

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

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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].

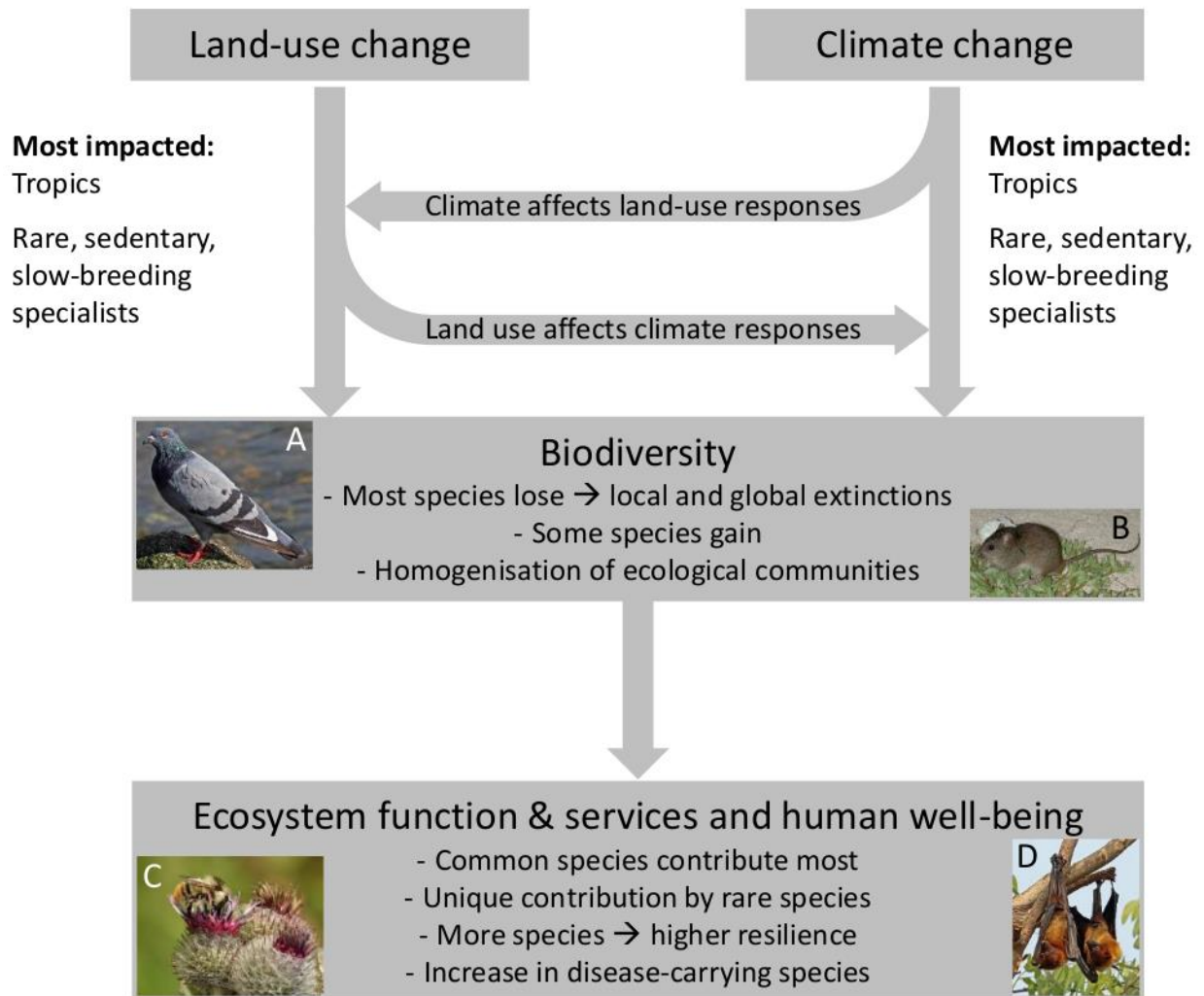
The present era is characterised by increasingly rapid changes to human and natural systems, in what has been termed the "Great Acceleration" [5]. Indeed, many scientists argue that we now exist in a new geological era dominated by human actions – the Anthropocene [6]. Two particularly significant changes 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

52 have an immediate cost for human food production [13,14], although the future resilience of natural
53 and agricultural systems likely depends on biodiversity being maintained [15]. Understanding the
54 complex synergies and trade-offs between human activities and biodiversity [14], especially in light
55 of the interactive and uneven responses of biodiversity to human activities, requires a major
56 advance in the underpinning science. One promising avenue is the development of robust predictive
57 models that can improve our understanding and drive more informed policy choices [16]. The
58 development of the United Nations Sustainable Development Goals [17] has emphasised the need to
59 balance biodiversity conservation and human well-being in national decision-making.

60 Evidence of the likely impacts of land-use and climate change is accumulating but remains
61 patchy. Important gaps in our knowledge include: 1) how these two major pressures on biodiversity
62 may interact; 2) whether the strength of their effects varies among species and locations; and 3) the
63 consequences of uneven biodiversity changes for ecosystem functioning and human well-being
64 (Figure 1). In this review, we synthesise the recent literature on land-use and climate impacts,
65 focusing on broad-scale analyses of terrestrial systems, discussing the mechanisms that may drive
66 important but under-studied interactions between these two drivers of change. We highlight the
67 unevenness in biodiversity responses, with certain geographical regions and species being
68 disproportionately sensitive, leading to a large-scale spatial homogenisation of ecological
69 communities. Finally, we discuss how the complex and uneven responses of biodiversity to land-use
70 and climate change are likely to impact the critical ecosystem functions and services on which the
71 natural world and human well-being rely. Although we primarily focus on terrestrial systems, both
72 land-use and climate change are also major threats to freshwater and coastal marine systems [18–
73 20].

74



75
 76 **Figure 1. Framework relating the effects of land-use, climate change and their interaction to uneven**
 77 **biodiversity changes, and the effect of such biodiversity changes on ecosystem functioning, services and**
 78 **human well-being.** Evidence suggests that tropical regions, and species that are rare, sedentary, slow-breeding
 79 and specialised on particular habitats and diets are consistently most impacted by land-use and climate change
 80 (see main text). A result of the same species being most impacted by both pressures is that certain species are
 81 doing particularly well in an era of global environmental change (such as pigeons in cities and farmland; A),
 82 while many others are declining (for example, the bramble cay melomys – B – went extinct as a result of
 83 climate-driven habitat loss [21]). Biodiversity changes have a substantial impact on the functioning of
 84 ecosystems, and the provision of ecosystem services on which human well-being relies. Two facets of
 85 biodiversity change that have been highlighted as having an important effect on human well-being are the
 86 large declines in pollinators, such as bumblebees (C), and increasing populations of certain species, such as
 87 flying foxes (D) that carry numerous human diseases. All images used here are published under Creative
 88 Commons licenses and were not altered in any way from the original form. A) Author: Charles J. Sharp;
 89 License: CC Attribution-Share Alike 4.0 International; Source: <https://bit.ly/2ssbjWu>. B) Author: Ian Bell, EHP,
 90 State of Queensland; License: CC Attribution 3.0 Australia; Attribution: State of Queensland; Source:
 91 <https://bit.ly/2W1Czsy>. C) Author: Ivar Leidus; License: CC Attribution-Share Alike 4.0 International; Source:
 92 <https://bit.ly/2Df72vD>. D) Author: Charles J Sharp; License: CC Attribution-ShareAlike 4.0 International; Source:
 93 <https://bit.ly/2VYfA1j>.

94
 95 **Pressures on biodiversity**

96
 97 The most important direct pressures on terrestrial biodiversity are habitat loss and degradation
 98 (driven mainly by human land use), climate change, invasive species, overexploitation, and pollution

99 [22,23]. Among these pressures, land-use and climate change are particularly significant. Habitat loss
100 and degradation have been identified as major threats to a large proportion of IUCN Red List
101 assessed species [22,23]. In contrast, a much smaller proportion of species are currently considered
102 to be threatened directly by climate change [22–25]. This is probably because habitat loss is a rapid
103 and easy-to-assess driver of species loss, whereas climate change is a more cryptic long-term driver
104 [25]. However, the pressure of climate change on biodiversity is likely to increase rapidly in the
105 future [9,26,27]. Already, greater declines in mammal and bird abundances have been observed in
106 areas where mean temperature has increased more rapidly [28].

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

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

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

137 138 **Interactions between land-use and climate change**

139
140 The consequences of pressures on biodiversity may be complicated if the effects of those pressures
141 interact with one another [10,46]. In comparison to the additive effect of multiple pressures (where
142 the effects of each pressure are combined assuming independence), interactions can result in either
143 greater (synergistic) or reduced (antagonistic) effects on biodiversity [10,47]. Land-use and climate
144 change have been found to interact in multiple ways [48–51]. The mechanisms are more likely to
145 lead to synergistic than to antagonistic interactions. However, it is often challenging in practice to
146 demonstrate robustly that interactions are occurring [47].

147 First, global climate change can affect the way biodiversity responds to land-use change.
148 Specifically, regions with warming temperatures and decreasing precipitation are expected to
149 experience the greatest impacts of habitat loss and fragmentation [49,52]. The resulting synergistic

150 interactions are predicted to intensify the impacts of land-use change in almost a fifth of the world's
151 ecoregions [50]. Of concern for species conservation, the most affected ecoregions are also highly
152 biodiverse, harbouring more than half of known terrestrial vertebrate species [50]. Climatic changes
153 can also affect population sizes, breeding systems, sex ratios and individual fitness, which can impact
154 a species' ability to respond to land-use change [53,54].

155 Second, land-use change can affect the way biodiversity responds to climate change, with
156 human land use and habitat fragmentation creating a hostile landscape and thus hindering species'
157 ability to track changes in climate [48,55,56]. Land-use change can also lead to localised climatic
158 changes, with human-disturbed habitats often hotter and drier than natural habitats [57–59].
159 Consequently, ecological communities within human-disturbed habitats (deforested areas,
160 agricultural lands, and cities) are generally composed of species that, on average, tolerate warmer
161 and drier climatic conditions compared to species within natural habitats [57,58,60,61]. These
162 differences in community composition may result directly from the local climatic changes or
163 indirectly, for example because of changes in habitat or vegetation structure [58,60]. Regardless of
164 the underlying mechanism, local temperature increases resulting from vegetation change will
165 exacerbate regional warming, with important consequences for biodiversity. The fact that both land-
166 use and climate change are likely to favour species that can tolerate climatic extremes is expected to
167 lead to a homogenisation of ecological communities, which may have negative impacts on
168 ecosystem functioning [62–64]. For example, experiments with microbial communities showed that,
169 under thermal stress, a greater number of species were required to maintain ecosystem function
170 [65]. Conversely, high-quality habitat, such as forests with denser canopies, can buffer the effect of
171 climatic changes, and may act as important refuges for species that are sensitive to climatic variation
172 [51,66,67]. Interestingly, in some cases urban environments may act as refugia for species that are
173 less able to tolerate the thermal extremes of managed (agricultural) ecosystems; for example, in
174 recent years, numerous Australian flying fox populations have moved into urban parkland to access
175 water and shelter [68]. Antagonistic interactions between land-use and climate change may occur if
176 human-altered landscapes also act as refugia for species unable to tolerate global climatic changes.
177 However, to our knowledge, there are currently no clear examples of such antagonistic interactions.
178 In part, this may be due to the difficulty in identifying these types of interaction [47].

179

180 **Unevenness in biodiversity changes**

181

182 *Geographic variation*

183

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

193 Since climatic conditions in the tropics are expected to exceed historic variability by the end of
194 this century [76], and rapid tropical land-use changes and human population growth are predicted in
195 many scenarios [77,78], there is an impending challenge for biodiversity conservation within this
196 realm [69]. This challenge may be exacerbated by governance issues [73], and the fact that much of
197 the impact of human actions on tropical biodiversity is a result of consumption in other countries
198 [79]. Consequently, mapping international trade in commodities and the resulting flows of
199 biodiversity impacts is a key area of research [79–81].

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

206

207 *Species variation*

208

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

215 It has long been suggested that biodiversity losses will impact rare species more than common
216 ones [84]. Rarity can be defined in several ways, including numerical rarity (i.e. low abundance),
217 geographical rarity (i.e. small range size) or specialisation to particular habitats [85]. Evidence
218 suggests that rare species have a disproportionately high risk of global extinction [86–88], and are
219 highly sensitive to land-use change [12,89–91]. Furthermore, rare species have been predicted
220 (using models) or hypothesised (based on expert opinion) to be at greater risk from future climatic
221 changes than common species [92,93]. Rarity may also mediate interactions between climate and
222 land-use change. For example, habitat specialists will likely be less able to shift their distributions
223 through human-dominated landscapes in response to climate [55]. The degree to which rare or
224 common species are likely to be sensitive to environmental changes depends on the ecosystem
225 being studied, the characteristics of species, and the spatial and temporal scales of the studies
226 [94,95]. The general tendency for rare, narrowly distributed and habitat-specialist species to be most
227 impacted by land-use and climate changes contributes to the observed spatial homogenisation of
228 biodiversity [33,34]. This reduced spatial turnover of species also leads to a reduction in global
229 biodiversity, as unique species are lost and replaced by a similar set of widespread species
230 everywhere [12,43,96].

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

241

242 **Effects of biodiversity change on ecosystem functioning**

243

244 Over the past 20 years, attitudes have shifted from biodiversity being a consequence of the
245 ecological and environmental properties of an ecosystem, to biodiversity being a key driver of
246 ecosystem functioning [102]. A positive relationship between biodiversity (typically measured as
247 species richness) and the magnitude and stability of ecosystem functioning (commonly measured as
248 plant productivity or standing biomass) has been well established through many local-scale
249 experimental and field studies [102–105]. As a result, changes in biodiversity due to human-driven
250 environmental change can have a large effect on plant productivity and stability [106]. For example,

251 land-use impacts on plant species diversity in tropical forests lead to decreased energy fluxes [107],
252 and in dryland ecosystems there is greater ecosystem stability when plant species diversity is high
253 [65]. At large scales, biodiversity is expected to have multiple, complex effects on different
254 ecosystem processes [108–112], but this remains uncertain because most previous studies have
255 been at conducted at small scales [113].

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

275

276 **Consequences for human well-being**

277

278 The framing of biodiversity conservation has changed over time from a ‘nature-for-nature’s sake’
279 perspective to one that recognises the interdependence of biodiversity, ecosystem function and
280 human well-being [127]. The ‘nature and people’ perspective [127] is now embedded within the
281 international discourse around conservation, including in the UN Sustainable Development Goals
282 [17], the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES) [128], and
283 research-policy agendas such as Planetary Health and One Health [129]. Connections between
284 biodiversity and human well-being are captured in the concept of ‘ecosystem services’ (see [130] for
285 a detailed review), or in more recently accepted terminology ‘nature’s contributions to people’
286 [131]. Contributions of the natural environment and biodiversity to human well-being can fall under
287 several categories, such as provisioning (e.g. crop production, clean water, timber, fuelwood, non-
288 timber forest products), regulating (e.g. carbon storage and sequestration, pollination, disease
289 regulation), and cultural services (e.g. aesthetic, spiritual, or recreational value) [4]. By impacting
290 ecological communities and processes, land-use and climate changes can alter the provision of
291 particular ecosystem services [132].

292 The best studied of the biodiversity-mediated regulating services is pollination. Pollinating
293 species are in widespread decline [133], in large part owing to land-use and climate change
294 [134,135]. For example, as agriculture expands to meet human food demands, croplands spread into
295 previously forested landscapes, which can have impacts on pollinator abundance [136] and,
296 ultimately, the yields of pollinator-dependent crops [137]. A reduction in agricultural productivity
297 caused by the loss of pollinating biodiversity may necessitate further land-use change, leading to a
298 positive feedback [138]. There is also evidence that climate change is negatively affecting pollinators
299 [135,139]. Given the increasing climate and land-use change predicted for the future, pollination
300 services are likely to be vulnerable. There is, however, uncertainty about the ability of novel species
301 to contribute to pollination when rarer and more sensitive species are lost [140].

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

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

314 Ecosystem services can also have more direct impacts on human health and well-being. Of
315 particular interest in the context of land-use and climate change is the mediation of zoonotic and
316 vector-borne human disease risk. Interactions between species-level host-parasite interactions,
317 overall community diversity and ecosystem structure can produce emergent effects on infectious
318 disease transmission and risk, including of significant human pathogens (e.g. Lyme disease,
319 hantaviruses, West Nile disease) [147–149]. However, evidence for a hypothesised general
320 prophylactic effect of biodiversity on pathogen transmission rates (the dilution effect) is patchy
321 [150], with recent evidence suggesting that ecological degradation can lead locally either to
322 increases or decreases in disease risk depending on host traits, behaviour and local ecological
323 context [151,152]. Across larger geographical areas or timescales, it is also possible that human risk
324 of specific diseases may predominantly be mediated by land-use and/or climate effects on particular
325 host or vector species, rather than by biodiversity loss *per se* [153–155].

326 Although ecosystem services provide a well-supported link between anthropogenic ecological
327 change and potential benefits or costs to human societies [130], quantifying whether these translate
328 to measurable, broader-scale outcomes for public health and well-being is a key emerging challenge
329 [104,156]. Confounding socioeconomic or demographic factors, which show latitudinal trends that
330 are coincident with biodiversity gradients [157], may mask any contributions of ecological change to
331 aggregate health metrics such as disease burden [158]. Furthermore, in the short-term, the benefits
332 to health and economies of land conversion for agriculture may significantly outweigh the costs of
333 degrading other services, whose long-term implications (e.g. reductions in carbon storage or water
334 provision, disease emergence) may not be felt for years or decades. Consequently, there is an urgent
335 need to improve understanding of the connections between biodiversity change, ecosystem services
336 and human well-being [156], and how these connections might be influenced by biodiversity
337 changes brought about by climate and land-use change.

338

339 **Summary points**

340

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

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- 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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392 All authors designed the structure of the review, contributed to writing, and checked the final

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394 **References**

- 395
- 396
- 397 [1] Grooten M, Almond REA. Living Planet Report - 2018: Aiming Higher. Gland,
- 398 Switzerland: 2018.
- 399 [2] Tittensor DP, Walpole M, Hill SLL, Boyce DG, Britten GL, Burgess ND, et al. A mid-term
- 400 analysis of progress toward international biodiversity targets. *Science* 2014;346:241–
- 401 4. doi:10.1126/science.1257484.
- 402 [3] Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, et al. High plant

- 403 diversity is needed to maintain ecosystem services. *Nature* 2011;477:199–202.
404 doi:10.1038/nature10282.
- 405 [4] Millennium Ecosystem Assessment. *Ecosystems and Human Well-being: Biodiversity*
406 *Synthesis*. Washington DC, USA: World Resources Institute; 2005.
- 407 [5] Steffen W, Broadgate W, Deutsch L, Gaffney O, Ludwig C. The trajectory of the
408 Anthropocene: The Great Acceleration. *Anthr Rev* 2015;2:81–98.
409 doi:10.1177/2053019614564785.
- 410 [6] Crutzen PJ. Geology of mankind. *Nature* 2002;415:23. doi:10.1038/415023a.
- 411 [7] Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, et al. Global effects of
412 land use on local terrestrial biodiversity. *Nature* 2015;520:45–50.
413 doi:10.1038/nature14324.
- 414 [8] Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across
415 natural systems. *Nature* 2003;421:37–42.
- 416 [9] Newbold T. Future effects of climate and land-use change on terrestrial vertebrate
417 community diversity under different scenarios. *Proc R Soc B Biol Sci*
418 2018;285:20180792. doi:10.1098/rspb.2018.0792.
- 419 [10] Oliver TH, Morecroft MD. Interactions between climate change and land use change
420 on biodiversity: attribution problems, risks, and opportunities. *Wiley Interdiscip Rev*
421 *Clim Chang* 2014;5:317–35. doi:10.1002/wcc.271.
- 422 [11] Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, et al. Primary forests are
423 irreplaceable for sustaining tropical biodiversity. *Nature* 2011;478:378–81.
424 doi:10.1038/nature10425.
- 425 [12] Newbold T, Hudson LN, Contu S, Hill SLL, Beck J, Liu Y, et al. Widespread winners and
426 narrow-ranged losers: land use homogenizes biodiversity in local assemblages
427 worldwide. *PLoS Biol* 2018;16:e2006841. doi:10.1371/journal.pbio.2006841.
- 428 [13] Mehrabi Z, Ellis EC, Ramankutty N. The challenge of feeding the world while
429 conserving half the planet. *Nat Sustain* 2018;1:409–12. doi:10.1038/s41893-018-
430 0119-8.
- 431 [14] Smith P. Managing the global land resource. *Proc R Soc B Biol Sci* 2018;285:20172798.
432 doi:10.1098/rspb.2017.2798.
- 433 [15] Oliver TH, Heard MS, Isaac NJB, Roy DB, Procter D, Eigenbrod F, et al. Biodiversity and
434 resilience of ecosystem functions. *Trends Ecol Evol* 2015;30:673–84.
435 doi:10.1016/j.tree.2015.08.009.
- 436 [16] Nicholson E, Fulton EA, Brooks TM, Blanchard R, Leadley P, Metzger JP, et al.
437 *Scenarios and Models to Support Global Conservation Targets*. *Trends Ecol Evol*
438 2019;34:57–68. doi:10.1016/j.tree.2018.10.006.
- 439 [17] Griggs D, Stafford-Smith M, Gaffney O, Rockström J, Öhman MC, Shyamsundar P, et
440 al. Sustainable development goals for people and planet. *Nature* 2013;495:305–7.
441 doi:10.1038/495305a.
- 442 [18] Kroon FJ, Thorburn P, Schaffelke B, Whitten S. Towards protecting the Great Barrier
443 Reef from land-based pollution. *Glob Chang Biol* 2016;22:1985–2002.
444 doi:10.1111/gcb.13262.
- 445 [19] Bryndum-Buchholz A, Tittensor DP, Blanchard JL, Cheung WWL, Coll M, Galbraith ED,
446 et al. Twenty-first-century climate change impacts on marine animal biomass and
447 ecosystem structure across ocean basins. *Glob Chang Biol* 2019;25:459–72.
448 doi:10.1111/gcb.14512.
- 449 [20] Mantyka-Pringle CS, Martin TG, Moffatt DB, Udy J, Olley J, Saxton N, et al. Prioritizing

450 management actions for the conservation of freshwater biodiversity under changing
451 climate and land-cover. *Biol Conserv* 2016;197:80–9.
452 doi:10.1016/j.biocon.2016.02.033.

453 [21] Watson J. Bring climate change back from the future. *Nature* 2016;534.

454 [22] Maxwell SL, Fuller RA, Brooks TM, Watson JEM. Biodiversity: The ravages of guns,
455 nets and bulldozers. *Nature* 2016;536:143–5. doi:10.1038/536143a.

456 [23] WWF. Living Planet Report 2014. Gland Switzerland: 2014.

457 [24] Keith DA, Mahony M, Hines H, Elith J, Regan TJ, Baumgartner JB, et al. Detecting
458 extinction risk from climate change by IUCN Red List criteria. *Conserv Biol*
459 2014;28:810–9. doi:10.1111/cobi.12234.

460 [25] Trull N, Böhm M, Carr J. Patterns and biases of climate change threats in the IUCN
461 Red List. *Conserv Biol* 2018;32:135–47. doi:10.1111/cobi.13022.

462 [26] Warren R, Price J, Graham E, Forstnerhaeusler N, VanDerWal J. The projected effect on
463 insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C.
464 *Science* 2018;360:791–5.

465 [27] Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. Impacts of climate
466 change on the future of biodiversity. *Ecol Lett* 2012;365–77. doi:10.1111/j.1461-
467 0248.2011.01736.x.

468 [28] Spooner FEB, Pearson RG, Freeman R. Rapid warming is associated with population
469 decline among terrestrial birds and mammals globally. *Glob Chang Biol*
470 2018;24:4521–31. doi:10.1111/gcb.14361.

471 [29] Foley JA, Defries R, Asner GP, Barford C, Bonan G, Carpenter SR, et al. Global
472 consequences of land use. *Science* 2005;309:570–4. doi:10.1126/science.1111772.

473 [30] Murphy GEP, Romanuk TN. A meta-analysis of declines in local species richness from
474 human disturbances. *Ecol Evol* 2014;4:91–103. doi:10.1002/ece3.909.

475 [31] Newbold T, Hudson LN, Arnell AP, Contu S, De Palma A, Ferrier S, et al. Has land use
476 pushed terrestrial biodiversity beyond the planetary boundary? A global assessment.
477 *Science* 2016;353:288–91.

478 [32] Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, Mac Nally R, et al.
479 Anthropogenic disturbance in tropical forests can double biodiversity loss from
480 deforestation. *Nature* 2016;535:144–7. doi:10.1038/nature18326.

481 [33] Gossner MM, Lewinsohn TM, Kahl T, Grassein F, Boch S, Prati D, et al. Land-use
482 intensification causes multitrophic homogenization of grassland communities. *Nature*
483 2016;540:266–9. doi:10.1038/nature20575.

484 [34] McKinney ML, Lockwood JL. Biotic homogenization: a few winners replacing many
485 losers in the next mass extinction. *Trends Ecol Evol* 1999;14:450–3.

486 [35] Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD. Rapid range shifts of species
487 associated with high levels of climate warming. *Science* 2011;333:1024–6.
488 doi:10.1126/science.1206432.

489 [36] Buitenwerf R, Rose L, Higgins SI. Three decades of multi-dimensional change in global
490 leaf phenology. *Nat Clim Chang* 2015;5:364–8. doi:10.1038/nclimate2533.

491 [37] Liu Q, Fu YH, Zhu Z, Liu Y, Liu Z, Huang M, et al. Delayed autumn phenology in the
492 Northern Hemisphere is related to change in both climate and spring phenology. *Glob*
493 *Chang Biol* 2016;22:3702–11. doi:10.1111/gcb.13311.

494 [38] Newson SE, Moran NJ, Musgrove AJ, Pearce-Higgins JW, Gillings S, Atkinson PW, et al.
495 Long-term changes in the migration phenology of UK breeding birds detected by
496 large-scale citizen science recording schemes. *Ibis (Lond 1859)* 2016;158:481–95.

- 497 doi:10.1111/IBI.12367.
- 498 [39] Visser ME, Perdeck AC, van Balen JH, Both C. Climate change leads to decreasing bird
499 migration distances. *Glob Chang Biol* 2009;15:1859–65. doi:10.1111/j.1365-
500 2486.2009.01865.x.
- 501 [40] Burns F, Eaton MA, Barlow KE, Beckmann BC, Brereton T, Brooks DR, et al.
502 Agricultural Management and Climatic Change Are the Major Drivers of Biodiversity
503 Change in the UK. *PLoS One* 2016;11:e0151595. doi:10.1371/journal.pone.0151595.
- 504 [41] Stephens PA, Mason LR, Green RE, Gregory RD, Sauer JR, Alison J, et al. Consistent
505 response of bird populations to climate change on two continents. *Science*
506 2016;352:84–7.
- 507 [42] Reino L, Triviño M, Beja P, Araújo MB, Figueira R, Segurado P. Modelling landscape
508 constraints on farmland bird species range shifts under climate change. *Sci Total*
509 *Environ* 2018;625:1596–605. doi:10.1016/j.scitotenv.2018.01.007.
- 510 [43] Thomas CD. Local diversity stays about the same, regional diversity increases, and
511 global diversity declines. *Proc Natl Acad Sci U S A* 2013;110:19187–8.
512 doi:10.1073/pnas.1319304110.
- 513 [44] Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. Future threats to
514 biodiversity and pathways to their prevention. *Nature* 2017;546:73–81.
515 doi:10.1038/nature22900.
- 516 [45] Kehoe L, Romero-Muñoz A, Polaina E, Estes L, Kreft H, Kuemmerle T. Biodiversity at
517 risk under future cropland expansion and intensification. *Nat Ecol Evol* 2017;1:1129–
518 35. doi:10.1038/s41559-017-0234-3.
- 519 [46] Brook BW, Sodhi NS, Bradshaw CJA. Synergies among extinction drivers under global
520 change. *Trends Ecol Evol* 2008;23:453–60. doi:10.1016/j.tree.2008.03.011.
- 521 [47] Côté IM, Darling ES, Brown CJ. Interactions among ecosystem stressors and their
522 importance in conservation. *Proc R Soc London Ser B, Biol Sci* 2016;283:20152592.
523 doi:10.1098/rspb.2015.2592.
- 524 [48] Eigenbrod F, Gonzalez P, Dash J, Steyl I. Vulnerability of ecosystems to climate change
525 moderated by habitat intactness. *Glob Chang Biol* 2015;21:275–86.
526 doi:10.1111/gcb.12669.
- 527 [49] Mantyka-Pringle CS, Martin TG, Rhodes JR. Interactions between climate and habitat
528 loss effects on biodiversity: a systematic review and meta-analysis. *Glob Chang Biol*
529 2012;18:1239–52. doi:10.1111/j.1365-2486.2011.02593.x.
- 530 [50] Segan DB, Murray KA, Watson JEM. A global assessment of current and future
531 biodiversity vulnerability to habitat loss-climate change interactions. *Glob Ecol*
532 *Conserv* 2016;5:12–21. doi:10.1016/j.gecco.2015.11.002.
- 533 [51] Terraube J, Villers A, Poudré L, Varjonen R, Korpimäki E. Increased autumn rainfall
534 disrupts predator–prey interactions in fragmented boreal forests. *Glob Chang Biol*
535 2017;23:1361–73. doi:10.1111/gcb.13408.
- 536 [52] Oliver I, Dorrough J, Doherty H, Andrew NR. Additive and synergistic effects of land
537 cover, land use and climate on insect biodiversity. *Landsc Ecol* 2016;31:2415–31.
538 doi:10.1007/s10980-016-0411-9.
- 539 [53] Opdam P, Wascher D. Climate change meets habitat fragmentation: linking landscape
540 and biogeographical scale levels in research and conservation. *Biol Conserv*
541 2004;117:285–97. doi:10.1016/j.biocon.2003.12.008.
- 542 [54] Verboom J, Schippers P, Cormont A, Sterk M, Vos CC, Opdam PFM. Population
543 dynamics under increasing environmental variability: implications of climate change

- 544 for ecological network design criteria. *Landsc Ecol* 2010;25:1289–98.
545 doi:10.1007/s10980-010-9497-7.
- 546 [55] Oliver TH, Gillings S, Pearce-Higgins JW, Brereton T, Crick HQP, Duffield SJ, et al. Large
547 extents of intensive land use limit community reorganization during climate warming.
548 *Glob Chang Biol* 2017;23:2272–83. doi:10.1111/gcb.13587.
- 549 [56] Schloss CA, Nuñez TA, Lawler JJ. Dispersal will limit ability of mammals to track
550 climate change in the Western Hemisphere. *Proc Natl Acad Sci U S A* 2012;109:8606–
551 11. doi:10.1073/pnas.1116791109/
552 /DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1116791109.
- 553 [57] Frishkoff LO, Hadly EA, Daily GC. Thermal niche predicts tolerance to habitat
554 conversion in tropical amphibians and reptiles. *Glob Chang Biol* 2015;21:3901–16.
555 doi:10.1111/gcb.13016.
- 556 [58] Frishkoff LO, Karp DS, Flanders JR, Zook J, Hadly EA, Daily GC, et al. Climate change
557 and habitat conversion favour the same species. *Ecol Lett* 2016;19:1081–90.
558 doi:10.1111/ele.12645.
- 559 [59] Senior RA, Hill JK, González del Pliego P, Goode LK, Edwards DP. A pantropical analysis
560 of the impacts of forest degradation and conversion on local temperature. *Ecol Evol*
561 2017;7:7897–908. doi:10.1002/ece3.3262.
- 562 [60] Barnagaud JY, Barbaro L, Hampe A, Jiguet F, Archaux F. Species' thermal preferences
563 affect forest bird communities along landscape and local scale habitat gradients.
564 *Ecography* 2013;36:1218–26. doi:10.1111/j.1600-0587.2012.00227.x.
- 565 [61] Piano E, De Wolf K, Bona F, Bonte D, Bowler DE, Isaia M, et al. Urbanization drives
566 community shifts towards thermophilic and dispersive species at local and landscape
567 scales. *Glob Chang Biol* 2017;23:2554–64. doi:10.1111/gcb.13606.
- 568 [62] Rezende EL, Castañeda LE, Santos M. Tolerance landscapes in thermal ecology. *Funct*
569 *Ecol* 2014;28:799–809. doi:10.1111/1365-2435.12268.
- 570 [63] García FC, Bestion E, Warfield R, Yvon-Durocher G. Changes in temperature alter the
571 relationship between biodiversity and ecosystem functioning. *Proc Natl Acad Sci*
572 2018;201805518. doi:10.1073/pnas.1805518115.
- 573 [64] Blüthgen N, Simons NK, Jung K, Prati D, Renner SC, Boch S, et al. Land use imperils
574 plant and animal community stability through changes in asynchrony rather than
575 diversity. *Nat Commun* 2016;7:10697. doi:10.1038/ncomms10697.
- 576 [65] García-Palacios P, Gross N, Gaitán J, Maestre FT. Climate mediates the biodiversity–
577 ecosystem stability relationship globally. *Proc Natl Acad Sci U S A* 2018;115:8400–5.
578 doi:10.1073/pnas.1800425115.
- 579 [66] Jarzyna MA, Zuckerberg B, Finley AO, Porter WF. Synergistic effects of climate and
580 land cover: grassland birds are more vulnerable to climate change. *Landsc Ecol*
581 2016;31:2275–90. doi:10.1007/s10980-016-0399-1.
- 582 [67] Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, et al. Thermal-
583 safety margins and the necessity of thermoregulatory behavior across latitude and
584 elevation. *Proc Natl Acad Sci U S A* 2014;111:5610–5. doi:10.1073/pnas.1316145111.
- 585 [68] Plowright RK, Eby P, Hudson PJ, Smith IL, Westcott D, Bryden WL, et al. Ecological
586 dynamics of emerging bat virus spillover. *Proc R Soc London Ser B, Biol Sci*
587 2015;282:20142124. doi:10.1098/rspb.2014.2124.
- 588 [69] Corlett RT. Climate change in the tropics: The end of the world as we know it? *Biol*
589 *Conserv* 2012;151:22–5. doi:10.1016/j.biocon.2011.11.027.
- 590 [70] Newbold T, Hudson LN, Hill SLL, Contu S, Gray CL, Scharlemann JPW, et al. Global

- 591 patterns of terrestrial assemblage turnover within and among land uses. *Ecography*
592 2016;39:1151–63. doi:10.1111/ecog.01932.
- 593 [71] Pacifici M, Visconti P, Butchart SHM, Watson JEM, Cassola FM, Rondinini C. Species'
594 traits influenced their response to recent climate change. *Nat Clim Chang*
595 2017;7:205–8. doi:10.1038/nclimate3223.
- 596 [72] Orme CDL, Davies RG, Burgess M, Eigenbrod F, Pickup N, Olson V a, et al. Global
597 hotspots of species richness are not congruent with endemism or threat. *Nature*
598 2005;436:1016–9. doi:10.1038/nature03850.
- 599 [73] Barlow J, França F, Gardner TA, Hicks CC, Lennox GD, Berenguer E, et al. The future of
600 hyperdiverse tropical ecosystems. *Nature* 2018;559:517–26. doi:10.1038/s41586-
601 018-0301-1.
- 602 [74] Moore RP, Robinson WD, Lovette IJ, Robinson TR. Experimental evidence for extreme
603 dispersal limitation in tropical forest birds. *Ecol Lett* 2008;11:960–8.
604 doi:10.1111/j.1461-0248.2008.01196.x.
- 605 [75] Janzen DH. Why Mountain Passes are Higher in the Tropics. *Am Nat* 1967;101:233–
606 49. doi:10.1086/282487.
- 607 [76] Mora C, Frazier AG, Longman RJ, Dacks RS, Walton MM, Tong EJ, et al. The projected
608 timing of climate departure from recent variability. *Nature* 2013;502:183–7.
609 doi:10.1038/nature12540.
- 610 [77] Popp A, Calvin K, Fujimori S, Havlik P, Humpenöder F, Stehfest E, et al. Land-use
611 futures in the shared socio-economic pathways. *Glob Environ Chang* 2017;42:331–45.
612 doi:10.1016/j.gloenvcha.2016.10.002.
- 613 [78] Lewis SL, Edwards DP, Galbraith D. Increasing human dominance of tropical forests.
614 *Science* 2015;349:827–32. doi:10.1126/science.aaa9932.
- 615 [79] Moran D, Kanemoto K. Identifying species threat hotspots from global supply chains.
616 *Nat Ecol Evol* 2017;1:0023. doi:10.1038/s41559-016-0023.
- 617 [80] Newbold T. The trouble with trade. *Nat Ecol Evol* 2019;3:522–3. doi:10.1038/s41559-
618 019-0816-3.
- 619 [81] Marques A, Martins IS, Kastner T, Plutzer C, Theurl MC, Eisenmenger N, et al.
620 Increasing impacts of land use on biodiversity and carbon sequestration driven by
621 population and economic growth. *Nat Ecol Evol* 2019;3:628–37. doi:10.1038/s41559-
622 019-0824-3.
- 623 [82] Joppa LN, Roberts DL, Myers N, Pimm SL. Biodiversity hotspots house most
624 undiscovered plant species. *Proc Natl Acad Sci U S A* 2011;108:13171–6.
625 doi:10.1073/pnas.1109389108.
- 626 [83] Phillips HRP, Newbold T, Purvis A. Land-use effects on local biodiversity in tropical
627 forests vary between continents. *Biodivers Conserv* 2017;26:2251–70.
628 doi:10.1007/s10531-017-1356-2.
- 629 [84] Gaston KJ. *Rarity*. Dordrecht: Springer Netherlands; 1994. doi:10.1007/978-94-011-
630 0701-3.
- 631 [85] Rabinowitz D. Seven forms of rarity. In: Syngé H, editor. *Biol. Asp. rare plant Conserv.*,
632 New York, NY: John Wiley & Sons Ltd.; 1981, p. 205–17.
- 633 [86] Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, et al.
634 Multiple causes of high extinction risk in large mammal species. *Science*
635 2005;309:1239–41. doi:10.1126/science.1116030.
- 636 [87] Purvis A, Gittleman JL, Cowlshaw G, Mace GM. Predicting extinction risk in declining
637 species. *Proc R Soc London Ser B, Biol Sci* 2000;267:1947–52.

- 638 doi:10.1098/rspb.2000.1234.
- 639 [88] Collen B, Dulvy NK, Gaston KJ, Gärdenfors U, Keith DA, Punt AE, et al. Clarifying
640 misconceptions of extinction risk assessment with the IUCN Red List. *Biol Lett*
641 2016;12:20150843. doi:10.1098/rsbl.2015.0843.
- 642 [89] Newbold T, Scharlemann JPW, Butchart SHM, Şekercioğlu ÇH, Alkemade R, Booth H,
643 et al. Ecological traits affect the response of tropical forest bird species to land-use
644 intensity. *Proc R Soc London Ser B Biol Sci* 2013;280:20122131.
645 doi:10.1098/rspb.2012.2131.
- 646 [90] Vetter D, Hansbauer MM, Végvári Z, Storch I. Predictors of forest fragmentation
647 sensitivity in Neotropical vertebrates: a quantitative review. *Ecography* 2011;34:1–8.
648 doi:10.1111/j.1600-0587.2010.06453.x.
- 649 [91] Nowakowski AJ, Thompson ME, Donnelly MA, Todd BD. Amphibian sensitivity to
650 habitat modification is associated with population trends and species traits. *Glob Ecol*
651 *Biogeogr* 2017;26:700–12. doi:10.1111/geb.12571.
- 652 [92] Pearson RG, Stanton JC, Shoemaker KT, Aiello-Lammens ME, Ersts PJ, Horning N, et al.
653 Life history and spatial traits predict extinction risk due to climate change. *Nat Clim*
654 *Chang* 2014. doi:10.1038/nclimate2113.
- 655 [93] Foden WB, Butchart SHM, Stuart SN, Vié JC, Akçakaya HR, Angulo A, et al. Identifying
656 the world's most climate change vulnerable species: a systematic trait-based
657 assessment of all birds, amphibians and corals. *PLoS One* 2013;8:e65427.
658 doi:10.1371/journal.pone.0065427.
- 659 [94] Hartley S, Kunin WE. Scale dependency of rarity, extinction risk, and conservation
660 priority. *Conserv Biol* 2003;17:1559–70. doi:10.1111/j.1523-1739.2003.00015.x.
- 661 [95] Bruelheide H, Dengler J, Purschke O, Lenoir J, Jiménez-Alfaro B, Hennekens SM, et al.
662 Global trait–environment relationships of plant communities. *Nat Ecol Evol*
663 2018;2:1906–17. doi:10.1038/s41559-018-0699-8.
- 664 [96] McGill BJ, Dornelas M, Gotelli NJ, Magurran AE. Fifteen forms of biodiversity trend in
665 the Anthropocene. *Trends Ecol Evol* 2015;30:104–13. doi:10.1016/j.tree.2014.11.006.
- 666 [97] Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, et al. Loss of
667 functional diversity under land use intensification across multiple taxa. *Ecol Lett*
668 2009;12:22–33. doi:10.1111/j.1461-0248.2008.01255.x.
- 669 [98] Rapacciuolo G, Marin J, Costa GC, Helmus MR, Behm JE, Brooks TM, et al. The
670 signature of human pressure history on the biogeography of body mass in tetrapods.
671 *Glob Ecol Biogeogr* 2017. doi:10.1111/geb.12612.
- 672 [99] La Sorte FA, Lepczyk CA, Aronson MFJ, Goddard MA, Hedblom M, Katti M, et al. The
673 phylogenetic and functional diversity of regional breeding bird assemblages is
674 reduced and constricted through urbanization. *Divers Distrib* 2018.
675 doi:10.1111/ddi.12738.
- 676 [100] Lavorel S, Garnier E. Predicting changes in community composition and ecosystem
677 functioning from plant traits: Revisiting the Holy Grail. *Funct Ecol* 2002.
678 doi:10.1046/j.1365-2435.2002.00664.x.
- 679 [101] Luck GW, Lavorel S, McIntyre S, Lumb K. Improving the application of vertebrate trait-
680 based frameworks to the study of ecosystem services. *J Anim Ecol* 2012.
681 doi:10.1111/j.1365-2656.2012.01974.x.
- 682 [102] Tilman D, Isbell F, Cowles JM. Biodiversity and Ecosystem Functioning. *Annu Rev Ecol*
683 *Evol Syst* 2014;45:471–93. doi:10.1146/annurev-ecolsys-120213-091917.
- 684 [103] Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, et al.

- 685 Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*
686 2006;443:989–92. doi:10.1038/nature05202.
- 687 [104] Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, et al. Biodiversity
688 loss and its impact on humanity. *Nature* 2012;486:59–67. doi:10.1038/nature11148.
- 689 [105] Duffy JE, Godwin CM, Cardinale BJ. Biodiversity effects in the wild are common and as
690 strong as key drivers of productivity. *Nature* 2017;549:261–4.
691 doi:10.1038/nature23886.
- 692 [106] Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB. Anthropogenic
693 environmental changes affect ecosystem stability via biodiversity. *Science*
694 2015;348:336–40.
- 695 [107] Barnes AD, Weigelt P, Jochum M, Ott D, Hodapp D, Haneda NF, et al. Species richness
696 and biomass explain spatial turnover in ecosystem functioning across tropical and
697 temperate ecosystems. *Philos Trans R Soc London Ser B, Biol Sci* 2016;371:20150279.
698 doi:10.1098/rstb.2015.0279.
- 699 [108] Brose U, Hillebrand H. Biodiversity and ecosystem functioning in dynamic landscapes.
700 *Philos Trans R Soc Ser B, Biol Sci* 2016;371:20150267. doi:10.1098/rstb.2015.0267.
- 701 [109] Lefcheck JS, Byrnes JEK, Isbell F, Gamfeldt L, Griffin JN, Eisenhauer N, et al.
702 Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats.
703 *Nat Commun* 2015;6:6936. doi:10.1038/ncomms7936.
- 704 [110] van der Plas F, Manning P, Soliveres S, Allan E, Scherer-Lorenzen M, Verheyen K, et al.
705 Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proc*
706 *Natl Acad Sci U S A* 2016;113:3557–62. doi:10.1073/pnas.1517903113.
- 707 [111] Isbell F, Cowles J, Dee LE, Loreau M, Reich PB, Gonzalez A, et al. Quantifying effects of
708 biodiversity on ecosystem functioning across times and places. *Ecol Lett*
709 2018;21:763–78. doi:10.1111/ele.12928.
- 710 [112] Thompson PL, Isbell F, Loreau M, O’Connor MI, Gonzalez A. The strength of the
711 biodiversity–ecosystem function relationship depends on spatial scale. *Proc R Soc*
712 *London Ser B, Biol Sci* 2018;285:20180038. doi:10.1098/rspb.2018.0038.
- 713 [113] Isbell F, Gonzalez A, Loreau M, Cowles J, Díaz S, Hector A, et al. Linking the influence
714 and dependence of people on biodiversity across scales. *Nature* 2017;546:65–72.
715 doi:10.1038/nature22899.
- 716 [114] Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, et al. Trophic
717 downgrading of planet Earth. *Science* 2011;333:301–6. doi:10.1126/science.1205106.
- 718 [115] Fung T, Farnsworth KD, Reid DG, Rossberg AG. Impact of biodiversity loss on
719 production in complex marine food webs mitigated by prey-release. *Nat Commun*
720 2015;6:6657. doi:10.1038/ncomms7657.
- 721 [116] Bracken MES, Low NHN. Realistic losses of rare species disproportionately impact
722 higher trophic levels. *Ecol Lett* 2012;15:461–7. doi:10.1111/j.1461-
723 0248.2012.01758.x.
- 724 [117] Jain M, Flynn DFB, Prager CM, Hart GM, DeVan CM, Ahrestani FS, et al. The
725 importance of rare species: a trait-based assessment of rare species contributions to
726 functional diversity and possible ecosystem function in tall-grass prairies. *Ecol Evol*
727 2014;4:104–12. doi:10.1002/ece3.915.
- 728 [118] Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, et al. Rare
729 species support vulnerable functions in high-diversity ecosystems. *PLoS Biol*
730 2013;11:e1001569. doi:10.1371/journal.pbio.1001569.
- 731 [119] Leitão RP, Zuanon J, Villéger S, Williams SE, Baraloto C, Fortunel C, et al. Rare species

732 contribute disproportionately to the functional structure of species assemblages.
733 Proceedings Biol Sci 2016;283:20160084. doi:10.1098/rspb.2016.0084.

734 [120] Soliveres S, Manning P, Prati D, Gossner MM, Alt F, Arndt H, et al. Locally rare species
735 influence grassland ecosystem multifunctionality. Philos Trans R Soc London Ser B,
736 Biol Sci 2016;371:20150269. doi:10.1098/rstb.2015.0269.

737 [121] Chapman ASA, Tunnicliffe V, Bates AE. Both rare and common species make unique
738 contributions to functional diversity in an ecosystem unaffected by human activities.
739 Divers Distrib 2018;24:568–78. doi:10.1111/ddi.12712.

740 [122] Hautier Y, Isbell F, Borer ET, Seabloom EW, Harpole WS, Lind EM, et al. Local loss and
741 spatial homogenization of plant diversity reduce ecosystem multifunctionality. Nat
742 Ecol Evol 2018;2:50–6. doi:10.1038/s41559-017-0395-0.

743 [123] Pasari JR, Levi T, Zavaleta ES, Tilman D. Several scales of biodiversity affect ecosystem
744 multifunctionality. Proc Natl Acad Sci U S A 2013;110:10219–22.
745 doi:10.1073/pnas.1220333110.

746 [124] Isbell F, Craven D, Connolly J, Loreau M, Schmid B, Beierkuhnlein C, et al. Biodiversity
747 increases the resistance of ecosystem productivity to climate extremes. Nature
748 2015;526:574–7. doi:10.1038/nature15374.

749 [125] Mori AS, Isbell F, Fujii S, Makoto K, Matsuoka S, Osono T. Low multifunctional
750 redundancy of soil fungal diversity at multiple scales. Ecol Lett 2016;19:249–59.
751 doi:10.1111/ele.12560.

752 [126] Soliveres S, van der Plas F, Manning P, Prati D, Gossner MM, Renner SC, et al.
753 Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality.
754 Nature 2016;536:456–9. doi:10.1038/nature19092.

755 [127] Mace GM. Whose conservation? Science 2014;345:1558–60.
756 doi:10.1126/science.1254704.

757 [128] Díaz S, Demissew S, Carabias J, Joly C, Lonsdale M, Ash N, et al. The IPBES conceptual
758 framework - connecting nature and people. Curr Opin Environ Sustain 2015;14:1–16.
759 doi:10.1016/j.cosust.2014.11.002.

760 [129] Whitmee S, Haines A, Beyrer C, Boltz F, Capon AG, Dias BF de S, et al. Safeguarding
761 human health in the Anthropocene epoch: report of the Rockefeller Foundation–
762 Lancet Commission on planetary health. Lancet 2015;386:1973–2028.

763 [130] Braat LC, de Groot R. The ecosystem services agenda: bridging the worlds of natural
764 science and economics, conservation and development, and public and private policy.
765 Ecosyst Serv 2012. doi:10.1016/j.ecoser.2012.07.011.

766 [131] Díaz S, Pascual U, Stenseke M, Martín-López B, Watson RT, Molnár Z, et al. Assessing
767 nature’s contributions to people. Science 2018;359:270–2.
768 doi:10.1126/science.aap8826.

769 [132] Bateman IJ, Harwood AR, Mace GM, Watson RT, Abson DJ, Andrews B, et al. Bringing
770 ecosystem services into economic decision-making: land use in the United Kingdom.
771 Science 2013;341:45–50. doi:10.1126/science.1234379.

772 [133] Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, et al.
773 Parallel declines in pollinators and insect-pollinated plants in Britain and the
774 Netherlands. Science 2006;313:351–4.

775 [134] De Palma A, Kuhlmann M, Bugter R, Ferrier S, Hoskins AJ, Potts SG, et al. Dimensions
776 of biodiversity loss: spatial mismatch in land-use impacts on species, functional and
777 phylogenetic diversity of European bees. Divers Distrib 2017;23:1435–46.
778 doi:10.1111/ddi.12638.

- 779 [135] Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, et al. Climate change
780 impacts on bumblebees converge across continents. *Science* 2015;349:177–80.
- 781 [136] Medan D, Torretta JP, Hodara K, de la Fuente EB, Montaldo NH, Fuente EB. Effects of
782 agriculture expansion and intensification on the vertebrate and invertebrate diversity
783 in the Pampas of Argentina. *Biodivers Conserv* 2011;20:3077–100.
784 doi:10.1007/s10531-011-0118-9.
- 785 [137] Winfree R, Reilly JR, Bartomeus I, Cariveau DP, Williams NM, Gibbs J. Species turnover
786 promotes the importance of bee diversity for crop pollination at regional scales.
787 *Science* 2018;359:791–3. doi:10.1126/science.aao2117.
- 788 [138] Aizen MA, Garibaldi LA, Cunningham SA, Klein AM. How much does agriculture
789 depend on pollinators? Lessons from long-term trends in crop production. *Ann Bot*
790 2009;103:1579–88. doi:10.1093/aob/mcp076.
- 791 [139] Giannini TC, Costa WF, Cordeiro GD, Imperatriz-Fonseca VL, Saraiva AM, Biesmeijer J,
792 et al. Projected climate change threatens pollinators and crop production in Brazil.
793 *PLoS One* 2017;12:e0182274. doi:10.1371/journal.pone.0182274.
- 794 [140] Stavert JR, Pattermore DE, Gaskett AC, Beggs JR, Bartomeus I. Exotic species enhance
795 response diversity to land-use change but modify functional composition. *Proc R Soc*
796 *London Ser B, Biol Sci* 2017;284:20170788. doi:10.1098/rspb.2017.0788.
- 797 [141] Sassen M, Sheil D, Giller KE. Fuelwood collection and its impacts on a protected
798 tropical mountain forest in Uganda. *For Ecol Manage* 2015;354:56–67.
799 doi:10.1016/j.foreco.2015.06.037.
- 800 [142] Chaudhary A, Burivalova Z, Koh LP, Hellweg S. Impact of forest management on
801 species richness: global meta-analysis and economic trade-offs. *Sci Rep* 2016;6:23954.
802 doi:10.1038/srep23954.
- 803 [143] Seidl R, Schelhaas M-J, Rammer W, Verkerk PJ. Increasing forest disturbances in
804 Europe and their impact on carbon storage. *Nat Clim Chang* 2014;4:806–10.
805 doi:10.1038/nclimate2318.
- 806 [144] Sullivan MJP, Talbot J, Lewis SL, Phillips OL, Qie L, Begne SK, et al. Diversity and
807 carbon storage across the tropical forest biome. *Sci Rep* 2017;7:39102.
808 doi:10.1038/srep39102.
- 809 [145] Delgado-Baquerizo M, Eldridge DJ, Maestre FT, Karunaratne SB, Trivedi P, Reich PB, et
810 al. Climate legacies drive global soil carbon stocks in terrestrial ecosystems. *Sci Adv*
811 2017;3:e1602008. doi:10.1126/sciadv.1602008.
- 812 [146] Chen W, Zhong J, Sun S, Xie Z, Zhou Y. Fuelwood collection depresses the seed-
813 dispersal service provided by rodents. *For Ecol Manage* 2017;406:53–60.
814 doi:10.1016/j.foreco.2017.10.008.
- 815 [147] Keesing F, Belden LK, Daszak P, Dobson A, Harvell CD, Holt RD, et al. Impacts of
816 biodiversity on the emergence and transmission of infectious diseases. *Nature*
817 2010;468:647–52. doi:10.1038/nature09575.
- 818 [148] Faust CL, McCallum HI, Bloomfield LSP, Gottdenker N, Dobson AP, Gillespie TR, et al.
819 Pathogen spillover during land conversion. *Ecol Lett* 2018;21:471–83.
820 doi:10.1111/ele.12904.
- 821 [149] Kilpatrick AM, Salkeld DJ, Titcomb G, Hahn MB. Conservation of biodiversity as a
822 strategy for improving human health and well-being. *Philos Trans R Soc Lond B Biol*
823 *Sci* 2017;372:20160131. doi:10.1098/rstb.2016.0131.
- 824 [150] Randolph S, Dobson A. Pangloss revisited: a critique of the dilution effect and the
825 biodiversity-buffers-disease paradigm. *Parasitology* 2012;139:847–63.

826 doi:10.1017/S0031182012000200.

827 [151] Faust CL, Dobson AP, Gottdenker N, Bloomfield LSP, McCallum HI, Gillespie TR, et al.
828 Null expectations for disease dynamics in shrinking habitat: dilution or amplification?
829 *Philos Trans R Soc Ser B, Biol Sci* 2017;372:20160173. doi:10.1098/rstb.2016.0173.

830 [152] Luis AD, Kuenzi AJ, Mills JN. Species diversity concurrently dilutes and amplifies
831 transmission in a zoonotic host–pathogen system through competing mechanisms.
832 *Proc Natl Acad Sci U S A* 2018;115:7979–84. doi:10.1073/pnas.1807106115.

833 [153] Suzán G, García-Peña GE, Castro-Arellano I, Rico O, Rubio A V., Tolsá MJ, et al.
834 Metacommunity and phylogenetic structure determine wildlife and zoonotic
835 infectious disease patterns in time and space. *Ecol Evol* 2015;5:865–73.
836 doi:10.1002/ece3.1404.

837 [154] Redding D, Atkinson P, Cunningham A, Iacono G Lo, Moses L, Wood J, et al. Impact of
838 global change on future Ebola emergence and epidemic potential in Africa. *BioRxiv*
839 2017:206169. doi:10.1101/206169.

840 [155] Tesla B, Demakovskiy LR, Mordecai EA, Bonds MH, Ngonghala CN, Brindley MA, et al.
841 Impacts of temperature on Zika virus transmission potential: combining empirical and
842 mechanistic modeling approaches. *BioRxiv* 2018. doi:10.1101/259531.

843 [156] Sandifer PA, Sutton-Grier AE, Ward BP. Exploring connections among nature,
844 biodiversity, ecosystem services, and human health and well-being: Opportunities to
845 enhance health and biodiversity conservation. *Ecosyst Serv* 2015;12:1–15.
846 doi:10.1016/j.ecoser.2014.12.007.

847 [157] Murray K, Olivero J, Roche B, Tiedt S, Guégan J. Pathogeography: leveraging the
848 biogeography of human infectious diseases for global health management. *Ecography*
849 2018;41:1–17. doi:10.1111/ecog.03625.

850 [158] Wood CL, McInturff A, Young HS, Kim D, Lafferty KD. Human infectious disease
851 burdens decrease with urbanization but not with biodiversity. *Philos Trans R Soc Ser*
852 *B, Biol Sci* 2017;372:20160122. doi:10.1016/S0140-6736(12)61689-4.

853 [159] IPCC. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II*
854 *and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate*
855 *Change*. Geneva, Switzerland: 2014.

856 [160] Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, et al. An
857 ecoregion-based approach to protecting half the terrestrial realm. *Bioscience*
858 2017;67:534–45. doi:10.1093/biosci/bix014.

859 [161] Kremen C, Merenlender AM. Landscapes that work for biodiversity and people.
860 *Science* 2018;362. doi:10.1126/science.aau6020.

861