Understanding how terrestrial vertebrate life-history strategies shape responses to climatic seasonality and landscape heterogeneity

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I, Gonzalo Albaladejo Robles, confirm that the work presented in this thesis is my own. If information was derived from other sources, I confirm that this has been indicated and properly referenced in the thesis.

Abstract

Life-history theory posits that species pace of life can be described based on species life-history traits: fast species, which have short lifespans and produce numerous offspring; and slow species, which have long lifespans but fewer offspring. A continuum of life-history strategies can be defined between these two extremes. Theoretically, these life-history strategies will give species competitive advantages under different environmental conditions. Fast species are expected to be favoured in more variable environments, whereas slow species are expected to thrive in more homogeneous or stable habitats. This hypothesis is deeply rooted in ecology and conservation, but it hasn´t been tested at a global scale. Filling this gap can allow us to better understand how species respond to anthropogenic environmental changes. In this thesis, I explore how life-history strategies and environmental factors influence the distributions, community composition, and population trends of terrestrial vertebrate species. In Chapter 3, I found that life-history strategies influence the probability of occurrence of species under different conditions of climatic seasonality and landscape heterogeneity. Extending my focus to whole species communities, I found that communities under human-impacted land uses, and climatically seasonal environments have species spanning a wider range of life-history types (life-history richness) and are dominated by fast species (Chapter 4). In my final experimental chapter, I investigated how populations of species with different life-history strategies change due to land-cover and climate warming. Here I show how fast species have benefited from recent land-cover conversions, while slow-lived species’ populations have declined (Chapter 5). Combined, these results show how species life-history influence key species responses to natural

gradients and environmental change, and which are the implications of these responses to the conservation of biodiversity. Individually, each experiment shows how the study of interactions between biodiversity and environmental conditions can benefit from the inclusion of species traits.

Impact Statement

We are facing a complex and global reaching biodiversity crisis. Humans have impacted the natural processes and systems that regulate the healthy functioning of the planet to the point that the natural services and goods that we, directly and indirectly, benefit from are at risk. As a result, global vertebrate populations have experienced strong declines, to the point that species extinction rates for vertebrate species are 100 times higher than those expected to be observed under natural conditions. Amongst the multiple threats that affect biodiversity now, human-driven land-use changes have been identified the most severe currently. Additionally, climate change is expected to become a predominant, if not the most important, driver of biodiversity loss in the next decades. Furthermore, these two drivers of biodiversity change can interact, creating still-unknown feedback mechanisms, and likely increasing biodiversity loss when compared to their individual effects.

Under these circumstances, and with the certainty that countermeasures are needed to avoid further environmental degradation, calls for major biodiversity conservation and planning policies have been made. Some of these policies, such as reintroduction programs or natural protected areas, have been proved to be effective strategies for attenuating biodiversity loss, at least temporarily. However, long-term planning and conservation measures require a deep understanding of how and why species respond positively or negatively to environmental changes. In this thesis, I explore how species life-history strategies and environmental conditions determine species' likelihood of presence, the composition of species communities and species' population trends.

My thesis findings can help to advance the field of trait-environment interactions, by showing a practical and generalized way to integrate species' life-history strategies into studies of biodiversity responses to environmental change. Furthermore, the results presented in this thesis increase our understanding of the underlying characteristics that determine species' responses to their environment. This, in turn, will aid in the creation of more precise scenarios of biodiversity change, which can help managers and conservationists to plan biodiversity conservation policies.

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to care for others. She’s an important part of who I am today. I know she would have been proud of me, because she always was, no matter what.

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Thesis outline of contents and contributions

Chapter 1

Introduction

In this chapter, I introduce the main concepts regarding the theoretical background of the thesis. Through the different sub-sections of this chapter, I expand on the idea that species' life histories might be used for the study of species' responses to environmental changes, and more precisely those disturbances driven by climate and land-use changes. By the end of this chapter, I introduce the main hypothesis and ideas of the thesis, as well as its overall aims.

Chapter 2

Methods

The methods chapter is aimed to introduce and explain in detail the methodological aspects that are common between the different experimental chapters. Along the different sections of this chapter, I introduce the methods used for the aggregation and correction of life-history traits and the methods I developed to classify species along different life-history gradients. Additionally, this chapter also serves as an expansion on life-history theory, presenting this from a more practical point of view.

Chapter 3

Life-history strategies shape responses of terrestrial amniotes to environmental heterogeneity

In this chapter, I explore if species life-history strategies determine the probability of occurrence of terrestrial vertebrate species (birds, mammals and reptiles) under different conditions of the landscape, land-cover, and climatic heterogeneity. This work was carried out in collaboration with Tim Newbold (TN, hereafter), Monika Bohm (MB hereafter) and Robin Freeman (RF hereafter). This work was conceived by me, with inputs from TN and MB. I designed the experimental framework and carried out the analysis. RF helped me with the earlier versions of the code. I wrote a paper proposal for this chapter (currently under review in Nature Communications) with the inputs of TN and MB.

Chapter 4

Land-use disturbance and temperature seasonality determine life-history diversity and pace of life of terrestrial vertebrate assemblages

In this chapter, I used the knowledge gained in my first chapter and applied it to the study of animal communities. In this case, I studied how land-use intensification, as well as landscape and climatic heterogeneity, shaped community life-history diversity and the overall pace of life. This work was carried out in collaboration with TN and MB. This work was conceived by me with the help of TN. I led the design, analysis, and writing of the chapter with inputs from TN and MB. This also includes a paper proposal submitted to Global Ecology and Biogeography in June 2022.

Chapter 5

Species life-history strategies affect population responses to temperature and land-cover changes

In this chapter, I investigate if the population trends of species with different life-history strategies respond differently to climate and land-use changes. This work was conceived by me with the inputs of TN and MB. As with the other chapters, I designed the experimental approach and wrote the paper proposal (submitted to Global Change Biology in April 2022). TN and MB gave me valuable feedback during this whole process, helping me to improve and polish my writing and analysis.

Chapter 6

Discussion and conclusions

In this chapter, I revisit the results from my experimental chapters and evaluate the key findings of this thesis concerning their contribution to life-history theory, and their implications for future research. I also reflect on the challenges associated with working with global data, the limitations of the experiments presented in this work and the potential of using different datasets and techniques to address these limitations. Additionally, I present new questions and research directions in the field of life-history theory and biodiversity response to change.

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Chapter 1: Introduction

1.1 The human-driven biodiversity crisis

The human species is deeply impacting the planet. For some authors, the effects of human activities on the biosphere and geosphere have marked the transition from the Holocene to a new geological era, the “Anthropocene” (Lewis & Maslin, 2015; Ruddiman, 2013). This transition into the Anthropocene has been marked by a substantial environmental degradation and by an increase in the rate of biodiversity loss, in what some authors define as the “sixth mass extinction” (Ceballos et al., 2015). Despite increased conservation efforts, the latest Living Planet Report (Collen et al., 2009) showed that global monitored vertebrate populations have declined by 68% since 1970 (WWF, 2020). The continuous decline in biodiversity does not just have a negative impact on ecosystems and species communities. Species support ecosystem services that are essential for human development and wellbeing. Services such as water and air purification, temperature regulation, soil maintenance, flood protection, disease regulation, pollination, and even human mental health depend on the good health of natural ecosystems (e.g Bartomeus et al., 2013; Oliver et al., 2015; Silva et al., 2021). Therefore, understanding the drivers causing biodiversity loss and finding mechanisms to predict and attenuate these losses is fundamental for the future of the biosphere and human wellbeing.

Among the numerous impacts that human activities have on natural systems, land-use change has been identified as a major driver of biodiversity change and species extinction while climate change is expected to become one of the predominant drivers of change in the next few decades (Maxwell et al., 2016). An expression of the scope and reach of land-use change and climate change on biodiversity can be found in the data compiled by the International Union for the Conservation of Nature (IUCN) Red List of Threatened species (Figure 1). The IUCN Red List is, to date, the world's most complete source of information on the global extinction risk of animals, plants, and fungus species (Figure 1). The IUCN Red List shows that 63% of the species classified as threatened with extinction (Vulnerable, Endangered, and Critically Endangered under the IUCN Red List categories) are negatively impacted by threats related to land-use change (Table 1 and Figure 1). The proportion of species threatened by climate change, according to the IUCN, is much smaller (about 9%) (Table 1 and Figure 1) (Maxwell et al., 2016). However, this low representation of climate change threats is probably due to the IUCN Red List species assessment process (Trull et al., 2018) and the low frequency at which those assessments are re-evaluated (Keith et al., 2014). Despite this, it is becoming established that climate change is having a profound impact on biodiversity, with some studies showing species distributional shifts, phenology changes and local extinctions (Elmhagen et al., 2015; Parmesan & Yohe, 2003; Sinervo et al., 2010; Stephens et al., 2016). Impacts of climate and land-use change on biodiversity are likely to increase in the near future (Rounsevell et al., 2006; Visconti et al., 2016). At the same time, future projections of human population predict 9-9.7 billion people by 2050 (United Nations, 2019; Tilman et al., 2017). This rise in population will be accompanied by an increase in demand by humans for resources, energy, housing/space, and food, with a resulting increase in pressure on natural systems (Steffen et al., 2015). This will inevitably lead to an increase in humans demands for resources, energy, space and food which, in turn, will lead to human-driven land-use and climate changes (Riahi et al., 2017), with their associated impacts on biodiversity (Newbold, 2018).

Future scenarios of biodiversity change need to consider the effects of land-use and climate change. But evaluating and predicting the impacts of these drivers on species and communities is, at best, challenging. First, threats do not usually appear as isolated phenomena, but rather like a combination of events that affect species' population stability. Some authors refer to these combinations of threats as syndromes or clusters (Bowler et al., 2020; Wraith & Pickering, 2018). Land-use and climate change interact in complex ways through changes in forcing and multiple biophysical and biogeochemical feedbacks across different spatial and temporal scales (Mbow, Reisinger, Canadell, & O'Brien, 2017; Northrup et al., 2019). Second, species response to these drivers are uneven with high variations among species, functional groups, ecosystems, and geographical regions (Newbold et al., 2020; Stephens et al., 2016; Williams et al., 2022). These factors add more uncertainty to the predictions of the effects of land-use and climate change on biodiversity. However, as human pressures on biodiversity and ecosystems increase, predictions of biodiversity change are more important than ever.

Table 1. First order threats and their associated second order associated threats and numerical codes according to the IUCN Red List Version 3.2 (IUCN, 2021). Only first and second order threats related with anthropogenic land-use (**bold blue**) and climate change (**bold green**) are shown (see Figure 1 for their frequency of appearance on the IUCN Red List). The full list of IUCN threats can be seeing in https://www.iucnredlist.org/resources/threat-classification-scheme.

First order threats	Second order threats	code
Residential & commercial development	**Housing & urban areas**	**1.1**
	Commercial & industrial areas	**1.2**
	Tourism & recreation areas	**1.3**
Agriculture & aquaculture	**Annual & perennial non-timber crops**	**2.1**
	Wood & pulp plantations	**2.2**
	Livestock farming & ranching	**2.3**
	Marine & freshwater aquaculture	2.4
Energy production & mining	**Oil & gas drilling**	**3.1**
	Mining & quarrying	**3.2**
	Renewable energy	**3.3**
Transportation & service corridors	**Roads & railroads**	**4.1**
	Utility & service lines	**4.2**
	Shipping lanes	4.3
	Flight paths	4.4
Climate change & severe weather	**Habitat shifting & alteration**	**11.1**
	Droughts	**11.2**
	Temperature extremes	**11.3**
	Storms & flooding	**11.4**
	Other impacts	**11.5**

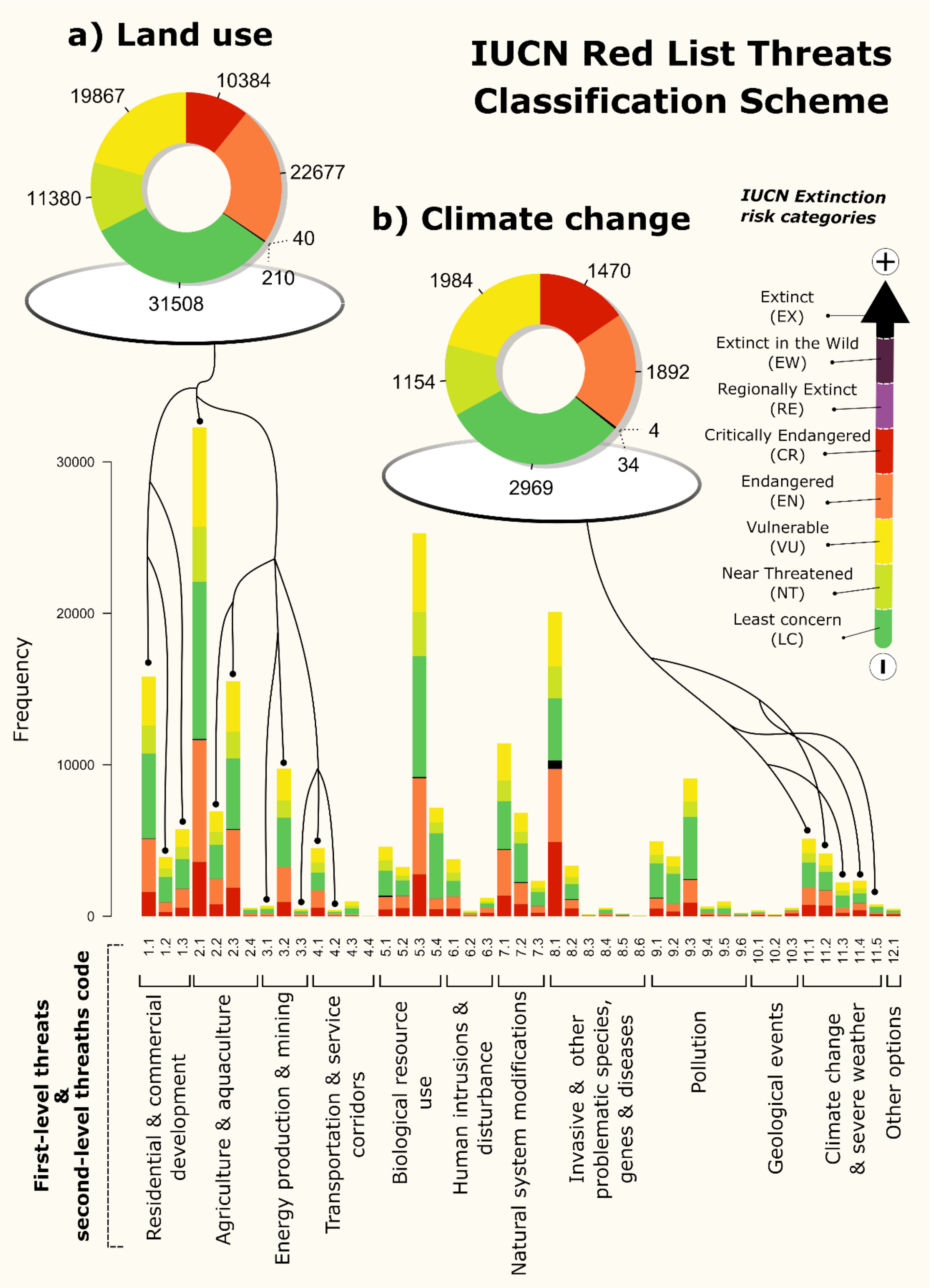

Figure 1. Frequency of appearance of the second-order IUCN Red List threats (Version 3.2, IUCN, 2021) broken down by IUCN species' extinction-risk categories. The second order threats denote subgroups medium to large scale threats for species that can by identified by IUCN Red List assessors. The same species can be affected by multiple threats, therefore the data presented here represent the frequency at which each second order threat appears and not the number of species that are affected by these threats.

1.2 Effects of land-use and climate change

The implications and impacts of land-use change, and climate change are different, and likely to act at different spatial and temporal scales. In order to design and promote effective biodiversity conservation strategies, it is imperative to understand why and how climate and land-use change affect biodiversity.

1.2.1 Land-use effects

Land-use change involves the transformation of natural or semi-natural habitats to human-altered landscapes, usually to optimize a small selection of provisioning ecosystems services for human exploitation, such as food production. Human land-use activities have a direct effect on more than 70% of the global ice-free land surface (Mbow, Reisinger, Canadell, & O'Brien et al., 2019). At a local scale, land-use changes can cause average declines of species richness of up to 24.8%, and up to approximately 40% of total abundance, when comparing human-dominated and non-impacted habitats, depending on land-use intensity and the climatic region in question (Murphy & Romanuk, 2014; Newbold et al., 2015). Not only does land use alter the richness and abundance of species, but it also causes a homogenization of habitat and species communities (Colléony & Shwartz, 2020; Gossner et al., 2016; Vellend et al., 2007). As a result of this taxonomic homogenization, communities become more similar to one another which in turn might cause a reduction of the resiliency of habitats to further environmental changes (Fricke & Svenning, 2020).

Human-dominated land uses are also associated with habitat fragmentation. We can define this fragmentation as the appearance of discontinuities in a habitat due to habitat loss (Fahrig, 2019). In this case, the origin of these discontinuities is not natural (wildfires, floods, or volcanic eruptions) but human-induced (urbanization, agriculture, or farming). A consequence of habitat fragmentation is the isolation and segregation of populations of plant and animals that inhabit the area (Carvajal et al., 2018; Rivera-Ortíz et al., 2015). Connectivity between populations is fundamental to promote dispersal, maintain genetic diversity, and for the realization of key ecosystem services such as seed dispersal (Dener et al., 2021; McConkey et al., 2012). For these reasons, species with low dispersal capabilities, such as small mammals, amphibians or reptiles, are expected to show the strongest responses to habitat fragmentation compared to species with high dispersal abilities such as birds, or large mammals (e.g Carvajal et al., 2018; Niebuhr et al., 2015).

Fragmentation derived from land-use activities not only limits the movement of species across the landscape, but also favours the introduction of alien invasive species (Ficetola et al., 2010; Honnay et al., 2002). The fragmentation of habitats promotes the creation of patches with relatively larger areas of transition from natural to artificial or semi-natural land covers. These transition areas are more permeable to invasive species (Phillips et al., 2005). These invasion episodes not only promote competition between native and invasive species, but also the spread of diseases between native and exotic fauna and flora (IUCN, 2021). This shows that the effects of habitat fragmentation are uneven across animal and plant species. Species' responses to fragmentation, and to land-use change itself, depend greatly on the intrinsic characteristics of species and individuals (e.g Youngquist & Boone, 2014).

1.2.2 Climate change

Climate change can impact organisms directly through changes in temperature and humidity, causing a reduction in individual fitness and survival (Mitchell et al., 2018; Pinsky et al., 2019; Sunday et al., 2014). One of the main effects of those direct impacts on biodiversity are changes in latitudinal and altitudinal species' ranges (Hitch & Leberg, 2007; Melles et al., 2011; Newbold et al., 2019; Parmesan & Yohe, 2003; Walther et al., 2005). The range, or distribution, of most species is marked by the set of climatic conditions in which they can fully develop their life cycles. Previous studies have found that, on average, species have changed their ranges towards the poles at a mean rate of 6.1-16.9 km per decade (Chen et al., 2011; Parmesan & Yohe, 2003). In mountain or high-altitude habitats, species have shifted to higher elevations at an average rate of 11 meters per decade (Chen et al., 2011), with observed changes that reached almost 300 meters for some groups and regions within the last few decades (Wilson et al., 2007). These changes in species natural ranges are likely to have direct consequences not only for the distribution of species, but also for the composition of communities and ecosystems (Hendershot et al., 2020).

Climate change is also causing phenological changes (Bellard et al., 2012). Natural climatic oscillations have been disrupted and, as a result, many biological responses that depend on these cyclic variations have been altered (Qiang Liu et al., 2016; Parmesan & Yohe, 2003). Patterns of bird migration have shifted earlier (Newson et al., 2016; Visser et al., 2009), creating a mismatch between bird communities and food availability with important repercussions for the reproductive outcome of vagrant bird populations (Jenni & Kéry, 2003; Newson et al., 2016; Visser et al., 2009). Similarly, plant growing seasons and leaf phenology have also been affected by climate change (Buitenwerf et al., 2015; Qiang Liu et al., 2016). Phenological changes can create knock-on impacts on other species such as asynchrony of pollinators and flowering (Bartomeus et al., 2013), plant-herbivore asynchrony (Donnelly et al., 2011), and even mismatches between agricultural systems and key environmental services such as water retention, pest control, and pollination (see Donnelly et al., 2011 for a full review of this subject).

Climate and land-use change interact, creating greater uncertainty in outcomes (Newbold et al., 2019). Local land-use changes can cause changes in local climatic conditions, with human-dominated land uses (e.g., croplands, urban areas, farmlands) having hotter and dryer climatic conditions than natural ecosystems (Williams & Newbold, 2020). Land-use changes are also likely to affect regional and global climate, by altering the emission and sequestration of greenhouse gases, and by changes in the reflection of solar energy from the Earth's surface (albedo) (Findell et al., 2017; Zhao et al., 2021). It is also predicted that extreme weather events such as droughts, heatwaves or heavy precipitations events will increase their likelihood, duration, and severity in more human-dominated land (e.g Miralles, Teuling, Van Heerwaarden, & De Arellano, 2014).

The interaction between land-use and climate change may have knock-on effects on biodiversity (Williams and Newbold, 2019). Changes in local climatic conditions (temperature, precipitation or moisture availability) caused by land-use change can have a direct effect on organisms' survival (Deutsch et al., 2008; Mitchell et al., 2018), and fitness (Hovinen et al., 2014; Kamel & Mrosovsky, 2006). Similarly, changes in local climatic conditions can have indirect effects on organisms through changes in vegetation, and the status of other species (e.g abundance or presence of competitors, predators/preys, etc…) (e.g Porter et al., 2000; Post et al., 1999; Schweiger et al., 2012).

1.3 Life-history theory and life-history strategies

Solutions to the biodiversity crisis must arise from a deep understanding of the main sources of biodiversity loss, and their impacts. Generalizable patterns of species' responses to environmental change need to be described to predict and attenuate the future impacts of climate and land-use change on biodiversity (Visconti et al., 2016). A fundamental obstacle when trying to describe global biodiversity patterns is that each species observes the environment on a unique suite of scales of space and time (Levin, 1992; McIntosh, 1991). This is the result of coevolutionary processes between an organism and its environment (Levin, 1992). Understanding how species characteristics, or traits, influence their response to environmental changes can allow us to build more informative and generalized scenarios of biodiversity change. In this context, life-history theory can offer us a good theoretical and practical ground to explore why and how species respond differently to land-use and climate changes.

Life-history theory attempts to use knowledge of how external and intrinsic factors affect the fitness of species, to understand how natural selection shapes organisms to achieve maximum fitness (Daniel et al., 2012; Dobson & Oli, 2008; Stearns, 2000; Zera & Harshman, 2001). Theoretically, and from an evolutionary point of view, traits related with ageing and reproduction (life-history traits) should always evolve to maximize survival and reproduction of species and populations, and thus the overall fitness of individuals (Houle, 2001). However, a series of intrinsic and external boundaries limit the behaviour of these traits, and hence the optimization of the fitness of species and hence the stability of populations. The intrinsic boundaries of species are termed trade-offs (Flatt & Heyland, 2011; Hillesheim & Stearns, 1992), and are intimately related to the allocation of energy and time. All energy or time displacement into growth or reproduction supposes a loss of fitness through one activity or the other.

Life-history traits can also be influenced by the environment (Dobzhansky, 1950; Hillesheim & Stearns, 1992; Salguero-Gómez et al., 2016; Schaffer, 1974). Species adapt their fitness through compromises between development and reproduction investment (intrinsic trade-offs), and the limitations set by the environment (food availability, climate, etc…). The *r*/*K*-selection theory (MacArthur & Wilson, 1967) applies this same principal of environmental filtering and theorizes how species with different life-history strategies fill their environment. From a biogeographical point of view, the theory states that where climates present greater seasonal contrasts or are more unstable, i.e., when seasonality and heterogeneity are high, survivor individuals will need to recolonize and form new populations each season. Under these circumstances, species with the ability to expand their populations rapidly and colonize new habitats will have greater fitness. In these cases, *r-selected* species, with a fast pace of life, will be favoured (MacArthur & Wilson, 1967). At the other extreme of the spectrum, where climates are less severe, and resources are more uniformly distributed among seasons, evolution should favour specialization and a higher efficiency of energy conversion into offspring. In this case, *K*-selected species, with a slow pace of life, will have a fitness advantage over *r*-selected species (MacArthur & Wilson, 1967). Under these hypotheses, the environment acts not only as a driver of change, by filtering species, but also as a major factor affecting species fitness and populations. Even though these ideas are deeply rooted in ecology, direct empirical links between species life histories and environmental changes are not yet clearly described (Stephen C. Stearns, 2000).

With a challenging horizon for biodiversity and conservation biology, new approaches with a solid ecological background are needed. During the following chapters of my thesis, I integrate life-history traits and strategies with different factors describing environmental heterogeneities, human impacts, and environmental changes to explain:

1) How species life histories influence their probability of occurrence under different scenarios of climatic seasonality, landscape heterogeneity, and topographic variation.

2) How life-history diversity and life-history strategies of terrestrial vertebrate species within a community are shaped by land-use impacts, climatic seasonality, and landscape heterogeneity.

3) How populations of terrestrial vertebrate species with different life histories have responded to recent land-cover and climatic changes.

The over-arching objective is to understand the ecological implications of life-history strategies for the distribution, configuration, and response of terrestrial vertebrate communities to environmental changes.

Chapter 2: Methods

During the experimental chapters of this thesis, I will explore in detail how life histories influence species' responses to environmental factors and environmental changes. Even though the questions and approaches of each chapter are different, all of them share some important technical details: the life-history trait data of terrestrial amniotes (birds, mammals and reptiles), and the way in which species are classified as fast or slow. To reduce redundancy between chapters, the general concepts and some technical details behind the life-history data processing and aggregation, as well as the life-history classification schemes used are presented here.

2.1 Species classification

A fundamental aspect of life-history theory is the classification of species, according to their life-history traits into broad life-history strategies. These life-history strategies are defined by the intrinsic trade-offs between species traits related to ageing (e.g., longevity, growth rates and maturity) and fecundity (e.g., litter/clutch size and frequency of reproduction) (Dobson & Oli, 2007, 2008). Depending on these trade-offs, species as well as individuals within a population can be allocated along a continuum from fast species, which display short lifespans and high fecundity, to slow species, with longer lifespans and lower fecundity (Dobson & Oli, 2007, 2008). However, the way in which species are allocated along this continuum can vary according to the underlaying assumptions on how life-history traits behave. This, ultimately, has led to the development of two life-history classification schemes, the body-mass continuum

(Stearns, 1983a; Read & Harvey, 1989) and the fast-slow continuum (Bielby et al., 2007; Dobson & Oli, 2008; Read & Harvey, 1989).

The body-mass continuum, is based on reinterpretations of MacArthur and Wilson's (1967) *r*/*K*-selection theory. According to the body mass continuum, *r*-selected species are going to present life-history traits associated with fast-lived species whereas *K*-selected species are going to present life-history traits associated with slow species (Pianka, 1970). Furthermore, species life-history traits are going to be closely related with the body mass of species (Boyce, 1984; Pianka, 1970; Scharf et al., 2015). Under the body-mass continuum, small species will typically spend less time growing and thus show early sexual maturity, and shorter lifespans (i.e., they tend to be fast species). Conversely, big species will tend to expend more time, and energy, in growing and therefore show late sexual maturity and longer lifespans (i.e., they tend to be slow species). One of the key assumptions of the body-mass continuum is the relationship of this continuum with environmental factors (Table 1). Small, fast-lived species are associated with unpredictable environments, while bigger slow lived species are associated with more stable environments (Table 1).

Table 2. Hypothesized characteristics of species with r and *K*-selected life-history strategies, adapted from Pianka (1970). 1 Type I survivorship curve; Negatively skew, is shown by members of a cohort which, having born at the same time, died at the same time after a lifespan characteristic of the species, for example elephants. 2 Type II survivorship curves; diagonal, individuals show a constant mortality rate for all the age groups, for example some rodent species. 3 Type III survivorship curve; positively skew, shows extremely high mortality during the early stages of development, but the few individuals that survive have a relatively large lifespan, for example sea turtles (Deevey, 1947).

	***r*-Selected species**	***K*-Selected species**
Climate preference	Variable and/or unpredictable	Fairly constant and/or predictable
Mortality	Often catastrophic, density-independent	More directed, density-dependent
Survivorship	Often Type III	Usually Type I and II
Population size	Variable in time, non-equilibrium; usually well below carrying capacity of environment; unsaturated communities or portions thereof; exploitation of empty niches, with frequent recolonization	More constant in time, equilibrium; at or near carrying capacity of the environment; saturated communities; usually no recolonization is necessary
Intra- and interspecific competition	Variable, often weak	Usually, strong
Selection favours	1. Rapid development	1. Slower development, greater competitive ability
	2. High maximum population growth rate	2. Survival and population stability
	3. Early reproduction	3. Delayed reproduction
	4. Small body size	4. Larger body size
	5. Semelparity	5. Iteroparity
Length of life	Shorter	Longer
Leads to	Offspring productivity	Offspring efficiency

Even though many species life-history traits correlate strongly with body mass (e.g de Fuentes-Fernández, Mercedes Suárez-Rancel, & Molina-Borja, 2016; Dunham & Miles, 1985; D. Western, 1979), there are a large number of situations in which the characteristics of the body-mass continuum made it problematic. The body-mass continuum relies heavily on the relationships of life-history traits and body-mass. However, body-mass is a factor that have huge influences on other species traits (Dobson & Oli, 2007; Dunham & Miles, 1985). For example, large species tend to be more dispersive (Stevens et al., 2013; Whitmee & Orme, 2013), and so, all else being equal, are better able to cope with spatial environmental heterogeneity. Therefore, if we use the body-mass continuum to evaluate the effects life-history strategies have on species response to environmental gradients, we ran into the problem that we are not only evaluating the influence of life-histories, but all the other aspects related with species body size (dispersal, metabolic rate, torpor, etc… Bonte et al., 2012; Merckx et al., 2018; Spence & Tingley, 2021 respectively). Thus the “true” effects of life-history strategies may be mask by body-size. Ultimately, this limits the ability of the body-mass continuum to compare the variation of life-histories among species of different taxa (Schaffer, 1974; Stearns, 1977; Stearns, 2000).

The fast-slow continuum is a modification of the body-mass continuum that tries to resolve some of the limitations of the former (Healy et al., 2019; Promislow & Harvey, 1990; Read & Harvey, 1989). The fast-slow continuum is based on the trade-offs between reproduction and survival that can be observed once the effects of body-mass and phylogeny have been controlled for (Dobson & Oli, 2007; Promislow & Harvey, 1990; Read & Harvey, 1989; Stearns, 2000). In other words, the fast-slow continuum shows the trade-offs of life-history traits relative to body size and phylogeny. The fast-slow continuum allows life-history strategies of different species and taxa to be compared without the effects of body size and kinship (e.g Capdevila et al., 2020; Soriano-Redondo et al., 2020)

Classifying species into general life-history strategies may be able to help us to simplify the diversity of response patterns that species display when traits are considered individually (e.g Newbold et al., 2013; Pacifici et al., 2015). This can be especially useful when dealing with multiple traits from a wide range of species in the same analysis. Furthermore, at a large taxonomical and geographical scales, the use of life-history strategies can help to find more simple and comparable patterns of species response to environmental factors (Carvajal et al., 2018; Stearns, 2000).

In this thesis I have used two methods to classify species into different life-history strategies following the theoretical principles of the body-mass and the fast-slow continuum. Both classification methods rely on Principal Component Analysis (PCA) to aggregate species-level life-history traits and describe the major axes of species life-history variation (Dobson & Oli, 2007; Soriano-Redondo et al., 2020). There is not a single life-history axis or a single body-mass or fast-slow continuum. For example, Dobson and Oli (2007), Soriano-Redondo et al., (2020), Cooke et al., (2019), and Salguero-Gómez et al., (2016) each use different combinations of traits to define the fast-slow continuum. Regardless of the combination of traits used, the axis reflecting the fast-slow or body-mass continuum, must reflect the expected trade-offs between ageing and fecundity. These trade-offs are reflected on the loading values of the trait variables on the different PCA axes, with ageing and fecundity variables taking opposite symbol loading values. Usually, these trade-offs tend to be present in the first axis of the PCA, whereas the second and third axis are considered complementary (e.g Salguero-Gómez, Jones, Jongejans, Blomberg, Hodgson, Mbeau-Ache, Zuidema, de Kroon, et al., 2016; Soriano-Redondo et al., 2020). In the case of this thesis, PCA axes were checked by inspecting the direction of loading values of the different life-history traits on each principal component (PC). This way, the PC axes that contained the expected trade-offs between life-history traits were described as the fast/slow or body/mass continuum (depending on the previous treatment of traits, see below).

Even though the body-mass and the fast-slow continuum are both derived from a PCA, the difference between these two continuums relies on the treatment of the selected life-history traits (See data section, below, for more details) prior to analysis. Since the body-mass continuum is based on original trait values and the influence body-mass have on them, the effects of body-mass and phylogeny, which strongly influence body-mass relationships between species, doesn't need to be factor out. Therefore, species life-history traits can be directly combined into a PCA. In this case, the values of the principal component axes describe the life-history variation associated with both body mass, phylogeny, and life-history trait variation (Stearns, 1983).

In the case of the fast-slow continuum, body mass and phylogeny are factors that need to be controlled. The most common approach to control for the effects of phylogeny and body mass is to use linear regression (Dobson & Oli, 2008; Soriano-Redondo et al., 2020; Stearns, 1983). For the purposes of this thesis, I have used linear mixed-effects models (LMMs). LMMs allow relationships between life-history traits and body mass to vary in slope, intercept, or both according to grouping factors (random effects) (Zuur et al., 2009). This in turn allowed me to include species from very different taxa in a single analysis, simplifying the workflow. To remove the effects of body mass and phylogenetic relationships from the selected life-history traits (See data section, below, for more details about the life-history trait selection), I regressed the life-history traits against body mass (as a fixed effect), using Family nested within Order nested within Class as random intercepts. I used taxonomic classification instead of phylogenies because, to date, there is no single or unified phylogenetic tree that contains information for all the species used in the analyses (chapters 3, 4 and 5). Even though large phylogenetic trees can be built using multiple partial phylogenetic trees, for some groups phylogenies are not yet well resolved (e.g Simões & Pyron, 2021), and might vary from study to study in a very short time periods (e.g Barrientos et al., 2021; Upham et al., 2019). Furthermore, for a large sample of species, no phylogenetic information is available yet. Residuals from the mixed-effects models were then used as life-history traits, adjusted for body mass and phylogeny ('adjusted traits' hereafter). Adjusted traits were then subjected to a PCA. The species position along these adjusted axes describes the variation in life-history traits without the effects of body mass and kinship (the fast-slow continuum).

This approach to species classification is repeated in chapters 3, 4 and 5. However, the statistical tools, data, and the life-history continuums used to explore the hypothesis of each experimental chapter varied due to new data availability, updated methods, data selection, and analysis objectives. These changes will be addressed in each chapter, with further details regarding software and statistical approaches.

2.2 Common data used for the analyses

2.2.1 Life-history data

There is not a single body-mass or fast-slow continuum. The classification of species into different life-history strategies relies on the selection of life-history traits and the relationships between them. For the objectives of this thesis, I have selected four traits to describe the life-history strategies of terrestrial vertebrates (birds, mammals, and reptiles): number of offspring per reproductive event (offspring); longevity, in years (longevity); age of female sexual maturity, in years (maturity); and the yearly number of reproductive events (reproduction events). In addition to these traits, I also gather information regarding species body mass, in grams. I selected these traits because: 1) they represent important reproductive characteristics (ageing, fecundity, and frequency of reproduction); 2) the relationships between these variables are likely to reflect the expected trade-offs between ageing and fecundity; and 3) these traits are available in the literature for a wide range of amniote species, which allowed me to compile a large dataset and increase the scope of the analysis.

I was able to collect life-history trait information for more than 20,000 species of terrestrial vertebrates. This dataset is the result of the combination of published and openly available databases of traits from a wide variety of sources. This database is still growing and has been an evolving project since the start of the thesis. Due to this, there are some differences between the datasets used for chapters 3, 4 and 5. These differences are related, mostly, with the number of species from which I have sufficient information at the time of each analysis, and the decision whether to use data imputation to increase the number of species for the analysis (Chapters 4 and 5) or to use only trait estimates as reported in the original databases (Chapter 3). In the case of Chapter 3, the data availability for the analysis was not as good as for Chapters 4 and 5 (Table 3) and therefore the imputation of data to increase the number of species was likely to return higher uncertainties than in Chapters 4 and 5. Furthermore, this first experiment represented the backbone of the thesis, if there was a relationship between species life-histories and environmental gradients it would be more likely to those relationships to be reflected on species communities and populations. For this reason, I was specially concern about possible bias on the life-history trait values. This also explains why the selection of data for the first experiment was stricter, in some ways, than for the rest of experiments. For example, for the first experimental chapter only trait representing average life-history trait values where used, whereas in the following experiments minimum and maximum values where averaged and included as final life-history trait values. Despite this, the data gathering, filtering, correction and aggregation procedures were consistent across the different chapters of this thesis.

I collected life-history-trait estimates from 25 (18 in the case of chapter 3) different databases of mammals, birds, and reptiles (*Table 3*). These studies spanned several decades, and therefore I expected species taxonomy to differ between studies. To resolve these taxonomic differences, I performed a taxonomic name resolution prior to the aggregation of the data (e.g., Etard, Morrill, & Newbold, 2020). The original species names given in the source publication were checked for possible typographic errors using the R package *taxize* Version 0.9.8 (Chamberlain et al., 2013). Checked names were then passed through the online repositories of the Integrated Taxonomic Information System (ITIS, http://www.itis.gov Version 26-July-2021) and the International Union for the Conservation of Nature (IUCN, http://www.iucnredlist.org Version 2021-1), where species synonyms, upward taxonomic classification (up to the level of Class) and currently accepted species names were retrieved. I choose this approach because, to date, there is not a global integrated taxonomic dataset that includes all the information needed (Cooke, Bates, et al., 2019; Etard et al., 2020). I selected two different taxonomic repositories to retrieve taxonomic information for as many species as possible. To be as consistent as possible, and to facilitate the integration of the trait data with other datasets, I prioritized the IUCN taxonomic information over that of ITIS.

This taxonomic revision and synonym resolution was applied to all datasets used in my analyses: species' spatial records, abundance or population data, community composition information, and life-history trait data.

Table 3. Studies and datasets used to collect life-history traits of terrestrial vertebrates. “x” indicates that a particular source contributed estimates of a trait. The column at the right of the table indicates in which chapters the different datasets were used.

Dataset	Body mass (grams)	Nº offspring (count)	Longevity (years)	Sexual maturity (years)	Nº reproductive events (count)	Chapters
Amat, 2008		x			x	4-5
Capellini et al., 2011	x	x				3-4-5
Cassill, 2019		x				3-4-5
Gonçalves et al., 2018	x					4-5
Grimm et al., 2014	x	x		x		3-4-5
Jones et al., 2009	x	x	x	x	x	3-4-5
Lobaina, 2014	x	x		x		3-4-5
Meiri, 2018	x	x				4-5
Myhrvold et al., 2015	x	x	x	x	x	3-4-5
Novosolov et al., 2013		x			x	4-5
Novosolov et al., 2017	x					3-4-5
Pacifici et al., 2013	x		x			3-4-5
Clutton-Brock et al., 1999		x		x		3-4-5
Polović et al., 2013		x			x	4-5
Sherman & Jarvis, 2002		x	x			3-4-5
Sherman et al., 1999		x	x			3-4-5
Schwarz & Meiri, 2017		x			x	3-4-5
Smith et al., 2003	x					3-4-5
Stark et al., 2018	x	x	x			4-5
Trochet et al., 2014	x	x		x		4-5
Scharf et al., 2015	x	x	x	x	x	3-4-5
Verde et al., 2013	x					3-4-5
Wilman et al., 2014	x					3-4-5
Tacutu et al., 2013	x	x	x	x	x	3-4-5
Bird et al., 2020			x	x		4-5

2.2.2 Trait filtering, correction, and aggregation

The trait databases encompass a wide variety of studies with different scopes and objectives. As a result, life-history traits are recorded in different units, under different standards and with different names. Due to this, it was necessary to establish a series of standards about nomenclature and units to collect and combine the traits of interest. To be included in the final trait dataset, I required that the original variables were clearly described (i.e., whether estimates refer to adult/juvenile, male/female individuals or minimum/maximum registered values) to group the data under a common descriptor. If the original data were presented transformed (e.g., log-transformed), the description must contain the specific transformation method used (so that the estimates can be back-transformed). Datasets were discarded if they did not meet these basic criteria.

Raw data were also subjected to a filtering process. To detect outlying values in the different datasets, I produced boxplots for each trait using species order as the grouping factor. Outliers from these exploratory analyses can reflect natural variability in the life-history traits or erroneous values. If the number of outliers was low, I checked values individually using scientific literature, field guides and expert knowledge. When the number of outliers was high (greater than 100), a random sample of 10% was retrieved and checked. If more than 20% of the selected observations were found to be erroneous, the whole dataset was discarded. I acknowledge that despite these efforts it is possible that erroneous estimates were included in the final dataset. Ideally data would have been checked individually, but for many species no independent estimates of the life-history traits of interest were available for comparison. In addition, the very large number of data (multiple traits from multiple datasets for more than 20,000 unique species) made a check of individual trait estimates impractical. Despite this, for most of the species used in the analysis, their final life-history traits are the combination of averaging traits from multiple datasets which are check individually for errors before. In turn, this makes the subset of species used for the final analysis less likely to contain erroneous trait information.

Once the taxonomy of the species was resolved, trait estimates transformed to the same units, and raw values checked for errors, the datasets were combined. I found life-history-trait and taxonomic information for 10,442 birds, 5,313 mammals and 5,371 reptiles. From this collection of species, 87% were present in multiple datasets, with multiple measurements for the same or different life-history traits. Therefore, trait information needed to be aggregated and unified. When multiple values, or minimum and maximum values, of the same life-history trait were available for the same species (either in the same or different datasets), (e.g., multiple records of longevity, etc…), values were log-transformed, the arithmetic mean was calculated, and back-transformed, prior to incorporation in the final trait dataset. After data aggregation, I had complete life-history-trait data for 3,347 (2,061 species in the case of the chapter 3) species (15% of the total number of species registered in the unified life-history-trait database): 1,431 mammals, 1,146 birds, and 770 reptiles. For the remaining 85% of species, I had estimates for at least 1 of the 5 life-history traits and therefore trait imputation was needed to include some of them in the analysis (e.g Chapter 4).

Chapter 3: Life-history strategies shape responses of terrestrial amniotes to environmental heterogeneity

3.1 Abstract

Life-history theories posit that fast-lived species will be favoured by environmental heterogeneity, whereas slow-lived species will thrive in more homogeneous habitats. This hypothesis is deeply rooted in ecology and conservation but has not been empirically tested at a global scale for terrestrial amniotes. Here, I perform a global cross-taxon study, analysing the influence of life-history strategies on the responses of 980 species of terrestrial amniotes (birds, mammals and reptiles) to environmental heterogeneity due to land-cover, climate seasonality, and topography. I find that species responses to environmental heterogeneity vary according to their sizes and life-history strategies: as expected, larger slow-lived species, and fast-lived species relative to their body size and phylogeny, were more likely to occur in heterogeneous and fragmented habitats. In contrast, smaller fast-lived species, and slower-lived species relative to their body size and phylogeny, were more likely to be present in homogeneous, less fragmented, and more climatically stable habitats. In the current context of accelerated environmental degradation, these results can be used to assess extinction risk of species with poor data coverage, and to forecast the response of biodiversity to future environmental changes. The observed patterns suggest a substantial reconfiguration of communities under future scenarios of climate and land-use changes.

3.2 Introduction

One major obstacle to understanding species' responses to environmental change is that species respond differently to the same drivers. Previous studies have shown that species traits are important determinants of species' sensitivity and response to land-use/land-cover differences (Börschig et al., 2013; Davies et al., 2009; De Palma et al., 2015; Newbold et al., 2013) and climate change (Pacifici et al., 2017). Trait-based approaches may therefore allow to understand differences in species' responses to environmental change, and to predict the responses of the many species for which empirical data is still rare, under the assumption that species that share traits are likely to respond similarly to environmental changes (Pigot et al., 2020).

Traits that shape species life-history strategy, such as fecundity and ageing, are fundamental to understanding species responses to change (Salguero-Gómez et al., 2016). These life-history traits can be grouped into life-history strategies to define how species grow, mature, and reproduce (Healy et al., 2019). Two basic life-history archetypes can be discerned: slow and fast. Slow species exhibit later sexual maturity and longer lifespans whereas, fast species tend to show early sexual maturity and short lifespans. Body size has a strong effect over other life-history traits (Hillesheim & Stearns, 1992; Sæther, 1987; Stearns, 1983), such that large species invest more time and energy into growing and due to this tend to have slow life histories. Contrary, small species require less time and energy to reach their maturity and therefore tend to exhibit fast life histories.

The concomitant change in life-history strategy and body mass is also termed the body-mass continuum (Pianka, 1970), under which small species tend to be closer to the fast end of the continuum and big species nearer the slow end

(Pianka, 1970). According to Pianka (1970), small and fast species will be more effective competitors in variable environments whereas big and slow species require more stable habitats to maintain their populations effectively. However, attempts to use the body-mass continuum to understand species' responses to environmental change may be complicated by conflicting effects of body size and life-history traits. For example, bigger vertebrate species are usually able to disperse over larger distances than small species (Sutherland et al., 2000) and are also more resilient to resource shortages (Lindstedt & Boyce, 1985), potentially allowing them to cope with environmental variation more easily than smaller species. Some of these problems can be solved by removing the effects of body mass and phylogeny from the classification of life-history strategies (Boyce, 1984; Promislow & Harvey, 1990; Read & Harvey, 1989). This way, species are classified as fast or slow relative to their body mass and phylogeny, along the so-called "fast-slow" continuum (Bielby et al., 2007; Read & Harvey, 1989; Stearns, 1983, 2000).

Environmental conditions may benefit certain life-history strategies by favouring or filtering out species with certain combinations of traits (Lebrija-Trejos et al., 2010; MacArthur & Wilson, 1967; Wiescher et al., 2012). Slow species transform and store energy more efficiently than fast species and, therefore, can compete in energy-limited or constant environments (Dobzhansky, 1950). On the other hand, fast species are more suited to exploit energy blooms, transforming energy quickly into reproduction at the cost of lower efficiency (Kooijman, 2013). Dobzhansky, (1950) hypothesised a latitudinal gradient, with slow species dominating in the more stable environments of the tropics, and fast species in the more energy-seasonal temperate environments. However, since Dobzhansky hypothesis were based on energy consumption and transformation into reproductive effort, the data required to run an empirical experiment does not exist yet and therefore these theories remain untested.

Extrinsic factors play a fundamental role in shaping species life-histories (Grether et al., 2001; Salguero-Gómez et al., 2016). For example, climatic seasonality is a strong determinant of primary productivity, which can both limit and favour the fitness of species with different life-history strategies. Similarly, community turn-over, both in time and space, is higher in degraded/fragmented landscapes (Laurance, 2002) and, therefore, I would expect fast-lived species to be more effective colonizers and to dominate these areas. Environmental characteristics such as climatic seasonality and landscape heterogeneity such as land-cover and topographic heterogeneity are important determinants of species distribution (Ficetola et al., 2010; Thuiller et al., 2004), dispersal (Daye & Healey, 2015; Youngquist & Boone, 2014), and species richness (Gossner et al., 2016; Vellend et al., 2007), and can have a direct impact on the effectiveness of species with different life-history strategies. However, little research has been carried out to establish explicit links between terrestrial vertebrate life-histories and environmental conditions (Carvajal et al., 2018; Stearns, 2000). Establishing explicit linkages between species life-history strategies, environmental conditions and species distributions could provide inferences beyond just the spatial distribution of species with repercussions for ecology and biodiversity conservation planning (Carvajal et al., 2018; Pollock et al., 2012).

Here, I explore how life-history strategies influence species' response to environmental heterogeneity due to land-cover heterogeneity, climate seasonality and topographic variation. I focus on the terrestrial amniote species: reptiles, mammals, and birds. This group of species is well represented in the literature, in terms of trait and spatial information. Furthermore, although these groups of species present strong physiological differences, they also share similar limitations in terms of reproduction (e.g. internal fertilisation and maturation or development of the embryo/egg, and large energy investment). I classify these species into slow or fast using the “body-mass” and the “fast-slow” continuums. In other words, I investigate both species overall life-history strategy (with species ranging from generally large and slow-lived to small and fast-lived), as well as their life-history strategy relative to body size and phylogeny (ranging from relatively slow-lived to relatively fast-lived, for a given body size and clade).

I hypothesize that responses will differ between these two life-history classification methods:

1. Under the “body-size” continuum, I predict that slower and bigger species will be favoured in less climatically seasonal areas, but also in more heterogeneous landscapes (in terms of land cover and topography). Big and slow species need more stable energy inputs, which will be provided by seasonal climatic stability. On the other hand, bigger species tend to have larger dispersal capabilities, which allows them to cross environmentally non-suitable areas to reach their optimal niche more easily. This way, highly movie species are able to cope with more heterogeneous landscapes.

2. Under the “fast-slow” continuum, without the influence of body-size and phylogeny, I predict that relatively fast species will be favoured in more heterogeneous, seasonal environments, since they have traits allowing rapid recolonization and expansion after a disturbance.

3.3 Materials and methods

3.3.1 Life history classification

To describe the life-history strategies of terrestrial vertebrates, I used two life-history classification schemes, the body-mass and the fast-slow continuum. As presented in Chapter 2, the classification of species along both continuums is based in four life-history traits: number of offspring per reproductive event (offspring); maximum recorded longevity, in years (longevity); age of female sexual maturity, in years (maturity); and the yearly number of reproductive events (reproduction events). I collected these data from 18 published and openly available databases of mammals, birds and reptiles (Table 3). In order to combine the data I ran a taxonomic matching analysis (Cooke, Eigenbrod, et al., 2019; Etard et al., 2020) using taxonomic information from various repositories: the International Union for Conservation of Nature Red List of Threatened Species Version 2021-1 (IUCN, 2021) (https://www.iucnredlist.org/); the Integrated Taxonomic Information System Version 26-july-2021 (ITIS, http://www.itis.gov); and the Global Biodiversity Information Facility Version 03-2021 (GBIF, http://www.gbif.org). I followed as much as possible the taxonomy underlying the IUCN Red List and stored additional taxonomic names from other repositories as synonyms. If a species was not available on the IUCN Red List, ITIS information was used instead; GBIF taxonomic information was used when no other sources were available (see Supporting Information for more details). Once taxonomy was resolved for all datasets, I aggregated the life-history traits of the different databases into a unified dataset.

Since trait data was skewed distributed, variables were log-transformed. In the case of the fast-slow continuum, linear mixed models (LMMs) were fitted using the *lme* function of the R package *nlme* Version 3.1-148 (Pinheiro et al., 2021) (details in Appendix 1 section 1) (see Chapter 2). The residuals from these models were then used as log-transformed trait variables, adjusted for body mass and phylogeny ('adjusted traits' from here on). Both the adjusted and non-adjusted life-history traits were subjected to PCA to form the fast-slow and body-mass continuum respectively (see Chapter 2) and the three first axes were extracted representing 81% and 94% of the total life-history trait variation respectively (see Appendix 1 Table S2 and Section 2 for a detailed description of the PCs of the body-mass and fast-slow continuums).

3.3.2 Species distribution information

I obtained spatial point data on the occurrence of species from GBIF using the R package *rgbif* Version 3.3.0 (S. Chamberlain, Barve, et al., 2020), and species range maps from the IUCN Red List of Threatened Species Version 2021-1 (IUCN, 2021). Only GBIF records from 2010 to 2019 were retrieved, to avoid as much as possible the spatial inaccuracies from older geo-referencing technology. Raw point information from GBIF contains erroneous or redundant points, and points with contradictory metadata (e.g. metadata country code does not match the geographic position of the point). Therefore, I discarded points with erroneous coordinates (e.g. missing or extra digits on the UTM coordinate values, mismatch between coordinates units and metadata, and coordinates assigned to country centroids); observations with duplicated coordinates (preserving only one observation for each coordinate combination); points that fell into the sea/ocean; and any observation where metadata mismatched between the spatial information and the observation (e.g. discrepancy between the point location and the region/country where the observation was taken). In addition to these filters, I also excluded all occurrences within a 1 km radius of museums, universities or known natural history collections, since species observations could correspond to specimens deposited or exhibited in those institutions' collections. All of these filtering steps were performed using the *CoordinateCleaner* R package Version 2.0-18 (Zizka et al., 2019).

Species occurrence information was further filtered using the range maps of the IUCN Red List of Threatened Species Version 2021-1 (IUCN, 2021). I am aware that IUCN range maps are not free of bias or errors, but they aim to represent a complete delimitation of species distributions (IUCN Red List Technical Working group, 2019). Observations which fell outside of a species' known or probable range (IUCN range maps presence codes 1 to 4; IUCN Red List Technical Working group, 2019) were removed. Since I am interested in the set of environmental conditions that allow these species to establish populations, I included native and invasive ranges (origin codes 1 to 6; IUCN Red List Technical Working group, 2019). Where IUCN range maps were unavailable (which was the case for 136 species), observations were manually checked using field guides and biodiversity atlases (e.g Billerman et al., 2019; Speybroeck et al., 2017; Wilson & Mittermeier, 2009). The remaining observations were presumed to be valid presence records. I acknowledge that GBIF records are patchy and biased. However, my objective was to test whether fast or slow species were more likely to be found in landscapes with different levels of heterogeneity, rather than to build species distribution models representing the complete range of species, thus I expected the data limitations to add noise rather than bias the results.

Since absence data are very scarce in GBIF, I created pseudo-absence records of the same number as presence records (Barbet-Massin et al., 2012). To create the pseudo-absences, I randomly distributed points inside a sampled area created by applying a 2-degree buffer to the IUCN range map of each species, following the method recommended by Barbet-Massin et al. (2012). For the 136 species for which IUCN range maps were not available, minimum convex polygons (MCP) were plotted around valid species observations to create species extent of occurrence maps, following the approach recommended for generating the IUCN range maps (IUCN, 201 C.E.), and a 2-degree buffer was added afterwards. Thus, I produced pseudo-absence records both in the range areas where species observations exist and, in the areas, where no observations have been recorded. I selected this approach to minimise the effects of potentially erroneous pseudo-absences, since these can lead to small inaccuracies or bias on correlative-type models (Barbet-Massin et al., 2012).

Distribution data were mapped onto grids at four spatial resolutions (1 × 1, 2 × 2, 5 × 5 and 10 × 10 km) with the same extent and resolution as the environmental variables (see below). GBIF contained information relative to the spatial uncertainty of records, and this allowed me to discard the presence points with a spatial uncertainty greater than the resolution of the grid. Thereafter, only one record (either presence or pseudo-absence) was retained for each cell of the corresponding grid. If both a pseudo-absence and a presence record were present within the same grid-cell, I preserved only the presence record. Thus, I obtained four different distribution data sets with presence and pseudo-absence records at 1 x 1, 2 x 2, 5 x 5 and 10 x 10 km grid resolution. From this dataset, only species with a minimum of 200 records (100 presence and 100 pseudo-absence) were selected for the analysis at each spatial resolution. I obtained sufficient distribution, taxonomic, and trait information for 980 species (230 mammals, 576 birds, and 174 reptiles) at 1 km resolution and for a minimum of

904 species at 10 km grid resolution. The total number of records (observations plus pseudo-absences) also varied according to the grid resolution used and ranged from more than 10 million, at 1 km grid resolution, to 6 million at 10 km grid resolution.

3.3.3 Heterogeneity variables

I defined heterogeneity as the set of land-cover, climatic seasonality and topography characteristics found in the environment. I selected six continuous environmental variables to describe heterogeneity, three describing land-cover heterogeneity, two describing climate seasonality, and one describing topographic heterogeneity.

Land-cover heterogeneities were based on remotely sensed data, specifically on textural features of the enhanced vegetation index (EVI). The EVI is a spectroscopy-based vegetation index that is particularly sensitive to changes in tree-canopy structure. I selected three independent EVI-derived variables to describe land-cover heterogeneity: 1) Coefficient of Variation; 2) Evenness; and 3) Correlation. These variables were extracted from Tuanmu and Jetz (2015) and capture different aspects of land-cover heterogeneity. The Coefficient of Variation captures variation between more heterogeneous types of land-cover (Tuanmu & Jetz, 2015), with a higher Coefficient of Variation corresponding to human-influenced land-cover types (such as built-up areas and croplands) and more patchy landscapes, while more natural land-cover types (e.g. grasslands, forests, shrublands, etc.) have a lower value. Evenness captures the probability of adjacent pixels having differently scaled EVI values (Tuanmu & Jetz, 2015).

Larger Evenness values are associated with natural forests and grasslands, and croplands and built-up areas and higher heterogeneity of land use. Shrublands and barren areas have more homogeneous EVI values and thus lower Evenness values (Tuanmu & Jetz, 2015). EVI Correlation measures the linear dependency between EVI values of adjacent cells (Tuanmu & Jetz, 2015), which can be interpreted as the spatial correlation of the vegetation cover. Higher Correlation values correspond to low fragmentation while low values are characteristic of highly fragmented landscapes. Combined, these three variables give an overall description of human-induced land-cover patchiness (Coefficient of Variation), natural heterogeneity (Evenness) and spatial fragmentation (Correlation). All the EVI derived variables are based on values of the MODIS EVI product (MOD13Q1 Version 5; 250-m resolution) corresponding to the period between 2001-2005 (Tuanmu & Jetz, 2015).

At coarse scales, climate is the main driver of biodiversity patterns (Gaston, 2000), and climatic heterogeneity is the main driver in the selection of life-history strategies (Dobzhansky, 1950; MacArthur & Wilson, 1963). Pianka (1970) theorised that climatically homogeneous habitats favour big and slow species, while climatically heterogeneous habitats benefit small and fast species. I account for climatic heterogeneity using two continuous variables: temperature which is calculated as and precipitation seasonality. These variables were obtained from the bioclimatic (BIOCLIM) variables of WorldClim Version 2.1 (https://www.worldclim.org): variables bio4 and bio15, respectively. These climatic variables are derived from long-term average climatic value (1970 to 2000), time-series of monthly averages by year, and also daily weather data. The final climatic variables are the result of averaging and interpolation annual temperature and precipitation range data. Higher values of these climatic variables represent greater within-year climatic variation.

Topography is another important aspect of environmental heterogeneity. I expect more topographically heterogeneous habitats, such as mountains, to be also influenced by more heterogeneous and unpredictable microclimatic conditions (Antonelli et al., 2018), thus promoting fast life-histories. I represent topographic heterogeneity as the standard deviation of elevation (‘SD elevation’ henceforth) (Amatulli et al., 2018; Barajas-Barbosa et al., 2020). SD elevation was retrieved from Amatulli et al. (2018) and is derived from the Global Multi-Resolution Terrain Elevation Data (https://doi.org/10.5066/F7J38R2N).

All variables were obtained as global raster datasets of 30-arc-seconds spatial resolution (approximately 1 km at the Equator). Since I am interested in testing my hypotheses at different scales, all heterogeneity layers were rescaled using the mean of the aggregated pixels to 2, 5 and 10 km resolution and resampled using bilinear interpolation. All these operations were performed using the *raster* R package Version 3.0-12 (Hijmans, 2020).

3.3.4 Statistical analysis

I used a hierarchical modelling approach to investigate the effect of the interaction between species life-history strategies and environmental heterogeneity on the probability of species occurrence, combining all information into a multispecies distribution model. To do so, I used a binomial generalized linear mixed-effects model (GLMM) with a logit link function, where the response is a binary variable describing the presence and pseudo-absences of species. Fixed effects were the environmental heterogeneity variables, the life-history axis, and the two-way interactions between each heterogeneity variable and each life-history axis. A significant interaction indicates that the species' response to that particular heterogeneity variable varies according to whether the species is large and slow or small and fast (body-mass continuum), or whether the species is slow or fast relative to its body size and phylogenetic position (fast-slow continuum). Species identity was included as a random intercept to account for variation among species. Since I expect responses to environmental heterogeneity to vary among species, I also added random slopes of each environmental heterogeneity variable, following Pollock et al. (2012).

Models were fitted by maximum likelihood, using an adaptative Gauss-Hermite quadrature approximation (Qing Liu & Pierce, 1994), implemented in the *lme4* R package Version 1.1-23 (Bates et al., 2015). I refitted the models at each spatial resolution: 1, 2, 5 and 10 km. Model fit was evaluated using the marginal and conditional pseudo-R^2 values for GLMM (Nakagawa et al., 2017). To satisfy the assumptions of linear relationships of the selected statistical analysis, environmental heterogeneity variables were normalized and centred using the Ordered-Quantile transformation (Qing Liu & Pierce, 1994) built into the *bestNormalize* R package Version 1.6.0 (Peterson & Cavanaugh, 2019).

The ability of models to correctly discriminate presences from pseudo-absences was evaluated using the area under the Receiver Operating Characteristic curve (AUC) (Hanley & McNeil, 1982). The AUC returns a value within the range of 0-1, where 0 is perfectly incorrect discrimination, 0.5 corresponds to the performance of a random classifier, and 1 corresponds to a perfect classification. All analysis, data manipulation, and spatial pre-processing was carried out using the R statistical software Version 3.6.3 (R Core Team, 2021).

Despite my efforts the dataset contains an unbalanced number of species from different classes. Birds represent more than 58% of the total species presented in the dataset, followed by mammals with a 23% and reptiles with 17%. To confirm that the patterns observed in the main model were not only the results of bird species responses to environmental heterogeneity, I ran individual models for each class of vertebrates (see Appendix 1 Section 3). From these individual models I extracted the strength of the effects (whether an effect is statistically significant or not) and the effects direction (the overall positive or negative effect on the response variable) and compared those against the main model.

3.4 Results

Both continuums showed the expected trade-offs, with life-history traits related with ageing (longevity and maturity) and fecundity (offspring and reproduction-events) showing opposite relationships on the first axis of the PCA (Figure 2.a-b). The position of species along the body-mass and fast-slow continuums often varied substantially (Figure 2). For example, the Asian water monitor (*Varanus salvator*), when classified under the body-mass continuum, fell in the middle part of the continuum (Figure 2.c). However, when this same species is classified under the fast-slow continuum it is located at the fast-end of the continuum (i.e., it has a fast life history for its body size and clade; Figure 2.d).

Species responses to environmental heterogeneity varied according to their life-history strategies with contrasting responses between the body-mass and fast-slow continuums (Figure 3). Here, I focused on the first principal component axis (PC) for each of the continuums at 1 km grid resolution. The first PC axis explained the largest proportion of trait variation, 59.53% in the case of the body mass continuum and 32.7% for the fast-slow continuum (Figure 2 and Appendix

1 Table S2). Results were consistent for the other axes and are presented in the Supplementary information (Appendix 1 Section 3 Table S3).

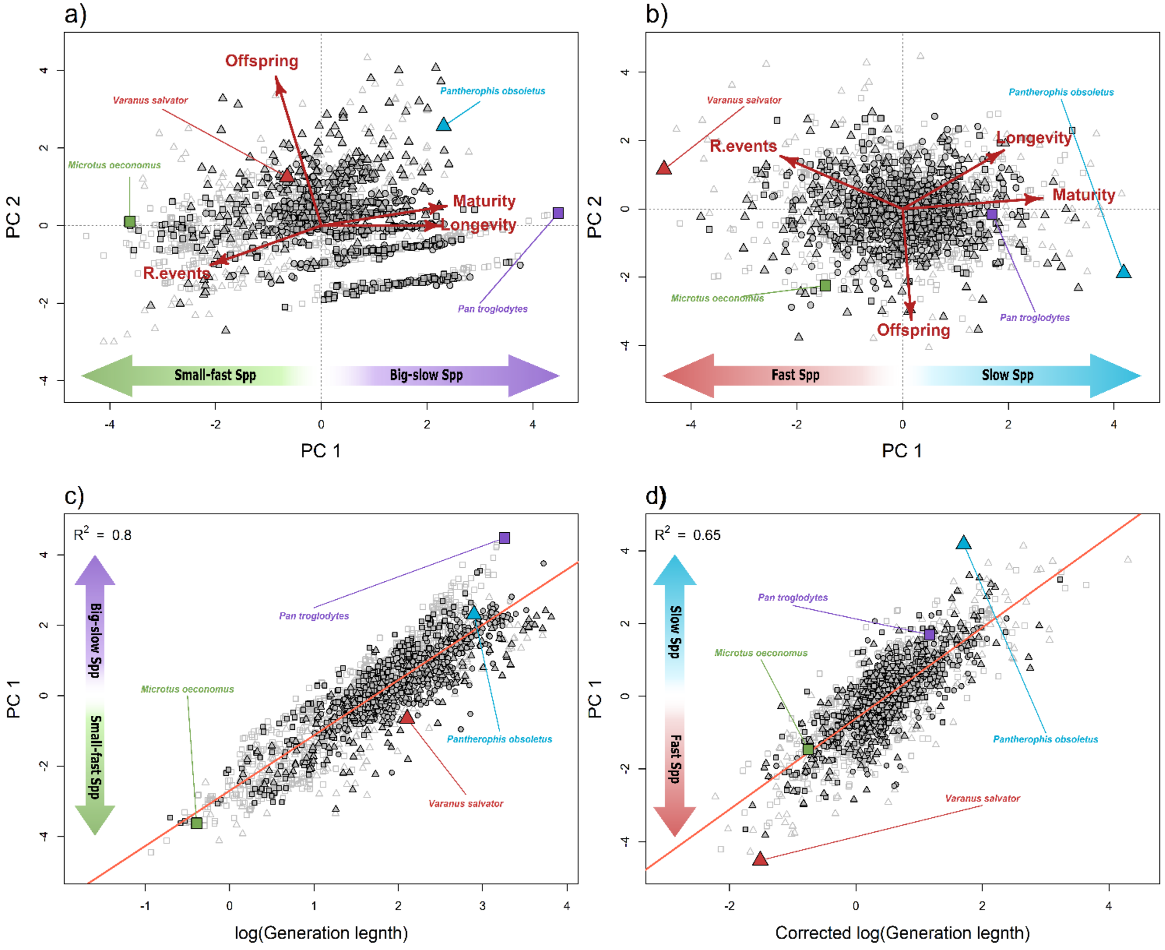

Figure 2. Score values for the first two axes of the body-mass (panel **a**) and fast-slow (panel **b**) continuums, and the correlation of the first axis of both continuums with generation length (panels **c** and **d** respectively). Each point, or score value, represents the position of a species on the body-mass or fast-slow continuum according to its life-history trait configuration. Scaled loading values of the life-history variables on the first and second axis of the body-mass and fast-slow continuums are shown in panels a and b (red lines). The different point shapes represent the main vertebrate classes included in the analysis (circles = birds; triangles = reptiles; and squares = mammals). Hollow shapes represent the position of all species used to calculate the life-history axes, whereas the filled points mark the species used in the analyses of responses to environmental heterogeneity. Coloured shapes represent example species near the extremes of the body-mass (green and purple) and fast-slow continuums (red and blue). Generation length (panels **c** and **d**) was calculated as specified in Pacifici et al. (2013), using raw life-history traits (panel **c**) and life-history traits adjusted for body-mass and phylogeny (panel **d**) (see Appendix 1 Section 2). R-squared values in panels c and d are from simple linear regressions. Orange lines in panels **c** and **d** represent the linear adjustment between generation length and the continuums.

Landscape heterogeneity had an important role in the probability of occurrence of species with different life-histories (Figure 3). Big and slow species were more likely to occur in naturally heterogeneous, artificially patchy, and fragmented landscapes (*Type II Wald Chi-square test,* χ^2= 52.5237, d.f=1, *p-value*< 0.0001; χ^2= 16.0908, d.f= 1,*p-value* < 0.0001; and χ^2= 53.3857, d.f=1,*p-value*< 0.0001 respectively) (Figure 3.a). To avoid extreme values and ensure robust predictions, I used the values corresponding to the 2.5 and 97.5 percentiles of my explanatory variables as the lower and higher values to fit the partial responses. Model partial responses showed that, when moving from low (2.5 percentile of the data) to highly (97.5 percentile of the data) artificial patchy habitats (EVI Coefficient of Variation), bigger slower-lived species were 25.48% more likely to occur when compared to smaller faster-lived species (Figure 4.a). When natural heterogeneity was high (higher values of EVI evenness) bigger slower-lived species were 27.24% more likely to occur than smaller faster-lived species (Figure 4.b). Similarly, when habitat fragmentation is high (lower values of EVI correlation) bigger slower-lived species are 24.48% more likely to occur than smaller faster-lived species (Figure 3.c). In contrast, slower species relative to their body size and phylogeny (hereafter termed slow) were less likely to be present in fragmented (χ^2= 10.6492, d.f=1, *p-value*= 0.0011) and artificially patchy landscapes (χ^2= 5.3072, d.f=1, *p-value*= 0.0212) than faster species relative to their body size and phylogeny (hereafter termed fast) (Figure 3.b). Slow species were 14.97% less likely to occur in artificial patchy landscapes (higher values of EVI Coefficient of Variation) (Figure 4.d), and 13.26% less likely to occur in more fragmented (lower values of EVI Correlation) habitats (Figure 4.f), compared to fast species.

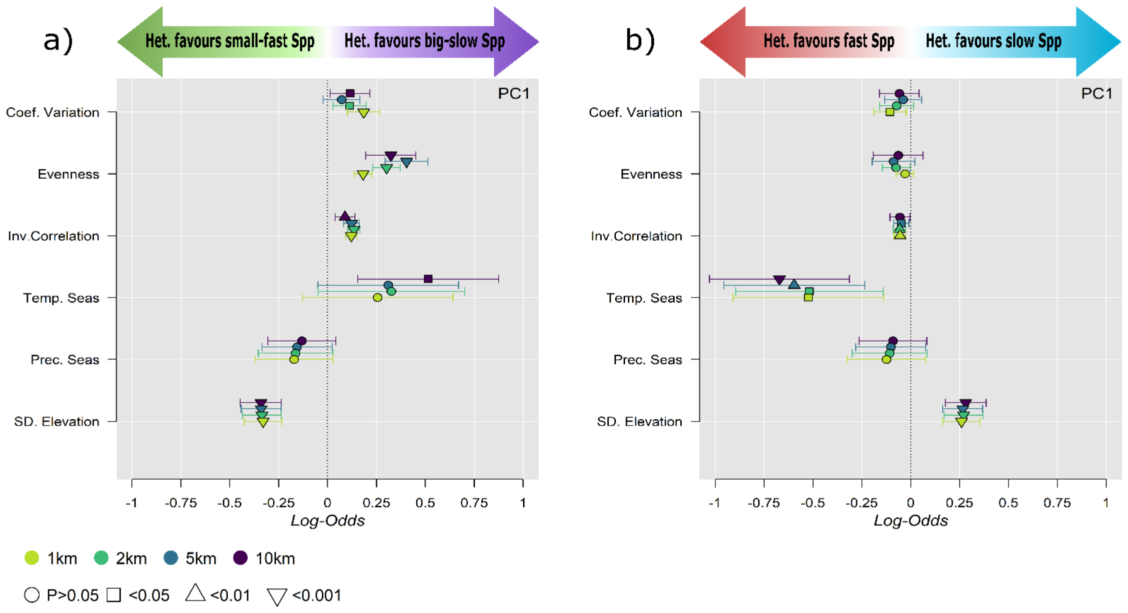

Figure 3. **Influence of life history on responses to environmental heterogeneity**. The log-odds describe how the probability of occurrence of species changes with increasing heterogeneity and increasing values along the first axes of the body-mass (panel **a**) and fast-slow continuums (panel **b**). Positive log-odds reflect increases with increasing heterogeneity in the probability of occurrence of big and slow species (panel **a**) or of slow species relative to body size and phylogeny (slow) (panel **b**). Negative values indicate a higher probability of occurrence of small and fast species (**a**), or of fast species relative to body size (**b**), with increasing heterogeneity. Values of EVI Correlation have been inverted (EVI Correlation × -1) in order that increasing heterogeneity is shown in the same direction as for the rest of the environmental variables ("Inv.Correlation"). Log-odds were calculated based on the models at 1, 2, 5 and 10 km grid resolution (colour gradient). The statistical significance of first-order interactions (life-history axis and environmental variables) is indicated by polygon shapes, bars and whiskers represent 95% confidence intervals (see Appendix 1 Table S4-5 for precise numerical values).

The association of life-history strategies with species' responses to climatic heterogeneity also differed between the two continuums (Figure 3). Species' position along the body-mass continuum did not show a significant association with their responses to temperature and precipitation seasonality (χ^2= 1.4335, d.f=1, *p-value*= 0.2311 and χ^2= 2.3697, d.f=1, *p-value*= 0.1237 respectively). In the case of the fast-slow continuum, the fastest species were 8.85% more likely to occur in areas of higher temperature seasonality when compared to the slowest species (χ^2= 5.9608, d.f=1, *p-value*= 0.0146) (Figure 5.d). Species' positions along the body-mass and fast-slow continuums also showed a strong association with their responses to topographic complexity. The biggest and slowest species were 29.93% more likely to occur in more topographically simple habitats (lower values of SD Elevation) than the smallest and most fast-lived species (Figure 5.c). In the case of the fast-slow continuum, the fastest species were 20.61% more likely to be present in topographically simple areas than slow species (Figure 5.f). These results for both continuums contradict my predictions, since I expected topographic heterogeneity to favour big slow-lived species, and fast species.

Although here I focused on the results for the models at 1 km resolution, the models at coarser spatial scales were qualitatively identical across different spatial grains (Figure 3). The proportion of variation in species occurrence explained by the models at different resolutions ranged between 0.11-0.12 for fixed effects and 0.76-0.81 for fixed and random effects combined, based on marginal and conditional pseudo-R^2 values, respectively (Nakagawa & Schielzeth, 2013). Models were effective at discriminating presence observations from pseudo-absences (AUC ranged from 0.83-0.84).

I observed differences in the strength and direction of responses between the vertebrates' class specific models and the main model (Appendix 1 Table S3). In terms of effect direction, the responses of birds, reptiles and mammals were mostly aligned with the main model. Reptiles showed the greatest discrepancies in terms of effects direction, but most of these differences were statistically not significant (Appendix 1 Table S3). Different classes also showed different sensitivities to the interaction of life-history axes and environmental variables (Appendix 1 Table S3). Birds was the group that showed the greatest sensitivity of all, with higher congruency with the main model. On the other hand, mammals showed the lowest of sensitivities but a high congruency with the main model. The full set of results is presented in the supplementary materials.

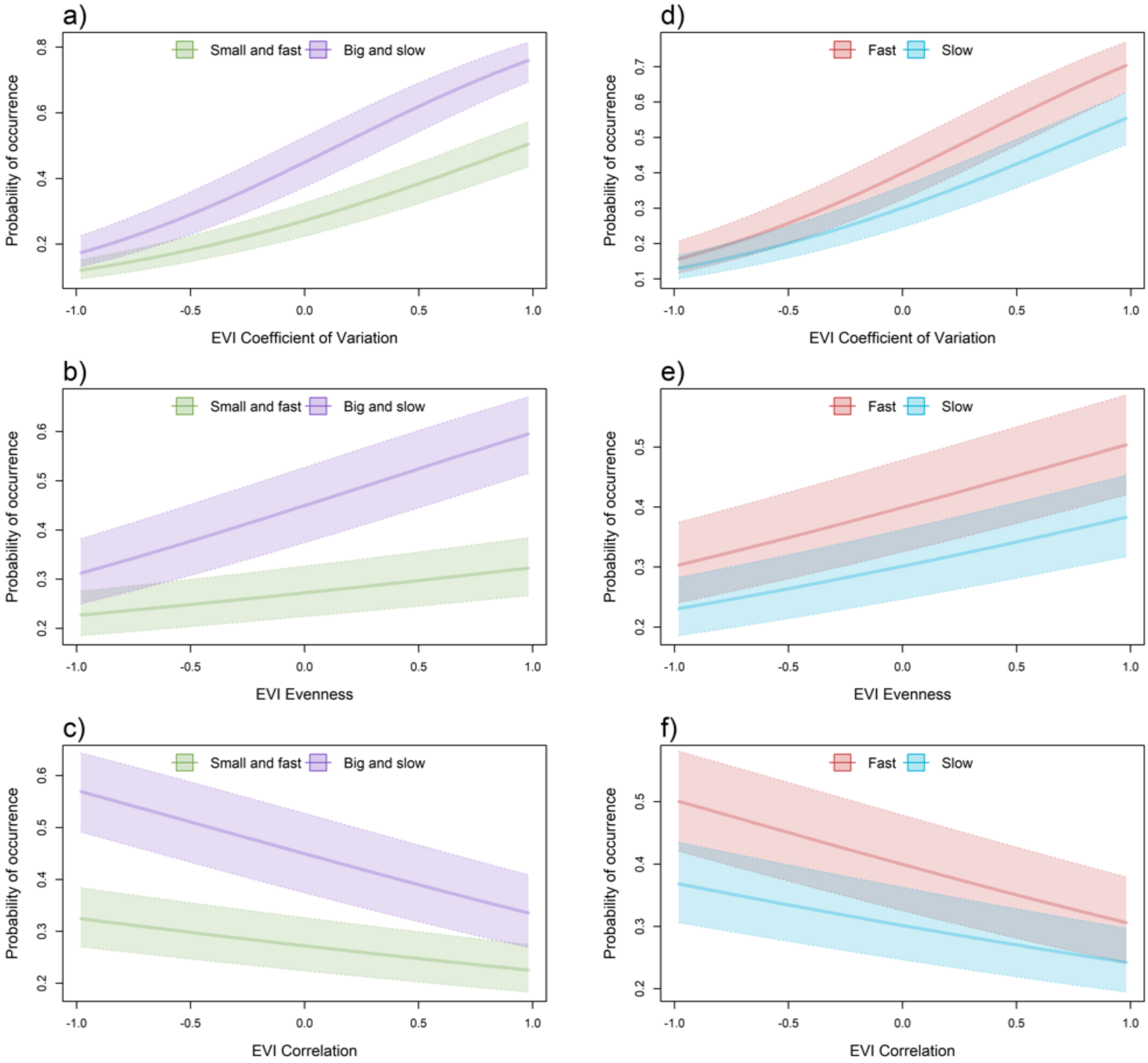

Figure 4. **Responses to land-cover heterogeneity of big and slow versus small and fast species (left-hand panels) and slow versus fast species relative to body size and phylogeny (right-hand panels)**. Effects of environmental heterogeneity variables are shown for species at the 2.5th and 97.5th percentile along the first principal component axis of life-history variation, for the models at 1 km grid resolution. Partial responses were calculated using the 2.5th and 97.5th percentile range of the of the heterogeneity variables. Shaded areas represent 95% confidence intervals around the fitted relationships. The values of EVI correlation are not inverted.

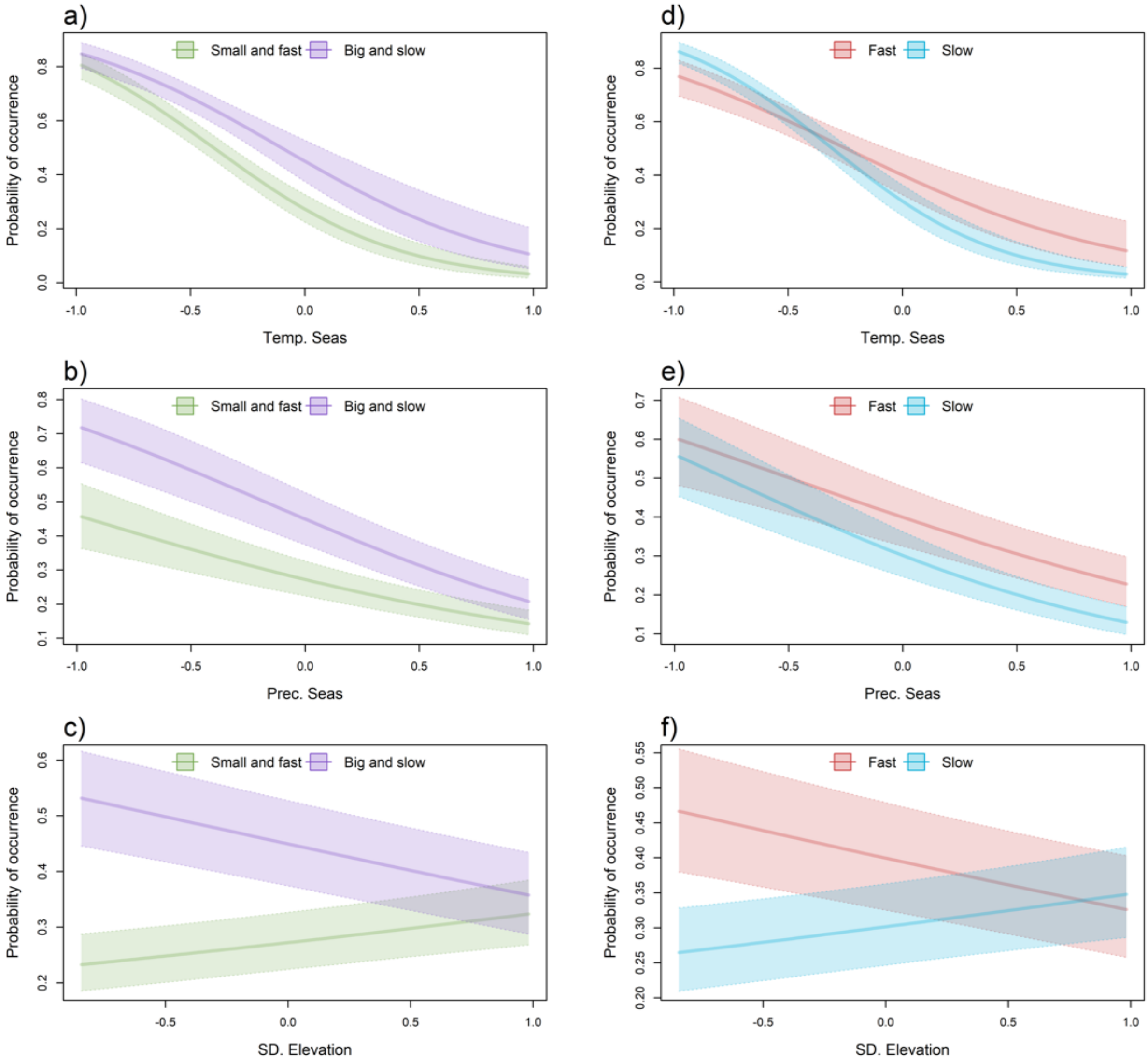

Figure 5. **Figure 5**. **Responses to climatic and topographic heterogeneity of big and slow versus small and fast species (left-hand panels) and slow versus fast species relative to body size and phylogeny (right-hand panels)**. As with **Figure 3**, effects of environmental heterogeneity variables are shown for species at the 2.5th and 97.5th percentile along the first principal component axis of life-history variation, for the models at 1 km grid resolution. Same as in Figure 3, partial responses were calculated using the 2.5th and 97.5th percentile range of the of the heterogeneity variables. Shaded areas represent 95% confidence intervals around the fitted relationships.

3.5 Discussion

I showed that there is a strong association between species' life-history strategies and their responses to environmental heterogeneity for terrestrial amniotes globally. Larger and slower species were favoured where land cover is more heterogeneous and fragmented (in both natural and artificial habitats), and in more topographically homogenous environments. After controlling for the effects of body mass and kinship on species' life histories, species with relatively slow life-history strategies were more likely to occur in areas where land cover is more homogeneous and less fragmented, where topographic heterogeneity is higher, and where temperature seasonality is lower.

The patterns I observed in the body-mass continuum can, in large part, be explained by the size of species: body-mass shows a correlation of 0.61 with the first axis of the body-mass continuum (Appendix 1 Table S2). Bigger species have higher dispersal capabilities than small species (Sutherland et al., 2000), are more energy efficient (Bonte et al., 2012), and are less likely to be preyed on during the dispersal phase than smaller species (Whitmee & Orme, 2013). This may give larger species more flexibility to move from one patch of suitable habitat to another (Niebuhr et al., 2015; Warzecha et al., 2016), which in turn may allow these species to compete more effectively in patchy and fragmented heterogeneous ecosystems. Furthermore, smaller fast-lived species are more likely to avoid large distance movements (Bonte et al., 2012; Sutherland et al., 2000; Whitmee & Orme, 2013) and are more likely to exploit topographically complex habitats that offer more shelter and a higher diversity of microhabitats

(Bátori et al., 2019). This can also explain why big and slow-lived species were more likely to be present in topographically homogeneous areas.

The results showed that fragmented, and artificially heterogeneous habitats favour fast-lived species. This same pattern has been found in other studies dealing with land-use changes (Börschig et al., 2013; Nordén et al., 2013). Together, these results suggest that habitats such as fragmented croplands will tend to be dominated by fast-lived species. My results further suggest that there will be an even stronger favouring of fast-lived species in habitats where temperature seasonality is higher.

Future land-use and climate changes are likely to produce large changes in environmental heterogeneity, likely increasing landscape patchiness and fragmentation, and increasing climatic variability (Newbold et al., 2019). This results point out that these environmental changes will be accompanied by the homogenization of ecological communities, favouring species with certain life histories while filtering out others (Brice et al., 2017; Gossner et al., 2016; Hidasi-Neto et al., 2019). Specifically, results show that the homogenization of communities caused by increasing heterogeneity in future is likely to be associated with a shift in community structure toward dominance by large species, and fast-lived species relative to body size. This homogenization of ecological community structure will have important consequences for biodiversity, ecosystem functioning, and ecosystem services (Newbold et al., 2019). Identifying which species and communities are more sensitive to these changes is imperative to understand the causes, patterns, and consequences of biodiversity loss.

This analysis has several necessary limitations. Spatial observations for reptiles and mammals were scarce compared to those of birds (Troudet et al., 2017). From the pool of 2,061 species for which I had complete trait information (706 birds, 932 mammals and 423 reptiles), I found spatial information for 82% of birds, 24% of mammals and 41% of reptiles. This greatly limited the final number of mammal and reptile species included in the model. The lack of absence records for species is also a challenge, although the use of pseudo-absences is likely to introduce random errors rather than bias (Wisz & Guisan, 2009). Both limitations are unlikely to be redressed soon, however, future models would greatly benefit from more complete and accurate data on species' distributions. Another challenge is that the availability of trait data differs greatly among taxonomic groups (Etard et al., 2020), with trait data for reptiles especially scarce.

The individual model for each vertebrate class remarks some of the aforementioned limitations. Vertebrate groups showed minor differences in the sensitivity and direction of the effects described by the main model. This was expected since, even though mammals, birds and reptiles share some characteristics, there are still physiological differences that can have a mayor effect on how these groups of species interact with its environment. For example, birds and mammals follow the Berman rule (a gradient of size from the tropics towards temperate and polar regions) (Meiri & Dayan, 2003) whereas reptiles (mostly lizards and snakes) follow the opposite pattern (Ashton & Feldman, 2003). This mean that there is going to be mismatch of size between reptiles and the rest of amniotes across a climatic gradient. This alone can explain some of the discrepancies between groups that we observed in the individual models. Despite these differences, the observed patterns are the results of the combination of all amniote groups. Since most discrepancies referred to sensitivity and considering that I controlled for the effects of species identity in my main model, I am confident in the patterns described here.

Although my results suggest a correlation between species life-history strategies and environmental heterogeneities, further research is needed to confirm the predictions made by Pianka (1970) and Mac Arthur & Wilson (1967) about the role of life-histories on the fitness and selection of species. A way to complement the findings of this study can include species metabolic rates and environmental energy availability. Metabolic rates are usually associated with the pace of life (e.g Auer et al., 2018): fast species present relatively higher metabolic rates than slow species (e.g Pettersen, White, & Marshall, 2016; Wiersma et al., 2007). Therefore, the dependency of species on energy availability is also different. This reasoning is coherent with Dobzhansky (1950) theory postulations that tropical and temperate areas show different yearly energy patterns (primary productivity) and therefore species are differently adapted to exploit this energy. Using distribution data from species with known metabolic rates and average yearly primary vegetation fluctuations (as a proxy for energy availability), I might be able to detect this pattern of energy availability variation, or energy seasonality, and species metabolic rate distributions. This could help to better understand the patterns observed in this experiment and to form a more cohesive species life-history distribution theory. The addition of this energy base dimension can also improve our understanding of how biodiversity might respond to future environmental changes.

In general, the observed responses matched my initial hypotheses: big and slow species, and fast species relative to their body size and phylogenetic position, are favoured in heterogeneous landscapes. Except for topographic variation that showed exactly the opposite pattern than hypothesized. These results point out that life-history strategies are important determinants of species distribution and responses to global environmental changes. However, the mechanisms driving these responses are still unclear. Further research into the response of more complete species archetypes (adding morphological, dietary, behavioural, and ecological traits), as well as focusing on smaller groups of species, is needed to clarify if the discrepancies I have observed are due to physiological or morphological differences. Either way, my results show that the way in which I combine life-history traits (the body-mass or fast-slow continuum) can have a substantial effect on the response patterns observed and their interpretation. By combining species life-history strategies with spatially and temporally explicit environmental information, I was able to get a more complete, and complex, picture of the factors driving species distribution. In the current context of accelerating rates of environmental change, these results can help to identify species most at risk of extinction and to project how biodiversity will respond to future land-use/cover and climate change scenarios.

Chapter 4: Land-use disturbance and temperature seasonality determine life-history diversity and pace of life of terrestrial vertebrate species assemblages

4.1 Abstract

Anthropogenic drivers of environmental degradation, such as land use, have caused substantial declines in local species richness. However, not all species respond equally to these changes with some increasing (winners) and others decreasing (losers) with repercussions for communities and ecosystems. The set of characteristics that determine which species are winners or losers is not well established. Life-history strategies, that summarize multiple life-history traits, are important factors shaping the distribution of terrestrial vertebrate species, but their influence and implications for species communities is still unknown. In this study, I explore how species' life histories vary across 2,974 globally distributed communities of vertebrate species under different land-use/cover and climatic conditions. I show that animal communities inhabiting more human-impacted and environmentally heterogeneous habitats are dominated by fast-lived species and present a higher diversity of life-history strategies. These results suggest that fast life histories are consistently favoured over slow life histories in more heterogeneous and human-disturbed habitats. Given the observed turnover of life histories, it is likely that there will be a substantial impact on the regulation of populations within communities. Furthermore, under current predictions of future anthropogenic threats, it is likely that land-use and climate change will coincide to drive further shifts towards the dominance of fast-lived species. The results of

these analysis can be used to forecast the composition of communities under different scenarios of land-use and climate change and to design conservations strategies aimed to alt community homogenization.

4.2 Introduction

Human-driven land-use changes and conversion of natural habitats present one of the main current threats to biodiversity (Harfoot et al., 2021; WWF, 2020), with human activities affecting more than 70% of the global ice-free land surface (Mbow, Reisinger, Canadell & O'Brien et al., 2019). This transformation of natural systems, often to optimize certain ecosystem services (e.g. food production, water retention), has negatively impacted biodiversity. At a local scale, human-driven land-use changes can cause reductions of species richness of up to 75%, and decreases of up to 40% in species abundance when compared to habitats with low human impacts (Murphy & Romanuk, 2014; Newbold et al., 2015). This biodiversity loss represents only a fraction of the issue, with species turnover being also crucial to understand ecosystem changes (e.g Clavel, Julliard, and Devictor 2011). Human-induced species turnover can lead to the homogenization of ecological communities (Clavel et al., 2011), which in turn can affect ecosystem resilience to other drivers of change such as climate change (Oliver et al., 2015). Therefore, it is imperative to understand how the species composition of ecological communities changes due to land-use pressures.

All species interact with their biotic and abiotic surroundings on different spatial and temporal scales (Levin, 1992). These interactions are constrained by species' morphological (e.g., size and locomotion type) and physiological (e.g., thermoregulation capabilities and metabolic rates) traits. In other words, traits are the expression of species adaptation and interactions to their biotic and abiotic environments and have a direct effect on how species respond to environmental changes (e.g Vandewalle et al. 2010; Nordén et al. 2013; Murray, Nowakowski, and Frishkoff 2021). Species that live in similar environments or that exploit the same resources are expected to share similar traits (e.g Pigot et al. 2020). Species with similar traits can be grouped into archetypes or functional groups (Kruk et al., 2017). Expanding this reasoning to assemblages of species, I can represent communities in terms of the diversity of species traits that determine when and where species can exist (McGill et al., 2006).

Probably one of the most used examples of trait archetypes in ecology is the fast-slow continuum which classifies species between two basic archetypes, slow and fast species (e.g Dobson and Oli 2007; Stearns 2000). This classification is based on the combination of traits related to fecundity and ageing, or life-history traits. Slow species are characterized by low reproductive rates, late sexual maturity, and longer lifespans (Healy et al., 2019; Pianka, 1970). Conversely, fast species are characterized by high reproductive rates, early sexual maturity, and short lifespans (Healy et al., 2019; Pianka, 1970). Between these two basic archetypes a continuum of life-history strategies can be described. Life-history strategies are directly related to the capacity of species to recover or maintain their populations after an environmental change (MacArthur & Wilson, 1967; Stearns, 2000). Theoretically, slow-lived species will be more sensitive to environmental changes than fast-lived species (Pianka, 1970). Therefore, life-history strategies should be important elements to consider when investigating how biodiversity responds to environmental changes.

Previous studies have shown the relationship between life-history strategies and, for example, species extinction risk (Reynolds, 2003; Hutchings, Myers, García, Lucifora, & Kuparinen, 2012; Tingley, Hitchmough, & Chapple, 2013), invasiveness (Allen et al., 2017; Capellini et al., 2015; Duyck et al., 2007), dispersal (Bonte et al., 2012; Soriano-Redondo et al., 2020) and spatial distribution (Chapter 3). Studies focusing on trait sensitivity to environmental changes have shown that traits such as body size, fecundity and diet are important determinants of species response to land-use change (Davies et al., 2009; Newbold et al., 2013) and that species with lower reproductive rates are more sensitive to climate change (Pacifici et al., 2017). Similarly, it has been observed that fast-lived species are more likely to be present in areas with higher values of climatic seasonality and landscape heterogeneity (Chapter 3). At a species level, most of these observations support the prediction that fast-lived species are better adapted to environmental impacts and that slow-lived species are much more sensitive to these changes (Pianka, 1970). However, the extent to which species responses lead to assemblage-level shifts in life-history strategies is still unknown.

I can study the life histories of communities as the range, average and, distribution of different reproductive and development strategies represented by the organisms within communities and ecosystems (adapted from Petchey and Gaston 2006). By doing these changes in the life-history diversity, and average life-history position (along a life-history continuum) of communities can be detected under different environmental conditions. Here, I present the first study exploring the relationships between life-history diversity and average position of terrestrial amniote communities (birds, reptiles, and mammals) along a fast-slow continuum, and key environmental drivers: climatic seasonality, land-use disturbance, and land-cover heterogeneity. In total, I included 2,424 globally distributed species assemblages, encompassing more than 3,000 species. I hypothesise that different combinations of environmental heterogeneity (climatic seasonality and land-cover heterogeneity) and land-use disturbance are going to lead to differences in the life-history diversity of communities (Figure 6). Under low environmental heterogeneity and low land-use disturbance, I expect life-history diversity to be high, with communities dominated by slow-lived species (baseline) (Figure 6). I expect communities under high environmental heterogeneity and low land-use disturbance to have a higher proportion of fast-lived species while retaining some slow-lived species such that life-history diversity remains high (Figure 6). At low environmental heterogeneity and high land-use disturbance, I expect communities to be strongly skewed towards the fast end of the fast-slow continuum, with a reduction in life-history diversity (Figure 6). When this increase in land-use disturbance is also accompanied by an increase in habitat heterogeneity, I expect communities to be dominated by fast-lived species, with the strongest reductions in life-history diversity (Figure 6).

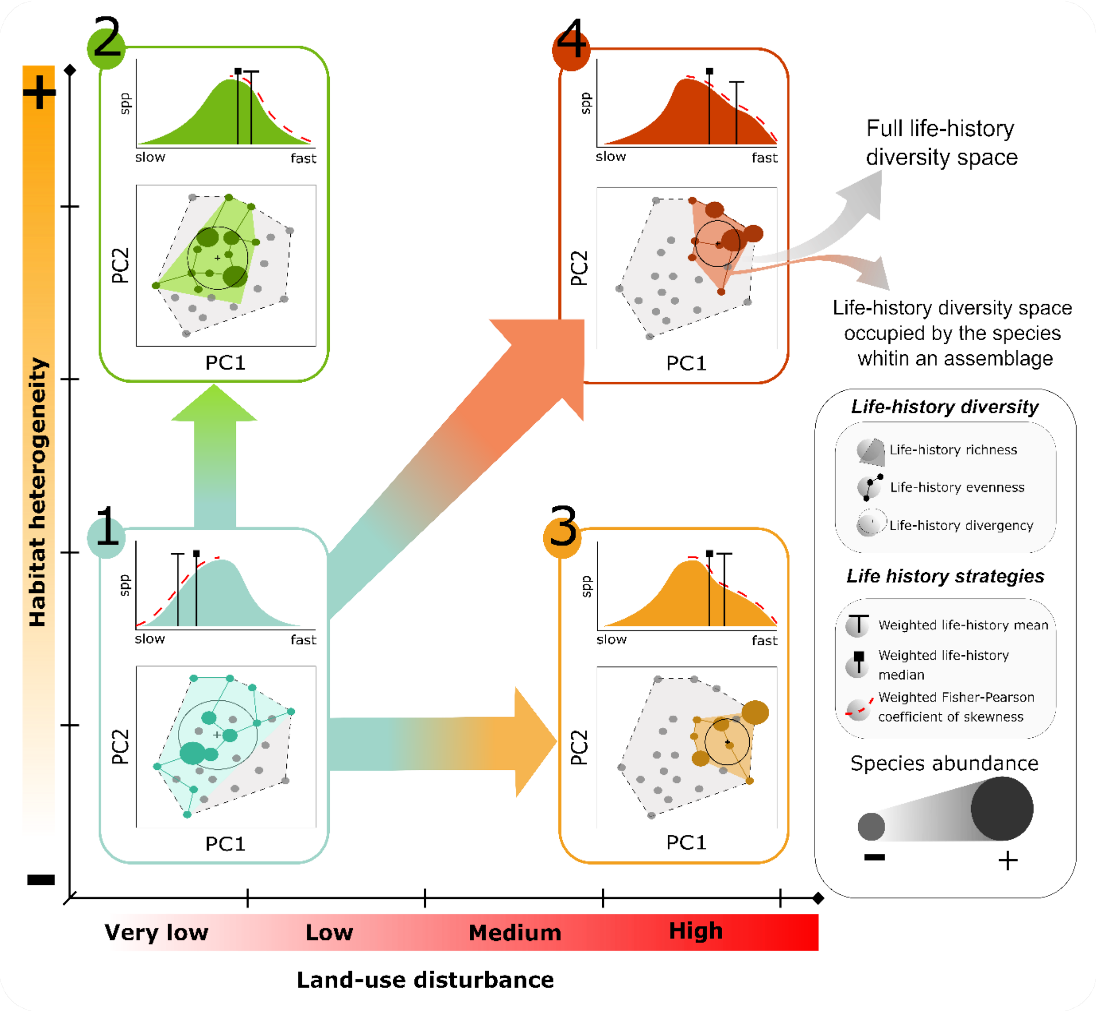

Figure 6. **Framework relating the effects of environmental heterogeneity (spatial land-cover heterogeneity and climate seasonality) and human land-use disturbance to life-history diversity and average life-history strategies of species assemblages.** Here I present three predictions about differences in the expected life-history diversity and average life-history strategies of assemblages in areas with different environmental heterogeneity and land-use disturbance: **a)** I expect increased environmental heterogeneity within natural habitats to favour the presence of fast-lived relative to slow-lived species within assemblages (higher life-history mean and skewness compared to areas of low environmental heterogeneity), with a reduction in life-history diversity (lower values of life-history richness, higher values of life-history divergence and lower values of life-history evenness) (boxes **1** and **2**); **b)** where increases in land-use disturbance are not accompanied by changes in environmental heterogeneity, I expect a dominance of faster-lived species (higher life-history mean and skewness), and also expect life-history diversity to be lower (lower values of life-history richness, higher values of life-history divergence, and lower values of life-history evenness) (boxes **1** and **3**); and **c)** where there is high environmental heterogeneity and high human land-use disturbance, I predict that communities will be dominated by fast-lived species (much higher life-history mean and skewness), with low life-history diversity (low life-history richness, high values of life-history divergence and low values of life-history evenness).

4.3 Material and methods

4.3.1 Species assemblage and land use

I retrieved data on terrestrial vertebrate community assemblage composition from the PREDICTS database (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems, https://doi.org/10.5519/0066354, downloaded 17-December-2021) (Hudson et al., 2017). This dataset contains records of species density, abundance, occurrence, and richness (richness records were discarded from this analysis) from more than 26,000 sites, distributed globally across 281 ecoregions (Olson et al. 2001), under different land-use conditions.

The PREDICTS database is hierarchically organized. Ecological surveys or scientific papers are included as “data sources” and are divided into different “studies” where sampling methods differed within a source. Data from a given source are also split into different studies if they covered very large geographic areas (e.g., multiple countries) to reduce the potential effects of biogeographic differences in species composition (Hudson et al., 2014). Studies are subsequently divided into sampled sites, with information on spatial location (geographical coordinates), species’ abundances/densities (in most cases) or occurrence, and the predominant land use and land-use intensity. Species assemblages are inferred from the records of the individual species sampled. The species’ data for certain PREDICTS sites are given as overall measures of species richness (only for 20 sites at which vertebrates were sampled). For the analysis, I required individual species records, and therefore species richness estimates were discarded from the analysis.

The land-use category of each site was assigned by the PREDICTS project team into 6 predefined classes (Hudson et al., 2014); 1) primary vegetation, natural vegetation with no evidence of past destruction; 2) secondary vegetation, sites where vegetation is recovering to a natural state either after a period of human-dominated land-use or after destruction by extreme natural events; 3) cropland, areas used for cultivation of herbaceous crops, including crops grown as livestock fodder; 4) pasture, 'land where livestock is known to be grazed regularly or permanently' (Hudson et al., 2014); 5) plantation forest, previously cleared areas planted with woody crops for commercial or subsistence exploitation; and 6) urban, areas with human settlements/buildings/parks where the primary vegetation has been removed or is intensively managed for civic or personal amenity (a more detailed description can be found in Hudson et al. 2014). The classification of site land-use and land-use intensity was made based on the habitat description given in the source publication or by consulting directly the original authors of the study (Hudson et al., 2014). Some sites in the PREDICTS database had insufficient information to classify land-use and land-use intensity, this later one was not considered for this analysis (68 sites). I grouped and excluded some land-use categories that presented very low frequencies: I included secondary vegetation as a single class (secondary vegetation is divided into 4 different categories in the PREDICTS database) and removed all sites within urban land use since these have a low representation in the PREDICTS dataset (about 4% of the total sites).

The PREDICTS database contains data for 5,839 species of terrestrial amniotes (birds, mammals, and reptiles) distributed across 8,028 different assemblages around the world. Due to the nature of the studies included in the PREDICTS database, primary vegetation is the most-sampled land-use type, constituting

37% of the sites included in the PREDICTS database. The second most abundant land-use type is cropland, with approximately 11% of the total sites. To ensure that the dataset was not strongly imbalanced towards primary vegetation, I removed studies that included more than twice as many primary vegetation sites as the sum of all the other land-use types. This threshold allowed us to remove those studies that included only primary vegetation sites, as well as those in which the proportion of primary vegetation were disproportionally high. This left us with a final set of 58 studies with 2,058 species assemblages (Figure 7). This dataset contained a more balanced representation of land-use types (611 assemblages in primary vegetation; 492 in secondary vegetation; 397 in plantation forest; 259 in pastures; and 299 species assemblages in croplands), as well as of life-history strategies.

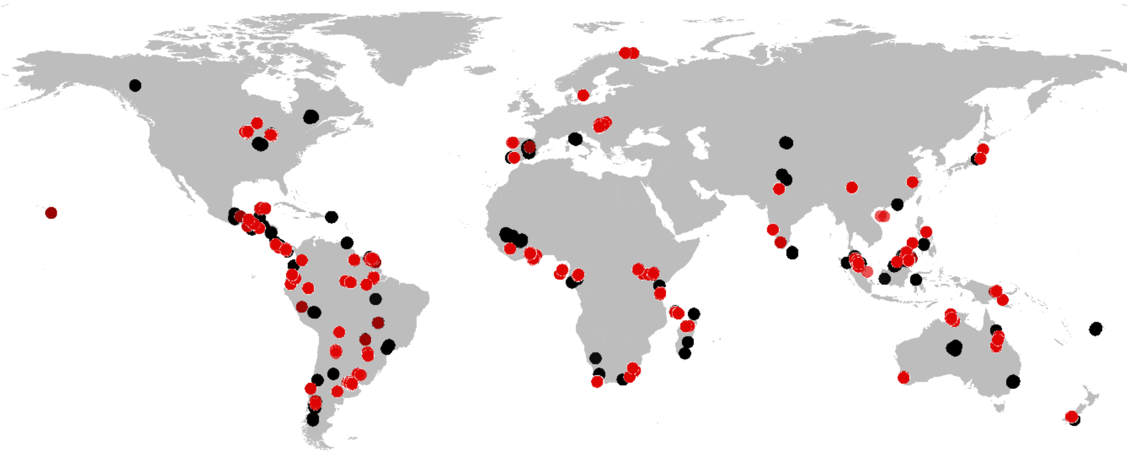

Figure 7. **Distribution of the PREDICTS database sites for terrestrial amniote species (birds, mammals, and reptiles).** The red points correspond to the species assemblages included in this study (minimum of 8 species per assemblage). Base map extracted from the Database of Global Administrative Areas (**GADM**) (https://gadm.org/) and projected using the WGS84 coordinate reference system (EPSG: 4326).

To combine the species assemblage information with the life-history trait information, control for possible errors, and present a final cohesive dataset, I ran a taxonomic and synonym resolution analysis on the dataset. I performed this correction and name resolution following Etard, Morrill, & Newbold (2020) and Cooke, Bates, and Eigenbrod (2019) followed as much as possible the taxonomy of the International Union for Conservation of Nature Red List (IUCN Red List, https://www.iucnredlist.org, Version 2021-1) or – if a species was not represented on the IUCN Red List - the Integrated Taxonomic Information System (ITIS, https://www.itis.gov, Version 26-july-2021). I gathered taxonomic information from multiple sources because, to date, there is no single dataset that contains all the taxonomic information needed to resolve potential synonyms, and to return a coherent and full taxonomic classification for the analysis (Cooke, Bates, et al., 2019; Etard et al., 2020). After this process, I ended up with 2,974 unique species (2,697 birds, 189 mammals and 88 reptiles).

All taxonomic information (synonyms, accepted names, and upward taxonomic classification to the level of class) was retrieved directly from the online repositories of the aforementioned institutions using the R package *taxize* Version 0.9.95 (S. Chamberlain, Szoecs, et al., 2020) (more details are given in Appendix 2 Section 1).

4.3.2 Trait data

I compiled life-history trait data from 24 open-access datasets and published scientific papers (Table 3). The final trait dataset encompassed more than 21,000 species of birds, mammals, and reptiles. The underlying trait data from those studies was collected over several decades. Consequently, there is not a cohesive taxonomy across them. For this reason, same as for the species assemblage data, I ran a taxonomic and synonym resolution analysis. After this, more than 87% of species for which I found trait information were represented in multiple trait datasets. When multiple estimates of life-history traits for the same species were available in the same or different datasets, values were log-transformed, and the arithmetic mean calculated. The mean estimate was then back-transformed and incorporated into the final trait dataset.

I found complete trait information for 15% of the species present in the life-history trait database, and 13% of the terrestrial vertebrate species sampled in the PREDICTS database (Table 4, Figure 8). Therefore, imputation was needed to get complete trait data for the 2,782 species present in the PREDICTS assemblages for which I had incomplete life-history trait information. To impute those missing values, I performed a random forest phylogenetic imputation (Penone et al., 2014), using the first ten eigenvectors derived from a synthetic TimeTree phylogenetic tree (Hedges et al. 2015). I could not find phylogenetic data for 24.16% of the species used for the imputation. To address this issue, I also added taxonomic class, order, and family, for which I had complete information, as a proxy for phylogeny (see also Appendix 2 Section 3). To add taxonomic classification into the imputation process I transformed the different taxonomic levels into numerical vectors. The combination of phylogeny and taxonomic information proved to be effective in reducing imputation bias (Appendix 2 Figure S1). In addition to the target species, I also included other terrestrial vertebrate species for which I had data for at least three of the five traits (a total of 6,644 extra species, see Table 4 & Figure 8). By doing this, I increased the overall trait completeness of the data used for the imputation, and reduced imputation errors (Appendix 2 Figure S1-2). Imputations were performed using the R package *missForest* Version 1.4 (Stekhoven et al., 2012) (for details see Appendix 2 Section 3).

Table 4. Percentage of "real" data (non-imputed) of each of the life-history traits present in the full data (species in the PREDICTs dataset and additional species) and the PREDICTs data (species used in the analysis). Percentages of non-imputed data are presented as total averages by life-history trait variable, life-history trait variable and class, and total overall completeness by dataset and class (**Overall completeness**). The total number of species and the number of species by class of each dataset can be seeing at the bottom of the table.

	All data			**PREDICTs data**		
Life-history Trait	**% of species with real data**			**% of species with real data**		
Number of offspring	0.9141194	Aves	0.8484	0.7754911	Aves	0.7604
		Mammals	0.9638		Mammals	0.8492
		Reptiles	0.9896		Reptiles	0.9291
Sexual maturity	0.4440632	Aves	0.3333	0.1954599	Aves	0.1741
		Mammals	0.6684		Mammals	0.4787
		Reptiles	0.3959		Reptiles	0.2677
Longevity	0.6101061	Aves	0.4547	0.3074524	Aves	0.2681
		Mammals	0.8213		Mammals	0.6230
		Reptiles	0.6718		Reptiles	0.4094
Body mass	0.9954252	Aves	0.9991	0.9975055	Aves	0.9996
		Mammals	0.9986		Mammals	1
		Reptiles	0.9837		Reptiles	0.9449
Yearly reproductive events	0.5786026	Aves	0.3911	0.2525725	Aves	0.2097
		Mammals	0.7139		Mammals	0.5213
		Reptiles	0.8023		Reptiles	0.5433
Overall completeness	0.7084633	Aves	0.6053	0.5198	Aves	0.4691
		Mammals	0.8332		Mammals	0.5806
		Reptiles	0.7687		Reptiles	0.6024

Number of species		**Number of species**	
Aves	4,638	Aves	2,697
Mammals	2,765	Mammals	189
Reptiles	2,215	Reptiles	88
Total	**9,618**	**Total**	**2,974**

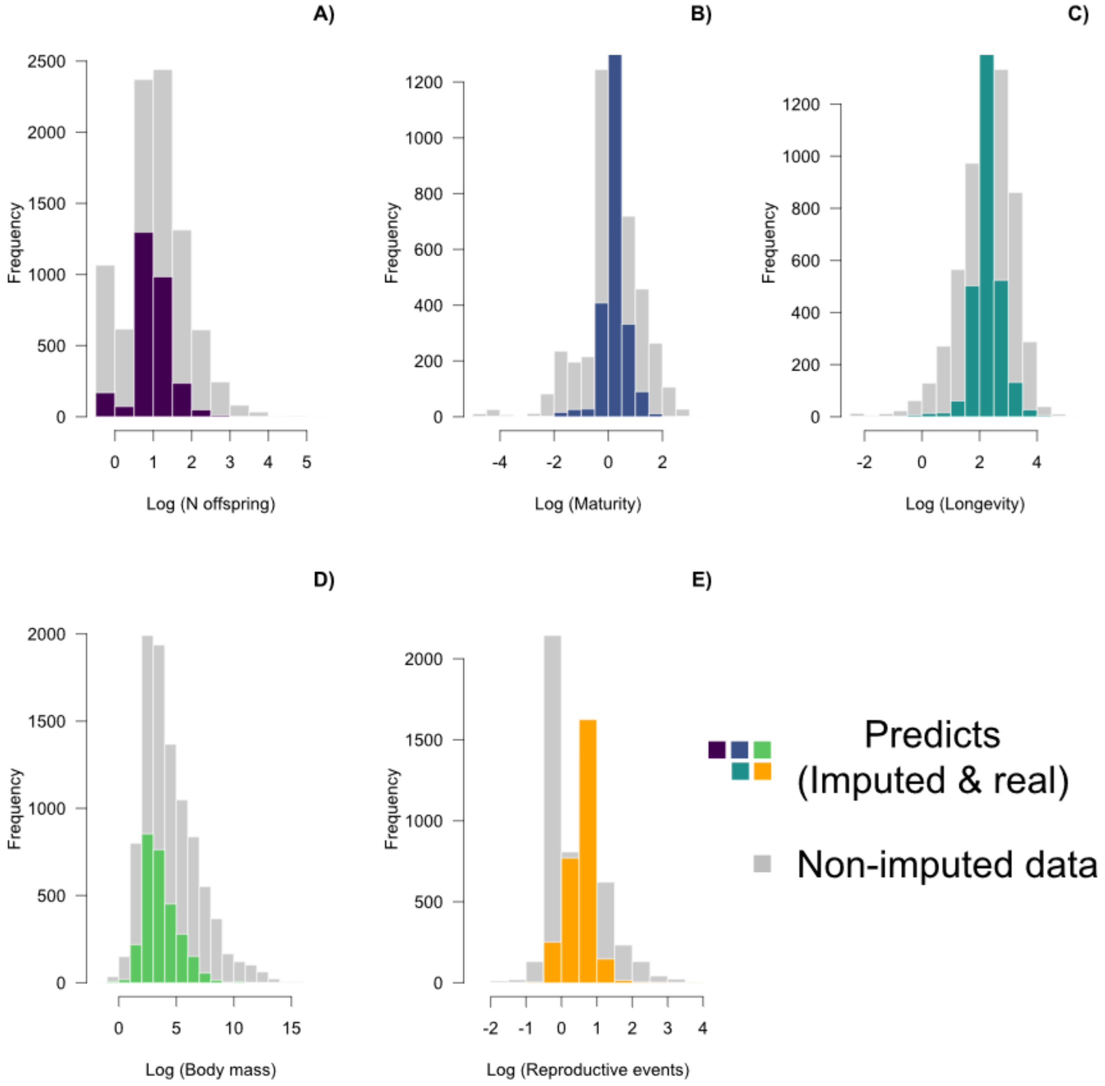

Figure 8. Distribution of the log-transformed life-history traits used to build the life-history diversity metrics and the fast-slow continuum; A) number of offspring; B) Maturity; C) Longevity; D) Body mass; and E) Yearly reproductive events (**reproductive events**). Colour filled histograms represent the distribution of life-history traits for the subset of species from the PREDICTs dataset (2,974 species; 2,697 birds, 189 mammals, and 88 reptiles)/ Grey shaded histograms represent the non-imputed data from the data used for imputations (9,618 species; 4,638 birds, 2,765 mammals, and 2,215 reptiles).

4.3.3 Life-history strategies

To place the species along the fast-slow continuum, first I removed the effects of body size and kinship from the life-history traits. Body size and phylogeny have a strong effect on life-history traits (Hillesheim & Stearns, 1992; Sæther, 1987; Stearns, 1983). Small species can grow faster and allocate more energy into reproduction than big species that require more time to reach their adult sizes and sexual maturity. This body-size influence can mask underlying important patterns of life-history variation (Dobson & Oli, 2007). At the same time, closely related species are likely to show similar body-sizes and reproductive strategies (Dobson & Oli, 2008; Stearns, 1983). Without removing the effects of these two factors from the life-history traits, comparisons between species of different size and taxonomic group are challenging, and could be misleading (Dobson & Oli, 2008; Stearns, 1983).

I performed this adjustment by regressing all the life-history traits against body mass, using linear mixed models (LMMs). To account for kinship, I included random intercepts representing the taxonomic classification of species (family nested within order, nested within class). All variables were log-transformed to account for the skewness of the data (for details, see the Appendix 2 Section 4). Residuals from these models were then used as log-transformed and body-mass-/kinship-adjusted trait variables in a Principal Component Analysis (Appendix 2 Table S4).

I applied this adjustment to all 9,618 species for which I could gather and impute life-history traits (see Appendix 2 Section 3 for details), representing 4,638 species, 2,765 mammals, and 2,215 reptiles. The first three axes of the PCA explained 82.6% of the total variation of the life-history traits and captured different facets of species' life-history strategies (Appendix 2 Table S4). The first PC represents the expected trade-offs between ageing and fecundity, thus representing the fast-slow continuum, classifying species from slow (low score values) to fast (high score values) (Appendix 2 Table S4). The second PC is mostly influenced by the number of reproductive events and classifies species from low productivity (low score values) to high productivity (high score values) (Appendix 2 Table S4). The third PC classifies species according to their longevity and number of offspring: species with low score values have shorter lifespans and low numbers of offspring, whereas species with high score values present longer lifespans and higher numbers of offspring (Appendix 2 Table S4).

Linear mixed-effects models were fitted using the R package *nlme* Version 3.1-157 (Pinheiro et al., 2021) and Principal Component Analysis was performed using the R package *ade4* Version 1.7-15 (Bougeard & Dray, 2018) (for details, see Appendix 2 Section 4).

4.3.4 Life-history metrics

To describe the life-history diversity of terrestrial vertebrate communities, I selected three different metrics, based on metrics commonly used in functional diversity studies (Mouillot et al., 2013; Villéger et al., 2008): life-history richness (LhR); life-history evenness (LhEv); and life-history divergence (LhDiv). These metrics are derived from their equivalent functional diversity metrics and are based here on the combination of the three life-history axes (Appendix 2 Table S4). Species richness can have a great impact on the calculation of functional diversity, and therefore also on the estimation of life-history diversity (Maire et al., 2015). There is no objective way in which to select an optimal number of species, however the methods used to calculate the life-history diversity metrics impose a minimum set of 8 species per assemblage (Villéger et al., 2008).

Life-history richness (LhR) is calculated as the volume of a three-dimensional convex hull formed by the three life-history axes. Communities with a greater variation of life-history strategies will show greater volumes, and thus higher life-history richness, compared to communities with a lower variety of life-history strategies. As with functional richness (Villéger et al., 2008), this metric is sensitive to the number of species included in the calculation.

Life-history evenness (LhEv) quantifies the regularity with which species fill the life-history space, formed by the life-history axes, weighted by species abundances. Values of LhEv are constrained between zero and one. When distances between species within the life-history space are regular, the index approaches one. LhEv decreases either when abundances are less evenly distributed among species or when life-history distances among species are less regular (Villéger et al., 2008).

Life-history divergence (LhDiv) represents how species abundances are spread within a volume defined by the life-history axes. In this case, the reference point is the centre of gravity or centroid of a volume formed by the life-history axes of the species within an assemblage. This index ranges between zero and one. When abundant species are very close to the centre of gravity (centre of the volume), relative to the rest of species the index gets close to zero. Conversely, if the most abundant species are located far away from the centre of gravity, the index approaches 1. Both LhEv and LhDiv are based on Euclidean distances between species and are independent of the convex hull area/volume, and thus the number of species (Villéger et al., 2008).

Differences in the values of the life-history diversity metrics among species assemblages will indicate overall changes in the life-history diversity of species, but do not allow us to detect if communities are becoming dominated by faster or slower species. Thus, I also calculated three metrics of central tendency and skewness, based on the first life-history axis, the fast-slow continuum: abundance-weighted life-history mean (LhM); abundance-weighted life-history median (LhMed); and abundance-weighted life-history skewness (LhSk). These three metrics describe how communities' life histories are positioned and distributed along the fast-slow continuum. Higher values of LhM and LhMed indicate that communities are dominated by faster species (i.e., where the most abundant species have faster life-history strategies), while lower values indicate that communities are dominated by slower species. LhSk indicates the skew in the distribution of assemblage life-history strategies. LhSk is estimated using the abundance-weighted Fisher coefficient of skewness (Chen, 1995). If LhSk has a value of zero, it means that the distribution of fast and slow life-history strategies is symmetrical in the assemblage. Negative or positive values of LhSk represent an asymmetry in the distribution of fast and slow life histories towards the fast (positive values of LhSk) or slow end of the continuum (negative values of LhSk).

4.3.5 Environmental heterogeneity

To evaluate the effect of environmental heterogeneity on the different life-history diversity and average life-history position variables, I selected a set of climate seasonality (describing changes in the overall climatic conditions within a year) and spatial land-cover heterogeneity variables. Land-cover heterogeneity variables were based on the textural features of the enhanced vegetation index (EVI), which captures spatial patterns in canopy structure and vegetation greenness. I selected two EVI-derived variables (Tuanmu & Jetz, 2015): EVI evenness (Evenness hereafter), and EVI correlation (Correlation hereafter). Evenness measures the numerical distance between EVI values of spatially adjacent pixels (Tuanmu & Jetz, 2015). This variable is sensitive to the structure of the vegetation canopy, with higher values associated with more heterogeneous or complex landscapes such as forests, grasslands, croplands, and built-up areas (Tuanmu & Jetz, 2015). Barren areas and shrublands have more homogeneous EVI values and therefore lower Evenness (Tuanmu & Jetz, 2015). Correlation measures the linear dependency between adjacent cells and can be interpreted as the spatial correlation of the vegetation cover (Tuanmu & Jetz, 2015). Higher correlation values are associated with low landscape fragmentation (e.g forest and grasslands), whereas lower values are associated with fragmented or patchy landscapes (e.g., croplands and urban areas) (Tuanmu & Jetz, 2015). The combination of these two variables, allowed us to define the overall landscape heterogeneity and fragmentation of the area surrounding each community. These variables, in combination with species life-history strategies, have proven to be important determinants of species spatial distribution (Chapter 3). All variables were downloaded directly from the EarthEnv project (http://www.earthenv.org/, Accessed 12th February 2021).

To account for climate heterogeneity, I considered temperature and precipitation seasonality. Both temperature and precipitation seasonality are important determinants of energy availability (Dobzhansky, 1950) and functional diversity patterns (Wieczynski et al., 2019), and have proven to be important factors for the distribution of species with different life-history strategies (Chapter 3). I extracted these two continuous variables from WorldClim Version 2.0 (https://www.worldclim.org/). This dataset contains climatic variables derived from long-term average climatic values, time-series of monthly averages by year, and daily weather data. The final climatic variables are the result of averaging and interpolation of averaged annual values from 1970 to 2000. Higher values of temperature and precipitation seasonality variables are associated with more climatically seasonal environments.

In addition to these variables, I included the land-use disturbance information from the PREDICTS database. Adding this information into the analysis allowed us to explore how human pressures, landscape heterogeneity, and climatic seasonality affects life-history diversity and average life-history position of terrestrial vertebrate communities.

4.3.6 Statistical analysis

To account for the hierarchical structure of the PREDICTS dataset, I used linear mixed-effects models. I fitted six models, one for each life-history diversity metric (life-history richness, life-history evenness, life-history divergence, weighted life-history mean, weighted life-history median, and weighted life-history skewness) as response variables. Explanatory variables were: 1. PREDICTS land-use category; 2. land-cover and climate heterogeneity variables (EVI correlation, EVI evenness, precipitation seasonality and temperature seasonality); 3. all the possible two-way interactions between land-use category and land-cover/climatic heterogeneity variables. Some of the life-history diversity metrics are known to be sensitive to the number of species in the community (Villéger et al., 2008). Even though the species assemblages were filtered based on the number of species within each community, this factor varied widely across communities (from 8 to 165). Therefore, I added the number of species in each community as a covariate in all models, to control for the possible effects of this variation between communities. To account for non-independence between species assemblages (samples that came from the same original source publication and study are not completely independent of one another), I added a random intercept in the form of the concatenation of source identity and study identity (see above for definitions of source and study, and Hudson et al., 2014 and S6 for more details). This random structure had a better model fit (according to AIC values) compared to other possible random-structure combinations tested: study identity nested within source identity; the combination of study identity and source identity; spatial block nested within study identity nested within source identity; spatial block, study identity and source identity combined; spatial block nested within study identity; spatial block and study identity combined; study identity; and source identity. None of the variables included in the models presented collinearity problems (variance inflation factors were lower than 5 for all explanatory variables, while pairwise correlation values were lower than 0.7 in all cases).

Models were fitted by restricted maximum likelihood, and further reduced using a backward stepwise selection procedure. In this process, the initial model is re-run multiple times dropping one of the terms that contribute to the increase of the overall AIC value of the model (Yamashita et al., 2007). This process was repeated until the model with the smallest AIC was found. This way, I found the best performing models for each life-history variable (Appendix 2 Table S5). LMMs were implemented in the R Package *lme4* Version 1.1-26 (Bates et al., 2015), and were then reduced using the *step* function implemented in the R package *lmerTest* Version 3.1-3 (Kuznetsova et al., 2017). Model fit was evaluated using conditional and marginal pseudo-R^2 values (Nakagawa et al., 2017), calculated using the R Package *MuMin* Version 1.43.17 (Barton, 2020).

To meet the linearity assumptions of the model, all variables were normalized using the Ordered-Quantile transformation (Qing Liu & Pierce, 1994) implemented in the R package *bestNormalize* Version 1.6.0 (Peterson & Cavanaugh, 2019).

The number and configuration of species in each site, as well as the number of species assemblages included in the analysis, can influence the inferred responses. Therefore, I evaluated the robustness of the results by re-running the models using different thresholds for the minimum number of species sampled within each assemblage. By changing this threshold, I was able to modify the number of species and sites included in the analysis. I compared thresholds of 10, 15 and 20 species, which gave me sample sizes of 1,886, 924 and 578 species assemblages, respectively.

4.4 Results

Assemblage life-history diversity and life-history strategies varied across land-use types, and with climate and land-cover heterogeneities. Assemblages in more human-impacted areas (plantation forest, pasture, and cropland) consisted of a greater range of life-history strategies (higher values of life-history richness) with a lower spread of dominant species (lower values of life-history divergence) (Figure 9, Table 5 and Appendix 2 Table S6). These land-use types were also associated with a decrease in the regularity of life-history strategies (lower values of life-history evenness) (Figure 9, Table 5 and Appendix 2 Table S6). Human-impacted land uses tended to be dominated by species with faster life-histories on average (higher values of weighted life-history mean, weighted life-history median, and weighted life-history skewness) compared to primary vegetation (Figure 9, Table 5 and Appendix 2 Table S7). Assemblages in areas of higher temperature seasonality also tended to present wider ranges of life-histories (higher values of life-history richness) and were also dominated by fast-lived species (higher values of weighted life-history mean and weighted life-history median) (Figure 10.a, Table 5-5 and Appendix 2 Table S6-S7). However, these patterns of response varied across land-use types, with species assemblages inhabiting agricultural land uses (pasture and cropland) being less sensitive to temperature seasonality (Figure 10.b-c, Appendix 2 Table S7). Similarly, assemblages in pasture with high values of vegetation heterogeneity (EVI evenness) presented lower values of life-history divergence (Figure 11, Table 5 and Appendix 2 S6).

Model performance varied depending on the life-history response variable considered. Life-history richness (LhR) presented the best fit, with values of conditional and marginal pseudo-R^2 scores of 0.755 and 0.191, respectively. The rest of the models had conditional pseudo-R^2 values ranging from 0.24 to 0.654 and marginal pseudo-R^2 values from 0.058 to 0.115 (for details on model performance see Appendix 2 Table S5; for a detailed comparison of model results see Appendix 2 Table S6-7).

Table 5. Results of the linear mixed-effects model (LMM) for the life-history diversity metrics (life-history richness, life-history evenness, and life-history divergence). ANOVA results based on a Kenward-Roger F test. Model terms included PREDICTS land use (**LU**), precipitation seasonality (**Prep**), temperature seasonality (**Temp**), and EVI correlation and evenness (**EVI Cor** and **EVI Eve** respectively). Terms given as '--' were not present in the respective model because they were excluded during the model selection procedure (see **Statistical analysis**). Significant terms are marked in bold with stars indicating the level of significance (P value: < 0.001***, < 0.01**, and < 0.05*). Individual model results are presented in Appendix 2 Table S6.

	Life-history richness		**Life-history evenness**		**Life-history divergence**	
	F-value : d.f.	p-value	F-value : d.f.	p-value	F-value : d.f.	p-value
LU	**10.348 : 4**	**<0.001*** **	**2.922 : 4**	**0.02***	2.111 : 4	0.076
Prep	0.724 : 1	0.395	--	--	--	--
Temp	**4.226 : 1**	**0.04***	1.04 : 1	0.309	--	--
EVI Cor	0.409 : 1	0.522			0.092 : 1	0.76
EVI Eve	0.217 : 1	0.641	1.172 : 1	0.991	0.012 : 1	0.911
LU: Prep	2.369: 4	0.05	--	--	--	--
LU: Temp	--	--	--	--	--	--
LU: EVI Cor	--	--	--	--	0.43 : 4	0.786
LU: EVI Eve	2.084 : 4	0.08	--	--	**2.611 : 4**	**0.0338***
Spp count	**601.765 : 1**	**<0.001*** **	**10.076: 1**	**0.001** **	1.75 : 1	0.186

Table 6. Results of the linear mixed-effects model (LMM) for the average and distribution of life-history strategies (life-history mean, life-history median, and life-history skewness). ANOVA results based on a Kenward-Roger F test. Model terms included PREDICTS land use (**LU**), precipitation seasonality (**Prep**), temperature seasonality (**Temp**), and EVI correlation and evenness (**EVI Cor** and **EVI Eve** respectively). Terms given as '--' were not present in the respective model because they were excluded during the model selection process (see **Statistical analysis**). Significant terms are marked in bold with stars indicating the level of significance (P value: < 0.001***, < 0.01**, and < 0.05*). Individual model results are presented in Appendix 2 Table S7.

	Life-history mean		**Life-history median**		**Life-history skewness**	
	F-value : d.f.	p-value	F-value : d.f.	p-value	F-value : d.f.	p-value
LU	**45.201 : 4**	**<0.001*** **	**20.579 : 4**	**<0.001*** **	**6.166 : 4**	**<0.001*** **
Prep	1.517 : 1	0.218	--	--	2.048 : 1	0.154
Temp	**8.201 : 1**	**0.004** **	**5.567 : 1**	**0.019***	**5.619 : 1**	**0.019***
EVI Cor	2.509 : 1	0.113	0.004 : 1	0.944	--	--
EVI Eve	--	--	--	--	--	--
LU: Prep	--	--	--	--	--	--
LU: Temp	**4.913 : 4**	**<0.001*** **	**2.732 : 4**	**0.027***	0.93 : 4	0.445
LU: EVI Cor	--	--	0.525 : 4	0.716	--	--
LU: EVI Eve	--	--	--	--	--	--
Spp count	0.371 : 1	0.542	**4.823 : 1**	**0.028***	**6.808 : 1**	**0.009** **

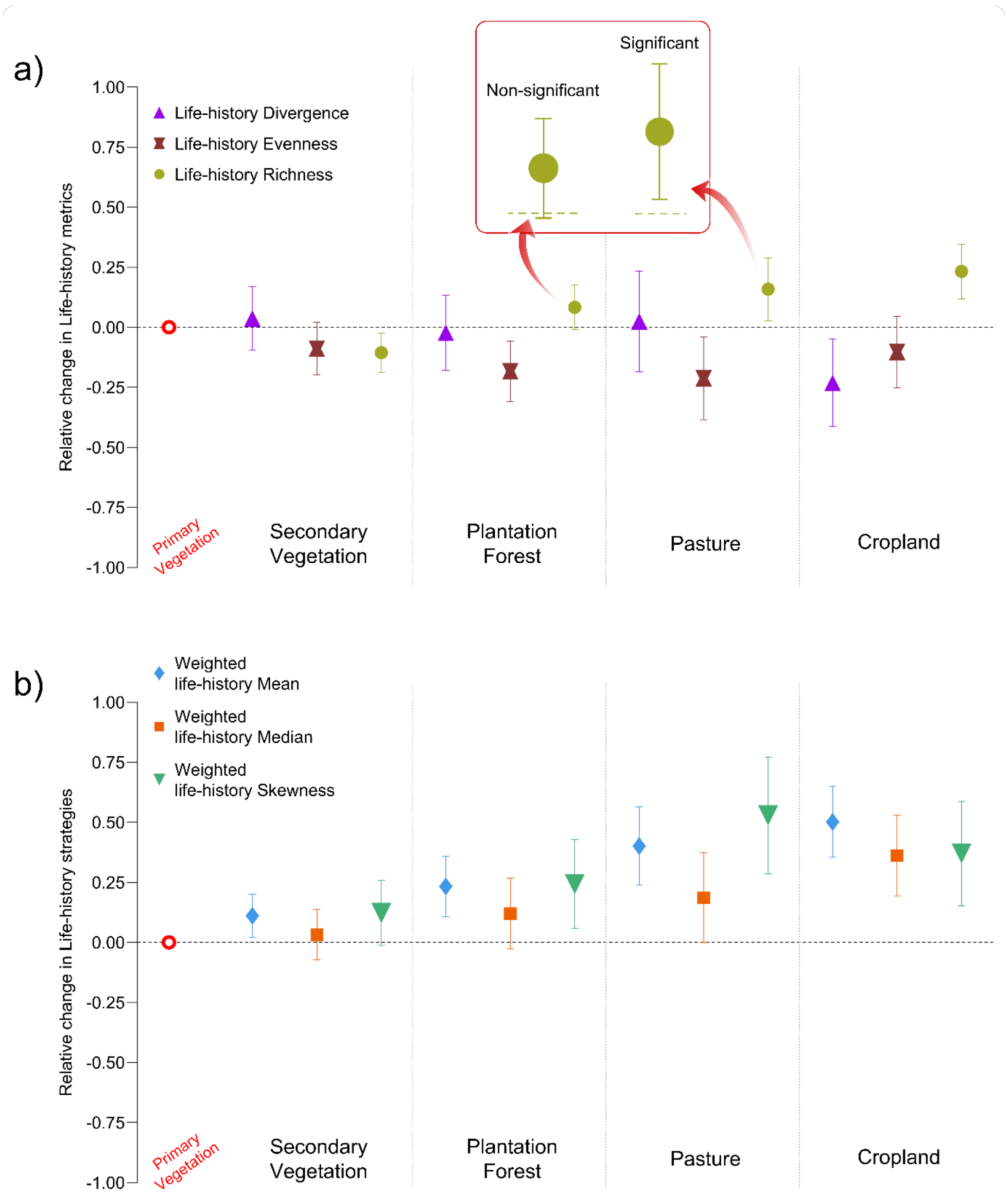

Figure 9. **Response to land use of life-history diversity and the average and distribution of life-history strategies. a**, responses of the life-history diversity metrics: life-history divergence, triangles; life-history evenness, hourglass shapes; and life-history richness, circles. **b**, responses of average life-history strategies (position of the community along the fast-slow continuum): weighted life-history mean, diamond; weighted life-history median, squares; and life-history skewness, inverted triangles. Points represent the change in response of the different metrics to land use when all the other variables included in the models are held at their means, this is their relative change. Primary vegetation is treated as the reference level (shown as empty red circles). Error bars represent 95% confidence intervals of the estimates; if this confidence intervals or the main points intersect with 0, term effects are considered non-statistically different from the reference level. If the term estimated effects and their respective confidence intervals do not intersect with 0, the term effects are considered statistically significantly different than the reference level (see Appendix 2 Table S6-S7 for the numeric values and model details). The total sample size in all cases was 2,058 assemblages (Primary vegetation=611; Secondary vegetation=492; Plantation Forest=397; Pasture=259; and Cropland=299).

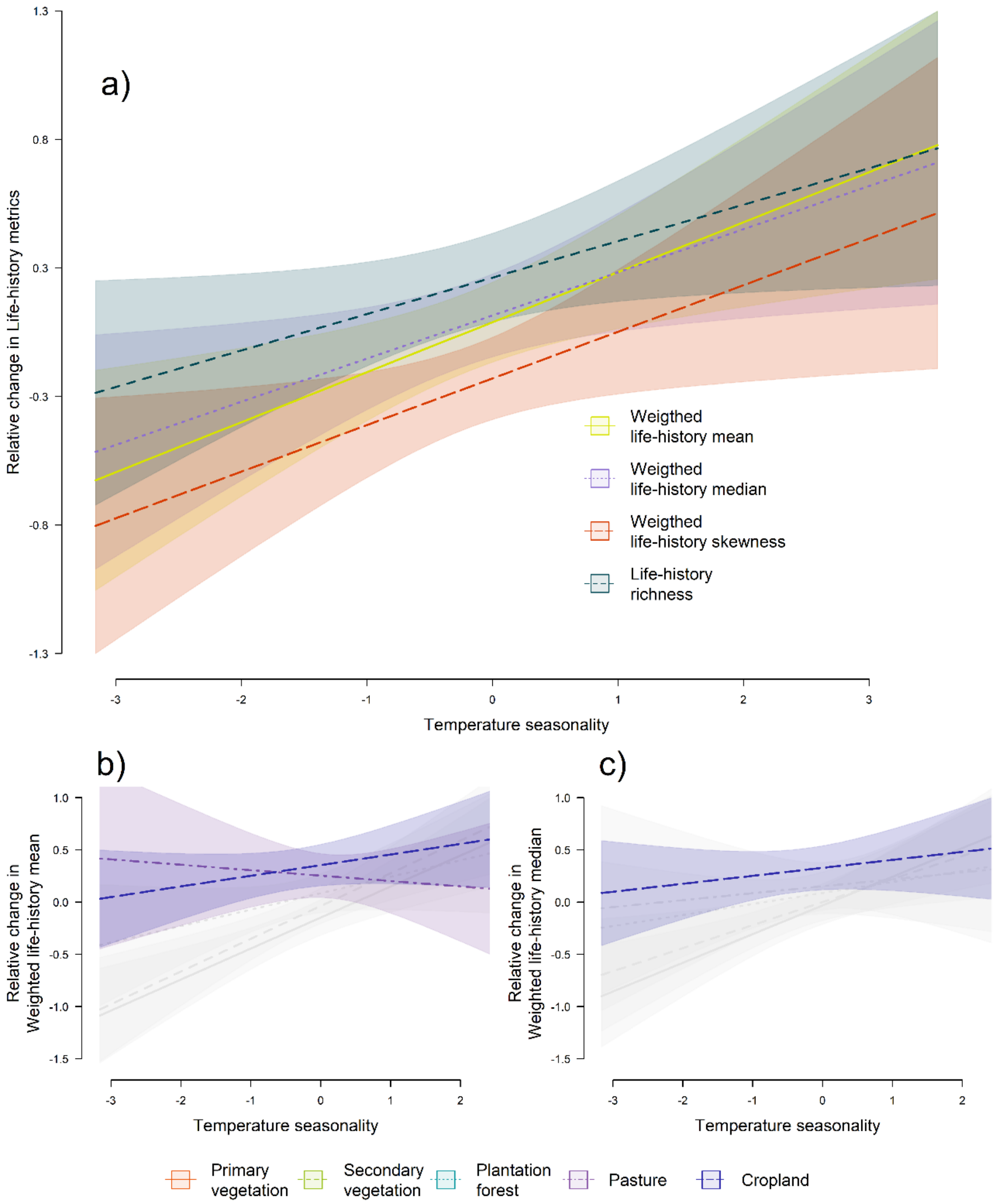

Figure 10. **Response of life-history metrics to temperature seasonality**. **a**, partial response of weighted life-history mean and median (solid and dotted line respectively), life-history skewness (long-dashed line), and life-history richness (short-dashed line) to temperature seasonality. **b** and **c** show the response of weighted life-history mean (**b**), and weighted life-history median (**c**) to temperature seasonality for individual land uses. In **b** and **c**, lines represent the different land uses; primary vegetation; secondary vegetation; plantation forest; pasture; and cropland. Coloured lines represent slopes that are statistically significantly different relative to primary vegetation (P < 0.05), and grey lines represent slopes that are not significantly different compared with primary vegetation (see Appendix 2 Table S6-S7 for significance levels and model details). Shaded areas, in all panels, represent 95% confidence intervals.

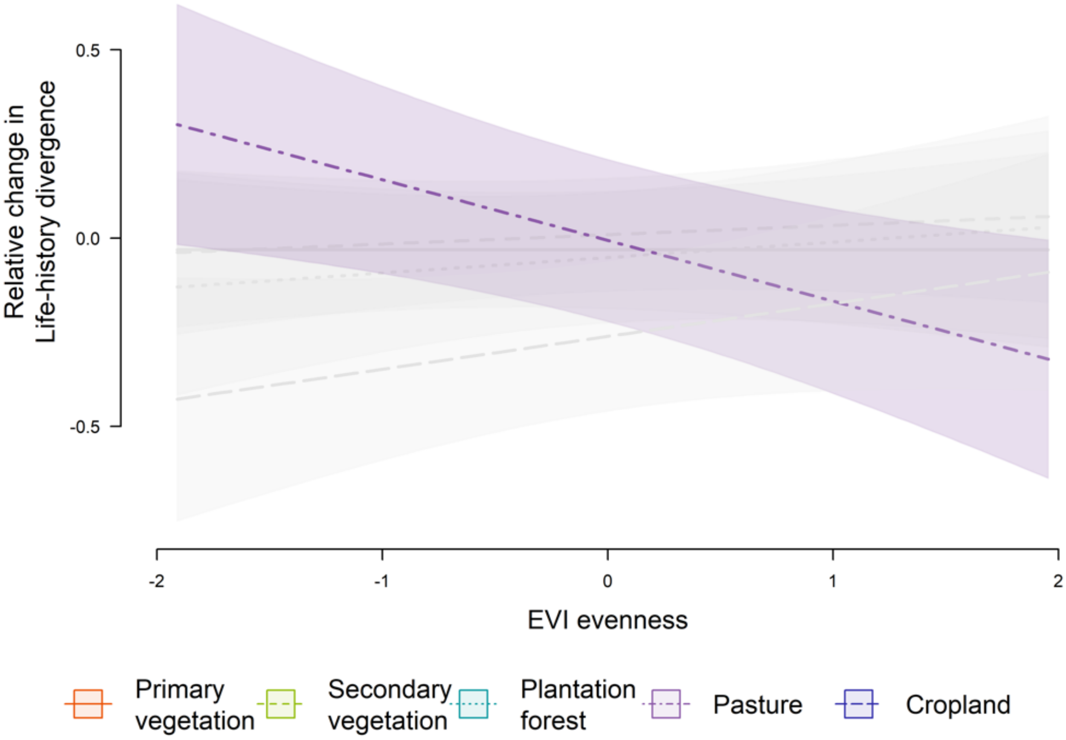

Figure 11. **Response of life-history divergence to vegetation heterogeneity (EVI evenness)** in different land uses. Lines represent the different land uses: primary vegetation; secondary vegetation; plantation forest; pasture; and cropland. Coloured lines represent slopes that are statistically significantly different relative to primary vegetation (P < 0.05), and grey lines represent slopes that are not significantly different compared with primary vegetation (see Table S6 for significance levels and model details). Shaded areas represent 95% confidence intervals.

4.4.1 Sensitivity analyses

The magnitude of the observed effects, but also their uncertainty, increased with higher thresholds for the minimum number of sampled species per assemblage (Appendix 2 Figure S5). Despite this variation in the strength of the inferred effects, most remained statistically significant across the different datasets (see Appendix 2 Figure S5 and Table S8). In terms of effect direction and statistical significance, results tended to be robust for some of the fast-slow continuum metrics (LhM, and LhMed), but more variable for LhEve and LhSk (Appendix 2 Figure S6 and Table S8).

4.5 Discussion

Here, I show that terrestrial amniote vertebrate communities (reptiles, birds, and mammals) inhabiting more human-impacted and environmentally heterogeneous habitats (in terms of climatic seasonality and land-cover heterogeneity): 1) are dominated by species located close to the fast end of the fast-slow continuum; and 2) have a higher diversity of life-history strategies. The results also show a shift toward dominance by fast species with an increase in temperature seasonality. However, species assemblages in more human-impacted land uses showed smaller differences in life-history strategies in response to temperature seasonality. Land-cover heterogeneity influenced life-history diversity (life-history richness and life-history divergence) depending on the land-use conditions. These findings support theoretical predictions that suggest that species inhabiting more variable environments are exposed to stochastic, or density-independent, mortality events and therefore their life cycles need to be fast to recover and maintain their populations (MacArthur & Wilson, 1967; Pianka, 1970).

As expected, species assemblages in more temperature-seasonal environments tended to become dominated by species with faster life-history strategies. Similar patterns have been observed when comparing life-history traits and life-history strategies of tropical and non-tropical vertebrate species (Wiersma et al. 2007). Importantly, I found that responses to temperature seasonality are land-use dependent, with more human-impacted habitats showing less pronounced changes. This can in part be explained by the communities that reside within different land uses. Human land uses impose a filter on species (Saladin et al., 2020; Vellend et al., 2007). Human-disturbed land uses are more likely to have lost narrowly distributed species (Newbold et al., 2018), which are more likely to have slow life-histories, in favour of more generalist species, which are usually characterized by fast life-history traits (Allen et al., 2017; Capellini et al., 2015). As a result, differences in assemblage structure along climate gradients within human-impacted habitats are likely to be more limited.

My previous chapter showed that fast-lived species are more likely to be present in more heterogeneous and climatically seasonal habitats (Chapter 3). Therefore, under these conditions, I expected to see a decrease in the range of life-histories (life-history richness) and an increase in the spread of dominant species (higher values of life-history divergence and lower values of life-history evenness). The observed results matched some of the predictions about life-history evenness but contradicted the expectations about life-history richness and life-history divergence. This can be in part explained because landscape heterogeneity generally has a positive effect on functional diversity (Hatfield et al., 2018). For example, heterogeneous pastures, surrounded by forest or containing small patches of trees, host a wider diversity of species (Athayde et al., 2015; Oksuz et al., 2020). In this case, life-history richness increased with the increase of climatic seasonality and human disturbance whereas life-history divergence remained mostly constant. These results suggest that communities are becoming dominated by fast-lived species with a low spread of species life-histories, highlighting the complex relationship between species traits, environmental complexity, and human impacts.

Although most results were consistent with the initial hypotheses, some were unexpected. For example, the fact that life-history richness increased in more temperature-seasonal and more human disturbed land uses. In part, this result can be explained by the behaviour of the convex volume used to calculate life-history richness. The convex volume is sensitive to the number of species in the community and the position of these species within life-history space (Villéger et al., 2008). In this case, only the species located at the edges of the volume contribute to the expansion/contraction of the convex hull. Therefore, if a community contained few species with highly contrasting life-history strategies, even if those species were not abundant, life-history richness will be high. This could occur if communities do not lose slow-lived species in human-impacted and temperature seasonal areas, while at the same time gaining fast-lived species. This explanation is consistent with observed responses of life-history skewness and life-history divergence. Both results suggest that changes in the community's life-history diversity are mostly driven by species with extreme life-history strategies. However, as with all correlative approaches, determining a definitive mechanism behind the observations is not possible.

It is obvious now that, to clearly understand which mechanisms are the main drivers of community life-history changes, further research is needed. In this aspect, beta-diversity partitioning can be a useful tool. Beta-diversity (β-div hereafter), among other things, describes changes on community composition (Tuomisto, 2010). Therefore, by looking at the changes on β-div across different land-uses and communities, we should be able to detect if life-histories strategies are being completely replaced across different communities or if certain land-uses are more prone to preserving certain life-histories while others become rarer. Similarly, we should expect some land-uses to be more redundant, in terms of life-history strategies, than others. For example, we can expect high human-disturbed habitats to share more species between them (anthropogenic homogenization of communities; e.g Brice, Pellerin, & Poulin, 2017; Gossner et al., 2016; Vellend et al., 2007), even if the distance between these habitats is large (e.g Clavel, Julliard, & Devictor, 2011), than pristine or less human-disturbed ecosystems. In this aspect, dissimilarity-distance curves might help us to better understand how life-history diversity change within different land-uses. Combining β-div partitioning with dissimilarity-distance curves might be a useful and informative way to shed some light into the mechanisms behind my results. However, other drivers such as extinction debts and interspecific competition might also be playing a fundamental role in the configuration of communities' life-histories. In those cases, mathematical simulations might aid to reconstruct the most likely mechanism of life-history community change.

The study, like all broad-scale analyses, includes many uncertainties. First, the fast-slow continuum is based on partially imputed data. Even though I took measures to minimize the imputation error (see Supplementary Material, S3 and S4), imputed estimates are associated with some level of uncertainty, which will carry over into the life-history classification. Second, the distribution of the communities is spatially biased. Most of the communities are in the tropics, in south and central America, and Oceania (Figure 7). I have more limited information for communities in North America, Europe, Eurasia, and Africa. Third, I am using spatial, rather than temporal data, so I am seeing a snapshot of species assemblages at the time of the sampling, rather than studying how species assemblages have changed over time due to environmental disturbances. Furthermore, this type of approach does not allow us to determine whether there might have been lags in the response of communities' life-histories. This can bias the inferences from spatial comparisons. Despite these limitations, I was able to encompass a wide range of life-history strategies, land-use types, land-cover heterogeneities, and climatic seasonality within the sample of vertebrate assemblages. I am confident that this combination of factors allowed us to build a fair representation of the state of communities' life-history diversity under multiple environmental conditions. The results from the sensitivity analysis (see Appendix 2 Section 6) suggested a good degree of consistency in the results.

The change of communities from slow to fast in human-impacted and climatically variable habitats is of concern for biodiversity conservation. Fast-lived species tend to be habitat and dietary generalists, widely distributed, and potentially invasive (Allen et al., 2017; Capellini et al., 2015). These species have the potential to displace more sensitive, narrow-ranged, specialist species, thus causing homogenization of communities, and potentially major disruptions of ecosystem function (e.g Fricke and Svenning 2020; Colléony and Shwartz 2020). Overall, my results provide consistent evidence that human impacts in the form of land use and changes in land-cover heterogeneity, as well as climatic seasonality, influence community life-history diversity and average life-history strategies, transforming natural vertebrate assemblages. Under the current predictions of future human population growth (Tilman et al., 2017), land-cover expansion (Riahi et al., 2017), and climate change (IPCC, 2021), the relationships observed in this study suggest that all those factors will coincide to drive further shifts toward dominance by fast-lived species into the future. These results have important implications for biodiversity conservation, community and ecosystem management, and biodiversity change.

Chapter 5: Species life-history strategies affect population responses to temperature and land-cover changes

5.1 Abstract

Despite an increase in conservation efforts, animal populations have experienced substantial declines in recent decades. It is therefore fundamentally important to understand which are the characteristics driving species response to environmental degradation. Theoretically, species life-history strategies are key determinants shaping the response of populations to environmental impacts. Despite this, the association between species life-histories and the response of populations to environmental changes has not been tested. In this experiment, I analysed the effects of recent land-cover and temperature changes on rates of population change of 1,072 populations from 461 terrestrial vertebrate species with different life-history strategies. I showed that populations of fast-lived species inhabiting areas that have experienced recent expansion of cropland or bare soil present positive populations trends whereas slow-lived species displayed negative population trends. Additionally, fast and slow-lived species showed overall positive and negative population trends respectively. When land-cover and life-history strategies interact, I found that fast-lived species tend to have positive population rates when cropland and bare-soil expand whereas slow-lived species showed negative population trends under the same conditions. These findings support previous hypotheses that fast-lived species are better adapted to recover their populations after a stochastic mortality event. With climate and land-use changes likely to increase in the near future, establishing clear links

between species characteristics and responses to these anthropogenic threats is fundamental to design and conduct conservation actions. The results of this study can be used to evaluate population sensitivity, assess extinction risk of species with poor data coverage and to predict future responses of biodiversity to environmental changes.

5.2 Introduction

We are facing a human-driven biodiversity crisis. The latest Living Planet Report estimated that monitored populations of the world's vertebrates have declined on average by 68% since 1970 (WWF, 2020), and that further decreases are expected into the future. Land-use change has been identified as one of the main drivers of global biodiversity loss (Newbold et al., 2015; WWF, 2020), while the effects of climate change on biodiversity are likely to intensify in the next decades (Newbold, 2018). In this context, prioritisation of especially sensitive biomes and species is essential to allocate conservation efforts and reduce biodiversity loss (Strassburg et al., 2020; Watson et al., 2020). However, to design long-term effective conservation strategies, we first need to understand the factors that determine how species and communities respond to environmental changes (D. Keith et al., 2015).

It is known that climate warming affects species and communities, causing species range shifts (Parmesan & Yohe, 2003), phenological changes and asynchrony of biological processes (Donnelly et al., 2011), and species extinctions (Román-Palacios & Wiens, 2020; Sinervo et al., 2010; Spooner et al., 2018). Similarly, land-use changes cause habitat destruction and fragmentation (Daye & Healey, 2015), homogenisation of communities (Gossner et al., 2016), and loss of species richness (Murphy & Romanuk, 2014). Furthermore, the interaction between climate warming and land-use change can exacerbate these effects (Northrup et al., 2019). Predicting how species are going to respond to climate and land-use changes is of paramount importance. Previous studies have shown that species with certain traits are more sensitive than others (e.g. Laliberté et al., 2010; Pacifici et al., 2015, 2017). However, these patterns varied across taxonomic groups and traits, making extrapolations of species' response to environmental change challenging (Laliberté et al., 2010; Pacifici et al., 2015, 2017). It is necessary then, to find a more generalized and taxon-independent approach to predict the response to environmental changes.

Species life-history strategies can serve as a proxy to evaluate species' sensitivity to environmental changes and extinction risk (Kosydar, 2014; Richards et al., 2021). Life-history strategies are defined by the intrinsic trade-offs between species traits related to ageing (e.g., longevity, growth rates or maturity) and fecundity (e.g., litter/clutch size or frequency of reproduction) (Dobson & Oli, 2007, 2008) Depending on their values of these life-history traits, species can be positioned along a continuum from fast- to slow-lived species (Stearns, 1983a; Read & Harvey, 1989). Species located towards the faster end of the continuum (fast species hereafter) have higher fecundity and shorter lifespans. In contrast, species closer to the slower end of the continuum (slow species hereafter) display longer lifespans and lower fecundity. Life-history strategies are important determinants of species' extinction risk (Hutchings et al., 2012; Tingley et al., 2013), invasiveness (Allen et al., 2017; Capellini et al., 2015), and dispersal (Bonte et al., 2012; Soriano-Redondo et al., 2020).

The two previous experimental chapters of this thesis have also shown that life-history strategies correlate with species' responses to habitat heterogeneity and land-use disturbance (Chapters 3 and 4 respectively). Additionally, animal communities tend to become dominated by fast-lived species in more human disturbed land use habitats (Chapter 4). Previous studies looking at traits related with ageing and fecundity have found that, In general, species with fast-lived related traits were more likely to be present in more human-impacted land-use areas whereas slow species thrive in less impacted habitats (Newbold et al., 2013). Fast and slow species also respond differently to climate change. Generally, species with fast life-history traits tolerate and, in some cases benefit, from climate warming (Lehmann et al., 2020; Pacifici et al., 2017). On the other hand, species with slow life-history traits were more sensitive to climate warming (Pacifici et al., 2017; Richards et al., 2021). This collection of evidence show that that life-histories are important factors influencing the response of species and communities to climate warming and human driven land-use disturbance. However, the role of species life-history strategies in shaping population trend responses to environmental changes is still unclear.

Theoretically, fast and slow species have different population-regulation mechanisms (MacArthur & Wilson, 1967). According to *r*/*K*-selection theory, fast species, or *r*-selected species, show density-independent or stochastic mortality events, with their populations unable to reach the environmental carrying capacity (MacArthur & Wilson, 1967; Pianka, 1970). Owing to their rapid fluctuations, populations of fast species are, theoretically, adapted to recover their populations faster than slow species (Pianka, 1970). Slow species, or *K*-selected species, show density-dependent mortality (MacArthur & Wilson, 1963; Pianka, 1970). These species are adapted to maintain stable populations close to the carrying capacity of the environment, and take longer to reach this population level after a stochastic mortality event (Pianka, 1970). For this reason, slow species are usually considered more sensitive to environmental changes and thus more likely to show population declines due to human impacts (e.g., Bird et al., 2020). Although these ideas are frequently used in ecology and conservation, the role of life-history strategies in shaping the response of species populations to environmental changes has not been empirically tested at a large scale (Stephen C. Stearns, 2000; W. J. Sutherland et al., 2013).

Large databases of population trends, such as the Living Planet Database (LPD) which holds the data underlying the Living Planet Index (LPI), allow us to explore changes in vertebrate populations over time. The LPI was developed to measure the changing state of the world's biodiversity (WWF, 2020), and relies on time-series data to calculate average rates of change in populations of terrestrial, freshwater, and marine vertebrate species. Although this index has been widely adopted to report on global (WWF, 2020) and local biodiversity changes (e.g., van Strien et al., 2016), the LPI is not free from bias or criticism. Studies analysing the robustness of the LPI, have shown major changes in global populations trends depending on the inclusion or removal of a small fraction of populations with extreme trends (Leung et al., 2020, see also Leung, Hargreaves, Greenberg, McGill, & Dornelas, 2022; Leung, Hargreaves, Greenberg, McGill, Dornelas, et al., 2022b, 2022a; Loreau et al., 2022; Mehrabi & Naidoo, 2022; Murali, de Oliveira Caetano, Barki, Meiri, & Roll, 2022; Puurtinen, Elo, & Kotiaho, 2022, for an extended discussion). Similarly, random population fluctuations can compromise the accuracy of the LPI even if, on average, populations remain stable, especially when populations are small (Buschke et al., 2021). Furthermore, the underlying time-series data are biased, with a disproportionate representation of osseous fishes and birds compared to other vertebrate groups (these two groups represent almost 70% of the total populations in the LPD), and also towards populations receiving conservation interventions (Murali et al., 2022). Some of the taxonomic and geographical bias has been addressed recently through the development of a weighted LPI (McRae et al., 2017). Most of these issues arise from a lack of population-monitoring data, a limitation not restricted to the LPI (Hochkirch et al., 2021).

Population-monitoring data for most species are still rare (e.g Bland & Böhm, 2016), but their use in conservation is of paramount importance. For example, some criteria of the IUCN Red List of Threatened Species are based on population sizes (criteria C and D) and declines (criteria A and C) (IUCN, 2021). In this context of data deficiency and increasing need for biodiversity conservation, establishing clear links between species life-history strategies and populations trends under environmental changes can help us to: 1) identify groups of species whose life-history strategies make then more likely to be sensitive to climate and land-use changes; 2) establish a more general or extrapolatable relationship between species traits and responses to environmental changes; and 3) better predict how poorly monitored species would respond to future climate and land-use changes.

In this study, I explore how populations of terrestrial amniote vertebrate species (birds, mammals, and reptiles) with different life-history strategies respond to recent climatic and land-use changes. To do this, I use the population trends reported in the public LPD, together with information on species' life-history strategies, and information on land-cover and temperature changes. I extracted mean annual rates of population, temperature and land-cover change for 1,072 populations of 461 species of birds, mammals, and reptiles (273, 137 and 51 species, respectively), distributed across 553 locations globally (Figure 12). I hypothesised that species with different life-history strategies will show distinct population trends depending on recent climate and land-use changes where they occur. Fast-lived species are better adapted to colonize and expand after a stochastic mortality event. Therefore, I expect fast species to show positive population trends in more human-disturbed habitats, for example areas where croplands or urban areas are expanding. Conversely, I expect slow species, under the same conditions, to present declining populations since they are generally more sensitive to stochastic mortality events. I expect a similar response to climate change, with populations of fast-lived species responding positively to temperature warming whereas populations of slow-lived species respond negatively.

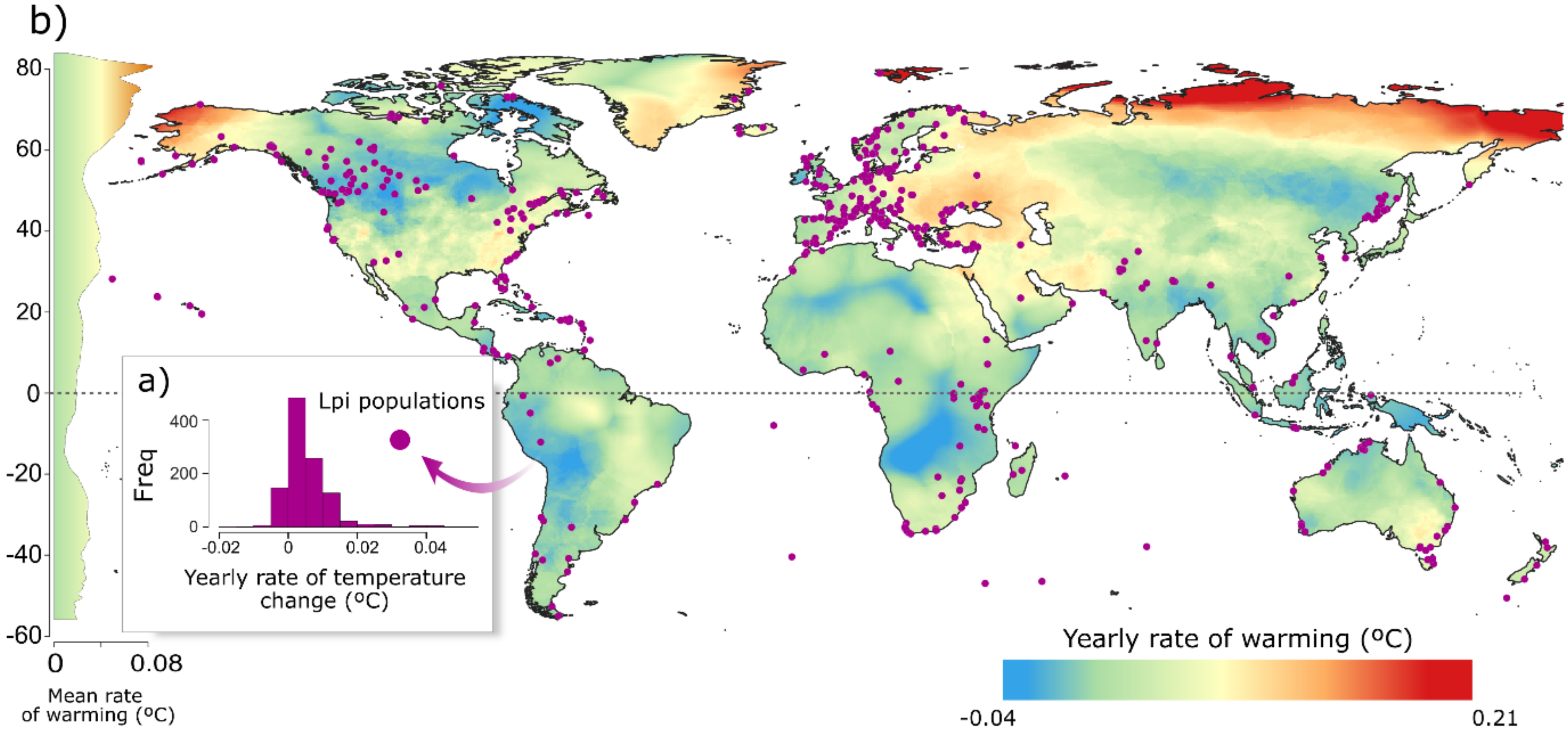

Figure 12. Distribution of the populations selected for the analysis (purple points), and the average rates of climate warming (annual mean temperature) for the period between 1992 and 2018 (base layer). Panel **a** show the yearly rate of temperature change (see **Climate and land-use data**) for the populations included in the analysis. Panel **b** shows the latitudinal mean yearly rate of warming. Yearly rates of warming were calculated using the Climatic Research Unit gridded Time Series or CRUTS Version 4.04 dataset (Harris, Osborn, Jones, & Lister, 2020). The outline world map was extracted from the Database of Global Administrative Areas (**GADM**) (https://gadm.org/). All the spatial information was projected using the WGS84 coordinate reference system (EPSG: 4326).

5.3 Materials and methods

5.3.1 Species populations trends

I extracted population trends from the public Living Planet Database (LPD) (https://livingplanetindex.org/home/index). This database contains time series information for 15,349 populations worldwide, of 4,182 different species of terrestrial, freshwater, and marine vertebrates. The LPD encompasses more than six decades of species monitoring data, from 1950 to 2018 (Collen et al., 2009; McRae et al., 2017). Time series in the LPD were collected from scientific studies, online databases and the grey literature (Collen et al., 2009), and must meet a series of criteria to be included in the LPD (see Loh et al., 2005 for a detailed list). Importantly, time series must have at least two time points, and the method used to calculate the species population size or abundance within a population time series must be compatible/comparable (e.g., count, density, abundance, etc…).

The choice to focus on amniote species was based on the reproductive similarities between these groups. Amniotes have internal fertilization, they carry the embryo or egg internally (at least during the early stages of development), they do not have larval stages, and the production of the embryo or egg requires a high investment of energy and time. I considered that these attributes made mammals, reptiles, and birds more feasible to group and compare than, for example, birds and amphibians. The public LPD contains data on 8,112 populations of terrestrial amniotes (54% of the total LPD data) from 2,357 species (1,494 birds, 636 mammals, and 227 reptiles). Only populations with at least 3 data points between 1992 and 2018, as well as having a known location (latitude and longitude), were included in the analysis. Further filtering was required to match the time periods covered by the environmental data (see **Climate and land-use data** for more details).

Overall, 2,561 populations in the LPD met my criteria. For this subset, I calculated rates of population change following the approach used for the LPI (Collen et al., 2009). Population rates of change must be comparable across populations. To accomplish this, population records were $\log_{10}$ transformed (Collen et al., 2009). Some populations contained zeros, which were replaced by 1% of the mean abundance recorded across the population time series in question (Collen et al., 2009). To calculate the annual rate of species population change, for each year and population, I required uninterrupted population trends (Spooner et al., 2018). However long-term and continuous population time series are still rare (Hochkirch et al., 2021), even in the LPD (http://stats.livingplanetindex.org/). Approximately 40% of the 2,561 populations contained missing observations. Therefore, I implemented imputation methods to fill those gaps and obtain continuous time series. I followed the imputation approach used for the LPI (Collen et al., 2009), adopting two methods to impute population observations depending on the number of real records available for each population time series: 1) a linear-regression interpolation was implemented when fewer than six real observations were available (Loh et al., 2005); or 2) for time series with six or more records, I implemented generalised additive models (GAMs). Linear regressions and GAMs were fitted for each time series using the population estimates as the response variable and year as the explanatory variable. In the case of the simple linear regression models only linear relationships were considered due to the low number of observations. In the GAMs, year was fitted with a smooth parameter, in the form of a penalised regression spline, of dimension equal to the length of the population time-series divided by two (Collen et al., 2009; McRae et al., 2017). Fitted GAMs and linear models were later used to impute missing values of their corresponding time series. I did not imputed values outside of the range (first to last year) of each time series. Model fit for both linear regression and GAMs was evaluated using R^2 values. Since I wanted to include only populations with low imputation uncertainties in my analysis, I selected those populations with an R^2 of at least 0.5 (following Spooner et al., 2018).

Another potential source of uncertainty arises from variability in time-series length. Short time-series are more likely to return false negative/positive trends, or to miss real and statistically significant population trends (Wauchope et al., 2019). To reduce this uncertainty, I discarded all populations with fewer than five observations (real or imputed) (Spooner et al., 2018) between the years 1992-2018. I select this time window to make the timespan covered by the LPD compatible with the land-cover data (see **Climate and land-use data** for more details). Although there is no standardised way to select the optimal length of a population time-series (Wauchope et al., 2019), the approach I used here offers an adequate time-series length while still having a large enough dataset in the end for analysis.

I used the imputed and real values of the selected population time-series (n_t) to calculate the annual ($\log_{10}$) rate of population change (λ_T) for each year and population, as described in equation 1. These values were then averaged to obtain the mean ($\log_{10}$) rate of population change for each population ($\overline{\lambda_T}$) (equation 2):

$$\lambda_t = log_{10}\left(\frac{n_t}{n_{t-1}}\right) \quad (1)$$

$$\overline{\lambda_T} = \frac{1}{T}\sum_{t=1}^{T}\lambda_t \quad (2)$$

where *n* represents real and imputed population measures, *t* represents the time/year at which the measure was taken/imputed, and *T* is the total number of years from the first to the last population estimates (Collen et al., 2009).

The final dataset contained average population trend estimates for 1,072 populations. These populations were distributed in 553 different locations across the world, and represented 461 different species (273 birds, 137 mammals, and 51 reptiles) (Figure 12). On average, after imputation, the populations had a mean time series length of 10 ± 4.2 records. Linear-regression interpolations were performed using the R package *stats* Version 4.0.2 (R Core Team, 2021), and GAMs were fitted using the R package *mgcv* Version 1.8-31 (Dunn & Smyth, 2018).

5.3.2 Climate and land-use data

I extracted temperature values from the Climatic Research Unit gridded Time Series (CRUTS) Version 4.04 dataset (Harris et al., 2020). This dataset contains monthly measurements of land-surface temperature at a grid resolution of 0.5º (≈ 55 km at the equator). To measure temperature warming, I use the monthly values of temperature to calculate the arithmetic mean temperature values for the years and locations of each population time series (Figure 12). Within each population time-series, I fitted linear regression models using yearly mean temperature as the response variable and year as the only explanatory variable.

The slope of these models was extracted and used as the average annual rate of temperature warming (ΔT in equation 3) for the time-period and location of each of the populations (Bowler et al., 2020; Spooner et al., 2018).

I gathered land-cover information from the European Space Agency Climate Change Initiative Land Cover Project (ESA CCI LCP, http://www.esa-landcover-cci.org) Version 2.0.7 (ESA-LC hereafter). This dataset contains global time series of land-cover data at a grid resolution of 300 m from 1992 to 2018. The ESA-LC consists of a map, in which each pixel on the grid is classified into one of 36 discrete land-cover types. To extract land-cover trends, I transformed the discrete categorisation of land-cover into the percent coverage of broader land-cover categories (Li et al., 2017). For this transformation, I used a cross-walking table between the ESA-LC classes and 14 simplified land-cover classes (Li et al., 2017): broadleaf evergreen trees; broadleaf deciduous trees; needleleaf evergreen trees; needleleaf deciduous trees; broadleaf evergreen shrubs; broadleaf deciduous shrubs; needleleaf evergreen shrubs; needleleaf deciduous shrubs; natural grass; bare-soil; cropland; snow/ice; urban; and water (see Table S3 for the cross-walking table). Following Li et al. (2017), I grouped all the tree and shrub land-use classes into two final classes: forest trees and shrubs, resulting in 8 final land-cover classes for my analysis. I then extracted the annual percentage change in each land-cover type for each population and time period within a 1-km-radius buffer around each population's location. I used this buffer because the LPD does not provide information about the spatial range occupied by each species populations. Instead, population's locations in the LPD are represented by discrete coordinates that can represent sample stations or the centroid of a grid or polygon of the surveyed area. Furthermore, this buffer covered the distances and areas usually covered during biodiversity monitoring (e.g Nalwanga et al., 2012; Newson et al., 2008), thus I was likely to include the habitats in which species were recorded. Finally, I calculated the mean annual rate of change of each of the land-cover classes for each population time-series ($\overline{Lu1}_T \ldots . + \overline{LuN}_T$, in equation 3) (Li et al., 2017).

All the spatial information was processed in R Version 4.0.2 (R Core Team, 2021) using the packages *raster* Version 3.3-13 (Hijmans, 2020), *maptools* Version 1.0-2 (Bivand & Lewin-Koh, 2020), and *rgdal* Version 1.5-16 (Bivand & Keitt, 2020).

5.3.3 Species life-history strategies

To classify the species according to their life-history strategies, I used the life-history dataset presented in Chapter 4. This dataset contains empirical and imputed estimates of life-history traits as well as values for the fast-slow continuum for 9,618 species of terrestrial amniotes (birds, mammals, and reptiles). The fast-slow continuum was defined based on four basic life-history traits: age of sexual maturity, average longevity, the average number of offspring per reproduction event, and the yearly number of reproductive events (Chapter 2). Before traits were used to define species life-histories, the influence of body mass and kinship was removed by regressing trait values against body mass using linear mixed-effects models (LMMs) (Chapter 2). Each life-history trait was log-transformed and regressed against log-transformed body mass, with higher taxonomic information, to the level of class, included as a nested random intercept (i.e., family nested within order, nested within class) (for details, see Appendix 2 Section 4). Residuals of those models were used as log-transformed and adjusted life-history traits and combined into a principal component analysis (PCA) to characterise species life-history strategies (Chapters 2).

Same as in Chapter 4, the first three axes of this PCA are assumed to describe species' life-history strategies and explained more than 80% of the observed life-history trait variation (see Chapter 4 Appendix 2 Section 4). The first axis (PC1) reflects the expected trade-offs between longevity and fecundity, and therefore was used to represent the fast-slow continuum (Chapter 4). Low score values of PC1 corresponded with species with delayed sexual maturity, longer lifespans, and lower sexual productivity, i.e., slow species (Chapter 4). On the other hand, species with high score values are characterised by shorter lifespans, earlier sexual maturity, and higher reproductive productivity, i.e., fast species (see Appendix 2 Section 4 for more details).

5.3.4 Taxonomic resolution

Both the LPD and the life-history dataset are the results of data compilation and aggregation of many underlying studies, spanning several decades. A consequence of this is that species taxonomy differs across and within datasets. Since I rely on the species binomial names to match each species with its corresponding life-history strategy and population trend, I needed to ensure that taxonomy was as consistent as possible. To resolve possible taxonomic mismatches, I performed a taxonomic name and synonym resolution (Cooke, Eigenbrod, et al., 2019; Etard et al., 2020). I followed the same approach as in Chapters 3 and 4. To update and correct the taxonomy as much as possible, I first checked species for typographical errors using the R package *taxize* Version 0.9.95 (S. Chamberlain, Szoecs, et al., 2020). Once original binomial names were corrected, these were passed through the online repositories of the International Union for Conservation of Nature Red List of Threatened Species (IUCN Red List, https://www.iucnredlist.org/ Version 2021-1) and the Integrated Taxonomic

Information System (ITIS, https://www.itis.gov/, as downloaded on 12th September 2021). If the species was present in these repositories, the matched scientific name was retrieved along with all its associated synonyms and higher-level taxonomic information. Wherever possible, I chose the matching binomial and taxonomic classification from the IUCN Red List. If a species binomial name was not recorded in the IUCN Red List, I used the binomial name and taxonomy retrieved from ITIS to match my datasets.

When all available taxonomic information was retrieved, a unified taxonomic table was created containing the species name as it appeared in the original datasets, the corrected binomial name, a unique matching binomial name for each species, a list of potential synonyms, and the higher taxonomic classification linked with the matching binomial name. I used this taxonomic table to unify binomial species names and higher taxonomy across the life-history database and the LPD. Once these fields were corrected, and all potential synonyms were resolved, the LPD and estimates of life-history strategies were finally merged.

5.3.5 Statistical analysis

The spatial distribution of population locations can lead to variations in population trends among locations and species that is unrelated to climate and land-cover change. To consider these possible effects, I included site and species identity as random intercepts in linear mixed-effects models (LMMs). To build the initial statistical model (equation 3), I used the mean rate of $\log_{10}$-transformed population change ($\overline{\lambda_T}$) as the response variable, with the rate of climate warming (ΔT), the mean rates of change for the land-cover types ($\overline{LuN_t}$), and species position along the fast-slow continuum (PC1) as fixed effects, along with all their two- and three-way interactions (equation 3). Final model selection was performed using a backward stepwise AIC model selection. In this approach all model terms are initially included in the model. Terms that contribute to increase the overall AIC value of the model were discarded one at a time and the new model re-evaluated (Yamashita et al., 2007). This process was repeated until the model with the lowest AIC was found (Yamashita et al., 2007).

$$\begin{aligned}\overline{\lambda_T} \sim \Delta T + PC1 + \overline{Lu1_T} .... + \overline{LuN_T} + {} & \Delta T:PC1 + \overline{Lu1_T}:PC1 + ... + \overline{LuN_T}:PC \\ & + \Delta T:PC1 + \overline{Lu1_T}:\Delta T + ... + \overline{LuN_T}:\Delta T \\ & + \overline{Lu1_T}:PC1:\Delta T + ... + \overline{LuN_T}:PC1:\Delta T + (1|Location) \\ & + (1|Species) \quad (3)\end{aligned}$$

The selection and data quality of my population time series can have a strong impact on the results. To evaluate the robustness of the results, I ran two different sensitivity analyses to investigate the effects of data quality and population selection on the results. To assess the effects of data quality, I resampled the LPD data using different R^2 thresholds. Lower R^2 are associated with poor imputation performance and therefore less accurate population trends. Conversely, high imputation accuracy is associated with higher R^2 values, and imputed values closer to real population values. Additionally, by changing the R^2 threshold from 0.5 (as used for the main results) to 0.3, 0.7 and 0.9 I modified the number of populations included in the model (1,108 for a threshold of 0.3, 996 for a threshold of 0.7, and 915 for a threshold of 0.9) as well as the quality/uncertainty of the data. To assess the effects of population selection on the results, I ran a second analysis in which I selectively removed populations with extreme values of $\overline{\lambda_T}$ (similar to Leung et al., 2020 and Murali et al., 2022). In this case, I created 3 different datasets by: 1) removing populations below the 2.5th percentile of $\overline{\lambda_T}$; 2) removing populations above the 97.5th percentile of $\overline{\lambda_T}$; and 3) preserving only the populations between the 2.5th and 97.5th percentiles of $\overline{\lambda_T}$.

The mixed-effects models were fitted using restricted maximum likelihood, implemented in the R package *lme4* Version 1.1-26 (Bates et al., 2015) and step backward AIC selection was implemented using the step function of the R package *stats* Version 4.0.5 (R Core Team, 2021). Model fit was evaluated using conditional and marginal pseudo-R^2 values calculated by the R package *MuMin* Version 1.43.17 (Barton, 2020). Statistical significance of fixed effects from the final models was assessed using the Wald chi-squared test, implemented using the R package *car* Version 3.0-9 (Fox & Weisberg, 2019). PCA analysis was performed using the R package *ade4* Version 1.7-15 (Bougeard & Dray, 2018).

5.4 Results

After model reduction and selection, my final model contained the following variables: rate of climate warming (ΔT); species position on the fast-slow continuum (*PC1*); mean annual rate of cropland change ($\overline{Crop_T}$), and its interaction with species life-history position ($\overline{Crop_T}{:}PC1$); mean annual rate of bare-soil change ($\overline{Bare\ Soil_T}$), its interaction with species life-history position ($\overline{Bare\ Soil_T}{:}PC1$), and the interaction between mean annual rate of bare-soil change and climate warming ($T\Delta{:}\overline{Bare\ Soil_T}$) (equation 4).

$$\overline{\lambda_T} \sim \Delta T + PC1 + \overline{Crop_T} + \overline{Bare\ Soil_T} + \overline{Crop_T}{:}PC1 + \overline{Bare\ Soil_T}{:}PC1 \\ +\ \Delta T{:}\overline{Bare\ Soil_T} + (1|Location) + (1|Species)\ (4)$$

Overall, populations of species inhabiting areas where cropland has expanded were decreasing, whereas populations inhabiting areas where cropland was contracting showed positive populations trends (Table 7, Figure 13.a). Fast-lived species tended to have more positive population trends than slow-lived species

(Table 7, Figure 13.b). Population trends of fast and slow species also varied according to land-cover changes (Table 7). Fast-lived species inhabiting areas that had experienced recent cropland and bare-soil expansion had positive population trends (Figure 13.c, and Figure 14.a). In contrast, populations of slow species inhabiting these areas tended to have negative population trends (Figure 13.c, and Figure 14.a).

Climate warming alone had no significant effect on population trends (Table 7), but the interactive effect of bare-soil expansion and climate warming did. Species populations subjected to both bare-soil expansion and climate warming presented negative population trends, whereas species populations in areas of bare-soil reduction and climate warming presented positive population trends (Figure 13.b). In areas where bare-soil cover was decreasing and temperature declines were observed, populations showed negative trends. Where temperatures decreased and bare soil expanded, populations showed positive population trends (Figure 13.b).

Table 7. **Estimates, standard errors, and results of an ANOVA type III Wald chi-square test for the model of population trends.** Statistically significant terms are marked in bold with stars indicating the level of significance (P < 0.1 = **.**; P < 0.05 = *; P < 0.01 = **; and P < 0.001 = ***). For all terms, the degrees of freedom for the Wald χ^2 test equals 1. Conditional and marginal pseudo-R^2 values are shown at the bottom of the table. Term names correspond to those in equation 3: $\Delta\mathrm{T}$, rate of temperature change; $\overline{\mathrm{Crop}}_{\mathrm{T}}$, rate of change for cropland land cover; $\overline{\mathrm{Bare\ soil}}_{\mathrm{T}}$, rate of change for bare-soil cover; and PC1, the life-history axis representing the fast-slow continuum.

Term	*Estimate*	*Std. Error*	χ^2	*P*
(Intercept)	0.0025	0.00281	0.871	0.3506
ΔT	0.0246	0.0024	0.0045	0.9462
PC1	**0.0052**	**0.0023**	**5.0484**	**0.0246 ***
$\boldsymbol{\overline{Crop}_T}$	**-1.4974**	**0.6943**	**4.6512**	**0.031 ***
$\overline{Bare\ Soil}_T$	5.1349	1.7809	0.6104	0.088 .
PC1 : $\boldsymbol{\overline{Crop}_T}$	**1.896**	**0.6017**	**9.9275**	**0.0016 ****
PC1 : $\boldsymbol{\overline{Bare\ Soil}_T}$	**2.7376**	**0.8676**	**9.9561**	**0.0016 ****
$\boldsymbol{\Delta T}$ **:** $\boldsymbol{\overline{Bare\ Soil}_T}$	**-718.4483**	**1.7971**	**7.0390**	**0.0079 ****

Conditional pseudo-R^2 = 0.25

Marginal pseudo-R^2=0.067

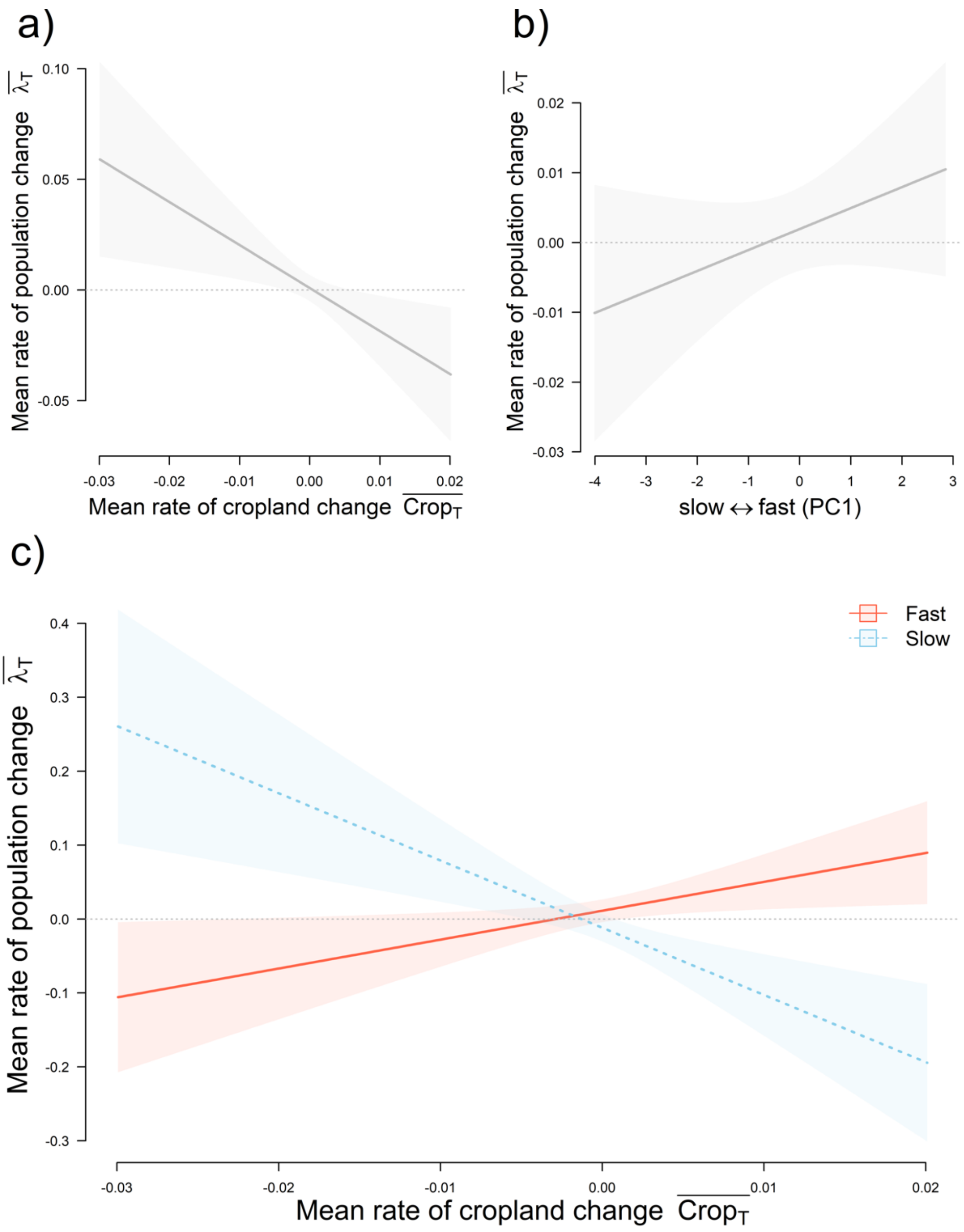

Figure 13. Responses of average population trends to: **a**, rate of cropland change; **b**, fast-slow continuum; and **c,** effects of the rate of cropland change for fast (red line/shaded area) and slow (blue dotted-line/shaded area) species separately. Predicted responses in **c** are shown for species located at both extremes of the fast-slow continuum sampled in the LPI localities used in the analysis. Shaded areas represent the 95% confidence intervals around the fitted relationships. Model estimates, standard errors and statistical significance of fixed effects are presented in Table 7.

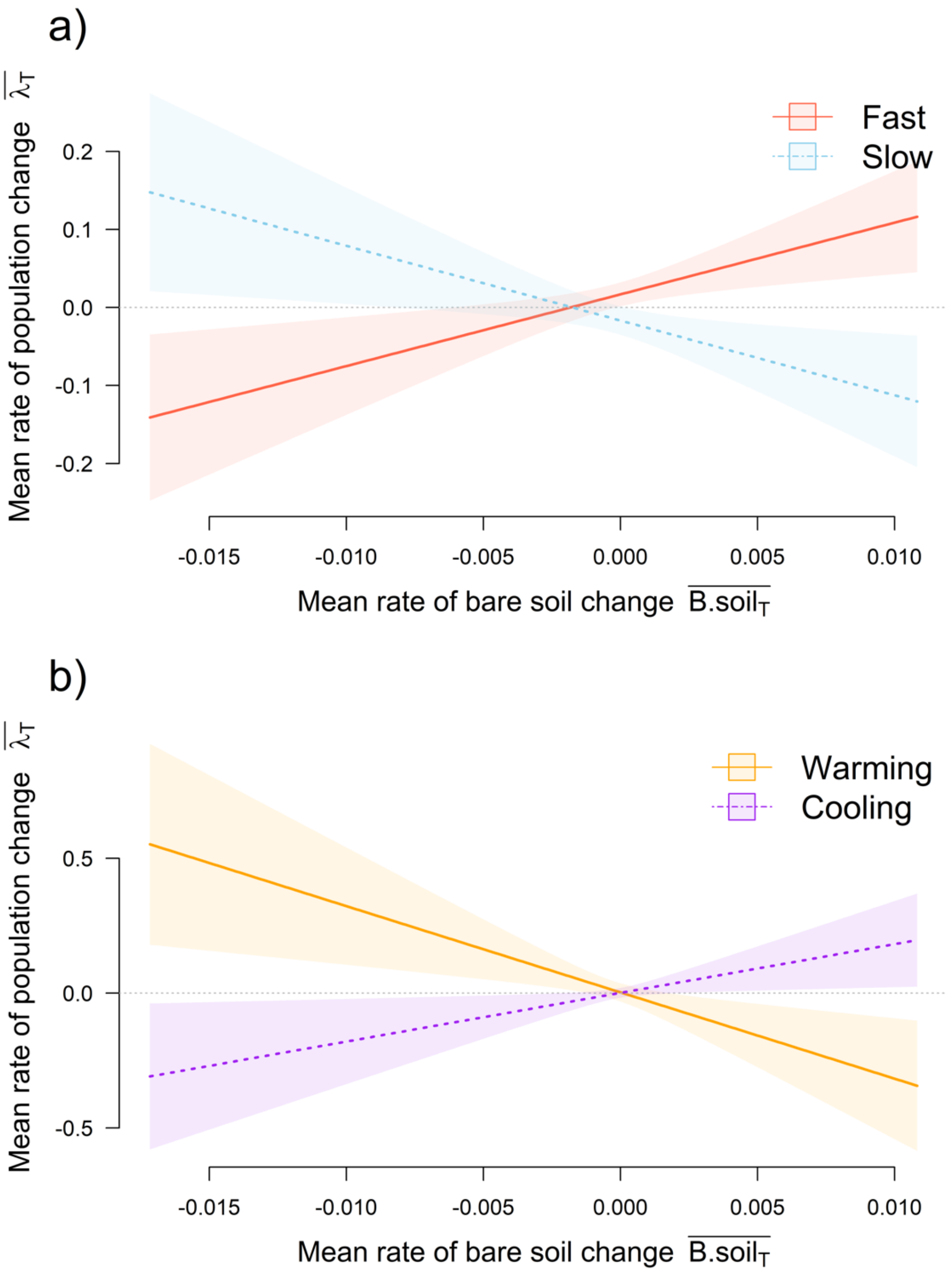

Figure 14. Responses of average population trends to: **a**, rate of bare-soil change for fast (red line/shaded area) and slow (blue dotted line/shaded area) species; and **b**, rate of bare-soil change for populations experiencing climate warming (gold line/shaded area) and climatic cooling (purple dotted-line/shaded area). Predicted responses in a) are shown for species with the highest and lowest values of the fast-slow continuum sampled in the LPI localities used in the analysis. Predicted responses in **b** are shown for the maximum and minimum rates of temperature warming recorded within the sampled localities. Shaded areas represent the 95% confidence intervals around the fitted relationships. Model estimates, standard errors and statistical significance of fixed effects are presented in *Table 7*.

5.4.1 Sensitivity analyses

The magnitude of the observed effects, as well as the 95% confidence intervals of the predicted estimates, remained mostly consistent and statistically significant across the datasets with different data-imputation quality (Appendix 3 Table S1). Conditional pseudo-R^2 values across these models ranged from 0.18 to 0.25, while marginal pseudo-R^2 values ranged from 0.069 to 0.074. Models with datasets compiled using a higher R^2 threshold for data imputation had higher marginal pseudo-R^2 values and lower values of conditional pseudo-R^2 values in the final models (Appendix 3 Table S1). When extreme values of $\overline{\lambda_T}$ were removed, models varied in terms of the direction and significance of environmental effects. When 2.5% of the populations with the most negative values of $\overline{\lambda_T}$ were removed, model effects showed the same direction but only the interactions between bare-soil and temperature warming and the fast-slow continuum remained statistically significant (see Table S2 for further details). I observed a similar trend when populations with both extremely positive and extremely negative values of $\overline{\lambda_T}$ were discarded (5% of the data) (Table S2). However, in this case only the interaction between bare-soil and temperature warming remained statistically significant (Table S2). When the 2.5% of the populations with the most positive values of $\overline{\lambda_T}$ were removed from the analysis, the fast-slow continuum, rate of cropland change and its interaction with the fast-slow continuum were statistically significant (Table S2). Overall, I detected changes on the sensitivity of the models fitted with different datasets and changes on the effects direction of temperature warming, although this term was not statistically significant in the original model.

5.5 Discussion

In this study, I showed that terrestrial vertebrate population trends vary according to interactions between land-cover and temperature changes (warming and cooling), as well as with species life histories. Specifically, I found that populations in areas that have experienced recent cropland and bare-soil expansions are more likely to present negative trends, and that species' populations trends are negative in areas that experienced both recent climate warming and bare-soil expansion. Species with different life-history strategies showed a distinct response to cropland and bare-soil expansion, with fast-lived species tending to show positive population trends, and slow-lived species tending to display negative trends. These findings support the hypothesis that fast-lived species are better adapted to colonize empty niches and recover after a stochastic mortality event or after environmental changes (MacArthur & Wilson, 1967; Pianka, 1970).

The effects of human land-use intensification on biodiversity are well documented and range from habitat fragmentation (e.g. de Oliveira, de Carvalho Júnior, Gomes, Guimarães, & McManus, 2017), to community homogenization (e.g. Vellend et al., 2007) and the introduction of invasive species (e.g. Soares et al., 2020). Thus, I expected to observe an effect of land-cover change on species population trends. I found that land-cover changes, more precisely those related with changes in the coverage of cropland and bare-soil, are important determinants of species' population trends, and that species respond differently to these changes according to their position along the fast-slow continuum of life histories. These observations match some of the theoretical predictions from MacArthur and Wilson (1967) and Pianka (1970). Fast-lived species are better adapted to rapidly increase their populations after a stochastic event, whereas slow-lived species are displaced or experience population declines (MacArthur & Wilson, 1967; Pianka, 1970). My results can help to explain previous findings that showed that terrestrial vertebrate communities under land-use conditions indicative of human disturbance were dominated by fast-lived species (Chapter 4).

It is well established that climate change has affected biodiversity (e.g Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Donnelly et al., 2011; Parmesan & Yohe, 2003), and that its effects are going to become more evident in the future (IPCC, 2021; Newbold, 2018). Previous studies have found a strong association between population declines/extirpations and climate warming in bird, mammal, and reptile populations (Sinervo et al., 2010; Spooner et al., 2018). I did not observe significant effects of climate warming on species population trends, probably because the time window was much shorter than those used in previous studies, which can influence the warming rates detected. Unlike land-use/cover change, which acts as a rapid and easy-to-detect driver of environmental change, the effects of climate change are still more challenging to detect (e.g Wu et al., 2015). Furthermore, the fact that climate warming effects are likely to act with a lag further complicates their detectability (e.g. Thompson & Ollason, 2001). Despite this, climate warming had a significant effect when interacting with land-cover changes. My results indicate that these interactions can lead to positive and negative changes in population trends depending on whether both factors follow the same trend (negative), or opposite (positive). My results show that relationships between land-cover change, climate warming and population trends are complex, and likely to vary across species.

From a theoretical point of view, I would expect for both fast and slow species to maintain average stable populations (MacArthur & Wilson, 1967). However, the results showed that, on average, fast-lived species showed positive population trends, while slow species were more likely to present negative population trends (Figure 3.b). This can, in part, be explained by the focus of this study. Biodiversity threats such as habitat destruction, pollution, or the introduction of invasive species, do not act in isolation but in complex clusters, in which multiple drivers can act at the same time and at different scales/intensities (Bowler et al., 2020; Wraith & Pickering, 2018). By focusing only on climate warming and land-cover changes I are likely missing other important drivers of biodiversity change that have an impact on species population trends and can be observed in the different average population trends of fast and slow species.

The sensitivity analysis showed that results were data sensitive. When different R^2 thresholds were used to include or discard populations from the analysis, larger datasets (lower R^2 thresholds) tended to return models with more statistically significant effects than models with more restricted data. Despite this, the direction and significance of the effects were consistent across datasets. When populations were discarded based on their rate of population change, the significance of effects varied greatly depending on which populations were discarded from the analysis. I can conclude, therefore, that my results were mostly driven by the effect of a small proportion of populations (2.5% to 5% of the total data) with extreme rates of change. These findings suggest that species' sensitivity to environmental change is not uniformly distributed across gradients of environmental change and life-history strategies but clustered, with some populations and species being particularly sensitive (Leung et al., 2020). The different sensitivity of species population rates to environmental changes, remarks the complexity of this types of interactions and the challenge of gather enough, and significant, information to run this type of analysis. Further research in this subject should rely on a combination of demographic simulations and lab experiments to clarify which are the aspects of life-history strategies that have a greater impact on the fitness and resilience of species populations.

Overall, my results show that populations of species with different life histories respond differently to environmental changes, with populations of fast-lived species being positively affected by climate warming and human-driven land-cover changes, and populations of slow-lived species negatively affected. Although I observed a clear relationship between life-history strategies and species response to environmental changes, some of the results, as well as the sensitivity analysis, exposed that additional information is needed to fully understand the characteristics that make species sensitive to environmental changes. With land-use and climate change expected to further increase in the near future (IPCC, 2021; Tilman et al., 2017), it is likely that this asymmetry in the response of fast and slow species to these drivers results in a turn-over of communities. Fast life histories are usually associated with invasive and generalist species (Allen et al., 2017; Cooke, Eigenbrod, et al., 2019), whereas slow life histories are usually associated with specialist species (Cooke, Eigenbrod, et al., 2019). The creation of conditions that favour fast-lived species, and the decline of slow-lived species, can lead to a further homogenization of communities, and the loss of important ecosystem services (Clavel et al., 2011). Establishing clear relationships between species traits and sensitivity to environmental change is fundamental to establish effective conservation strategies and halt biodiversity degradation. Here, I have shown that life-history traits are a useful tool to study species' population responses to climate and land-cover changes.

Chapter 6: Discussion

6.1 Introduction

Human activities are shaping the landscape and climate of the planet with important repercussions for biodiversity and human wellbeing (Naeem et al., 2016). Among the different threats, anthropogenic land-use changes have been identified as one of the main forces driving biodiversity change globally (Maxwell et al., 2016) (Figure 1). In addition, climate change is likely to become one of the main drivers of biodiversity change in the near future (Newbold, 2018; Visconti et al., 2016). With a global estimated of 9 to 9.7 billion people expected by 2050 (United Nations et al., 2019; Tilman et al., 2017), these and other anthropogenic threats are likely to intensify. Thus, it is more important than ever to enact policies that secure the healthy functioning of the biosphere in the future (Naeem et al., 2016; Titley et al., 2021). However, such planning must come from a deep understanding of the causes and consequences of species' responses to environmental change.

Species do not respond to environmental changes equally, with some species benefitting (winners) and others losing (losers) (Colléony & Shwartz, 2020; Dornelas et al., 2018; Sinervo et al., 2010; Stephens et al., 2016). Therefore, it is of paramount importance to understand which are the characteristics, or traits, that shape species responses to environmental changes. This will help us to: 1) better understand the implications of climate and land-use change for biodiversity; 2) build more precise scenarios of biodiversity change (Carvajal et al., 2018; Stephen C. Stearns, 2000); and 3) to design more effective conservation and prioritization strategies. Trait-based approaches, in which the response to environmental changes of species with different traits is compared (e.g Chaparro-Pedraza & de Roos, 2019; Pollock et al., 2012), have been proving an effective strategy for disentangling why species show different sensitivity to, for example, land-use and climate change (Murray, Justin Nowakowski, et al., 2021; Pacifici et al., 2015). However, when species sensitivity to environmental change is evaluated using individual traits, results can be contradictory (when related traits show opposite responses to environmental gradients/changes) or challenging to interpret (there is not a clear connection between the observed response and the environmental gradients/changes observed).

In this thesis, I have tried to avoid the limitations of traditional multi-trait approaches by describing common patterns of trait variation and classifying species according to these patterns. These common patterns of trait variation can be described by aggregating multiple traits under a single measure that reflects the relationships of those traits (e,g Cooke et al., 2019). This way we should be able to reflect all trait relationships under a unified metric that can be used to analyse species relationships to environmental variation. In this thesis, I have focused on terrestrial vertebrate life-history strategies. Species life-history strategies describe de general relationships between traits related with ageing and fecundity (Dobson & Oli, 2007; Healy et al., 2019). Previous studies have demonstrated that traits related with life-history strategies are relevant elements shaping important ecological factors such as species responses to climate change, species extinction risk, species invasiveness potential, and population resilience (Allen et al., 2017; Bird et al., 2020; Capdevila et al., 2022; Pacifici et al., 2017; Richards et al., 2021). However, most studies exploring life-history strategies are focused on the variation and relationships of these strategies within groups of species, rather than on their relationships with environmental variables

(Capdevila et al., 2020; Dobson & Oli, 2007; Dunham & Miles, 1985). As a result, previous research has left the practical and theoretical advantages of grouping traits under common life-history strategies unexplored (e.g Cooke et al., 2019; Stearns, 2000). By classifying species according to their life-history strategies, I was able to: 1) simplify the outcomes of the models, by combining life-history traits into main axes of life-history variation (either the fast-slow or body-mass continuums); 2) improve the interpretability of model results when clear relationships between species traits can be described (in this case the relationship between life-history traits); and 3) develop an expandable and flexible approach to relate species life-histories and environmental gradients. Through the different chapters of this thesis, I have expanded on one fundamental question: what are the ecological implications of life-history strategies for the distribution, configuration, and response of terrestrial vertebrate communities to environmental changes? The three research chapters of this thesis explore different aspects of the relationships between species' life histories and environmental variables.

6.2 Main results

My first study (Chapter 3) focuses on the relationship between life-history strategies, in this case the body-mass (Pianka, 1970) and fast-slow (Dunham & Miles, 1985; Read & Harvey, 1989) continuums, and the spatial distribution of species. In this chapter, I show that larger and slower-lived species (the body-mass continuum) tend to be favoured by habitat heterogeneity (particularly land-cover heterogeneity, temperature seasonality, and habitat fragmentation) and that elevation heterogeneity reduce their probability of occurrence. Meanwhile, faster species, relative to their size and phylogeny (the fast-slow continuum), are also favoured by habitat heterogeneity (metrics mentioned above) but their probabilities of occurrence are lower on areas with higher elevation heterogeneity. These results are important for various reasons. First, it supports the predictions of MacArthur and Wilson (1967) and Pianka (1970) that there is a relationship between species life-history strategies and basic environmental gradients. This is the first time that these theories have been empirically explored at a global scale. Second, it demonstrates the usefulness of using species life-histories to explore global patterns of species distribution. Additionally, I also found that the way in which life-history traits are processed and combined, either to form the fast-slow or body-mass continuum, can have a strong impact on the patterns of response observed and its interpretation.

Generally, traits reflect the adaptation and interaction of species to their environment and shape the way in which species respond to environmental changes (Vandewalle et al. 2010; Nordén et al. 2013; Murray, Nowakowski, and Frishkoff 2021). Species that inhabit similar environments or that exploit the same resources are expected to share similar traits (e.g Pigot et al. 2020) and to some extent to respond similarly to environmental changes. Therefore, we can define a community as the diversity of traits that determine when and where species can exist (McGill et al., 2006). Given the association between species life-histories strategies and environmental heterogeneities found in Chapter 3, I would expect for those effects to transpire down to species assemblages. This way, species assemblages in more climatic seasonal and human-impacted habitats will be mostly dominated by fast-lived species. Contrary, I expect species assemblages in less human-impacted and climatically seasonal environments to be predominantly dominance by slow-lived species. In Chapter 4, I study how species life-histories may affect the composition of species assemblages under different environmental conditions and levels of human impact. I show that life-history diversity and the overall pace of life of the species inhabiting a community is related with the land-use and climatic conditions of their habitat. Communities inhabiting human-disturbed and climatically seasonal environments have a higher life-history richness, but are dominated by fast-lived species. Previous studies have shown similar patterns, with animal species with higher fecundity, and shorter lifespans being more likely to be present in more human-impacted habitats (e.g Börschig et al., 2013; Newbold et al., 2013). However, those studies focused on narrower taxonomic groups and on specific regions or locations. The results of my research clearly show, for the first time, how both climatic seasonality and human disturbances act as environmental filters favouring predominantly species with fast life-history strategies, and how these changes can be observed at a community level. Additionally, this is the first time these patterns of life-history variation have been observed in a global multi cross-taxon analysis. These results support previous predictions that point out that animal life-history strategies will shift towards fast-lived and highly fecund species due to human pressures (Cooke, Eigenbrod, et al., 2019).

Chapters 3 and 4 show that species' life-history strategies determine the probability of occurrence of species, and the relative dominance of species within communities affected by climatic seasonality and different levels of human disturbance. These results suggest that populations of fast- and slow-lived species might respond differently to environmental changes (Capdevila et al., 2022; Cooke, Eigenbrod, et al., 2019; Ye et al., 2014). However, they only represent snapshots of species distributions and communities, and do not show how populations of fast and slow species behave over time under environmental changes. Theoretically, fast- and slow-lived species present different population resilience to environmental impacts (Capdevila et al., 2022). Empirical studies have shown that some life-history traits are highly correlated with the potential resilience of populations, i.e., their potential to recover to equilibrium after an impact (Capdevila et al., 2022), but have not explored how populations of fast- and slow-lived species respond to land-cover and temperature changes. In Chapter 5, I focus on how the populations of fast- and slow-lived species behave when subjected to recent environmental impacts, in this case temperature and land-cover changes. The results of this study show that under the expansion of human-dominated land covers (bare-soil and croplands), fast-lived species tend to present positive population trends whereas slow-lived species tend to show negative population trends. Temperature change impacts on species populations depends on recent land-cover changes, with species inhabiting warming areas that have suffered recent bare-soil expansion displaying negative population trends. Species inhabiting cooling areas that have suffered recent bare-soil expansion displayed positive populations trends. This is the first study that shows a clear association between species' population trends, environmental changes and species' life-histories.

6.3 Limitations

Both, the methods used to carry out the analysis as well as the datasets used, have their limitations. Despite using some of the biggest and most complete datasets on biodiversity such as the PREDICTS database (https://doi.org/10.5519/0066354), the International Union for Conservation of Nature (IUCN) Red List (https://www.iucnredlist.org/), the Living Planet Database (LPD; https://livingplanetindex.org/home/index), and the Global Biodiversity Information Facility (GBIF; https://www.gbif.org). There was a limited overlap between the species covered by these datasets and the species with life-history information. This limited the number of species included in each analysis. Additionally, each dataset contains its own biases (see discussion sections in Chapters 3, 4 and 5). For example, the IUCN Red List (IUCN, 2021) presents precise spatial information for most mammals and almost all birds, but only general distribution polygons (with lower accuracy) for a large number of reptiles and amphibians. Similarly, the LPD contains population data mostly for osseous fishes and birds, and have an over-representation of species that are under conservation actions (Murali et al., 2022; WWF, 2020). The biases towards mammals and birds are also reflected in the life-history trait data. I was able to compile complete life-history trait information (i.e., information for all the five traits considered) for only 11.55% of the 6,665 species of reptiles present in my dataset. It is also important to note that the studies I have carried out in this thesis are only possible for vertebrates, for which life-history trait, spatial and population data are available. As a result, I have neglected the most diverse group of animals, the invertebrates. These limitations are not unique to my work (Bland & Böhm, 2016; Hochkirch et al., 2021), but it does highlight that efforts are needed in order to obtain data for important yet under-represented groups.

In addition to data biases, since my results are all based on correlative analyses, it is not possible to establish clear mechanisms by which life-history strategies shape species' responses to environmental gradients and environmental changes. To clearly disentangle mechanisms, further research and more mechanistic approaches are needed (e.g., Buckley et al., 2010). Such mechanistic approaches can be challenging when focusing on vertebrate life-histories and will required a careful and systematic selection of model species. For example, slow species generation times might create an obstacle to study the long-term response of populations to environmental changes. This, in turn, will also require holding individuals in captivity for long periods of time, controlling at the same time the conditions of the experiments. A way to overcome these potential challenges may be to study the evolution of populations of microorganisms or insects with different life cycles and subjected to different environmental conditions.

6.4 Key findings, implications, and future research

Overall, results were consistent across chapters and suggest that terrestrial vertebrate life-history strategies are important factors shaping species' responses to environmental variables. Together, the results highlighted that human-driven environmental changes, in the form of land-use and land-cover changes are consistently favouring fast-lived species. Conversely, slow-lived species are being filtered out by those same human-induced environmental changes. Simultaneously, temperature seasonality and temperature warming are also favouring fast-lived species and negatively affecting slow-lived species. Altogether, my three experiments suggest that human-disturbances and environmental heterogeneities, promote the expansion, dominance, and population growth of fast-lived species.

Although the results from the different experiments point in the same direction, the proportion of variability explained by the models was low. Even though these results are in line with other studies exploring similar ecological questions (Le Provost et al., 2020; Murray, Nowakowski, et al., 2021; Spooner et al., 2018; Wieczynski et al., 2019), they also suggest that the addition of more information is needed to obtain a more complete understanding of the patterns observed. My results could be made more informative by constructing more complex species strategies or archetypes. Aggregating other species traits alongside life-history traits may aid us to better understand species respond to environmental changes. For example, previous experiments have shown that behaviour (Briscoe et al., 2014), diet (Leclerc et al., 2020), climatic tolerance (Williams et al., 2022), and morphology (Lyons et al., 2010; Merckx et al., 2018) are important factors affecting species' responses to environmental gradients and changes. Moreover, other threats, such as invasive species or pollution, might be acting on species' populations at the same time as climate warming and land-cover changes. Therefore, a more complete consideration of species' traits and biodiversity threats would likely increase our understanding of how traits influence the response of species to environmental changes.

The results of the studies presented in this thesis show how species' life-history strategies are significant correlates of species' distributions, community composition, and population responses to environmental changes. Furthermore, taken together, the results highlight an asymmetry in the response to environmental changes/gradients of fast and slow-lived species. Throughout the different experiments, I have focused on two main ecological gradients (land-cover heterogeneity and climatic seasonality) and two human-driven environmental changes, climate warming/cooling and land-use/cover changes. With land-use can climate change likely to increase in the near future (IPCC, 2021; Tilman et al., 2017), it is also highly probable that the observed asymmetries in species' responses will promote: 1) The expansion of fast-lived species ranges through changes in landscape heterogeneity and climatic seasonality; 2) A reduction on the diversity and average pace of life of species assemblages due to the increase of human-disturbances in the form of land-use expansion and intensification; and 3) the reduction of populations of slow-lived species and an increase of fast-lived species' populations. These potential changes towards fast-lived communities are of interest for biodiversity conservation. Fast-lived species are more likely to be generalist and invasive species (Allen et al., 2017; Cooke, Eigenbrod, et al., 2019). In contrast, slow-lived species are usually related with specialist more sensitive to extinction and vulnerable to population declines species (Capdevila et al., 2022). Therefore, the promotion of conditions that favour fast-lived species and reduces slow-lived species can lead not only to a further homogenization of communities but to the loss of key specialist species. Subsequently, the shift towards fast-lived species strategies can lead to the potential degradation of important ecosystem services (Clavel et al., 2011; Cooke, Eigenbrod, et al., 2019) with implications for biodiversity and humans (Mbow, Reisinger, Canadell, & O'Brien et al., 2019).

The results presented in this thesis open a new and exciting avenue of research in the field of life-histories and trait-based ecology. Part of those new opportunities of research are on the field of island biogeography. Even though the foundational hypothesis of this work is based on the island biogeography theory from McArthur and Wilson (1967), this thesis does not include a chapter dedicated to the evolution, composition, or comparison of life-histories between islands systems and continents. From a merely theoretical point of view, a simple comparison of the life-history strategies of island and non-island related taxa might give us extensive information about the island syndromes and life-history evolution. From a more practical point of view, this could inform us about the vulnerability of island communities to environmental changes, their functional redundancy, and their resilience against environmental changes. A body of research dedicated to the study of the evolution of life-histories on islands is a natural step forward from the results presented in this thesis.

The life-history strategies described in this thesis cover a significantly small portion of the total dimensional space that conforms the trait-space of any living organism. However, using that small portion of the trait-space, I have been able to find clear and significant ecological patterns. It is therefore logic to expect a larger proportion of that trait-space to return a stronger ecological signal and provide a more complete explanation of such signal. The construction of more complex and complete species trait-spaces, or species archetypes, might help us explain one of the main themes or questions posed within this thesis: why do species respond differently to environmental changes? Behavioral and dietary traits, in combination with morphological and life-history traits, can be used to classify species into functional groups, or archetypes, and to evaluate their response to environmental gradients. If distinct response patterns are found between archetypes, we might start looking at species and communities from a trait-environment perspective. This will not only have implications for future research but also for conservation. If we can predict the response of species to environmental changes based on their trait configuration, extinction risk assessments could be, at least partially, carried out based on species trait information. Similarly, if common patterns of trait configuration are found amongst known invasive species, the invasive potential of species can be stablished beforehand. This could help preventing further introduction of potentially invasive species.

Other research questions worth exploring have also emerged from each of the experimental chapters. Chapter 3 suggests it is necessary to combine metabolic rates and life-history strategies in a more ecologically meaningful way. Although there is a theoretical relationship between life-history strategies, metabolic rate and environmental energy availability, predictions from those theories have not been tested. Additionally, the combination of these two dimensions might give us more information about the processes driving species distributions, energy use and species fitness under landscape and energy heterogeneities. The results from Chapter 4 show that the configuration of life-history strategies varied according to land-use changes but did not explain the mechanism behind those changes. Other methods explicitly accounting for dissimilarities between communities, life-history strategies turnover, and substitutions might shed some light into the mechanisms behind those changes. These same methods can be used to explore how different land-uses impact life-history diversity and how this diversity change spatially. Additionally, life-histories assemblages can also be studied from a demographical and competition perspective. Simulations of multiple species and populations might help us to better understand the mechanism behind community life-history diversity. At the same time, these methods might allow us to include other important drivers of community change such as extinction and invasion rates. Finally, Chapter 5 points to the potential of combining different types of information to answer ecological questions and shows that data limitations can have a significant effect on the species/populations observed responses. Undoubtably, future research can benefit from such a combination of datasets and methods to mitigate the effects of these limitations.

Establishing clear relationships between species traits and sensitivity to environmental change is fundamental to establish effective conservation strategies and halt biodiversity degradation. Since information regarding the precise distribution, population trends, and status for many species is unknown, being able to predict the response of species to environmental changes, based on their traits can be a powerful tool for conservation scientist and managers.

More comprehensive and complete trait-based approaches may help us to better prioritise conservation efforts, to predict with a lower uncertainty what would be the response and likely composition of communities under future scenarios of environmental change, and to evaluate the sensitivity to extinction of species from which population or distributional data is not available. Clearly, to achieve this life-histories are not enough and that additional traits are needed. In this regard, the same approach as used to correlate species life-history continuums and environmental characteristics could also be used to build more complex species archetypes incorporating morphological, dietary, and even behavioural traits. This will might allow to test other hypotheses regarding the different response of species to environmental gradients. For example, is there a difference in the response of carnivore fast-lived species to environmental changes when compared to herbivores or omnivore fast-lived species? Or between flying or non-flying species with similar life-history strategies? This way, the results of this thesis set a strong precedent to explore species responses to environmental changes, human-impacts and climate change from a more informative and simplified trait-based perspective. This ultimately, will lead to the design of better conservation actions.

6.5 Conclusions

Threats to biodiversity are likely to increase in the near future, driven by increases in the human population, and changes in human consumption patterns (IPCC, 2021; Tilman et al., 2017). Land-use changes are expected to intensify globally (Tilman et al., 2017), and even with substantial reductions in energy and fossil-fuel use, global temperatures are likely to increase by 1.5-2°C by 2050 (IPCC, 2021). Consequently, both land-use and climate change are likely to increase their impacts on biodiversity (IPCC, 2021; Newbold, 2018). Thus, it is more important than ever to understand how and why species respond to environmental degradation, and why individual species respond differently. The studies presented in this thesis build on the knowledge of how species life-history strategies affect responses to environmental heterogeneity, human-disturbance, and environmental changes. Overall, my results show that environmental heterogeneity and change, in the form of land-cover heterogeneity/change and climate change/seasonality, tend to favour fast-lived species while filtering out slow-lived ones. The results from this thesis help us to understand better the interspecific variation observed in responses to environmental changes, their implication for the configuration of communities, and differences in the trajectory of populations. Such an understanding is fundamental for the development of species conservation plans, species prioritization schemes, and ultimately to help preserve global biodiversity.

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Appendix 1: Supplementary materials Chapter 3

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Section 1: Trait data

Section 1.1. Trait data completeness

The completeness of life-history trait data for each species was calculated as the proportion of the four traits which had an estimate. An aligned-rank-transformation ANOVA was performed to compare trait completeness values across vertebrate classes using the *ARTool* R package Version 0.10.8 (Wobbrock et al., 2011) and results were plotted using the *emmeans* R package Version 1.5.0 (Lenth, 2020). This analysis revealed significant variation in average trait-data completeness among vertebrate classes (F=1532.5, d.f.=3, *p*-value<0.001) (Figure S1). Mammals had the highest completeness (mean = 0.506 ± 0.339 sd), followed by birds (mean=0.365 ± 0.242 sd), while reptiles had the least complete trait information on average (mean= 0.299 ± 0.291 sd) (Figure S1). These findings are broadly consistent with those of a previous study (Etard et al., 2020), although it is surprising that mammals show a higher data completeness than birds. This can be explained by two factors; first, the traits selected for this analysis, especially those related to ageing (longevity and maturity), are more abundant for mammals than for birds. Second, the availability of data, in terms of open access and public trait information, was greater for mammals than for birds. Third, although I could not find bird data for some important traits, I did find extensive information for traits such as body-mass. As a result, the trait dataset contained a much large quantity of bird species than mammals or reptiles (9,655 birds compare to 4,638 mammals). Mammals are the group best represented in terms of trait information with almost 25% with complete trait information. By contrast, birds and reptiles presented values of trait completeness of 9.5% and 8.2%.

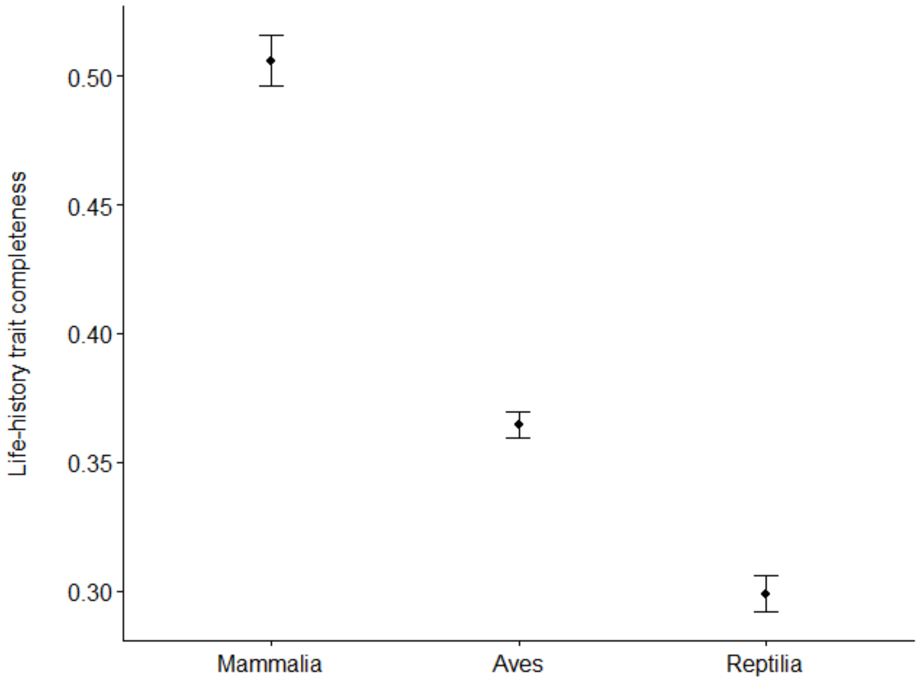

Figure S1. Life-history trait completeness across terrestrial amniote classes. Points show means as estimated by the ANOVA analysis, while error bars show 95% confidence intervals.

To check the spatial distribution of the life-history traits I used species distribution maps from the IUCN Red List Version 2021-1(IUCN, 2021). Species for which I had spatial distributions (presence codes 1-4 and origin codes 1-6, IUCN, 2021) had these distributions transformed into raster surfaces, using the completeness of trait data of each species as the pixel value. Raster-layers were stacked, and mean values were calculated for each class individually and for all species (Figure S2). By doing this I found that trait completeness also varied spatially for each of the vertebrate classes (Figure S2). Mammals have high completeness of trait information across most of the northern hemisphere, but lower completeness in the Amazon basin and the Brazilian coast, eastern and central Africa, and south-eastern Asia (Figure S2). Trait data for reptiles is relatively complete in North America, Europe, some regions of Asia, the Middle East, India, Australia and the humid subtropical areas of Morocco and Algeria but low everywhere else

(Figure S2). The completeness of life-history trait data for birds included in this study was generally low across all regions. Better-represented areas were central and northern Africa, western Europe, western North America, Central America, some portions of the Amazon basin, and the humid subtropical and temperate grassland areas of South America (Figure S2). From the spatial patterns of all species, it can be concluded that the dataset is poorly representing the southern and central regions of the African continent. Lower values of data completeness are also associated with the Amazon basin for all groups as well as south-east Asia.

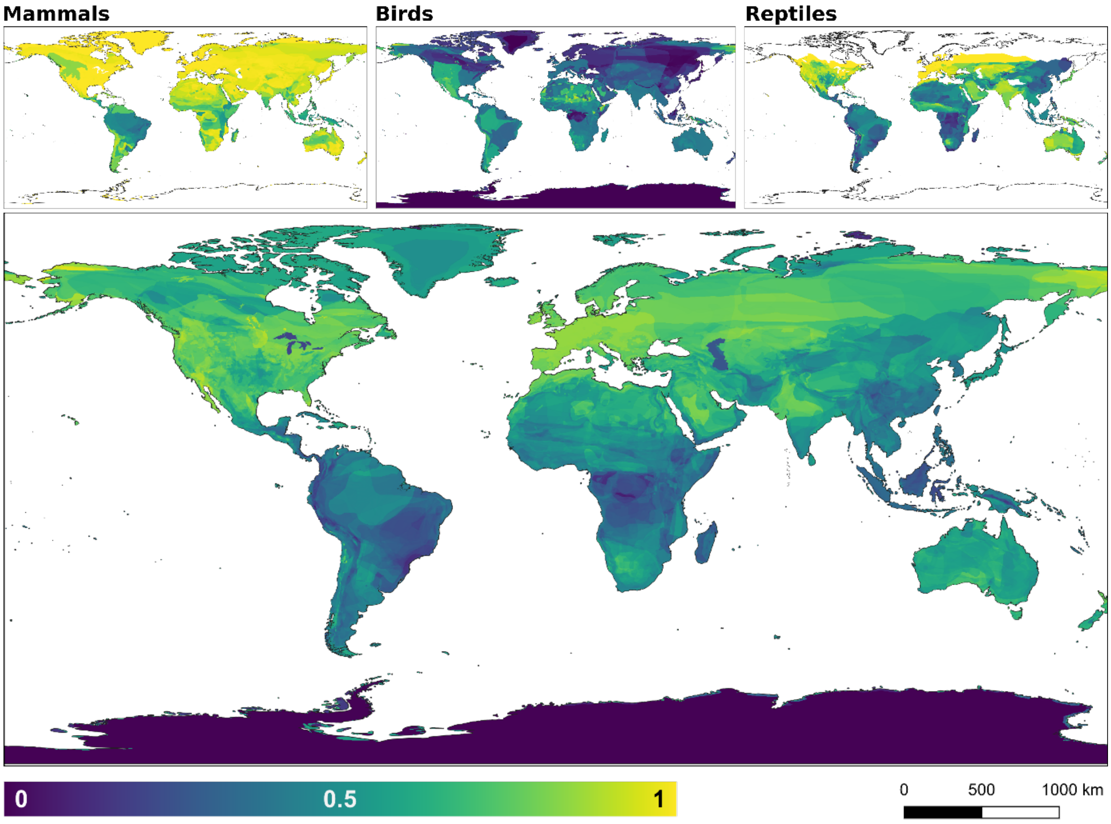

Figure S2. Trait-data completeness for the individual classes of terrestrial amniotes (top panels) and combined (bottom panel). Values range from 0, indicating that no life-history traits estimates are available for any species, to 1, indicating that all species in an area have estimates for all four life-history traits. A total of 17,062 mammal, bird and reptile species, for which IUCN range maps (Version 2021-1(IUCN, 2021)) are available, are considered in this map.

Section 1.2 Trait adjustment

For the construction of the fast-slow continuum, life-history traits needed to be adjusted for body mass and taxonomy. Linear regression approaches have been used previously for this purpose (Dobson & Oli, 2008; Schwarz & Meiri, 2017; Stearns, 1983). For this study, I used linear mixed-effects models (LMM), allowing us to account for the effect of taxonomic relationships. Linear mixed-effects models were fitted using restricted maximum likelihood (REML), using body mass as the explanatory variable and the life-history traits (offspring, longevity, maturity, reproduction events) as response variables in four separate models. To deal with the skewness of the trait data, all variables were $\log_e$ transformed. I used a nested random-effect structure, with family nested within order nested within class, to control for species taxonomic relationships. I used this approach instead of a phylogenetic correction because at the time I could not build a unified and comprehensive phylogenetic tree that included all the species included in the analysis. An exponential variance structure was added to the model to deal with residual heteroskedasticity. This structure modelled the variance of the residuals as σ^2 multiplied by an exponential function of the variance-covariate of the explanatory variables multiplied by a parameter δ, which allows for a different spread of residuals across factor levels (Zuur et al., 2009). I selected this model structure after testing combinations of different random effects and variance structures. Model selection was based on the Akaike Information Criterion (AIC), the Bayesian Information Criterion (BIC), and the marginal and conditional R^2 values (Nakagawa et al., 2017).

Residuals from these models were used as log-transformed trait values adjusted for the effects of body mass and phylogeny (‘adjusted traits’ from now on). These adjusted traits (offspring, longevity, maturity, and reproduction events) were then used to build the fast-slow continuum, using Principal Component Analysis. Linear mixed-effects models were fitted using the *lme* function of the R package *nlme* Version 3.1-148 (Pinheiro et al., 2021). AIC and BIC selection parameters were extracted using the R package *stats* Version 3.6.1 (R Core Team, 2021). Marginal and conditional R^2 values were calculated using the *rsquaredGLMM* function of the R package *MuMln* Version 1.43.17 (Barton, 2020).

The absolute correlation of unadjusted life-history traits with body mass ranged from r = 0.21 for the number of offspring to 0.62 for longevity (Table S1). Longevity and maturity were highly correlated with each other (r = 0.76), while offspring and reproductive events showed the weakest correlation (r = 0.11) (Table S1). When the effects of body mass and phylogeny were removed from the life-history traits, correlations of these variables with body mass were approximately zero (first row on the right-hand side of Table S1). This also significantly reduced the correlation between life-history traits, by nearly 70% on average (remaining rows on the right-hand side of Table S1).

Table S1. Spearman rank correlation between unadjusted and adjusted life-history trait variables; offspring; longevity; number of reproductive events per-year (Re-events in the table); maturity; and body mass.

	Unadjusted				Adjusted			
	Offspring	Maturity	Maturity	Re-events	Offspring	Maturity	Longevity	Re-events
Body mass	-0.212***	0.549***	0.625***	-0.434***	0.000	-0.002	0.000	0.002
Offspring		-0.178***	-0.230***	0.117***		-0.021	-0.052*	-0.094***
Maturity			0.762***	-0.658***			0.165	-0.212***
Longevity				-0.545***				-0.075**

***P ≤ 0.0001,**P ≤ 0.001,*P ≤ 0.05

Section 2: Life-history classification

2.1. Body-mass continuum

I classified 2,061 species of terrestrial amniote vertebrates under the body-mass continuum (Figure S3). Variables related to ageing, i.e. longevity and female maturity, loaded positively with the first principal components axis, while variables related to reproductive outcome, i.e. number of offspring and number of reproductive events, showed negative loading values on this axis (Table S2). The second axis of the body-mass continuum was highly influenced by the number of offspring (loading value of 0.96, explaining more than 90% of the total variation of this axis; Table S2). The third axis was highly influenced by longevity and number of reproduction events, both loading positively and explaining almost 95% of the total variation of this axis.

The first axis of the body-mass continuum classified species from small, short-lived species with high reproductive outcome (lower score values) to large, long-lived species with a low reproductive outcome (higher score values). Scores from the second axis classified species into those with few offspring (low values) to those with a higher number of offspring (higher values). Lower score values of the third axis were characteristic of species with shorter reproductive lifespan and less frequent reproduction events, while higher values indicated species with longer lifespans and more frequent reproduction events.

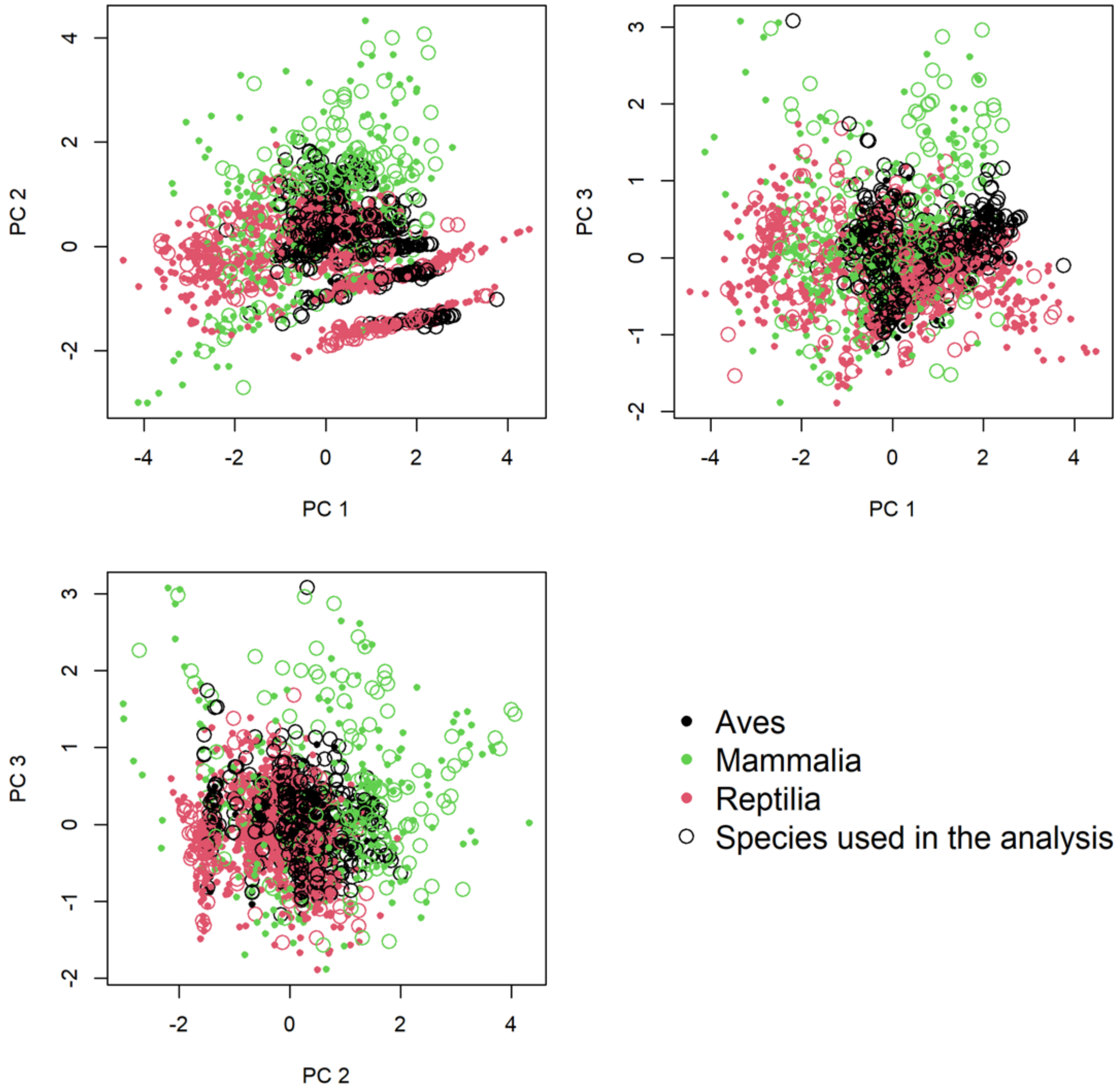

Figure S3. Score values for the first three PCs of the body-mass continuum. Each point, or score value, represents the position of a species on the body-mass continuum according to its life-history trait configuration. The different colours represent the main vertebrate classes included in the analysis; hollow circles indicate the position of the species used for the final analysis whereas solid circles represent the total set of species used to calculate the body-mass continuum. In positioning species along the body-mass continuum, I included more species than could be considered in the final analyses to reduce biases.

Section 2.2. *Fast-slow continuum*

The same 2,061 species as for the body-mass continuum were classified along the fast-slow continuum (Figure S4). Loading values for the first principal components axis showed the expected trade-offs between traits, with longevity and female maturity loading positively, and frequency of reproduction events negatively (Table S2). The second axis was mostly influenced by the number of offspring, with a negative loading, contributing more than 67% to its variability (Table S2). The third axis was mostly influenced by longevity and number of offspring, both loading positively (Table S2).

Low score values of the first axis of the fast-slow continuum corresponded with short-lived species with a high number of reproduction events, while higher score values corresponded with long-lived species with less frequent reproduction events. Lower score values of the second axis were related to species with a higher number of offspring, and higher scores to species that produce fewer offspring. High score values of the third axis described species with long lifespans and a high number of offspring, while lower score values of this continuum represented species with short lifespans and fewer offspring.

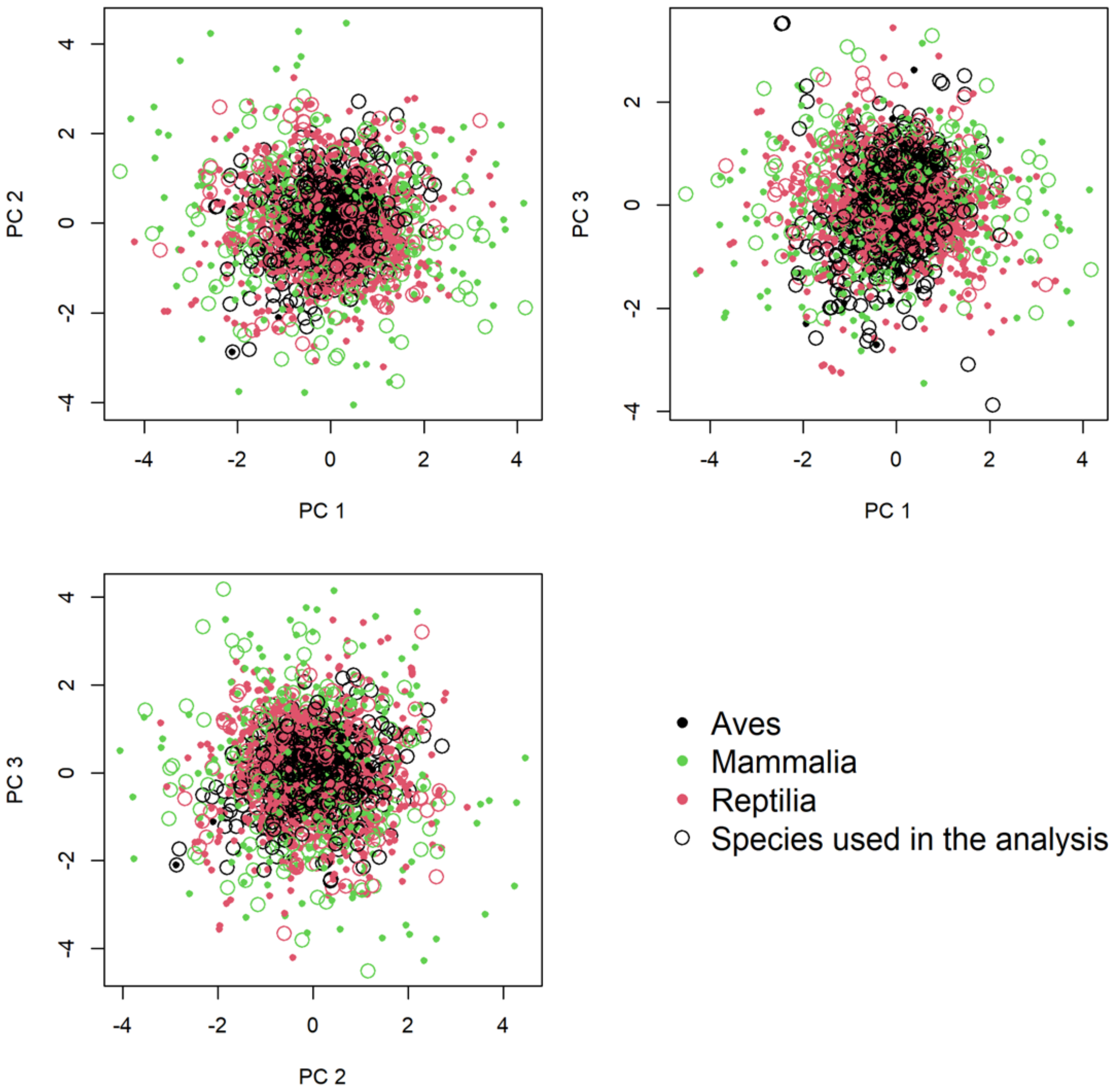

Figure S4. Score values for the first three PCs of the fast-slow continuum. Each point, or score value, represents the position of a species on the fast-slow continuum according to its life-history trait configuration. The different colours represent the main vertebrate classes included in the analysis. Hollow circles indicate the position of the subset of species used for the final analysis. The solid-coloured circles represent the total set of species used to calculate the fast-slow continuum. In positioning species along the fast-slow continuum, I included more species than could be included in the final analysis to reduce bias.

Table S2. Factor loadings (Load) and the percentage contribution to the principal components (Contr) of each life-history trait variable; number of offspring per reproductive event (Offspring), longevity in years (Longevity); number of reproduction events per-year (Re-event); and age at sexual maturity (Maturity). Correlation of the PC with body-mass (Cor-Bm); the PC eigenvalue ('Eig'), and percentages of explained and cumulative variance (Ex-var, Cum-var) of each PC under the body-mass and fast-slow continuums.

	Body-mass Continuum						Fast-slow Continuum					
	PC1		*PC2*		*PC3*		*PC1*		*PC2*		*PC3*	
	Load	Contr	Load	Contr	Load	Contr	Load	Contr	Load	Contr	Load	Contr
Offspring	-0.216	4.67	0.96	93.31	0.138	1.9	0.051	0.264	-0.823	67.78	0.507	25.73
Longevity	0.571	32.55	0.025	0.06	0.568	32.27	0.482	23.19	0.416	17.3	0.738	54.4
Re-event	-0.526	27.62	-0.221	4.88	0.786	61.82	-0.582	33.83	0.375	14.06	0.36	12.95
Maturity	0.593	35.15	0.132	1.74	0.2	4.01	0.653	42.71	0.092	0.84	-0.263	6.92

Cor-Bm	0.612	-0.025	0.12	-0.003	0.0003	0.0002
Eig	2.381	0.943	0.459	1.308	1.071	0.869
Ex-var	59.53	23.57	11.48	32.707	26.783	21.729
Cum-var	59.53	83.106	94.588	32.707	59.49	81.218

Section 3: Class specific models

To test the potential changes of the response across amniote classes of species to environmental heterogeneity due to life-history strategies, I fitted class specific models using the same approach as for the main model. I used a binomial generalized linear mixed-effects model (GLMM) with a logit link function and a binomial distribution (binary response variable, presence = 1; pseudo-absence= 0). The explanatory variables were the environmental heterogeneity metrics, the life-history axis, and the two-way interaction between the environmental variables and the life-history axis. Species identity was included as a random intercept to account for variation among species. Same as with the main model, I expected responses to environmental heterogeneity to vary among species. To account for this, I added random slopes in the form of each environmental variable.

Individual models were fitted for birds, mammals and reptiles using maximum likelihood, using an adaptative Gauss-Hermite quadrature approximation (Liu & Pierce, 1994), using the *lme4* R package Version 1.1-23 (Bates et al., 2015). Same as with the main model, each class model was refitted at each spatial resolution: 1, 2, 5 and 10 km grid resolution. I evaluated model fit using the marginal and conditional pseudo-R^2 values for GLMM (Johnson, 2014; Nakagawa et al., 2017; Nakagawa & Schielzeth, 2013). All environmental heterogeneity variables were normalized using the Ordered-Quantile transformation (Liu & Pierce, 1994) built into the *bestNormalize* R package Version 1.6.0 (Peterson & Cavanaugh, 2019). The ability of models to correctly discriminate presences from pseudo-absences was evaluated using the area under the Receiver Operating Characteristic curve (AUC) (Hanley & McNeil, 1982). The AUC returns a value within the range of 0-1, where 0 is perfectly incorrect discrimination, 0.5 corresponds to the performance of a random classifier, and 1 corresponds to a perfect classification. All analysis, data manipulation, and spatial pre-processing was carried out using the R statistical software Version 3.6.3 (R Core Team, 2021).

Section 3.1. *Model summary at 1 km grid resolution*

Table S3. Summary of the Generalized Linear Mixed-effects Models (GLMM´s) at 1-km resolution. The direction of the effects ("+" = positive and, "-" = negative effects), and the significance (*P values*) for each effect in the model are included (left and right sides of the table, respectively). Shaded grey and green areas represent overlap in sensitivity and response direction between the full model (mammals, birds and reptiles combined) and the models for each vertebrate class. Interactions between life-history axes and environmental variables are shown for the body-mass continuum (top half of the table), and fast-slow continuum (bottom half of the table).

	Direction of the effects at 1 km				Significance of the effects at 1 km			
Effects	Complete	Birds	Mammals	Reptiles	Complete	Birds	Mammals	Reptiles
	Body-mass continuum							
Coef. Variation:PC.1	"+"	"+"	"-"	"-"	6.04e-05	4.27e-07	6.75e-01	4.37e-04
Evenness:PC.1	"+"	"+"	"+"	"-"	4.25e-13	1.33e-05	4.46e-03	7.08e-01
Correlation:PC.1	"-"	"-"	"-"	"+"	2.74e-13	2.61e-14	1.25e-01	8.80e-03
Temp. Seas:PC.1	"+"	"-"	"+"	"-"	2.31e-01	2.04e-01	2.44e-02	8.21e-01
Prec. Seas:PC.1	"-"	"-"	"+"	"-"	1.24e-01	4.65e-01	6.16e-01	2.01e-01
SD. Elevation:PC.1	"-"	"-"	"-"	"-"	6.89e-10	8.36e-11	6.15e-01	2.19e-01
Coef. Variation:PC.2	"+"	"+"	"+"	"+"	5.43e-02	1.52e-01	3.34e-01	1.97e-02
Evenness:PC.2	"+"	"+"	"+"	"+"	6.94e-03	1.12e-04	3.72e-02	1.00e-02
Correlation:PC.2	"-"	"-"	"-"	"-"	1.60e-02	1.04e-04	2.10e-01	2.45e-02
Temp. Seas:PC.2	"-"	"-"	"+"	"-"	9.39e-01	1.24e-01	6.21e-01	9.20e-01
Prec. Seas:PC.2	"-"	"-"	"+"	"+"	9.53e-01	1.20e-01	4.92e-01	7.58e-01
SD. Elevation:PC.2	"-"	"-"	"-"	"-"	1.59e-05	4.89e-07	5.99e-02	1.54e-01
Coef. Variation:PC.3	"+"	"+"	"+"	"+"	3.40e-07	2.06e-01	2.06e-01	4.04e-06
Evenness:PC.3	"+"	"+"	"+"	"+"	2.04e-01	5.00e-01	5.00e-01	7.95e-07
Correlation:PC.3	"-"	"-"	"-"	"-"	1.90e-07	8.80e-02	8.80e-02	1.32e-06
Temp. Seas:PC.3	"+"	"+"	"+"	"+"	1.55e-01	1.29e-02	1.29e-02	2.29e-01
Prec. Seas:PC.3	"+"	"+"	"+"	"-"	3.38e-01	7.09e-02	7.09e-02	5.45E-01
SD. Elevation:PC.3	"-"	"-"	"-"	"-"	2.26e-09	3.71e-04	3.71e-04	2.82e-07
	Fast-slow continuum							
Coef. Variation:PC.1	"-"	"-"	"+"	"+"	0.0212	0.0262	0.5579	0.7914
Evenness:PC.1	"-"	"+"	"-"	"-"	0.2468	0.0662	0.0165	0.8423
Correlation:PC.1	"+"	"+"	"+"	"+"	0.0011	0.0795	0.1783	0.2478
Temp. Seas:PC.1	"-"	"+"	"-"	"-"	0.0146	0.6156	0.0275	0.3697
Prec. Seas:PC.1	"-"	"-"	"-"	"+"	0.2664	0.3699	0.0097	0.3169
SD. Elevation:PC.1	"+"	"+"	"+"	"+"	0.0000	0.0061	0.0019	0.0073

Coef. Variation:PC.2	"-"	"-"	"+"	"-"	0.1000	0.0183	0.8217	0.3998
Evenness:PC.2	"-"	"+"	"-"	"-"	0.5478	0.5371	0.1106	0.1249
Correlation:PC.2	"+"	"+"	"+"	"+"	0.0528	0.1110	0.4141	0.1082
Temp. Seas:PC.2	"+"	"+"	"+"	"-"	0.3251	0.9996	0.1212	0.4073
Prec. Seas:PC.2	"-"	"-"	"-"	"+"	0.9130	0.7435	0.9125	0.7042
SD. Elevation:PC.2	"+"	"+"	"+"	"+"	0.0047	0.0079	0.0705	0.1433
Coef. Variation:PC.3	"-"	"-"	"+"	"-"	0.0988	0.1225	0.3459	0.1359
Evenness:PC.3	"-"	"+"	"-"	"-"	0.6462	0.9877	0.4990	0.0820
Correlation:PC.3	"+"	"+"	"+"	"+"	0.0121	0.0017	0.6045	0.0697
Temp. Seas:PC.3	"-"	"-"	"-"	"+"	0.1767	0.7699	0.1026	0.8104
Prec. Seas:PC.3	"-"	"-"	"-"	"+"	0.0169	0.0615	0.0004	0.1386
SD. Elevation:PC.3	"+"	"+"	"+"	"+"	0.0171	0.3163	0.5536	0.0044

Section 3.2. *Full Model by grid resolution*

Table S4. Model estimates and p-values for the interaction of life-history axes and environmental heterogeneity variables for the full (birds, mammals, and reptiles) Generalized Linear Mixed Models (GLMMs) at different spatial resolutions. Along with the spatial resolution at which the analysis was carried out, I also included the number of species in each model (presented as Spp).

	1 km Spp=980		2 km Spp=958		5 km Spp=933		10 km Spp=904	
	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value
	Body-mass continuum							
Coef. Variation:PC.1	0.1844	0.0001	0.1121	0.0185	0.0716	0.1724	0.1152	0.0414
Evenness:PC.1	0.1815	0.0000	0.3017	0.0000	0.4037	0.0000	0.3235	0.0000
Correlation:PC.1	-0.1213	0.0000	-0.1343	0.0000	-0.1223	0.0000	-0.0888	0.0017
Temp. Seas:PC.1	0.2560	0.2312	0.3260	0.1179	0.3100	0.1212	0.5144	0.0102
Prec. Seas:PC.1	-0.1715	0.1237	-0.1638	0.1217	-0.1567	0.1156	-0.1317	0.1737
SD. Elevation:PC.1	-0.3301	0.0000	-0.3363	0.0000	-0.3398	0.0000	-0.3410	0.0000
Coef. Variation:PC.2	0.0861	0.0543	0.0612	0.1864	0.0381	0.4501	0.0104	0.8470
Evenness:PC.2	0.0659	0.0069	0.0493	0.1972	0.0261	0.6550	0.0466	0.4931
Correlation:PC.2	-0.0390	0.0160	-0.0125	0.4664	0.0321	0.1293	0.0580	0.0318
Temp. Seas:PC.2	-0.0159	0.9391	0.0626	0.7575	-0.0007	0.9970	0.1221	0.5222
Prec. Seas:PC.2	-0.0064	0.9528	0.0298	0.7714	0.0775	0.4160	0.0659	0.4744
SD. Elevation:PC.2	-0.2249	0.0000	-0.2030	0.0002	-0.1606	0.0030	-0.1697	0.0023
Coef. Variation:PC.3	0.3061	0.0000	0.2919	0.0000	0.3088	0.0000	0.2500	0.0006
Evenness:PC.3	0.0419	0.2036	0.0809	0.1158	0.0328	0.6757	0.0607	0.5068
Correlation:PC.3	-0.1132	0.0000	-0.1084	0.0000	-0.0920	0.0013	-0.0559	0.1269
Temp. Seas:PC.3	0.3963	0.1553	0.4181	0.1241	0.4318	0.0940	0.4093	0.1090
Prec. Seas:PC.3	0.1392	0.3384	0.1575	0.2542	0.1458	0.2565	0.1601	0.1963
SD. Elevation:PC.3	-0.4178	0.0000	-0.4266	0.0000	-0.4343	0.0000	-0.4141	0.0000
	Fast-slow continuum							
Coef. Variation:PC.1	-0.1062	0.0212	-0.0718	0.1335	-0.0384	0.4649	-0.0585	0.2995
Evenness:PC.1	-0.0290	0.2468	-0.0746	0.0586	-0.0881	0.1460	-0.0634	0.3702
Correlation:PC.1	0.0542	0.0011	0.0568	0.0013	0.0479	0.0291	0.0552	0.0505
Temp. Seas:PC.1	-0.5238	0.0146	-0.5178	0.0136	-0.5960	0.0029	-0.6714	0.0007
Prec. Seas:PC.1	-0.1242	0.2664	-0.1073	0.3135	-0.1018	0.3055	-0.0904	0.3468
SD. Elevation:PC.1	0.2602	0.0000	0.2706	0.0000	0.2665	0.0000	0.2815	0.0000
Coef. Variation:PC.2	-0.0908	0.1000	-0.0752	0.1859	-0.0939	0.1324	-0.0879	0.1849
Evenness:PC.2	-0.0180	0.5478	-0.0722	0.1225	-0.0876	0.2233	-0.1093	0.1895
Correlation:PC.2	0.0382	0.0528	0.0443	0.0333	0.0713	0.0060	0.0769	0.0199
Temp. Seas:PC.2	0.2533	0.3251	0.1926	0.4411	0.1583	0.5076	0.1734	0.4602
Prec. Seas:PC.2	-0.0147	0.9130	-0.0118	0.9261	0.0607	0.6093	0.0899	0.4290

SD. Elevation:PC.2	0.1818	0.0047	0.1856	0.0050	0.1988	0.0032	0.1884	0.0060
Coef. Variation:PC.3	-0.1053	0.0988	-0.0828	0.2100	-0.0949	0.1901	-0.1022	0.1823
Evenness:PC.3	-0.0157	0.6462	-0.0195	0.7184	0.0203	0.8072	0.0074	0.9387
Correlation:PC.3	0.0568	0.0121	0.0545	0.0225	0.0472	0.1129	0.0574	0.1309
Temp. Seas:PC.3	-0.4023	0.1767	-0.4506	0.1209	-0.4787	0.0845	-0.4762	0.0806
Prec. Seas:PC.3	-0.3714	0.0169	-0.3730	0.0117	-0.3245	0.0190	-0.3604	0.0063
SD. Elevation:PC.3	0.1780	0.0171	0.1685	0.0290	0.1629	0.0381	0.1678	0.0348

Section 3.3. *Partial for birds by grid resolution*

Table S5. Model estimates and p-values for the GLMM's of birds at different spatial resolutions. Only the interaction effects between the life-history axes (body-mass and fast-slow continuum, upper and lower half of the table respectively) and the environmental variables are shown. Along with the spatial resolution at which the analysis was carried out, I included the number of species in each model (presented as Spp).

	1 km Spp=576		2 km Spp=571		5 km Spp=570		10 km Spp=562	
	Estimate	*p-value*	Estimate	*p-value*	Estimate	p-value	Estimate	*p-value*
	Body-mass continuum							
Coef. Variation:PC.1	0.3795	0.0000	0.3571	0.0000	0.3224	0.0001	0.3556	0.0001
Evenness:PC.1	0.1606	0.0000	0.1923	0.0004	0.2518	0.0015	0.1980	0.0365
Correlation:PC.1	-0.2013	0.0000	-0.2148	0.0000	-0.2114	0.0000	-0.1702	0.0003
Temp. Seas:PC.1	-0.3832	0.2041	-0.4252	0.1561	-0.3506	0.2322	-0.3227	0.2488
Prec. Seas:PC.1	-0.1362	0.4648	-0.1380	0.4377	-0.1632	0.3345	-0.1816	0.2631
SD. Elevation:PC.1	-0.5745	0.0000	-0.5952	0.0000	-0.5513	0.0000	-0.4965	0.0000
Coef. Variation:PC.2	0.1150	0.1523	0.0914	0.2743	-0.0022	0.9804	-0.0298	0.7635
Evenness:PC.2	0.1538	0.0001	0.1605	0.0057	0.1852	0.0286	0.1975	0.0502
Correlation:PC.2	-0.1107	0.0001	-0.0948	0.0021	-0.0317	0.4126	0.0332	0.5041
Temp. Seas:PC.2	-0.4954	0.1238	-0.4881	0.1267	-0.4054	0.1931	-0.3677	0.2165
Prec. Seas:PC.2	-0.3094	0.1200	-0.2563	0.1773	-0.2315	0.1980	-0.2181	0.2079
SD. Elevation:PC.2	-0.4755	0.0000	-0.4828	0.0000	-0.3818	0.0000	-0.3272	0.0004
Coef. Variation:PC.3	0.1936	0.2062	0.1787	0.3002	0.2358	0.2801	0.2484	0.2616
Evenness:PC.3	0.0571	0.4995	0.2502	0.0894	0.2429	0.3540	0.1508	0.6029
Correlation:PC.3	-0.0868	0.0880	-0.1314	0.0292	-0.1010	0.2275	-0.0953	0.3712
Temp. Seas:PC.3	2.2003	0.0129	2.0032	0.0225	1.9894	0.0194	2.2255	0.0136
Prec. Seas:PC.3	0.7006	0.0709	0.5562	0.1246	0.1984	0.5307	0.2180	0.4714
SD. Elevation:PC.3	-0.6403	0.0004	-0.7573	0.0001	-0.8961	0.0000	-0.9458	0.0000
	Fast-slow continuum							
Coef. Variation:PC.1	-0.1673	0.0262	-0.1500	0.0556	-0.1459	0.0887	-0.1749	0.0623
Evenness:PC.1	0.0676	0.0662	0.0959	0.0768	0.1186	0.1386	0.1718	0.0725
Correlation:PC.1	0.0463	0.0795	0.0512	0.0733	0.0537	0.1399	0.0572	0.2228
Temp. Seas:PC.1	0.1519	0.6156	0.1684	0.5756	0.1214	0.6815	-0.0006	0.9984
Prec. Seas:PC.1	-0.1677	0.3699	-0.1343	0.4519	-0.1167	0.4941	-0.1133	0.4899
SD. Elevation:PC.1	0.2436	0.0061	0.2460	0.0061	0.2240	0.0110	0.2017	0.0202
Coef. Variation:PC.2	-0.1934	0.0183	-0.2065	0.0152	-0.2448	0.0082	-0.2493	0.0145
Evenness:PC.2	0.0249	0.5371	0.0428	0.4683	0.1500	0.0834	0.2309	0.0267
Correlation:PC.2	0.0460	0.1110	0.0522	0.0937	0.0506	0.2000	0.0462	0.3649
Temp. Seas:PC.2	0.0002	0.9996	-0.0248	0.9395	0.0080	0.9800	-0.0099	0.9743
Prec. Seas:PC.2	-0.0665	0.7435	-0.0607	0.7537	-0.0731	0.6916	-0.1019	0.5682

SD. Elevation:PC.2	0.2566	0.0079	0.2676	0.0059	0.2952	0.0019	0.2688	0.0044
Coef. Variation:PC.3	-0.1339	0.1225	-0.1105	0.2226	-0.1053	0.2904	-0.1538	0.1588
Evenness:PC.3	0.0007	0.9877	-0.0034	0.9563	0.0318	0.7328	0.0553	0.6189
Correlation:PC.3	0.0958	0.0017	0.1093	0.0010	0.1236	0.0035	0.1609	0.0032
Temp. Seas:PC.3	-0.1015	0.7699	-0.2029	0.5581	-0.2710	0.4298	-0.2394	0.4659
Prec. Seas:PC.3	-0.4019	0.0615	-0.4321	0.0360	-0.3501	0.0773	-0.2999	0.1163
SD. Elevation:PC.3	0.1023	0.3163	0.1012	0.3283	0.0729	0.4759	0.0399	0.6928

Section 3.4. *Partial for mammals by grid resolution*

Table S6. Model estimates and p-values for the GLMM’s of mammals at different spatial resolutions. Only the interaction effects between the life-history axes (body-mass and fast-slow continuum, upper and lower half of the table respectively) and the environmental variables are shown. Along with the spatial resolution at which the analysis was carried out, I included the number of species in each model (presented as Spp).

	1 km Spp=230		2 km Spp=217		5 km Spp=200		10 km Spp=190	
	Estimate	*p-value*	Estimate	*p-value*	Estimate	*p-value*	Estimate	*p-value*
	Body-mass continuum							
Coef. Variation:PC.1	-0.0321	0.6755	-0.1238	0.1496	-0.1688	0.1264	-0.0858	0.4530
Evenness:PC.1	0.1212	0.0045	0.2830	0.0001	0.4084	0.0022	0.2589	0.0872
Correlation:PC.1	-0.0396	0.1249	-0.0819	0.0069	-0.0802	0.0568	-0.0670	0.2182
Temp. Seas:PC.1	0.9950	0.0244	1.1202	0.0102	1.1615	0.0068	1.5711	0.0008
Prec. Seas:PC.1	0.0974	0.6156	0.0898	0.6182	-0.0391	0.8065	-0.0150	0.9239
SD. Elevation:PC.1	-0.0452	0.6150	-0.0598	0.5440	-0.0962	0.3786	-0.1612	0.1504
Coef. Variation:PC.2	0.1124	0.3342	0.0951	0.4681	0.0859	0.5984	0.0318	0.8475
Evenness:PC.2	0.1330	0.0372	0.1634	0.1442	0.1818	0.3550	0.2310	0.2878
Correlation:PC.2	-0.0483	0.2095	-0.0631	0.1662	0.0132	0.8315	-0.0072	0.9269
Temp. Seas:PC.2	0.3358	0.6207	0.3515	0.6017	-0.0965	0.8797	0.1141	0.8659
Prec. Seas:PC.2	0.2029	0.4924	0.1093	0.6916	0.1541	0.5117	0.1119	0.6176
SD. Elevation:PC.2	-0.2578	0.0599	-0.2578	0.0877	-0.2796	0.0827	-0.3454	0.0319
Coef. Variation:PC.3	0.1936	0.2062	0.1787	0.3002	0.2358	0.2801	0.2484	0.2616
Evenness:PC.3	0.0571	0.4995	0.2502	0.0894	0.2429	0.3540	0.1508	0.6029
Correlation:PC.3	-0.0868	0.0880	-0.1314	0.0292	-0.1010	0.2275	-0.0953	0.3712
Temp. Seas:PC.3	2.2003	0.0129	2.0032	0.0225	1.9894	0.0194	2.2255	0.0136
Prec. Seas:PC.3	0.7006	0.0709	0.5562	0.1246	0.1984	0.5307	0.2180	0.4714
SD. Elevation:PC.3	-0.6403	0.0004	-0.7573	0.0001	-0.8961	0.0000	-0.9458	0.0000
	Fast-slow continuum							
Coef. Variation:PC.1	0.0489	0.5579	0.1076	0.2540	0.2253	0.0578	0.2078	0.0947
Evenness:PC.1	-0.1105	0.0165	-0.2872	0.0004	-0.4262	0.0030	-0.4645	0.0046
Correlation:PC.1	0.0375	0.1783	0.0750	0.0237	0.1060	0.0204	0.1429	0.0160
Temp. Seas:PC.1	-1.0655	0.0275	-1.1699	0.0152	-1.5935	0.0006	-1.9412	0.0001
Prec. Seas:PC.1	-0.5480	0.0097	-0.4814	0.0152	-0.3414	0.0466	-0.3911	0.0210
SD. Elevation:PC.1	0.3040	0.0019	0.3554	0.0010	0.3862	0.0010	0.4076	0.0008
Coef. Variation:PC.2	0.0232	0.8217	0.0662	0.5632	0.0614	0.6749	0.0482	0.7414
Evenness:PC.2	-0.0902	0.1106	-0.2200	0.0247	-0.2920	0.0984	-0.3418	0.0759
Correlation:PC.2	0.0275	0.4141	0.0519	0.1921	0.0768	0.1678	0.1019	0.1447
Temp. Seas:PC.2	0.9245	0.1212	0.8162	0.1637	0.3583	0.5325	0.2768	0.6435
Prec. Seas:PC.2	-0.0287	0.9125	-0.0176	0.9419	0.2326	0.2732	0.2267	0.2559

SD. Elevation:PC.2	0.2188	0.0705	0.2472	0.0609	0.2433	0.0947	0.1972	0.1687
Coef. Variation:PC.3	0.1390	0.3459	0.1685	0.3107	0.2009	0.3482	0.2008	0.3610
Evenness:PC.3	-0.0547	0.4990	-0.0841	0.5543	-0.1267	0.6239	-0.0727	0.8018
Correlation:PC.3	0.0250	0.6045	0.0914	0.1118	0.0863	0.2876	0.1122	0.2828
Temp. Seas:PC.3	-1.3947	0.1026	-1.3430	0.1142	-1.5287	0.0695	-1.3656	0.1324
Prec. Seas:PC.3	-1.3248	0.0004	-1.2058	0.0006	-0.8671	0.0055	-0.9750	0.0013
SD. Elevation:PC.3	0.1030	0.5536	0.1083	0.5721	0.1488	0.4858	0.1965	0.3649

Section 3.5. *Partial for reptiles by grid resolution*

Table S7. Model estimates and p-values for the GLMM's of reptiles at different spatial resolutions. Only the interaction effects between the life-history axes (body-mass and fast-slow continuum, upper and lower half of the table respectively) and the environmental variables are shown. Along with the spatial resolution at which the analysis was carried out, I included the number of species in each model (presented as Spp).

	1 km Spp=174		2 km Spp=170		5 km Spp=163		10 km Spp=152	
	Estimate	*p-value*	Estimate	*p-value*	Estimate	*p-value*	Estimate	*p-value*
	Body-mass continuum							
Coef. Variation:PC.1	-0.4098	0.0004	-0.3734	0.0030	-0.2876	0.0394	-0.0790	0.6046
Evenness:PC.1	-0.0271	0.7081	-0.0703	0.5845	-0.1504	0.4986	-0.1498	0.5867
Correlation:PC.1	0.1077	0.0088	0.1057	0.0260	0.1629	0.0134	0.1434	0.1092
Temp. Seas:PC.1	-0.1978	0.8205	-0.3543	0.6704	-1.1061	0.1438	-0.9821	0.1772
Prec. Seas:PC.1	-0.5477	0.2006	-0.6775	0.0965	-0.4831	0.2237	-0.4562	0.2202
SD. Elevation:PC.1	-0.1926	0.2190	-0.1965	0.2278	-0.1831	0.3072	-0.1267	0.5355
Coef. Variation:PC.2	0.1867	0.0197	0.0879	0.3079	0.0310	0.7422	-0.0949	0.3566
Evenness:PC.2	0.1292	0.0100	0.2488	0.0049	0.4054	0.0068	0.4335	0.0194
Correlation:PC.2	-0.0649	0.0245	-0.0715	0.0307	-0.0736	0.1025	-0.0623	0.3035
Temp. Seas:PC.2	-0.0595	0.9202	0.2325	0.6791	0.6177	0.2189	0.7556	0.1184
Prec. Seas:PC.2	0.0898	0.7582	0.1398	0.6121	0.0428	0.8710	0.0233	0.9245
SD. Elevation:PC.2	-0.1534	0.1540	-0.1416	0.2022	-0.1406	0.2403	-0.1462	0.2828
Coef. Variation:PC.3	0.3695	0.0000	0.2406	0.0054	0.1153	0.2184	-0.1062	0.3023
Evenness:PC.3	0.2481	0.0000	0.4512	0.0000	0.6426	0.0000	0.8156	0.0000
Correlation:PC.3	-0.1372	0.0000	-0.1056	0.0012	-0.0740	0.0948	0.0099	0.8688
Temp. Seas:PC.3	0.7203	0.2286	0.9410	0.0994	1.2278	0.0147	1.3027	0.0072
Prec. Seas:PC.3	-0.1782	0.5447	-0.1127	0.6880	-0.0710	0.7880	0.0381	0.8779
SD. Elevation:PC.3	-0.5542	0.0000	-0.5439	0.0000	-0.5745	0.0000	-0.5979	0.0000
	Fast-slow continuum							
Coef. Variation:PC.1	0.0183	0.7914	0.0163	0.8286	-0.0223	0.7837	-0.0678	0.4472
Evenness:PC.1	-0.0086	0.8423	0.0217	0.7784	0.0838	0.5153	0.0623	0.6957
Correlation:PC.1	0.0285	0.2478	0.0058	0.8396	-0.0389	0.3163	-0.0217	0.6794
Temp. Seas:PC.1	-0.4629	0.3697	-0.3148	0.5238	-0.0078	0.9858	0.1165	0.7800
Prec. Seas:PC.1	0.2541	0.3169	0.2989	0.2184	0.2227	0.3308	0.3069	0.1509
SD. Elevation:PC.1	0.2504	0.0073	0.2552	0.0087	0.2572	0.0132	0.2823	0.0167
Coef. Variation:PC.2	-0.0670	0.3998	-0.0178	0.8347	0.0228	0.8050	0.0279	0.7824
Evenness:PC.2	-0.0757	0.1249	-0.2094	0.0166	-0.3250	0.0264	-0.4288	0.0178
Correlation:PC.2	0.0448	0.1082	0.0165	0.6057	0.0529	0.2259	0.0482	0.4151
Temp. Seas:PC.2	-0.4929	0.4073	-0.5128	0.3614	-0.1744	0.7260	-0.1665	0.7263
Prec. Seas:PC.2	0.1115	0.7042	0.1088	0.6947	0.1040	0.6900	0.1993	0.4117

SD. Elevation:PC.2	0.1574	0.1433	0.1418	0.2003	0.1346	0.2538	0.1959	0.1441
Coef. Variation:PC.3	-0.1629	0.1359	-0.1017	0.3851	-0.0823	0.5141	-0.0220	0.8718
Evenness:PC.3	-0.1175	0.0820	-0.2571	0.0322	-0.3035	0.1295	-0.4307	0.0763
Correlation:PC.3	0.0705	0.0697	0.0504	0.2536	0.0326	0.5853	0.0136	0.8652
Temp. Seas:PC.3	0.1960	0.8104	0.1542	0.8419	0.0698	0.9181	-0.1559	0.8076
Prec. Seas:PC.3	0.5979	0.1386	0.6131	0.1082	0.5180	0.1467	0.3745	0.2523
SD. Elevation:PC.3	0.4226	0.0044	0.4316	0.0048	0.4358	0.0071	0.4799	0.0079

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Appendix 2: Supplementary materials Chapter 4

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Section 1: Life-history trait compilation and taxonomic matching

I selected a total of five life-history traits: species body mass in grams; number of offspring per reproductive event; species longevity in years; age of sexual maturity in years; and yearly number of reproductive events. These traits were compiled from 24 different open-access datasets and published scientific articles (Table S1). Some of these datasets contained multiple records for each life-history trait per species, as well as maximum and minimum values (e.g. maximum/minimum values of number of offspring). In these cases, trait records were log-transformed, the arithmetic mean calculated, and the resulting values were back-transformed and used as average life-history values for the species.

Studies incorporated into our trait dataset spanned several decades, therefore I expected species taxonomy to differ between studies. To resolve taxonomic differences, I performed a taxonomic name resolution prior to the aggregation of the data. The original species names, as given in the source publications, were checked for possible typographic errors using the R package *taxize* Version 0.9.8 (Chamberlain et al., 2013). Checked names were then passed through the online repositories of the International Union for the Conservation of Nature (IUCN, http://www.iucnredlist.org Version 2021-1) and the Integrated Taxonomic Information System (I, http://www.itis.gov Version 26-July-2021) , where species synonyms, upward taxonomic classification (up to the level of Class) and currently accepted species names were retrieved. To date, there is not a global integrated taxonomic dataset that includes all the information needed (Cooke et al., 2019; Etard et al., 2020). By selecting two different taxonomic repositories I attempted to fill possible gaps and retrieve taxonomic information for as many species as possible. To be as consistent as possible, I prioritized the IUCN taxonomic information over IITIS.

Table S8. Studies and datasets used to collect life-history traits of terrestrial vertebrates. “x” indicates that a particular source contributed estimates of a trait. Life-history traits included; Bm, body-mass (grams); Noffs, number of offspring (count); Lon, longevity (years); Sm, sexual maturity (years); and ReEv, reproductive events (count).

Dataset	Bm	Noffs	Lon	Sm	ReEv
Amat, 2008		x			x
Capellini, Venditti, & Barton, 2011	x	x			
Cassill, 2019		x			
Gonçalves et al., 2018	x				
Grimm, Prieto Ramírez, Moulherat, Reynaud, & Henle, 2014	x	x		x	
Jones et al., 2009	x	x	x	x	x
Lobaina, 2014	x	x		x	
Meiri, 2018	x	X			
Myhrvold et al., 2015	x	x	x	x	x
Novosolov, Raia, & Meiri, 2013		x			x
Novosolov et al., 2017	x				
Pacifici et al., 2013	x		x		
Clutton-Brock et al., 1999		x		x	
Polović, Pešić, Ljubisavljević, & Čadenović, 2013		x			x
Sherman & Jarvis, 2002		x	x		
P. W. Sherman, Braude, & Jarvis, 1999		x	x		
Schwarz & Meiri, 2017		x			x
Smith et al., 2003	x				
Stark, Tamar, Itescu, Feldman, & Meiri, 2018	x	x	x		
Trochet et al., 2014	x	x		x	
Scharf et al., 2015	x	x	x	x	x
Verde Arregoitia, Blomberg, & Fisher, 2013	x				
Wilman et al., 2014	x				
Bird et al., 2020			x	x	

Section 2: Trait filtering, correction, and aggregation

The trait databases encompass a wide variety of studies with different scopes and objectives. As a result, traits are recorded in different units, under different standards and labelled with different names. Due to this, it is necessary to establish a series of standards, about nomenclature and units, to collect and combine the traits of interest. To be included in the final trait dataset, the original variables had to be clearly described (i.e., whether estimates refer to adult/juvenile, male/female individuals or minimum/maximum registered values) to group the data under a common descriptor. If the original data are presented as transformed values (e.g., log transformed), the description must contain the specific transformation method used (so that the estimates can be correctly back-transformed). Datasets were discarded if they did not meet these criteria.

Raw data were also subjected to a filtering process. To detect abnormal values in the different datasets, I produced boxplots for each trait using species order as the grouping factor (Chapter 2). Outliers from these exploratory analyses can reflect natural variability in the life-history traits or erroneous values. If the number of outliers was low, I checked values individually using scientific literature, field guides and expert knowledge. When the number of outliers was high, a random sample of 10% was retrieved and checked (Chapter 2). If more than 20% of the selected observations were found to be erroneous, the whole dataset was discarded (Chapter 2). I acknowledge that despite these efforts it is possible that erroneous estimates were included in our final dataset. Ideally data would have been checked individually, but for many species no independent estimates were available for contrast. In addition, the very large amount of data (multiple traits for more than 20,000 species) made a check of individual trait estimates impractical.

Once the taxonomy of the species was resolved, and trait estimates transformed to the same units and checked for errors, the data were combined. I found life-history trait and taxonomic information for 21,126 unique species (10,442 birds, 5,313 mammals and 5,371 reptiles). More than 87% of these species were present in multiple datasets. When multiple life-history trait records were present for the same species across different datasets, values were log-transformed, the arithmetic mean was calculated and these back-transformed values were used as final trait values for the species. All species trait values were incorporated into a unified dataset including the final life-history trait values, species taxonomy, and matched binomial names. After data aggregation, I had complete life-history trait data for 3,347 species (15% of the total number of species in the unified life-history-trait database): 1,431 mammals, 1,146 birds and 770 reptiles.

Section 3: Trait imputation

The focus of this study was on the amniote vertebrate species from the PREDICTS database. The selection of studies and sites included in this study contained a total of 2,947 unique species (after taxonomic correction): 2,697 birds; 189 mammals; and 88 species of reptiles. From the original pool of species in our life-history trait database (21.123 species; 10,441 birds, 5,312 mammals; and 5,370 reptiles), only 3,347 had complete life-history trait information. From those species, only 462 were also sampled in the PREDICTS database. To fill gaps in my data, I performed a phylogenetic trait imputation. This method can deal with highly dimensional data and can also model complex interactions and non-linear relationships between variables (Stekhoven et al., 2012). Random forests imputation has been shown to perform better, or similarly, compared with other more time consuming and restricted imputation methods (Penone et al., 2014). In addition to the trait data and following the recommendations of Penone et al. (2014), I added phylogenetic information in the form of species phylogenetic eigenvectors (Diniz-Filho et al., 2012; Diniz Filho et al., 2015). Phylogenetic eigenvectors represent phylogenetic distances among species.

There is not a single global consensus phylogenetic tree that includes all the species in our analysis. To obtain the phylogenetic eigenvectors, I used the Interactive Tree of Life (iTOL) (https://itol.embl.de/) and the TimeTree (Hedges et al., 2015) online interface (timetree.org). I constructed two consensus species-level phylogenetic trees using the interactive Tree of Life (iTOL) through the R package *rotl* Version 3.0.10.9000 (Michonneau et al., 2016), and the TimeTree online interface tool. The methods used to construct these trees and the information included in them differ. The iTOL is based on a synthetic rooted tree in which all branches have equal lengths. In contrast, the tree resulting from TimeTree presents divergence times between species. Because of this, tree branches have different lengths. Once the phylogenetic trees were constructed, eigenvectors were calculated using a principal coordinate analysis (PCoA) in the R package *PVR* Version 1.0 (Santos, 2018), and the first 10 phylogenetic eigenvectors of each species and tree were extracted to use in the life-history-trait imputations.

To refine the parameters of the random forest imputation (e.g. number of trees, number of iterations and source of phylogenetic information), I ran preliminary tests on four datasets that contained our five life-history traits, simulated to exhibit different proportions of missing data (30%, 50%, 60% and 80%), and the first 10 phylogenetic eigenvectors (following Penone et al., 2014 and Etard et al., 2020) from the iTOL and TimeTree. In our case, there were no values of body-mass missing from the data targeted for imputation (the complete life-history trait data contains only 1.9% of missing values for body-mass) and, consequently I did not remove values from this trait. In total, I used 8 different datasets corresponding to the combinations of proportion of missing data (4 different proportions) and phylogenetic information (2 different sources of phylogenetic information). I created these different datasets using a set of species for which I had a complete sample of traits and phylogenetic eigenvectors from TimeTree and the iTOL. In total, a subsample of 2,501 species was selected and trait values were removed at random until I had the desired proportions of missing data. I performed imputations using different numbers of trees, from 50 to 300, for each dataset and extracted the overall normalized root-square mean values (NRMSE). The NRMSE ranges from 0 to 1 and measures the correspondence between estimated and observed values (Hyndman & Koehler, 2006), with values close to 0 representing higher accuracy while values around 1 are related with low imputation accuracy. I performed all imputations using the random forest algorithm implemented in the R package *missForest* Version 1.4 (Stekhoven et al., 2012). For the final set of imputation parameters, I also calculated the NRSME for each imputation test and life-history trait (Figure S2).

I was unable to find phylogenetic information for all species, including 25% of the species sampled in the PREDICSTS database. To account for kinship among these species in the imputations, I used species taxonomy (Class, Order and Family) as variables for the trait imputation. Since our random forest algorithm cannot handle factor variables with more than 32 levels (Stekhoven et al., 2012), I transformed our taxonomic information into numerical vectors (‘transformed taxonomy' hereafter) and added these new vectors as variables into the imputation process. I repeated the previous tests but substituted the phylogenetic information with the transformed taxonomy. I also tested imputation performance with and without taxonomic information (Figure S1.b and S1.a respectively). Additionally, I also tested whether the addition of both phylogenetic eigenvectors and transformed taxonomic information improved the overall imputation accuracy. Results from these tests included imputations with phylogenetic eigenvectors from iTOL and transformed taxonomy (Figure S1.e) and imputations using the phylogenetic eigenvectors from TimeTree along with the transformed taxonomy (Figure S1.f).

The results from these preliminary tests showed that trait imputation improved slightly with the addition of phylogenetic information (i.e., lower NRMSE). These improvements were independent of the type of eigenvectors used, with both iTOL and Time Tree showing similar imputation accuracy when compared to imputations using only trait information. (Figure S1.a, and S2.c-d). Similarly, the addition of taxonomic information improved imputation accuracy when compared to using only life-history trait information (Figure S1.a, and S2.b). The simultaneous addition of taxonomic and phylogenetic information (either from iTOL or TimeTree) improved imputation accuracy when compared to using those variables in isolation (Figure S1.b-d and S2.e-f). As expected, lower proportions of missing information led to greater imputation accuracy in all cases (Figure S1 and S2). The increase in the number of trees used for the imputation did not improve imputation accuracy when 80% of the data was missing (Figure S1). This indicated that, with this amount of data missing, the algorithm in not able to improve its accuracy with the increment of trees. However, the increase of number of trees had a limited positive effect, improvement of imputation accuracy, when missing data ranged from 30% to 60%. These improvements were in all cases small and almost neglible after reaching 100-200 trees (Figure S1).

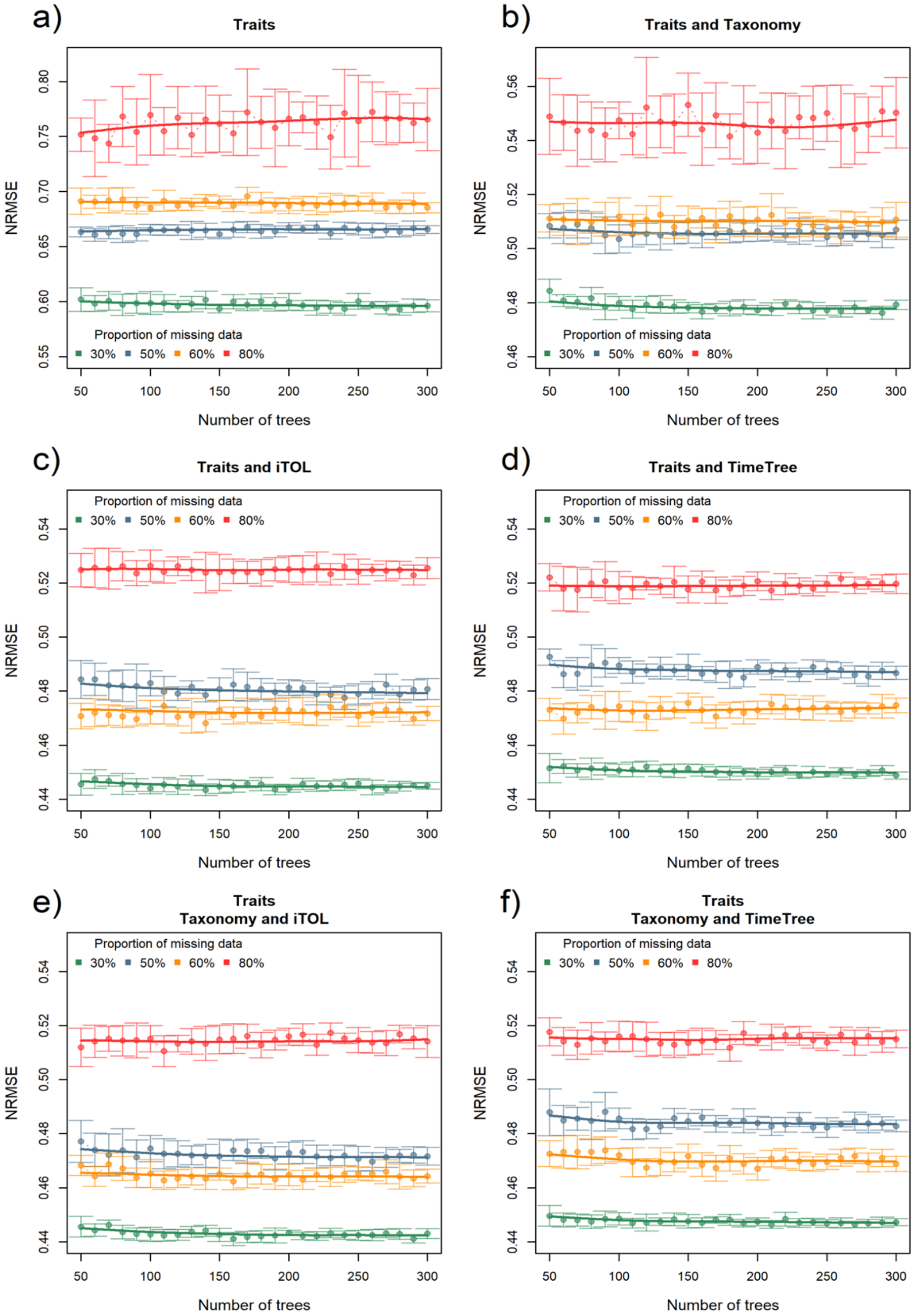

Figure S1. Mean real imputation errors (**NRMSE**) for random forests imputations with different numbers of trees using; **a)** only trait information; **b)** traits and taxonomic information; **c)** traits and the first 10 eigenvectors of iTOL; **d)** traits and the first 10 TimeTree-derived eigenvectors; **e)** traits and the first 10 iTOL-derived eigenvectors along with taxonomic information; and **f)** traits and the first 10 TimeTree-derived eigenvectors plus species' taxonomic information. Points represent the mean values of MRIE calculated after 10 imputations, and error bars represent ± 1 standard deviation. Solid lines represent the fitted values of generalized additive models (GAM) with smoothed partial residuals regression splines, calculated by generalized maximum likelihood, fitted using the R package *gam* Version 1.20 (Hastie, 2020). Colours represent datasets with different percentage of missing values. The different percentages of missing data were obtained by removing, at random, trait values from a dataset of 2,501 species for which I had complete trait, phylogenetic, and taxonomic information.

For the final test, I set the number of trees at 150 and the maximum number of iterations to 15 and used the data with the lowest percentage of missing information to extract the NRMSE of the different combinations of datasets and the individual life-history variables. The results of this test pointed out that the inclusion of extra information, whether in the form of taxonomy or phylogenetic eigenvectors, improved the accuracy of imputations (values of NRMSE closer to 0) (Figure S3.b). In terms of test performance, the addition of extra information either in the form of taxonomic or phylogenetic information improved life-history trait imputation (Figure S2.b). The test that used both taxonomic and phylogenetic eigenvectors were the ones that showed the lowest NRMSE. In this aspect TimeTree and iTOL eigenvectors perform similarly, with almost no differences in the values of RMSE between the tests performed using both phylogenies. A similar pattern can be observed when considering the NRMSE of the individual life-history traits. Life-history traits imputed using only the trait information showed greater NRMSE values than those imputed using the traits values and taxonomic or phylogenetic information (Figure S2.a). When adding extra information, NRMSE values were lower than 0.6 for all life-history variables but yearly reproductive events. This life-history trait was the one that presented higher NRMSE values whereas number of offspring was the one that showed the strongest improvement in terms of imputation accuracy (Figure S2.a). Similarly, than with the imputation accuracy of the different test, life-history traits imputed that combined taxonomy and phylogenetic eigenvectors presented the higher accuracy, with little differences between the TimeTree and iTOL phylogenies (Figure S2.a). Overall, life-history trait imputation performed well for the set of parameters selected (30% of missing data, 150 trees, 15 iterations, either with the phylogenetic information from TimeTree or iTOL and the transformed taxonomy).

In summary: 1) phylogenetic information from TimeTree produced greater imputation accuracy than the phylogenetic data from iTOL; 2) in order to keep precise imputations, the percentage of missing data had to be low, in our case less or equal to 30%; 3) When missing information was between 30% and 60% imputation accuracy increased with the number of trees; 4) in all cases, the combined inclusion of phylogenetic and taxonomic information improved imputation accuracy.

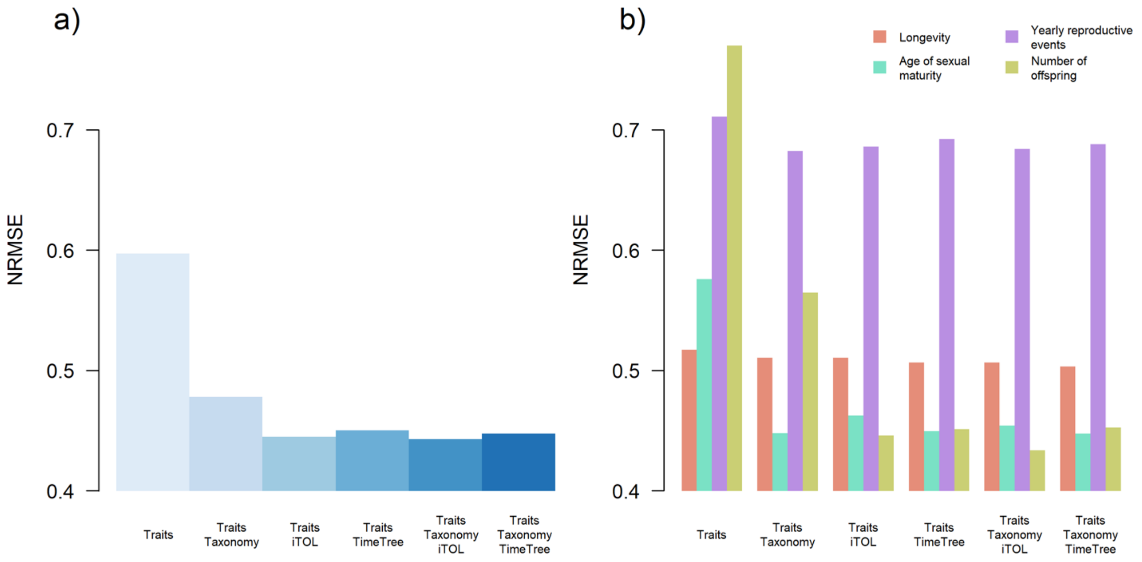

Figure S2. Normalized root-square mean values (NRMSE) for each dataset combination (panel **a**) and imputed life-history traits by dataset combination (panel **b**). Displayed NRMSE are based on imputations using 150 trees and 15 maximum iterations of the random-forest algorithm. Lower

NRMSE values are related with higher imputation accuracy while NRMSE values closer to 1 are associated with low imputation accuracy.

Based on the results from the tests, and since I had trait information for a large number of species, I controlled the proportion of missing information by including the species from the selected PREDICTS assemblages along with all the species present in our life-history dataset that had values for at least three out of five life-history traits. Thus, a total of 9,618 species (2,765 mammals, 4,638 birds and 2,215 reptiles) were selected. This trait dataset had an average trait completeness of 70.84%. In terms of phylogenetic information, I choose TimeTree. During the test both iTOL and TimeTree performed similarly, however the percentage of species for which I had phylogenetic information was higher in the case of TimeTree (68.13% of the species included in the final imputation). I added the upward taxonomic classification (class, order, and family) for all species (as numerical variables), and the first 10 phylogenetic eigenvectors from TimeTree for the species that had this information. I set the parameters of the random forest algorithm to 150 trees and a maximum of 15 iterations. The values for the final imputed traits were calculated by averaging the results of 100 imputations (Figure S4).

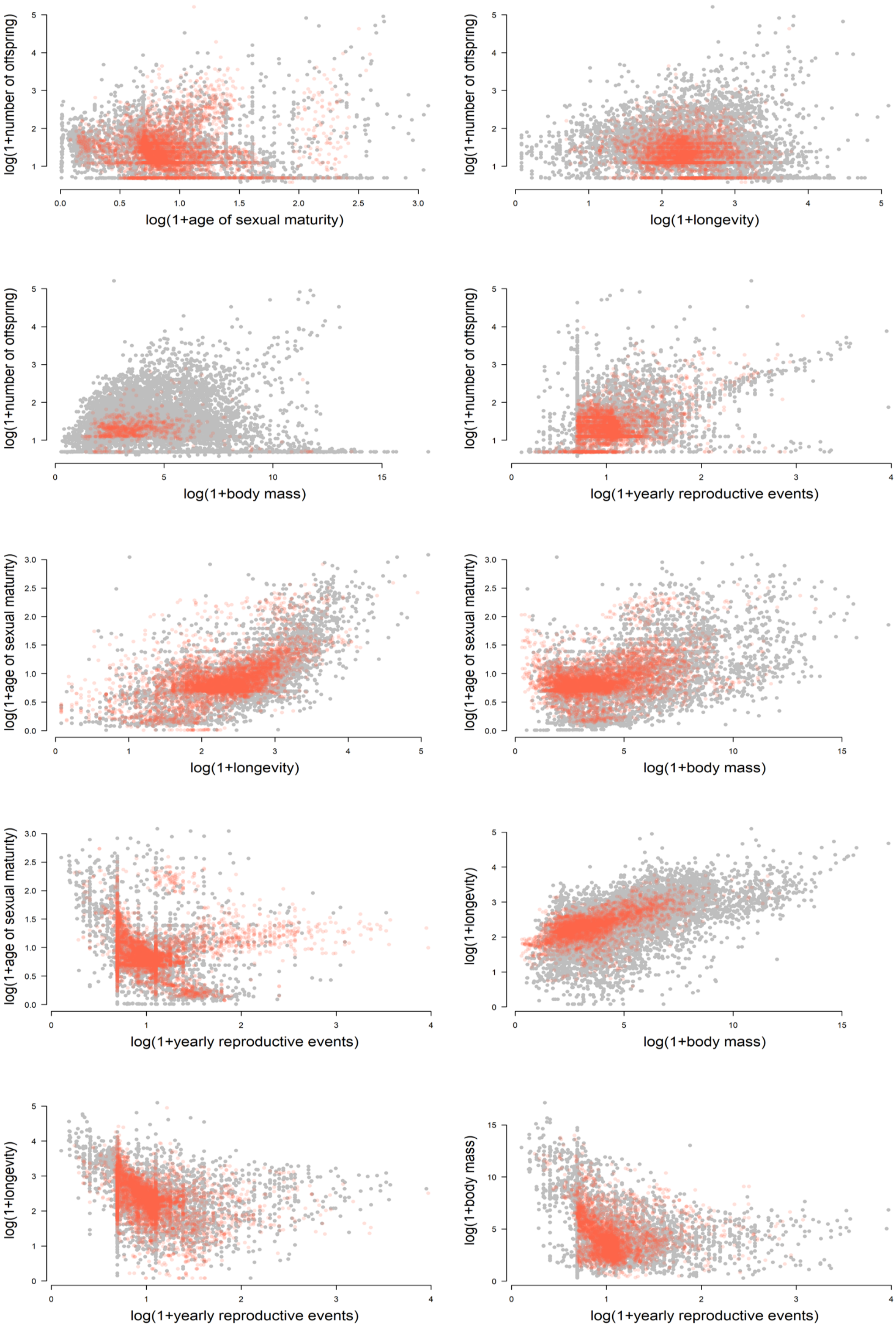

Figure S3. Plots of the pairwise relationships between log-transformed values of the life-history traits. Grey dots represent pairs of non-imputed life-history-trait values, whereas red dots represent pairs of life-history traits where at least one of the two values was imputed using a random forest phylogenetic imputation (details see text S.3).

Section 4: The fast-slow continuum

To place our species along the fast-slow continuum, I first needed to remove the effects of body size and kinship from the life-history traits (e.g Dobson & Oli, 2007). Body mass is an important factor that affects other fundamental traits (Stearns, 1983). Large species tend to spend more time growing, are more likely to present late sexual maturity, and have greater lifespans and fewer offspring than small, fast-growing species. This makes the comparison of life histories between species of different size challenging, and thus body size is a factor that must be accounted for (Dobson & Oli, 2007). To remove the effects of body mass I regress each life-history trait against body mass using linear mixed-effects models (LMM), fitted using restricted maximum likelihood. Before running this analysis, all variables were log-transformed to deal with the skewness of the trait data. To control for relatedness between species, I added taxonomic information as a nested random intercept (family nested within order nested within class). I used this approach because, as I stated before in section S3, I could not build a complete phylogenetic tree for all species. To control for residual heteroscedasticity, I added an exponential variance structure. This structure modelled the variance of the residuals as σ^2 multiplied by an exponential function of the covariance matrix of our explanatory variables multiplied by a parameter δ, which allows for a different spread of residuals across factor levels (Zuur et al., 2009). Table S3 contains additional information about the models used. Linear mixed-effects models were fitted using the lme function of the R package *nlme* Version 3.1-157 (Pinheiro et al., 2021). Residuals from these models were used as trait values adjusted for the effects of body mass and taxonomic relationships ('adjusted traits' from now on).

Adjusted traits were subjected to a Principal Component Analysis (PCA), and the first three axes, or principal components (**PC**), were retrieved as our life-history axes. These three axes encompassed 82.59% of the total variance in our life-history traits (Table S4). The first axis explained more than 32% of the total variance and reflects the expected trade-offs between fecundity and longevity. As such, I considered this axis to represent the fast-slow continuum. The second and third life-history axes represent different aspects of species life histories. All variables loaded positively with the second PC (Table S4 and Figure S4), but the variables that had a major contribution on this axis were yearly reproduction events and sexual maturity. For the third axis, number of offspring and longevity loaded negatively with the third axis whereas sexual maturity and the number of yearly reproductive events loaded positively (Table S4 and Figure S4).

Table S3. Linear mixed-effects models used to adjust trait estimates to account for the effects of body mass and taxonomic relationships of mammals, birds and reptiles in our analysis. Fixed-effects coefficients and random effects are presented. Fixed effects contain the parameter estimate for each explanatory variable value (**value**), their standard deviation (**stDev**), and the **t-value** (derived using the Satterthwaite t-test approximation, see Kuznetsova et al., 2017) along with its corresponding P value (**P**). Model performance metrics – the Akaike information criterion (**AIC**) and the Bayesian information criterion (**BIC**) – are displayed below the fixed effects. I present the variance and standard deviation associated with each random effect (**Variance** and **stDev** respectively), the fraction of total variance explained by those factors (**Exp-var**), the total variance explained by the random effects (**Total var**), and the residual variance unexplained by the random effects (**Residual**). Models have a sample size of 9,618 species (4,638 birds, 2,765 mammals, and 2,215 reptiles). Random effects included were Family (**Fam**) nested within Order (**Or**) nested within Class (**Cl**).

Longevity

	Fixed					*Random*			
	value	**stDev**	**t**	**P**		**Variance**	**stDev**	**Exp-var**	**Total var**
intercept	1.802	0.23150	7.782	0.000	**Cl**	0.146	0.383	0.364	0.742
log(Bm)	0.147	0.004	38.020	0.000	**Cl/Or**	0.108	0.328	0.268	
AIC	8321.590				**Cl/Or/Fam**	0.044	0.211	0.110	
BIC	8371.789				**Residual**	0.104	0.322		

Sexual Maturity

	Fixed					*Random*			
	value	**stDev**	**t**	**P**		**Variance**	**stDev**	**Exp-var**	**Total var**
intercept	0.805	0.266	3.029	0.003	**Cl**	0.204	0.452	0.614	0.785
log(Bm)	0.071	0.002	33.355	0.000	**Cl/Or**	0.057	0.239	0.171	
AIC	-3783.776				**Cl/Or/Fam**	0.043	0.207	0.129	
BIC	-3733.578				**Residual**	0.028	0.169		

Number of offspring

	Fixed					*Random*			
	value	**stDev**	**t**	**P**		**Variance**	**stDev**	**Exp-var**	**Total var**
intercept	1.255	0.450	2.788	0.005	**Cl**	0.594	0.770	0.685	0.794
log(Bm)	0.056	0.003	17.364	0.000	**Cl/Or**	0.094	0.307	0.109	
AIC	3906.995				**Cl/Or/Fam**	0.122	0.350	0.141	
BIC	3957.193				**Residual**	0.056	0.237		

Number of yearly reproductive events

	Fixed					*Random*			
	value	**stDev**	**t**	**P**		**Variance**	**stDev**	**Exp-var**	**Total var**
intercept	1.098	0.088	2.788	0.005	**CI**	0.020	0.141	0.109	0.195
log(Bm)	-0.027	0.003	17.364	0.000	**CI/Or**	0.016	0.126	0.087	
AIC	1658.531				**CI/Or/Fam**	0.047	0.218	0.260	
BIC	1708.729				**Residual**	0.099	0.315		

Table S4. Factor loadings and contribution percentage to the principal components of each life-history trait variable (number of offspring, longevity, yearly reproduction events, and sexual maturity). Correlation of the different principal components (**PC**) with body mass (**Correlation Bm**) are also shown here along with the eigenvectors, eigenvalues, explained variance and cumulative explained variance (**Exp-Variance** and **Cum-Variance** respectively) for the three main life-history axes.

	PC1		***PC2***		***PC3***	
	Loadings	**Contribution**	**Loadings**	**Contribution**	**Loadings**	**Contribution**
Number of offspring	0.5921	35.0619	0.1281	1.6424	-0.5841	34.1286
Longevity	-0.4794	22.3968	0.0332	0.1107	-0.8034	64.5570
Yearly reproduction events	0.2963	8.7843	0.8351	69.7457	0.0587	0.3447
Sexual maturity	-0.5759	33.1668	0.5338	28.5011	0.0984	0.9694
Correlation Bm	-0.009		0.01		0.007	
Eigenvalues	1.2963		1.0549		0.9524	
Exp-Variance	32.4093		26.3726		17.4064	
Cum-Variance	32.4093		58.7821		82.5935	

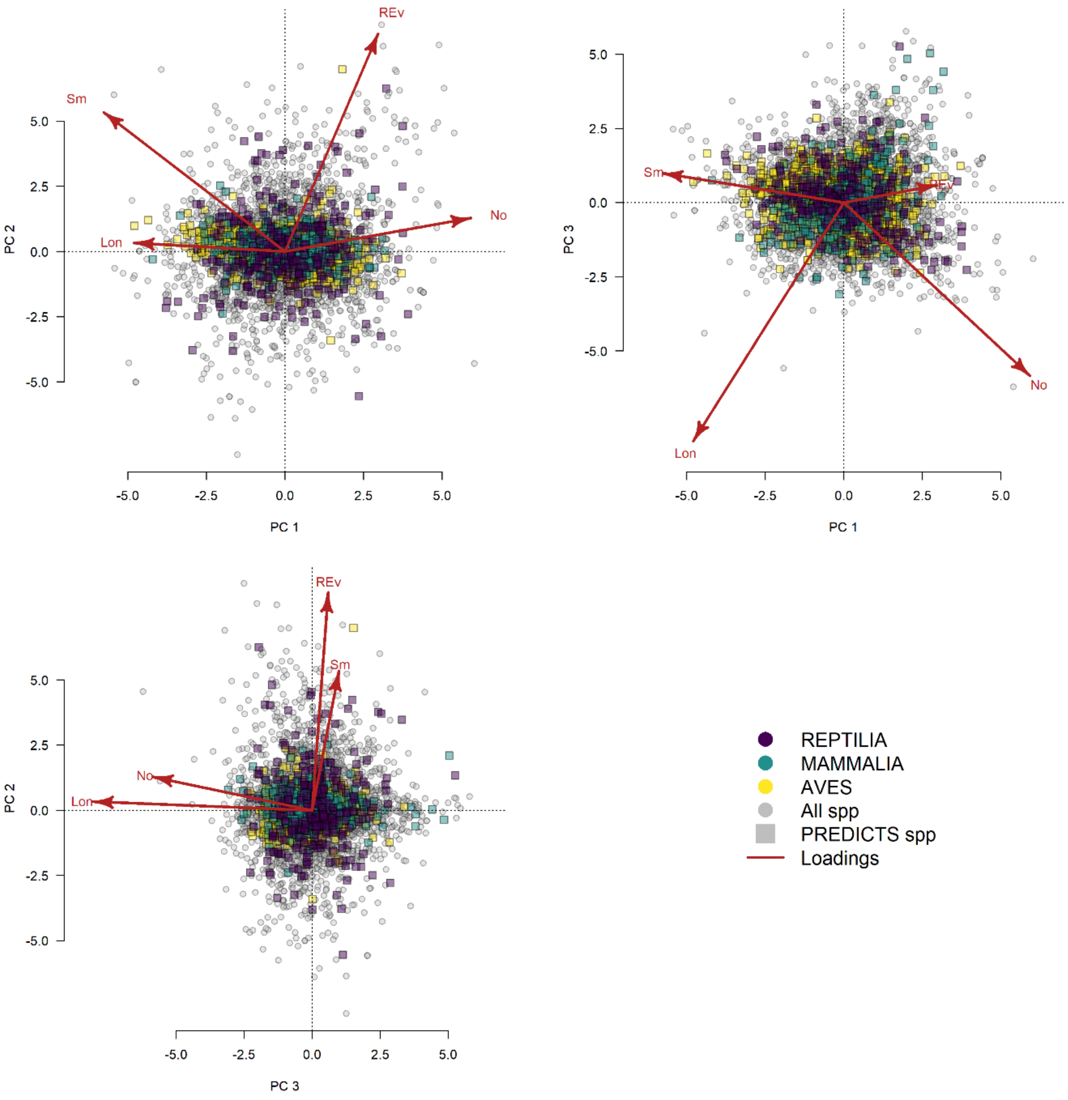

Figure S4. Score values for the three life-history axes. Each point represents the position of a species in life-history diversity space according to their life-history-trait combination. The different colours represent the main vertebrate classes included in the sampled PREDICTS dataset (2,974 different species; 2,697 birds; 189 mammals, and 88 reptiles), while the grey circles represent the rest of the species used for the life-history classification. Arrows represent the direction and influence of the loading values for each life-history variable (**Sm**, sexual maturity; **No**, number of offspring; **Lon**, longevity; and **REv**, yearly reproductive events) on the different life-history axes. Loading values have been 10x rescaled for representation purposes.

Section 5: Statistical analysis

All variables were transformed using Ordered-Quantile transformation (Liu & Pierce, 1994) using the R package *bestNormalize* Version 1.7.0 (Peterson & Cavanaugh, 2020). This transformation method produced the same results as using a log transformation but led to better model convergence. Variables were assessed for multicollinearity using variance inflation factors (Zuur et al., 2009) with a maximum threshold of 5. In addition, if any pair of variables had a Pearson correlation coefficient greater than 0.7, the variable considered to be ecologically more informative was retained and the other discarded.

To select the best-performing model for each of the life-history metrics, I first fitted maximally complex linear and quadratic models. These complex models contained all our normalized explanatory variables as well as all possible two-way interactions between land-use and environmental variables. Three and four-way interactions cause convergence and residual-autocorrelation issues, and so were not considered in this analysis. With this maximally complex model, I considered a combination of different random-effects structures, selecting the structure that best fit the data (i.e., the model with the minimum AIC value). Once the random-effects structure had been selected, the maximally complex models were subjected to backward stepwise AIC variable selection method. Using this method, models were re-fitted multiple times, dropping one of the terms that contribute to the increase of overall model AIC at each run, until the model with the lowest AIC was found (Yamashita et al., 2007). The final models were checked for residual spatial autocorrelation, heteroscedasticity and normality of the residuals, and multicollinearity using the R package *performance* Version 0.7.1 (Lüdecke et al., 2021). Model fit was evaluated using conditional and marginal pseudo-R^2 values (Nakagawa et al., 2017) using the R package *MuMin* Version 1.43.17 (Barton, 2020). All analyses were carried out in R Version 4.0.5 (R Core Team, 2021). The parameters of the final models are presented in Table S5 and the detailed results of the main models are presented in Table S6-7.

Table S5. Final model formulations and performance metrics for each life-history metric (**Variable**). Formulae display the abbreviated form of the variables; LhDiv, Life-history divergence; LhEv, life-history evenness; LhR, life-history richness; LhM, weighted life-history mean; LhMed, weigthed life-history median; LhSk, weighted life-history skewness; LU, land-use; EVIcorr, EVI correlation; EVIeve, EVI evenness; SpCount, number of species per site; TempSea, temperature seasonality; PreTemp, precipitation seasonality; SS, study identity. AIC and BIC stand for Akaike and Bayesian information criterion respectively, R^2 conditional and R^2 marginal, correspond to the models' pseudo R^2 values (Johnson, 2014; Nakagawa et al., 2017).

Variable	Life-history Divergence (LhDiv)		
Formula	LhDiv ~ LU + EVIcorr + EVIeve + LU: EVIcorr + LU: EVIeve + SpCount		
R-effects	1 | SS		
AIC	**BIC**	**R^2 conditional**	**R^2 marginal**
5619.950	5721.280	0.246	0.013
Variable	Life-history Evenness (LhEv)		
Formula	LhEv ~ LU + EVIeve + TempSea + EVIeve:TempSea + SpCount		
R-effects	1 | SS		
AIC	BIC	R^2 conditional	R^2 marginal
4923.877	4985.802	0.467	0.015
Variable	Life-history richness (LhR)		
Formula	LhR ~ LU + EVIcorr + EVIeve + PreSea + TempSea + LU:EVIeve + LU:PreSea + SpCount		
R-effects	1 | SS		
AIC	**BIC**	**R^2 conditional**	**R^2 marginal**
3454.792	367.381	0.755	0.191
Variable	Weighted life-history mean (LhM)		
Formula	LhM ~ LU + EVIcorr + PreSea + TempSea + LU:TempSea + C_SpCount		
R-effects	1 | SS		
AIC	**BIC**	**R^2 conditional**	**R^2 marginal**
3690.630	3775.073	0.654	0.115
Variable	Weighted life-history median (LhMed)		
Formula	LhMed ~ LU + EVIcorr + TempSea + LU:EVIcorr + LU:TempSea + C_SpCount		
R-effects	1 | SS		
AIC	**BIC**	**R^2 conditional**	**R^2 marginal**
4284.490	4385.820	0.576	0.058

<table>
<tr><th>Variable</th><th colspan="3">Weighted Life-history skewness (LhSk)</th></tr>
<tr><td>Formula</td><td colspan="3">LhSk ~ LU + PreSea + TempSea + LU:TempSea + C_SpCount</td></tr>
<tr><td>R-effects</td><td colspan="3">1 | SS</td></tr>
<tr><td>AIC</td><td>BIC</td><td>R^2 conditional</td><td>R^2 marginal</td></tr>
<tr><td>5369.756</td><td>5448.569</td><td>0.428</td><td>0.080</td></tr>
</table>

Table S6. Linear mixed-effect model (LMM) results for the life-history diversity metrics (life-history richness, life-history evenness, and life-history divergence). Model fixed terms, first column from the left, include PREDICTS land use (**LU**) with the respective classes (**PV**, primary vegetation; **SV**, secondary vegetation; **PF**, plantation forest; **Pa**, pasture; and **Cr**, cropland), precipitation seasonality (**Prep**), temperature seasonality (**Temp**), EVI correlation and evenness (**EVI Cor** and **EVI Eve** respectively). Terms given as '--' were not present in the respective model because they were excluded during model selection. In all cases t-values were derived using the Satterthwaite t-test approximation (Kuznetsova et al., 2017). Significant terms are marked in bold, and stars indicate indicated the level of significance: ***, P < 0.001; **, 0.001 < P < 0.01; *, 0.01 < P < 0.05.

	Life-history richness		**Life-history evenness**		**Life-history divergence**	
	Estimate ± sd	t	Estimate ± sd	t	Estimate ± sd	t
LU:						
PV (intercept)	0.181 ± 0.094	1.925	**-0.216 ± 0.092**	**-2.34***	-0.029 ± 0.079	-0.371
SV	**-0.105 ± 0.041**	**-2.545***	-0.089 ± 0.055	-1.604	-0.036 ± 0.067	0.544
PF	0.158 ± 0.066	1.772	**-0.183 ± 0.064**	**-2.84****	-0.023 ± 0.079	-0.289
Pa	**0.158 ± 0.066**	**2.381***	**-0.212 ± 0.087**	**-2.42***	0.024 ± 0.107	0.226
Cr	**0.232 ± 0.057**	**6.198*****	-0.102 ± 0.075	-1.357	**-0.231 ± 0.093**	**-2.48***
Prep	0.003 ± 0.057	0.052	--		--	--
Temp	**0.147 ± 0.071**	**2.069***	-0.076 ± 0.077	-0.99	--	--
EVI Cor	0.008 ± 0.012	0.64	--	--	-0.025 ± 0.039	-0.636
EVI Eve	0.027 ± 0.025	1.05	0.012 ± 0.02	0.591	<-0.001 ± 0.045	-0.002
LU: Prep						
SV: Prep	**0.093 ± 0.037**	**2.494***	--	--	--	--
PF: Prep	**0.098 ± 0.043**	**2.247***	--	--	--	--
Pa: Prep	0.024 ± 0.062	0.397	--	--	--	--
Cr: Prep	0.056 ± 0.065	0.874	--	--	--	--
LU: Temp						
SV: Temp	--	--	--	--	--	--
PF: Temp	--	--	--	--	--	--
Pa: Temp	--	--	--	--	--	--
Cr: Temp	--	--	--	--	--	--
LU: EVI Cor						
SV: EVI Cor	--	--	--	--	0.0705 ± 0.058	1.198
PF: EVI Cor	--	--	--	--	0.052 ± 0.062	0.838
Pa: EVI Cor	--	--	--	--	0.0083 ± 0.076	0.108
Cr: EVI Cor	--	--	--	--	0.027 ± 0.072	0.384
LU: EVI Eve						
SV: EVI Eve	-0.025 ± 0.034	-0.744	--	--	0.0248± 0.062	0.397
PF: EVI Eve	**-0.118 ± 0.042**	**-2.799****	--	--	0.0411± 0.075	0.547

Pa: EVI Eve	-0.02 ± 0.044	-0.468	--	--	**-0.161 ± 0.076**	**-2.095***
Cr: EVI Eve	-0.046 ± 0.043	-1.075	--	--	0.087 ± 0.079	1.099
Spp count	**0.47 ± 0.019**	**24.57*****	**-0.88 ± 0.026**	**-3.29****	-0.039 ± 0.029	-1.329

Table S7. Linear mixed-effect model (LMM) results for average life-history strategy (life-history mean, life-history median, and life-history skewness). Model fixed terms, first column from the left, include PREDICTS land use (**LU**) with the respective classes (**PV**, primary vegetation; **SV**, secondary vegetation; **PF**, plantation forest; **Pa**, pasture; and **Cr**, cropland), precipitation seasonality (**Prep**), temperature seasonality (**Temp**), EVI correlation and evenness (**EVI Cor** and **EVI Eve** respectively). Terms given as '--' were discarded from the model during model selection. In all cases t-values were derived using the Satterthwaite t-test approximation (Kuznetsova et al., 2017). Significant terms are marked in bold, and stars indicate the level of significance: ***, P < 0.001; **, 0.001 < P < 0.01; *, 0.01 < P < 0.05.

	Life-history mean		**Life-history median**		**Life-history skewness**	
	Estimate ± sd	t	Estimate ± sd	t	Estimate ± sd	t
Land-use						
PV (intercept)	**-0.15 ± 0.087**	**-1.751**	-0.032 ± 0.091	-0.358	**-0.381 ± 0.094**	**-4.023****
SV	**0.11 ± 0.046**	**2.39***	0.031 ± 0.053	0.6	0.122 ± 0.069	1.769
PF	**0.232 ± 0.064**	**3.607*****	0.119 ± 0.075	1.591	**0.242 ± 0.094**	**2.568***
Pa	**0.401 ± 0.082**	**4.837*****	**0.186 ± 0.095**	**1.949**	**0.529 ± 0.124**	**4.262****
Cr	**0.501 ± 0.075**	**6.67*****	**0.361 ± 0.085**	**4.208*****	**0.37 ± 0.11**	**3.344*****
Prep	-0.060 ± 0.048	-1.24	--	--	0.004 ± 0.051	0.082
Temp	**0.296 ± 0.073**	**4.041*****	**0.274 ± 0.078**	**3.477****	**0.316 ± 0.072**	**4.332*****
EVI Cor	0.02 ± 0.013	1.584	0.013 ± 0.026	0.484	--	--
EVI Eve	--	--	--	--	--	--
LU: Prep			--	--		
SV: Prep	--	--	--	--	--	--
PF: Prep	--	--	--	--	--	--
Pa: Prep	--	--	--	--	--	--
Cr: Prep	--	--	--	--	--	--
LU: Temp						
SV: Temp	-0.016 ± 0.048	0.342	-0.054 ± 0.055	-0.969	-0.006 ± 0.062	-0.111
PF: Temp	-0.139 ± 0.081	-1.7	-0.169 ± 0.093	-1.813	0.061 ± 0.098	0.627
Pa: Temp	**-0.348 ± 0.123**	**-2.815****	-0.208 ± 0.014	-1.461	**-0.261 ± 0.116**	**-2.238***
Cr: Temp	**-0.195 ± 0.057**	**-3.39*****	**-0.198 ± 0.065**	**-3.018****	**-0.15 ± 0.055**	**-2.701****
LU: EVI Cor						
SV: EVI Cor	--	--	-0.009 ± 0.035	-0.226	--	--
PF: EVI Cor	--	--	-0.026 ± 0.041	-0.641	--	--
Pa: EVI Cor	--	--	-0.062 ± 0.049	-1.271	--	--
Cr: EVI Cor	--	--	-0.04 ± 0.043	-0.923	--	--
LU: EVI Eve						
SV: EVI Eve	--	--	--	--	--	--
PF: EVI Eve	--	--	--	--	--	--

Pa: EVI Eve	--	--	--	--	--	--
Cr: EVI Eve	--	--	--	--	--	--
Spp count	-0.012 ± 0.02	-0.61	**0.051 ± 0.023**	**2.201***	**-0.077 ± 0.029**	**-2.618***

Section 6: Sensitivity analysis

To test the robustness of our analyses, I re-ran our models using different subsets of the original PREDICTS database. These subsets were selected by changing the threshold minimum number of species per community from 8, to 10, 15 and 20. A higher threshold allows us to increase the requirements for an assemblage to be included and therefore it reduces sample size from 2,424 (minimum of 8 spp per community) to 2,185 or 1,262 and 651 species assemblages (minimum of 10, 15 and 20 spp per assemblage respectively). I observed an increase in the strength of the differences among land uses with a more restrictive threshold for the number of species per assemblage (Figure S6). Similarly, confidence intervals got wider with an increase in the minimum number of species per assemblage (Figure S6). Despite this, results were consistent for the weighted life-history mean across all land uses and for life-history richness, weighted life-history median and life-history skewness for pasture and croplands (Figure S5).

To summarize the results from the sensitivity analysis, I calculated the statistical significance of the fixed effects from the different models using the Kenward Rogers F test (Kenward & Roger, 1997) implemented in the R package *car* Version 3.0-9 (Fox & Weisberg, 2019) (Table S8). Overall, models showed similar results regardless of the dataset used (Figure S6 and Table S8). Modelled responses to land use were consistent for all models and datasets, except for those related with life-history evenness (Table S8). In this case, effects were not significant for the models using species thresholds of 10, 15 and 20. I observed a higher variability in the statistical significance of fixed effects when evaluating the interactions between land use and the heterogeneity variables (Table S8).

This highlights that changes in sample size can have a large impact on the sensitivity of the models to detect statistically significant interactions.

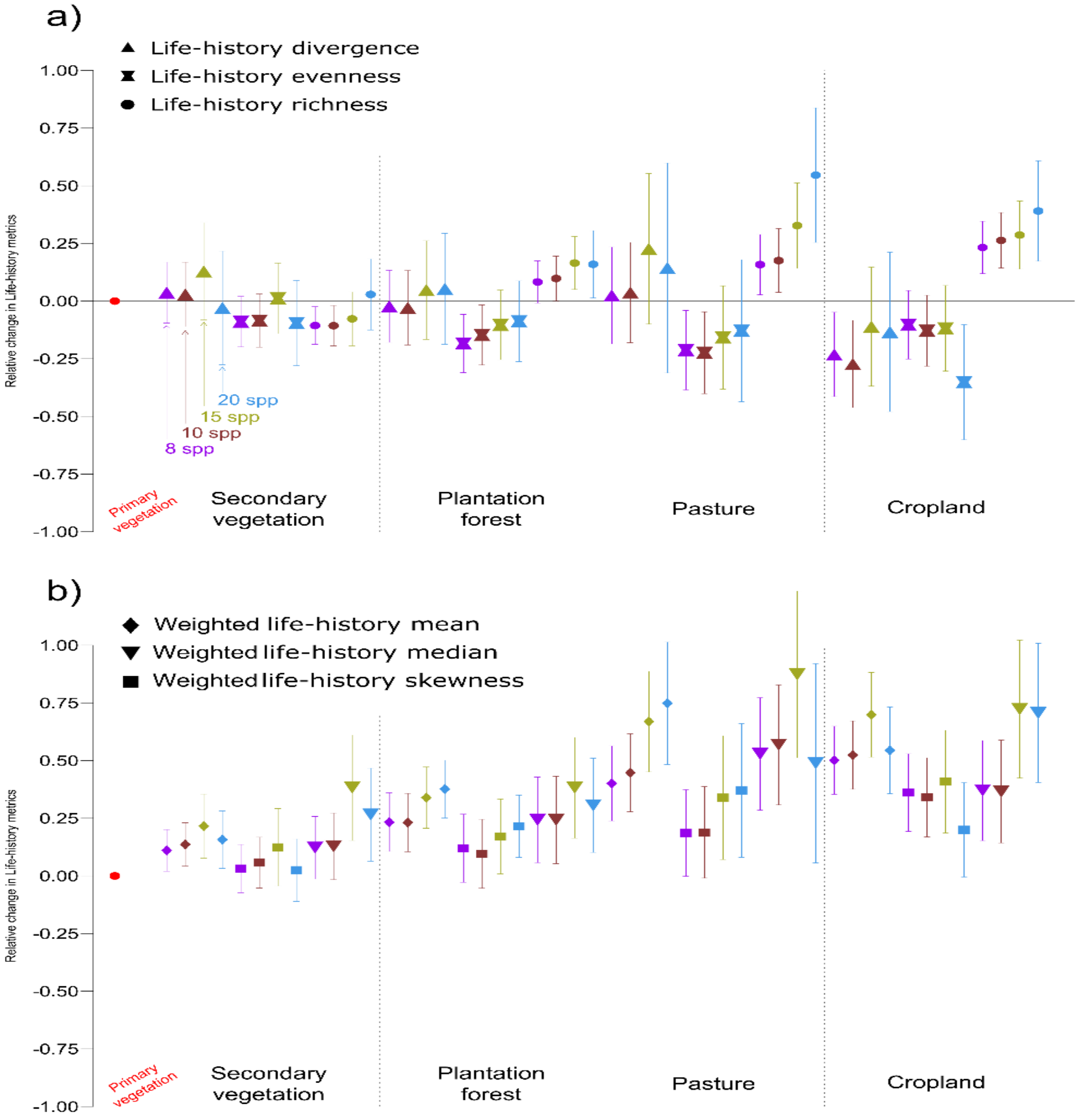

Figure S5. Response of life-history metrics and life-history strategies to land use (primary vegetation, secondary vegetation, plantation forest, pasture, and cropland). Responses, ordered from left to right and in different colors, correspond to models using 8, 10, 15, and 20 species thresholds, as marked in panel **a** (sample size of 2,058, 1,886, 924, and 578 species assemblages respectively). Shapes represent the different life-history metrics: life-history divergence (triangles); life-history evenness (hourglass shaped); life-history richness (circle); weighted life-history mean (diamond); weighted life-history median (squares); and weighted life-history skewness (inverted triangles). Points represent the response of the different metrics to land use when all the other variables included in the models are held at their means. Primary vegetation is the intercept, marked by a red circle; bars represent 95% confidence intervals of the estimates.

Table S8. Kenward-Rogers F test results for the fixed effects (leftmost column) of the different linear mixed-effects models (LMM). For each fixed effect, the F and P values of the Kenward-

Rogers F test are presented. Models are grouped into columns according to the dataset used to fit them. Information about the minimum number of species used to filter the PREDICTS dataset (**spp**), and the number of species assemblages included (**N**) in each dataset is presented in the column headers. Green shaded fields show statistical coherence between models fitted with different datasets. Statistically significant effects are marked with different superscripts: *, P < 0.05; **, P < 0.01; and ***, P < 0.001.

	8 spp (N=**2,058**)		10 spp (N=**1,886**)		15 spp (N=**924**)		20spp (N=**578**)	
Life-history divergence								
	F	***P***	***F***	***P***	***F***	***P***	***F***	***P***
Land use	2.111	0.076	2.485	0.041*	0.997	0.407	0.109	0.979
EVI Correlation	0.09	0.76	0.398	0.528	0.081	0.775	0.136	0.711
EVI evenness	0.012	0.911	0.056	0.811	0.019	0.887	<0.001	0.99
Land-use: EVI Correlation	0.43	0.786	0.236	0.917	0.64	0.633	3.017	0.017*
Land use: EVI Evenness	2.611	0.033*	4.462	0.001**	2.346	0.052	2.806	0.025*
Life-history evenness								
Land use	2.922	0.02*	2.245	0.061	1.162	0.325	1.974	0.096
EVI evenness	0.0001	0.991	0.207	0.648	0.582	0.445	0.31	0.577
Temp Sea	1.04	0.309	1.197	0.275	2.61	0.108	0.837	0.362
EVI evenness: Temp Sea	3.877	0.049*	4.529	0.033*	12.536	<0.001***	9.714	0.001**
Life-history richness								
Land use	10.348	<0.001***	10.815	<0.001***	10.671	<0.001***	7.584	<0.001***
EVI correlation	0.409	0.522	0.943	0.331	0.806	0.369	0.341	0.559
EVI evenness	0.2172	0.641	1.323	0.25	0.4319	0.511	0.011	0.913
Prep Sea	0.724	0.395	1.01	0.315	0.481	0.488	0.079	0.777
Temp Sea	4.226	0.04*	3.013	0.083	5.237	0.023*	11.996	<0.001***
Land use: EVI evenness	2.084	0.08	1.649	0.159	2.039	0.086	1.394	0.234
Land use: Prep Sea	2.369	0.05	2.194	0.067	2.126	0.075	1.711	0.145
weighted life-history mean								
Land use	45.201	<0.001***	45.089	<0.001***	42.902	<0.001***	29.094	<0.001***
EVI correlation	2.509	0.113	2.188	0.139	1.048	0.306	2.638	0.104
Prep Sea	1.517	0.218	2.526	0.112	3.659	0.056	0.152	0.696
Temp Sea	8.201	0.004**	11.553	<0.001***	7.085	0.008**	26.733	<0.001***
Land use: Temp Sea	4.913	<0.001***	5.213	<0.001***	3.526	0.007**	2.863	0.028*
weighted life-history median								
Land use	20.579	<0.001***	18.556	<0.001***	16.275	<0.001***	12.97	<0.001***
EVI correlation	0.004	0.944	0.0137	0.906	0.156	0.692	1.655	0.198

Temp Sea	5.567	0.019*	7.181	0.007**	2.562	0.111	20.202	<0.001***
Land use: EVI correlation	0.525	0.716	0.941	0.439	0.755	0.554	3.326	0.01*
Land use: Temp Sea	2.732	0.027*	3.337	0.009**	3.548	0.006**	6.462	<0.001***
life-history skewness								
Land use	6.166	<0.001***	5.904	<0.001***	6.601	<0.001***	7.801	<0.001***
Prep Sea	2.048	0.154	1.841	0.176	0.002	0.96	<0.001	0.988
Temp Sea	5.619	0.019*	5.336	0.022*	0.725	0.396	3.598	0.061
Land use: Temp Sea	0.93	0.454	0.936	0.442	3.195	0.012*	4.396	0.001**

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Appendix 3: Supplementary materials chapter 5

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Section 1: Sensitivity analysis

Section 1.1. Methods

The set of populations included in the analysis, their spatial location, and their time-series length can have a strong impact on the capacity to detect environmental and population changes (Wauchope et al., 2019). The data used to run the main analysis contains population trends based on time series, for which some estimates had been imputed using GAMs or log-linear regression (for details, see main text). Populations with imputed values are associated with an R^2 value (derived from the model used to impute the data) that serves as a measure of imputation quality: higher values of R^2 are associated with higher imputation accuracy (higher quality) and lower values are associated with lower imputation accuracy (lower quality). To test the robustness of the observed results, I re-ran the final selected linear mixed-effects model (LMM) (see **equation 4** in main text) using three different imputation R^2 thresholds: 0.3, 0.7, and 0.9 (a threshold of 0.5 was used for the main analysis). This filtering resulted in three datasets; R^2-0.3 = 1,108 populations; R^2-0.7 = 996 populations; and R^2-0.9 = 915 populations.

Additionally, to test the impacts of population selection on the results observed, I re-ran the main model on 3 different subsets of our dataset, specifically subsets in which populations with extreme rates of population change ($\overline{\lambda_T}$) were selectively removed (e.g Leung et al., 2020; Murali, de Oliveira Caetano, Barki, Meiri, & Roll, 2022). This way, a **no-lower-extreme** dataset was created by selecting all the populations with a $\overline{\lambda_T}$ above the 2.5th percentile (the most negative declines were removed). Similarly, a **no-upper-extreme** dataset was created by selecting all the populations with $\overline{\lambda_T}$ below the 97.5th percentile (the most positive increases were removed). A third dataset, **no-extremes**, was created by selecting the populations between the 2.5-97.5th percentiles of $\overline{\lambda_T}$ (both extremely negative and positive rates of population change were removed). The final sample size was 1,018 populations for **no-extremes,** and 1,045 populations for the **no-lower/no-upper-extreme** datasets respectively.

All models were fitted using restricted maximum likelihood, implemented in the R package *lme4* Version 1.1-26 (Bates, Mächler, Bolker, & Walker, 2015). Random sampling was performed using the R *set.seed* and *sample* functions, both implemented in the R package *base* Version 4.0.2 (R Core Team, 2021). Model fit was evaluated using conditional and marginal pseudo-R^2 values calculated by the R package *MuMin* Version 1.43.17 (Barton, 2020). Wald chi-square test was implemented using the R package *car* Version 3.0-9 (Fox & Weisberg, 2019).

Section 1.2. Results

Overall, fixed effects were broadly consistent across datasets irrespective of the threshold imputation R^2. In terms of significance of effects, rate of cropland change was the only that differed depending on R^2 threshold used. This term was statistically significant when populations with R^2 values of 0.3-0.5 were included in the analysis, but non-significant when a more restrictive threshold for the inclusion of populations was used (R^2 values between 0.7 and 0.9). Despite this, the direction of all effects was consistent across the different datasets (Table S1).

The results from the models in which extremely low/high values of $\overline{\lambda_T}$ were removed showed greater differences from the main model. When the upper and lower-most $\overline{\lambda_T}$ were removed from the data (**no-extremes**), only the interaction between climate warming and bare-soil land-cover remained both statistically significant and with the same direction effect (Table S2). For the same dataset (**no-extremes**) climate warming alone also showed a change in its effect direction, when compared to the main model, but was statistically non-significant . When the populations with the lowest $\overline{\lambda_T}$ were removed from the analysis (**no-lower-extreme**), the effects of the interaction of the fast-slow continuum and bare-soil land-cover, and the interaction of climate warming and bare-soil land-cover matched the main model in both statistical significance and direction (Table S2). In this case, all effects directions matched the pattern observed in the main model (Table S2). For the model in which the populations with the higher $\overline{\lambda_T}$ were removed (**no-upper-extreme**), the fast-slow continuum, rate of cropland change, and the interaction between these variables showed the same direction and statistical significance as the main model (Table 2). The direction of the rest of the effects matched the same pattern as the main model, with the exception of climate warming, but were not statistically significant (Table 2).

Table S1. Estimate (± standard error) and results of an ANOVA type III Wald chi-square test for species population trends models using datasets sampled at different imputation R^2 thresholds. Dataset size for each model is denoted by **N** and presented along with the R^2 threshold used for the filtering of populations at the top of each set of metrics. Statistically significant terms are marked in bold with stars indicating the level of significance ($P < 0.1$ = .; $P < 0.05$ = *; $P < 0.01$ = **; and $P < 0.001$ = ***). The degrees of freedom for all terms were equal to 1. Model conditional and pseudo-R^2 values are shown at the bottom of the table. Fixed effects included in the models were: ΔT, rate of temperature change; $\overline{Crop_T}$, rate of change for cropland land cover; $\overline{Bare\ soil_T}$, rate of change for bare soil cover; and PC1, the fast-slow continuum (see also equation 4 in the main text). Green shaded fields denote agreement between the sensitivity test models and the main model.

	R^2 = 0.3; N= 1,108			**R^2 = 0.5; N= 1,072**			**R^2 = 0.7; N= 996**			**R^2 = 0.9; N= 915**		
	Estimate	χ^2	p	Estimate	χ^2	p	Estimate	χ^2	p	Estimate	χ^2	p
(Intercept)	0.0022 ± 0.0028	0.6097	0.4349	0.0025 ± 0.0032	0.8711	0.3507	0.0036 ± 0.0029	1.5509	0.2130	**0.0055 ± 0.0029**	**3.6136**	**0.0573 .**
ΔT	0.003 ± 0.0024	0.0137	0.9068	0.0246 ± 3.3658	0.0045	0.9463	<0.0001 ± 0.0025	0.0000	0.9970	0.0003 ± 0.0026	0.0166	0.8976
PC1	**0.0052 ± 0.0023**	**5.3038**	**0.0213***	**0.0052 ± 0.0023**	**5.0484**	**0.0246***	**0.0059 ± 0.0024**	**5.9357**	**0.0148***	**0.0065 ± 0.0024**	**7.3435**	**0.0067****
$\overline{Crop_T}$	**-1.4983 ± 0.6796**	**4.8599**	**0.0275***	**-1.4970 ± 0.6943**	**4.6512**	**0.0310***	-1.2895 ± 0.7159	3.2443	0.0717 .	-1.1153 ± 0.7135	2.4430	0.1181
$\overline{Bare\ Soil_T}$	1.4428 ± 1.7695	0.6649	0.4148	5.1350 ± 3.015	0.6105	0.4346	2.3248 ± 1.9109	1.4802	0.2237	2.3564 ± 1.8935	1.5487	0.2133
PC1: $\overline{Crop_T}$	**1.8382 ± 0.5713**	**10.3509**	**0.0013****	**1.8960 ± 0.6018**	**9.9276**	**0.0016****	**1.7831 ± 0.6369**	**7.8372**	**0.0051****	**1.7055 ± 0.6373**	**7.1612**	**0.0074****
PC1: $\overline{Bare\ Soil_T}$	**2.745 ± 0.8555**	**10.2942**	**0.0013****	**2.7380 ± 0.8676**	**9.9562**	**0.0016****	**2.8866 ± 0.8921**	**10.4687**	**0.0012****	**2.9393 ± 0.8982**	**10.7091**	**0.0011****
ΔT : $\overline{Bare\ Soil_T}$	**-4.773 ± 1.7726**	**7.2516**	**0.0071****	**-718.4 ± 270.8**	**7.0390**	**0.0080****	**-5.8548 ± 1.9913**	**8.6440**	**0.0033****	**-6.1629 ± 2.0646**	**8.9100**	**0.0028****
C-pseudo-R^2	0.2557			0.2488			0.2343			0.1869		
M-pseudo-R^2	0.0685			0.0668			0.0687			0.0736		

Table S2. Estimate (± standard error) and results of an ANOVA type III Wald chi-square test for the species population trends models using datasets from which populations with extreme populations trends have been removed. In the case of the **no-extremes** model, populations with extremely negative and positive population trends were removed (data trimmed at the 2.5 and 97.5 percentiles). For the **no-lower-extreme** models, populations with trends below the 2.5th percentile were discarded. In the case of **no-upper-extreme**, populations with trends above the 97.5 percentile were discarded. Dataset size for each model is denoted by **N** and presented along with the model's name. Statistically significant terms are marked in bold with stars indicating the level of significance ($P < 0.1$ = .; $P < 0.05$ = *; $P < 0.01$ = **; and $P < 0.001$ = ***). Degrees of freedom for all terms were equal to 1. Model conditional and pseudo-R^2 values are shown at the bottom of the table. Fixed effects included in the models were: ΔT, rate of temperature change; $\overline{Crop_T}$, rate of change for cropland land-cover; $\overline{Bare\ soil_T}$, rate of change for bare soil cover; and PC1, the fast-slow continuum (see also equation 4 in the main text). Green shaded fields denote agreement between the sensitivity test models and the main model.

	No-extremes; N= 1,018			**No-lower-extreme; N= 1,045**			**No-upper-extreme; N= 1,045**		
	Estimate	χ^2	*p-value*	Estimate	χ^2	*p-value*	Estimate	χ^2	*p-value*
(Intercept)	0.0033 ± 0.0025	1.7494	0.1860	**0.0068 ± 0.0029**	**5.4445**	**0.0196***	-0.0012 ± 0.003	0.1503	0.6983
ΔT	-0.0497 ± 0.2709	0.0337	0.8543	0.0891 ± 0.3176	0.0787	0.7791	-0.1347 ± 0.3287	0.1681	0.6818
PC1	0.0018 ± 0.0017	1.0309	0.3099	0.0028 ± 0.0020	1.9454	0.1631	**0.0039 ± 0.0021**	**3.5214**	**0.0606 .**
$\overline{Crop_T}$	-0.8173 ± 0.5484	2.2209	0.1362	-0.4713 ± 0.6377	0.5462	0.4599	**-1.9383 ± 0.6402**	**9.1673**	**0.0025****
$\overline{Bare\ Soil_T}$	2.7716 ± 2.2939	1.4599	0.2270	5.4665 ± 2.6299	4.3205	0.0377*	2.4317 ± 2.7658	0.7730	0.3793
PC1: $\overline{Crop_T}$	0.5483 ± 0.51	1.1557	0.2824	0.3243 ± 0.5863	0.3059	0.5802	**2.0806 ± 0.5396**	**14.8656**	**0.0001*****
PC1: $\overline{Bare\ Soil_T}$	0.4963 ± 0.6851	0.5249	0.4688	**2.0439 ± 0.7567**	**7.2968**	**0.0069****	1.0751 ± 0.8117	1.7544	0.1853
ΔT : $\overline{Bare\ Soil_T}$	**-396.7622 ± 212.47**	**3.4869**	**0.0619 .**	**-778.9622 ± 240.23**	**10.5142**	**0.0012****	-338.9939 ± 257.67	1.7307	0.1883
C-pseudo-R^2	0.2038			0.2575			0.2405		
M-pseudo-R^2	0.0223			0.073			0.0353		

Table S3. Cross-walk table for the transformation of ESA-CCI land-cover classes into coarser categories used to measure land-cover change in this analysis (adapted from Li et al., 2017). Unified land covers are: TBe, tree broadleaf evergreen; TBd, tree broadleaf deciduous; TNe, tree needleleaf evergreen; TNd, tree needleleaf deciduous; SBe, shrub broadleaf evergreen; SBd, shrub broadleaf deciduous; SNe, shrub needleleaf evergreen; SNd, shrub needleleaf deciduous; NB, natural grass; Cr, crop; Bs, bare-soil; Wr, water; S/I, snow/ice; Ur, urban; and Nt, no data. Values show the % contribution to the final land-cover class for each of the original ESA-CCI-LCP (http://www.esa-landcover-cci.org) classes.

		Unified land-cover														
Pix	**ESA CCI description**	**TBe**	**TBd**	**TNe**	**TNd**	**SBe**	**SBd**	**SNe**	**SNe**	**NG**	**Cr**	**Bs**	**Wr**	**S/I**	**Ur**	**Nt**
0	No data															100
10	Cropland, rainfed									10	90					
11	Herbaceous cover									10	90					
12	Tree or shrub cover						70				30					
20	Cropland, irrigated or post-flooding										100					
30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover)(<50%)	5	5			5	5	5		15	60					
40	Mosaic natural vegetation (tree, shrub, herbaceous cover (>50%)/ cropland (<50%)	7.5	7.5			10	15	10		30	20					
50	Tree cover, broadleaved, evergreen, close to open (>15%)	90				5	5									
60	Tree cover, broadleaved, deciduous, closed to open (>15%)		50				20			30						
61	Tree cover, broadleaved, deciduous, croloasdeldea (f> 40%)		70				15			15						
62	Tree cover, broadleaved, deciduous, open (15-40%)		30				25			45						
70	Tree cover, needleleaved, evergreen, closed to open (>15%)			70		5	5	5		15						
71	Tree cover, needleleaved, evergreen, closed (>40%)			70		5	5	5		15						
72	Tree cover, needleleaved, evergreen, open (15-40%)							25		45						
80	Tree cover, needleleaved, deciduous, closed to open (>15%)				50	2.5	2.5	2.5	12.5	30						
81	Tree cover, needleleaved, deciduous, closed (>40%)				70	5	5	5		15						
82	Tree cover, needleleaved, deciduous, open (15-40%)				30				25	45						
90	Tree cover, mixed leaf type (broadleaved and needleleaved)		30	20	10	5	5	5		25						

100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	10	20	5	5	5	10	5		40						
110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	5	10	5		5	10	5		60						
120	Shrubland					15	30	15		40						
121	Shrubland evergreen					30		30		40						
122	Shrubland deciduous						60			40						
130	Grassland									100						
140	Lichens and mosses									100						
150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)		5	5			5	5		30		50				
152	Sparse shrub (<15%)						10	10		30		50				
153	Sparse herbaceous cover (<15%)									50		50				
160	Tree cover, flooded, fresh or brackish water	37.5	37.5							25						
170	Tree cover, flooded, saline water	75				25										
180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water						25	15		60						
190	Urban areas														100	
200	Bare areas											100				
201	Consolidated bare areas											100				
202	Unconsolidated bare areas											100				
210	Water bodies												100			
220	Permanent snow and ice													100		

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