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

2   **climate change**

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

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

Introduction

Global biodiversity is continuing to decline despite increasing conservation efforts[1–4]. On the other hand, recent years have seen increases in people's awareness of the scale of biodiversity change and of the important roles that biodiversity plays, and also increases in funding for many aspects of conservation work and in the designation of protected areas[5]. 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 biodiversity[5]. There remain many gaps in our understanding of the effects of

44   biodiversity pressures globally[6], gaps which need to be addressed to understand better how to

45   reduce the downward biodiversity trend.

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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 pressures[8]. 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 biased[11], 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 climate[14]

61   (and sometimes other aspects of the environment, including land use[10]). 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 margin[15]). 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   drylands[19], 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 others[20].

77   This long history of human use is likely to have already filtered out the most sensitive species even

78   from natural habitats[21], 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   elsewhere[22]. Smaller range size has been associated with a disproportionate sensitivity to both land-

81   use change[18] and climate change[23]. Third, there is a greater proportion of dietary and habitat

82   specialist species found within tropical areas than in other biomes[24]. Dietary and habitat specialists

83   have been shown to be most sensitive to both human land use[25,26] and climate change[27]. Fourth,

84   tropical species tend to have a slower 'pace of life', having smaller numbers of offspring and

85   maturing more slowly than other species[28]. 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 use[25]

87   and to climate change[27]. 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 limits[29]. 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   changes[30]. 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 distribution[4]. 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 habitats[34]. 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 biodiversity[39] (in the Extended Data, we also present

114   responses to land use of total community abundance and a measure based on the endemicity 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 2013[40]. 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 distributions[9] 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 simultaneously[9], 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**

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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).

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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).

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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**

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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 data[19].

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 habitats[42]. 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 change[43] 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 disturbance[21].

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 expansion[45], and to be among the first areas to experience

253 unprecedented temperatures as a result of climate change[46]. 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 areas[47]. 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 species[48] and in

263 numbers of endemic species[49], 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 areas[50].

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 changes[51], and synthetic models of land-use

272 impacts may generally underestimate sensitivity because of the difficulty of establishing baseline

273 conditions without human influence[52]. 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 latitudes[53]. 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 here[35], 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 biased[11]. 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   use[40] were compiled to be as geographically representative as possible, and biomes were sampled

291   roughly in proportion to their area[56]. 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 biodiversity[39]. We show that similar

295   patterns in land-use responses are obtained for two other measures based on abundance or species

296   endemicity (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

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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 framework[57], 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 ecoregions[60], which are a nested sub-unit of biomes[61]. 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 ecoregions[62]. 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 available[61], 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) database[63], 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

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352 include the effects of land use directly into species distribution models[10]. 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 models[64]. For global multi-clade analyses, however, it remains

355 necessary to use separate modelling paradigms[9]. 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 Project[63]. This database is a global collation of published comparisons of ecological

364 assemblages across different types of land use, both natural and human-dominated[56]. We excluded

365 any studies that focused on a single species, because these cannot be expected to give a reliable

366 estimate of species richness[1]. 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 follows[56]: 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 fungi[40]. 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 models[65] 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 differences[1]. We additionally included a random intercept of site

395 identity (i.e. an observation-level random intercept), to account for the over-dispersion present[66].

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

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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 biodiversity[39]. 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 community[1], and the

412   average range size of species within the community (weighted by species' abundance)[18]. The latter

413   metric captures the degree of endemicity of species within each community, and so may be a more

414   sensitive metric of the effects of land use[18]. 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   made[18] 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 calculation[18]).

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 models[9]. 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 occupancy[67], they are the best data with

434   which to capture broad-scale responses to climate change of a large number of species[9]. The

435   published distribution models[9] 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) scenarios[68] 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 presented[9], 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

Temperature and precipitation seasonality estimates were derived directly from WorldClim Version

1.4[69] (bioclimatic variables, Bio4 and Bio15, respectively) at 10-arc-minute spatial resolution.

Thermal and precipitation position indices were estimates of the community-average position of

species within their observed (i.e. realised) thermal and precipitation niches (i.e. a value of 0 would

indicate that all species were at their lower thermal or precipitation niche limits, i.e. cold and dry

limits, respectively; whereas a value of 1 would indicate that all species were at their hot or wet

niche limits). For each vertebrate species (species that have relatively reliable information on broad-

scale distribution), we estimated position within niche limits based on the minimum and maximum

conditions experienced throughout its distribution. Estimates of species distributions were the

extent-of-occurrence maps as described above. We did not use GBIF data (see above) to estimate

position within species' thermal and precipitation niches, because the patchy and biased nature of

the GBIF data[11] means that estimates of the precise position of range (and thus climatic niche)

boundaries are likely to be unreliable. We processed the distribution maps by: 1) excluding areas

where species are considered to be vagrant, or present only during migration; 2) excluding areas

outside the known elevational limits for the species; and 3) resampling the maps to a 10-km

cylindrical equal-area (Behrmann) spatial projection. The grain size of 10 km was selected as a

reasonable trade-off between precision and map accuracy. We defined the limits of a species

thermal niche as the minimum across its distribution of the minimum temperature of the coldest

month (bioclimatic variable 'bio6' from WorldClim Version 1.4[69]) and the maximum across its

distribution of the maximum temperature of the warmest month ('bio5'). For precipitation, we

defined niche limits as the minimum across a species' distribution of the total precipitation in the

driest month ('bio14') and the maximum across the distribution of the total precipitation in the

wettest month ('bio13'). For a given location, we then calculated a species' thermal or precipitation

position as the average across the year of the monthly average maximum temperature or monthly

507   total precipitation values – also obtained from WorldClim Version 1.4[69] – 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 use[45]. 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 species[70], and the time since this

520   level of conversion occurred has been shown previously to explain responses of biodiversity to land

521   use[1].

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 1.1-3[71] 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

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: $R^2_{conditional}$ =

734   0.61, $R^2_{marginal}$ = 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_{cells} = 236,527), tropical

740   grasslands (Trop G, n_{cells} = 203,690), drylands (Dry, n_{cells} = 279,178), Mediterranean (Med, n_{cells} = 31,630),

741   temperate forest (Temp F, n_{cells} = 170,680), temperate grasslands (Temp G, n_{cells} = 144,369) and boreal forest

742   (Bor F, n_{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 × 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 (χ^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 °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