiliation (extreme value and range-wide variation; to test for patterns in the response to land use of abundances (log(x+1) transformed) of species groups with different climatic niches); this was completed, and the linear mixed-effects models were run following the same methods as used in Chapter 3. I also found the correlation between the species-level climatic niche properties calculated using the distribution maps and GBIF data (table S3.2).

The results were generally qualitatively and quantitatively very similar when running models with species' realised niches estimated from GBIF data (table S3.2, fig. S3.1–3) to those reported in Chapter 3. The main difference was that, for CWMmax(Pp_{max}), even though the direction of the effect of land use on this community-average climatic niche property was the same as reported in Chapter 3, the interaction between land use and geographic zone was not significant when using GBIF data (fig. S3.2).

Table S3.2: Correlation (Pearson's correlation coefficient, *r*) between the species-level climatic niche properties produced when using IUCN (for mammals, amphibians, and reptiles) or BirdLife International (for birds) range maps (IUCN 2016, BirdLife International 2012) versus occurrence data from GBIF (GBIF 2015). The climatic niche properties include the extreme (maximum [Max] or minimum [Min]) or range-wide variation (standard deviation) in one of four climatic variables (maximum temperature of the warmest month [T_{max}], minimum temperature of the coldest month [T_{min}], precipitation of the wettest month [Pp_{max}] and precipitation of the driest month [Pp_{min}]).

Climatic niche property	*r*
$MaxT_{max}$	0.799
T_{max} variation	0.562
$MinT_{min}$	0.867
T_{min} variation	0.713
$MaxP_{max}$	0.784
Pp_{max} variation	0.631
$MinP_{min}$	0.650
Pp_{min} variation	0.752

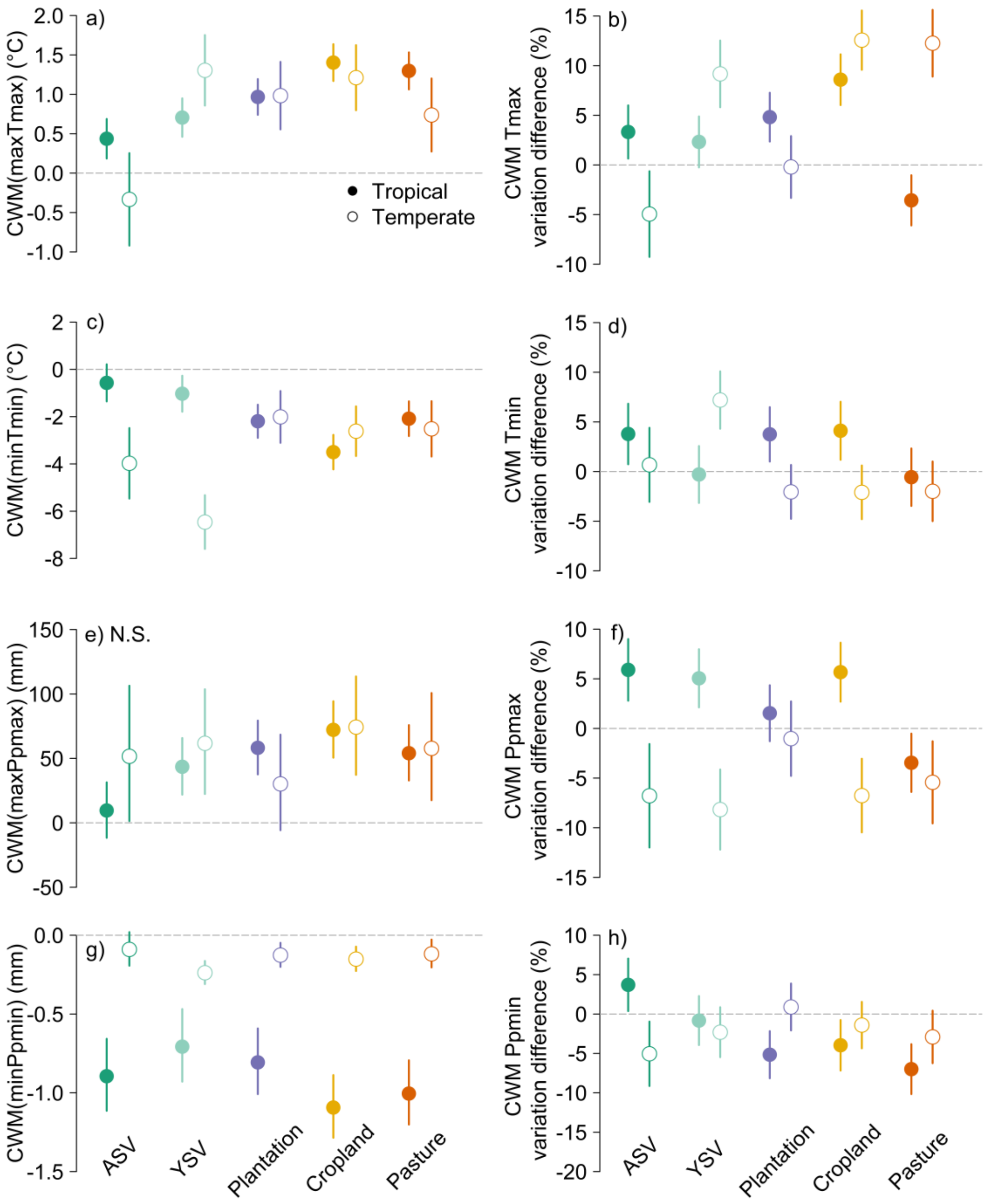


Figure S3.1: Geographic variation (tropical vs. temperate latitudes) in modelled differences across land uses in community weighted mean (CWM) maximum (max, a, e) or minimum (min, e, g) and range-wide variation (b, d, f, h) in maximum temperature of the warmest month (a, b), minimum temperature of the coldest month (c, d), precipitation of the wettest month (e, f) and precipitation of the driest month (g, h). All values are relative to assemblages within primary vegetation (which is represented by the dotted line). Error bars show 95% confidence intervals. ASV and YSV denote advanced and young secondary vegetation, respectively. Community weighted means were produced using data from GBIF. Transformed values were back-transformed from the log-scale used for analysis before plotting. N.S. denotes that the interaction between land use and geographic zone was not significant in that model.

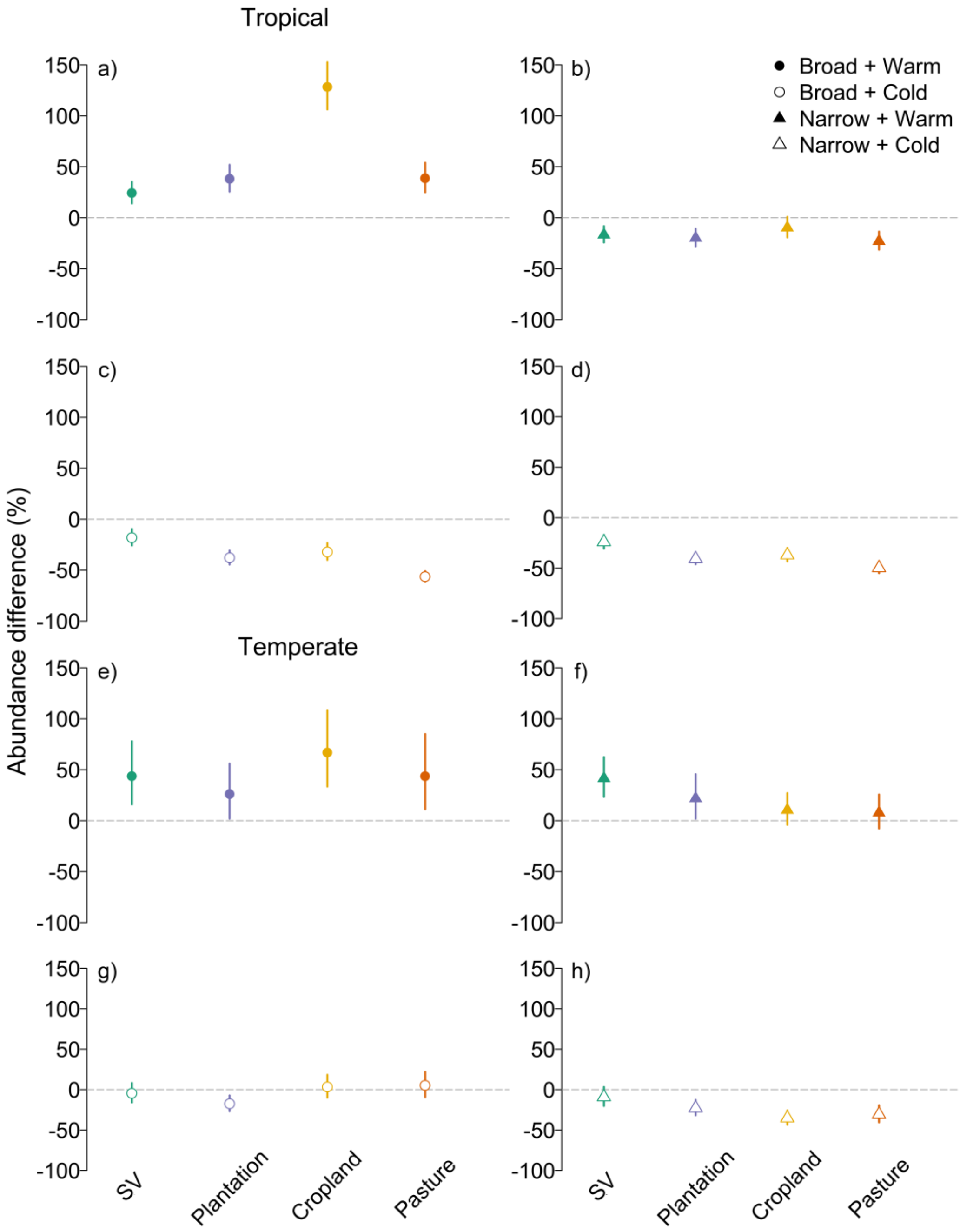


Figure S3.2: The total abundance of species with different thermal (T_{max}) niches at tropical (a-d) and temperate (e-h) latitudes across human-altered land uses, relative to assemblages within primary vegetation (dotted line). Species groups differ in the range-wide variation of thermal (T_{max}) conditions experienced over their range (‘broad’ vs. ‘narrow’) and maximum T_{max} value (‘warm’ vs. ‘cold’). Error bars show

95% confidence intervals; SV denotes secondary vegetation (consisting of the young and advanced secondary vegetation land-use categories). Values were back-transformed from the log-scale used for analysis before plotting. Species thermal niches were produced using data from GBIF.

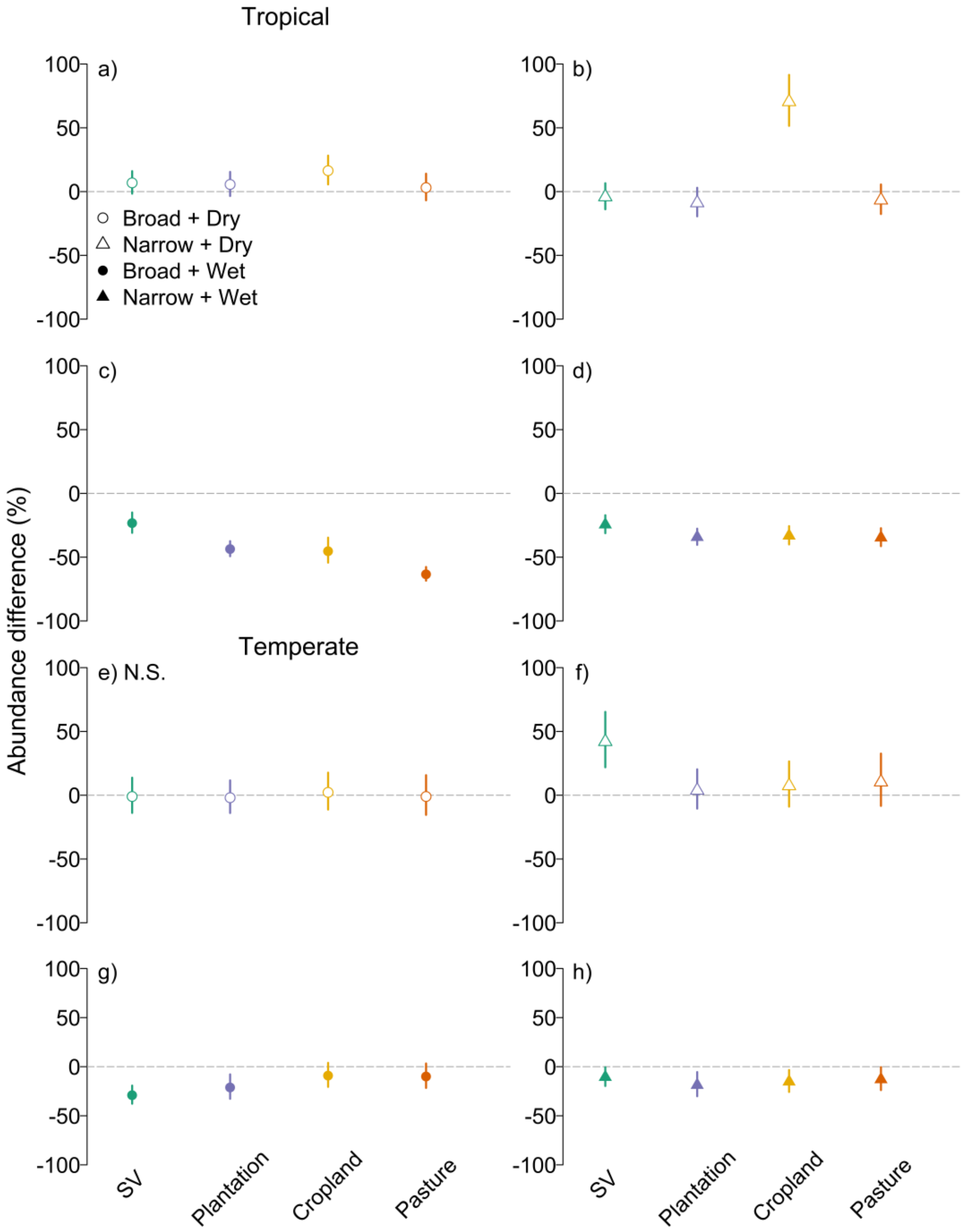
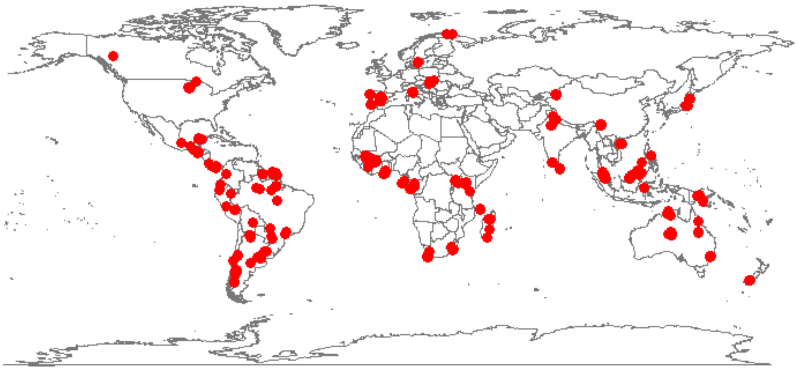


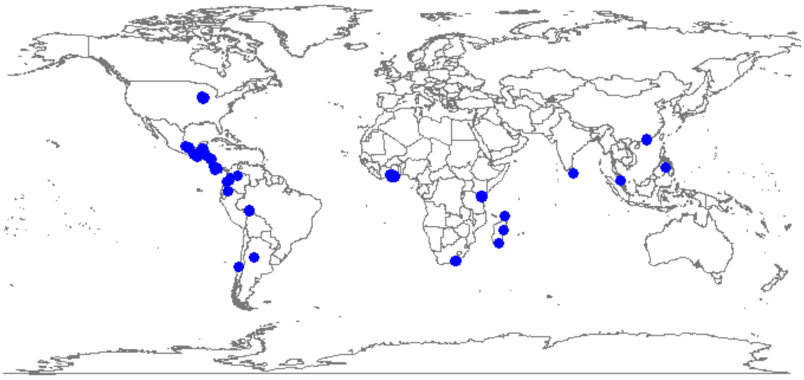
Figure S3.3: The total abundance of species with different precipitation niches (Pp_{min}) at tropical (a-d) and temperate (e-h) latitudes across human-altered land uses, relative to assemblages within primary vegetation (dotted line). Species groups differ in range-wide variation in precipitation (Pp_{min}) levels experienced throughout their range ('broad' vs. 'narrow') and minimum Pp_{min} values ('dry' vs. 'wet'). Error bars show 95% confidence intervals; SV denotes secondary vegetation (consisting of the young and advanced secondary vegetation land-use categories). Values were back-transformed from the log-scale used for analysis before plotting. Species precipitation niches were produced using data from GBIF. N.S. denotes that the effect of land use was not significant within that species group.

Section 3: Further details on the PREDICTS Project database

a) Endothermic assemblages



b) Ectothermic assemblages



c) Both

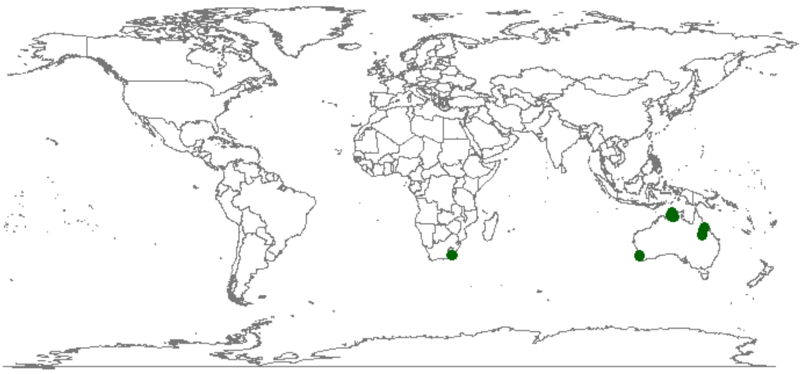


Figure S3.4: Locations of each study site ($n_{assemblages}$ = 6,123) from the PREDICTS Project database included in my analyses, split into those studies that looked at (a) solely endothermic vertebrates (mammals and birds), (b) solely ectothermic vertebrates (reptiles and amphibians) and (c) both endothermic and ectothermic vertebrates; base map from R package ‘maps’ v.3.3.0 (Becker & Wilks 2018).

Spatial extent of studies

Table S3.3: The number of assemblages in which species from each vertebrate class were recorded and the maximum linear extent sampled for 95% of PREDICTS sites that were included in my analyses, to the nearest metre.

Taxonomic group	Number of assemblages	Bounds of maximum linear extent for 95% of sites (m)	
		Lower	Upper
Mammalia	1542	15	5000
Aves	4199	40	2000
Reptilia	785	31	1923
Amphibia	885	31	1049

Section 4: Community unweighted means

I also calculated CWMs that were not weighted by species abundance (termed here community unweighted means) for the mean climatic extreme values and range-wide climatic variation of each assemblage. Using these, I produced models using the same methods as with the community-average climatic niche models (in Chapter 3) to explore whether the average climatic maximum or minimum or range-wide variation of a species assemblage differed between land uses when these values were not weighted by species abundance.

Using CWMs weighted (i.e., average for an individual within a community) versus unweighted (i.e., average for a species within a community) by species abundance made very little difference to the results when testing the effect of land use and the interaction between land use and geographic zone (fig. S3.5).

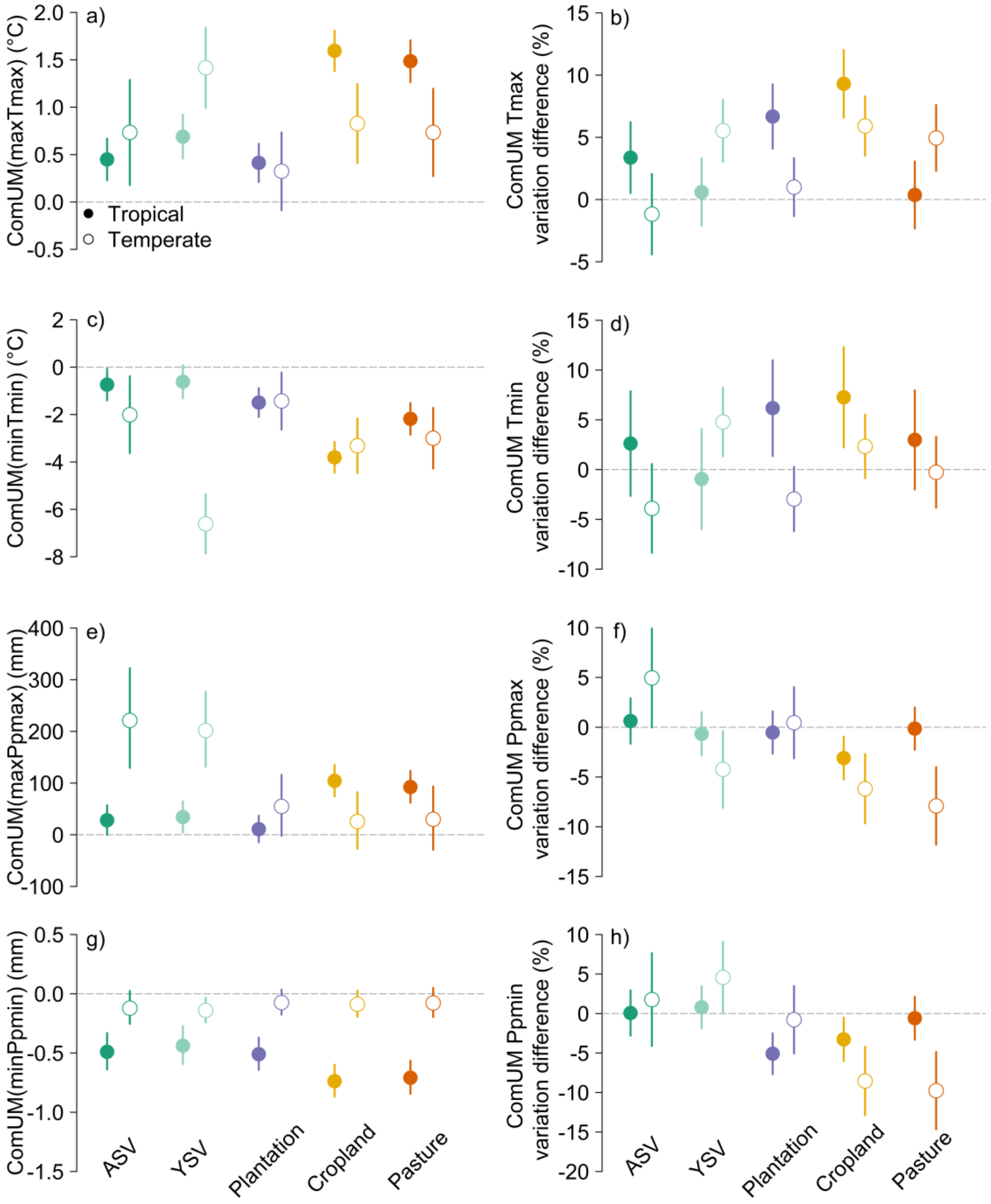


Figure S3.5: Geographic variation (tropical vs. temperate latitudes) in differences across land uses in community unweighted mean (ComUM) maximum (max, a, c) or minimum (min, e, g) and range-wide variation (b, d, f, h) of maximum temperature of the warmest month (a, b), minimum temperature of the coldest month (c, d), precipitation of the wettest month (e, f) and precipitation of the driest month (g, h). All values are relative to assemblages within primary vegetation (dotted line). Error bars show 95% confidence intervals. ASV and YSV denote advanced and young secondary vegetation, respectively. Transformed values were back-transformed from the log-scale used for analysis before plotting.

Section 5: Correlation between climatic niche properties

Table S3.4: The correlation (Spearman rank correlation) between the community-average climatic niche properties: the climatic extreme (maximum [Max] or minimum [Min]) and range-wide variation in maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) and precipitation of the driest month (Pp_{min}).

	Max T_{max}	T_{max} variation	Min T_{min}	T_{min} variation	Max Pp_{max}	Pp_{max} variation	Min Pp_{min}	Pp_{min} variation
Max T_{max}								
T_{max} variation	0.625							
Min T_{min}	-0.621	-0.913						
T_{min} variation	0.696	0.889	-0.928					
Max Pp_{max}	0.491	0.356	-0.358	0.490				
Pp_{max} variation	-0.053	-0.046	0.172	0.008	0.524			
Min Pp_{min}	-0.563	-0.455	0.473	-0.468	-0.158	0.094		
Pp_{min} variation	0.002	-0.100	0.047	0.037	0.378	0.327	0.148	

Section 6: Species groups with different climatic niches

Table S3.5: The number of species within each climatic niche group included in the abundance analysis. These groups were formed by splitting around the within-study medians of climatic extreme values and range-wide variation with regards to (a) maximum temperature of the warmest month (T_{max}) or (b) precipitation of the driest month (Pp_{min}).

		Climatic extreme			
a)		T_{max} maximum			
		Warm		Cold	
		Tropics	Temperate	Tropics	Temperate
T_{max} variation	Wide	581	290	345	123
	Narrow	248	175	1598	593
b)		Pp_{min} minimum			
		Wet		Dry	
		Tropics	Temperate	Topics	Temperate
Pp_{min} variation	Wide	583	106	1240	431
	Narrow	323	98	626	546

Table S3.6: Number of assemblages within each land use for each of the four species group with distinct climatic niches (see table S3.5) with regards to (a) maximum temperature of the warmest month (T_{max}) and (b) precipitation of the driest month (Pp_{min}). Advanced and young secondary vegetation land-use classes were combined to become 'secondary vegetation'.

Climatic niche			Land Use					Total
			Primary vegetation	Secondary vegetation	Plantation	Cropland	Pasture	
a) T_{max}								
	Warm and broad	Tropics	1156	744	691	439	543	3573
		Temperate	709	219	258	484	274	1944
	Warm and narrow	Tropics	1250	762	844	435	517	3808
		Temperate	544	127	166	278	252	1367
	Cold and broad	Tropics	884	498	684	399	518	2983
		Temperate	568	117	214	272	257	1428
	Cold and narrow	Tropics	1362	802	865	439	552	4020
		Temperate	635	207	85	226	267	1420
b) Pp_{min}								
	Wet and broad	Tropics	524	431	457	101	140	1653
		Temperate	310	60	84	218	257	929
	Wet and narrow	Tropics	925	510	578	390	487	2890
		Temperate	539	198	81	225	263	1306
	Dry and broad	Tropics	1343	763	854	435	550	3945
		Temperate	666	224	225	484	282	1881
	Dry and narrow	Tropics	1179	561	655	415	537	3347
		Temperate	747	198	258	485	283	1971

Section 7: Range-wide climatic variation and range size

Table S3.7: The correlation between community-average range-wide climatic variation and community-average range size. The latter were acquired from Newbold et al. (2018); the methods used to estimate these range sizes are described briefly in Chapter 3. Range-wide climatic variation was calculated for the following climatic variables: maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) and precipitation of the driest month (Pp_{min}).

	Community-average range-wide climatic variation			
	T_{max}	T_{min}	Pp_{max}	Pp_{min}
Community-average range size	0.661	0.773	-0.050	0.038

Section 8: Comparing endotherms and ectotherms

I also tested for differences between endothermic and ectothermic assemblages, as ambient climatic conditions affect them differently due to their distinct physiologies (Deutsch et al., 2008; Frishkoff et al., 2016; McNab 2012; Senior et al., 2017).

Methods

These models were run in the same way as the models looking at geographic differences in Chapter 3, but with thermoregulatory strategy (endothermic vs. ectothermic) and its interaction with land use included as fixed effects instead of geographic zone. The 391 communities (5.73% of all communities) that sampled for endotherms *and* ectotherms were removed from these analyses. The secondary vegetation land-use classes were grouped together (to become 'secondary vegetation'), and pasture and cropland were grouped to become an 'agriculture' land-use class (the only grouping in this analysis that failed to reach my target minimum threshold of 50 communities was in the range-wide climatic variation analyses for ectothermic assemblages in secondary vegetation where n = 34; table S3.8). For the final statistical models used, see table S3.9. I also tested for spatial autocorrelation in the residuals of all my models using Moran's I tests.

Table S3.8: The number of endothermic and ectothermic assemblages within each land-use type included in the models comparing these two groups. The numbers in parentheses denote the number of assemblages included in the models testing effects of land use on the community-average range-wide variation in climatic conditions.

Assemblage	Land use				Total
	Primary vegetation	Secondary vegetation	Plantation	Agriculture	
Endothermic	1697 (1456)	859 (719)	873 (661)	1638 (1433)	5067 (4289)
Ectothermic	226 (133)	56 (34)	262 (207)	121 (73)	665 (447)

Table S3.9: The final statistical models for the analyses of community-average climatic niches after backwards stepwise selection of fixed effects, following the methods proposed by Zuur et al. (2009). Response variables were the community weighted means (CWM) for the extremes of the four focal climatic variables (CWM(maxT_{max}), CWM(minT_{min}), CWM(maxPp_{max}), CWM(minPp_{min})) or STD (the community weighted mean of the standard deviation of the climatic variables across the species range, which I used to calculate community-average range-wide variation) for each climatic variable (maximum temperature of the warmest month, STD_Tmax; minimum temperature of the coldest month, STD_Tmin; precipitation of the wettest month, STD_Ppmax; precipitation of the driest month, STD_Ppmin). Community weighted means for extremes of precipitation variables were log(x+1) transformed. Random intercepts included study identity (SS, added to account for differences between studies in sampling methods and response variables) and spatial block within study (SSB, to account for the spatial structure of sites sampled within each study). The explanatory variables considered as fixed effects included land use (LU), thermoregulatory strategy (EE; endothermic vs. ectothermic assemblages) and the interaction between the two ('×' between variables indicate that the interaction between those two variables was significant). In addition, the climatic variable in question at the study site and the site's elevation were also added into models as continuous covariates (for all models apart from those focusing on maximum temperature of the warmest month, where elevation was not added because it correlated strongly with maximum temperature itself; see Chapter 3); for range-wide climatic variation analyses community weighted mean range sizes (Range) were also added as a continuous covariate; I fit linear terms for these three covariates.

<table>
<tr><th colspan="3">Model</th></tr>
<tr><td>Endotherms vs. ectotherms</td><td>Climatic extreme</td><td></td></tr>
<tr><td></td><td></td><td>CWM(maxTmax) ~ LU + EE + LU×EE + Tmax + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td></td><td>CWM(minTmin) ~ LU + EE + LU×EE + Tmin + Elevation + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td></td><td>CWM(maxPpmax) ~ LU + EE + Elevation + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td></td><td>CWM(minPpmin) ~ LU + EE + LU×EE + Elevation + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>Climatic variation</td><td></td></tr>
<tr><td></td><td></td><td>STD_Tmax ~ LU + EE + LU×EE + Range + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td></td><td>STD_Tmin ~ LU + EE + LU×EE + Tmin + Elevation + Range + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td></td><td>STD_Ppmax ~ LU + EE + LU×EE + Range + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td></td><td>STD_Ppmin ~ LU + EE + LU×EE + Ppmin + Elevation + Range + (1|SS) + (1|SSB)</td></tr>
</table>

Results

Endothermic and ectothermic assemblages differed in their climatic niches across land uses for all climatic variables apart from community-average maximum Pp_{max} (land use by thermoregulatory strategy interaction, $p < 0.05$, apart for CWM(maxPp_{max}) where $p = 0.34$; fig. S3.6, table S3.10). Ectothermic and endothermic assemblages differed most in agricultural land uses (pasture and cropland), in which ectothermic assemblages tended to show stronger relative shifts toward species affiliated with warmer T_{max}, whereas endothermic assemblages showed stronger shifts towards colder T_{min} affiliations (fig. S3.6).

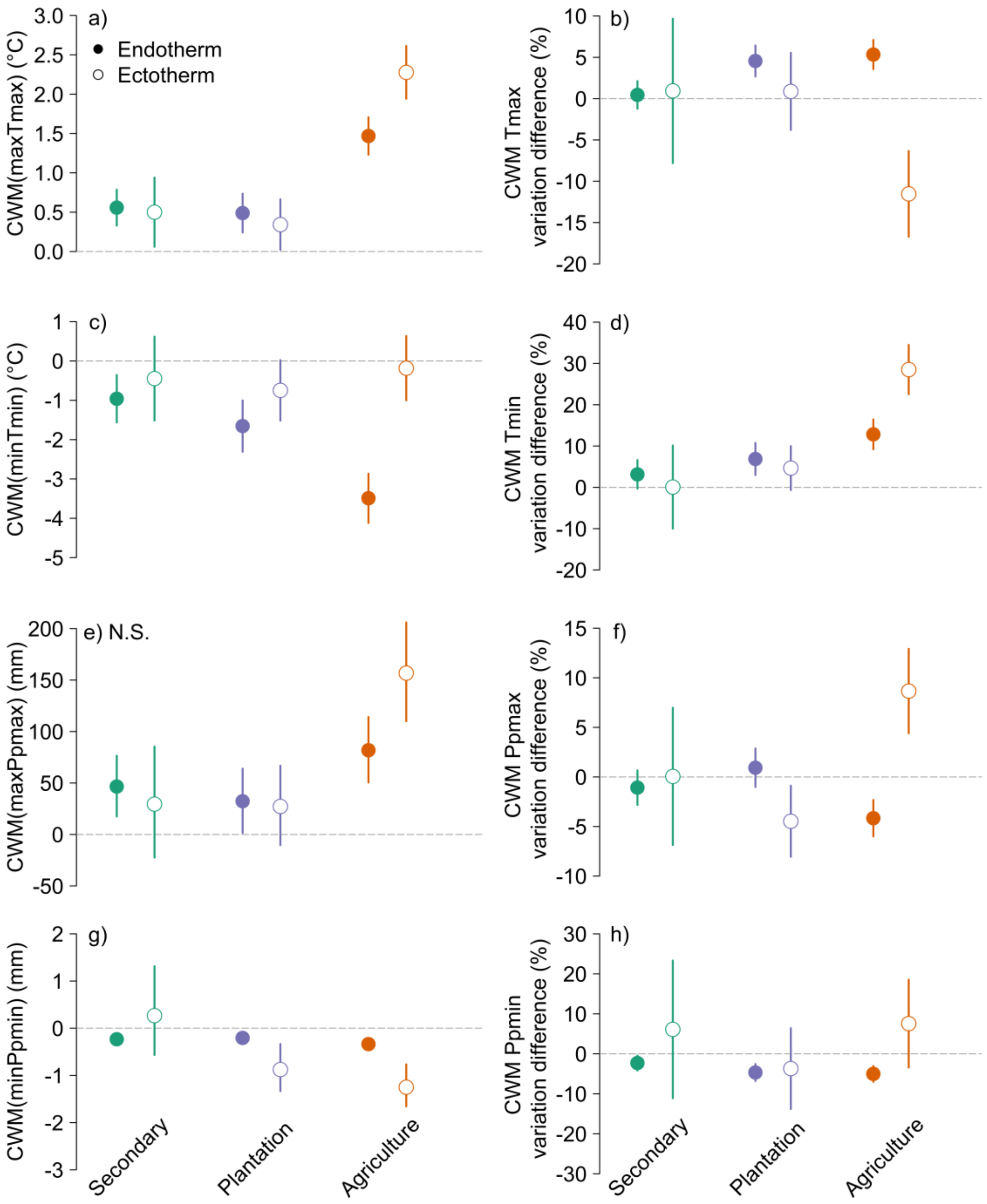


Figure S3.6: Variation between endothermic and ectothermic assemblages across land-use types in community weighted mean (CWM) maximum (max, a, c) or minimum (min, e, g) and range-wide variation (b, d, f, h) of maximum temperature of the warmest month (a, b), minimum temperature of the coldest month (c, d), precipitation of the wettest month (e, f) and precipitation of the driest month (g, h). Values are relative to assemblages within primary vegetation (dotted line). Error bars show 95% confidence intervals; community-average extreme or range-wide variation significantly differ from those within primary vegetation when the error bars for that land use do not cross the dotted line. Transformed values were back-transformed from the log-scale used for analysis before plotting. N.S. denotes models in which the interaction between land use and thermoregulatory strategy was not significant.

Table S3.10: The statistical results from the likelihood ratio tests investigating the effect of the interaction between land use and thermoregulatory strategy (endothermic vs. endothermic). Response variables were community weighted mean for the climatic extreme (maximum [max] or minimum [min]) or range-wide variation in one of four climatic variables (maximum temperature of the warmest month [T_{max}], minimum temperature of the coldest month [T_{min}], precipitation of the wettest month [Pp_{max}] and precipitation of the driest month [Pp_{min}]).

Model (in parentheses is the fixed effect for which the statistical results are provided)	Climatic niche property	Results from likelihood ratio tests		
		χ^2	Degrees of freedom	*p*-value
Endotherm vs. ectotherm (interaction between land use and thermoregulatory strategy)	CWM(maxT_{max})	8.03	3,12	0.045
	T_{max} variation	143.95	3,13	<0.001
	CWM(minT_{min})	15.87	3,13	0.001
	T_{min} variation	20.57	3,14	<0.001
	CWM(maxPp_{max})	3.38	3,13	0.337
	Pp_{max} variation	19.74	3,14	<0.001
	CWM(minPp_{min})	27.52	3,13	<0.001
	Pp_{min} variation	30.17	3,14	<0.001

Table S3.11: Spatial autocorrelation in the community-level model residuals; a Moran's I test was applied to the residuals of the final models for each individual underlying study separately (Newbold et al., 2015), with the percentage of studies that had $p < 0.05$ shown below. The climatic niche properties modelled were the community weighted mean for the extreme value (maximum [max] or minimum [min]) or range-wide variation in one of four climatic variables (maximum temperature of the warmest month [T_{max}], minimum temperature of the coldest month [T_{min}], precipitation of the wettest month [Pp_{max}] and precipitation of the driest month [Pp_{min}]).

Model	Climatic niche property	Percentage of studies for which $p < 0.05$
Endotherm vs. ectotherm	CWM(maxT_{max})	5.48
	T_{max} variation	3.28
	CWM(minT_{min})	8.00
	T_{min} variation	3.39
	CWM(maxPp_{max})	0
	Pp_{max} variation	8.20
	CWM(minPp_{min})	1.39
	Pp_{min} variation	6.90

Discussion

Endothermic and ectothermic assemblages differed in the magnitude, and sometimes direction, of community-average climatic niches across human-altered land uses relative to primary vegetation. Differences were often largest in agricultural land uses (cropland and pastures) and was particularly strong for thermal niche properties. For ectotherms, agriculture appears to be favouring hot-specialists (species affiliated with higher maximum temperatures and less range-wide variation in T_{max}), potentially due to the strong influence of temperature on ectotherm's basic physiological functions (Deutsch et al., 2008). Additionally, to survive hotter temperatures, ectotherms rely on access to cool microhabitats (shade or burrows) to thermoregulate (Kearney, Shine, & Porter, 2009; Sunday et al., 2014), which may be lacking in agriculture. Endotherms affiliated with cold extremes appeared to be favoured in human-altered habitats, especially in agricultural land uses; this may be due to the strong limiting effect of cold extremes on the distributions of birds and mammals (Khaliq, Böhning-Gaese, Prinzinger, Pfenninger, & Hof, 2017). With more data, it would be interesting to also look at the similarities/differences between wet-skinned (i.e., amphibians) and dry-skinned (i.e., endotherms and reptiles) species.

Section 9: Model structure and further statistical results

Table S3.12: The final statistical models for the analyses of community-average climatic niches after backwards stepwise selection of fixed effects, following the methods proposed by Zuur et al. (2009). Response variables were the community weighted means for the extremes (maximum or minimum) of the four focal climatic variables (CWM(maxT_{max}), CWM(minT_{min}), CWM(maxPp_{max}), CWM(minPp_{min})) or STD (the community weighted mean of the standard deviation of the climatic variables across the species range, which I used to calculate community-average range-wide variation) for each climatic variable (maximum temperature of the warmest month, STD_Tmax; minimum temperature of the coldest month, STD_Tmin; precipitation of the wettest month, STD_Ppmax; precipitation of the driest month, STD_Ppmin). Community weighted means for extremes of precipitation variables were log(x+1) transformed. Random intercepts included study identity (SS, added to account for differences between studies in sampling methods and response variables) and spatial block within study (SSB, to account for the spatial structure of sites sampled within each study). The explanatory variables considered as fixed effects included land use (LU) and geographic zone (GZ; temperate versus tropical latitudes) and its interaction with land use; '×' between variables indicate that the interaction between those two variables was significant. In addition, the climatic variable in question at the study site and the site's elevation were also added into models as continuous covariates (for all models apart from those focusing on maximum temperature of the warmest month, where elevation was not added; see Chapter 3); for range-wide climatic variation analyses community weighted mean range sizes (Range) were also added as a continuous covariate; I fit linear terms for these three covariates.

Model		
Community-average climatic niche models	Climatic extreme	
		CWM(maxT$_{max}$) ~ LU + GZ + LU×GZ + Tmax + (1|SS) + (1|SSB)
		CWM(minT$_{min}$) ~ LU + GZ + LU×GZ + Tmin + Elevation + (1|SS) + (1|SSB)
		Log(CWM(maxPp$_{max}$)+1) ~ LU + GZ + LU×GZ + Elevation + (1|SS) + (1|SSB)
		Log(CWM(minPp$_{min}$)+1) ~ LU + GZ + LU×GZ + Elevation + (1|SS) + (1|SSB)
	Climatic variation	
		STD_Tmax ~ LU + GZ + LU×GZ + Range + (1|SS) + (1|SSB)
		STD_Tmin ~ LU + GZ + LU×GZ + Tmin + Elevation + Range + (1|SS) + (1|SSB)
		STD_Ppmax ~ LU + GZ + LU×GZ + Range + (1|SS) + (1|SSB)
		STD_Ppmin ~ LU + GZ + LU×GZ + Ppmin + Elevation + Range + (1|SS) + (1|SSB)

Table S3.13: The final statistical models for the abundance analyses after the backwards stepwise selection of fixed effects. Response variables were the abundance (transformed using log(x+1); LogAbund) of species groups with different climatic niches (separately for maximum temperature [T$_{max}$] and minimum precipitation [Pp$_{min}$]). Species within each assemblage analysed were split into 4 groups around the within-study medians of climatic extreme (maximum of T$_{max}$ or minimum of Pp$_{min}$) and range-wide variation (T$_{max}$ or Pp$_{min}$). For the temperature variable, groups included species with (1) warm and broad, (2) warm and narrow, (3) cold and broad or (4) cold and narrow T$_{max}$ niches. For the precipitation variable, groups included species with (1) dry and broad, (2) dry and narrow, (3) wet and broad or (4) wet and narrow Pp$_{min}$ niches. Random intercepts included study identity (SS, added to account for differences between studies in sampling methods and response variables) and spatial block within study (SSB, to account for the spatial structure of sites sampled within each study). Land use (LU) was always considered as an explanatory variable, so added as a fixed effect. The climatic variable in question at the study site was considered as a fixed, continuous covariate; site elevation was also considered as a continuous fixed effect for the temperate models focusing on precipitation of the driest month (see Chapter 3); I fit linear terms for both of these covariates.

Abundance model

<table>
<tr><td>Maximum temperature of the warmest month</td><td colspan="2">Tropical latitudes</td></tr>
<tr><td></td><td>1)</td><td>LogAbund ~ LU + Tmax + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>2)</td><td>LogAbund ~ LU + Tmax + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>3)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>4)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td colspan="2">Temperate latitudes</td></tr>
<tr><td></td><td>1)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>2)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>3)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>4)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td>Precipitation of the driest month</td><td colspan="2">Tropical latitudes</td></tr>
<tr><td></td><td>1)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>2)</td><td>LogAbund ~ LU + Ppmin + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>3)</td><td>LogAbund ~ LU + Ppmin + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>4)</td><td>LogAbund ~ LU + Ppmin + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td colspan="2">Temperate latitudes</td></tr>
<tr><td></td><td>1)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>2)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>3)</td><td>LogAbund ~ LU + (1|SS) + (1|SSB)</td></tr>
<tr><td></td><td>4)</td><td>LogAbund ~ LU + Elevation + (1|SS) + (1|SSB)</td></tr>
</table>

Full statistical results

Table S3.14: The statistical results from the likelihood ratio tests investigating the effect of land use and the interaction between land use and geographic zone. Response variables were community weighted means for the climatic extreme (maximum [Max] or minimum [Min]) or range-wide variation of one of four climatic variables (maximum temperature of the warmest month [T_{max}], minimum temperature of the coldest month [T_{min}], precipitation of the wettest month [Pp_{max}] and precipitation of the driest month [Pp_{min}]).

The effect for which the statistical results are provided	Climatic niche property	Results from likelihood ratio tests		
		χ^2	Degrees of freedom	*p*-value
Land use	Max T_{max}	238.79	5,11	<0.001
	T_{max} variation	67.12	5,11	<0.001
	Min T_{min}	170.26	5,12	<0.001
	T_{min} variation	22.56	5,12	<0.001
	Max Pp_{max}	71.74	5,10	<0.001
	Pp_{max} variation	30.07	5,11	<0.001
	Min Pp_{min}	105.07	5,11	<0.001
	Pp_{min} variation	24.38	5,13	<0.001
Interaction between geographic zone and land use	Max T_{max}	38.23	5,16	<0.001
	T_{max} variation	99.41	5,17	<0.001
	Min T_{min}	99.14	5,17	<0.001
	T_{min} variation	62.38	5,18	<0.001
	Max Pp_{max}	84.73	5,17	<0.001
	Pp_{max} variation	14.24	5,18	0.014
	Min Pp_{min}	14.39	5,17	0.013
	Pp_{min} variation	19.05	5,18	0.002

Table S3.15: The statistical results from the likelihood ratio tests looking at the effect of land use on the abundance of species groups with different climatic niche properties. Species groups were formed by splitting assemblages within the PREDICTS Project database around the within-study medians of climatic extreme (maximum or minimum) and range-wide variation in (a) maximum temperature of the warmest month (T_{max}) or (b) precipitation of the driest month (Pp_{min}).

Model	Species group	Geographic zone	Statistical results for the land use term		
			χ^2	Degrees of freedom	*p*-value
a) T_{max}	Broad and warm	Tropics	155.29	4,9	<0.001
		Temperate	9.32	4,8	0.053
	Narrow and warm	Tropics	35.57	4,9	<0.001
		Temperate	4.51	4,9	0.341
	Broad and cold	Tropics	236.55	4,8	<0.001
		Temperate	36.60	4,8	<0.001
	Narrow and cold	Tropics	132.30	4,8	<0.001
		Temperate	17.84	4,8	0.001
b) Pp_{min}	Broad and dry	Tropics	37.25	4,8	<0.001
		Temperate	6.71	4,9	0.152
	Narrow and dry	Tropics	191.06	4,9	<0.001
		Temperate	10.25	4,8	0.036
	Broad and wet	Tropics	184.26	4,9	<0.001
		Temperate	7.49	4,8	0.112
	Narrow and wet	Tropics	78.74	4,9	<0.001
		Temperate	17.35	4,9	0.002

Spatial autocorrelation results

I tested for spatial autocorrelation in the residuals of all my models using Moran's I tests (Newbold et al. 2018; table S3.16-17).

Table S3.16: Spatial autocorrelation in the residuals of the community-average climatic niche models; a Moran's I test was applied to the residuals of the final models for each individual underlying study separately, with the percentage of studies that had $p < 0.05$ shown below. The climatic niche properties modelled were the community weighted means for the climatic extreme (maximum [Max] or minimum [Min]) or range-wide variation in one of four climatic variables (maximum temperature of the warmest month [T_{max}], minimum temperature of the coldest month [T_{min}], precipitation of the wettest month [Pp_{max}] and precipitation of the driest month [Pp_{min}]).

Model	Climatic niche property	Percentage of studies for which $p < 0.05$
Community-average climatic niche models	Max T_{max}	5.33
	T_{max} variation	1.54
	Min T_{min}	5.26
	T_{min} variation	4.62
	Max Pp_{max}	0
	Pp_{max} variation	9.23
	Min Pp_{min}	1.37
	Pp_{min} variation	6.25

Table S3.17: Spatial autocorrelation in the abundance model residuals; a Moran's I test was applied to the residuals of the abundance models for each individual underlying study separately, with the percentage of studies that had $p < 0.05$ shown below. Species groups were formed by splitting assemblages within the PREDICTS Project database around the within-study medians of climatic extreme (maximum T_{max} or minimum Pp_{min}) and range-wide variation (T_{max} or Pp_{min}).

Model	Species group	Geographic zone	Percentage of studies for which $p < 0.05$
a) T_{max}	Broad and warm	Tropics	9.76
		Temperate	8.00
	Narrow and warm	Tropics	2.78
		Temperate	11.76
	Broad and cold	Tropics	7.69
		Temperate	5.56
	Narrow and cold	Tropics	6.98
		Temperate	15.00
b) Pp_{min}	Broad and dry	Tropics	4.55
		Temperate	4.17
	Narrow and dry	Tropics	3.23
		Temperate	8.33
	Broad and wet	Tropics	11.54
		Temperate	25.00
	Narrow and wet	Tropics	9.09
		Temperate	6.25

Section 10: Habitat specialisation

Using species' habitat preferences extracted from IUCN (2017), a species-level habitat breadth index was produced by weighting each habitat used by its importance and suitability to the species (as recorded within IUCN 2017) and then summing these together (table S3.18). Habitats that were classed as of major importance to the species were given a weight of 1, while habitats that were less important or suitable (e.g., marginal habitats) were given lower weights (table S3.18); the index was robust to different weighting systems (A. Etard, unpublished data). Thus, higher indices represent species inhabiting a greater range of habitats. I calculated the correlation between the species-level climatic niche properties and this habitat breadth index; these correlations were all low ($|r| < 0.41$, table S3.19).

Table S3.18: The weighting system used to produce a species-level habitat breadth index based on their habitat preferences (IUCN 2017). Each habitat was assigned a weight depending on its importance and suitability to the species (reproduced with permission from A. Etard). Dashes denote categories that do not exist (a habitat cannot have a classification of major importance and marginal or unknown suitability).

Suitability	Major importance		
	Yes	No	Unknown
Suitable	1.0	0.5	1.0
Marginal	---	0.3	0.3
Unknown	---	0.3	1.0

Table S3.19: The correlation (Pearson's correlation coefficient, *r*) between species-level climatic niche properties and their habitat breadth (using the habitat breadth index produced by A. Etard; $n_{species}$ = 3,119). The species-level climatic niche properties include the climatic extreme (maximum [Max] or minimum [Min]) or the range-wide variation in maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) and precipitation of the driest month (Pp_{min}).

Climatic niche property	*r*
Max T_{max}	0.409
T_{max} variation	0.360
Min T_{min}	-0.384
T_{min} variation	0.367
Max Pp_{max}	0.283
Pp_{max} variation	0.121
Min Pp_{min}	-0.119
Pp_{min} variation	-0.039

Forest specialisation

To further explore the relationship between species' climatic niches and their habitat affiliations, using the above habitat preferences (IUCN 2017), I extracted data on forest use. Forest canopies buffer climatic extremes (Barnagaud, Barbaro, Hampe, Jiguet, & Archaux, 2013; Ewers & Banks-Leite, 2013). Consequently, if species' climatic niches are a product of the spatial (and climatic) distribution of their critical habitats, then the loss of forest specialists from human-disturbed habitats may be a driver in the shift towards community-average realised climatic niches that encompass greater extremes in climatic variables in these human-altered sites. Therefore, to check that my results were not being driven by a loss of forest specialists, I explored the climatic niche properties of forest specialists and the influence of excluding forest specialists from the models on the results. A species was classified as a forest specialist if natural forest habitats were considered as being of 'major' importance according to the IUCN habitat classification (rather than suitable, marginal, or unsuitable), otherwise the species was classified as a non forest-specialist (although because estimates are lacking for some species, I cannot say for certain a species is *not* a forest specialist). The habitats in the IUCN classification that were considered to be natural forest were: Forest – Subtropical/Tropical Moist Lowland; Forest – Subtropical/Tropical Moist Montane; Forest – Subtropical/Tropical Dry; Forest – Temperate; Forest – Subtropical/Tropical Swamp; Forest – Boreal; Forest – Subartic; Forest – Subtropical/Tropical Mangrove Vegetation Above High Tide Level; Forest – Subantarctic.

First, I compared the difference in species-level climatic niche properties between forest specialists and non forest-specialists (fig. S3.7).

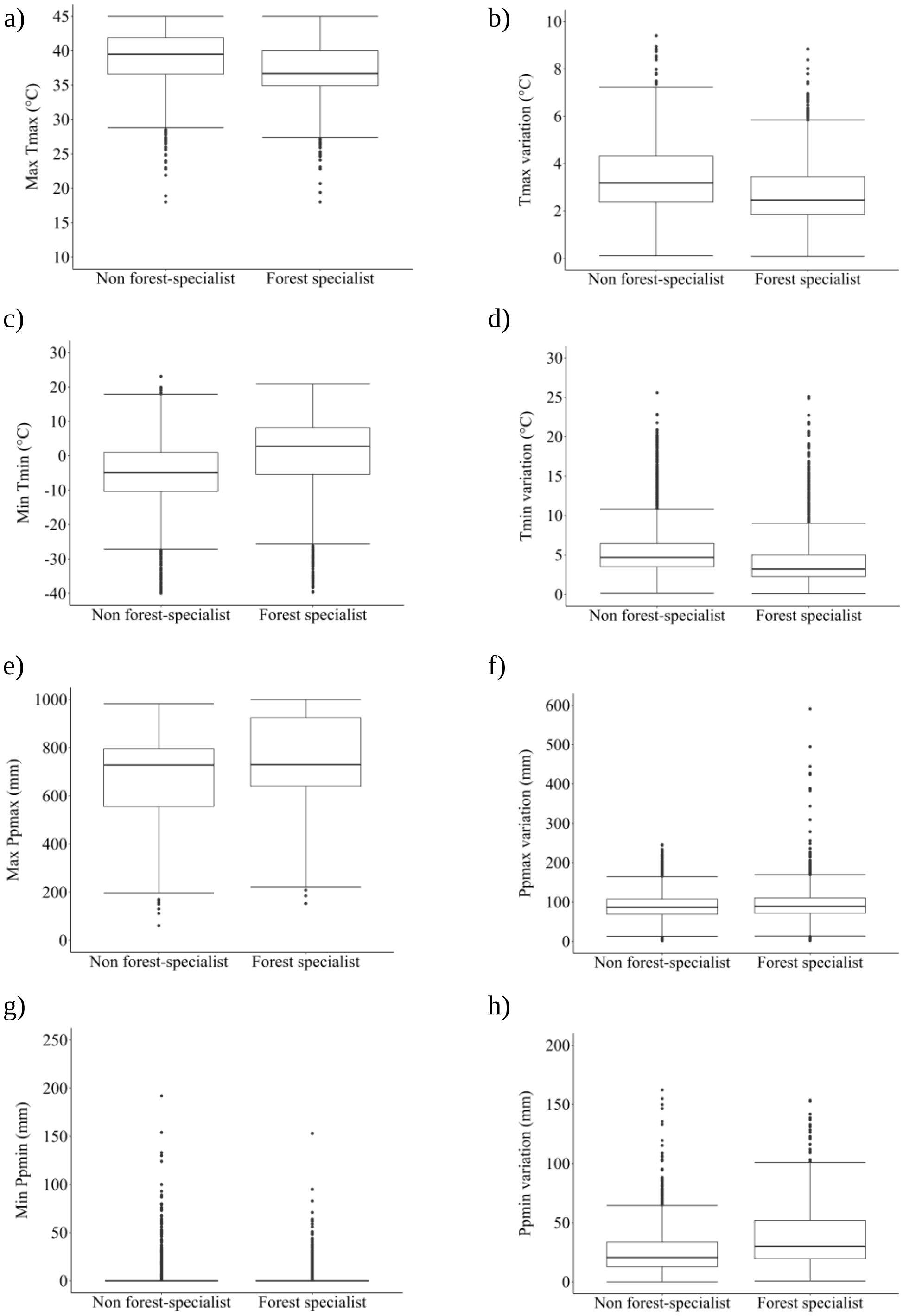


Figure S3.7: Comparisons between species classed as forest specialists and non forest-specialists for the following climatic niche properties: species-level climatic maximum (max, a, c) or minimum (min, e, g) and range-wide variation in (b, d, f, h) of maximum temperature of the warmest month (a, b), minimum temperature of the coldest month (c, d), precipitation of the wettest month (e, f) and precipitation of the driest month (g, h).

Second, to investigate the influence of habitat specialisation on my results, I ran two sets of simple models, run following the same method to my community-average climatic niche models in Chapter 3, but excluding geographic zone and its interaction with land use. All species were included in the first set of models (fig. S3.8), but in the second set, species classed as forest specialists were excluded (fig. S3.9). Although there were some differences between species-level climatic niche properties for forest versus non forest-specialists (fig. S3.7), the results from the models excluding forest specialists were qualitatively and quantitatively very similar to the models including all species (fig. S3.8-9).

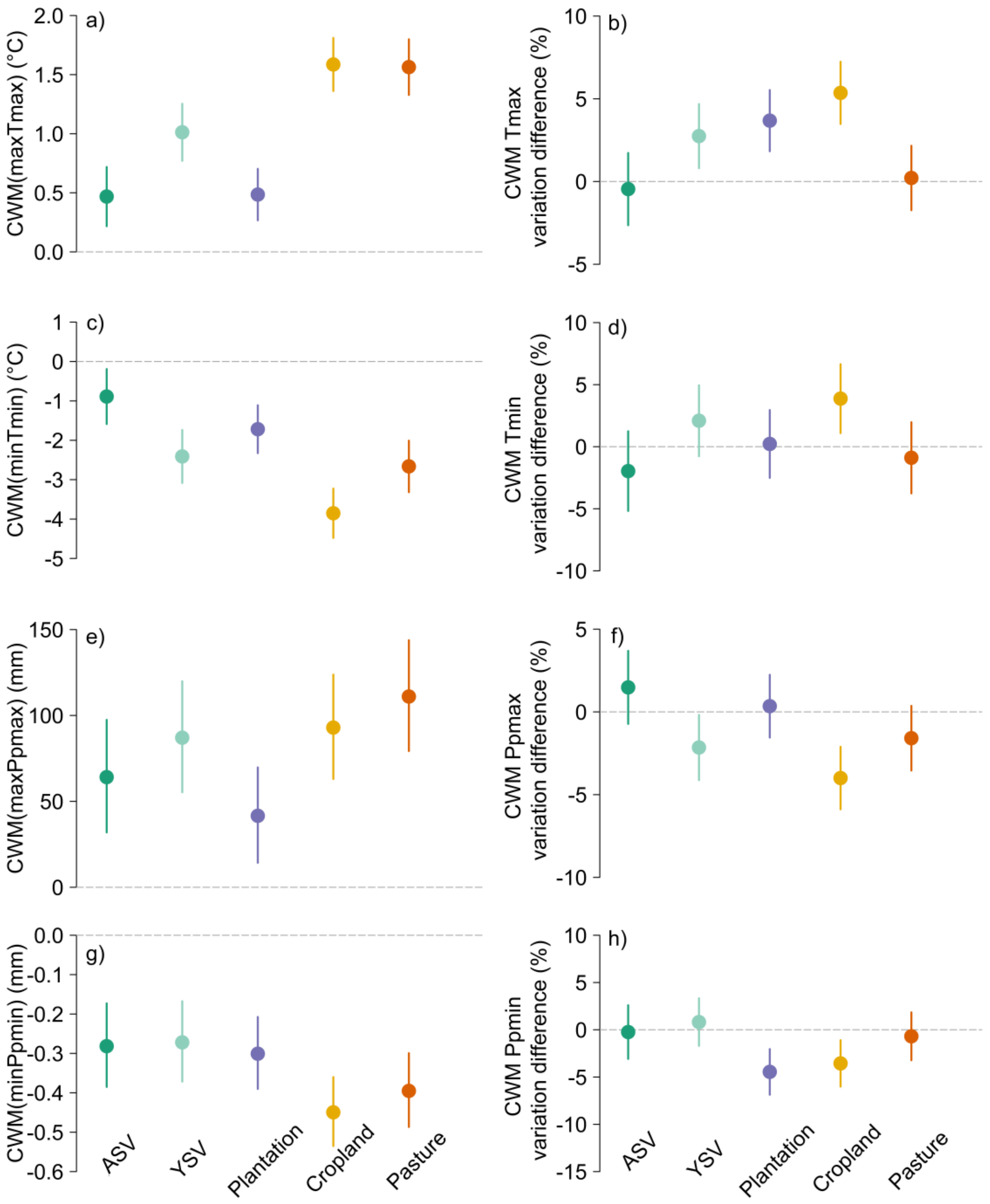


Figure S3.8: Difference across land uses in community weighted mean (CWM) maximum (max, a, c) or minimum (min, e, g) and range-wide variation (b, d, f, h) in maximum temperature of the warmest month (a, b), minimum temperature of the coldest month (c, d), precipitation of the wettest month (e, f) and precipitation of the driest month (g, h). All values are relative to assemblages within primary vegetation (dotted line). Error bars show 95% confidence intervals; community-average extreme value (maximum or minimum) or range-wide variation significantly differ from those within primary vegetation when the error bars for that land use do not cross the dotted line. ASV and YSV denote advanced and young secondary vegetation, respectively. Transformed values were back-transformed from the log-scale used for analysis before plotting.

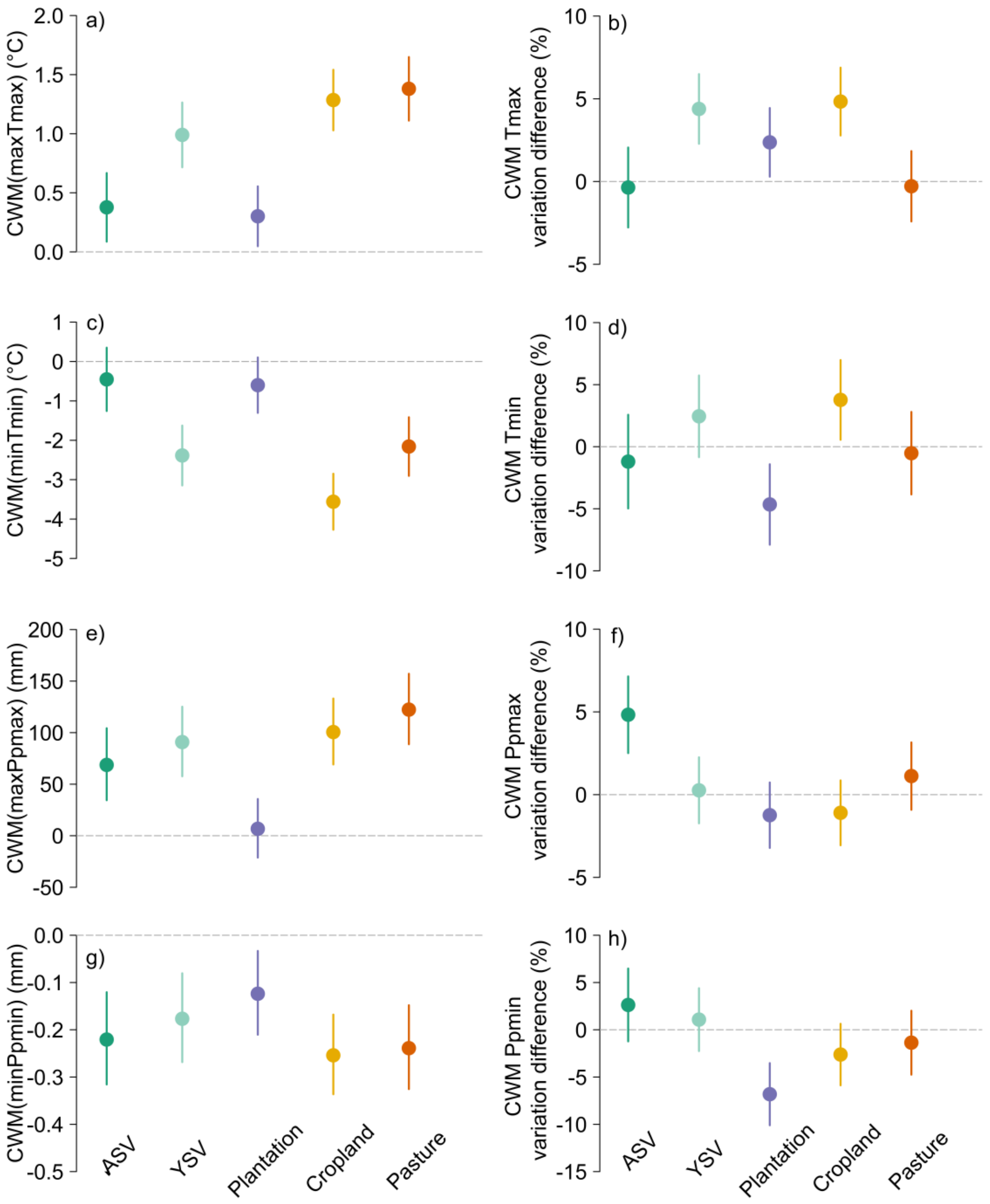


Figure S3.9: Difference across land uses, when forest specialists are excluded, in community weighted mean (CWM) maximum (max, a, c) or minimum (min, e, g) and range-wide variation (b, d, f, h) in maximum temperature of the warmest month (a, b), minimum temperature of the coldest month (c, d), precipitation of the wettest month (e, f) and precipitation of the driest month (g, h). All values are relative to assemblages within primary vegetation (dotted line). Error bars show 95% confidence intervals; community-average extreme value or range-wide variation significantly differ from those within primary vegetation when the error bars for that land use do not cross the dotted line. ASV and YSV denote advanced and young secondary vegetation, respectively. Transformed values were back-transformed from the log-scale used for analysis before plotting.

Section 11: Migratory birds

For migrating species, using entire distributions may lead to unreliable/inaccurate estimates of realised climatic niches owing to the species' potential ability to use movement to avoid certain climatic conditions (Robinson et al., 2009). Thus, when producing community-average climatic niche properties (Chapter 3), I compared the results with and without migratory birds included (migratory status was derived from BirdLife International's World Bird Database; BirdLife International (2018); table S3.20). There were 2,158 non-migratory and 551 migratory species of bird within those species included in my analyses (BirdLife International 2018). When I excluded the migratory bird species and recalculated the community weighted means (CWMs) for each climatic niche property, the values were highly correlated with the CWMs that included migratory bird species (table S3.20).

Table S3.20: Correlation (Pearson correlation coefficient, *r*) between the community weighted means produced with and without migratory bird species included for each community-average climatic niche property. The climatic niche properties included the community weighted means for the climatic extreme (maximum [Max] or minimum [Min]) or range-wide variation experienced across a species' range in one of four climatic variables (maximum temperature of the warmest month [T_{max}], minimum temperature of the coldest month [T_{min}], precipitation of the wettest month [Pp_{max}] and precipitation of the driest month [Pp_{min}]). Migratory data were extracted from BirdLife International's World Bird Database (BirdLife International 2018).

Climatic niche property	*r*
Max T_{max}	0.930
T_{max} variation	0.943
Min T_{min}	0.954
T_{min} variation	0.917
Max Pp_{max}	0.850
Pp_{max} variation	0.943
Min Pp_{min}	0.998
Pp_{min} variation	0.983

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Appendix 2: Supplementary materials for Chapter 4

The sections contained in this appendix are:

Section 1: Land-use type definitions

Table S4.1: Classifications of the land-use types and land-use intensity (reproduced from Hudson et al., 2014). For the analyses in Chapter 4, I removed minimally-used urban sites.

Level 1 Land Use	Predominant Land Use	Minimal use	Light use	Intense use
No evidence of prior destruction of the vegetation	Primary Vegetation	Any disturbances identified are very minor (e.g., a trail or path) or very limited in the scope of their effect (e.g., hunting of a particular species of limited ecological importance).	One or more disturbances of moderate intensity (e.g., selective logging) or breadth of impact (e.g., bushmeat extraction), which are not severe enough to markedly change the nature of the ecosystem. Primary sites in suburban settings are at least Light use.	One or more disturbances that is severe enough to markedly change the nature of the ecosystem; this includes clear-felling of part of the site too recently for much recovery to have occurred. Primary sites in fully urban settings should be classed as Intense use.
Recovering after destruction of the vegetation	Mature Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
Recovering after destruction of the vegetation	Intermediate Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
Recovering after destruction of the vegetation	Young Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use

Human use (agricultural)	Plantation forest	Extensively managed or mixed timber, fruit/coffee, oil-palm or rubber plantations in which native understorey and/or other native tree species are tolerated, which are not treated with pesticide or fertiliser, and which have not been recently (< 20 years) clear-felled.	Monoculture fruit/coffee/rubber plantations with limited pesticide input, or mixed species plantations with significant inputs. Monoculture timber plantations of mixed age with no recent (< 20 years) clear-felling. Monoculture oil-palm plantations with no recent (< 20 years) clear-felling.	Monoculture fruit/coffee/rubber plantations with significant pesticide input. Monoculture timber plantations with similarly aged trees or timber/oil-palm plantations with extensive recent (< 20 years) clear-felling.
Human use (agricultural)	Cropland	Low-intensity farms, typically with small fields, mixed crops, crop rotation, little or no inorganic fertiliser use, little or no pesticide use, little or no ploughing, little or no irrigation, little or no mechanisation.	Medium intensity farming, typically showing some but not many of the following: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, no crop rotation, mechanisation, monoculture crop. Organic farms in developed countries often fall within this category, as may high-intensity farming in developing countries.	High-intensity monoculture farming, typically showing many of the following features: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, mechanisation, no crop rotation.
Human use (agricultural)	Pasture	Pasture with minimal input of fertiliser and pesticide, and with low stock density (*not* high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture either with significant input of fertiliser or pesticide, or with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture with significant input of fertiliser or pesticide, *and* with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).
Human use (urban)	Urban	Extensive managed green spaces; villages.	Suburban (e.g., gardens), or small managed or unmanaged green spaces in cities.	Fully urban with no significant green spaces.

Section 2: Comparison with GBIF

I extracted occurrence data from the Global Biodiversity Information Facility (GBIF 2015) for terrestrial vertebrate species in the PREDICTS Project database included in my final dataset. For these species, the maximum temperature of the warmest month, minimum temperature of the coldest month and precipitation of the wettest and driest months (WorldClim version 1.4; Hijmans, Cameron, Parra, Jones, & Jarvis 2005) were extracted for each recorded location within GBIF. Then, for each species the extremes (maximum and minimum) of these values were found and used as the species' thermal and precipitation tolerance limits. For each population, climatic positions were found in the same way as described in Chapter 4, but by using the species' realised climatic tolerance limits from GBIF rather than those extracted using species' distribution maps (the correlations between the two methods of estimating climatic position can be found in table S4.2). Following this, I ran the same set of models as in Chapter 4, but used the climatic positions found using GBIF data, rather than species' range maps. The results were very similar to those reported in Chapter 4 (figs. S4.1-2).

Table S4.2: Correlations (Pearson's correlation coefficient, *r*), between populations' climatic positions estimated by using species' distribution maps (BirdLife International 2012; IUCN 2016) versus using occurrence data from the Global Biodiversity Information Facility (GBIF 2015).

Climatic position	*r*
Maximum temperature of warmest month	0.834
Minimum temperature of coldest month	0.675
Precipitation of wettest month	0.806
Precipitation of driest month	0.834

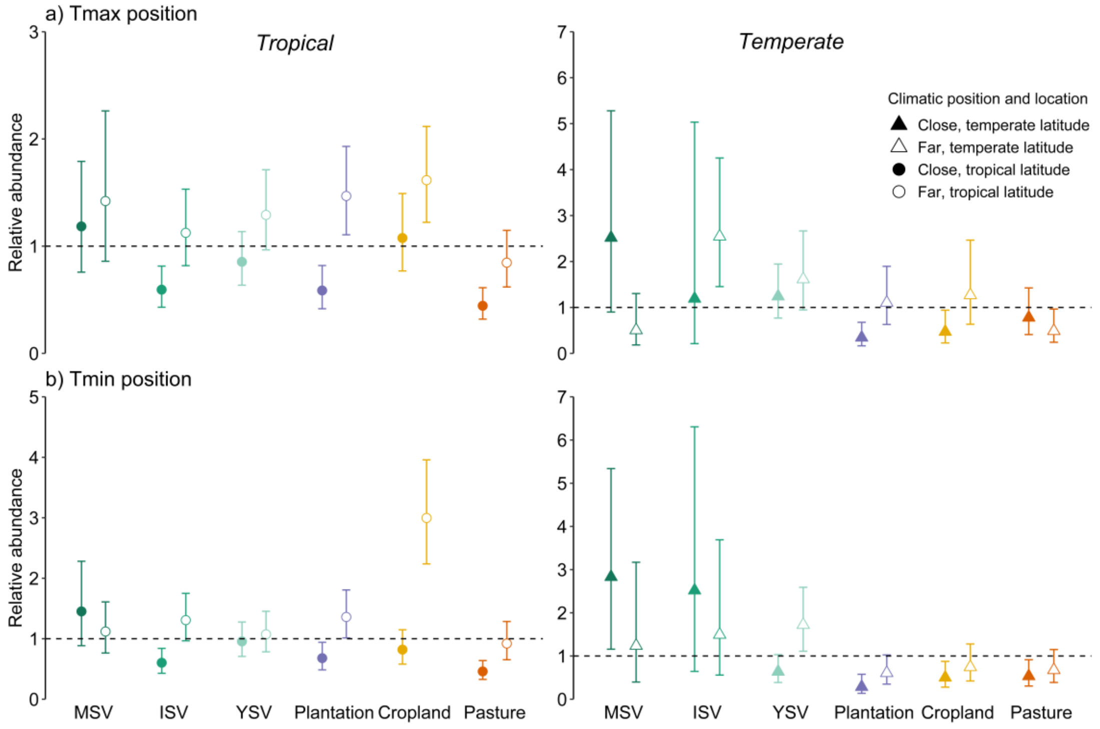


Figure S4.1: The abundance of species within each land-use type, relative to abundance in primary vegetation (indicated by the dotted line), for populations with T_{max} or T_{min} positions 'close' or 'far' from their thermal tolerance limits (calculated using occurrence data from the Global Biodiversity Information Facility) at tropical and temperate latitudes. For (a) a population's T_{max} position, 'close' and 'far' refer to a position of 0.9 and 0.7, respectively, for both tropical and temperate latitudes. For (b) a population's T_{min} position, 'close' and 'far' refer to a position of 0.2 and 0.6 at tropical latitudes, and 0.1 and 0.4 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of T_{max} or T_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively.

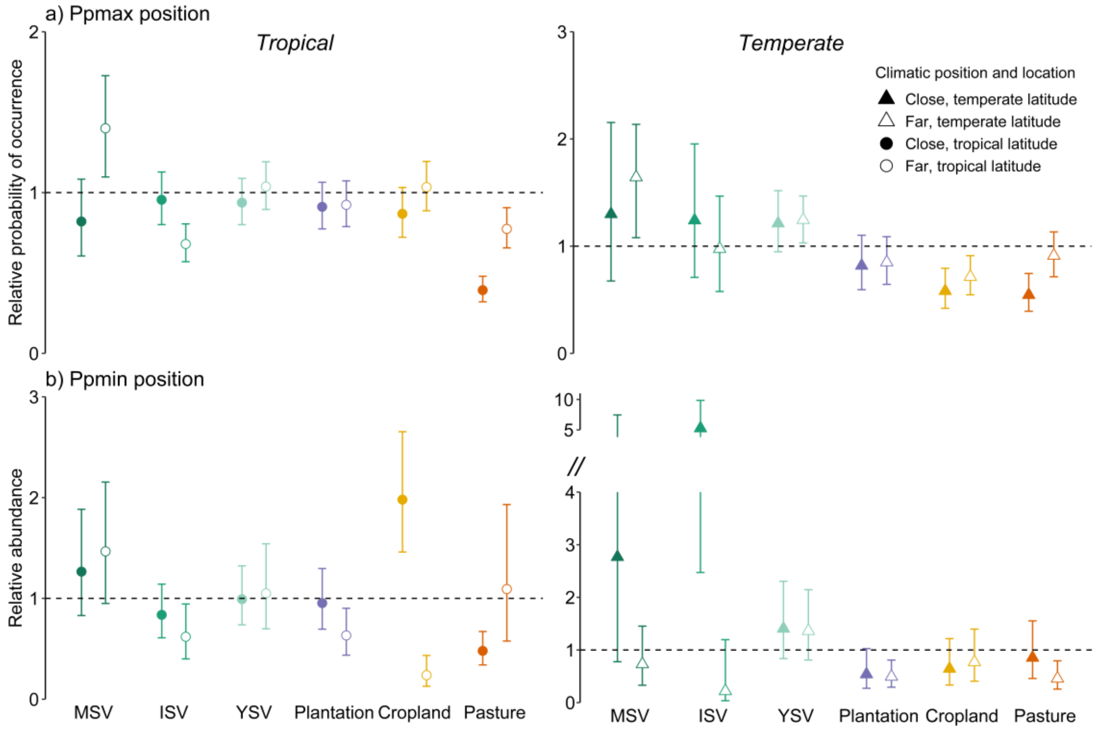


Figure S4.2: The (a) probability of occurrence or (b) abundance of species within each land-use type, relative to that in primary vegetation (indicated by the dotted line), for populations with (a) Pp_{max} or (b) Pp_{min} positions 'close' or 'far' from their precipitation tolerance limits (calculated using occurrence data from the Global Biodiversity Information Facility) at tropical and temperate latitudes. For (a) a population's Pp_{max} position, 'close' and 'far' refer to a position of 0.6 and 0.2 at tropical latitudes, and 0.4 and 0.1 at temperate latitudes, respectively. For (b) a population's Pp_{min} position, 'close' and 'far' refer to a position of 0 and 0.2 at tropical latitudes, and 0 and 0.1 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of Pp_{max} or Pp_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively. I plot relative probability of occurrence (rather than relative abundance) for Pp_{max} positions because a population's Pp_{max} position was not found to have a significant effect on abundance, and so was not included in the final abundance (given presence) model. I use a broken y-axis (represented by //) on the plot for Pp_{min} position at temperate latitudes so that the smaller effect sizes can be more easily interpreted.

Section 3: Including populations recorded outside of their species' stated distribution

To check the influence of excluding populations outside of their species' ranges as stated by the IUCN (2016) and BirdLife International (2012), I ran two sets of models that had the same structure as the final models in Chapter 4 but did not include the distance to range edge main effect or its interaction with land use. One set of models was run for the same populations included in the models in Chapter 4 (i.e., excluding populations that fell outside the species' range maps, but the models excluded the distance to range edge covariate). The other model set included populations both inside and outside of their species' ranges. The main qualitative results of these models were on the whole very similar (figs. S4.3-6). The exception to this was the relationship between a population's Pp_{min} position and their relative abundance within tropical pastures – when populations inside and outside of their species' ranges were included, the relationship matched that observed within cropland and plantations, with populations experiencing minimum monthly precipitation closer to the species' dry limit having higher relative abundances than populations further from this limit, whereas this was not the case for the models only containing populations within their stated species' ranges (figs. S4.4, S4.6).

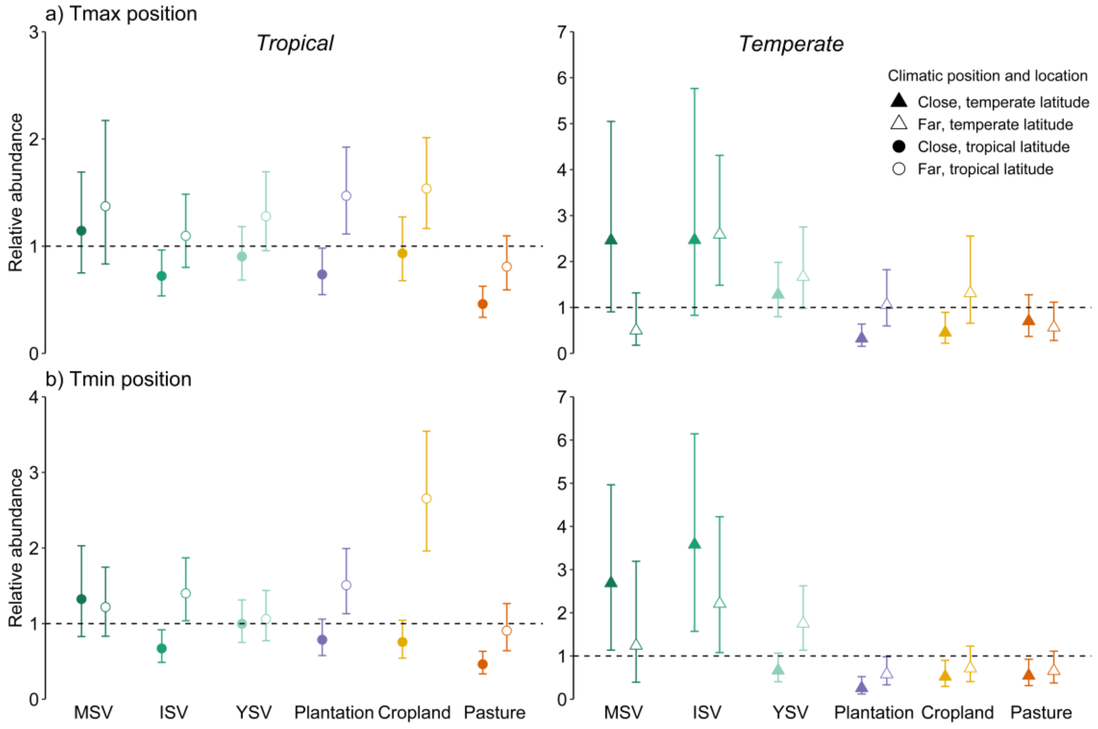


Figure S4.3: The abundance of species within each land-use type, relative to abundance in primary vegetation (indicated by the dotted line), for populations with T_{max} or T_{min} positions 'close' or 'far' from their thermal tolerance limits at tropical and temperate latitudes (including the same populations as included in the models presented in Chapter 4, but excluding the distance to range edge covariate from the models). For (a) a population's T_{max} position, 'close' and 'far' refer to a position of 0.9 and 0.7, respectively, for both tropical and temperate latitudes. For (b) a population's T_{min} position, 'close' and 'far' refer to a position of 0.2 and 0.6 at tropical latitudes, and 0.1 and 0.4 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of T_{max} or T_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively.

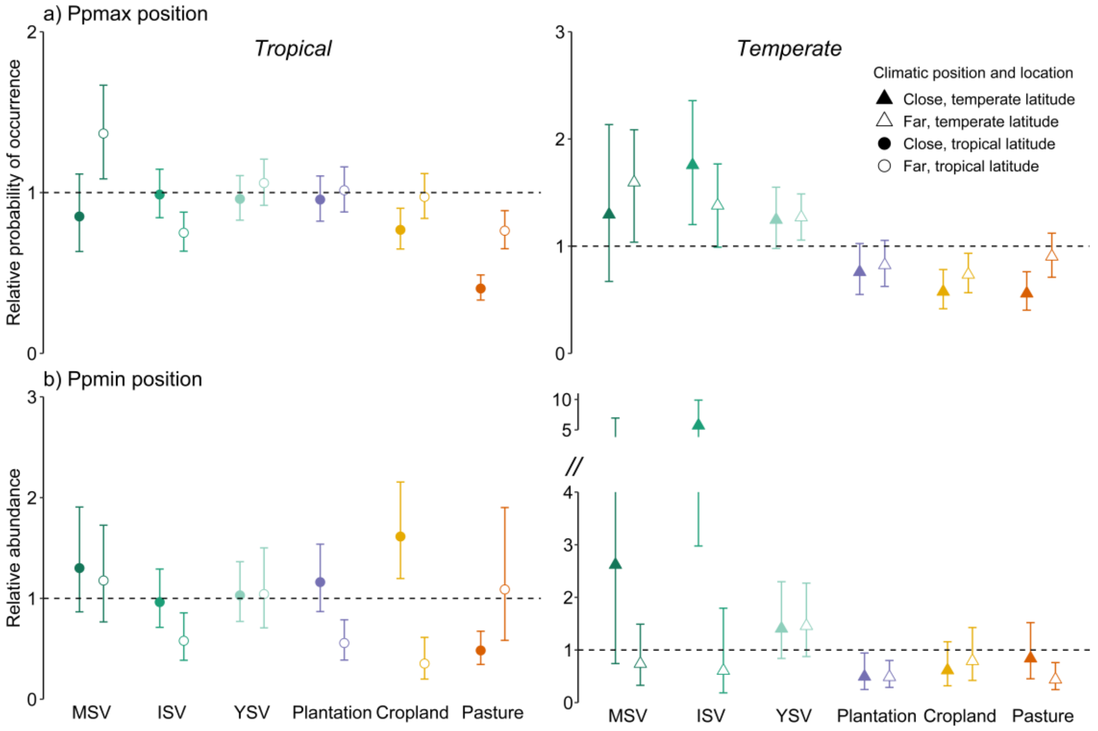


Figure S4.4: The (a) probability of occurrence or (b) abundance of species within each land-use type, relative to that in primary vegetation (indicated by the dotted line), for populations with (a) Pp_{max} or (b) Pp_{min} positions 'close' or 'far' from their precipitation tolerance limits at tropical and temperate latitudes (including the same populations as included in the models presented in Chapter 4, but excluding the distance to range edge covariate from the models). For (a) a population's Pp_{max} position, 'close' and 'far' refer to a position of 0.6 and 0.2 at tropical latitudes, and 0.4 and 0.1 at temperate latitudes, respectively. For (b) a population's Pp_{min} position, 'close' and 'far' refer to a position of 0 and 0.2 at tropical latitudes, and 0 and 0.1 at temperate latitudes, respectively. These positions reflect the 10^{th} and 90^{th} percentile of Pp_{max} or Pp_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively. I plot relative probability of occurrence (rather than relative abundance) for Pp_{max} positions because a population's Pp_{max} position was not found to have a significant effect on abundance, and so was not included in the final abundance (given presence) model. I use a broken y-axis (represented by //) on the plot for Pp_{min} position at temperate latitudes so that the smaller effect sizes can be more easily interpreted.

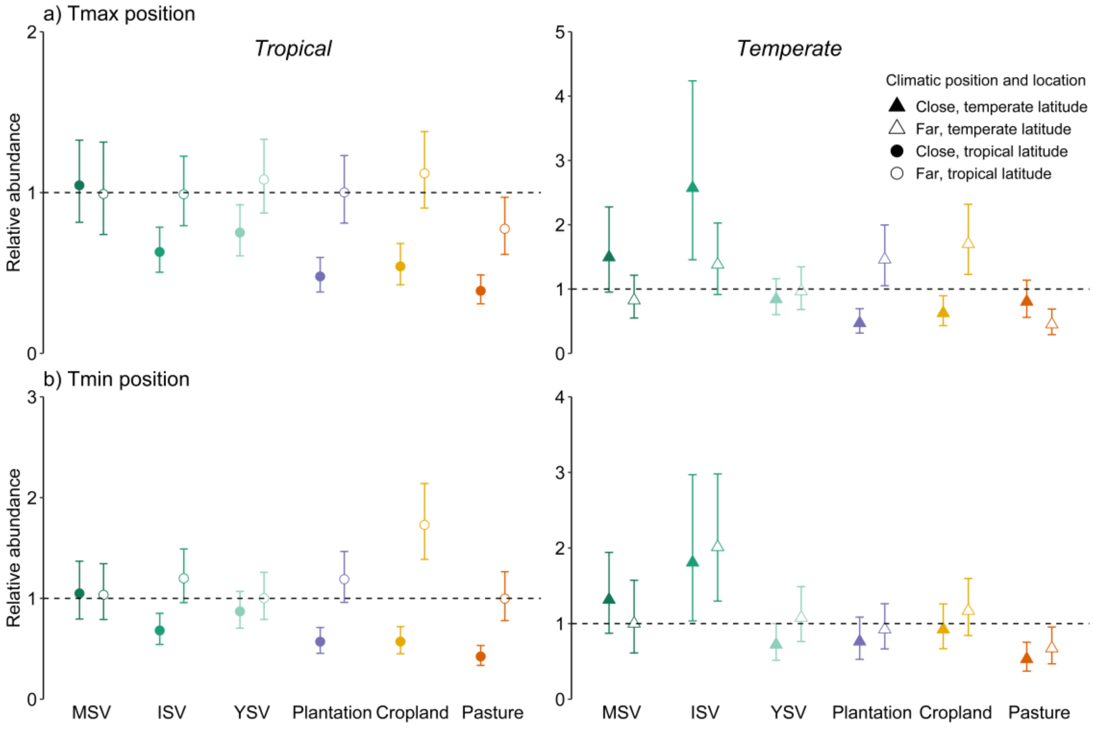


Figure S4.5: The abundance of species within each land-use type, relative to abundance in primary vegetation (indicated by the dotted line), for populations with T_{max} or T_{min} positions 'close' or 'far' from their thermal tolerance limits at tropical and temperate latitudes (including populations recorded inside and outside of their species' distributions as stated by the IUCN and BirdLife International, and excluding the distance to range edge covariate from the models). For (a) a population's T_{max} position, 'close' and 'far' refer to a position of 0.9 and 0.7, respectively, for both tropical and temperate latitudes. For (b) a population's T_{min} position, 'close' and 'far' refer to a position of 0.2 and 0.6 at tropical latitudes, and 0.1 and 0.5 at temperate latitudes, respectively. These positions reflect the 10^{th} and 90^{th} percentile of T_{max} or T_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively.

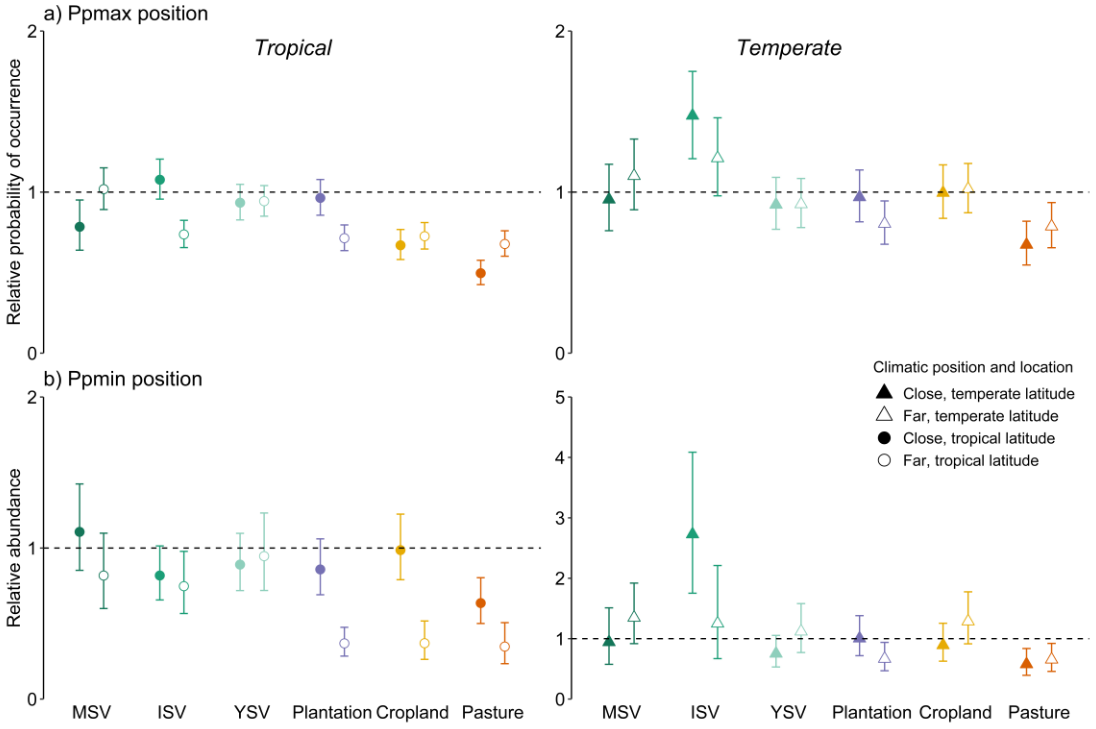


Figure S4.6: The (a) probability of occurrence or (b) abundance of species within each land-use type, relative to that in primary vegetation (indicated by the dotted line), for populations with (a) Pp_{max} or (b) Pp_{min} positions 'close' or 'far' from their precipitation tolerance limits at tropical and temperate latitudes (including populations recorded inside and outside of their species' distributions as stated by the IUCN and BirdLife International, and excluding the distance to range edge covariate from the models). For (a) a population's Pp_{max} position, 'close' and 'far' refer to a position of 0.7 and 0.2 at tropical latitudes, and 0.4 and 0.1 at temperate latitudes, respectively. For (b) a population's Pp_{min} position, 'close' and 'far' refer to a position of 0 and 0.2 at tropical latitudes, and 0 and 0.1 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of Pp_{max} or Pp_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively. I plot relative probability of occurrence (rather than relative abundance) for Pp_{max} positions because a population's Pp_{max} position was not found to have a significant effect on abundance, and so was not included in the final abundance (given presence) model.

Section 4: Further information on the results

Table S4.3: The number of populations from the PREDICTS Project dataset included in the final abundance given presence models (and, in parentheses, probability of occurrence models) across each land-use type, along with the number of sites that were sampled and the studies that these originated from.

Land use	Number of					
	Populations		Sites		Studies	
	Tropics	Temperate	Tropics	Temperate	Tropics	Temperate
Primary vegetation	4,382 (26,138)	1,265 (6,339)	957 (1,426)	425 (809)	70 (81)	30 (32)
Mature secondary vegetation	381 (2,896)	30 (155)	119 (173)	10 (42)	14 (15)	5 (5)
Intermediate secondary vegetation	1,227 (5,820)	51 (113)	205 (252)	38 (42)	29 (31)	6 (7)
Young secondary vegetation	1,259 (7,880)	243 (1,070)	192 (304)	97 (188)	24 (25)	8 (11)
Plantation	1,379 (8,885)	143 (734)	459 (819)	78 (232)	33 (41)	13 (13)
Cropland	888 (9,948)	410 (2,783)	246 (429)	160 (453)	14 (16)	7 (9)
Pasture	788 (11,269)	482 (2,522)	245 (537)	168 (235)	20 (21)	10 (10)
Urban	222 (569)	171 (886)	41 (41)	74 (91)	2 (2)	3 (3)

Table S4.4: For each land-use type, the number of species (out of the 2,103 species with occurrence data) with *more than one* distinct measure for each climatic position and distance to range edge (these do not equate to the number of species recorded in more than one location, because some populations may have the same climatic position or distance to range edge measure at different locations within their range), and the average difference between the minimum and maximum value of each climatic position or distance to range edge for these species. T_{max} position relates to the maximum temperature of the warmest month a population experiences compared to their thermal tolerance limits; T_{min} position relates to the minimum temperature of the coldest month a population experiences compared to their thermal tolerance limits; Pp_{max} position relates to the precipitation of the wettest month a population experiences compared to their precipitation tolerance limits; Pp_{min} position relates to the precipitation of the driest month a population experiences compared to their precipitation tolerance limits (see Chapter 4 for more information on how these were calculated).

Land-use type	Number of species with more than one measure (and the average difference between each species' minimum and maximum value)				
	T_{max} position	T_{min} position	Pp_{max} position	Pp_{min} position	Distance to range edge
Primary vegetation	1341 (0.06)	1220 (0.08)	1356 (0.10)	1210 (0.03)	1444 (0.14)
Mature secondary vegetation	110 (0.03)	98 (0.05)	116 (0.05)	109 (0.03)	116 (0.08)
Intermediate secondary vegetation	550 (0.04)	486 (0.06)	532 (0.08)	521 (0.03)	620 (0.12)
Young secondary vegetation	717 (0.04)	627 (0.04)	719 (0.05)	680 (0.02)	756 (0.09)
Plantation	628 (0.05)	597 (0.06)	627 (0.06)	572 (0.03)	629 (0.09)
Cropland	417 (0.05)	417 (0.06)	412 (0.10)	413 (0.03)	425 (0.11)
Pasture	507 (0.05)	507 (0.05)	505 (0.07)	498 (0.02)	510 (0.13)
Urban	57 (0.03)	46 (0.09)	46 (0.08)	46 (0.03)	57 (0.20)

Table S4.5: The correlations (Spearman correlation, *p*) between the four climatic positions and distance to range edge for those populations with occurrence data. T_{max} position relates to the maximum temperature of the warmest month a population experiences compared to their thermal tolerance limits; T_{min} position relates to the minimum temperature of the coldest month a population experiences compared to their thermal tolerance limits; Pp_{max} position relates to the precipitation of the wettest month a population experiences compared to their precipitation tolerance limits; Pp_{min} position relates to the precipitation of the driest month a population experiences compared to their precipitation tolerance limits.

	T_{max} position	T_{min} position	Pp_{max} position	Pp_{min} position	Distance to range edge
T_{max} position					
T_{min} position	0.31				
Pp_{max} position	0.32	0.18			
Pp_{min} position	-0.12	0.14	0.18		
Distance to range edge	0.36	-0.11	0.05	-0.17	

Table S4.6: The climatic positions of populations with occurrence data relative to their species-level realised climatic tolerance limits (0 = at lower thermal or precipitation tolerance limit, 1 = at upper thermal or precipitation tolerance limit) for each climatic variable focused on, and the percentage of values that fell beyond 0 or 1.

Climatic variable	Range of climatic positions	Percentage of datapoints beyond the 0 and 1 bounds (%)
Maximum temperature of warmest month	0.38 – 1.18	0.07
Minimum temperature of coldest month	-0.36 – 0.81	0.02
Precipitation of wettest month	0.02 – 1.08	0.24
Precipitation of driest month	-0.02 – 0.40	0.13

Distance to range edge

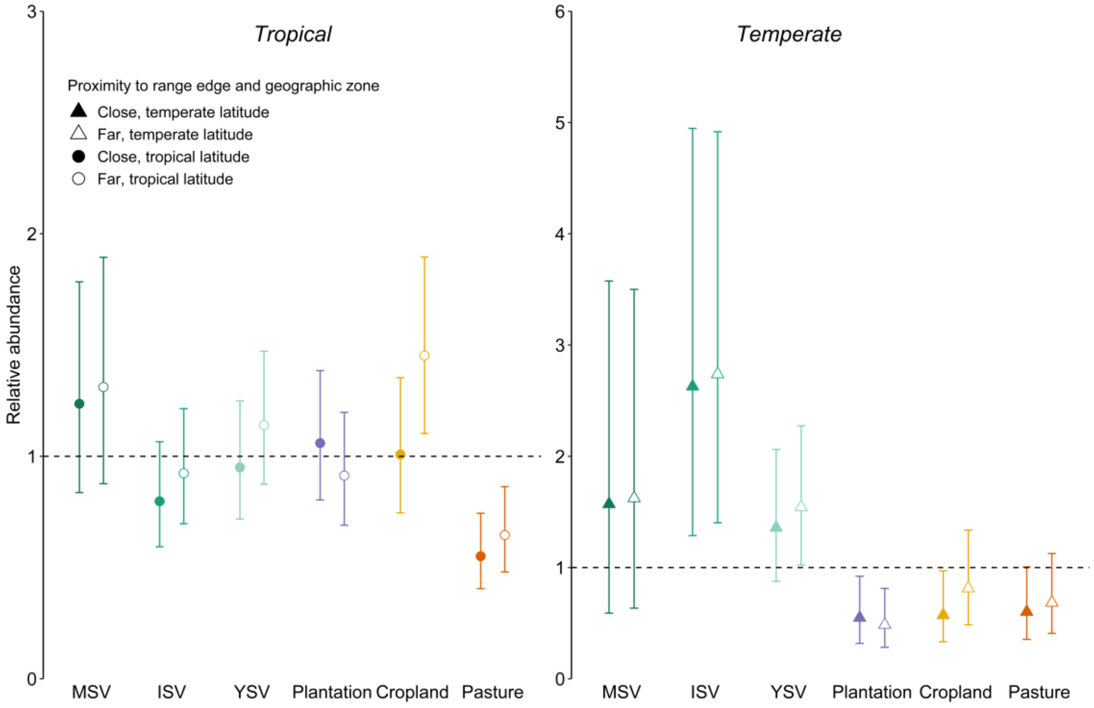


Figure S4.7: The abundance of species within each land-use type, relative to abundance in primary vegetation (indicated by the dotted line), for populations 'close' or 'far' from their range edge, split by geographic zone (tropical or temperate latitude). For a population's proximity to range edge, 'close' refers to a position of 0 (i.e., at their range edge) and 'far' refers to a position of 0.5 at tropical latitudes and 0.4 at temperate latitudes (i.e., around half-way between a species' range centre and edge). These positions reflect the 10th and 90th percentile of distance to range edge measures (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively. The *p*-values from the backwards stepwise selection process for distance from range edge were, $p_{\mathrm{P(Occ)}} < 0.001$, $p_{\mathrm{LogAbund}} = 0.012$, and for the interaction between land-use type and distance from range edge, $p_{\mathrm{P(Occ)}} = 0.003$, $p_{\mathrm{LogAbund}} = 0.208$.

Comprehensive plots for each climatic position

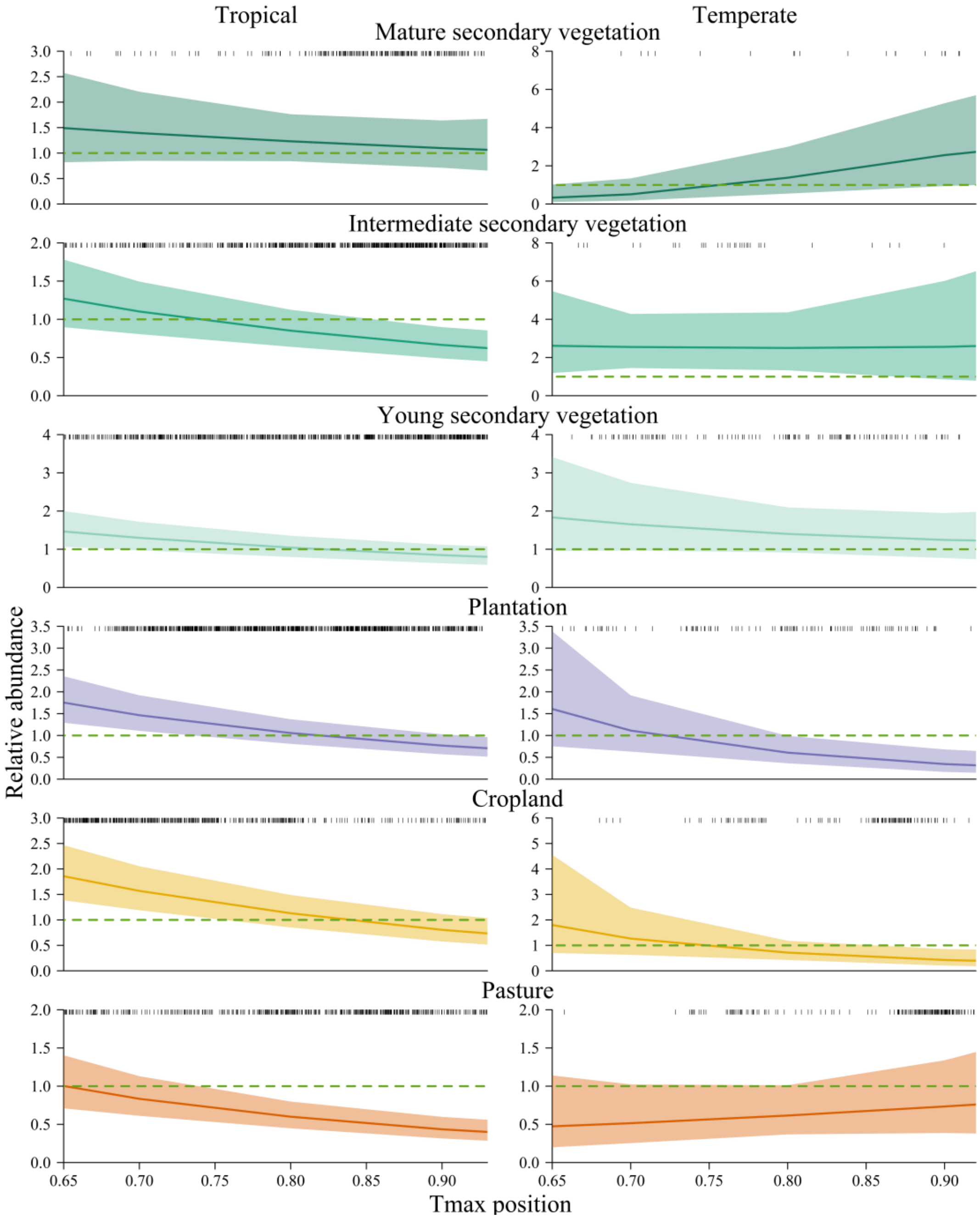


Figure S4.8: The relative abundance of species within each land-use type, in comparison to abundance in primary vegetation (indicated by the dotted line), depending on the population's T_{max} position, standardised to between 0 (species' realised minimum temperature tolerance limit) and 1 (species' realised maximum temperature tolerance limit). Error margins denote ±1 standard error; rug plots above each plot show the distribution of populations across the standardised climatic positions within each land use. The x-axes are truncated at the 5th and 95th percentile of T_{max} positions for each geographic zone in the data analysed.

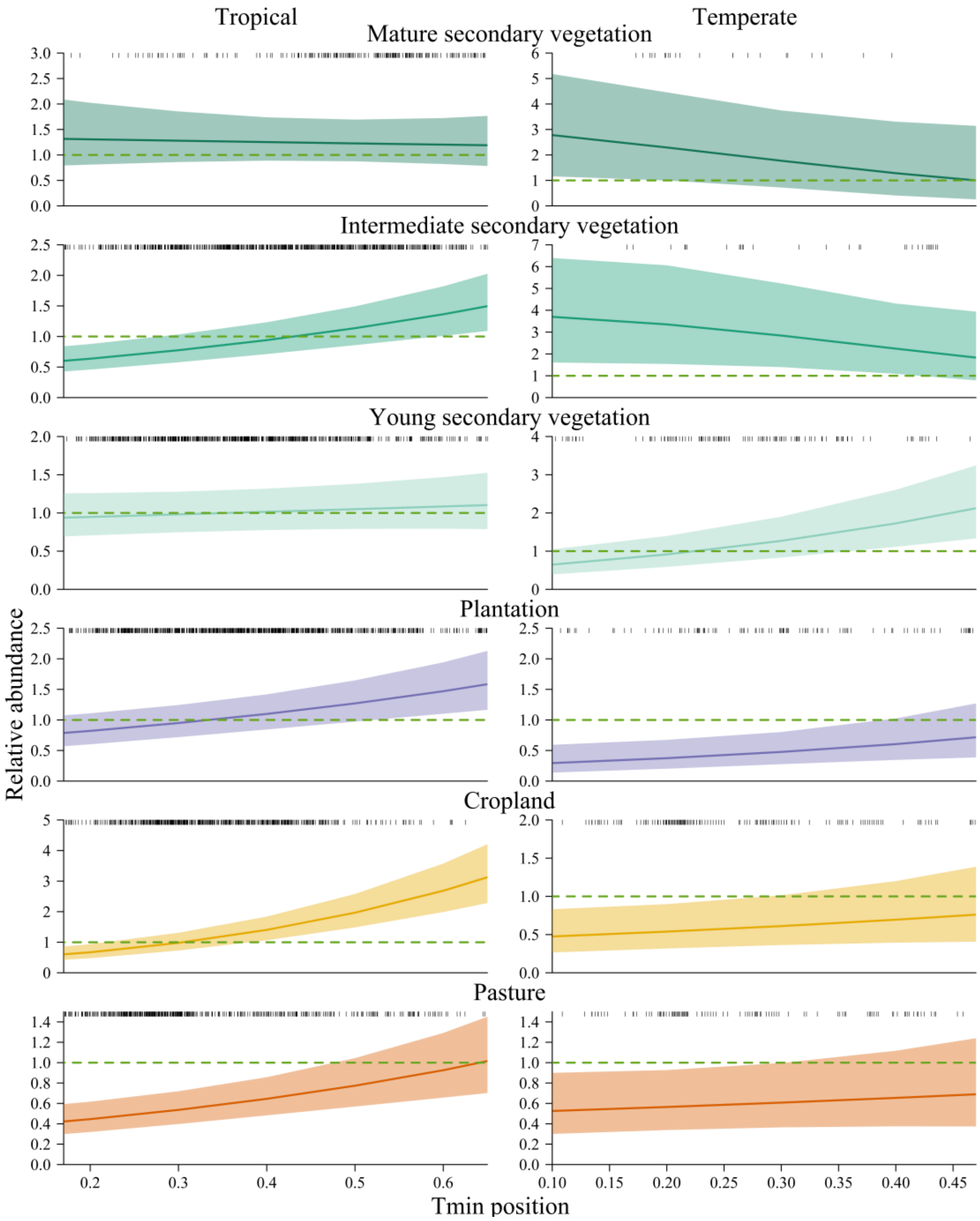


Figure S4.9: The relative abundance of species within each land-use type, in comparison to abundance in primary vegetation (indicated by the dotted line), depending on the population's T_{min} position, standardised to between 0 (species' realised minimum temperature tolerance limit) and 1 (species' realised maximum temperature tolerance limit). Error margins denote ±1 standard error; rug plots above each plot show the distribution of populations across the standardised climatic positions within each land use. The x-axes are truncated at the 5th and 95th percentile of T_{min} positions for each geographic zone in the data analysed.

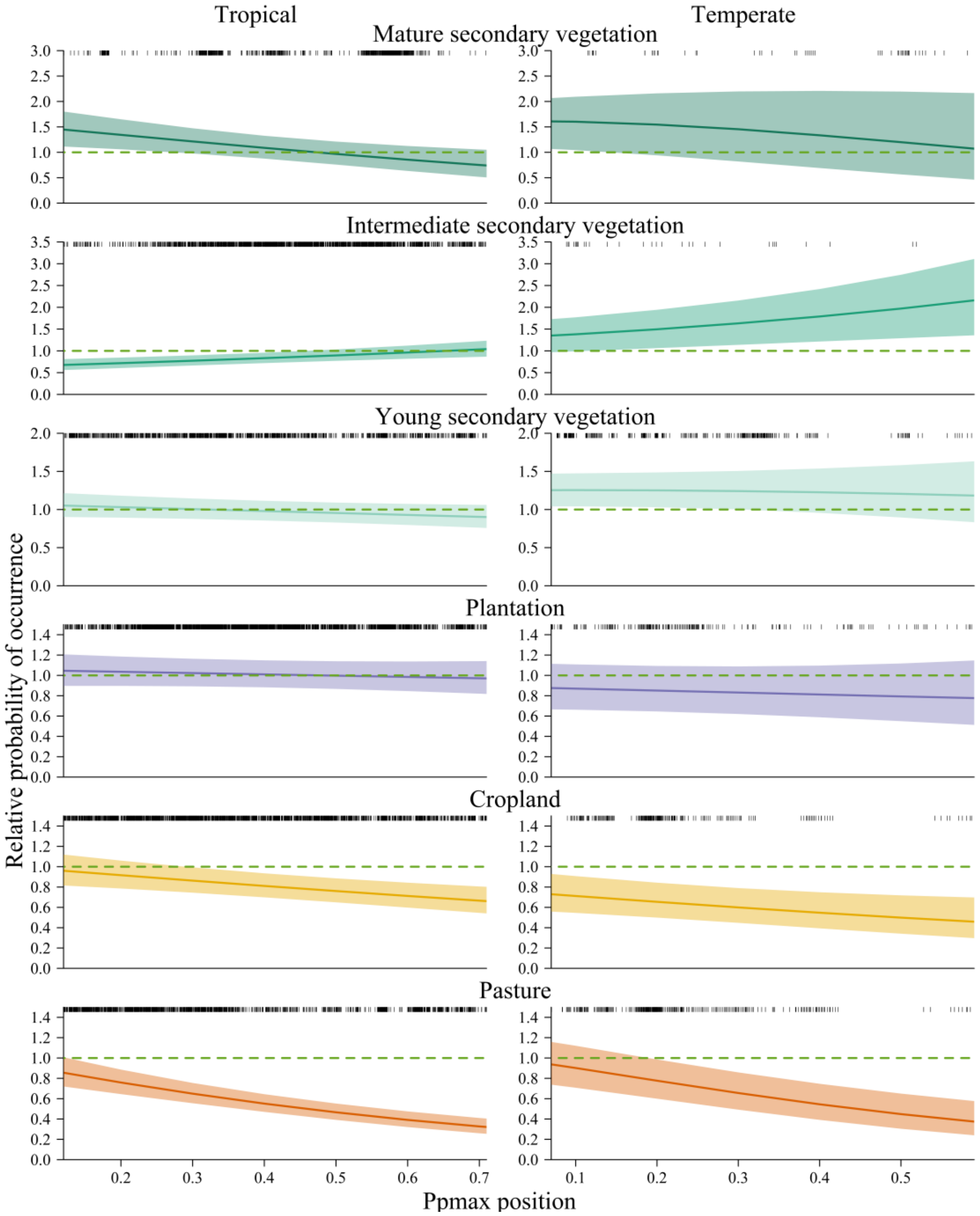


Figure S4.10: The relative probability of occurrence of species within each land-use type, in comparison to that in primary vegetation (indicated by the dotted line), depending on the population's Pp_{max} position, standardised to between 0 (species' realised dry limit) and 1 (species' realised wet limit). I plot relative probability of occurrence (rather than relative abundance) for Pp_{max} positions because a population's Pp_{max} position was not found to have a significant effect on abundance, and so was not included in the final abundance (given presence) model (see Chapter 4). Error margins denote ±1 standard error; rug plots above each plot show the distribution of populations across the standardised climatic positions within each land use. The x-axes are truncated at the 5th and 95th percentile of Pp_{max} positions for each geographic zone in the data analysed.

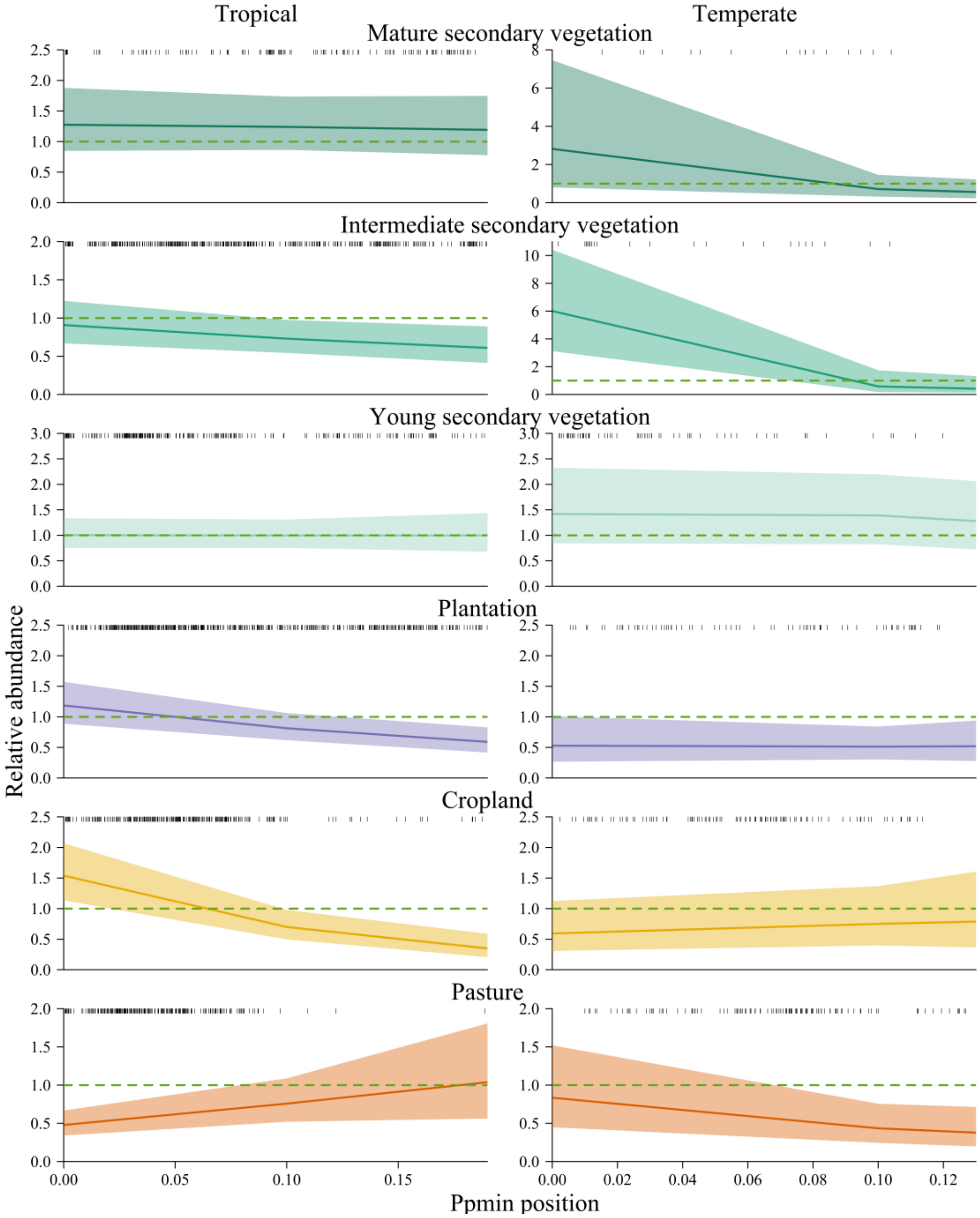


Figure S4.11: The relative abundance of species within each land-use type, in comparison to abundance in primary vegetation (indicated by the dotted line), depending on the population's Pp_{min} position, standardised to between 0 (species' realised dry limit) and 1 (species' realised wet limit). Error margins denote ±1 standard error; rug plots above each plot show the distribution of populations across the standardised climatic positions within each land use. The x-axes are truncated at the 5th and 95th percentile of Pp_{min} positions for each geographic zone in the data analysed.

Section 5: Probability of occurrence and abundance (given presence) plots

In my analysis I employed a two-stage modelling approach (similar to a hurdle model), which combined a probability of occurrence model with an abundance (given presence) model. Below I plot out the results from these two models separately. I do not show the results for Pp_{max} position because this variable was not included in the final abundance model, and the results for this variable's effect on probability of occurrence have already been plotted in Chapter 4.

Probability of occurrence plots

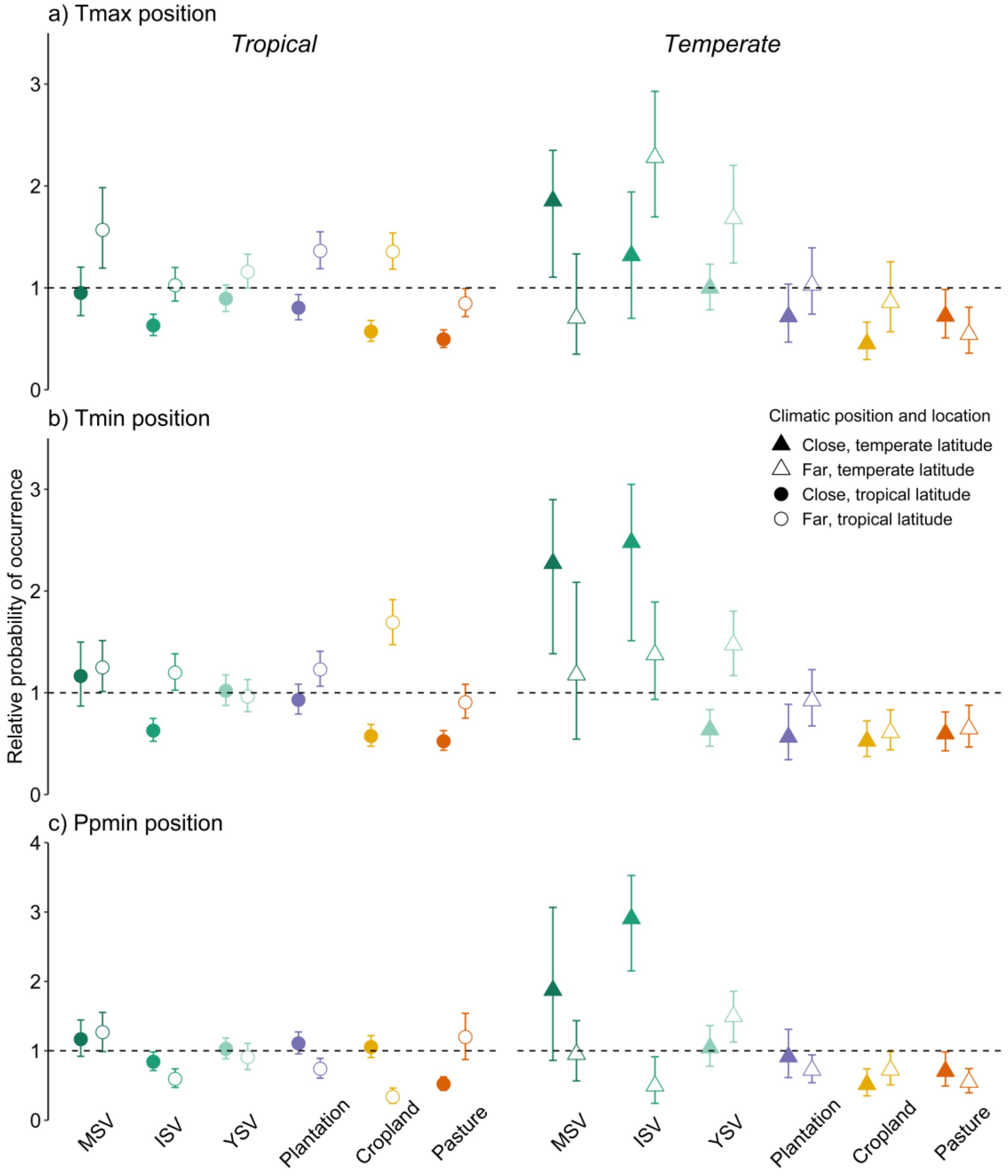


Figure S4.12: The probability of occurrence of species within each land-use type, relative to that in primary vegetation (indicated by the dotted line), for populations with T_{max}, T_{min} or Pp_{min} positions 'close' or 'far' from their climatic tolerance limits at tropical and temperate latitudes. For (a) a population's T_{max} position, 'close' and 'far' refer to a position of 0.9 and 0.7, respectively, for both tropical and temperate latitudes. For (b) a population's T_{min} position, 'close' and 'far' refer to a position of 0.2 and 0.6 at tropical latitudes, and 0.1 and 0.4 at temperate latitudes, respectively. For (c) a population's Pp_{min} position, 'close' and 'far' refer to a position of 0 and 0.2 at tropical latitudes, and 0 and 0.1 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of T_{max}, T_{min} or Pp_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively.

Abundance (given presence) plots

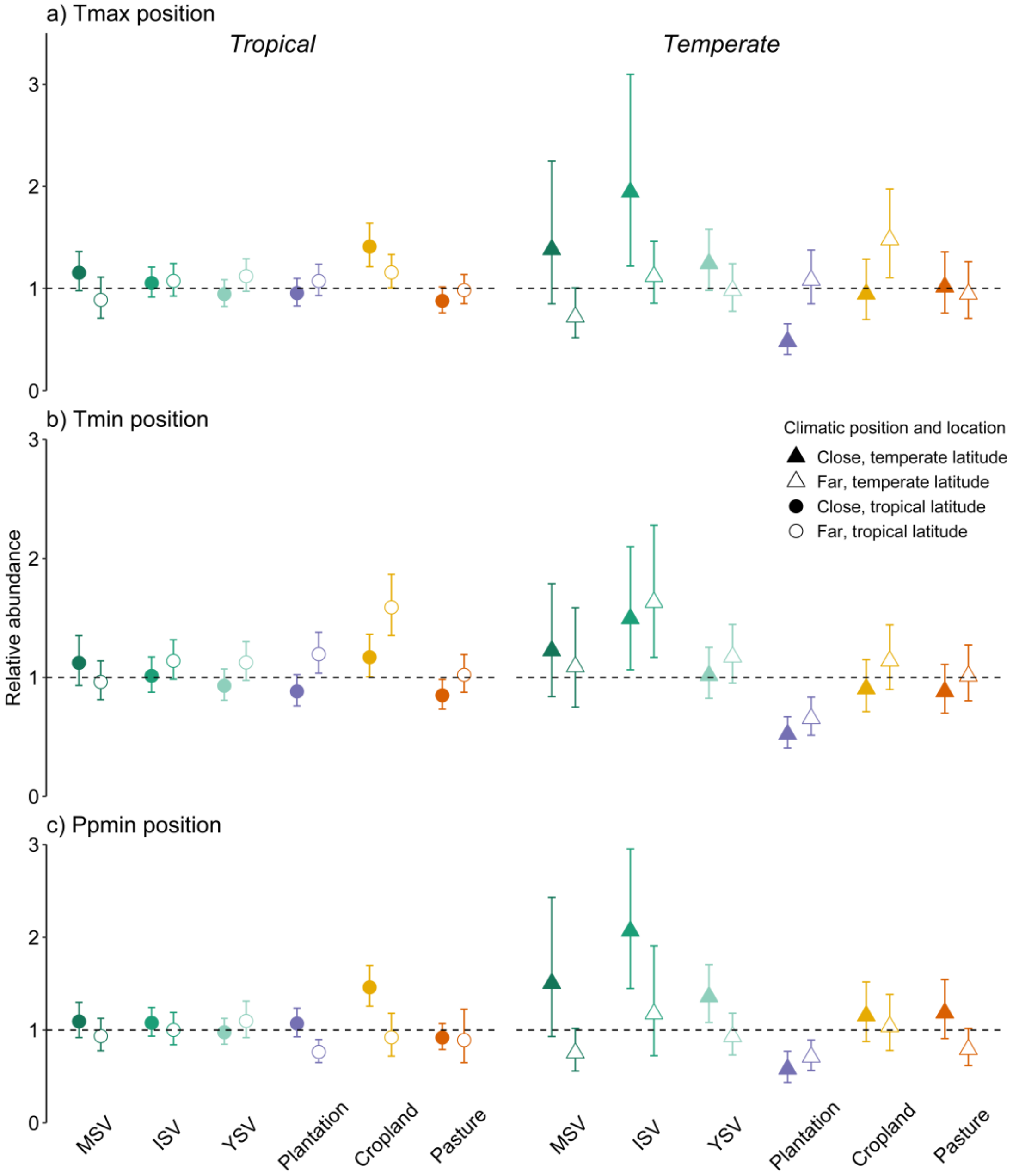


Figure S4.13: The abundance (given presence) of species within each land-use type, relative to that in primary vegetation (indicated by the dotted line), for populations with T_{max}, T_{min} or Pp_{min} positions 'close' or 'far' from their climatic tolerance limits at tropical and temperate latitudes. For (a) a population's T_{max} position, 'close' and 'far' refer to a position of 0.9 and 0.7, respectively, for both tropical and temperate latitudes. For (b) a population's T_{min} position, 'close' and 'far' refer to a position of 0.2 and 0.6 at tropical latitudes, and 0.1 and 0.4 at temperate latitudes, respectively. For (c) a population's Pp_{min} position, 'close' and 'far' refer to a position of 0 and 0.2 at tropical latitudes, and 0 and 0.1 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of T_{max}, T_{min} or Pp_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively.

Section 6: Severity of decline following land conversion

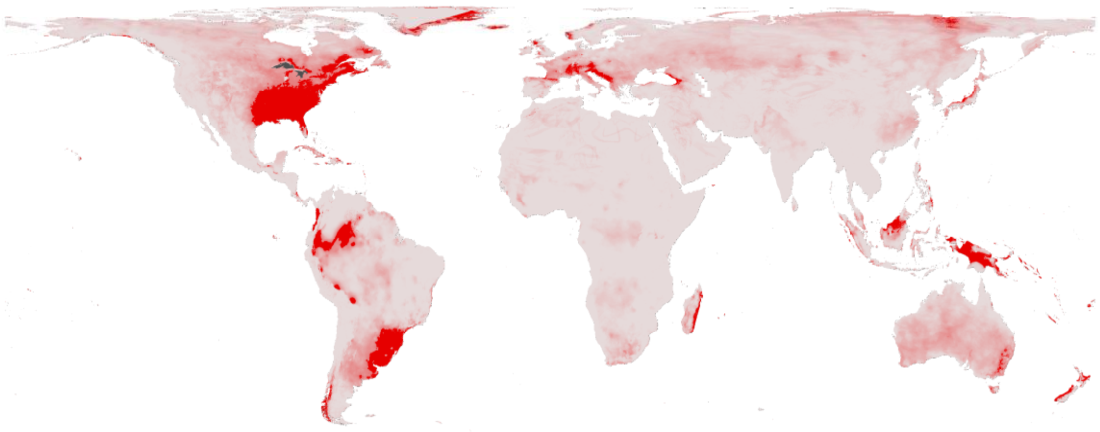
Table S4.7: A reminder of the final probability of occurrence (P(Occ)) and abundance (LogAbund) models followed by the relevant coefficients (to 3 decimal places) used to produce estimates of relative abundance in croplands and pastures, which were used to explore terrestrial vertebrate community-average severity of decline following conversion of primary vegetation to agriculture. Models were selected following the methods in Chapter 4, with main effects and interactions used to estimate severity of decline (following Orme et al., 2019). Variables included land use (LU), geographic zone (GZ; i.e., whether the location was at tropical (Trop) or temperate (Temp) latitudes), the population's distance from their species' range edge (standardised to between 0 (at range edge) and 1 (centre of range); Dist) and the population's climatic position (standardised to between 0 and 1) with regard to one of four climatic variables (T_{max} – maximum temperature of the warmest month; T_{min} – minimum temperature of the coldest month; Pp_{max} – precipitation of the wettest month; Pp_{min} – precipitation of the driest month; Hijmans et al. 2005). In the final models, a nested random-intercept term for study (SS; to account for study-dependent variation in methods or measures used) and for sampled site within studies (SSBS) was included in all models, along with a random-intercept term for species name (Species).

	Occurrence model						Abundance model					
	P(Occ) ~ Intercept + LU + GZ + T_{max} + T_{min} + Pp_{min} + Pp_{max} + Dist + LU×GZ + LU×Dist + LU×T_{max} + LU×T_{min} + LU×Pp_{max} + LU×Pp_{min} + T_{max}×GZ + T_{min}×GZ + Pp_{max}×GZ + Pp_{min}×GZ + LU×T_{max}×GZ + LU×T_{min}×GZ + LU×Pp_{min}×GZ + (1|SS) + (1|SSBS) + (1|Species)						LogAbund ~ Intercept + LU + GZ + T_{max} + T_{min} + Pp_{min} + Dist + LU×GZ + LU×T_{max} + LU×T_{min} + LU×Pp_{min} + GZ×T_{max} + GZ×Pp_{min} + LU×T_{max}×GZ + LU×Pp_{min}×GZ + (1|SS) + (1|SSBS) + (1|Species)					
	Primary vegetation		Cropland		Pasture		Primary vegetation		Cropland		Pasture	
	Trop	Temp	Trop	Temp	Trop	Temp	Trop	Temp	Trop	Temp	Trop	Temp
Intercept	0.752		0.752		0. 752		3.836		3.836		3.836	
LU	-----		-0.184		-0.483		-----		0.222		-0.076	
Dist	0.487		0.487		0.487		0.186		0.186		0.186	
T_{max}	2.423		2.423		2.423		0.153		0.153		0.153	
T_{min}	-0.474		-0.474		-0.474		-0.463		-0.463		-0.463	
Pp_{max}	-0.242		-0.242		-0.242							
Pp_{min}	2.547		2.547		2.547		0.817		0.817		0.817	
GZ	-----	-0.157	-----	-0.157	-----	-0.157	-----	0.008	-----	0.008	-----	0.008
LU × GZ	-----	-----	-----	-0.326	-----	-0.218	-----	-----	-----	-0.086	-----	-0.005
LU × Dist	-----		1.000		0.335							
LU × T_{max}	-----		-5.886		-3.587		-----		0.985		-0.564	

LU × T_{min}	-----		3.826		1.751		-----		0.765		0.462	
LU × Pp_{max}	-----		-0.802		-1.934		▨	▨	▨	▨	▨	▨
LU × Pp_{min}	-----		-7.493		5.633		-----		-2.303		-0.153	
T_{max} × GZ	-----	3.034	-----	3.034	-----	3.034	-----	1.632	-----	1.632	-----	1.632
T_{min} × GZ	-----	-0.179	-----	-0.179	-----	-0.179	▨	▨	▨	▨	▨	▨
Pp_{max} × GZ	-----	-1.832	-----	-1.832	-----	-1.832	▨	▨	▨	▨	▨	▨
Pp_{min} × GZ	-----	3.629	-----	3.629	-----	3.629	-----	-0.242	-----	-0.242	-----	-0.242
T_{max} × LU × GZ	-----	-----	-----	1.411	-----	4.675	-----	-----	-----	-3.214	-----	0.919
T_{min} × LU × GZ	-----	-----	-----	-3.140	-----	-1.346	▨	▨	▨	▨	▨	▨
Pp_{min} × LU × GZ	-----	-----	-----	10.822	-----	-9.468	-----	-----	-----	1.247	-----	-3.868

Grey cells represent those variables that were not considered in the model because they were not significant and were not nested within higher-order interactions. ‘-----’ denotes terms that were reference levels and so contained within the intercept.

a) Cropland



b) Pasture

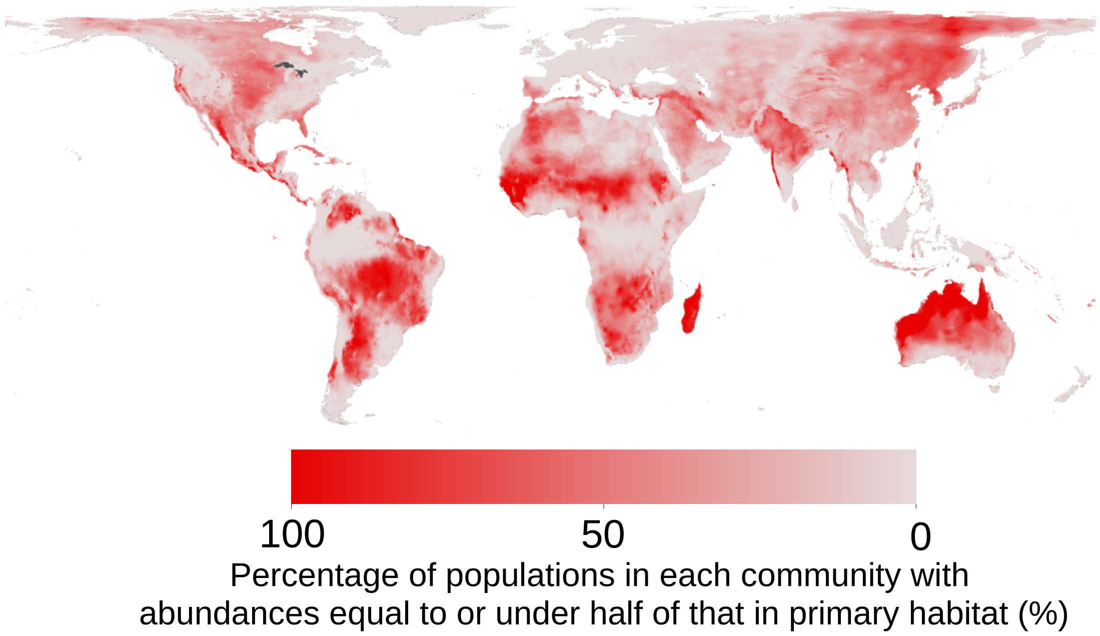


Figure S4.14: The percentage of terrestrial vertebrate populations within each community (10 × 10-km pixel) with expected abundances less than half of that in primary vegetation following conversion to (a) cropland and (b) pasture, based on the population's climatic position (all else held equal). I present global maps (Behrmann projection) to demonstrate how the average severity of decline within communities may differ due to the local climatic changes following agricultural conversion, whilst recognising that land conversion from primary vegetation to cropland or pasture is not possible, or has already happened, for large parts of the world (although these maps could also be useful in highlighting areas in which habitat restoration may be more beneficial, based on the climatic positions of the local populations). Dark grey areas represent locations that were not covered by any of the species' ranges in our dataset (some of the Great Lakes in North America, for example).

I also produced maps of estimated community-average probability of occurrence in cropland and pasture relative to that in primary vegetation, based on the climatic positions of populations within each community. I carried this out for the same set of 22,267 species as described in Chapter 4 for the maps of community-average relative abundance. Similarly, for each species, I produced maps of T_{max}, T_{min}, Pp_{max} and Pp_{min} (WorldClim Version 1.4; Hijmans et al., 2005) across their distribution and standardised them to between 0 and 1 in the same way as described in Chapter 4. Then, using the main-effect and interaction estimates (table S4.7) from the final probability of occurrence model, I found the model-estimated probability of occurrence of each species across their range, based on their climatic position, in primary vegetation (*PV*), cropland (*Cr*) and pasture (*Pa*). Following this, I expressed each species' probability of occurrence (*P(Occ)*) in cropland and pasture relative to that in primary vegetation (i.e., relative probability of occurrence, *RP(Occ)*; equation S4.1 and S4.2, for relative probability of occurrence within cropland and pasture, respectively):

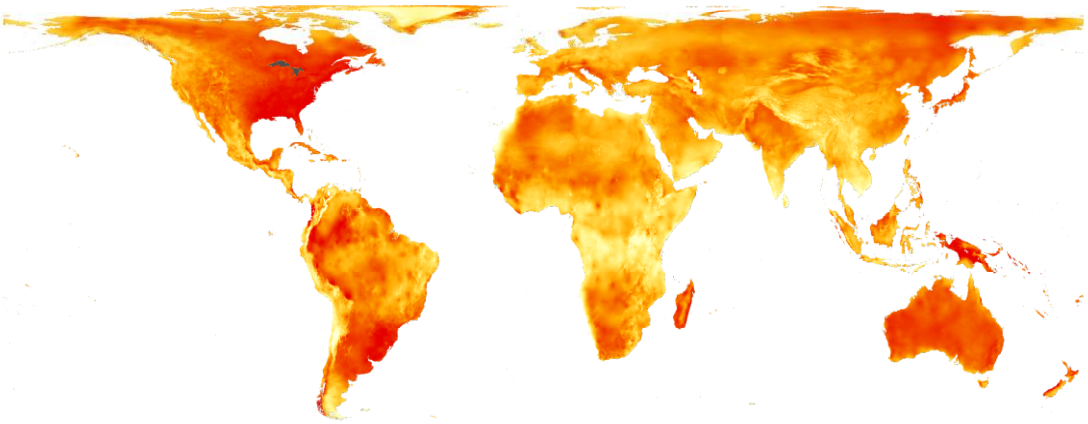
$$\text{(S4.1)} \qquad RP(Occ)_{Cr} = \frac{P(Occ)_{Cr}}{P(Occ)_{PV}}$$

$$\text{(S4.2)} \qquad RP(Occ)_{Pa} = \frac{P(Occ)_{Pa}}{P(Occ)_{PV}}$$

I then averaged and plotted the species-level results within each 10 × 10-km grid cell to display community-average probability of occurrence following conversion of primary vegetation to cropland or pasture, where the 'community' included all the populations whose species' range covered that cell (fig. S4.15).

Again, to ensure I did not extrapolate beyond the limits of my data, I found the predicted relative probability of occurrence within cropland and pasture for each population from the PREDICTS database included in my models (again using the main-effect and interaction estimates from my models). I then averaged these predicted values for populations in cropland or pasture within each PREDICTS site, producing site-level-average (i.e., community-average) relative probability of occurrences, and extracted the minimum and maximum site-level average relative probability of occurrence for each land use. Finally, when producing the global maps described above showing the community-average probability of occurrence, I only plotted values that fell within these limits (which included values for the vast majority of the Earth's surface).

a) Cropland



b) Pasture

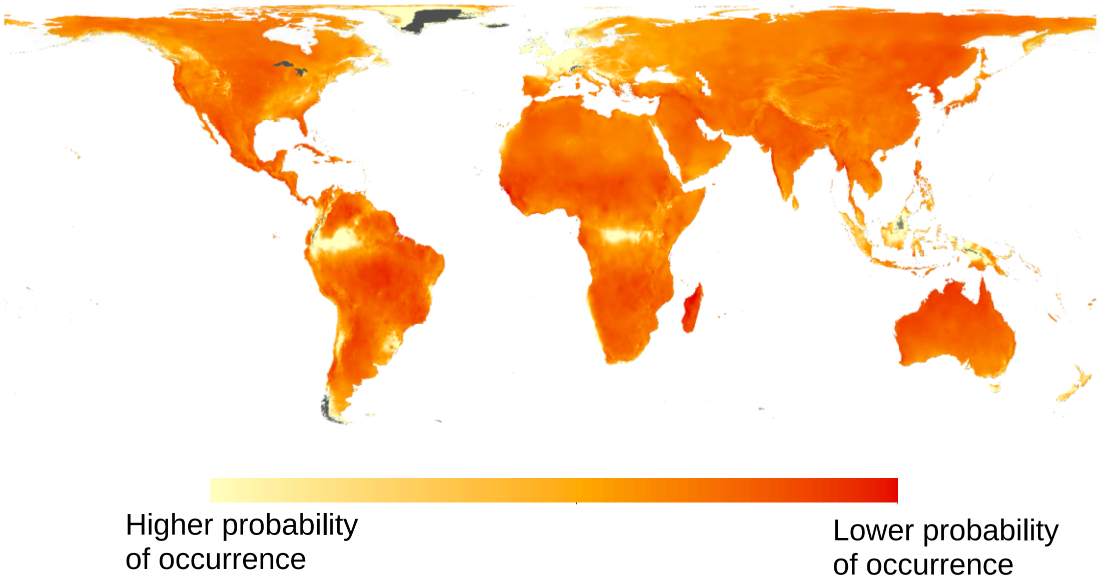


Figure S4.15: The community-average (10 × 10-km pixel) probability of occurrence for terrestrial vertebrates within (a) cropland and (b) pasture relative to that in primary vegetation, based on the climatic position of populations within each community. I present global maps (Behrmann projection) to demonstrate how the average probability of occurrence within communities may differ due to the local climatic changes following agricultural conversion, whilst recognising that land conversion from primary vegetation to cropland or pasture is not possible, or has already happened, for large parts of the world (although these maps could also be useful in highlighting areas in which habitat restoration may be more beneficial, based on the climatic positions of the local populations). Dark grey areas represent locations that were not covered by any of the species' ranges in my dataset (some of the Great Lakes in North America, for example), or where community-average measures were beyond the limits of my dataset (see methods above). The scale of community-average probability of occurrence is separate for each map: the deepest red (lowest relative probability of occurrence) represents a value of 0.12 (to 2 decimal places) in both cropland and pasture, the lightest yellow (highest relative probability of occurrence) represents values of above 2 and up to 1.66 (to 2 decimal places) in cropland and pasture, respectively, and the middle colour of orange represents values of 1 (probability of occurrence equal to that in primary habitat) for both land uses.

Section 7: Endotherm models

I ran a separate set of models that only included species of mammals and birds. This was to ensure that my results were consistent for endothermic species, who may be less affected by local climatic changes. The results of these models (fig. S4.16-17) were very similar to those including both ectotherms and endotherms (see Chapter 4).

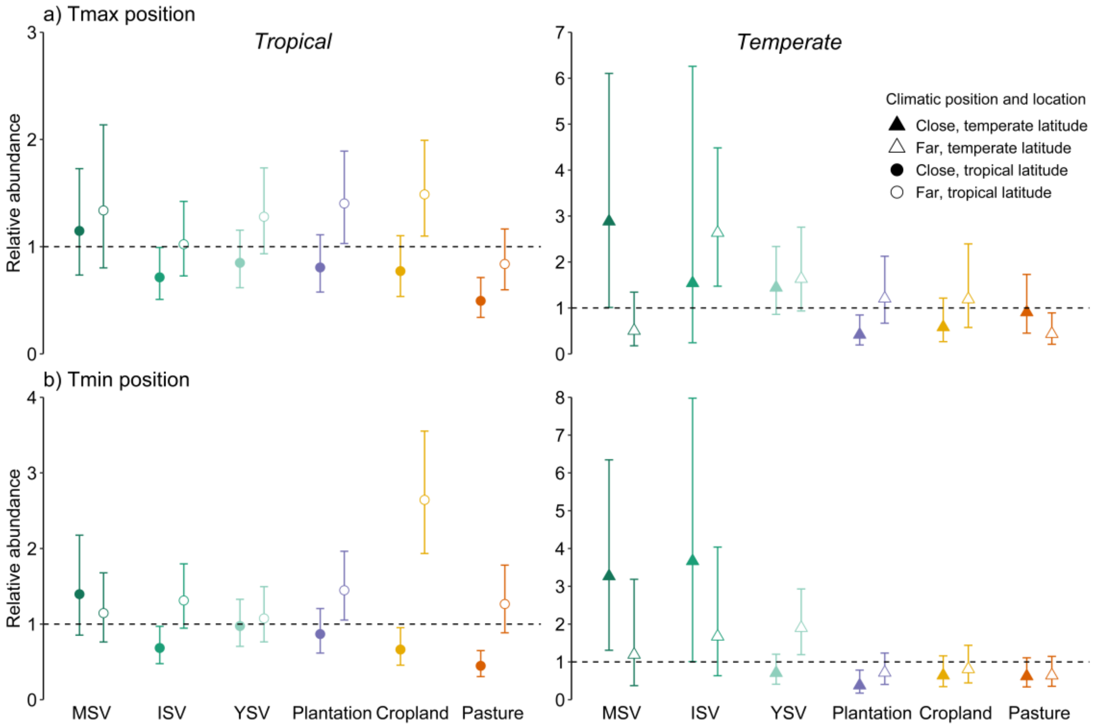


Figure S4.16: The abundance of endothermic species within each land-use type, relative to abundance in primary vegetation (indicated by the dotted line), for populations with T_{max} or T_{min} positions ‘close’ or ‘far’ from their thermal tolerance limits at tropical and temperate latitudes. For (a) a population’s T_{max} position, ‘close’ and ‘far’ refer to a position of 0.9 and 0.7, respectively, for both tropical and temperate latitudes. For (b) a population’s T_{min} position, ‘close’ and ‘far’ refer to a position of 0.2 and 0.6 at tropical latitudes, and 0.1 and 0.4 at temperate latitudes, respectively. These positions reflect the 10^{th} and 90^{th} percentile of T_{max} or T_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively.

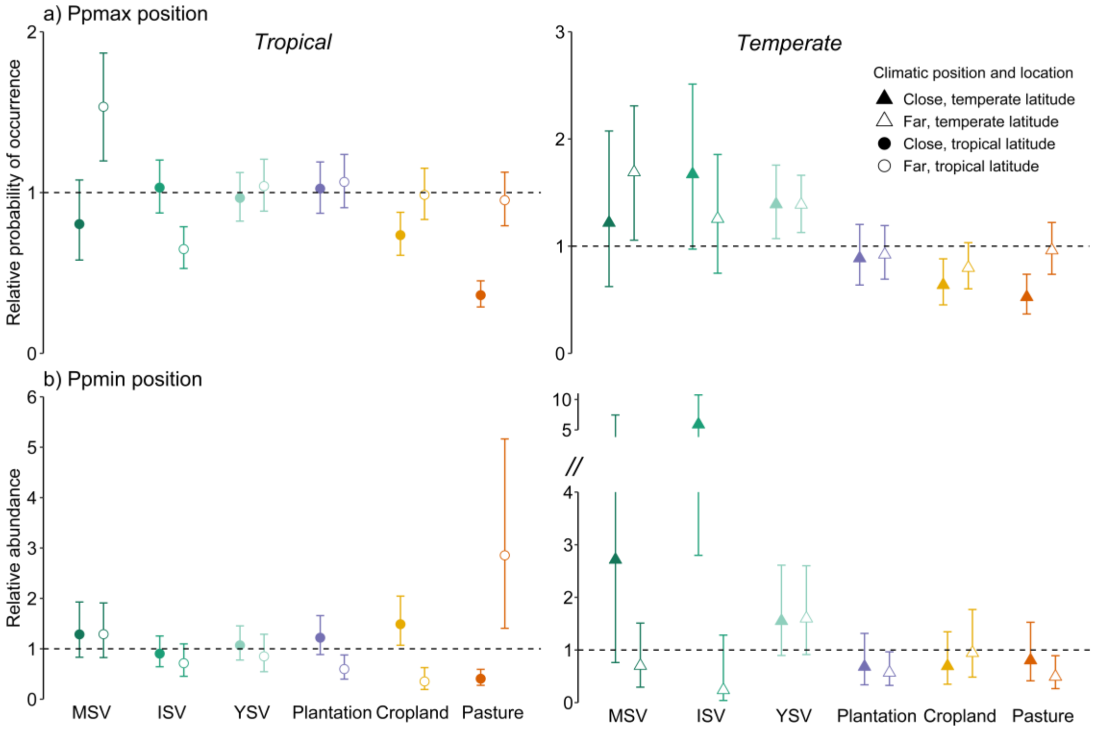


Figure S4.17: The (a) probability of occurrence or (b) abundance of endothermic species within each land-use type, relative to that in primary vegetation (indicated by the dotted line), for populations with (a) Pp_{max} or (b) Pp_{min} positions ‘close’ or ‘far’ from their precipitation tolerance limits at tropical and temperate latitudes. For (a) a population’s Pp_{max} position, ‘close’ and ‘far’ refer to a position of 0.6 and 0.1 at tropical latitudes, and 0.4 and 0.1 at temperate latitudes, respectively. For (b) a population’s Pp_{min} position, ‘close’ and ‘far’ refer to a position of 0 and 0.2 at tropical latitudes, and 0 and 0.1 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of Pp_{max} or Pp_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively. I plot relative probability of occurrence (rather than relative abundance) for Pp_{max} positions because a population’s Pp_{max} position was not found to have a significant effect on abundance, and so was not included in the final abundance (given presence) model. I use a broken y-axis (represented by //) on the plot for Pp_{min} position at temperate latitudes so that the smaller effect sizes can be more easily interpreted.

Section 8: Excluding forest specialists

I extracted data on habitat preferences for the vertebrate species included in my models (IUCN 2017). I classified a species as a 'forest specialist' if natural forest habitats (Forest – Subtropical/Tropical Moist Lowland; Forest –Subtropical/Tropical Moist Montane; Forest – Subtropical/Tropical Dry; Forest – Temperate; Forest – Subtropical/Tropical Swamp; Forest – Boreal; Forest – Subartic; Forest – Subtropical/Tropical Mangrove Vegetation Above High Tide Level; Forest – Subantarctic) were considered as being of 'major' importance to the species (rather than suitable, marginal, or unsuitable), according to the IUCN habitat classification. Then, this time excluding forest specialist species, I ran the final models stated in Chapter 4. The probability of occurrence model included 48,125 populations, consisting of 907 species, and the abundance (given presence) included 6,728 populations, from 700 species. The results of these (figs. S4.18-19) were very similar to those including forest specialist species.

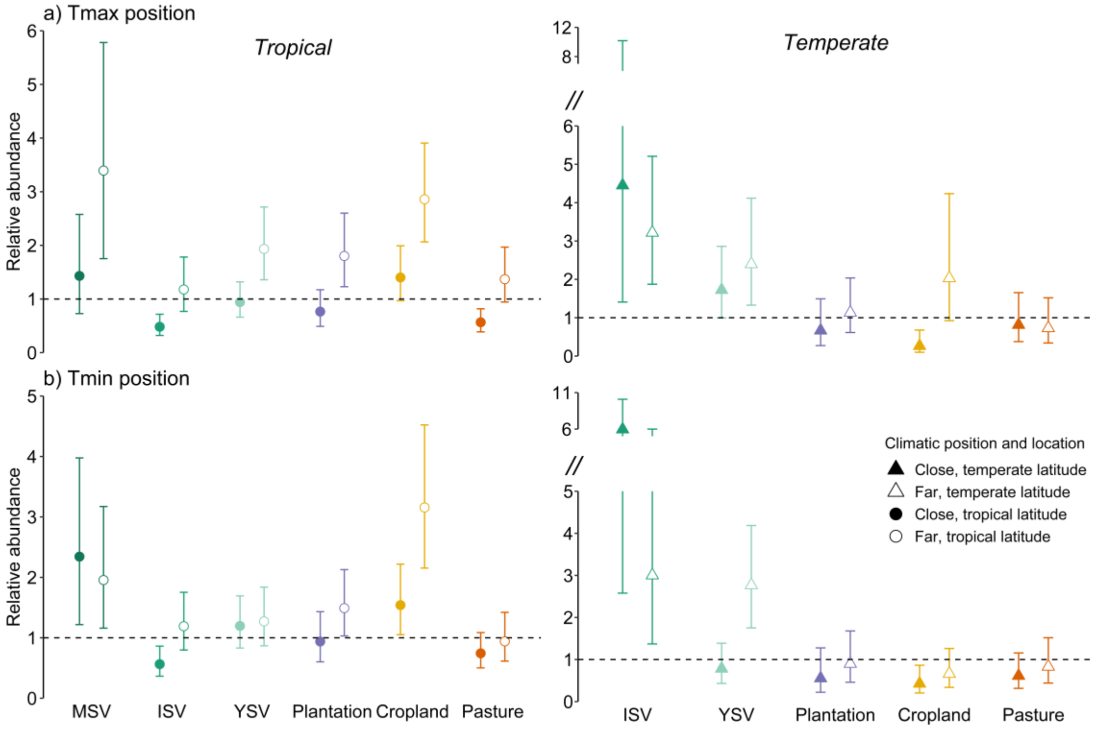


Figure S4.18: The abundance of species (excluding those classified as forest specialists) within each land-use type, relative to abundance in primary vegetation (indicated by the dotted line), for populations with T_{max} or T_{min} positions 'close' or 'far' from their thermal tolerance limits at tropical and temperate latitudes. For (a) a population's T_{max} position, 'close' and 'far' refer to a position of 0.9 and 0.7, respectively, for both tropical and temperate latitudes. For (b) a population's T_{min} position, 'close' and 'far' refer to a position of 0.2 and 0.6 at tropical latitudes, and 0.1 and 0.4 at temperate latitudes, respectively. These positions reflect the 10^{th} and 90^{th} percentile of T_{max} or T_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively. Results for MSV at temperate latitudes are not shown as there were only nine populations in this grouping after excluding forest specialists, which resulted in large error bars for this grouping. I use broken y-axes (represented by //) on the plots for temperate latitudes so that the smaller effect sizes can be more easily interpreted.

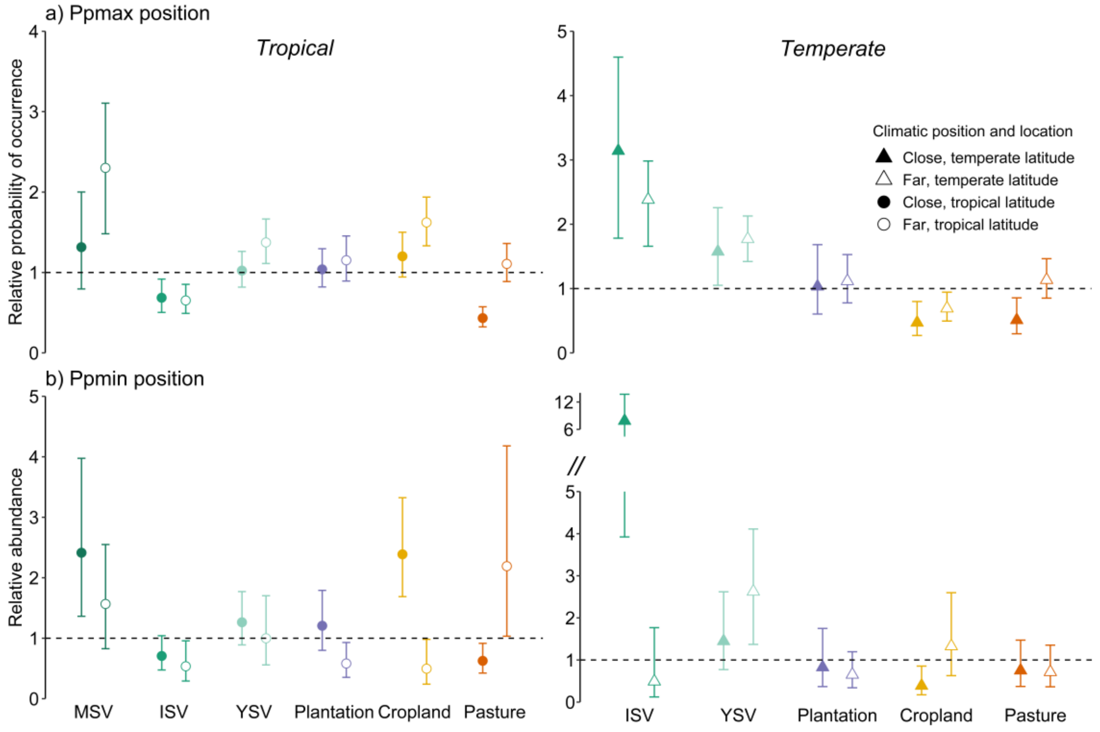


Figure S4.19: The (a) probability of occurrence or (b) abundance of species (excluding those classified as forest specialists) within each land-use type, relative to that in primary vegetation (indicated by the dotted line), for populations with (a) Pp_{max} or (b) Pp_{min} positions 'close' or 'far' from their precipitation tolerance limits at tropical and temperate latitudes. For (a) a population's Pp_{max} position, 'close' and 'far' refer to a position of 0.6 and 0.2 at tropical latitudes, and 0.4 and 0.1 at temperate latitudes, respectively. For (b) a population's Pp_{min} position, 'close' and 'far' refer to a position of 0 and 0.2 at tropical latitudes, and 0 and 0.1 at temperate latitudes, respectively. These positions reflect the 10^{th} and 90^{th} percentile of Pp_{max} or Pp_{min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ±1 standard error. MSV, ISV, and YSV stand for mature, intermediate, and young secondary vegetation, respectively. Results for MSV at temperate latitudes are not shown as there were only nine populations in this grouping after excluding forest specialists, which resulted in large error bars for this grouping. I plot relative probability of occurrence (rather than relative abundance) for Pp_{max} positions because a population's Pp_{max} position was not found to have a significant effect on abundance, and so was not included in the final abundance (given presence) model. I use a broken y-axis (represented by //) on the plot for Pp_{min} position at temperate latitudes so that the smaller effect sizes can be more easily interpreted.

Section 9: Coefficient comparison with MCMCglmm models

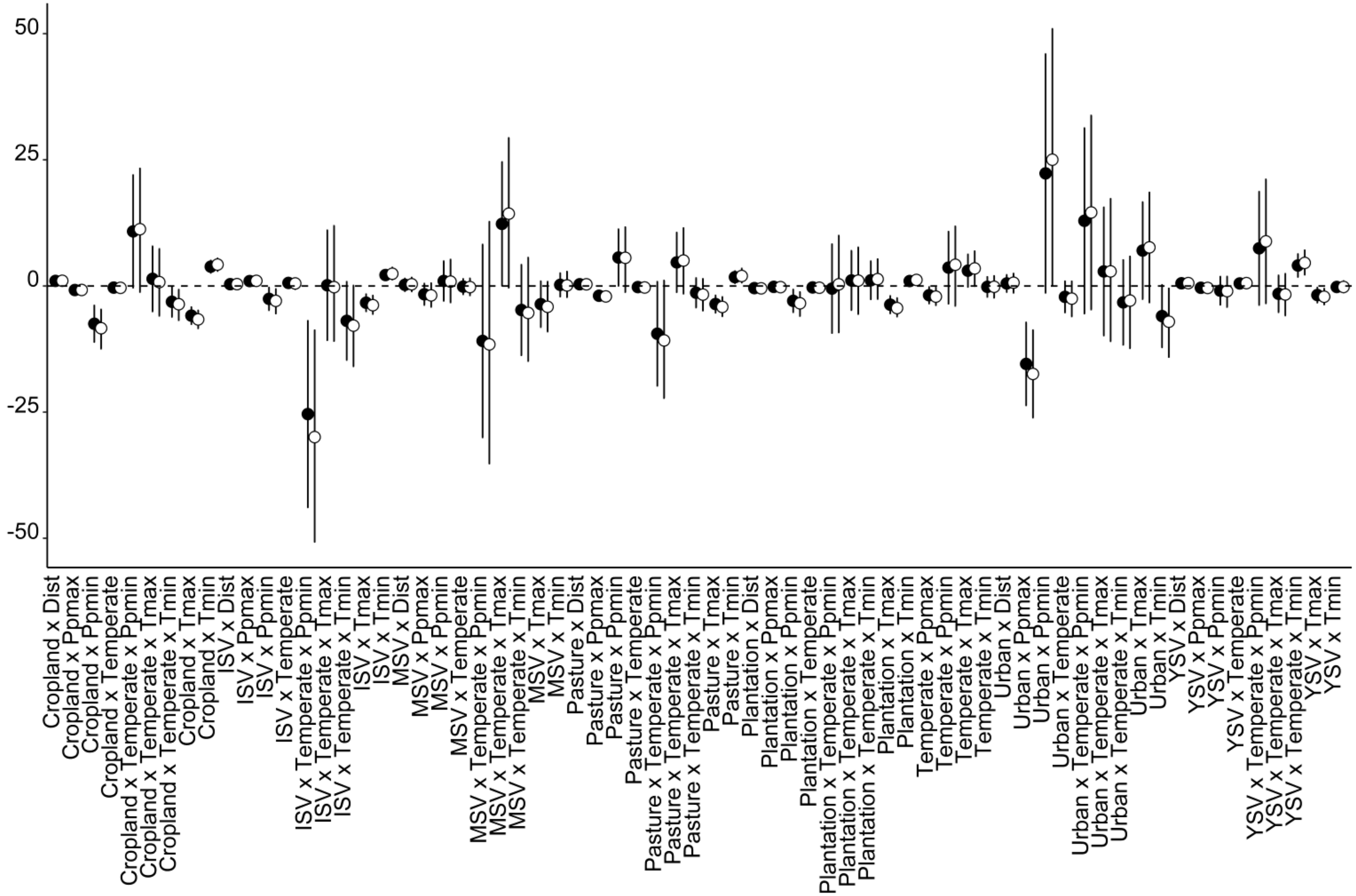


Figure S4.20: The coefficients of the interaction terms from the reported probability of occurrence models using the package ‘lme4’ (filled circles; Bates et al., 2015) compared to those produced using a Bayesian modelling approach with the package ‘MCMCglmm’ (open circles; Hadfield, 2010). The interactions included the geographic zone (tropical [reference level] or temperate), land-use class (primary vegetation [reference level], mature secondary vegetation [MSV], intermediate secondary vegetation [ISV], young secondary vegetation [YSV], plantation, cropland, pasture or urban), climatic position (with regard to maximum temperature of the warmest month [Tmax], minimum temperature of the coldest month [Tmin], precipitation of the wettest [Ppmax] or driest [Ppmin] month) and distance to range edge (Dist). Error bars denote 95% confidence intervals (for the models produced using ‘lme4’) or credible intervals (for models produced using ‘MCMCglmm’).

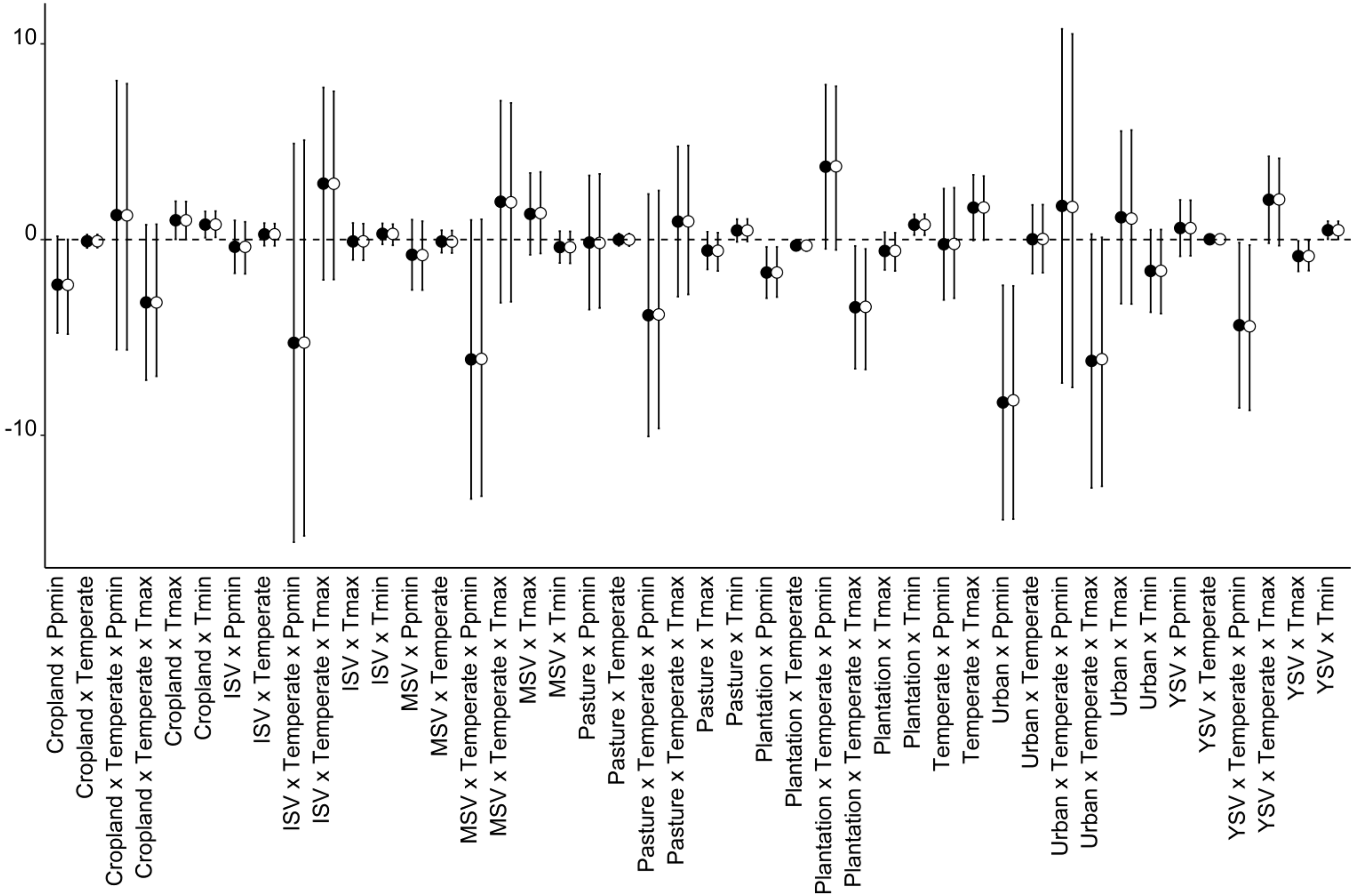

10
0
-10
Cropland x Ppmin
Cropland x Temperate
Cropland x Temperate x Ppmin
Cropland x Temperate x Tmax
Cropland x Tmax
Cropland x Tmin
ISV x Ppmin
ISV x Temperate
ISV x Temperate x Ppmin
ISV x Temperate x Tmax
ISV x Tmax
ISV x Tmin
MSV x Ppmin
MSV x Temperate
MSV x Temperate x Ppmin
MSV x Temperate x Tmax
MSV x Tmax
MSV x Tmin
Pasture x Ppmin
Pasture x Temperate
Pasture x Temperate x Ppmin
Pasture x Temperate x Tmax
Pasture x Tmax
Pasture x Tmin
Plantation x Ppmin
Plantation x Temperate
Plantation x Temperate x Ppmin
Plantation x Temperate x Tmax
Plantation x Tmax
Plantation x Tmin
Temperate x Ppmin
Temperate x Tmax
Urban x Ppmin
Urban x Temperate
Urban x Temperate x Ppmin
Urban x Temperate x Tmax
Urban x Tmax
Urban x Tmin
YSV x Ppmin
YSV x Temperate
YSV x Temperate x Ppmin
YSV x Temperate x Tmax
YSV x Tmax
YSV x Tmin

Figure S4.21: The coefficients of the interaction terms from the reported abundance (given presence) models using the package ‘lme4’ (filled circles; Bates et al., 2015) compared to those produced using a Bayesian modelling approach with the package ‘MCMCglmm’ (open circles; Hadfield, 2010). The interactions included the geographic zone (tropical [reference level] or temperate), land-use class (primary vegetation [reference level], mature secondary vegetation [MSV], intermediate secondary vegetation [ISV], young secondary vegetation [YSV], plantation, cropland, pasture or urban) and climatic position (with regard to maximum temperature of the warmest month [Tmax], minimum temperature of the coldest month [Tmin] or driest [Ppmin] month). Error bars denote 95% confidence intervals (for the models produced using ‘lme4’) or credible intervals (for models produced using ‘MCMCglmm’).

Section 10: Comparing models with random-intercept vs. random-slope terms

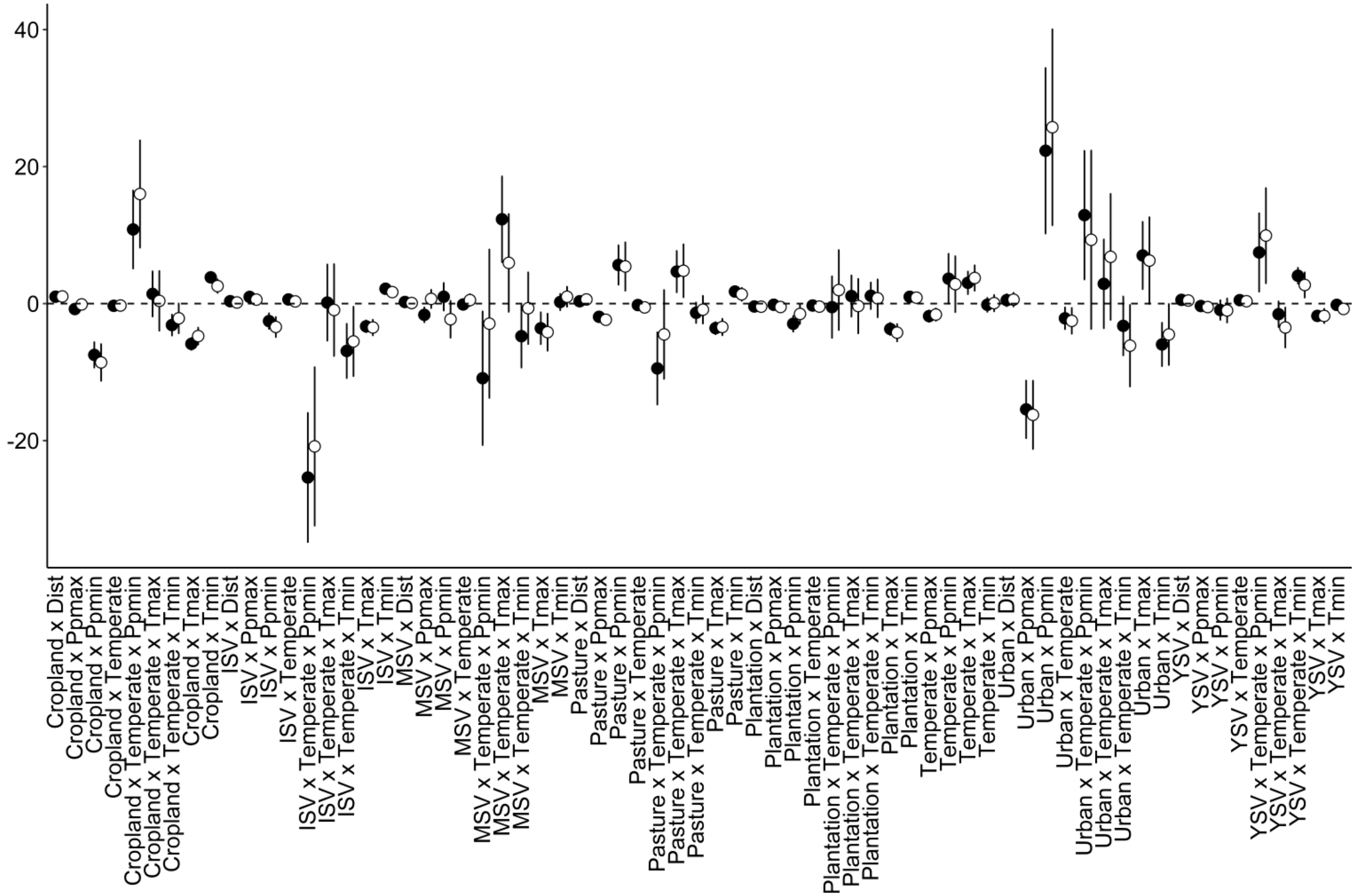


Figure S4.22: The coefficients of the interaction terms from the reported probability of occurrence models using random-intercept terms (filled circles) compared to those including random-slope terms to account for species differences in responses to climatic position and land-use type (open circles). The interactions included the geographic zone (tropical [reference level] or temperate), land-use class (primary vegetation [reference level], mature secondary vegetation [MSV], intermediate secondary vegetation [ISV], young secondary vegetation [YSV], plantation, cropland, pasture or urban), climatic position (with regard to maximum temperature of the warmest month [Tmax], minimum temperature of the coldest month [Tmin], precipitation of the wettest [Ppmax] or driest [Ppmin] month) and distance to range edge (Dist). Error bars denote ±1 standard error.

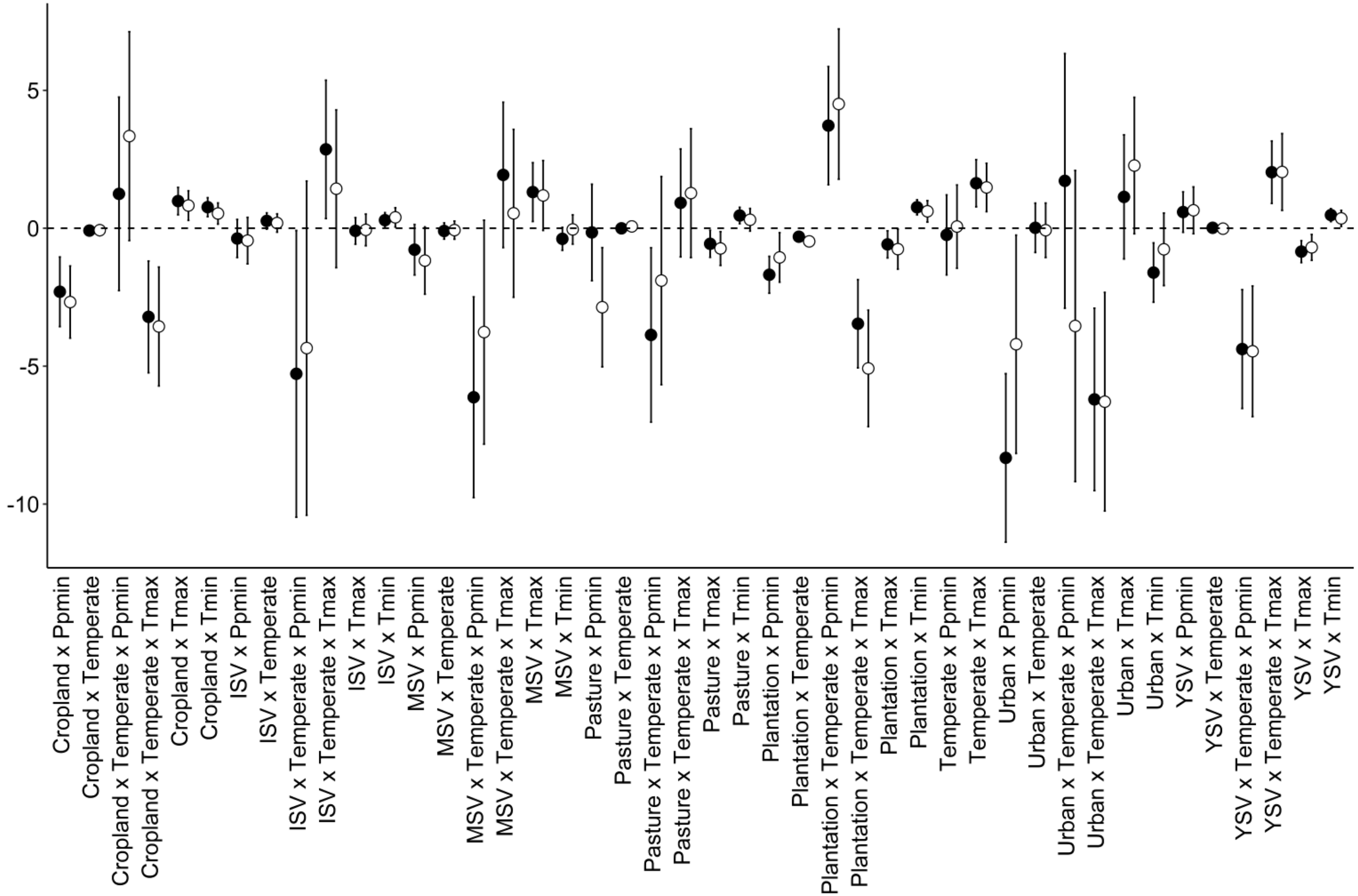

5
0
-5
-10
Cropland x Ppmin
Cropland x Temperate
Cropland x Temperate x Ppmin
Cropland x Temperate x Tmax
Cropland x Tmax
Cropland x Tmin
ISV x Ppmin
ISV x Temperate
ISV x Temperate x Ppmin
ISV x Temperate x Tmax
ISV x Tmax
ISV x Tmin
MSV x Ppmin
MSV x Temperate
MSV x Temperate x Ppmin
MSV x Temperate x Tmax
MSV x Tmax
MSV x Tmin
Pasture x Ppmin
Pasture x Temperate
Pasture x Temperate x Ppmin
Pasture x Temperate x Tmax
Pasture x Tmax
Pasture x Tmin
Plantation x Ppmin
Plantation x Temperate
Plantation x Temperate x Ppmin
Plantation x Temperate x Tmax
Plantation x Tmax
Plantation x Tmin
Temperate x Ppmin
Temperate x Tmax
Urban x Ppmin
Urban x Temperate
Urban x Temperate x Ppmin
Urban x Temperate x Tmax
Urban x Tmax
Urban x Tmin
YSV x Ppmin
YSV x Temperate
YSV x Temperate x Ppmin
YSV x Temperate x Tmax
YSV x Tmax
YSV x Tmin

Figure S4.23: The coefficients of the interaction terms from the reported abundance (given presence) models using random-intercept terms (filled circles) compared to those including random-slope terms to account for species differences in responses to climatic position and land-use type (open circles). The interactions included the geographic zone (tropical [reference level] or temperate), land-use class (primary vegetation [reference level], mature secondary vegetation [MSV], intermediate secondary vegetation [ISV], young secondary vegetation [YSV], plantation, cropland, pasture or urban), climatic position (with regard to maximum temperature of the warmest month [Tmax], minimum temperature of the coldest month [Tmin], precipitation of the wettest [Ppmax] or driest [Ppmin] month). Error bars denote ±1 standard error.

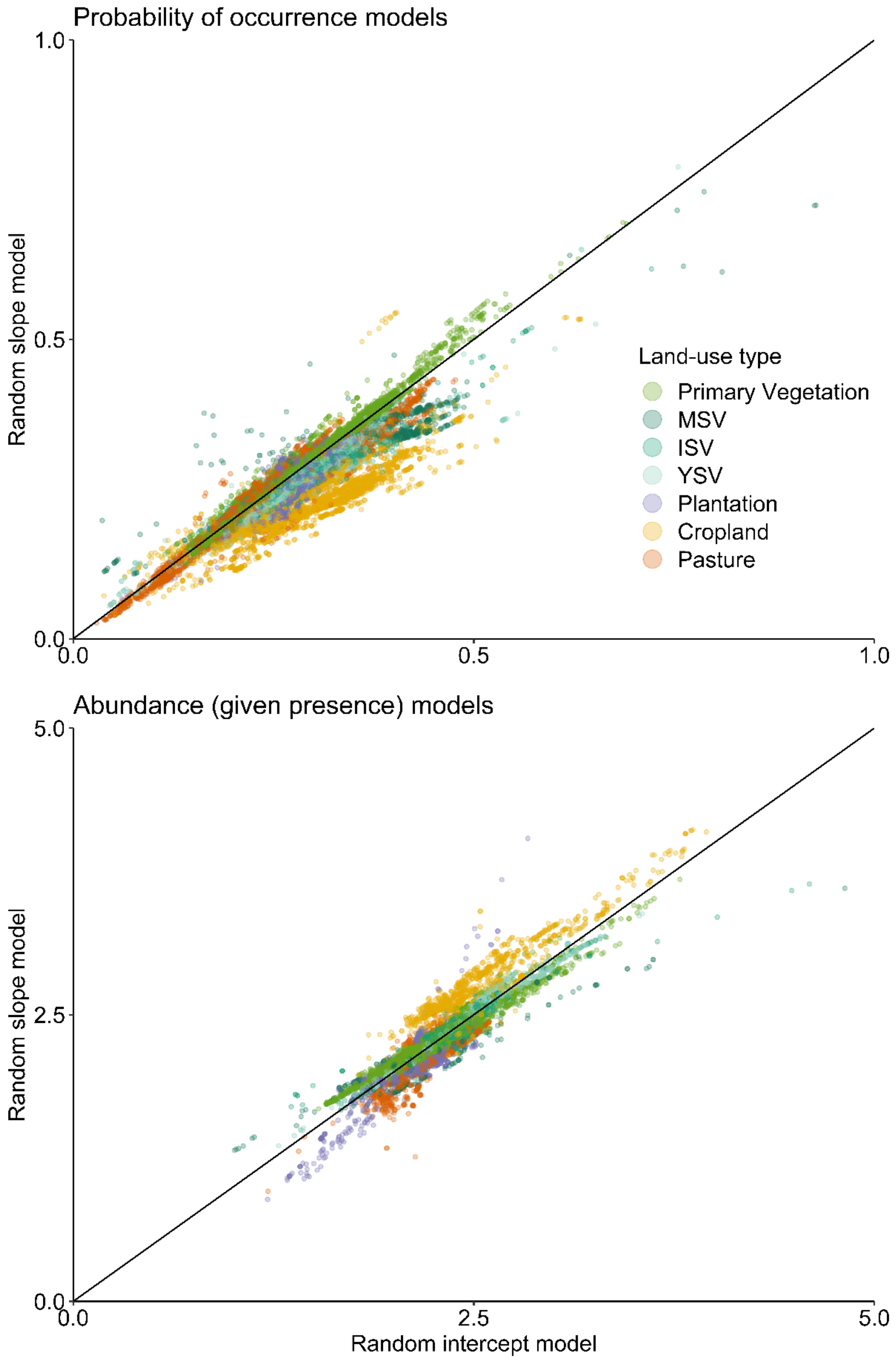


Figure S4.24: Comparing fitted values from the models using random-intercept terms to those including random-slope terms (to account for species differences in responses to climatic position and land-use type). Points are coloured by the land-use type the population was recorded within. For the probability of occurrence models, fitted values for 20,000 (from 88,0007) random datapoints are plotted; for the abundance models, all fitted values (13,321 values) are shown.

Section 11: Bibliography

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Appendix 3: Supplementary materials for Chapter 5

The sections contained in this appendix are:

Section 1: Land-use categories

Table S5.1: The 37 land-cover classes classified by the European Space Agency Climate Change Initiative (ESA CCI; ESA Land Cover CCI project team, Defourny, 2019), and the land-use categories I grouped them into for my analysis (closely following the groupings used by the Intergovernmental Panel on Climate Change for change detection; Defourny et al., 2017). The classes were also grouped (with a weighting system) to form a semi-natural habitat (SNH) category, in order to calculate change in land use surrounding populations. In this weighting system, I used the maximum percentage cover of a specific land use (detailed in the ESA's land-use categories) to weight each category (for example, the category 'Tree cover, broadleaved, deciduous, closed to open (>15%)' was given a weighting of 1, as it could cover 100% of the 300 × 300-m area, whereas the category 'Tree cover, broadleaved, deciduous, open (15-40%)' was given a weighting of 0.4, as this could cover a maximum of 40% of the 300 × 300-m area). Non-SNH categories were given a weighting of 0.

The land-use category used in my analysis	Land cover classification system used in the ESA CCI land-cover maps[▲]			Included as semi-natural habitat? (Y/N)	Weighting system
Agriculture	10		Rainfed cropland	N	0
		11	Herbaceous cover	N	0
		12	Tree or shrub cover	N	0
	20		Irrigated cropland	N	0
	30		Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	N	0
	40		Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)	N	0
	100[+]		Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	N	0
Forest	50		Tree cover, broadleaved, evergreen, closed to open (>15%)	Y	1
	60		Tree cover, broadleaved, deciduous, closed to open (>15%)	Y	1
		61	Tree cover, broadleaved, deciduous, closed (>40%)	Y	1
		62	Tree cover, broadleaved, deciduous, open (15-40%)	Y	0.4
	70		Tree cover, needleleaved, evergreen, closed to open (>15%)	Y	1

		71	Tree cover, needleleaved, evergreen, closed (>40%)	Y	1
		72	Tree cover, needleleaved, evergreen, open (15-40%)	Y	0.4
	80		Tree cover needleleaved, deciduous, closed to open (>15%)	Y	1
		81	Tree cover, needleleaved, deciduous, closed (>40%)	Y	1
		82	Tree cover, needleleaved, deciduous, open (15-40%)	Y	0.4
	90		Tree cover, mixed leaf type (broad leaved and needleleaved)	Y	1
	160		Tree cover, flooded, fresh or brackish water	Y	1
	170		Tree cover, flooded, saline water	Y	1
Grassland	110		Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	Y	0.5
	130		Grassland	Y	1
Wetland	180		Shrub or herbaceous cover, flooded, fresh-saline or brackish water	Y	1
Urban	190		Urban	N	0
Other	120		Shrubland	Y	1
		121	Evergreen shrubland	Y	1
		122	Deciduous shrubland	Y	1
	140		Lichens and mosses	N	0
	150		Sparse vegetation (tree, shrub, herbaceous cover)	N	0
		152	Sparse shrub (<15%)	N	0
		153	Sparse herbaceous cover (<15%)	N	0

	200		Bare areas		N	0
		201		Consolidated bare areas	N	0
		202		Unconsolidated bare areas	N	0
Water*	210		Water		N	0
Snow and ice*	220		Permanent snow and ice		N	0

* I did not consider these categories in my analysis, so removed populations starting in these areas.

[+] This was classed as agriculture due to personal communications with members of the Sentinel (Social and Environmental Trade-Offs in African Agriculture) Project (www.sentinel-gcrf.org), who have found that this land-use category was commonly cropland with sparse trees.

[▲] The 37th class is a No Data class.

Section 2: Map of populations

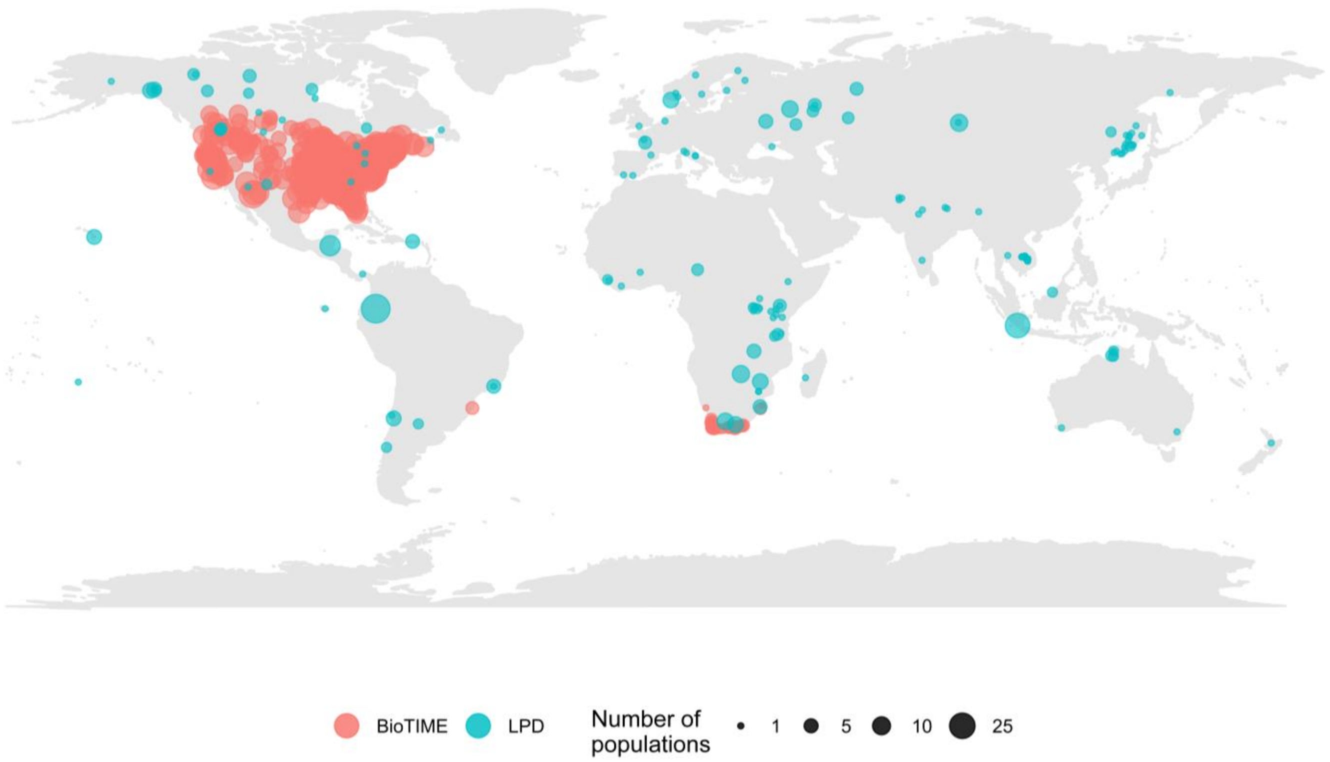

Figure S5.1: The location of terrestrial vertebrate populations included in the final dataset. The size reflects the number of populations at that location, with colours differentiating the Living Planet dataset (LPD) and BioTIME dataset.

Section 3: Further information on the results

Table S5.2: The correlations (Spearman correlation, p) between the continuous variables considered in the backwards stepwise selection. These variables were: average annual rate of change in semi-natural habitat (SNH_rate), starting climatic positions with regard to T_{max} (Tmax_pos), T_{min} (Tmin_pos), Pp_{max} (Ppmax_pos) and Pp_{min} (Ppmin_pos), average annual rate of change in climate with regard to maximum temperature of the warmest month (MaxT_rate), minimum temperature of the coldest month (MinT_rate), precipitation of the wettest (MaxP_rate) and driest (MinP_rate) months, and distance to range edge (Stand_dist).

	SNH_rate	Tmax_pos	Tmin_pos	Ppmax_pos	Ppmin_pos	MaxT_rate	MinT_rate	MaxP_rate	MinP_rate	Stand_dist
SNH_rate										
Tmax_pos	-0.027									
Tmin_pos	0.002	0.331								
Ppmax_pos	-0.025	0.325	-0.032							
Ppmin_pos	0.015	0.193	-0.013	0.461						
MaxT_rate	-0.025	-0.257	-0.146	-0.249	-0.433					
MinT_rate	0.034	-0.337	-0.355	-0.156	-0.070	0.094				
MaxP_rate	0.065	-0.073	-0.057	-0.126	0.238	-0.218	0.188			
MinP_rate	0.062	-0.424	-0.243	-0.101	-0.279	0.125	0.337	0.176		
Stand_dist	-0.071	0.209	0.013	0.127	0.091	0.104	-0.129	-0.230	-0.216	

Section 4: Comparing climatic position measures

To check the robustness of my climatic position measure, I also calculated starting climatic position using the average maximum and minimum temperature and precipitation conditions (CRU Time-series data v. 4.03; Harris & Jones, 2020) in the three years up to and including the first year of a population's time-series (instead of just using data from the first year, as described in Chapter 5). I then ran a model (using the same structure as described in Chapter 5) using this climatic position measure. The results (figs. S5.2-3) were very similar to those reported in Chapter 5.

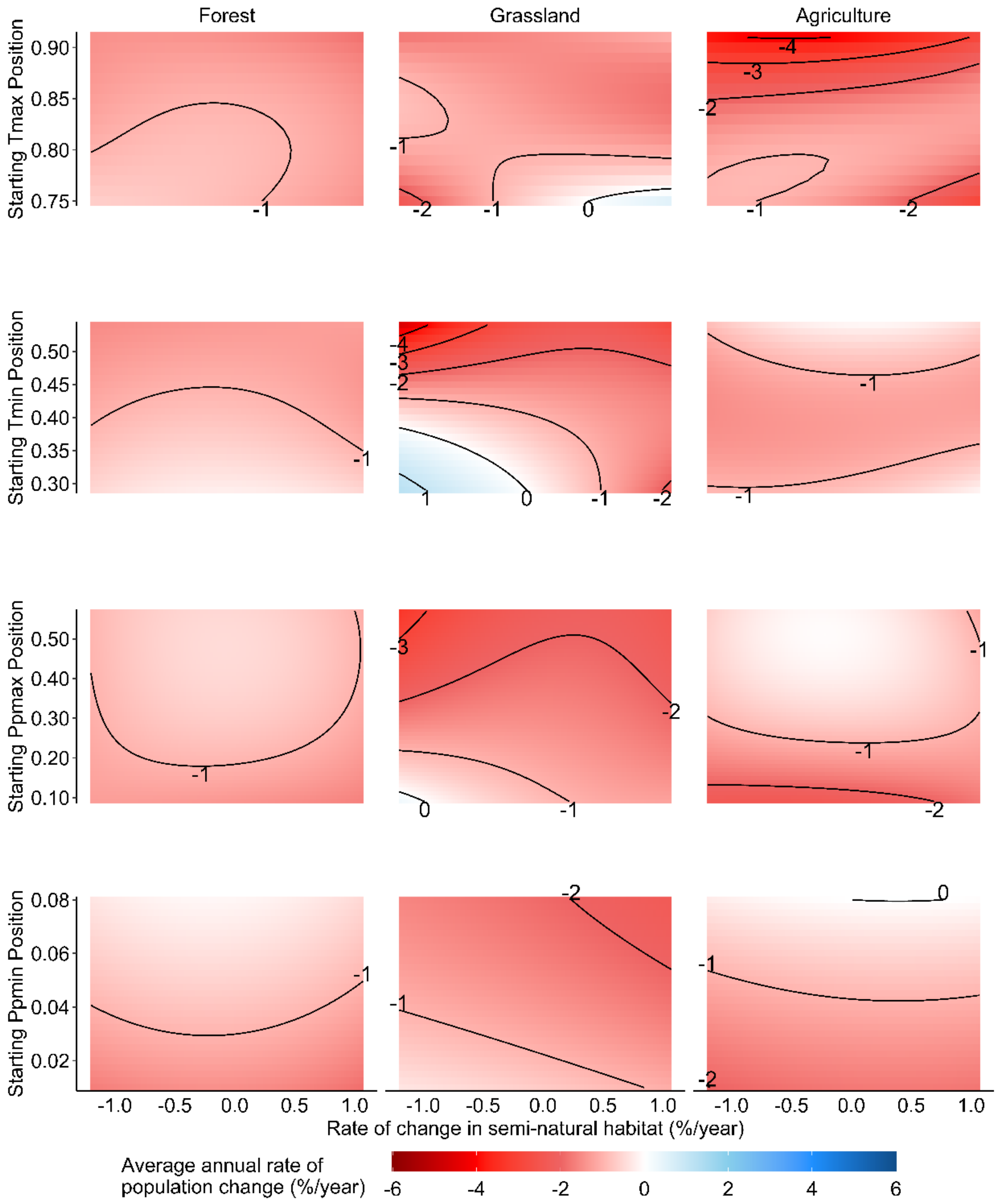

Figure S5.2: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) a population's starting climatic position (calculated using the average maximum and minimum temperature and precipitation conditions in the three years up to and including the first year of a population's time-series) with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

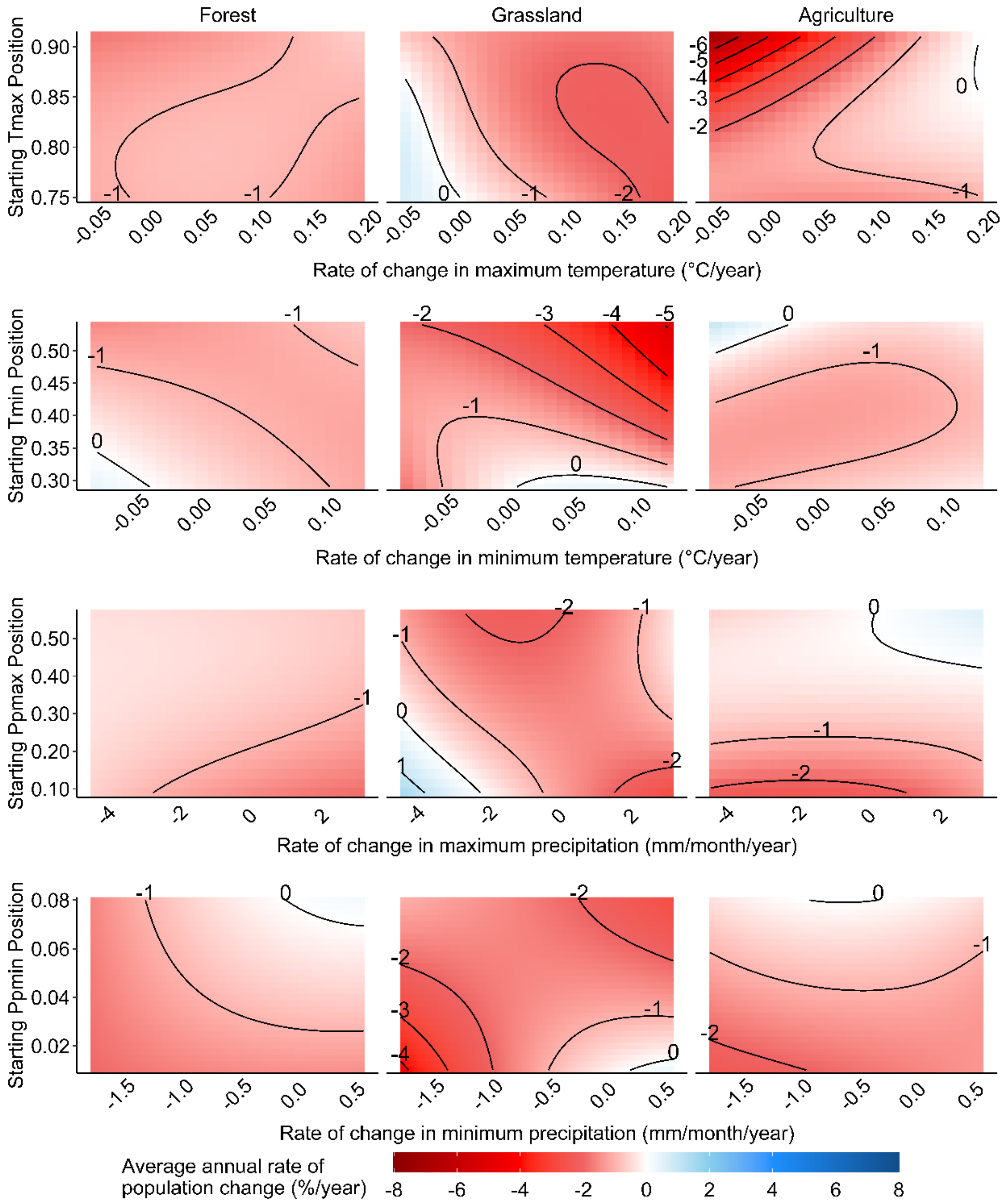

Figure S5.3: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in climate; and (ii) a population's starting climatic position (calculated using the average maximum and minimum temperature and precipitation conditions in the three years up to and including the first year of a population's time-series). Climatic variables considered were maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month

(Pp_{max}), and precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

Further, to check the robustness of my estimates of climatic limits, as well as calculating species' climatic limits as described in Chapter 5, I also (1) used the CRU Time-series data v. 4.03 (Harris & Jones, 2020), extracting climatic data from 1992, to calculate species' climatic limits (rather than using WorldClim data), and (2) used occurrence records from the Global Biodiversity Information Facility (GBIF; GBIF 2015, https://www.gbif.org) to estimate climatic limits. From GBIF, I extracted occurrence records for each species in my final dataset (324 species were also found in GBIF) and, for each species, used the highest maximum temperature of the warmest month, lowest minimum temperature of the coldest month, highest precipitation of the wettest month and lowest precipitation of the driest month (WorldClim version 1.4; Hijmans, Cameron, Parra, Jones, & Jarvis 2005) across these locations to define the species' thermal and precipitation tolerance limits. Following this, for the populations in my final dataset, climatic positions were calculated in the same way as described in Chapter 5, but using the species' estimated realised climatic tolerance limits found using the two methods above. The correlations between the starting climatic positions estimated using the different methods are presented below (table S5.3).

Table S5.3: Correlations (Pearson's correlation coefficient, *r*), between populations' starting climatic positions estimated by using species' distribution maps (described in Chapter 5; BirdLife International 2012; IUCN 2016a-b, 2017a-c, 2018a-b, 2019a-c) and WorldClim climate maps (Hijmans et al., 2005) and (1) using species' distribution maps and climate data from the CRU Time-series data (Harris & Jones, 2020), or (2) using occurrence data from the Global Biodiversity Information Facility (GBIF 2015) and WorldClim climate maps. Climatic positions were produced for four climatic variables: maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), and precipitation of the wettest (Pp_{max}) and driest (Pp_{min}) months (see Chapter 5).

Climatic position	Estimated using IUCN or BirdLife International distribution maps and CRU climate data	Estimated using GBIF occurrence data and WorldClim climate maps
T_{max}	0.93	0.87
T_{min}	0.93	0.78
Pp_{max}	0.90	0.88
Pp_{min}	0.93	0.90

I also reran my final model twice, replacing the climatic position measures with those calculated by (1) using CRU Time-series data and (2) using GBIF data to estimate climatic limits. Results of the model run using the climatic positions calculated using climatic limits derived from CRU Time-series data were very similar to the results presented in Chapter 5 (figs. S5.4-5). The pattern of results using climatic positions derived from GBIF data was on the whole very similar to the results reported in the Chapter 5, with the exception that there was a slight difference in trend for the interaction between starting Pp_{max} position and rate of change in maximum precipitation for populations starting in grasslands (figs. S5.6-7).

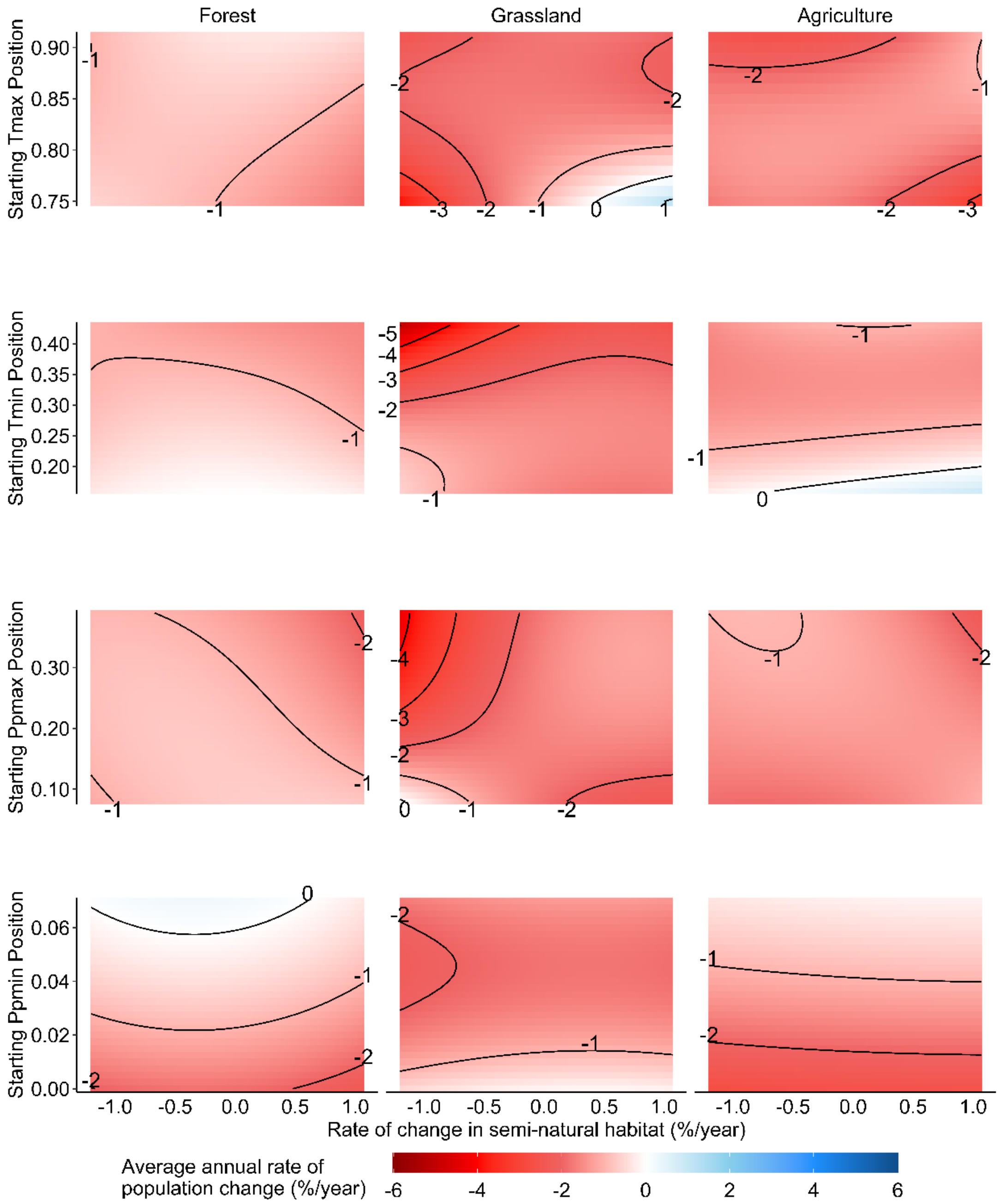

Figure S5.4: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) a population's starting climatic position (calculated using CRU Time-series data, extracting climatic data from 1992, to estimate species' climatic limits) with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

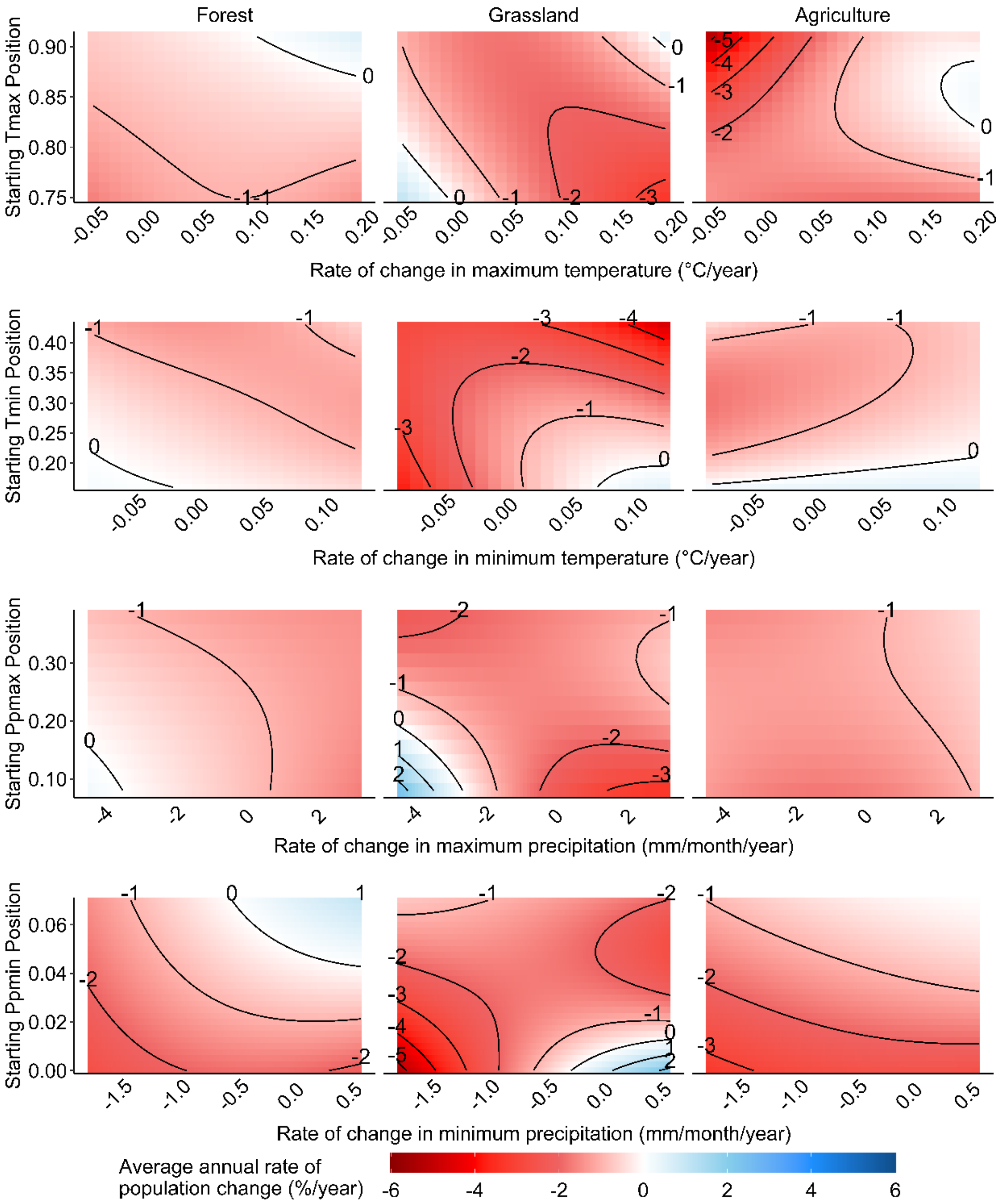

Figure S5.5: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in climate; and (ii) a population's starting climatic position (calculated using CRU Time-series data, extracting climatic data from 1992, to estimate species' climatic limits). Climatic variables considered were maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}), and precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

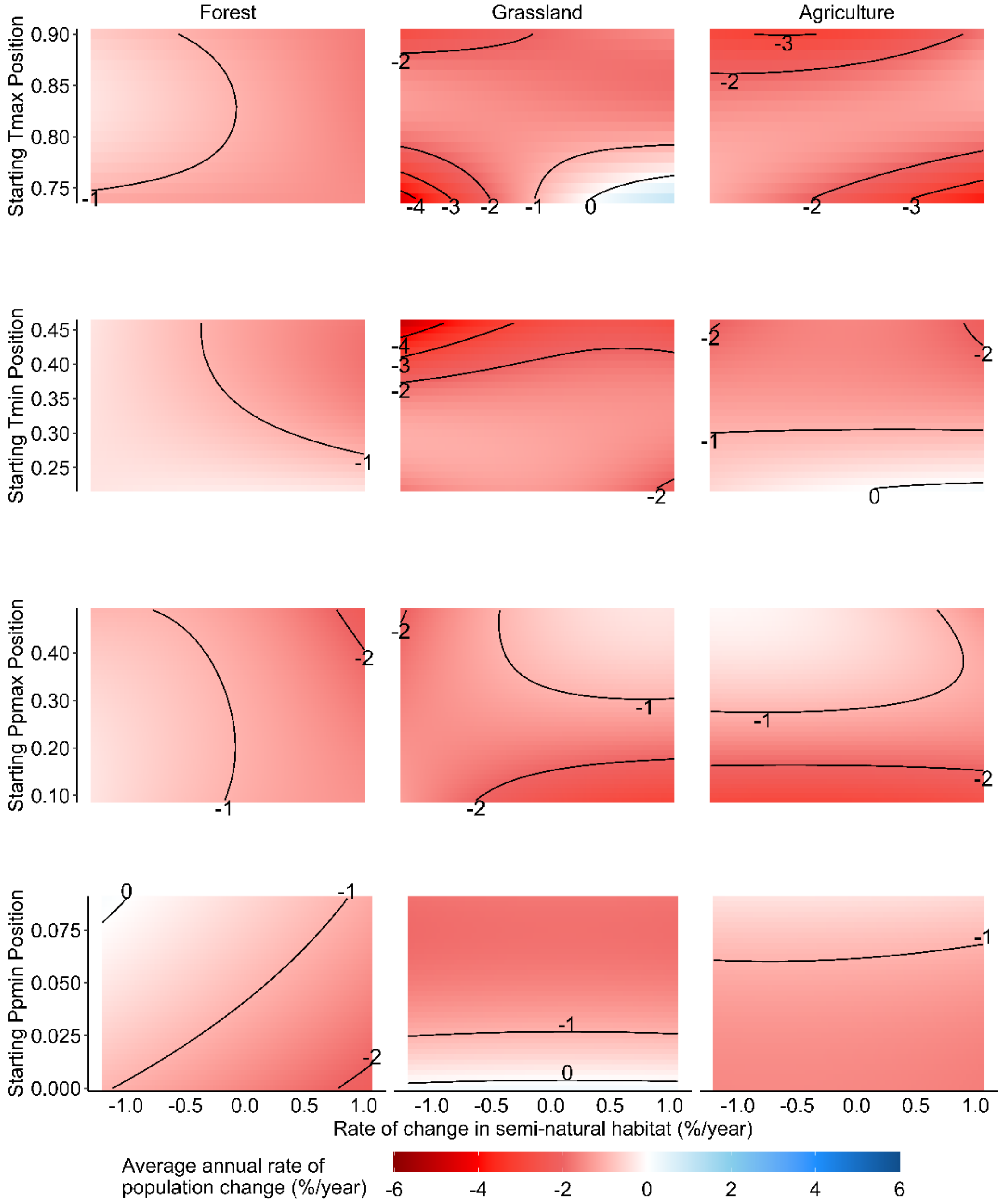

Figure S5.6: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) a population's starting climatic position (calculated using GBIF occurrence data to estimate species' climatic limits) with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

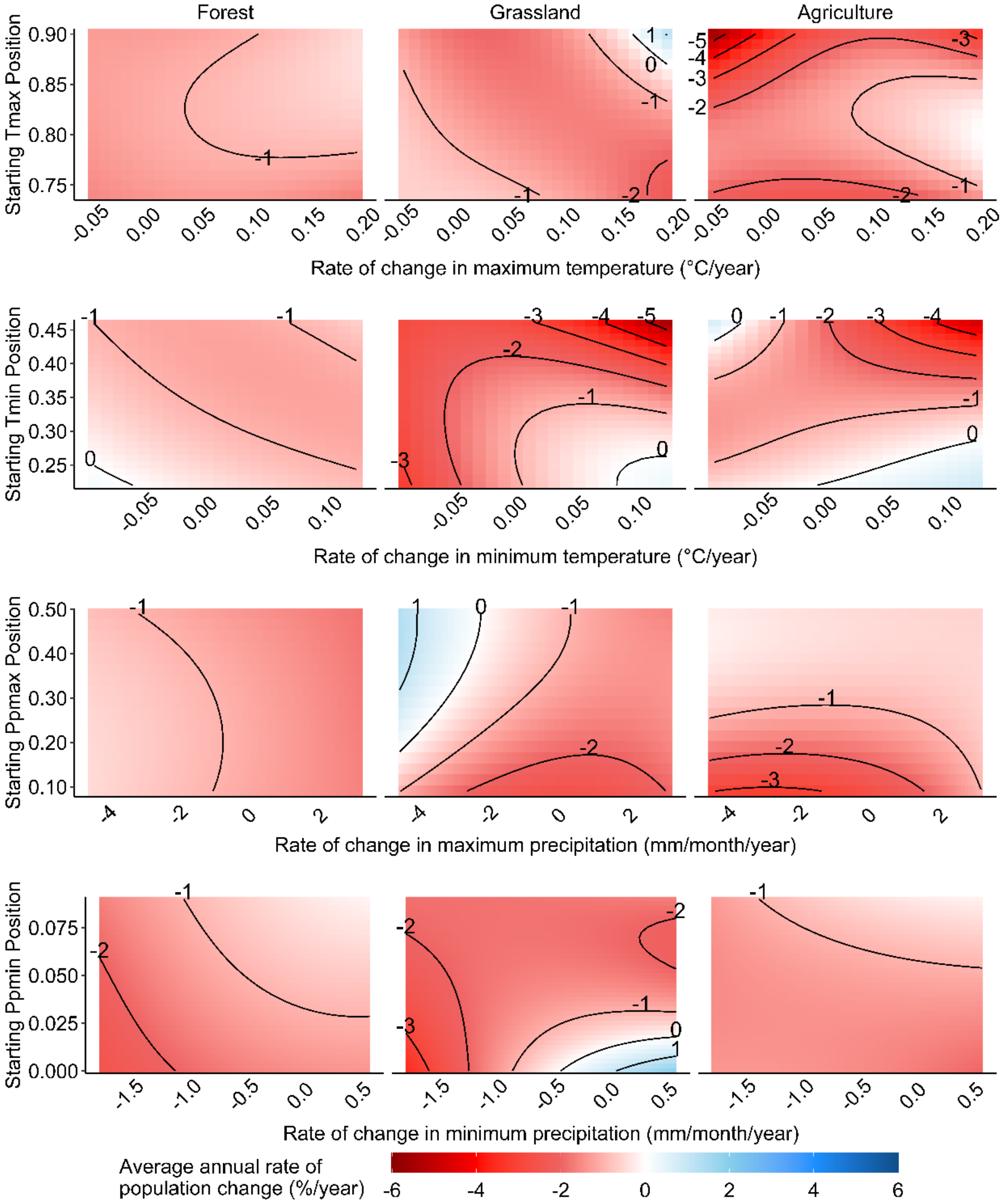

Figure S5.7: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in climate; and (ii) a population's starting climatic position (calculated using GBIF occurrence data to estimate species' climatic limits). Climatic variables considered were maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}), and precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

Section 5: Models including starting percentage of semi-natural habitat

As a sensitivity test, I ran the final model reported within Chapter 5, but included the percentage of semi-natural habitat (SNH) within a 1 km radius in the first year a population was measured, instead of starting land-use type, in the model. The percentage of surrounding SNH was added into the model as a continuous linear fixed-effect, and included in all the same interactions as was starting land-use type. The results are presented below (figs. S5.8-11).

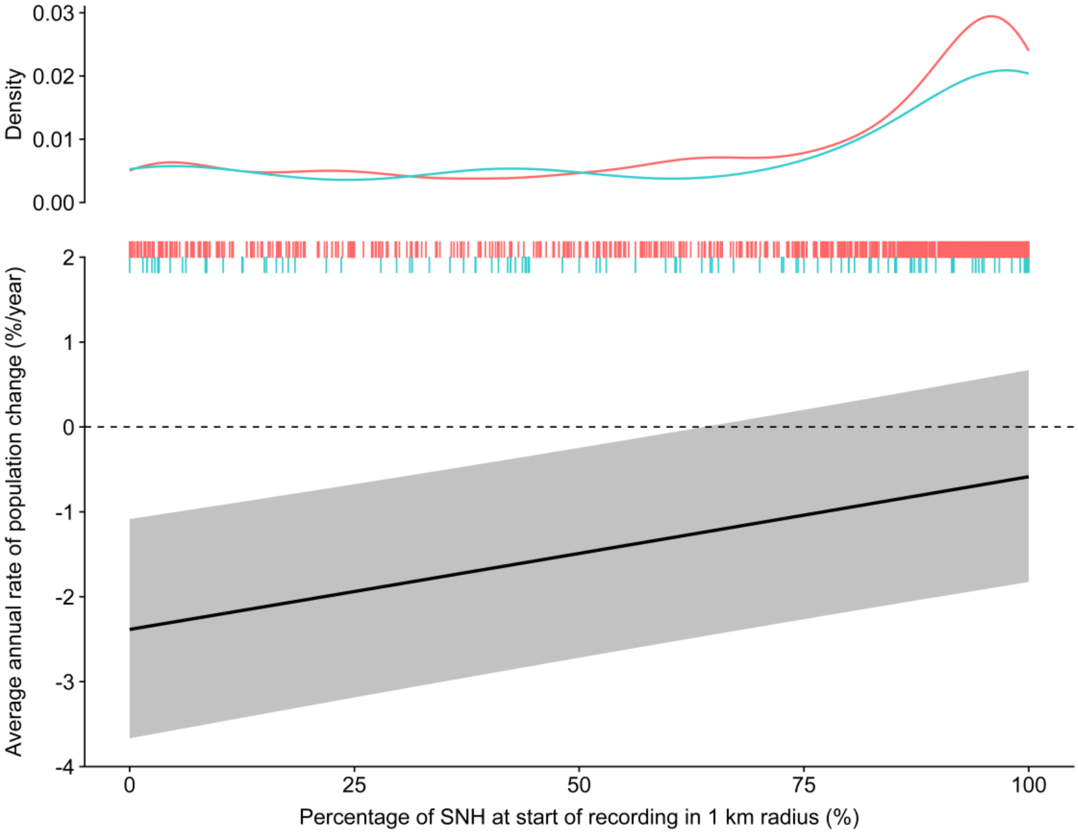

Figure S5.8: The average annual rate of population change depending on the percentage of semi-natural habitat (SNH) within a 1 km radius of the population in the first year they were measured. Error margins denote ±1 standard error. The density and rug plots at the top of the figure show the distribution of populations from the Living Planet database (blue) and BioTIME database (red).

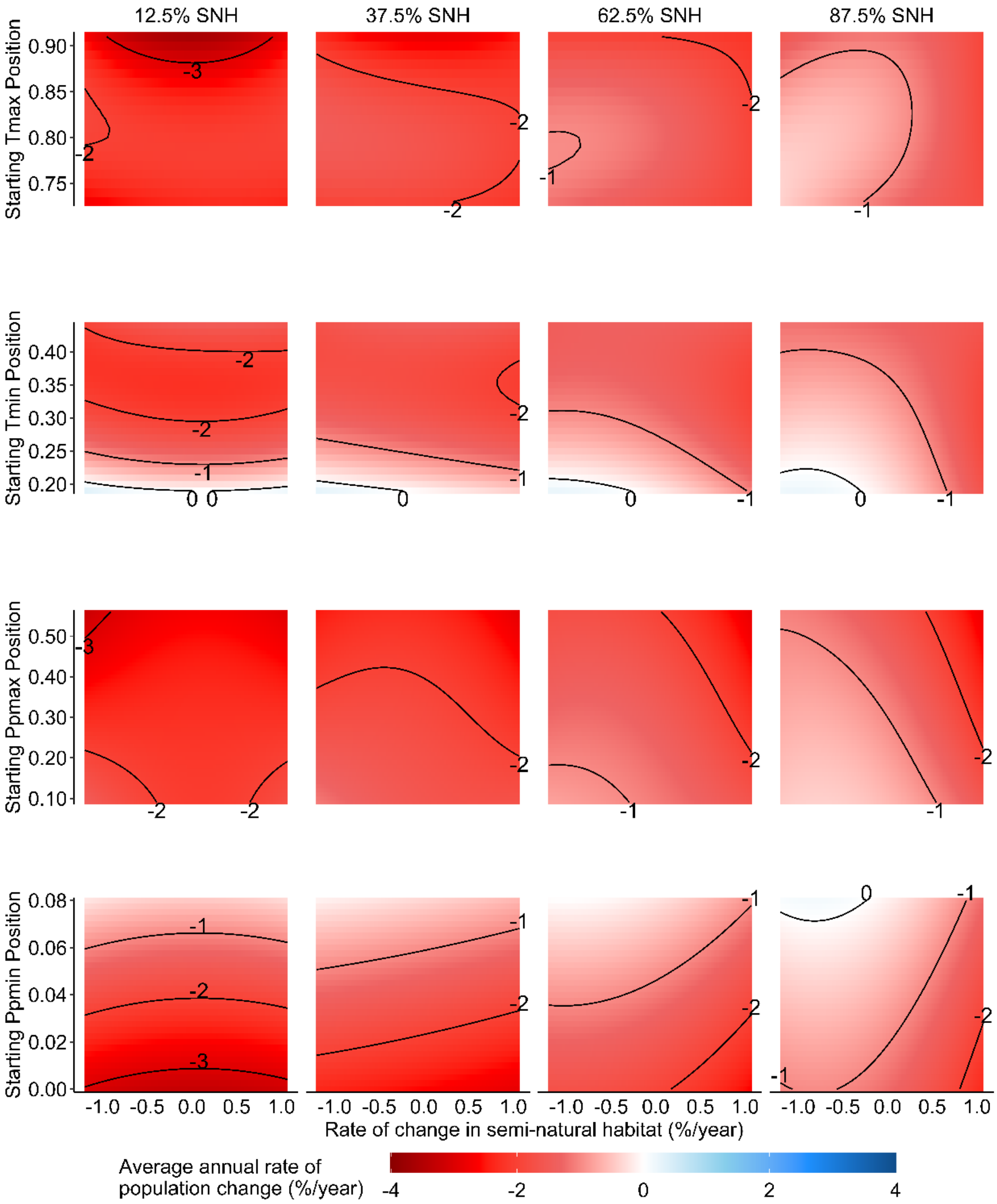

Figure S5.9: The average annual rate of population change (percentage change per year) for populations starting in areas with different percentages of semi-natural habitat (SNH) in the surrounding 1 km radius (rather than starting land-use type), depending on: (i) the average annual rate of change in semi-natural habitat; and (ii) a population's starting climatic position with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable.

Contour lines (and labels) indicate changes in average annual rate of population change.

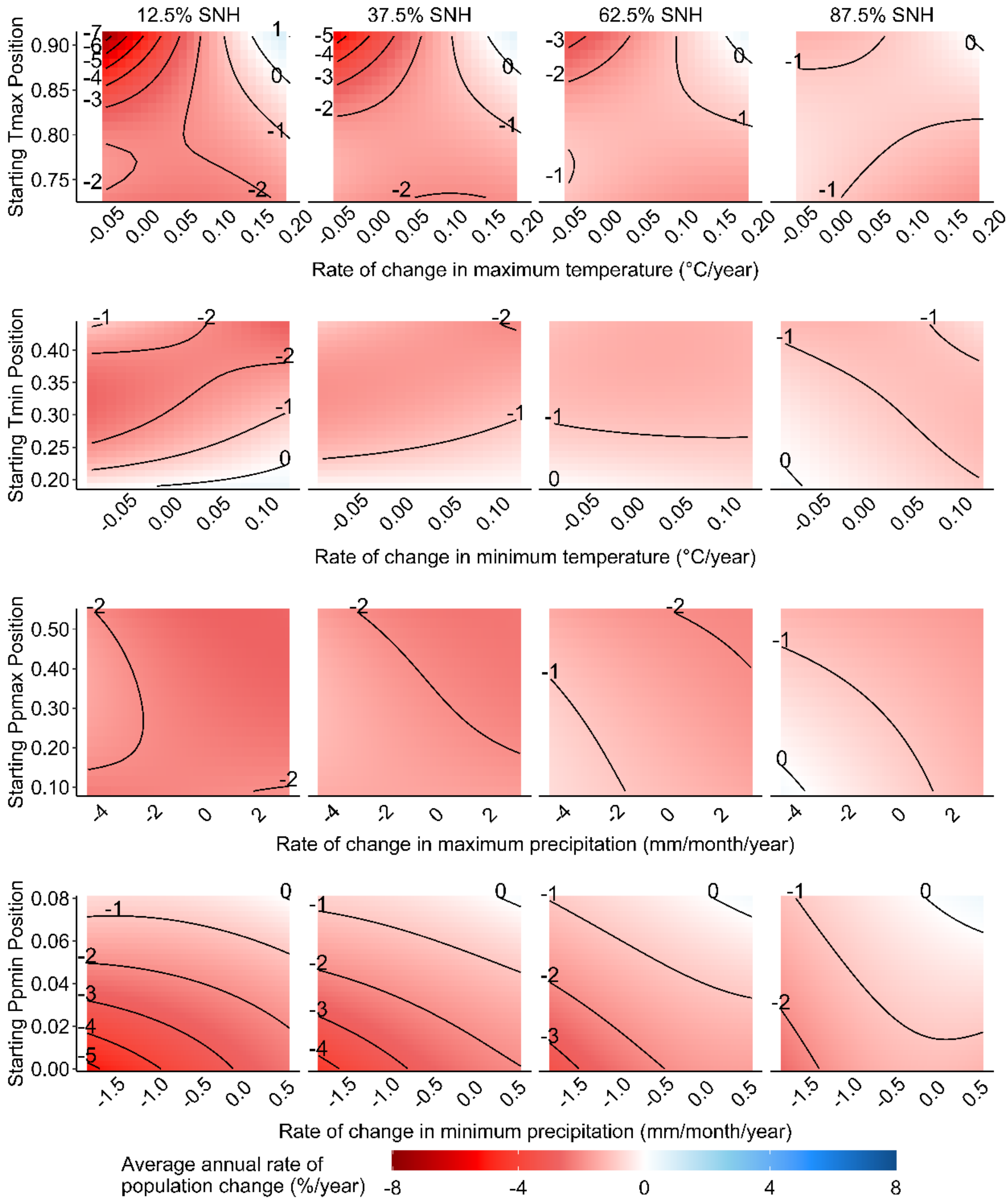

Figure S5.10: The average annual rate of population change (percentage change per year) for populations starting in areas with different percentages of semi-natural habitat (SNH) in the surrounding 1 km radius (rather than starting land-use type), depending on: (i) the average annual rate of change in climate; and (ii) a population's starting climatic position. Climatic variables considered were maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}), and precipitation of the driest month (Pp_{min}).

The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

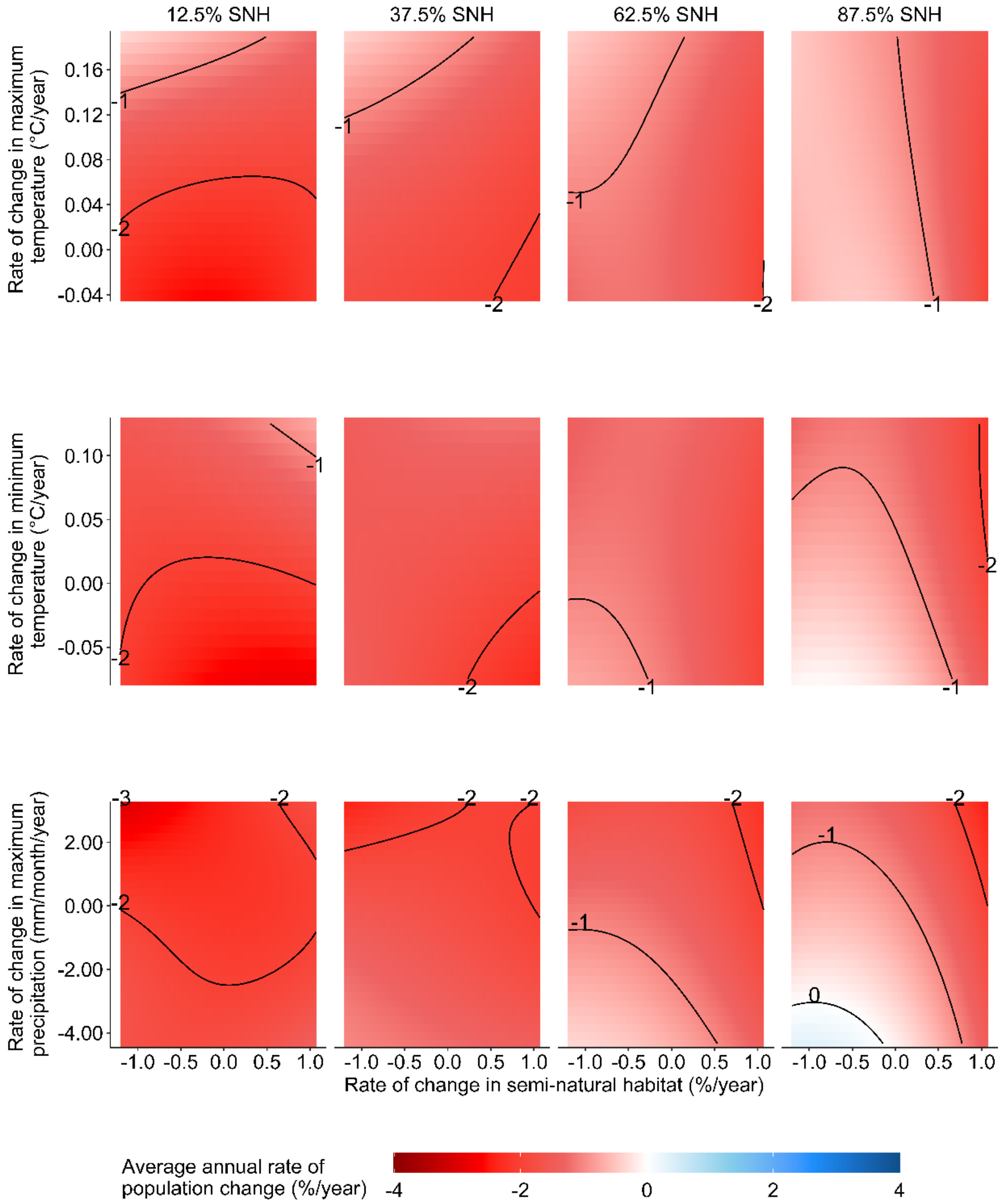

Figure S5.11: The average annual rate of population change (percentage change per year) for populations starting in areas with different percentages of semi-natural habitat (SNH) in the surrounding 1 km radius (rather than starting land-use type), depending on: (i) the average annual rate of change in semi-natural habitat; and (ii) rate of change in climate with regard to maximum temperature of the warmest month (°C/year), minimum temperature of the coldest month (°C/year), and precipitation of the wettest month (monthly mm/year). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

Section 6: Comparison between land cover datasets

To check the consistency of land-use types across data sources, I downloaded a global map of terrestrial habitat types for the year 2015 (Jung et al., 2020a, 2020b) and compared it to the 2015 land cover map from the European Space Agency Climate Change Initiative (ESA CCI; ESA Land Cover CCI project team, Defourny, 2019) used in my analysis. For each unique site (n = 1,151) within my dataset, whether there was a population estimate for a population there in the year 2015 or not, I extracted the site's land-use type from both the 2015 ESA land cover map (using the same broader categories of agriculture, forest, grassland, wetland, urban, and other, as for the starting land-use types in Chapter 5) and Jung et al.'s (2020a) terrestrial habitat map. I grouped Jung et al.'s (2020a) habitat types into broader categories (grouping A) based on their IUCN habitat classification scheme, and further into a smaller number of categories (grouping B) to match those groups used for starting land-use types in my analysis (although wetland and urban populations were removed from the main model due to small sample sizes; table S5.4). Then, for each location, I compared the extracted land uses. In particular, I wanted to ensure that there were not a large number of plantations or pastures at sites that I classed as forest or grasslands, respectively, as land-cover maps may miss these land uses.

For 71% of locations, the land-use type extracted from the ESA land cover map matched that from Jung et al.'s (2020a) terrestrial habitat map. For the other sites, the land uses differed, and I detail these differences in table S5.5.

Table S5.4: The land-use type groupings used for the global map of terrestrial habitat types (Jung et al., 2020a). Grouping A groups the habitats into broader categories and grouping B further groups the habitats to match those used for starting land-use types in my analysis.

IUCN habitat classification scheme used by Jung et al. (2020a)	**Grouping A**	**Grouping B**
1. Forest	Forest	Forest
1.1. Forest – Boreal		
1.2. Forest - Subarctic		
1.3. Forest – Subantarctic		
1.4. Forest – Temperate		
1.5. Forest – Subtropical/tropical dry		
1.6. Forest – Subtropical/tropical moist lowland		
1.7. Forest – Subtropical/tropical mangrove vegetation above high tide level		
1.8. Forest – Subtropical/tropical swamp		
1.9. Forest – Subtropical/tropical moist montane		
2. Savanna	Savanna	Grassland
2.1. Savanna - Dry		
2.2. Savanna - Moist		
3. Shrubland	Shrubland	Other
3.1. Shrubland – Subarctic		
3.2. Shrubland – Subantarctic		

3.3. Shrubland – Boreal		
3.4. Shrubland –Temperate		
3.5. Shrubland – Subtropical/tropical dry		
3.6. Shrubland – Subtropical/tropical moist		
3.7. Shrubland – Subtropical/tropical high altitude		
3.8. Shrubland – Mediterranean-type shrubby vegetation		
4. Grassland	Grassland	Grassland
4.1. Grassland – Tundra		
4.2. Grassland – Subarctic		
4.3. Grassland – Subantarctic		
4.4. Grassland – Temperate		
4.5. Grassland – Subtropical/tropical dry		
4.6. Grassland – Subtropical/tropical seasonally wet/flooded		
4.7. Grassland – Subtropical/tropical high altitude		
5. Wetlands (inland)	Wetland	Wetland
5.1. Wetlands (inland) – Permanent rivers/streams/creeks (includes waterfalls)		
5.2. Wetlands (inland) – Seasonal/intermittent/irregular rivers/streams/creeks		
5.3. Wetlands (inland) – Shrub dominated wetlands		
5.4. Wetlands (inland) – Bogs, marshes, swamps, fens, peatlands		

5.5. Wetlands (inland) – Permanent freshwater lakes (over 8 ha) 5.6. Wetlands (inland) – Seasonal/intermittent freshwater lakes (over 8 ha) 5.7. Wetlands (inland) – Permanent freshwater marshes/pools (under 8 ha) 5.8. Wetlands (inland) – Seasonal/intermittent freshwater marshes/pools (under 8 ha) 5.9. Wetlands (inland) – Freshwater springs and oases 5.10. Wetlands (inland) – Tundra wetlands (inc. pools and temporary waters from snowmelt) 5.11. Wetlands (inland) – Alpine wetlands (inc. temporary waters from snowmelt) 5.12. Wetlands (inland) – Geothermal wetlands 5.13. Wetlands (inland) – Permanent inland deltas 5.14. Wetlands (inland) – Permanent saline, brackish or alkaline lakes 5.15. Wetlands (inland) – Seasonal/intermittent saline, brackish or alkaline lakes and flats 5.16. Wetlands (inland) – Permanent saline, brackish or alkaline marshes/pools 5.17. Wetlands (inland) – Seasonal/intermittent saline, brackish or alkaline marshes/pools 5.18. Wetlands (inland) – Karst and other subterranean hydrological systems (inland)		
6. Rocky Areas (e.g., inland cliffs, mountain peaks)	Rocky areas	---
7. Caves & Subterranean Habitats (non-aquatic) 7.1. Caves and Subterranean Habitats (non-aquatic) – Caves 7.2. Caves and Subterranean Habitats (non-aquatic) – Other subterranean habitats	Caves and subterranean habitats	---
8. Desert	Desert	Other

8.1. Desert – Hot		
8.2. Desert – Temperate		
8.3. Desert – Cold		
9. Marine Neritic	Marine Neritic	Marine Neritic^{+}
9.1. Marine Neritic – Pelagic		
9.2. Marine Neritic – Subtidal rock and rocky reefs		
9.3. Marine Neritic – Subtidal loose rock/pebble/gravel		
9.4. Marine Neritic – Subtidal sandy		
9.5. Marine Neritic – Subtidal sandy-mud		
9.6. Marine Neritic – Subtidal muddy		
9.7. Marine Neritic – Macroalgal/kelp		
9.8. Marine Neritic – Coral Reef		
9.8.1. Outer reef channel		
9.8.2. Back slope		
9.8.3. Foreslope (outer reef slope)		
9.8.4. Lagoon		
9.8.5. Inter-reef soft substrate		
9.8.6. Inter-reef rubble substrate		
9.9 Seagrass (Submerged)		

9.10 Estuaries		
10 Marine Oceanic	Marine Oceanic	---
10.1 Epipelagic (0–200 m)		
10.2 Mesopelagic (200–1,000 m)		
10.3 Bathypelagic (1,000–4,000 m)		
10.4 Abyssopelagic (4,000–6,000 m)		
11 Marine Deep Ocean Floor (Benthic and Demersal)		
11.1 Continental Slope/Bathyl Zone (200–4,000 m)		
11.1.1 Hard Substrate		
11.1.2 Soft Substrate		
11.2 Abyssal Plain (4,000–6,000 m)		
11.3 Abyssal Mountain/Hills (4,000–6,000 m)		
11.4 Hadal/Deep Sea Trench (>6,000 m)		
11.5 Seamount		
11.6 Deep Sea Vents (Rifts/Seeps)		
12 Marine Intertidal	Marine Intertidal	---
12.1 Rocky Shoreline		
12.2 Sandy Shoreline and/or Beaches, Sand Bars, Spits, etc.		
12.3 Shingle and/or Pebble Shoreline and/or Beaches		

12.4 Mud Shoreline and Intertidal Mud Flats		
12.5 Salt Marshes (Emergent Grasses)		
12.6 Tidepools		
12.7 Mangrove Submerged Roots		
13 Marine Coastal/Supratidal	Marine Coastal	---
13.1 Sea Cliffs and Rocky Offshore Islands		
13.2 Coastal Caves/Karst		
13.3 Coastal Sand Dunes		
13.4 Coastal Brackish/Saline Lagoons/Marine Lakes		
13.5 Coastal Freshwater Lakes		
14 Artificial - Terrestrial	Artificial – terrestrial	---
14.1 Arable Land	Arable land	Agriculture
14.2 Pastureland	Pastureland	
14.3 Plantations	Plantations	
14.4 Rural Gardens	Rural gardens	Urban
14.5 Urban Areas	Urban areas	
14.6 Subtropical/Tropical Heavily Degraded Former Forest	Heavily degraded former forest	---
15 Artificial - Aquatic	Artificial – aquatic	---

15.1 Water Storage Areas [over 8 ha]		
15.2 Ponds [below 8 ha]		
15.3 Aquaculture Ponds		
15.4 Salt Exploitation Sites		
15.5 Excavations (open)		
15.6 Wastewater Treatment Areas		
15.7 Irrigated Land [includes irrigation channels]	Artificial – irrigated land and flooded agricultural land	---
15.8 Seasonally Flooded Agricultural Land		
15.9 Canals and Drainage Channels, Ditches	Artificial – aquatic	---
15.10 Karst and Other Subterranean Hydrological Systems [human-made]		
15.11 Marine Anthropogenic Structures		
15.12 Mariculture Cages		
15.13 Mari/Brackish-culture Ponds		
16 Introduced Vegetation	Introduced vegetation	---
17 Other	Other	---
18 Unknown	Unknown	---

--- denotes that no locations were within this land-use type, so it was not put into a grouping.

[+] Sites in Marine Neritic land-use types were kept in their own grouping, not placed into one of those used in my main analysis.

Table S5.5: The number of sites from the final dataset in each land use under the 2015 ESA CCI land cover map and Jung et al.’s (2020a) terrestrial habitat map for 2015 (using Grouping A). The shaded grey boxes indicate agreement between the two maps (which included 71% of sites in the final dataset).

		ESA CCI land cover map					
		Forest	Grassland	Agriculture	Other	Urban	Wetland
Jung et al.’s (2020a) terrestrial habitat map (Grouping A)	Forest	633	20	40	27	1	0
	Grassland	14	22	22	26	0	1
	Savanna	7	1	9	7	0	0
	Arable land	4	6	100	1	0	0
	Pasturelands	7	6	10	2	1	0
	Plantation	24	4	3	1	0	0
	Shrubland	58	14	20	38	2	0
	Urban	0	3	4	0	6	0
	Rural gardens	0	0	2	0	0	0
	Wetland	1	0	1	0	0	0
	Marine neritic	2	0	1	0	0	0

Section 7: Rate of change in forest

As a sensitivity test, using the same structure of the final model reported in Chapter 5, I ran another model that included average annual rate of change in the percentage of forest (instead of SNH) within a 1 km radius of the population. This model explained less variance in rate of population change compared to the model presented in Chapter 5, but overall patterns in forest and agriculture were similar (figs. S5.12-13). Predictably, there were small differences in rates of population change for those populations starting in grassland when rate of change in forest was included in the model rather than SNH. The results for the three-way interactions that included this variable (starting land-use type × rate of change in forest × starting climatic position, and starting land-use type × rate of change in forest × rate of change in climate) are plotted below (figs. S5.12-13).

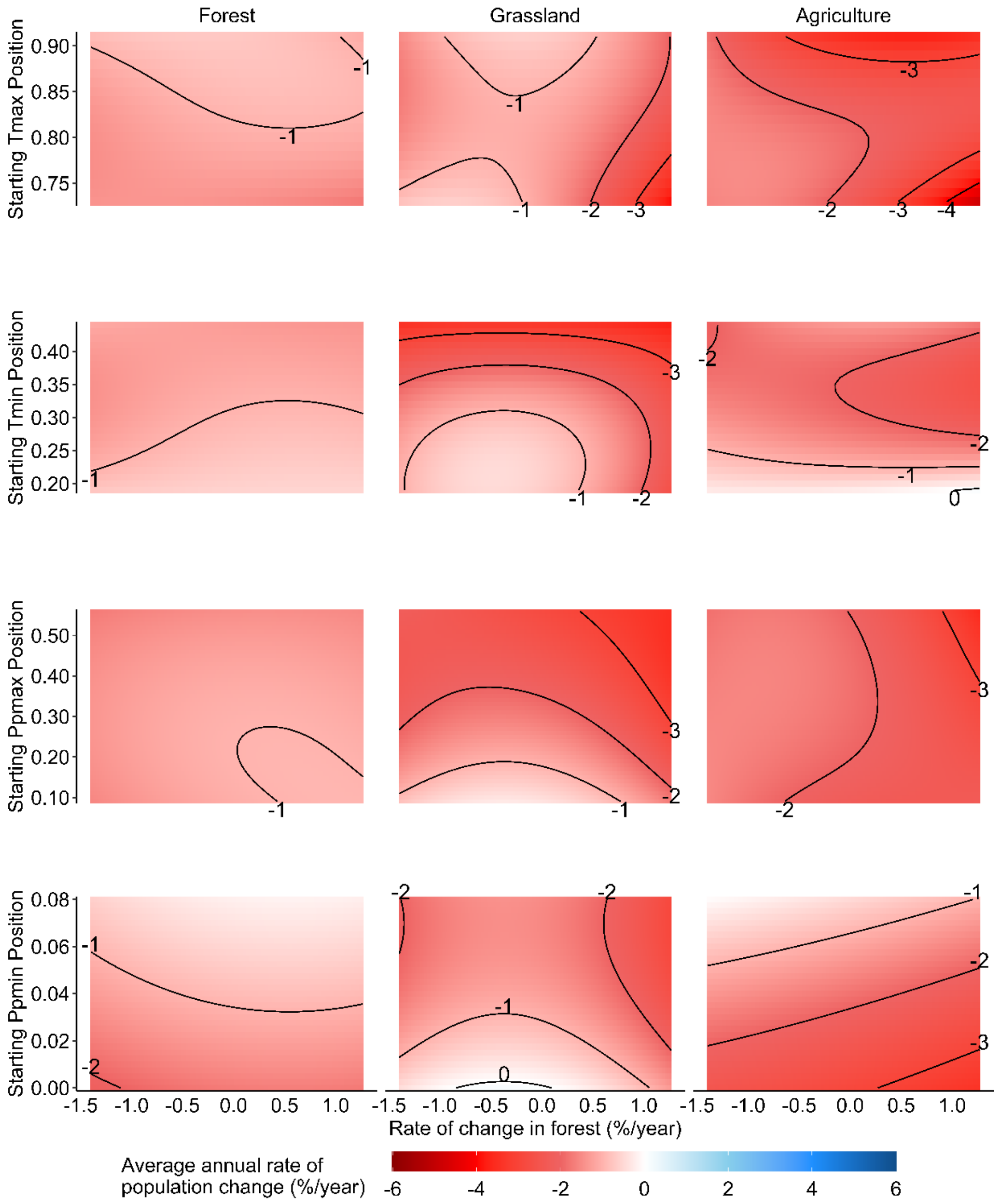

Figure S5.12: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of forest (rather than semi-natural habitat) within a 1 km radius; and (ii) a population's starting climatic position with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

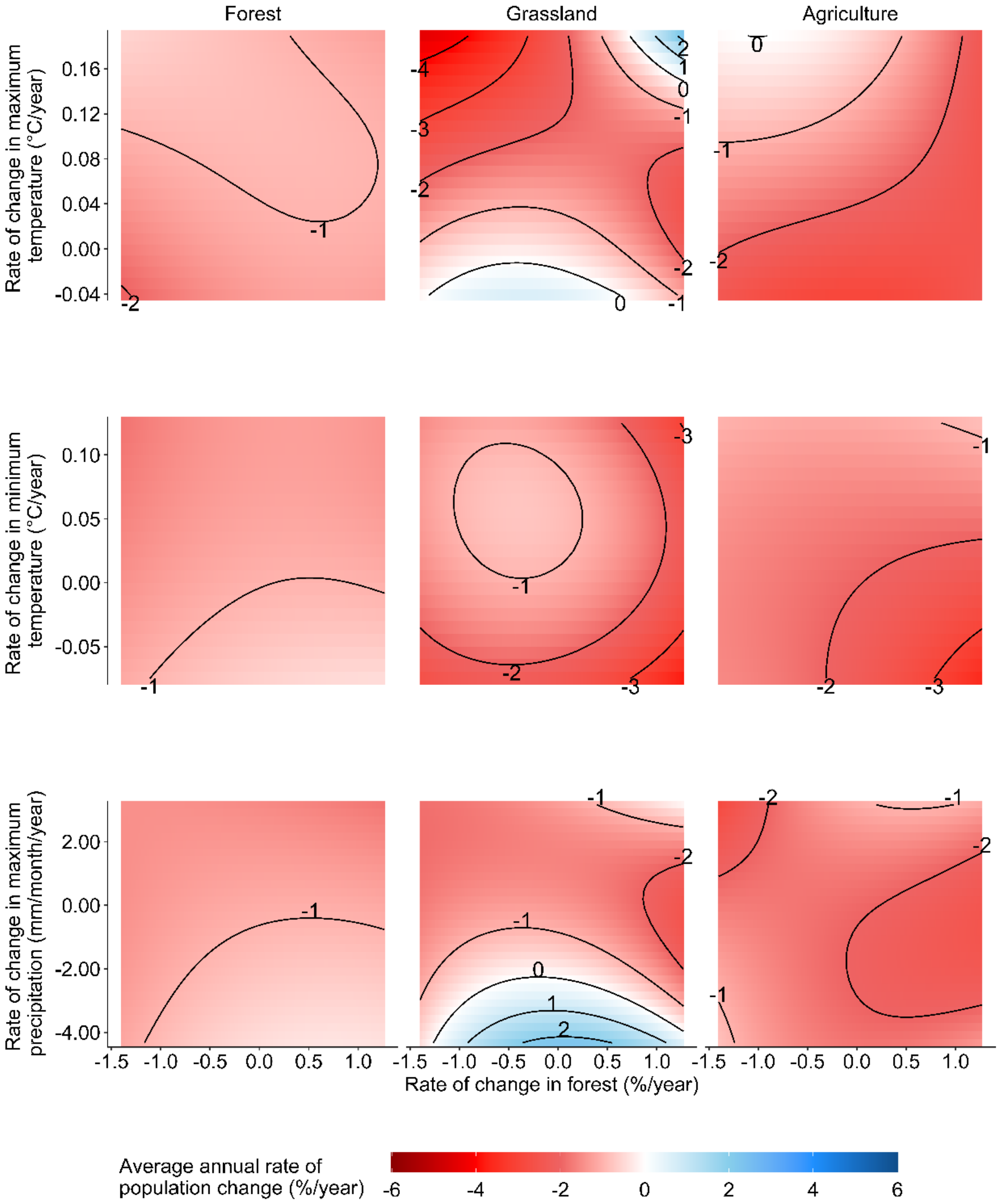

Figure S5.13: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of forest (rather than semi-natural habitat) within a 1 km radius; and (ii) average annual rate of change in climate with regard to maximum temperature of the warmest month (°C/year), minimum temperature of the coldest month (°C/year), and precipitation of the wettest month (monthly mm/year). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change. If comparing this plot to figure 5.5 in Chapter 5, note the differences in scale for the average annual rate of population change.

Section 8: Only including populations whose time-series had $R^2 \geq 0.5$ when fit to the GAM

I ran a model, using the same structure as the model in Chapter 5, but only including populations that had $R^2 \geq 0.5$ when fit to the generalised additive model (GAM), which left 1,639 populations (93 mammal, 1520 bird, 11 amphibian, and 15 reptile populations). In general, even though this model predicted more extreme annual rates of population change (in both the positive and negative direction), the overall patterns were very similar to that highlighted in the main model (figs. S5.14-16). The only slight differences in patterns were found for populations starting within grassland for a couple of the interactions (figs. S5.15-16), which may be due to the smaller number of populations starting in grassland included in this model (n = 201). This model had a higher marginal R^2 than the model reported in Chapter 5, which may have been for a couple of reasons, including: (1) the time-series with greater variation in population measures over time have been removed, and (2) for some populations excluded from this model, larger variation in their population measures may be due to particular events (e.g., policy implementation, poisoning, or wild fires), that cannot be explained well by the variables in my model.

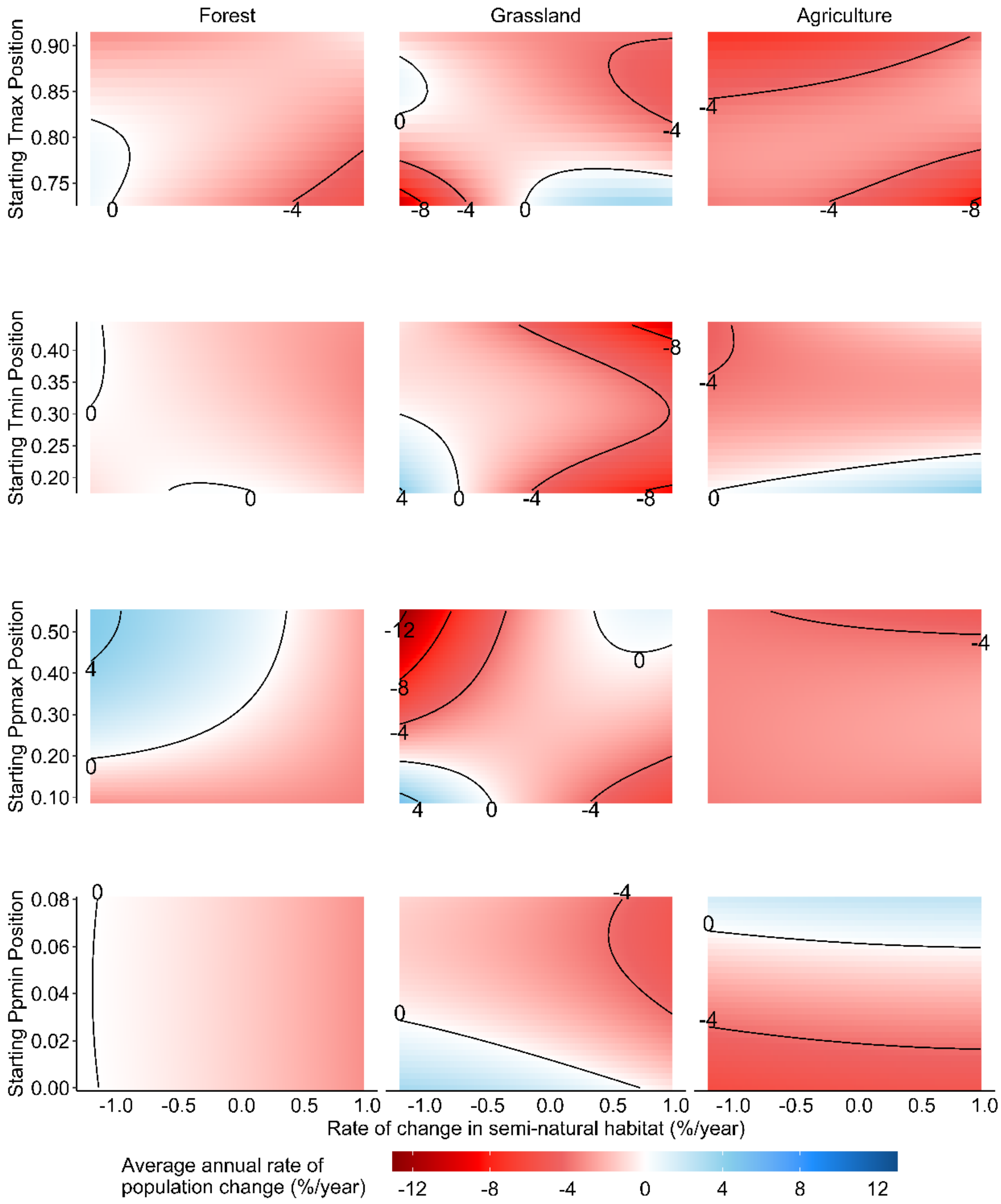

Figure S5.14: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) a population's starting climatic position with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). Only population time-series with $R^2 \geq 0.5$ when fitted to the GAM were included in this model. The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

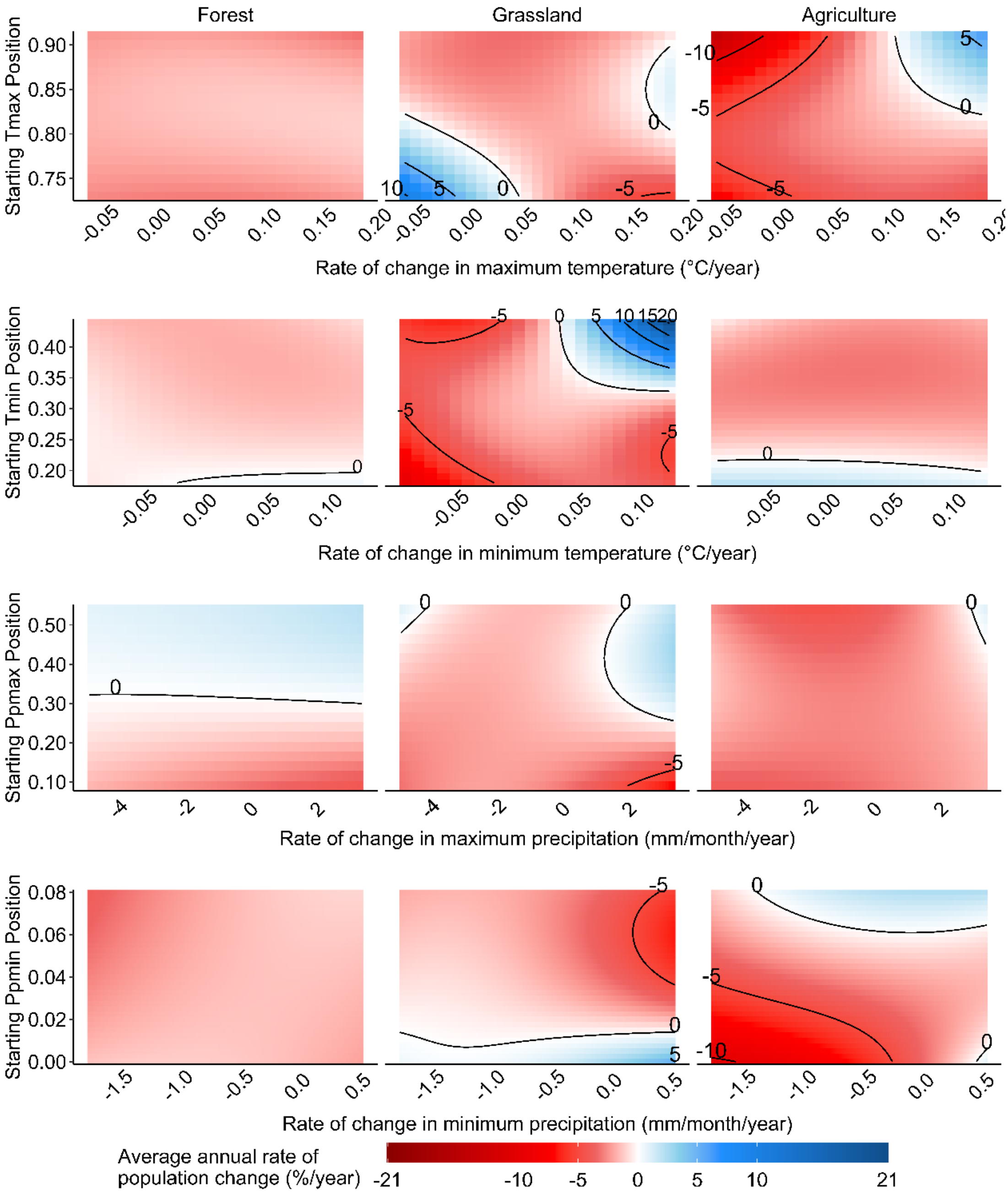

Figure S5.15: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in climate; and (ii) a population's starting climatic position. Climatic variables considered were maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}), and precipitation of the driest month (Pp_{min}). Only population time-series with $R^2 \geq 0.5$ when fitted to the GAM were included in this model. The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

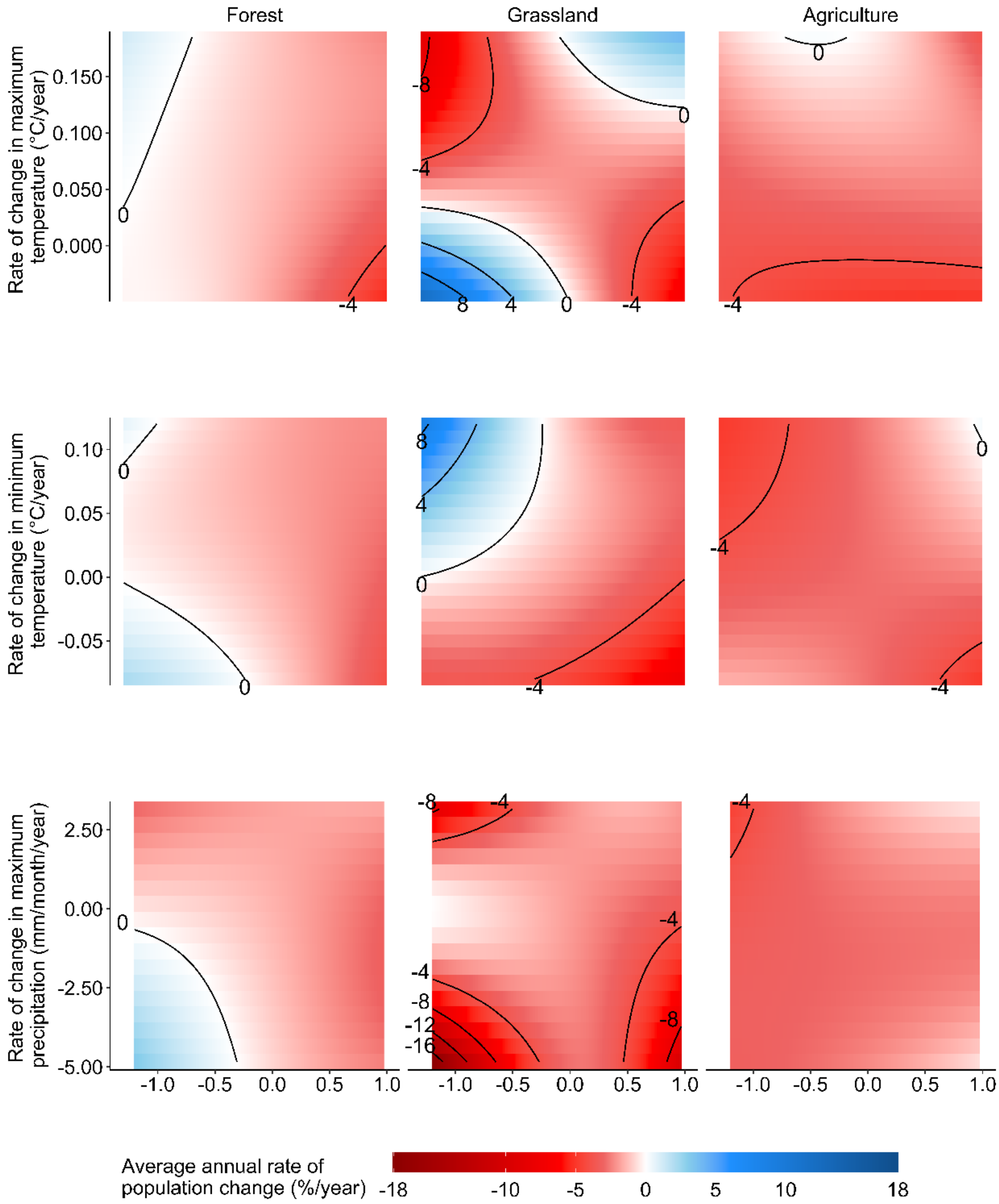

Figure S5.16: The average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) average annual rate of change in climate with regard to maximum temperature of the warmest month (°C/year), minimum temperature of the coldest month (°C/year), and precipitation of the wettest month (monthly mm/year). Only population time-series with $R^2 \geq 0.5$ when fitted to the GAM were included in this model. The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

Section 9: Excluding extreme values

To ensure my results reported were not being influenced by extreme positive or negative rates of population change, I excluded time-series with $\overline{\lambda_{\boldsymbol{Y}}}$ above and below the upper and lower 97.5th and 2.5th percentile, respectively (which removed 358 populations; table S5.6), and ran the model as described in Chapter 5. The results for the three focal three-way interactions are plotted below (figs. S5.17-19).

Table S5.6: Summary statistics for the population time-series analysed when populations with extreme rates of change (above and below the upper and lower 97.5th and 2.5th percentile, respectively) were removed from the final dataset. The table is split by the database the populations originated from (Living Planet database, [Living Planet Index database, January 2020], and the BioTIME database [Dornelas et al., 2018]). The average annual rate of change in semi-natural habitat refers to change within a 1 km radius surrounding each population. Fitted values were based on fixed effects only.

	Living Planet database	BioTIME database
Number of populations analysed	312	6453
Average annual rates of population change (% / year)		
Mean of observed (and fitted) values	-0.71 (-0.11)	-0.06 (-0.42)
Median of observed (and fitted) values	-0.17 (-0.31)	0 (-0.44)
Number of populations with a positive (↑) or negative (↓) values	↑ 137 ↓ 175	↑ 3135 ↓ 3180
Mean length of population time-series (years)	13	15
Number of countries populations originated from	39	4
Average annual rates of change in semi-natural habitat		
Range (% / year)	-4.06 – 3.97	-7.27 – 9.24
Mean (% / year)	-0.05	0.02
Median (% / year)	0	0.03
Number of populations with a positive (↑) or negative (↓) values	↑ 126 ↓ 139	↑ 3731 ↓ 2460
Percentage of populations starting in each starting land-use type (%, to 1 decimal place)		
Forest	62.8	54.5
Grassland	3.8	11.5
Agriculture	16.0	28.2
Other	17.3	5.8

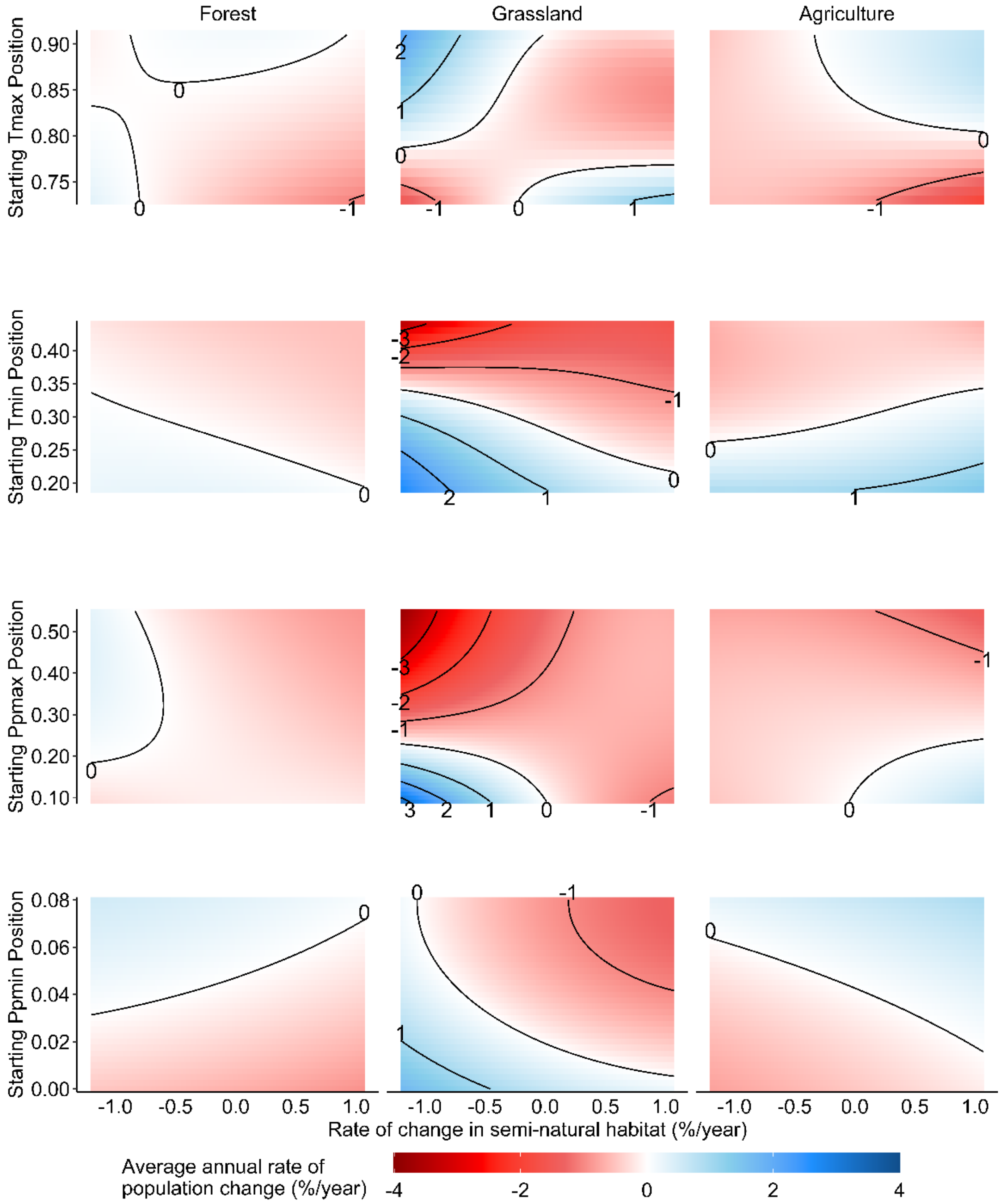

Figure S5.17: After excluding populations with extreme rates of population change (above and below the upper and lower 97.5th and 2.5th percentile, respectively), the average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) a population's starting climatic position with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

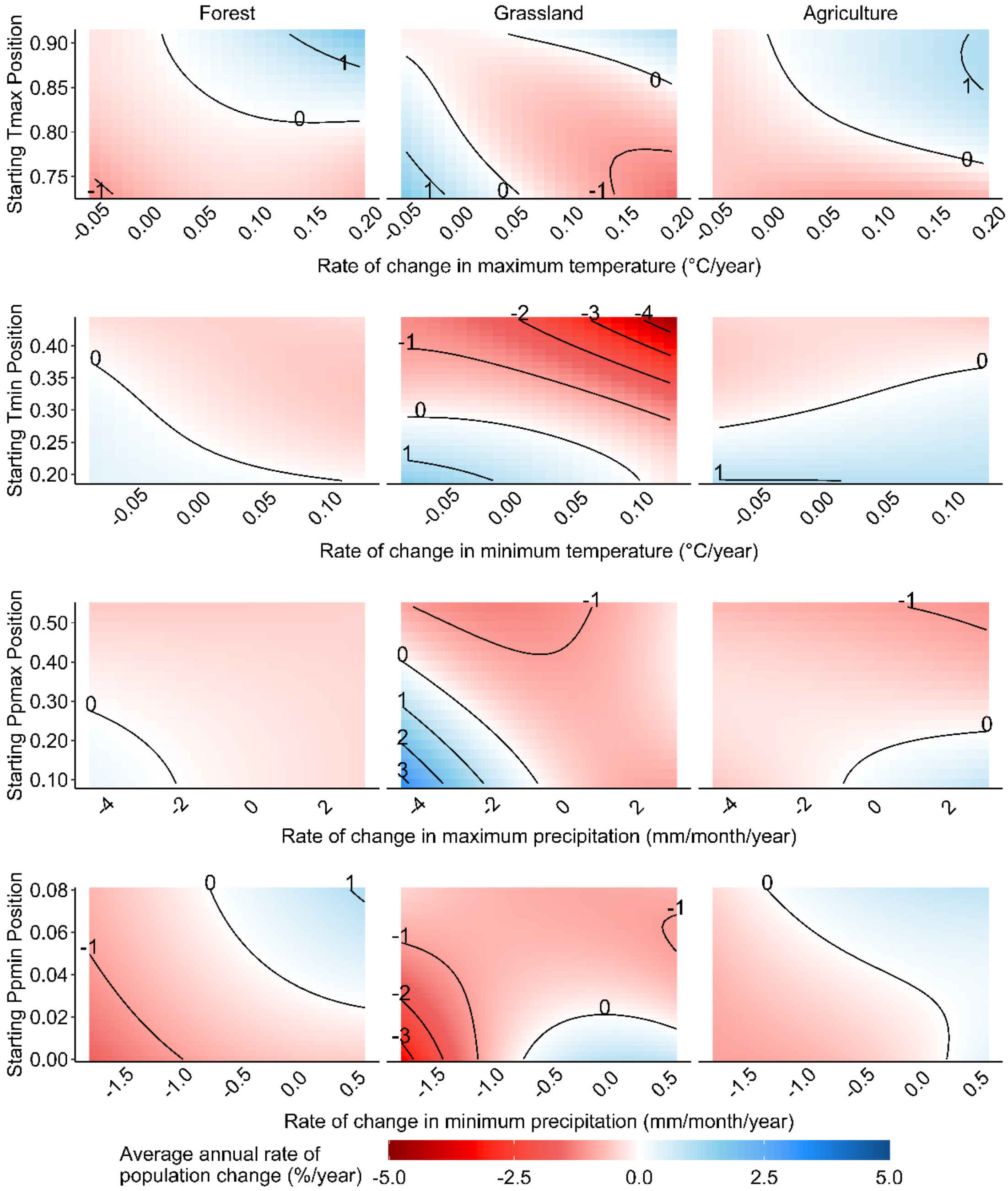

Figure S5.18: After excluding populations with extreme rates of population change (above and below the upper and lower 97.5th and 2.5th percentile, respectively), the average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in climate; and (ii) a population’s starting climatic position. Climatic variables considered were maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}), and precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

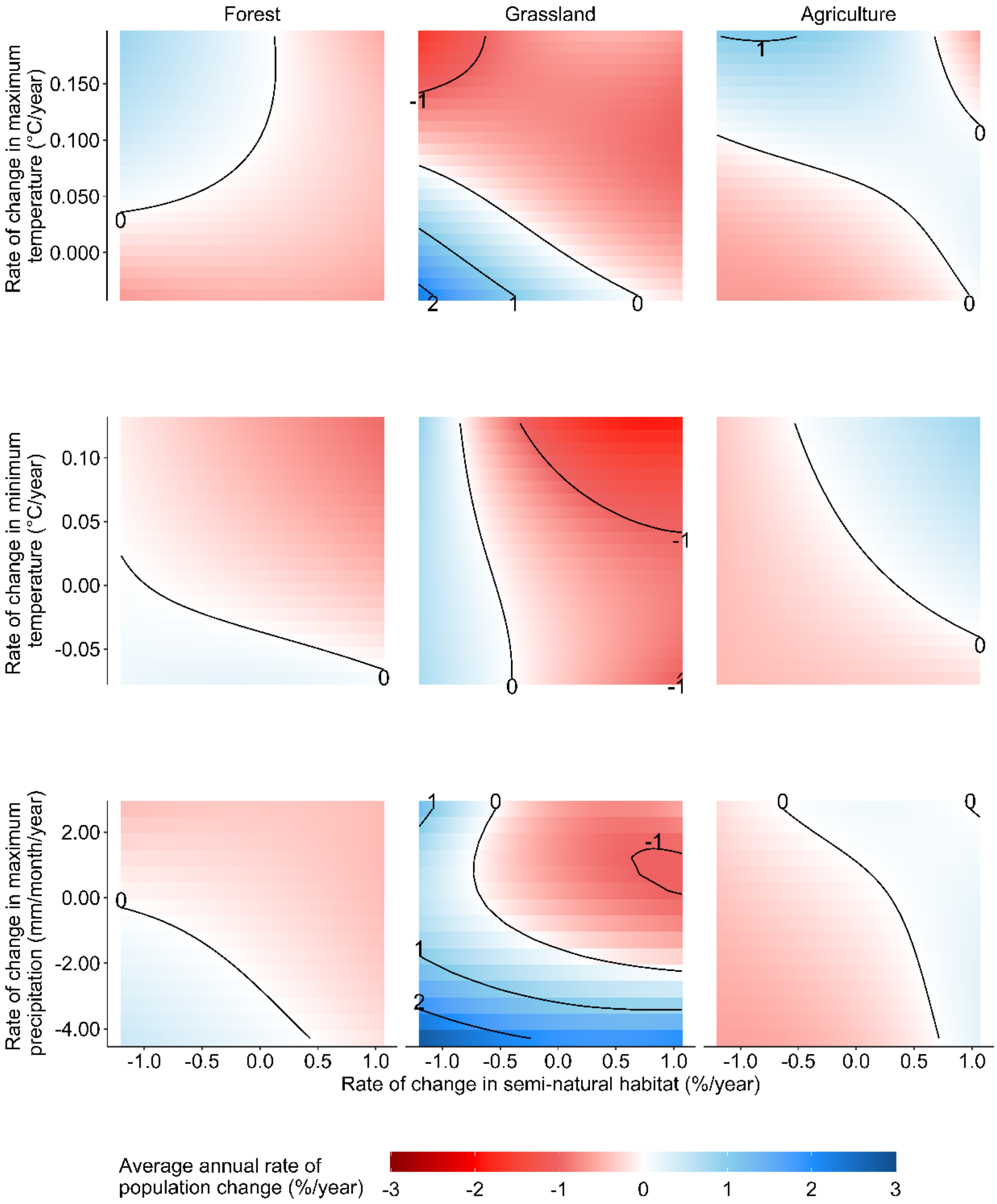

Figure S5.19: After excluding populations with extreme rates of population change (above and below the upper and lower 97.5th and 2.5th percentile, respectively), the average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) average annual rate of change in climate with regard to maximum temperature of the warmest month (°C/year), minimum temperature of the coldest month (°C/year), and precipitation of the wettest month (monthly mm/year). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

Section 10: Excluding *Gyps*

There were three species within the dataset from the genus *Gyps* (a genus of Old World vultures) – *Gyps bengalensis* (11 populations), *G. indicus* (1 population) and *G. tenuirostris* (5 populations). A previous study (Green et al., 2020) found that this genus had a big influence on model estimates, so I removed these species from the dataset, and ran the model described in Chapter 5 again. The results for the three focal three-way interactions are plotted below (figs. S5.20-22).

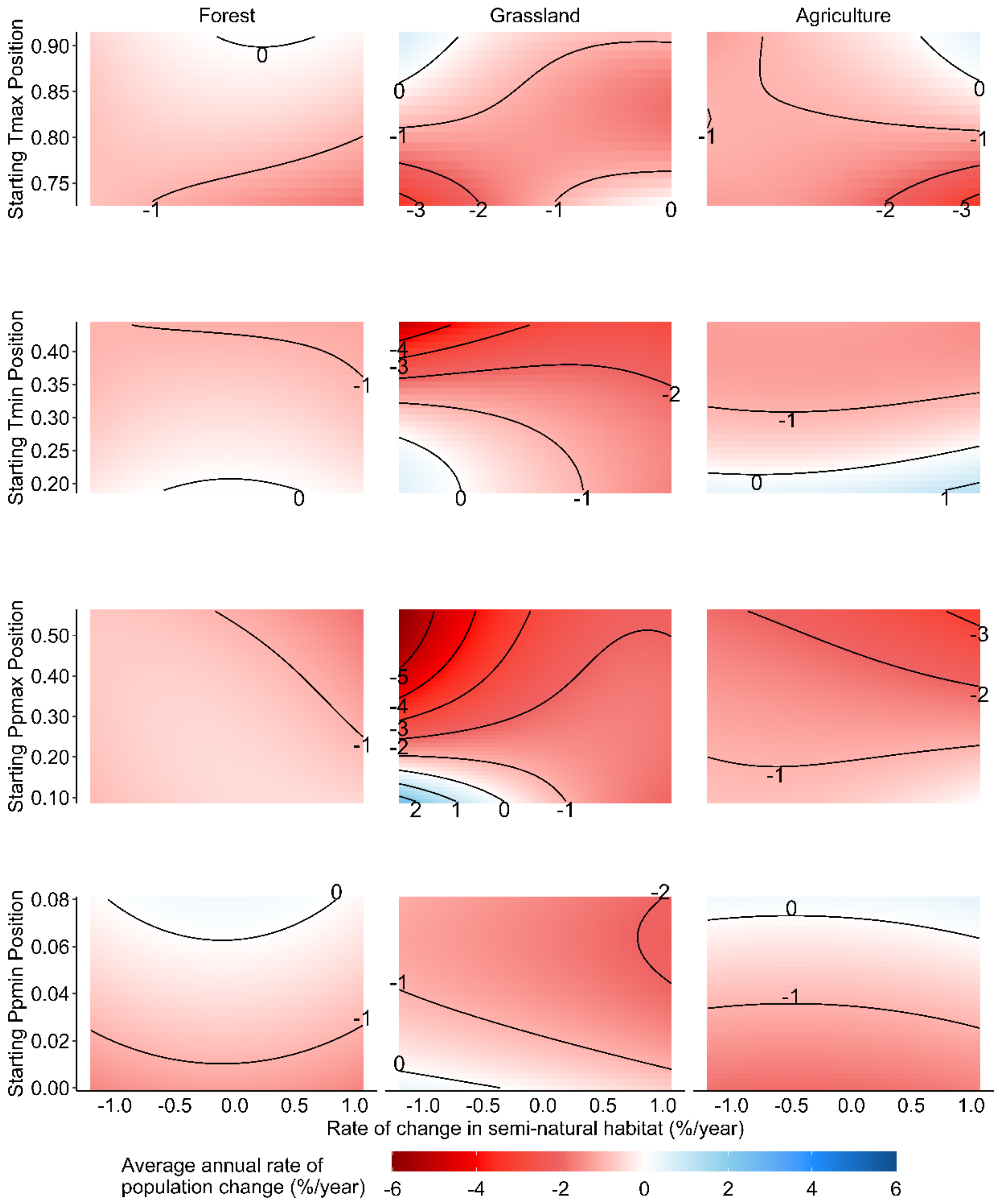

Figure S5.20: Excluding species within the genus *Gyps*, the average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) a population's starting climatic position with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

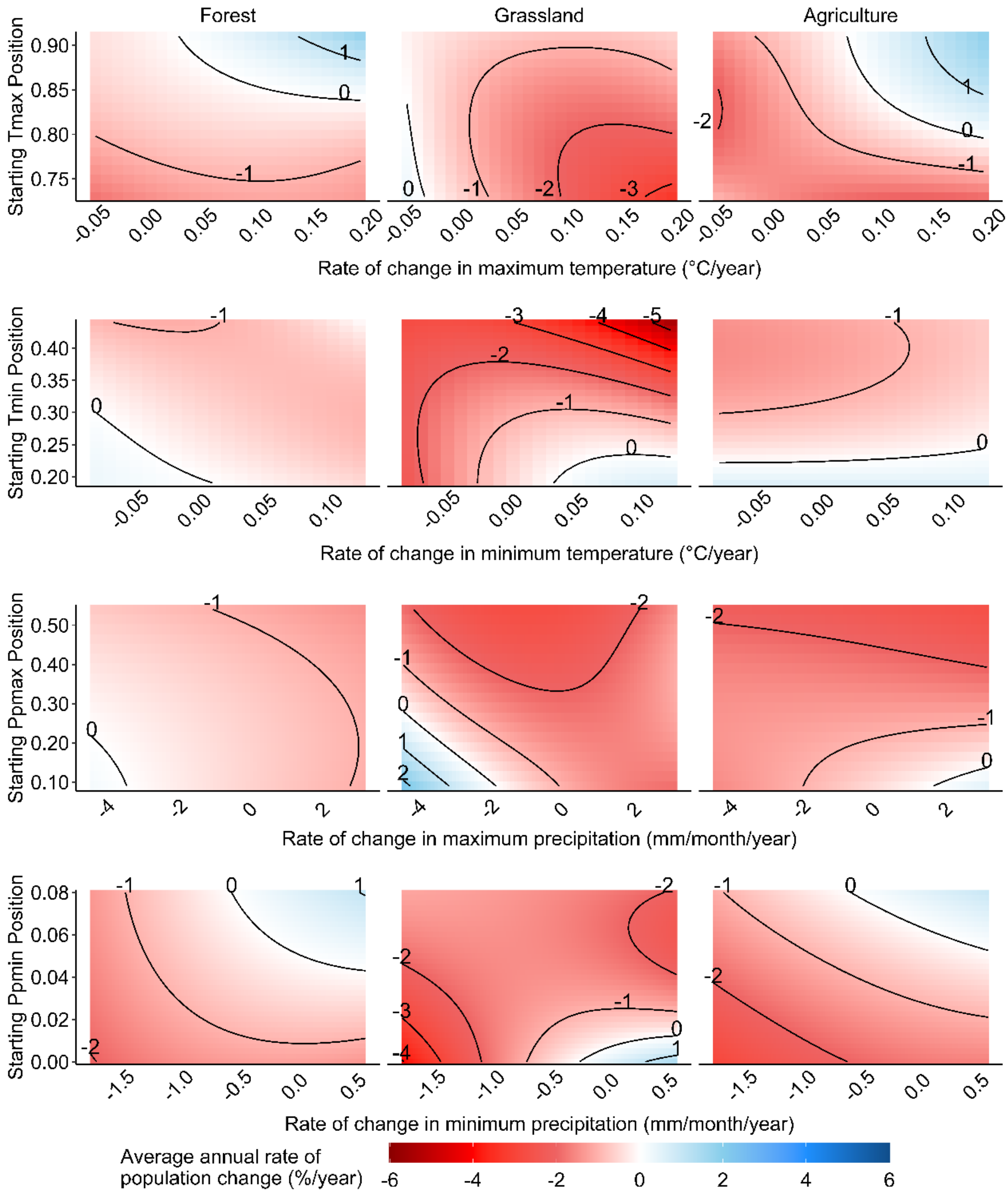

Figure S5.21: Excluding species within the genus *Gyps*, the average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in climate; and (ii) a population's starting climatic position. Climatic variables considered were maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}), and precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

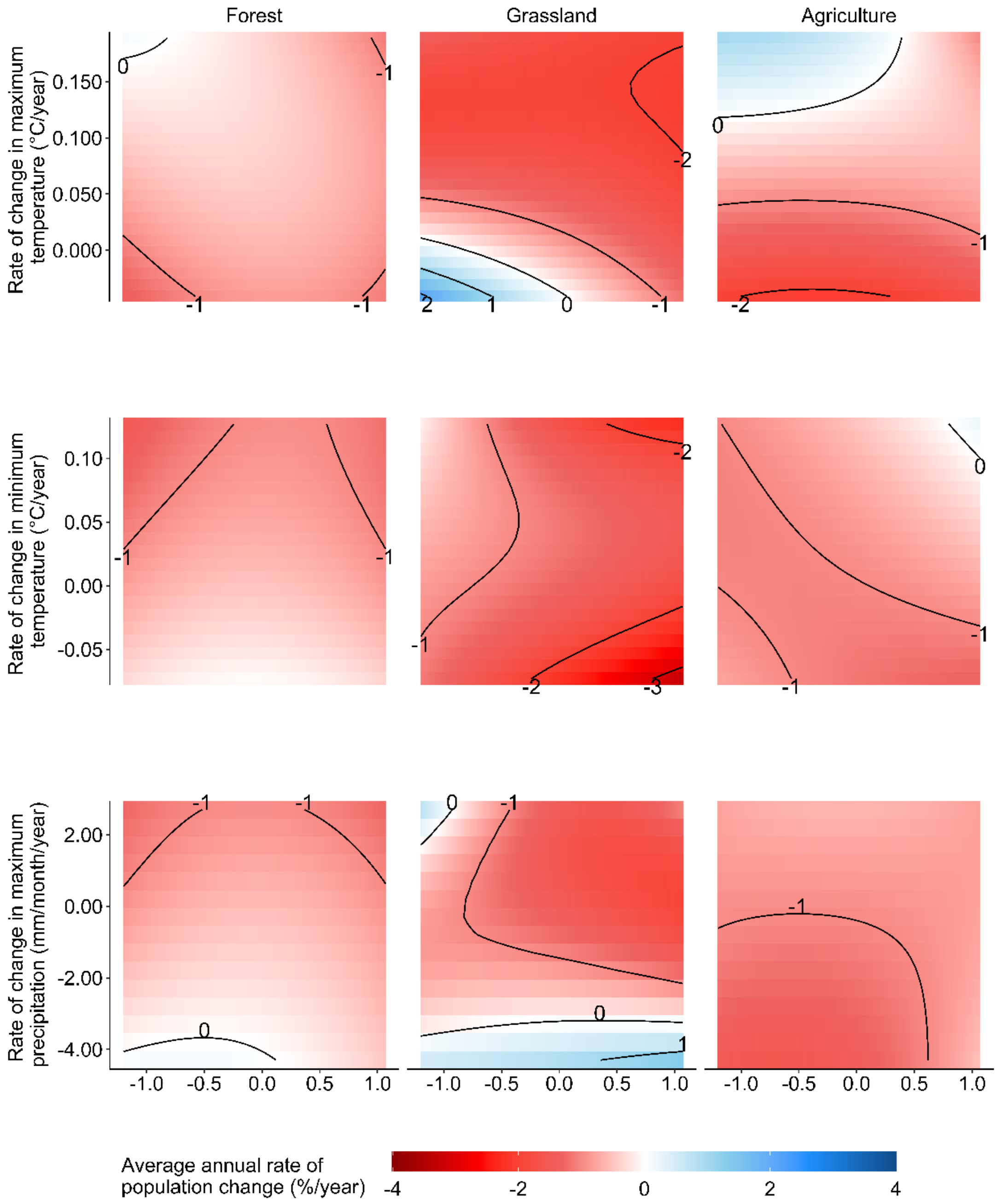

Figure S5.22: Excluding species within the genus *Gyps*, the average annual rate of population change (percentage change per year) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) average annual rate of change in climate with regard to maximum temperature of the warmest month (°C/year), minimum temperature of the coldest month (°C/year), and precipitation of the wettest month (monthly mm/year). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change.

Section 11: Including populations recorded outside of their species' ranges

I ran a model with the same structure as the final model in Chapter 5, this time including the populations that were recorded outside of their species' ranges as stated by the BirdLife International (2012) and IUCN (2016a-b, 2017a-c, 2018a-b, 2019a-c) distribution maps. This was completed to ensure that removing these populations (originally done so that I could include the distance to range edge measure in the model selection process), did not affect my results. The results of the models including populations outside of their reported species' ranges (figs. S5.23-25) were very similar to those presented in Chapter 5.

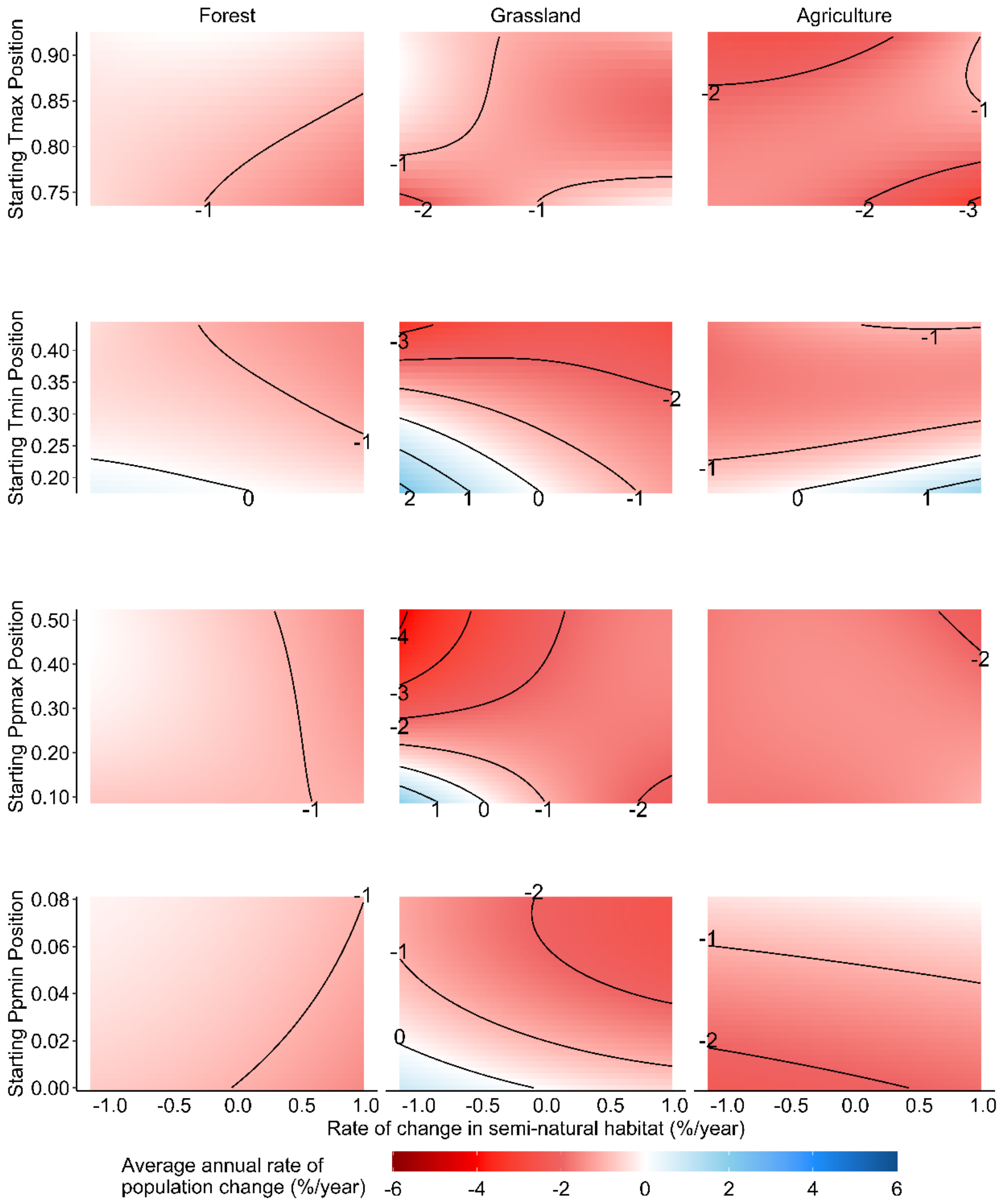

Figure S5.23: The average annual rate of population change (including populations both inside and outside of their reported species' ranges) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) a population's starting climatic position with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}) or precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change (percentage change per year).

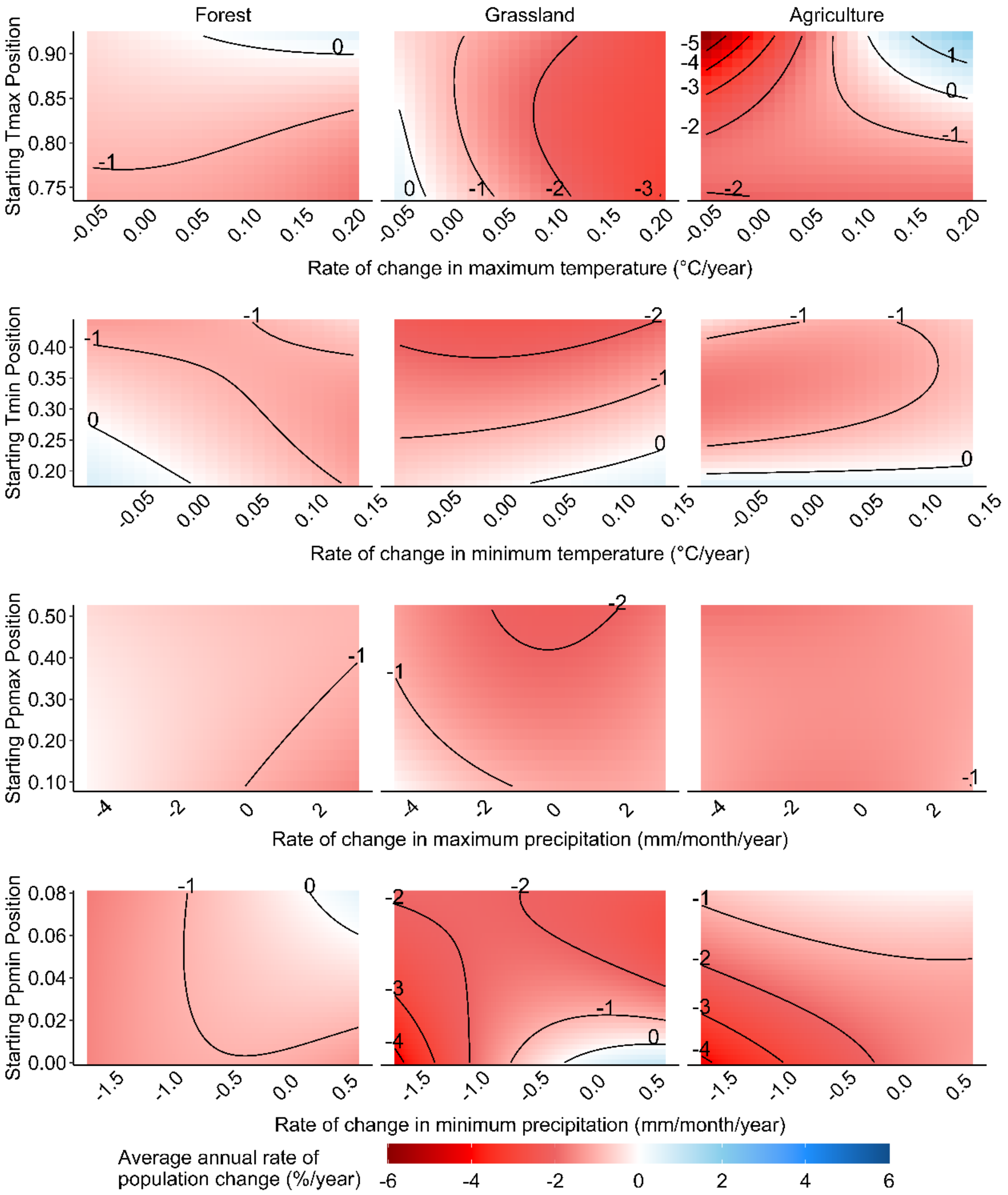

Figure S5.24: The average annual rate of population change (including populations both inside and outside of their reported species' ranges) across different starting land-use types, depending on: (i) the average annual rate of change in climate; and (ii) a population's starting climatic position. Climatic variables considered were maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}), precipitation of the wettest month (Pp_{max}), and precipitation of the driest month (Pp_{min}). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change (percentage change per year).

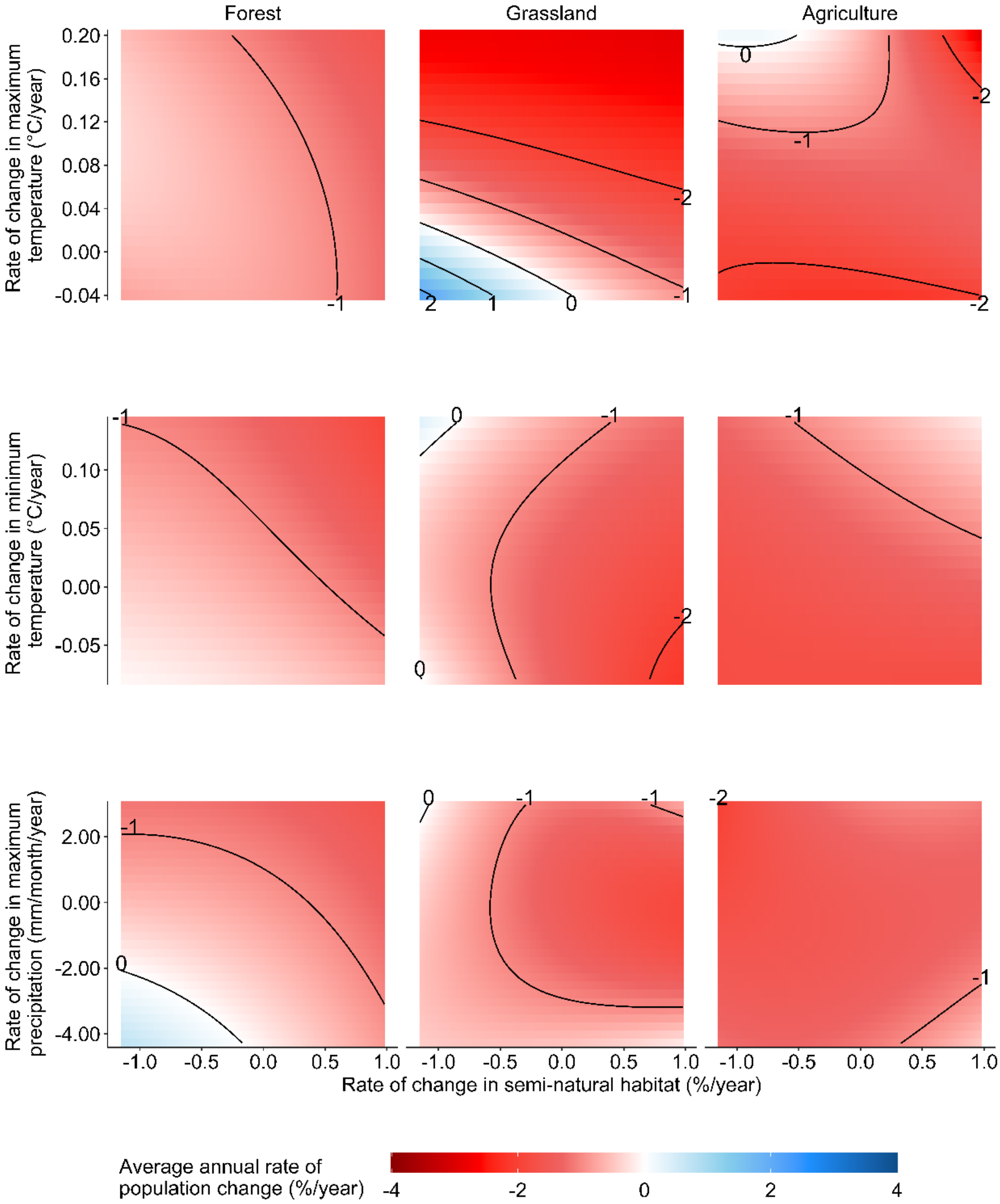

Figure S5.25: The average annual rate of population change (including populations both inside and outside of their reported species' ranges) across different starting land-use types, depending on: (i) the average annual rate of change in the percentage of semi-natural habitat within a 1 km radius; and (ii) average annual rate of change in climate with regard to maximum temperature of the warmest month (°C/year), minimum temperature of the coldest month (°C/year), and precipitation of the wettest month (monthly mm/year). The x- and y-axes are truncated at the 10th and 90th percentile of sampled values of each variable. Contour lines (and labels) indicate changes in average annual rate of population change (percentage change per year).

Section 12: Cross validation tests

I ran leave-one-out cross validation tests of my final model to check there were no overly influential species (figs. S5.26-27) or locations (figs. S5.28-29) within my dataset.

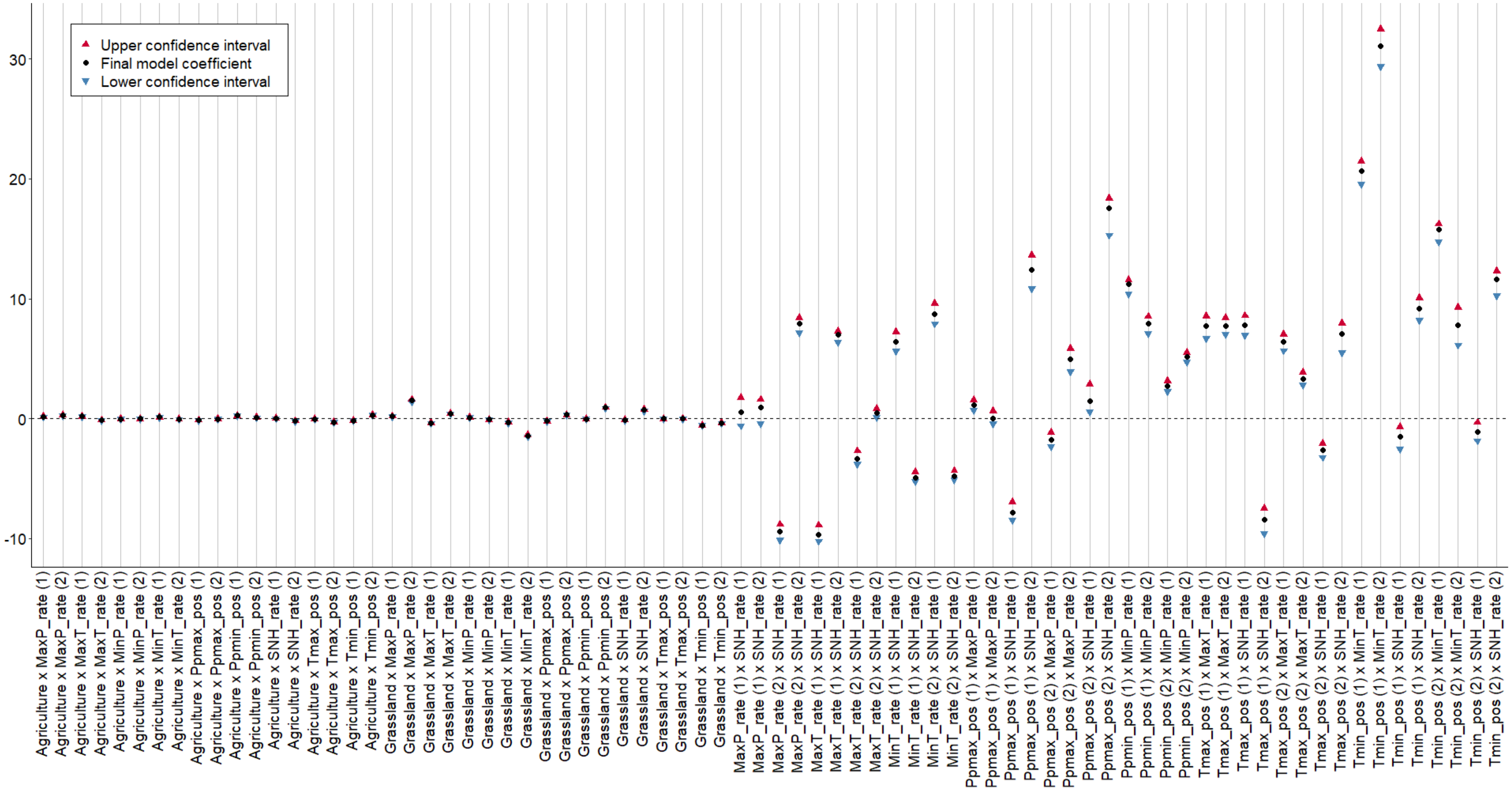

Figure S5.26: The orthogonal polynomial coefficients of the two-way interactions included in the final model and plotted in Chapter 5, along with the 95% confidence intervals around the estimated coefficients when each species in my dataset was removed one at a time and the model

rerun. The final model included starting land-use type (forest [reference level], agriculture, grassland or other), the average annual rate of change in semi-natural habitat (SNH_rate), starting climatic positions with regard to T_{max} (Tmax_pos), T_{min} (Tmin_pos), Pp_{max} (Ppmax_pos) and Pp_{min} (Ppmin_pos), average annual rate of change in climate with regard to maximum temperature of the warmest month (MaxT_rate), minimum temperature of the coldest month (MinT_rate), precipitation of the wettest (MaxP_rate) and driest (MinP_rate) months. The continuous variables in the model were run as second-degree (i.e., quadratic) orthogonal polynomials. Numbers in parentheses refer to the linear (1) or quadratic (2) components of the polynomial terms.

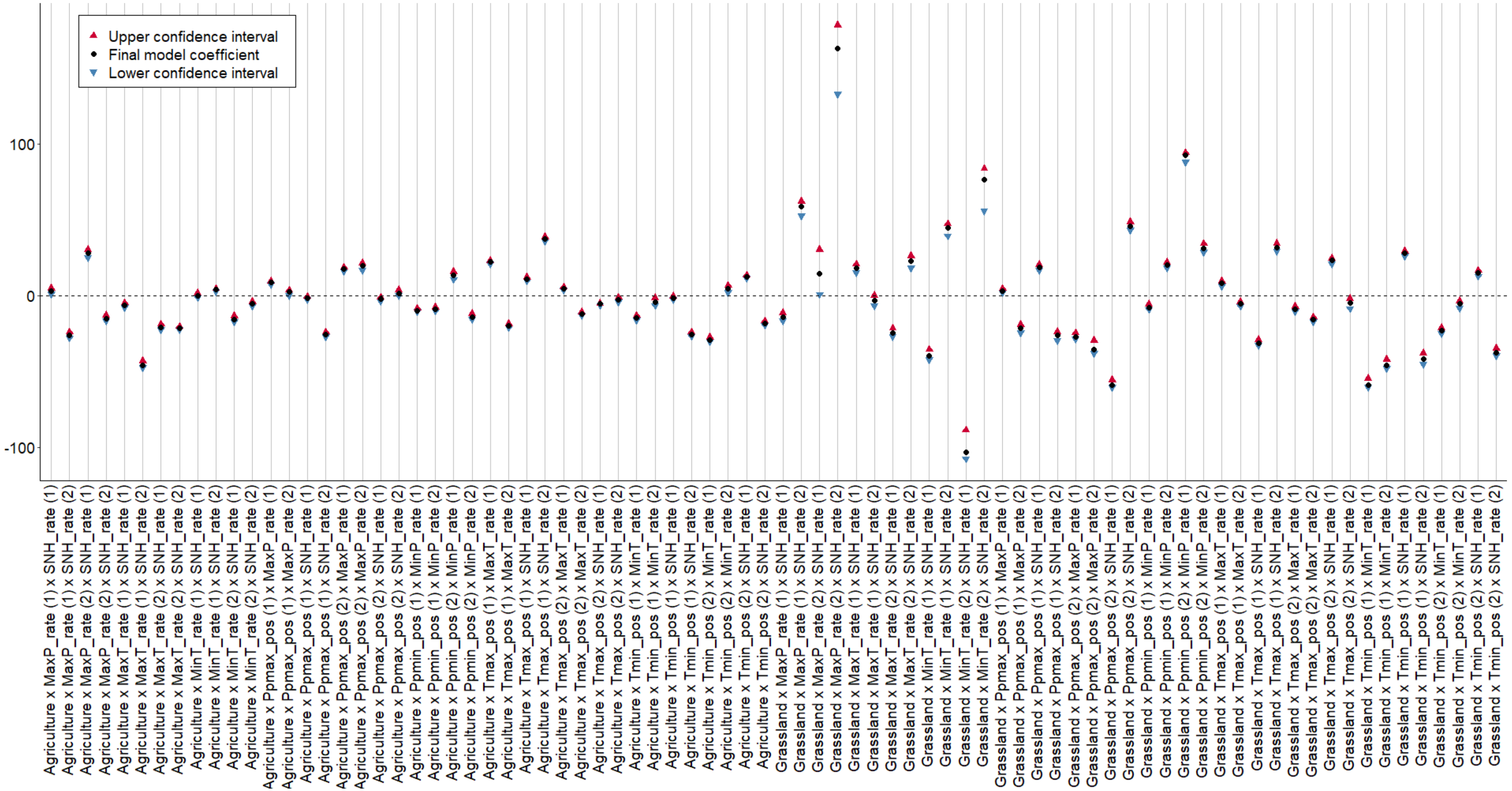

Figure S5.27: The orthogonal polynomial coefficients of the three-way interactions included in the final model and plotted in Chapter 5, along with the 95% confidence intervals around the estimated coefficients when each species in my dataset was removed one at a time and the model

rerun. The final model included starting land-use type (forest [reference level], agriculture, grassland or other), the average annual rate of change in semi-natural habitat (SNH_rate), starting climatic positions with regard to T_{max} (Tmax_pos), T_{min} (Tmin_pos), Pp_{max} (Ppmax_pos) and Pp_{min} (Ppmin_pos), average annual rate of change in climate with regard to maximum temperature of the warmest month (MaxT_rate), minimum temperature of the coldest month (MinT_rate), precipitation of the wettest (MaxP_rate) and driest (MinP_rate) months. The continuous variables in the model were run as second-degree (i.e., quadratic) orthogonal polynomials. Numbers in parentheses refer to the linear (1) or quadratic (2) components of the polynomial terms.

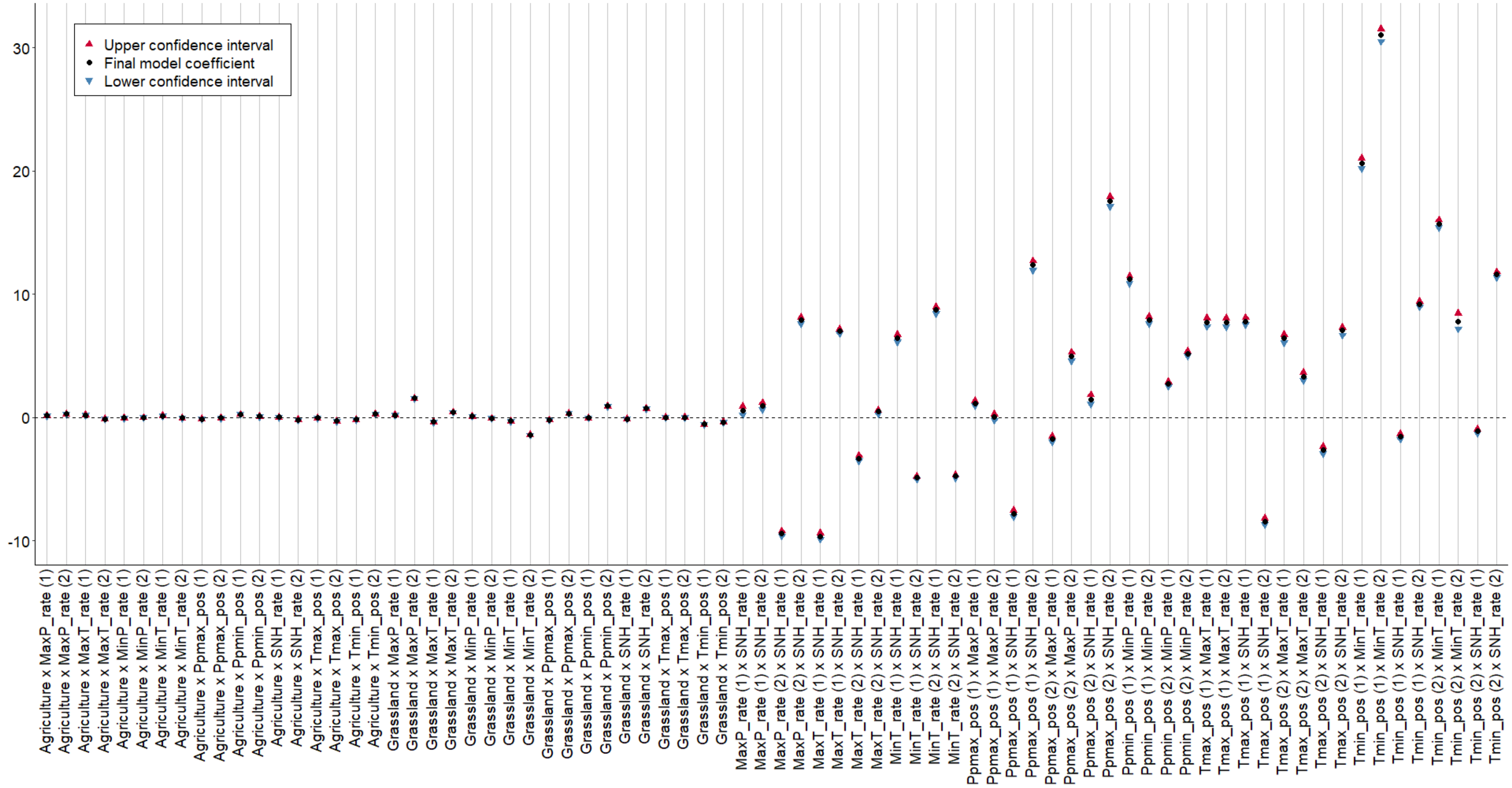

Figure S5.28: The orthogonal polynomial coefficients of the two-way interactions included in the final model and plotted in Chapter 5, along with the 95% confidence intervals around the estimated coefficients when each location in my dataset was removed one at a time and the model rerun.

The final model included starting land-use type (forest [reference level], agriculture, grassland or other), the average annual rate of change in semi-natural habitat (SNH_rate), starting climatic positions with regard to T_{max} (Tmax_pos), T_{min} (Tmin_pos), Pp_{max} (Ppmax_pos) and Pp_{min} (Ppmin_pos), average annual rate of change in climate with regard to maximum temperature of the warmest month (MaxT_rate), minimum temperature of the coldest month (MinT_rate), precipitation of the wettest (MaxP_rate) and driest (MinP_rate) months. The continuous variables in the model were run as second-degree (i.e., quadratic) orthogonal polynomials. Numbers in parentheses refer to the linear (1) or quadratic (2) components of the polynomial terms.

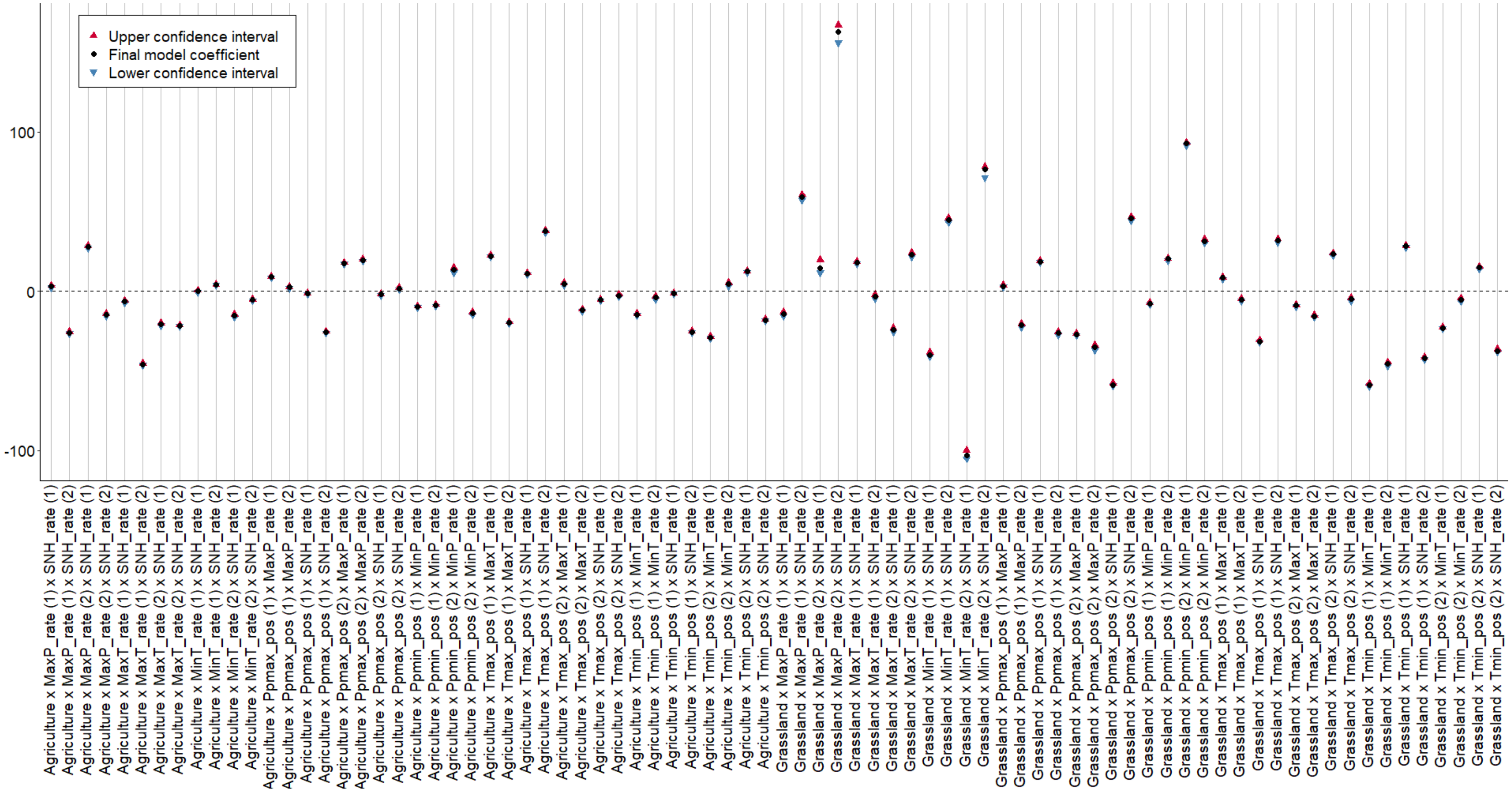

Figure S5.29: The orthogonal polynomial coefficients of the three-way interactions included in the final model and plotted in Chapter 5, along with the 95% confidence intervals around the estimated coefficients when each location in my dataset was removed one at a time and the model

rerun. The final model included starting land-use type (forest [reference level], agriculture, grassland or other), the average annual rate of change in semi-natural habitat (SNH_rate), starting climatic positions with regard to T_{max} (Tmax_pos), T_{min} (Tmin_pos), Pp_{max} (Ppmax_pos) and Pp_{min} (Ppmin_pos), average annual rate of change in climate with regard to maximum temperature of the warmest month (MaxT_rate), minimum temperature of the coldest month (MinT_rate), precipitation of the wettest (MaxP_rate) and driest (MinP_rate) months. The continuous variables in the model were run as second-degree (i.e., quadratic) orthogonal polynomials. Numbers in parentheses refer to the linear (1) or quadratic (2) components of the polynomial terms.

Section 13: BioTIME references

Listed below are the data sources for the data extracted from BioTIME that were included in this study:

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- USFS “Landbird Monitoring Program (UMT-LBMP).” US Forest Service. Available at: http://www.avianknowledge.net/, accessed 2012.
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IUCN (2017a). The IUCN Red List of Threatened Species. Versions 2017-1, 2017-2, 2017-3. http://www.iucnredlist.org

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Appendix 4: Further publications

Below, I provide details of two other published papers on which I am co-author and which I contributed to by using the expertise and knowledge acquired over the course of my PhD. I do not include the typeset versions, as this would infringe the journals' copyright policies.

1) Newbold, T., Adams, G. L., Albaladejo Robles, G. Boakes, E. H., Braga Ferreira, G., Chapman, A. S., … Williams, J. J. (2019). Climate and land-use change homogenise terrestrial biodiversity, with consequences for ecosystem functioning and human well-being. *Emerging Topics in Life Sciences*, *3*(2), 207-219. DOI: 10.1042/ETLS20180135
    - For this publication, I helped design the structure of the review, contributed substantially to the writing of the sections on geographic unevenness in biodiversity changes and interactions between land-use and climate change, and provided feedback on the rest of the manuscript.

2) Newbold, T., Oppenheimer, P., Etard, A., & Williams, J. J. (2020). Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. *Nature Ecology and Evolution, 4*, 1630-1638. DOI: 10.1038/s41559-020-01303-0
    - For this publication, I provided analytical help and substantial input to the writing of the manuscript.