Climate and land-use change homogenise terrestrial biodiversity, with consequences for ecosystem functioning and human well-being

Tim Newbold[1], Georgina L. Adams[1], Gonzalo Albaladejo Robles[1,2], Elizabeth H. Boakes[1], Abbie S. A. Chapman[1], Adrienne Etard[1], Guilherme Braga Ferreira[1,2], Rory Gibb[1], Joseph Millard[1,2], Charlotte L. Outhwaite[1], Jessica J. Williams[1]

[1]Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, United Kingdom
[2]Institute of Zoology, Zoological Society of London, Regent's Park, London, United Kingdom

Corresponding author: Tim Newbold (t.newbold@ucl.ac.uk)

Abstract

Biodiversity continues to decline under the effect of multiple human pressures. We give a brief overview of the main pressures on biodiversity, before focusing on the two that have a predominant effect: land-use and climate change. We discuss how interactions between land-use and climate change in terrestrial systems are likely to have greater impacts than expected when only considering these pressures in isolation. Understanding biodiversity changes is complicated by the fact that such changes are likely to be uneven among different geographic regions and species. We review the evidence for variation in terrestrial biodiversity changes, relating differences among species to key ecological characteristics, and explaining how disproportionate impacts on certain species are leading to a spatial homogenisation of ecological communities. Finally, we explain how the overall losses and homogenisation of biodiversity, and the larger impacts upon certain types of species, are likely to lead to strong negative consequences for the functioning of ecosystems, and consequently for human well-being.

Introduction

The latest Living Planet Report estimates that vertebrate populations have declined by 60% since 1970 [1]. Despite significant increases in conservation efforts over the last decade, anthropogenic pressures on biodiversity continue to increase [2]. As a result, few of the latest set of internationally agreed targets (the Convention on Biological Diversity's Aichi 2020 targets) are likely to be achieved [2]. The continued global loss of biodiversity has important consequences for humans. Species support critical ecosystem functions [3], which in turn provide services essential to human well-being such as water purification, flood protection, disease regulation and pollination [4].

The present era is characterised by increasingly rapid changes to human and natural systems, in what has been termed the "Great Acceleration" [5]. Indeed, many scientists argue that we now exist in a new geological era dominated by human actions – the Anthropocene [6]. Two particularly significant changes involve the ever-increasing amount of the land surface used for human activities, and the rising concentration of greenhouse gases in the atmosphere, leading to climate change [5]. The resulting profound impacts on biodiversity [7,8] are expected to accelerate in the coming decades [9]. Effects on biodiversity may be greater than previously thought, as the pressures from land use and climate are likely to interact [10]. Furthermore, evidence suggests that biodiversity responses to changes in climate and land use are uneven, with variation among species and geographical regions [9,11,12]. Interactive effects and uneven responses are likely to lead to unanticipated outcomes for biodiversity, ecosystem functions and, ultimately, human well-being.

Although we rely on biodiversity for supporting key ecosystem functions and services, much of human progress has come through activities that directly impact ecological communities, in particular our use of the land to build homes and grow food. Conservation efforts may therefore have an immediate cost for human food production [13,14], although the future resilience of natural and agricultural systems likely depends on biodiversity being maintained [15]. Understanding the complex synergies and trade-offs between human activities and biodiversity [14], especially in light of the interactive and uneven responses of biodiversity to human activities, requires a major advance in the underpinning science. One promising avenue is the development of robust predictive models that can improve our understanding and drive more informed policy choices [16]. The development of the United Nations Sustainable Development Goals [17] has emphasised the need to balance biodiversity conservation and human well-being in national decision-making.

Evidence of the likely impacts of land-use and climate change is accumulating but remains patchy. Important gaps in our knowledge include: 1) how these two major pressures on biodiversity may interact; 2) whether the strength of their effects varies among species and locations; and 3) the consequences of uneven biodiversity changes for ecosystem functioning and human well-being (Figure 1). In this review, we synthesise the recent literature on land-use and climate impacts, focusing on broad-scale analyses of terrestrial systems, discussing the mechanisms that may drive important but under-studied interactions between these two drivers of change. We highlight the unevenness in biodiversity responses, with certain geographical regions and species being disproportionately sensitive, leading to a large-scale spatial homogenisation of ecological communities. Finally, we discuss how the complex and uneven responses of biodiversity to land-use and climate change are likely to impact the critical ecosystem functions and services on which the natural world and human well-being rely. Although we primarily focus on terrestrial systems, both land-use and climate change are also major threats to freshwater and coastal marine systems [18–20].

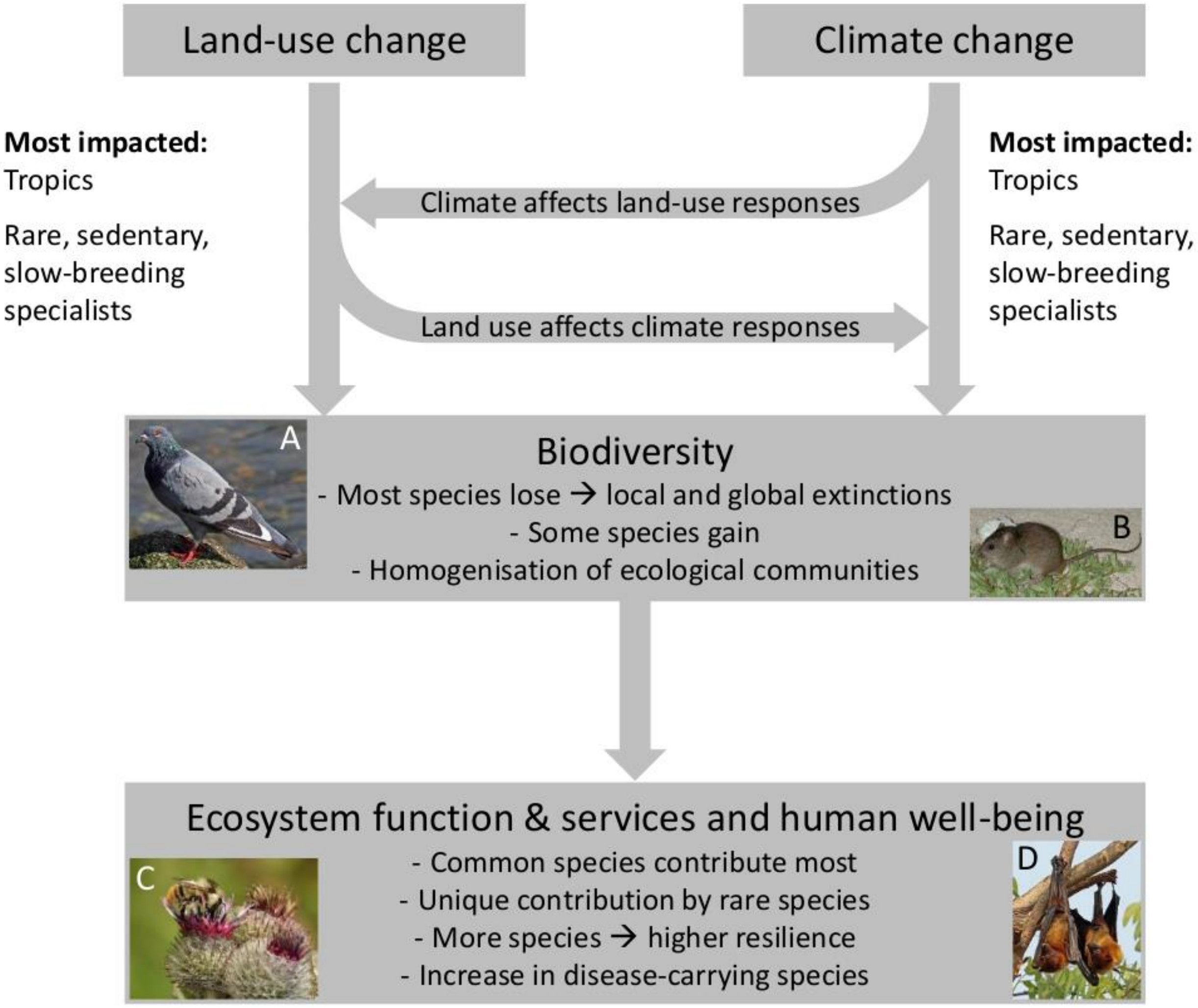

Figure 1. Framework relating the effects of land-use, climate change and their interaction to uneven biodiversity changes, and the effect of such biodiversity changes on ecosystem functioning, services and human well-being. Evidence suggests that tropical regions, and species that are rare, sedentary, slow-breeding and specialised on particular habitats and diets are consistently most impacted by land-use and climate change (see main text). A result of the same species being most impacted by both pressures is that certain species are doing particularly well in an era of global environmental change (such as pigeons in cities and farmland; A), while many others are declining (for example, the bramble cay melomys – B – went extinct as a result of climate-driven habitat loss [21]). Biodiversity changes have a substantial impact on the functioning of ecosystems, and the provision of ecosystem services on which human well-being relies. Two facets of biodiversity change that have been highlighted as having an important effect on human well-being are the large declines in pollinators, such as bumblebees (C), and increasing populations of certain species, such as flying foxes (D) that carry numerous human diseases. All images used here are published under Creative Commons licenses and were not altered in any way from the original form. A) Author: Charles J. Sharp; License: CC Attribution-Share Alike 4.0 International; Source: https://bit.ly/2ssbjWu. B) Author: Ian Bell, EHP, State of Queensland; License: CC Attribution 3.0 Australia; Attribution: State of Queensland; Source: https://bit.ly/2W1Czsy. C) Author: Ivar Leidus; License: CC Attribution-Share Alike 4.0 International; Source: https://bit.ly/2Df72vD. D) Author: Charles J Sharp; License: CC Attribution-ShareAlike 4.0 International; Source: https://bit.ly/2VYfA1j.

Pressures on biodiversity

The most important direct pressures on terrestrial biodiversity are habitat loss and degradation (driven mainly by human land use), climate change, invasive species, overexploitation, and pollution

[22,23]. Among these pressures, land-use and climate change are particularly significant. Habitat loss and degradation have been identified as major threats to a large proportion of IUCN Red List assessed species [22,23]. In contrast, a much smaller proportion of species are currently considered to be threatened directly by climate change [22–25]. This is probably because habitat loss is a rapid and easy-to-assess driver of species loss, whereas climate change is a more cryptic long-term driver [25]. However, the pressure of climate change on biodiversity is likely to increase rapidly in the future [9,26,27]. Already, greater declines in mammal and bird abundances have been observed in areas where mean temperature has increased more rapidly [28].

Land-use change, principally to grow food and provide settlements for humans, has altered natural landscapes substantially [29]. At a local scale, land-use changes cause reductions of species richness by around 75% and of organism abundance by 40% in human-impacted compared to undisturbed habitats [7,30]. As a result of the high proportion of the land surface that is used by humans, it is estimated that the average ecological community has lost somewhere between 13% and 25% of its naturally occurring species [7,31]. Habitat degradation without significant loss of vegetation cover can also have negative impacts on biodiversity. For example, some Amazonian forests may have lost around half of their conservation value due to anthropogenic disturbance such as selective logging and wildfires [32]. In addition to effects on local ecosystems, land-use change also causes homogenisation of biodiversity across space, leading to ecological communities becoming more similar to one another [12,33,34].

Climate change has affected biodiversity via range shifts, local extinctions and phenological changes. Species are moving their ranges poleward at a rate of 16.9 km per decade, and to higher elevations at a rate of 11 m per decade [35]. Effects on phenological patterns [8] have included global changes in leaf phenology [36], a later end to the vegetation growing season [37], and changes in migration patterns in birds [38,39]. However, the effect of climate change on species is mixed, with both winners and losers [40–42], and the numbers of species inhabiting some regions is predicted to increase [43].

With the human population set to reach 9 billion by 2050, pressure on biodiversity due to climate change and human land use will increase [7,9,44]. Global projections have suggested that the average ecological community could lose as many as 38% of its species as a result of combined land-use and climate impacts under current trajectories [9]. Future expansion of land use alone is expected to cause a 17% loss of species from the average community under business-as-usual, while projections for the Amazon and Afrotropical regions have predicted a 30% decline in species abundance [45]. The effects of climate change will accelerate in the near future, and are predicted to exceed the impacts of land-use change by the middle of this century [9]. Under business-as-usual trends, climate change is predicted to cause more than half of species to lose over half of their range area by 2100 [26]. In contrast, fewer than 10% of species are expected to lose more than half of their range area if international commitments (such as under the Paris climate agreement) are honoured [26].

Interactions between land-use and climate change

The consequences of pressures on biodiversity may be complicated if the effects of those pressures interact with one another [10,46]. In comparison to the additive effect of multiple pressures (where the effects of each pressure are combined assuming independence), interactions can result in either greater (synergistic) or reduced (antagonistic) effects on biodiversity [10,47]. Land-use and climate change have been found to interact in multiple ways [48–51]. The mechanisms are more likely to lead to synergistic than to antagonistic interactions. However, it is often challenging in practice to demonstrate robustly that interactions are occurring [47].

First, global climate change can affect the way biodiversity responds to land-use change. Specifically, regions with warming temperatures and decreasing precipitation are expected to experience the greatest impacts of habitat loss and fragmentation [49,52]. The resulting synergistic interactions are predicted to intensify the impacts of land-use change in almost a fifth of the world's ecoregions [50]. Of concern for species conservation, the most affected ecoregions are also highly biodiverse, harbouring more than half of known terrestrial vertebrate species [50]. Climatic changes can also affect population sizes, breeding systems, sex ratios and individual fitness, which can impact a species' ability to respond to land-use change [53,54].

Second, land-use change can affect the way biodiversity responds to climate change, with human land use and habitat fragmentation creating a hostile landscape and thus hindering species' ability to track changes in climate [48,55,56]. Land-use change can also lead to localised climatic changes, with human-disturbed habitats often hotter and drier than natural habitats [57–59]. Consequently, ecological communities within human-disturbed habitats (deforested areas, agricultural lands, and cities) are generally composed of species that, on average, tolerate warmer and drier climatic conditions compared to species within natural habitats [57,58,60,61]. These differences in community composition may result directly from the local climatic changes or indirectly, for example because of changes in habitat or vegetation structure [58,60]. Regardless of the underlying mechanism, local temperature increases resulting from vegetation change will exacerbate regional warming, with important consequences for biodiversity. The fact that both land-use and climate change are likely to favour species that can tolerate climatic extremes is expected to lead to a homogenisation of ecological communities, which may have negative impacts on ecosystem functioning [62–64]. For example, experiments with microbial communities showed that, under thermal stress, a greater number of species were required to maintain ecosystem function [65]. Conversely, high-quality habitat, such as forests with denser canopies, can buffer the effect of climatic changes, and may act as important refuges for species that are sensitive to climatic variation [51,66,67]. Interestingly, in some cases urban environments may act as refugia for species that are less able to tolerate the thermal extremes of managed (agricultural) ecosystems; for example, in recent years, numerous Australian flying fox populations have moved into urban parkland to access water and shelter [68]. Antagonistic interactions between land-use and climate change may occur if human-altered landscapes also act as refugia for species unable to tolerate global climatic changes. However, to our knowledge, there are currently no clear examples of such antagonistic interactions. In part, this may be due to the difficulty in identifying these types of interaction [47].

Unevenness in biodiversity changes

Geographic variation

The impacts of land-use and climate change on biodiversity are predicted to vary spatially across the globe, which has important consequences for the conservation of biodiversity, and for the effects that biodiversity changes may have on ecosystems and human well-being. The tropics are repeatedly emphasised as showing disproportionately large losses of biodiversity [10,12,46,69–71], and contain a disproportionate number of species threatened with extinction [72,73]. Future responses of tropical species to climate change may be hindered by their lower dispersal abilities [74], and by their lower tolerance of climatic variation as a result of evolving in a climate that has historically been relatively stable [70,71,75]. In addition, it is likely that tropical species are currently living closer to their upper thermal limits compared to species within the temperate realm [67].

Since climatic conditions in the tropics are expected to exceed historic variability by the end of this century [76], and rapid tropical land-use changes and human population growth are predicted in many scenarios [77,78], there is an impending challenge for biodiversity conservation within this realm [69]. This challenge may be exacerbated by governance issues [73], and the fact that much of the impact of human actions on tropical biodiversity is a result of consumption in other countries [79]. Consequently, mapping international trade in commodities and the resulting flows of biodiversity impacts is a key area of research [79–81].

The disproportionate effects of land-use and climate change on tropical ecosystems is a major concern for biodiversity conservation, given the large number of species found within the tropics. At least 78% of species, including many endemic species, occur in tropical ecosystems [73]. Moreover, the tropics are likely home to most currently undiscovered species [73,82]. Even within the tropics, certain areas are more impacted than others, with Asian biodiversity often emerging as being particularly sensitive to land-use change [11,83].

Species variation

Climate and land-use effects on biodiversity are also expected to fall unevenly on different species. The need to understand which species are likely to be most vulnerable to environmental changes has led to increasing efforts to identify characteristics associated with sensitivity. We focus here on two aspects of this work: first, whether rare or common species are more vulnerable; and second, whether there are ecological characteristics (traits) of species that are consistently associated with species' responses.

It has long been suggested that biodiversity losses will impact rare species more than common ones [84]. Rarity can be defined in several ways, including numerical rarity (i.e. low abundance), geographical rarity (i.e. small range size) or specialisation to particular habitats [85]. Evidence suggests that rare species have a disproportionately high risk of global extinction [86–88], and are highly sensitive to land-use change [12,89–91]. Furthermore, rare species have been predicted (using models) or hypothesised (based on expert opinion) to be at greater risk from future climatic changes than common species [92,93]. Rarity may also mediate interactions between climate and land-use change. For example, habitat specialists will likely be less able to shift their distributions through human-dominated landscapes in response to climate [55]. The degree to which rare or common species are likely to be sensitive to environmental changes depends on the ecosystem being studied, the characteristics of species, and the spatial and temporal scales of the studies [94,95]. The general tendency for rare, narrowly distributed and habitat-specialist species to be most impacted by land-use and climate changes contributes to the observed spatial homogenisation of biodiversity [33,34]. This reduced spatial turnover of species also leads to a reduction in global biodiversity, as unique species are lost and replaced by a similar set of widespread species everywhere [12,43,96].

The sensitivity of species to environmental change is also mediated by their ecological characteristics (or traits) [71,89,91,92], leading to observed changes in the functional diversity of ecological communities with land-use and climate change [97–99]. Traits that determine species' sensitivity to environmental changes are often referred to as "response traits" (in contrast to "effect traits" that determine species contributions' to ecosystem function – see below) [100,101]. Importantly, some traits emerge as determining species' responses to both land-use and climate change. Slower-breeding species with low mobility, and narrow food and habitat requirements have been shown to be disproportionately sensitive to both pressures [71,89,90,92,93]. Identifying which species traits confer greater risk to anthropogenic changes and which are likely to modify ecosystem processes is key for predicting the future of ecological communities and processes.

Effects of biodiversity change on ecosystem functioning

Over the past 20 years, attitudes have shifted from biodiversity being a consequence of the ecological and environmental properties of an ecosystem, to biodiversity being a key driver of ecosystem functioning [102]. A positive relationship between biodiversity (typically measured as species richness) and the magnitude and stability of ecosystem functioning (commonly measured as plant productivity or standing biomass) has been well established through many local-scale experimental and field studies [102–105]. As a result, changes in biodiversity due to human-driven environmental change can have a large effect on plant productivity and stability [106]. For example, land-use impacts on plant species diversity in tropical forests lead to decreased energy fluxes [107], and in dryland ecosystems there is greater ecosystem stability when plant species diversity is high [65]. At large scales, biodiversity is expected to have multiple, complex effects on different ecosystem processes [108–112], but this remains uncertain because most previous studies have been at conducted at small scales [113].

Different species have been shown to promote ecosystem functioning at different times, places and environmental contexts [3]. Contributions to ecosystem functioning depend on ecological characteristics ("effect traits") [100]. Functional effect traits are often the same as those associated with a high sensitivity to environmental change (response traits – see above), in which case environmental change could result in larger-than-expected changes in ecosystem functions. Disproportionate losses of large-sized and high-trophic-level taxa (both of which are often most impacted by environmental changes) may lead to more negative changes in ecosystem functioning than caused by random losses [114,115]. Furthermore, rare species contribute unique traits to communities and thus are likely to support distinct functions in many systems [116–120], although in an undisturbed system both rare and common taxa have been shown to make unique contributions [121]. In addition to the effects of local losses of biodiversity, homogenisation across space, such as caused by the disproportionate loss of rare species, has also been associated with an independent negative effect on ecosystem functioning [110,122]. For example, a study of 65 grasslands worldwide showed that naturally diverse communities, with a high turnover of species across space, had the greatest ecosystem multifunctionality (functions such as soil carbon storage, aboveground live biomass and litter decomposition were measured) [122]. Overall, therefore, systems with a large number of species, a high turnover of species in space, and a diversity of different types of species, are likely to be more resistant and resilient to environmental change through high and stable ecosystem functioning [123–126].

Consequences for human well-being

The framing of biodiversity conservation has changed over time from a 'nature-for-nature's sake' perspective to one that recognises the interdependence of biodiversity, ecosystem function and human well-being [127]. The 'nature and people' perspective [127] is now embedded within the international discourse around conservation, including in the UN Sustainable Development Goals [17], the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES) [128], and research-policy agendas such as Planetary Health and One Health [129]. Connections between biodiversity and human well-being are captured in the concept of 'ecosystem services' (see [130] for a detailed review), or in more recently accepted terminology 'nature's contributions to people' [131]. Contributions of the natural environment and biodiversity to human well-being can fall under several categories, such as provisioning (e.g. crop production, clean water, timber, fuelwood, non-timber forest products), regulating (e.g. carbon storage and sequestration, pollination, disease regulation), and cultural services (e.g. aesthetic, spiritual, or recreational value) [4]. By impacting ecological communities and processes, land-use and climate changes can alter the provision of particular ecosystem services [132].

The best studied of the biodiversity-mediated regulating services is pollination. Pollinating species are in widespread decline [133], in large part owing to land-use and climate change [134,135]. For example, as agriculture expands to meet human food demands, croplands spread into previously forested landscapes, which can have impacts on pollinator abundance [136] and, ultimately, the yields of pollinator-dependent crops [137]. A reduction in agricultural productivity caused by the loss of pollinating biodiversity may necessitate further land-use change, leading to a positive feedback [138]. There is also evidence that climate change is negatively affecting pollinators [135,139]. Given the increasing climate and land-use change predicted for the future, pollination services are likely to be vulnerable. There is, however, uncertainty about the ability of novel species to contribute to pollination when rarer and more sensitive species are lost [140].

Provisioning services have also been an important research focus for understanding the interactions between land use and human well-being. For instance, the removal of trees for fuel to cook food is a common practice in many countries across the globe, but can degrade forest systems, potentially leading to longer-term feedbacks on people [141,142].

Land use can also affect Earth-system feedbacks, by altering local microclimates and the balance of carbon stocks. These interactions are clearly seen in forests, through impacts of land-use change on tree diversity, biomass, and carbon storage [143]. However, the nature and scale-dependence of the relationships between land use, diversity, and carbon storage remain unclear in many cases [144], particularly when past climates have influenced carbon in present-day soils [145]. In addition, the picture is further complicated when the land used for provisioning services drives trade-offs with other ecosystem services. For example, fuelwood collection in China impairs seed-dispersal services by rodents [146].

Ecosystem services can also have more direct impacts on human health and well-being. Of particular interest in the context of land-use and climate change is the mediation of zoonotic and vector-borne human disease risk. Interactions between species-level host-parasite interactions, overall community diversity and ecosystem structure can produce emergent effects on infectious disease transmission and risk, including of significant human pathogens (e.g. Lyme disease, hantaviruses, West Nile disease) [147–149]. However, evidence for a hypothesised general prophylactic effect of biodiversity on pathogen transmission rates (the dilution effect) is patchy [150], with recent evidence suggesting that ecological degradation can lead locally either to increases or decreases in disease risk depending on host traits, behaviour and local ecological context [151,152]. Across larger geographical areas or timescales, it is also possible that human risk of specific diseases may predominantly be mediated by land-use and/or climate effects on particular host or vector species, rather than by biodiversity loss *per se* [153–155].

Although ecosystem services provide a well-supported link between anthropogenic ecological change and potential benefits or costs to human societies [130], quantifying whether these translate to measurable, broader-scale outcomes for public health and well-being is a key emerging challenge [104,156]. Confounding socioeconomic or demographic factors, which show latitudinal trends that are coincident with biodiversity gradients [157], may mask any contributions of ecological change to aggregate health metrics such as disease burden [158]. Furthermore, in the short-term, the benefits to health and economies of land conversion for agriculture may significantly outweigh the costs of degrading other services, whose long-term implications (e.g. reductions in carbon storage or water provision, disease emergence) may not be felt for years or decades. Consequently, there is an urgent need to improve understanding of the connections between biodiversity change, ecosystem services and human well-being [156], and how these connections might be influenced by biodiversity changes brought about by climate and land-use change.

Summary points

- Land use and climate are already having profound effects on terrestrial biodiversity, and their effects are likely to accelerate in the coming decades. Our understanding of how climate and land use might interact in their effects on biodiversity is still very limited, but early evidence points toward a synergistic interaction. Overall, it is therefore likely that biodiversity changes will be greater than suggested by the majority of previous large-scale studies that have treated pressures additively or in isolation.
- The effects of pressures on biodiversity do not fall evenly on all species. While most species are impacted negatively by land-use or climate change, some benefit. Characteristics such as rarity, slow breeding, low mobility and specific food and habitat requirements are associated with a high degree of sensitivity to both pressures. The replacement of many distinctive species with a few tolerant species bearing the same characteristics is already leading to a global homogenisation of biodiversity.

- The loss of particular types of species, and the associated homogenisation of biodiversity, has important implications for the functioning of ecosystems and for the ecosystem services (or nature's contributions to people) on which humans rely. The links between biodiversity changes and ecosystem functioning and services remain unclear, but it is certain that we are losing important groups (such as pollinators). It is also very likely that the homogenisation of biodiversity will reduce the resilience of ecosystem functioning to future environmental changes. Finally, in many cases, it appears that among those species that are tolerant of human activities are species that could have detrimental effects on human health (i.e. reservoirs of zoonotic disease).
- Effects of environmental changes on biodiversity also fall unevenly geographically. The tropics, especially the Southeast Asian tropics, consistently emerge as having biodiversity that is particularly sensitive to land-use and climate changes. This is a concern for human societies, given that the most rapid future population increases will occur in the tropics, and much of the future expansion in agriculture must also take place here (often supplying consumption in other countries).
- Overall, the evidence suggests that to avoid large-scale losses of biodiversity we need to reduce the major pressures on biodiversity from land-use and climate change, by mitigating greenhouse gas emissions [159], preserving remaining natural habitats in protected areas [160], and improving the conservation of biodiversity within areas used by humans [161]. We also need to improve our understanding of the interactions between the effects of land-use and climate change, and the link between biodiversity change and ecosystem functions and services. However, the available evidence already points toward profound and uneven biodiversity changes, with important effects, in most cases negative, for ecosystems and human societies.

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Author contributions

All authors designed the structure of the review, contributed to writing, and checked the final version.

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