Humans have been modifying Earth’s ecosystems for thousands of years. Archaeological and palaeontological evidence suggest that human activities may have played a major role in the extinction of Australian’s megafauna as early as fifty thousand years ago (Johnson *et al.* 2016; Miller *et al.* 2016; Van Der Kaars *et al.* 2017). The subsequent arrival of modern humans in other parts of the world has also been associated with extinctions, of the megafauna in particular (Sandom *et al.* 2014; Broughton & Weitzel 2018). However, the global signature of human presence on Earth has never been as prominent as in the recent decades. The past two hundred years have been characterised by a sharp increase in the rates of human-driven changes at the planetary scale, termed “the Great Acceleration” (Steffen *et al.* 2015). To emphasize the recent impacts of human activities on the Earth’s systems, Crutzen & Stoermer (2000) proposed that we have entered a new geological epoch, which they called “the Anthropocene”. Although the formal acceptation of this epoch and the timing of its start are still debated within the stratigraphic community (Lewis & Maslin 2015; Monastersky 2015), the coined term reflects the profound effects of humans on planetary processes and on the biosphere, such that its use has largely surpassed the geological field (Malhi 2017).

The Anthropocene can be characterised with Earth-system and socio-economic indicators (Steffen *et al.* 2011; Biermann *et al.* 2016). Two of the major signatures are the human-driven transformations of the land surface and the changes in atmospheric composition, associated with the onset of anthropogenic climate change (Lewis & Maslin 2015). Altogether, the development of human activities at unprecedented scales and magnitude of has led to the alteration of many ecosystems. As a result of combined anthropogenic pressures, the world’s biodiversity has been changing (Dirzo *et al.* 2014; McGill *et al.* 2015; Johnson *et al.* 2017; Daru *et al.* 2021). Decreases in a range of biodiversity indicators have been reported for many taxonomic groups (Butchart *et al.* 2010). Human-mediated invasions and translocations of species, coupled with local declines in native species, have promoted biotic homogenisation (Newbold *et al.* 2018; Finderup Nielsen *et al.* 2019; Daru *et al.* 2021). In addition, species have gone extinct at higher rates than expected from natural background variability, with current extinction rates estimated to exceed those inferred from fossil records by a hundred to a thousand times (Barnosky *et al.* 2011; De Vos *et al.* 2015). Biodiversity loss and ecosystem change have become such major issues in the 21th century that the prevention of biodiversity erosion and the protection of ecosystems have become priority goals on international agendas (Convention on Biological Diversity 2020; Hoban *et al.* 2020). Indeed, it is now well established that biodiversity is tightly linked with ecosystem functioning and ecosystem services delivery (Duraiappah *et al.* 2005, Oliver *et al.* 2015, Hooper *et al.* 2005), and thus ultimately, with human well-being. However, the difficulty in achieving global conservation goals – such as the failure to reach the Aichi targets (Buchanan *et al.* 2020) – highlights the need strengthen global conservation efforts if we are to protect biodiversity and related ecosystem services from global threats (Butchart *et al.* 2016).

1. *Land-use change and climate change, two major drivers of global biodiversity loss in the Anthropocene*

The biggest anthropogenic threats to biodiversity have been well characterised (Maxwell *et al.* 2016). Currently, land-use change is the primary driver of global biodiversity loss (Newbold *et al.* 2015; Chaudhary *et al.* 2018; Jetz & Pyron 2018; Powers & Jetz 2019). However, the negative effects of climate change on biodiversity could equate those of land-use change in their magnitude by 2070 (Newbold 2018), emphasizing that together, these two threats urge towards immediate mitigation and conservation action.

*Land-use change*

Land-use change refers to the process by which humans transform the landscape to achieve socio-economic needs, such that the use of the land is characterised by the main purpose it fulfils (in other words, land use describes the human intent behind a particular land cover; Lambin *et al.* 2001). Land-use change includes transitions from natural to anthropized landscapes, as exemplified by agricultural-driven deforestation in tropical areas (Jayathilake *et al.* 2021); land-use change also describes transitions between different forms of human-dominated land uses, with, for instance, the expansion of urban areas over agricultural lands (Ustaoglu & Williams 2017). Although humans have been modifying terrestrial ecosystems for millennia – between 75% and 95% of the total land surface could have been altered by human activities (Ellis *et al.* 2013, 2021) –, only during the past three centuries has the terrestrial surface made the transition from mostly wild to mostly human-dominated (Ellis *et al.* 2010). The most important driver behind this transition has been agricultural expansion, with major increases in cropland and grazing areas from the mid-18th century (Figure 1). In the recent decades, the expansion of grazing areas and animal feed crops, fuelled by the rising demand in animal products, has been identified as the most important driver of land-use change (Alexander *et al.* 2015).

Chart

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**Figure 1: Land surface (and land-surface proportion) used for agricultural purposes between 2000 BCE and 2016.** Data from the HYDE database (Goldewijk *et al.* 2017), downloaded from <https://ourworldindata.org/land-use> (24/01/2022).

The effects of land-use change on biodiversity have been characterised at local, regional and global scales – although global-scale studies represent a small proportion of the published research (Davison *et al.* 2021). Overall, published research highlights the negative impacts of land-use change on species richness and abundance (Newbold *et al.* 2015), as well as key impacts of future land-use change scenarios for ecosystem processes and services (Lawler *et al.* 2014). For example, and although they currently represent a small proportion of the terrestrial surface (about 1%; Goldewijk *et al.* (2017)), urban areas have been expanding at faster rates than urban populations themselves (Seto *et al.* 2010), and can cause considerable damage to biodiversity and ecosystem services. In particular, the expansion of impervious surfaces has been linked to reduction in species richness (Souza *et al.* 2019; Yan *et al.* 2019) and to increases in ecological risks (e.g., due to flooding, Hou *et al.* 2022). However, another important aspect of land-use change for biodiversity outcomes is the level of intensity at which the land is used to fulfil its purpose. For instance, introducing and managing green spaces can lead to positive biodiversity outcomes in urban environments (Ives *et al.* 2016; Aronson *et al.* 2017). Yet, land-use intensity has not been explicitly considered by a majority of past studies investigating impacts of land-use change on biodiversity (Davison *et al.* 2021), despite its likely importance for biodiversity (Dullinger *et al.* 2021; Millard *et al.* 2021).

*Climate change*

According to the World Meteorological Organization, climate change is defined as long-term changes (i.e, at least over several decades) to the mean state or to the variability of the climate, attributable to human activity or to natural causes. There is a strong scientific consensus that current climate change (starting ~A.D. 1850) is the result of human activity, and that it is has been onset by the human-driven changes to atmospheric composition (Crowley 2000; IPCC 2013; Maibach *et al.* 2014). Current manifestations of climate change include rising average temperatures (Valipour *et al.* 2021; Figure 2), increases in the frequency of extreme events (Seneviratne *et al.* 2012) and changes in global rainfall patterns (Dore 2005; Trenberth 2011).

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**Figure 2: Land surface temperature anomaly between A.D 1880 and A.D. 2022.** Data retrieved from the National Oceanic and Atmospheric Administration – National Centers for Environmental Information, downloaded from [https://www.ncdc.noaa.gov/cag/](https://www.ncei.noaa.gov/cag/) (May 2022), and plotted for the month of March. The anomalies are calculated with reference to the global temperature average for the 20th century.

There is accumulating empirical evidence that climate change affects biodiversity globally, with documented changes in phenology (Inouye 2022), in the geographical distributions of species (Chen *et al.* 2011; Lenoir & Svenning 2015), and in species physiology (Pörtner & Farrell 2008; Chown *et al.* 2010). Climate-change impacts on individual species have consequences for whole communities, through the disruptions of species interactions, which can in turn exacerbate impacts on individual species (Cahill *et al.* 2013; Kharouba *et al.* 2018).

Projecting future land-use and climate-change impacts on biodiversity highlights the key role of human-development scenarios for global biodiversity outcomes (Newbold 2018) and for the long-term viability of animal populations (Spooner *et al.* 2018). As the world’s population continues to grow and as the demand for food, energy and other commodities keeps rising, rates of global land-use and climate change are unlikely to curb without the implementation of strong international regulations and consumption changes (Intergovernmental Panel on Climate Change 2022; Stehfest *et al.* 2019). In this context, evaluating the effects of land-use and climate change on biodiversity and associated ecosystem services has become vital in order to put into place mitigation measures. In particular, understanding what makes species more sensitive to land-use and climate change can help conservation efforts.

1. *Informing and prioritising vertebrate conservation with trait-based approaches*

*Ecological importance of terrestrial vertebrates and current threats*

Vertebrates play significant roles in ecosystem functioning and support a wide range of processes, most notably as pollinators (Ratto *et al.* 2018), seed dispersers (Tiffney 2004), regulators of lower trophic levels (Barber *et al.* 2010; Salo *et al.* 2010; Luck *et al.* 2012; Lin *et al.* 2018; Zhang *et al.* 2018), nutrient cyclers (Wilson & Wolkovich 2011; Inger *et al.* 2016; Cunningham *et al.* 2018) and ecosystem engineers (Severtsov 2012). Vertebrates are also important for human societies, both culturally and as sources of proteins (Hirons *et al.* 2016; Albert *et al.* 2018; Alves *et al.* 2018), and figure among the most charismatic species (Courchamp *et al.* 2018). Despite their cultural and ecological importance, terrestrial vertebrates are highly threatened by human activities. The latest Living Planet Report revealed that vertebrate populations have decreased by 70% on average since 1970 (WWF 2020). According to the IUCN Red List of Threatened Species, about 41% of assessed amphibian species are classified as threatened, 26% of the mammals, 21% of the reptiles and 13% of the birds (IUCN 2022, <https://www.iucnredlist.org/resources/summary-statistics>). A recent assessment of vertebrates listed in the IUCN Red List of Threatened Species highlights habitat destruction as the predominant human threat (Cox *et al.* 2022), but direct exploitation also figures among the major factors of decline (Monastersky 2014). Although climate change is not the principal driver of current population declines (Caro *et al.* 2022), the first extinction of a mammal attributed to anthropogenic climate was reported in 2016 (Watson 2016). Future projections highlight that. Further, land-use changes have negative effects on local vertebrate diversity, with reductions in species richness and abundance.

*Using traits to understand species responses to environmental change*

Despite the global average declines reported for vertebrate populations, not all species respond similarly to environmental changes. Past studies have highlighted interspecific variation in the growth rates of different populations under similar conditions (ref) and in species responses to land-use and climate change (ref). Some species may benefit from global changes, while others are projected to decline (ref). One of the reasons why species differ in their ability to cope with disturbances is that species present different intrinsic characteristics, or traits. Although the formal definition of ‘a trait’ can vary depending on studies, in this thesis, I consider traits to be characteristics measurable at the organismal level, that likely influence organismal fitness and performance (this is the definition adopted in McGill 2006). The idea that species traits mediate species responses to environmental change was formalized in the “response-effect” framework, developed on the grounds of plant ecology (refs), where traits that influence species responses to environmental change were termed “response traits” (and those that underpin ecological processes were termed “effect traits”). One of the appeals of trait-based approaches is that individual species are no longer the focus of biodiversity investigations. Rather, traits become “common currencies” across species, which is of particular interest for conservation when long-term population data are lacking for some species. Indeed, if species’ responses to human threats consistently relate to certain traits, it may be possible to generalise patterns and estimate the responses of species for which population data is not available (Verberk *et al.* 2013). As such, traits have been used to assess species vulnerability to global changes (in particular to climate change, refs), with frameworks assuming that species traits predict species sensitivity to environmental change. To date, the empirical evidence linking traits showing that traits explain species responses to human threats relies mostly on correlative assessments conducted at local to regional scale (refs). In particular, traits have been used to explain species responses to land use and land-use intensity (refs). Trait-based approaches have also been used to understand species responses to climate change (with studies focusing on range shifts; range filling), and . Although response traits to land-use and climate change have been identified in various vertebrate taxa (refs), whether the effects of such traits can be generalised geographically and taxonomically remains largely uncertain, emphasising the need for global comparative assessments of the relationships between traits and species responses to human threats. The overarching aims of my thesis are to investigate whether species traits are associated with species land-use responses and species climate-change sensitivity, at global scales, and comparatively across the four vertebrate classes. I also aim to highlight some of the consequences of global changes for ecosystem functioning. Throughout my thesis, assemblage-level and species-level responses to land use and land-use intensity are assessed using a “space-for-time” approach (refs). To this end, I use one of the most comprehensive databases recording species occurrence and abundance in different land uses (the PREDICTS database, Hudson *et al.* (2014, 2017)). I estimate sensitivity to climate change from properties of species climatic niche space, and thus I do not assess species responses to climate change (which would require to integrate exposure to climate change).

1. *Aims, hypotheses and outline of the following Chapters*

One of the obstacles that have hindered the application of trait-based approaches at large scales in animal taxa is the lack of a centralised repository for readily available trait data, as emphasized by the recent calls to compile and release trait data for animals (Junker *et al.* 2022). Thus, collecting trait data and investigating the current availability of the data for terrestrial vertebrates was an important and necessary prerequisite to any analysis. In Chapter 2, I present a trait data collection for terrestrial vertebrates. Because using similar traits in the different vertebrate classes is necessary to be able to make comparisons among vertebrate classes, I target seven traits that are commonly used in any taxonomic group: body mass/size, a proxy for lifespan, litter/clutch size, trophic level, diel activity, habitat breadth, and a broad degree of habitat specialisation. Because of data limitation constraints, I am not able to consider intraspecific variation in the data compilation. Chapter 2 assesses the availability of the trait data across the terrestrial vertebrate classes, and investigates whether the trait data present global taxonomic, phylogenetic and spatial biases. On the basis of past work (Titley *et al.* 2017), I hypothesize that amphibians and reptiles are undersampled compared to mammals and birds. Further, I hypothesize that trait data are less abundant for the narrower-ranging species and in species-richer regions. This Chapter was published in *Global Ecology and Biogeography* (Etard *et al*. 2020).

At the assemblage level, multidimensional trait composition can be summarised with functional diversity indices (). Past research has shown that human threats reshape the functional composition Functional diversity indices are useful to understand effects of as they allow to capture into single indices. To the best of my knowledge, a global assessment of how the functional diversity of terrestrial vertebrate assemblages respond to land use and land-use intensity, within and across taxonomic classes, has not yet been undertaken. Chapter 3 aims to fill in this gap, by investigating the effects of land use and land-use intensity on the functional diversity of local vertebrate assemblages. To this end, I combine the trait data collected in Chapter 2 with the PREDICTS database. After imputing missing trait values (evidenced in Chapter 2), I investigate the effects of land use on the functional diversity of local terrestrial vertebrate assemblages, across and within vertebrate classes. I hypothesize that the functional diversity of vertebrate assemblages in disturbed land uses is lower than in undisturbed land uses. I further predict that decreases in functional diversity in disturbed land uses are driven by high levels of functional loss and that observed declines in functional diversity exceed those expected from random species loss. This Chapter was published in *Ecology Letters* (Etard *et al*. 2022).

Chapter 3 highlights the effects of land-use change on the functional composition of vertebrate assemblages but does not allow to assess the effects of particular traits on species land-use responses, as multidimensional trait variation is summarised into single indices of functional diversity. Thus, in Chapter 4, I investigate whether ecological traits and geographical range area are associated with species land-use responses and species climate-change sensitivity, comparatively among the terrestrial vertebrate classes. I enhance the trait data compiled in Chapter 2 with diet information for vertebrate species. I investigate whether there are associations between ecological traits (including geographical range area) and species land-use responses on the one hand, and between ecological traits and species climate-change sensitivity on the other hand. I further assess whether these associations can be generalised across classes and threats by looking for emerging patterns in the associations between traits and land-use responses and between traits and climate-change sensitivity. To the best of my knowledge, Chapter 4 constitutes the first global comparative assessment, among vertebrate classes, of associations between traits and species land-use responses and between traits and species climate-change sensitivity.

Chapter 5 develops our understanding of the impacts of land-use change on ecosystem functioning by focusing on species energetic requirements. First, I assess the effects of land use on the total energetic requirements of vertebrate assemblages. Second, I assess whether species energetic requirements influence species persistence in disturbed land uses. To this end, I collect resting metabolic rates for vertebrate species, which I use as a proxy for species-level energetic expenditure, and I combine these estimates with the PREDICTS database. Assuming that there is less energy available in disturbed land uses, I hypothesize that the assemblage-level energetic requirements of vertebrates are lower in disturbed land uses compared to undisturbed land uses, and that species with lower mass-independent energetic requirements are favoured over species with higher mass-independent energetic requirements in disturbed land uses. Chapter 5 highlights the impacts of land-use change on vertebrate community metabolism.

Finally, inChapter 6, I summarise the findings of this thesis, I highlight some of the limitations and I examine the relevance of the findings for the field. By investigating whether traits are associated with species land-use responses and climate-change sensitivity across the terrestrial vertebrates, my thesis furthers our understanding of what could render species more sensitive to human threats, underlines possible modifications to ecosystem functioning and stresses the role and usefulness of vertebrate trait data for understanding species and community responses to human pressures.