

1 **Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and**
2 **climate change**

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16 **Global biodiversity is undergoing rapid declines, driven in large part by changes to land use and**
17 **climate. Global models help to understand the consequences of environmental changes for**
18 **biodiversity, but tend to neglect important geographical variation in the sensitivity of biodiversity**
19 **to these changes. Here we test whether biodiversity responses to climate change and land-use**
20 **change differ among biomes (geographical units that have marked differences in environment and**
21 **species composition). We find the strongest negative responses to both pressures in tropical**
22 **biomes and in the Mediterranean. A further analysis points toward similar underlying drivers for**
23 **the sensitivity to each pressure: we find greater reductions in species richness in the most human-**
24 **disturbed land uses and more negative predicted responses to climate change in areas of lower**
25 **climatic seasonality, and in areas where a greater proportion of species are near their upper**
26 **temperature limit. Within the land uses most heavily modified by humans, reductions in**
27 **biodiversity were particularly large in regions where humans have come to dominate the land**
28 **more recently. Our results will help to improve predictions of how biodiversity is likely to change**
29 **with ongoing climatic and land-use changes, suggesting particularly large declines in the tropics**
30 **where much future agricultural expansion is expected to occur. This finding could help to inform**
31 **the development of the post-2020 biodiversity framework, by highlighting the under-studied**
32 **regions where biodiversity losses are likely to be particularly large.**

33

34 **Keywords: biodiversity, biomes, climate change, global, land use, model**

35

36 **Introduction**

37

38 **Global biodiversity is continuing to decline despite increasing conservation efforts¹⁻⁴. On the other**
39 **hand, recent years have seen increases in people’s awareness of the scale of biodiversity change and**
40 **of the important roles that biodiversity plays, and also increases in funding for many aspects of**
41 **conservation work and in the designation of protected areas⁵. It is likely that the failure of these**

42 increased conservation efforts to improve the state of biodiversity is caused by a continuing increase
43 in the pressures on biodiversity⁵. There remain many gaps in our understanding of the effects of
44 biodiversity pressures globally⁶, gaps which need to be addressed to understand better how to
45 reduce the downward biodiversity trend.

46

47 Broad-scale models play a vital role in efforts to understand biodiversity change^{7,8}, although they
48 tend to focus on better-understood pressures⁸. Models can be used to attribute differences in
49 biodiversity to putative pressures, generally pointing to large impacts of climate and land-use
50 change^{1,2,4,9,10}. Currently, the available biodiversity data are patchy and biased¹¹, and so models are
51 necessary even to predict present-day biodiversity for many under-sampled species and locations.
52 For exploring the future, biodiversity models can be applied to different alternative scenarios in an
53 attempt to identify societal pathways that have a more positive outcome for biodiversity^{1,9,12,13}.

54

55 Most broad-scale biodiversity models neglect important geographical variation in the sensitivity of
56 biodiversity to human pressures. At the global scale, two main modelling approaches are used to
57 capture the effects of land-use and climate change, both of which use spatial patterns to predict
58 changes over time ('space-for-time substitution'). Responses of species to spatial variation in climate
59 are typically represented using species distribution models, which use statistical methods to relate
60 broad-scale data on a species' observed distributions to spatial variables describing the climate¹⁴
61 (and sometimes other aspects of the environment, including land use¹⁰). While species distribution
62 models represent the response of each species individually, and thus implicitly capture geographical
63 variation in sensitivity, it is rare to quantify that variation explicitly (although a recent study showed
64 that tropical terrestrial communities have a smaller climate safety margin¹⁵). Globally, responses to
65 land-use change have typically been assessed using statistical models that assess spatial differences
66 in biodiversity across land-use types based on collations of fine-scale data^{1,16}. These models
67 generally assume that differences in biodiversity among land uses are constant across the whole

68 terrestrial surface of the world^{1,16}, although some models have considered tropical-temperate and
69 taxonomic differences^{17,18}. A recent study based on time-series data showed more negative
70 biodiversity trends in tropical, temperate and Mediterranean biomes than in boreal areas or
71 drylands¹⁹, highlighting important geographical differences in biodiversity change, likely driven in
72 part by differences in the sensitivity of biodiversity to the major pressures.

73

74 There are several ecological and environmental differences among biomes that may cause
75 geographical differences in the sensitivity of biodiversity. First, certain biomes (principally those in
76 temperate areas) have been impacted by humans for a much longer period of time than others²⁰.
77 This long history of human use is likely to have already filtered out the most sensitive species even
78 from natural habitats²¹, which is likely to lead to a smaller response of biodiversity to contemporary
79 land-use change. Second, species have on average smaller range sizes in tropical biomes than
80 elsewhere²². Smaller range size has been associated with a disproportionate sensitivity to both land-
81 use change¹⁸ and climate change²³. Third, there is a greater proportion of dietary and habitat
82 specialist species found within tropical areas than in other biomes²⁴. Dietary and habitat specialists
83 have been shown to be most sensitive to both human land use^{25,26} and climate change²⁷. Fourth,
84 tropical species tend to have a slower 'pace of life', having smaller numbers of offspring and
85 maturing more slowly than other species²⁸. At least for birds, long generation time (which is
86 associated with a slow pace of life) has been shown to confer greater sensitivity to human land use²⁵
87 and to climate change²⁷. Fifth, the position of populations within species' geographical distributions
88 and climatic niche limits (i.e. the observed climatic conditions that species inhabit) varies across
89 biomes. Tropical biomes have a high proportion of populations living near the edge of their
90 distribution and at the upper end of species' thermal limits, while high latitudes have a greater
91 proportion of populations at lower thermal limits²⁹. Similarly, species' upper and lower moisture
92 limits will most often be reached in moist and dry biomes, respectively. In general, species near the
93 edges of their geographical distribution have been shown to be more sensitive to environmental

94 changes³⁰. For bumblebees, recent climate change has been shown to impact most strongly those
95 communities where a greater proportion of species are near the upper temperature limit of their
96 observed distribution⁴. Land uses heavily modified by humans tend, on average, to be hotter and
97 drier than natural habitats, which has led to shifts in ecological assemblages by favouring species
98 associated with these climatic conditions^{31–33}. The generally reduced canopy cover in heavily
99 modified land uses means that there is also less of a buffering of temperature extremes compared to
100 natural habitats³⁴. Together, these differences in local climatic conditions in heavily modified land
101 uses are favouring species that can tolerate greater extremes of climate (i.e., hotter maximum
102 temperatures, colder minimum temperatures, and wetter and drier precipitation extremes)^{31,32,35}.
103 Finally, the very existence of biomes, with their widely differing vegetation structure, is caused by
104 differences in climatic properties. In particular, tropical biomes have a lower degree of seasonality
105 than temperate and high-latitude biomes. Species that have evolved to tolerate the narrower range
106 of climatic and other environmental conditions within tropical biomes are likely to be more sensitive
107 to environmental changes than those that evolved in areas with greater environmental
108 variability^{36,37}. Indeed, responses to both climate and land-use change have been shown to be most
109 negative in areas of low climatic seasonality or among species inhabiting these areas^{18,27,38}.

110

111 Here we ask whether sensitivity of biodiversity to climate and land-use change differs across biomes.
112 We focus on species richness as a measure of biodiversity, which is easy to measure but captures
113 only some of the many dimensions of biodiversity³⁹ (in the Extended Data, we also present
114 responses to land use of total community abundance and a measure based on the endemism of
115 species in the community). We further test the extent to which variation in the sensitivity of species
116 richness is correlated with environmental and ecological differences among biomes that are
117 hypothesised to influence sensitivity (climatic seasonality, average position of species within their
118 climatic niche limits, and length of human land-use history). We hypothesise that tropical biomes
119 will show the most negative responses because they harbour species known to be most sensitive on

120 average to both pressures (slow-breeding specialists with small range sizes, which have evolved
121 under more stable climatic conditions with a shorter history of land-use change), and because
122 populations in tropical biomes tend to be nearer their upper thermal limits than elsewhere.
123 Responses to land-use change may also be disproportionately negative in biomes with relatively
124 drier climates because populations will tend to be closer to species' lower moisture limits.

125

126 To assess sensitivity to land-use change, we used mixed-effects models to compare species richness
127 among land uses, using data from the PREDICTS database (Extended Data 1), which contains samples
128 of communities from different land uses, mostly collected between 2000 and 2013⁴⁰. Land uses
129 considered were: primary vegetation (natural habitat, not known to have been destroyed in the
130 past), secondary vegetation (natural habitat, recovering after being destroyed by human actions or
131 extreme natural events), plantation forest (areas used to grow woody crops), cropland (areas used
132 to grow herbaceous crops, including for livestock fodder), and pasture (areas used to graze
133 livestock). In the final models, plantation forests and croplands were grouped into a single
134 'Harvested agriculture' category. The hierarchical structure of the land-use analysis means that
135 differences in biodiversity among land uses are estimated within individual studies that span limited
136 climatic gradients. Our estimates of likely sensitivity to climate change were based on a published
137 ensemble of future projections of climate effects on species distributions⁹ between a 1960-1990
138 baseline and the future period 2061-2080 (assuming intermediate 'limited' dispersal ability; see
139 Methods). We calculated sensitivity as the predicted change in grid-cell species richness per degree
140 Celsius of expected mean temperature increase. The use of different input datasets and methods to
141 estimate land-use and climate sensitivity was necessitated because we currently lack the data
142 required to consider both pressures simultaneously⁹, and because climate and land use operate on
143 biodiversity at very different scales. Land-use sensitivity was estimated using observed responses,
144 whereas climate sensitivity was estimated based on future predicted changes because global
145 datasets do not yet exist to allow a broad assessment of sensitivity to observed climate change.

146 Nevertheless, for both pressures we express biodiversity changes in terms of species richness, so
147 relative sensitivities across biomes should be comparable.

148

149 **Results**

150

151 Spatial differences in biodiversity among land uses varied strongly across biomes (Figure 1; Extended
152 Data 2). In secondary vegetation, species richness was more than 40% lower on average than in
153 primary vegetation in the Mediterranean biome, around 10% lower in tropical forests and grasslands
154 (although not significantly so in the latter case), and similar or even higher than in primary
155 vegetation in temperate forests, temperate grasslands and drylands (Figure 1). In pastures, species
156 richness was between 20 and 40% lower compared to primary vegetation in tropical forests and
157 grasslands and in the Mediterranean biome, 17% lower in temperate grasslands, and similar or even
158 higher than primary vegetation in temperate forest and drylands (Figure 1). Finally, for harvested
159 croplands (woody plantations and herbaceous croplands), average species richness reductions were
160 between 20 and 40% for the tropical forest, temperate grassland and Mediterranean biomes,
161 between 15 and 20% for tropical grasslands and temperate forests respectively, and around 10% for
162 drylands (although not a significant reduction in the last case; Figure 1). Alternative groupings of
163 either the land-use or biome classification did not markedly improve the fit of the models to the data
164 (Extended Data 3 & 4). Patterns were similar for two alternative measures of biodiversity: total
165 community abundance and community-average range size (Extended Data 5 & 6).

166

167 The sensitivity of vertebrate biodiversity to a 1°C increase in annual average temperature also varied
168 widely across biomes (Figure 2; climate sensitivity was estimated by projecting biodiversity change
169 against projected climate change between a 1960-1990 baseline and the future period 2061-2080,
170 and then dividing by projected temperature change across the same time period). The most
171 sensitive biomes were tropical forests, tropical grasslands and Mediterranean areas, with median

172 projected local declines of between 10 and 13% in species richness for each degree of climate
173 warming (Figure 2). Drylands showed intermediate sensitivity, with estimated declines of 5% of
174 species for every degree increase in temperature. Finally, the biomes estimated to have the least
175 sensitivity to climate change were temperate forests (median of 2% loss per degree of climate
176 warming), temperate grasslands (1.5% loss) and boreal forests (1% gain). Results were qualitatively
177 very similar regardless of the emissions scenario assumed, but absolute sensitivities were less
178 negative in most cases for the low-emissions (RCP 2.6) compared to the high-emissions (RCP 8.5)
179 scenario: tropical forests = -14%; tropical grasslands = -9.7%; Mediterranean = -6.1%; Drylands = -
180 2.8%; temperate forests = +1.4%; temperate grasslands = +1.4%; boreal forests = +7% (Extended
181 Data 7).

182

183 Three biomes stood out for having large biodiversity reductions in land uses heavily modified by
184 humans and a high sensitivity to climate warming: tropical forests, tropical grasslands and
185 Mediterranean environments. These biomes showed an approximately 30% reduction in species
186 richness in the most modified land uses compared to primary vegetation, and a 10-12% average
187 local loss of species for each degree of climate warming (Figure 3). In contrast, the other biomes
188 showed smaller sensitivities that were less consistent for land-use change and climate change
189 (Figure 3).

190

191 Exploratory analyses suggested that both land-use and climate sensitivity may be associated with
192 the same underlying factors (Table 1; Figure 4, where the sensitivity of biodiversity to land use for
193 any given value of an explanatory variable is inferred as the relative species richness in disturbed
194 land uses compared to the species richness in primary vegetation; Figure 5). The sensitivity of
195 biodiversity to both climate change and to land use was greatest in areas with the lowest seasonality
196 of both temperature and precipitation (Figure 4a, b; Figure 5a, b), and where a higher proportion of
197 species were near the upper edge of their observed thermal niche (although for land use this was

198 only true for harvested agriculture, not pasture; Figure 4c; Figure 5c). Contrary to our predictions,
199 reductions in species richness in the most human-modified land uses (especially pastures) were
200 greatest in areas where a higher proportion of species were near the centre of their precipitation
201 niche (Figure 4d). As expected, responses to land use were strongest in areas that have experienced
202 land-use impacts more recently (Figure 4e; this explanatory variable was not expected to have an
203 effect on sensitivity to climate change, and so was not included in the analysis of climate responses).
204 Although the explanatory variables helped to explain variation in sensitivity to land use among
205 biomes, there remained a significant interaction between land use and biome in explaining species
206 richness ($\chi^2_{18,72} = 170$, $P < 0.001$). Owing to the need to use separate modelling paradigms for climate
207 and land-use effects, we were not able to consider here any effects on biodiversity of interactions
208 between land-use change and climate change, nor whether the effects of such interactions were
209 strongest in certain biomes. This question should be addressed in future studies.

210

211 **Discussion**

212

213 Our results demonstrate that species' sensitivity to climate and land-use change varies
214 geographically, and that high sensitivity to these two pressures coincides in the same parts of the
215 world. The existence of such strong geographical variation implies that attempts to extrapolate
216 inferences about the impact of climate and land-use change from well-studied areas^{1,4,41} to other
217 parts of the world may be misleading. In particular, we find that tropical biomes (forests and
218 grasslands) and the Mediterranean biome have a particularly high sensitivity to both pressures. We
219 caution that quantitative comparisons of responses to climate change versus land-use change should
220 not be made because of the very different scales at which these pressures operate, and because of
221 the different methods used to assess their impacts. Nevertheless, the relative sensitivity of biomes
222 to each pressure should be unaffected by the different methods used. Our results support previous
223 studies that have shown greater reductions in biodiversity in heavily human-modified land uses in

224 tropical compared to temperate areas^{17,18}, but go further in showing differences among individual
225 biomes. Our results are also consistent with a recent study showing similar geographical variation in
226 historical biodiversity change using time-series data¹⁹.

227

228 The explanatory variables we considered help to explain geographical variation in the sensitivity of
229 biodiversity, but do not completely explain the observed differences in biodiversity sensitivity among
230 biomes. As expected, sensitivity to both pressures was highest in places with low climatic
231 seasonality, probably because species confined to less-seasonal environments are not as resilient to
232 environmental changes^{18,27,36}. Sensitivity was also high in areas where a majority of species approach
233 the hottest temperatures within their observed distributions (for land use this was true for
234 harvested agriculture, but not for pastures used for livestock grazing). The disproportionate
235 biodiversity reductions in agriculture in areas dominated by species near their upper temperature
236 limits probably results from the fact that heavily human-modified land uses tend to have hotter
237 maximum temperatures than natural habitats⁴². The results with regard to precipitation were more
238 equivocal. Unexpectedly, there were greater biodiversity reductions in the most modified land uses
239 where there were more species approaching the centre of their precipitation niche (Figure 4).
240 Precipitation patterns, and resulting changes in moisture availability, are not predicted to change as
241 consistently and monotonically as temperature either with regional climate change⁴³ or with human
242 land use^{33,44}. As expected, the effects of human land use were strongest in areas that have
243 experienced a relatively short history of land-use disturbance. This is consistent with suggestions
244 that a longer period of disturbance filters out the most sensitive species from ecological
245 communities rendering the remaining communities less sensitive to further disturbance²¹.

246

247 Future efforts to model broad-scale biodiversity changes should consider geographical variation in
248 the sensitivity of biodiversity. Previous models, especially those focusing on the effects of land-use
249 change, have generally ignored geographical variation in sensitivity altogether^{1,9,16}. The existence of

250 wide differences among regions in the sensitivity of biodiversity to environmental changes has
251 important implications for predictions of future biodiversity. Tropical biomes are predicted to
252 experience most future agricultural expansion⁴⁵, and to be among the first areas to experience
253 unprecedented temperatures as a result of climate change⁴⁶. The disproportionate sensitivity of
254 tropical biodiversity that we find thus implies that future biodiversity changes may be larger than
255 suggested by most previous models.

256

257 The disproportionate sensitivity of tropical and Mediterranean biomes points to important gaps in
258 our understanding of the ecology and conservation of these areas⁴⁷. Data on biodiversity are patchy,
259 and often show strong bias toward temperate forests and grasslands^{11,19}. Our results suggest that
260 the under-studied biodiversity of tropical biomes is most sensitive to major environmental changes,
261 supporting previous research that has highlighted the sensitivity of tropical biodiversity to land-use
262 change^{17,18}. Tropical and Mediterranean areas are the richest in overall numbers of species⁴⁸ and in
263 numbers of endemic species⁴⁹, and so higher proportional losses of species in these biomes will
264 translate into even larger losses in absolute terms. We need more research to understand better the
265 causes and consequences of the sensitivity of tropical and Mediterranean biodiversity. The growing
266 availability of databases describing changes in biodiversity over time will likely allow progress in this
267 area, although such databases still under-represent tropical areas⁵⁰.

268

269 Broad-scale models of the response of biodiversity to both land-use and climate change have a
270 number of important known limitations. Both model types ignore important ecological effects such
271 as biotic interactions and adaptation to environmental changes⁵¹, and synthetic models of land-use
272 impacts may generally underestimate sensitivity because of the difficulty of establishing baseline
273 conditions without human influence⁵². To affect the qualitative patterns of biodiversity sensitivities
274 across biomes, any model artefacts would have to affect disproportionately certain biomes over
275 others. This may be true for some of the ecological limitations of the models. For example, biotic

276 interactions are thought to be relatively more important in shaping biodiversity in tropical than
277 temperate latitudes⁵³. A failure to account for biotic interactions and other factors limiting species'
278 distributions will influence the inference of climatic niche limits, which determine expected
279 responses to climate change in the models. Unfortunately, data on true physiological limits are
280 available for too few species to include in an analysis such as is presented here³⁵, but future studies
281 should explore this question further. Our results suggest an important role of climatic variation in
282 explaining the observed sensitivity of biomes. However, in the correlative analysis we present here,
283 we cannot rule out the possibility that climate determines the distribution of biomes, but that some
284 other feature of biomes (for example, vegetation differences or differences in species composition
285 unrelated to climate) determines sensitivity. Data limitations are another potential source of bias, if
286 data quantity or quality differ markedly across biomes. For assessing climate impacts, we used
287 globally consistent data on the extent of species ranges^{54,55}, rather than opportunistically-collected
288 data that tend to be geographically biased¹¹. Nevertheless, differences in the accuracy of these
289 range estimates across biomes are very likely. Similarly, the data used to assess responses to land
290 use⁴⁰ were compiled to be as geographically representative as possible, and biomes were sampled
291 roughly in proportion to their area⁵⁶. Yet, as with the data on species' ranges, we cannot rule out
292 geographical variation in data quality. We focus in this study on species richness as a biodiversity
293 measure that can be estimated by both the modelling approaches we use, while acknowledging that
294 species richness cannot capture the many dimensions of biodiversity³⁹. We show that similar
295 patterns in land-use responses are obtained for two other measures based on abundance or species
296 endemism (Extended Data 5 & 6), but future modelling work should aim to represent a broader
297 suite of biodiversity metrics. Finally, it was not possible to isolate completely observed responses to
298 climate change and land-use change, given that both pressures are operating within complex real-
299 world ecological systems. While the hierarchical structure of the models of land-use responses, with
300 differences in biodiversity fitted within individual studies that span relatively small climatic

301 gradients, should factor out most effects of regional climate change, climate inevitably plays a role in
302 shaping observed responses (indeed, we show this to be the case in our analyses).

303

304 In conclusion, we have shown that biodiversity in tropical and Mediterranean biomes is
305 disproportionately sensitive to both land-use and climate change, which has important implications
306 for conservation in these areas. Further work is needed to incorporate differences in sensitivity into
307 broad-scale models of biodiversity changes. Moreover, results such as these can contribute to the
308 discussions around the post-2020 biodiversity framework⁵⁷, by highlighting the disparity in how
309 environmental changes impact biodiversity in different geographic regions of the world and showing
310 a disproportionate sensitivity of the under-studied tropics. Importantly, our results suggest that the
311 high level of land-use and climate change expected in tropical biomes in the coming decades will
312 affect ecological communities that are particularly sensitive to these environmental changes, and
313 thus biodiversity declines may be stronger than previous models have implied.

314

315 **Methods**

316

317 *Defining biomes*

318

319 There are several schemes by which the world can be divided into biogeographical units, differing in
320 the set of species they contain^{58–60}. A recent global study showed marked changes in species
321 composition across the boundaries of ecoregions⁶⁰, which are a nested sub-unit of biomes⁶¹. For
322 understanding large-scale differences in the sensitivity of biodiversity to environmental changes, a
323 coarser division into biomes is more practical than an ecoregion-based division, given the paucity of
324 biodiversity data for most ecoregions^{11,40}.

325

326 We derived estimates of the spatial distribution of biomes from The Nature Conservancy's map of
327 global ecoregions⁶². This map divides the world into 16 different biomes, 11 of which we considered
328 in this study: Tropical and Subtropical Moist Broadleaf Forests; Tropical and Subtropical Dry
329 Broadleaf Forests; Tropical and Subtropical Coniferous Forests; Temperate Broadleaf and Mixed
330 Forests; Temperate Conifer Forests; Boreal Forests/Taiga; Tropical and Subtropical Grasslands,
331 Savannas and Shrublands; Temperate Grasslands, Savannas and Shrublands; Montane Grasslands
332 and Shrublands; Mediterranean Forests, Woodlands and Scrub, and Deserts and Xeric Shrublands.
333 Biomes excluded owing to a paucity of biodiversity data were: Tundra; Mangroves; Flooded
334 Grasslands and Savannas; Inland Water; and Rock and Ice. Although a newer version of this map is
335 available⁶¹, it is unlikely that its use would have made a noticeable difference to the broad-scale
336 patterns we report here. The biome classification is already built into the PREDICTS (Projecting
337 Responses of Ecological Diversity in Changing Terrestrial Systems) database⁶³, which we used to
338 assess responses to land-use change (see below). For the assessment of sensitivity to climate
339 change, we simply overlaid the map of biomes with the projections of ecological community change
340 under future climate scenarios (see below).

341

342 *Framework for modelling biodiversity responses*

343

344 We used mixed-effects models to estimate differences in biodiversity among different land-use
345 types, and species distribution models to project likely biodiversity responses to climate change.
346 Treating the effects of land use and climate in separate models is often necessitated by the fact that
347 these pressures operate at very different spatial scales, and because the data documenting
348 responses to the two pressures don't transcend the different scales (data on species distributions
349 are typically not accurate enough to capture effects of land use, while data on the effects of land use
350 do not span large enough climatic gradients to capture the effects of regional climate change)⁹. In
351 some regions, distribution and land-use data are sufficiently accurately resolved that it is possible to

352 include the effects of land use directly into species distribution models¹⁰. Alternatively, for some
353 well-known taxonomic groups, expert knowledge can be used to predict species' responses to land-
354 use change in species distribution models⁶⁴. For global multi-clade analyses, however, it remains
355 necessary to use separate modelling paradigms⁹. The difference in methods used means that the
356 absolute estimates of responses to each pressure are not directly comparable. Nevertheless, the
357 relative sensitivities of biodiversity to each pressure across biomes should be unaffected. All input
358 datasets are detailed in Extended Data 8.

359

360 *Estimating biodiversity response to land use*

361

362 We obtained data describing differences in biodiversity among land-use types from the database of
363 the PREDICTS Project⁶³. This database is a global collation of published comparisons of ecological
364 assemblages across different types of land use, both natural and human-dominated⁵⁶. We excluded
365 any studies that focused on a single species, because these cannot be expected to give a reliable
366 estimate of species richness¹. Original samples were collected in the field between 1984 and 2013
367 (95% of locations were sampled since 2000). The PREDICTS database is structured such that data
368 from each published Source may be divided into one or more Studies, distinguished if the data were
369 collected using a different sampling protocol. Studies may be divided into one or more Spatial
370 Blocks, within which one or more distinct Sites are sampled. The data for each Site consists of a list
371 of taxa, in most cases with recorded abundances, but sometimes just simple presence or absence (a
372 very small number of records give the overall species richness of a group of species). The
373 predominant land use at each site was classified based on the description of the sampled habitat as
374 given in the original source publication, as follows⁵⁶: primary vegetation describes natural habitat
375 with no record of historical destruction of the vegetation (including remnant patches in urban
376 areas); secondary vegetation describes natural habitat that is known to have been destroyed
377 historically, either by human actions or extreme natural events, but which is now recovering to its

378 natural state; plantation forests are areas used for cultivation of woody crops (such as fruit, oil-palm,
379 coffee or timber plantations); cropland is land used for cultivating herbaceous crops (including
380 fodder for livestock); pastures are areas regularly or permanently used for livestock grazing; and
381 urban areas are those used for human settlements or civic amenity, or areas where the vegetation
382 has been transformed for human recreation. We excluded urban land use in this study, because
383 there were too few urban samples to allow a consideration of biome differences. The PREDICTS
384 database contains data for 47,044 species of vertebrates, invertebrates, plants and fungi⁴⁰. The
385 dataset analysed in this study were from 20,585 sites in 11 out of 14 of the world's terrestrial biomes
386 (the tundra, flooded grasslands and mangroves biomes were discarded from the analysis because
387 they were represented by too few sites) and from 91 of the world's countries.

388

389 We used mixed-effects models⁶⁵ to fit differences in sampled species richness as a function of land
390 use and biome. We modelled species richness using generalised linear mixed-effects models with a
391 Poisson distribution of errors. We included a random intercept of study identity to account for the
392 differences in sampling protocols among studies, and to ensure that comparisons were made within
393 studies that spanned relatively small environmental gradients, thus excluding most effects of climate
394 change on observed biodiversity differences¹. We additionally included a random intercept of site
395 identity (i.e. an observation-level random intercept), to account for the over-dispersion present⁶⁶.

396 Some combinations of land use and biome are poorly sampled, so using the finest divisions of these
397 variables (i.e. all 11 biomes and all 5 land uses) would reduce the potential generality of our findings.

398 Therefore, we initially sought the most parsimonious groupings of land use and biome for explaining
399 observed differences in species richness. For example, croplands and pastures could be grouped
400 together as a single 'agriculture' class, or tropical conifer forest, tropical moist broadleaf forest and
401 tropical dry broadleaf forest could be grouped as 'tropical forest'. Using the finest division of biomes,
402 we compared different groupings of land use. Separately, using the finest division of land uses, we
403 compared different groupings of biome. For all four sets of models, we selected the one with the

404 lowest AIC value as the best-fitting. We then fit a final model of species richness using the
405 combination of the best-fitting land-use grouping and the best-fitting biome grouping. This
406 procedure allowed us to maximise the generality of our results, without unduly sacrificing
407 explanatory power. We focus in the main text on changes in species richness, which can be
408 measured more-or-less consistently with respect to both land-use change and climate change.
409 However, species richness does not capture all facets of biodiversity³⁹. To test whether the
410 estimated sensitivity of biodiversity to land-use change was influenced by choice of biodiversity
411 metric, we repeated the models also for the total sampled abundance of each community¹, and the
412 average range size of species within the community (weighted by species' abundance)¹⁸. The latter
413 metric captures the degree of endemism of species within each community, and so may be a more
414 sensitive metric of the effects of land use¹⁸. We estimated the average range size of species within
415 each community using published estimates already calculated for the communities sampled in the
416 PREDICTS database (DOI: 10.6084/m9.figshare.7262732.v1)¹⁸. These estimates were originally
417 made¹⁸ by: 1) taking all records for each species from the Global Biodiversity Information Facility
418 (GBIF) database; 2) mapping these records onto a 110-km equal-area (Behrmann projection) grid; 3)
419 summing the total area of the occupied grid cells (which should be relatively insensitive to
420 geographical outliers among the biodiversity records); and 4) calculating the average area-of-
421 occupancy across all species within any sampled community in the PREDICTS database, weighted by
422 species' abundance (see ref. 18 for full details). We assumed that the GBIF records would be
423 adequate for estimating broad relative differences in species' area of occupancy (indeed, previous
424 analyses have shown that effects of these range size estimates on responses to land use are
425 relatively robust to alternative methods of calculation¹⁸).

426

427 *Estimating biodiversity sensitivity to climate change*

428

429 We obtained our estimates of the predicted response of biodiversity (vertebrate assemblage species
430 richness) to climate change from published projections based on species distribution models⁹. These
431 projections were derived using species' distribution data for 20,938 terrestrial vertebrate species
432 from published extent-of-occurrence range maps^{54,55}. While such maps tend to underestimate the
433 full extent of species' ranges while overestimating local occupancy⁶⁷, they are the best data with
434 which to capture broad-scale responses to climate change of a large number of species⁹. The
435 published distribution models⁹ used an ensemble of five modelling algorithms (DOMAIN, BIOCLIM,
436 Maxent, Generalised Linear Models and Random Forests), fit using the dismo package Version 1.1-4
437 in R. For any given location (10-km grid cell) we took the median of the projections across the
438 ensemble. Each range map was converted to a raster at 10-km spatial resolution, using a cylindrical
439 equal-area projection. Each occupied cell was considered a presence record in the distribution
440 models. The Maxent algorithm drew 10,000 background points from all grid cells (occupied and
441 unoccupied) within realm-biome combinations containing at least one presence record. For the
442 Generalised Linear Models and Random Forests, pseudo-absence records were drawn at random
443 from unoccupied cells within realm-biome combinations that also contain a presence record. The
444 distribution of each species was modelled as a function of four climatic variables shown to have
445 good explanatory power for vertebrate distributions: minimum temperature of the coldest month,
446 total annual precipitation, growing degree days and water balance. Distribution models were
447 evaluated against a reserved 20% of records, using the Area Under the Receiver Operating
448 Characteristic Curve (AUC) statistic; all models with an AUC > 0.8 were retained. The distribution
449 models were projected onto current and future climate estimates under the Representative
450 Concentration Pathways (RCP) scenarios⁶⁸ derived from the Worldclim Version 1.4 database.
451 Continuous predictions from all models were converted to a binary prediction of presence or
452 absence using a threshold that minimizes the difference between model sensitivity and specificity. In
453 the original paper in which these projections were presented⁹, three dispersal scenarios were used:
454 no dispersal, unlimited dispersal, and intermediate 'limited' dispersal. In this study, we focused on

455 the projections under 'limited' dispersal. Birds and mammals were assumed to be able to expand
456 their ranges by 3 km per year, and reptiles and amphibians by 0.5 km per year (see ref. 9 for full
457 details of the distribution modelling and projection methods). To estimate the sensitivity of
458 ecological communities to climate change across space, here we took the future projections (from a
459 1960-1990 baseline until the period 2061-2080) of percentage change in the number of species
460 present in each location (negative for species loss, positive for species gain) divided by the number
461 of degrees by which annual average temperature is expected to increase within the same timeframe
462 and under the same scenario (negative for projected decreases in temperature). We obtained the
463 latter estimates of change in annual mean temperature also from the WorldClim Version 1.4
464 database. Because biodiversity may show a non-linear response to climate warming, we tested the
465 robustness of the results to using two different RCP climate scenarios with varying overall projected
466 temperature increase: the RCP2.6 scenario, which is characterised by strong climate-mitigation
467 efforts, and RCP8.5, which represents a high-emissions scenario.

468

469 *Explaining biome differences in biodiversity sensitivity to land use and climate change*

470

471 In order to attempt to explain any observed differences in biodiversity sensitivity among biomes, we
472 considered a set of factors that differ among biomes and that have been hypothesised or shown to
473 influence differences in biodiversity among land uses or the response of species to climate change:
474 climate (temperature and precipitation) seasonality; the community-average position of species with
475 respect to their observed climatic (temperature and precipitation) niche limits; and the number of
476 years since the landscape was substantially impacted by human land-use activities. We initially
477 considered two other variables (the average proportion of habitat specialists within a community;
478 and the average range-size of species within a community). However, these variables were strongly
479 correlated with others and can be less reliably measured across the breadth of species considered in
480 this study.

481

482 Temperature and precipitation seasonality estimates were derived directly from WorldClim Version
483 1.4⁶⁹ (bioclimatic variables, Bio4 and Bio15, respectively) at 10-arc-minute spatial resolution.

484

485 Thermal and precipitation position indices were estimates of the community-average position of
486 species within their observed (i.e. realised) thermal and precipitation niches (i.e. a value of 0 would
487 indicate that all species were at their lower thermal or precipitation niche limits, i.e. cold and dry
488 limits, respectively; whereas a value of 1 would indicate that all species were at their hot or wet
489 niche limits). For each vertebrate species (species that have relatively reliable information on broad-
490 scale distribution), we estimated position within niche limits based on the minimum and maximum
491 conditions experienced throughout its distribution. Estimates of species distributions were the
492 extent-of-occurrence maps as described above. We did not use GBIF data (see above) to estimate
493 position within species' thermal and precipitation niches, because the patchy and biased nature of
494 the GBIF data¹¹ means that estimates of the precise position of range (and thus climatic niche)
495 boundaries are likely to be unreliable. We processed the distribution maps by: 1) excluding areas
496 where species are considered to be vagrant, or present only during migration; 2) excluding areas
497 outside the known elevational limits for the species; and 3) resampling the maps to a 10-km
498 cylindrical equal-area (Behrmann) spatial projection. The grain size of 10 km was selected as a
499 reasonable trade-off between precision and map accuracy. We defined the limits of a species
500 thermal niche as the minimum across its distribution of the minimum temperature of the coldest
501 month (bioclimatic variable 'bio6' from WorldClim Version 1.4⁶⁹) and the maximum across its
502 distribution of the maximum temperature of the warmest month ('bio5'). For precipitation, we
503 defined niche limits as the minimum across a species' distribution of the total precipitation in the
504 driest month ('bio14') and the maximum across the distribution of the total precipitation in the
505 wettest month ('bio13'). For a given location, we then calculated a species' thermal or precipitation
506 position as the average across the year of the monthly average maximum temperature or monthly

507 total precipitation values – also obtained from WorldClim Version 1.4⁶⁹ – after rescaling the raw
508 climatic variables to take values of 0 and 1 at species’ estimated niche limits. Finally, for every
509 location (10-km grid cells), we estimated the community-average thermal and precipitation position
510 indices as the average of the species-level values for all species potentially occurring within a grid
511 cell, with potential occurrence defined using the same distribution maps as before. We resampled all
512 climatic variables to the same 10-km equal-area projection as the distribution maps.

513

514 Our estimates of the length of time that a landscape had been substantially impacted by human
515 land-use activities was based on the HYDE reconstruction of historical land use⁴⁵. Specifically, we
516 calculated the number of years since each 0.5° grid cell is estimated to have first surpassed 30%
517 conversion of natural habitat to human-dominated uses (croplands, pastures and urban
518 environments). A 30% threshold has been suggested previously to represent a level at which
519 significant effects of fragmentation will begin to be felt for some species⁷⁰, and the time since this
520 level of conversion occurred has been shown previously to explain responses of biodiversity to land
521 use¹.

522

523 To test the importance of these factors in explaining land-use responses, we fit more complex
524 mixed-effects models of species richness as a function not only of land use and biome interactions,
525 but also of land use in interaction with the additional explanatory variables. We fit the additional
526 explanatory variables and their interactions with land use as fixed effects in the model, allowing
527 quadratic terms for the continuous explanatory variables because we hypothesised that the
528 responses would likely be non-linear. The random-effects structures were the same as for the earlier
529 models of land-use responses: site identity nested within study identity. We used backward stepwise
530 model selection to exclude non-significant terms (likelihood-ratio test, $\alpha = 0.05$).

531

532 To explain geographical variation in the sensitivity of vertebrate assemblages to climate change, we
533 modelled the estimates of percent species richness change per degree of temperature change (see
534 above) as a function of the same explanatory variables as used for analysing land-use responses. We
535 initially fit these models using ordinary least squares regression, allowing only linear terms for the
536 continuous variables, because over-fitting was likely with such a large sample (all terrestrial 10-km
537 grid cells). Since species richness, species richness change and all of the explanatory variables are
538 likely to show strong, positive spatial autocorrelation, we repeated all of the models using spatial
539 autoregression (using the lagsarlm function in the spdep package Version 1.1-3⁷¹ in R).

540

541 **Author Contributions**

542

543 T.N. and P.O conceived and designed the study and carried out the main analyses. A.E. and J.J.W.
544 input analytical tools and important insight on aspects of the work. T.N. wrote the final manuscript,
545 with substantial inputs from all authors.

546

547 **Data availability**

548

549 All data required to run the analyses are published on FigShare:

550 <http://doi.org/10.6084/m9.figshare.12674372>.

551

552 **Code availability**

553

554 All code used in the analyses is publicly available at:

555 <https://github.com/timnewbold/BiomeSpecificResponsesPublic>.

556

557 **Competing Interests**

558

559 The authors declare no competing interests.

560

561 **Acknowledgments**

562

563 This work was supported by a Royal Society University Research Fellowship to T.N. J.J.W. and A.E.

564 were supported by research grants from the Royal Society, awarded to T.N. T.N. was also supported

565 by grants from the Natural Environment Research Council (NE/R010811/1) and the Leverhulme Trust

566 (RPG-2015-073).

567

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720

721 **Figure Legends**

722

723 **Figure 1. Differences in species richness among land-use types, across different biomes:** a) Tropical forest; b)
724 Tropical grasslands; c) Drylands; d) Mediterranean; e) Temperate forest; and f) Temperate grassland. Plots
725 show the percentage change in species richness compared to primary vegetation (PV), in secondary vegetation
726 (SV), pasture (PAS) and areas of harvested agriculture (woody plantations and herbaceous croplands; HARV).
727 Error bars show 95% confidence intervals. Sample sizes at the bottom of each panel refer to the number of
728 sites in each combination of land use and biome. The most complex models were the best fitting – including
729 the finest division of both biome and land use, and their interaction (Extended Data 3 & 4). However, because
730 relatively few sites were sampled in some biomes and thus to maximise the number of biomes for which we
731 could make a reasonably confident inference of land-use responses, we show here the results based on a
732 coarser division of both biome and land use. The model with coarser land-use and biome groupings still
733 showed a relatively similar fit to the data compared to the most complex models (Species richness: $R^2_{\text{conditional}} =$
734 0.61 , $R^2_{\text{marginal}} = 0.025$).

735

736 **Figure 2. Predicted sensitivity of biodiversity to climate change across biomes.** Shown is the predicted
737 percentage change in vertebrate species richness for each °C of climate warming expected under the RCP 8.5
738 scenario. Results were qualitatively very similar under the lower-emissions RCP2.6 scenario (Extended Data 7).
739 Biomes considered were tropical forest (Trop F, total number of 10-km grid cells, $n_{\text{cells}} = 236,527$), tropical

740 grasslands (Trop G, $n_{\text{cells}} = 203,690$), drylands (Dry, $n_{\text{cells}} = 279,178$), Mediterranean (Med, $n_{\text{cells}} = 31,630$),
741 temperate forest (Temp F, $n_{\text{cells}} = 170,680$), temperate grasslands (Temp G, $n_{\text{cells}} = 144,369$) and boreal forest
742 (Bor F, $n_{\text{cells}} = 168,005$). Thick horizontal black lines show median values across all grid cells within the biome,
743 boxes extend to the first and third quartiles, and whiskers to $1.5 \times$ the inter-quartile range.

744

745 **Figure 3. Relationship across biomes between climate and land-use sensitivity.** We estimate climate
746 sensitivity as the predicted percentage species richness change of the average ecological assemblage under
747 1°C of warming under the RCP 8.5 scenario. We estimated land-use sensitivity as the average percentage
748 difference in species richness between human-dominated land uses (plantation forests, cropland and pasture)
749 and primary vegetation.

750

751 **Figure 4. Patterns of species richness among land-use types moderated by putative explanatory variables.**
752 Shown are the results of mixed-effects models that fit the interaction between land use and each explanatory
753 variable: a) temperature seasonality, b) precipitation seasonality, c) average proximity of species in an
754 assemblage to lower (value = 0.0) or upper (value = 1.0) monthly temperature limits based on species'
755 observed distributions; d) average proximity of species in an assemblage to lower or upper maximum
756 precipitation limits based on species' observed distributions; e) the number of years since the landscape
757 became at least 30% converted to human-dominated land uses. All interactions between land use and the
758 explanatory variables had a significant association with species richness ($\chi^2 > 23$, $P < 0.001$; Table 1). Sensitivity
759 at a given value of an explanatory variable is inferred as the relative reduction in species richness in disturbed
760 land uses compared with the species richness in primary vegetation.

761

762 **Figure 5. Relationships of predicted biodiversity sensitivity to climate change with putative explanatory**
763 **variables.** a) temperature seasonality; b) precipitation seasonality, c) average proximity of species in an
764 assemblage to lower (value = 0.0) or upper (value = 1.0) monthly temperature limits based on species'
765 observed distributions; d) average proximity of species in an assemblage to lower or upper maximum
766 precipitation limits based on species' observed distributions. We estimated climate sensitivity as the
767 percentage change in species richness for each $^\circ\text{C}$ of warming expected under the RCP 8.5 climate scenario.

768 Relationships are shown here for a random sample of 10,000 10-km grid cells from across the world's
769 terrestrial surface. We derived fitted relationships (shown by red lines) from a simple linear model relating
770 climate sensitivity to each variable, but the direction and significance of relationships was consistent when
771 using a spatial autoregressive model.

772

773 **Tables**

774

775 **Table 1. Statistics for the ability of potential explanatory variables to explain responses of species richness**

776 **to land use.** Shown are the statistics (Chi-squared values, χ^2 ; degrees of freedom, DF; and P values from

777 likelihood-ratio tests) describing the effect on species richness of interactions between the explanatory

778 variables and land use (using the most parsimonious classification, highlighted in bold in Extended Data 3).

Interaction with land use	χ^2	DF	P
Biome	170	18,70	< 0.001
Temperature seasonality	23.8	6, 70	< 0.001
Precipitation seasonality	67.3	6, 70	< 0.001
Thermal position	70.3	6, 70	< 0.001
Precipitation position	203.5	6, 70	< 0.001
Time since landscape conversion to human-dominated land uses	25.8	6, 70	< 0.001

779