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## 15 **Global effects of land use on local terrestrial biodiversity**

16  
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63 **Human activities, especially conversion and degradation of habitats, are causing global**  
64 **biodiversity declines. How local ecological assemblages are responding is less clear – a**  
65 **concern given their importance for many ecosystem functions and services. We analyze**  
66 **a terrestrial assemblage database of unprecedented geographic and taxonomic coverage**  
67 **to quantify local biodiversity responses to land-use and related changes. In the worst-**  
68 **impacted habitats, these pressures reduce within-sample species richness by an average**  
69 **of 76.5%, total abundance by 39.5% and rarefaction-based richness by 40.3%. We**  
70 **estimate that, globally, these pressures have already slightly reduced average within-**  
71 **sample richness (by 13.6%), total abundance (10.7%) and rarefaction-based richness**  
72 **(8.1%), with changes showing marked spatial variation. Rapid further losses are**  
73 **predicted under a business-as-usual land-use scenario: within-sample richness is**  
74 **projected to fall by a further 3.4% globally by 2100, with losses concentrated in**  
75 **biodiverse but economically poor countries. Strong mitigation can deliver much more**  
76 **positive biodiversity changes (up to a 1.9% average increase) that are less strongly**  
77 **related to countries' socioeconomic status.**

78

79 Biodiversity faces growing pressures from human actions, including habitat conversion and  
80 degradation, habitat fragmentation, climate change, harvesting and pollution<sup>1</sup>. As a result,  
81 global assessments show that species' extinction risk is increasing on average while  
82 population sizes are declining<sup>1,2</sup>. Such assessments have usually focused on data-rich  
83 vertebrates, so might not reflect broader biodiversity<sup>3</sup>. Furthermore, most have concentrated  
84 on the global status of species, whereas the long-term security of many ecosystem functions  
85 and services – especially in changing environments – is likely to depend upon local  
86 biodiversity<sup>4–6</sup>. Average trends in local diversity remain unclear: analyses of temporal  
87 changes in assemblages have suggested no systematic change in species richness<sup>7,8</sup>, but the  
88 available times-series data might under-represent transitions between land-use types<sup>9</sup> and  
89 population time series suggest vertebrate populations have declined sharply in recent  
90 decades<sup>3</sup>.

91 Spatial comparisons provide an alternative source of evidence on how human pressures  
92 affect biodiversity, assuming that differences in pressures have caused observed biodiversity  
93 differences between otherwise matched sites<sup>10–12</sup>. The prevalence of published spatial  
94 comparisons makes it possible to go beyond particular taxa or regions<sup>11,12</sup> to develop global,  
95 taxonomically representative models. Furthermore, the willingness of many researchers to  
96 share their raw data makes it possible to consider multiple aspects of biodiversity, rather than  
97 the single, simple metrics of most existing models<sup>10</sup> which cannot capture all key aspects of  
98 diversity<sup>13</sup>.

99 We present the most geographically and taxonomically representative models to date of  
100 how several aspects of the composition and diversity of terrestrial assemblages respond to

101 multiple human pressures. The explanatory variables in our models most directly measure  
102 land use and infrastructure, but might correlate<sup>14,15</sup> with two other important pressures –  
103 harvesting and invasive species – for which comparable high-resolution spatial data are  
104 unavailable globally. We exclude climate change effects because they are not captured well  
105 by spatial comparisons. We use our models to infer past net changes in assemblages since  
106 1500, project future changes over this century under different socioeconomic scenarios of  
107 land use, and relate projected national changes in local biodiversity to socioeconomic  
108 variables and natural biodiversity.

109 Our models of local within-sample species richness (hereafter ‘richness’), rarefaction-  
110 based species richness (hereafter ‘rarefied richness’), total abundance, compositional turnover  
111 and average organism size are based on among-site comparisons of ecological assemblage  
112 composition collated from the literature as part of the PREDICTS project<sup>16</sup>. The dataset  
113 consisted of 1,130,251 records of abundance and 320,924 of occurrence or species richness at  
114 11,525 sites (2-360 sites per study, median 15; Figure 1a). These data, from 284 publications  
115 (see Methods), represent 26,953 species – 1.4% of the number formally described<sup>17</sup> – and 13  
116 of the 14 terrestrial biomes (Extended Data Figure 1). Each site was scored for six putative  
117 pressures: land use<sup>11</sup> and use intensity<sup>18</sup>, land-use history<sup>19</sup>, human population density<sup>20</sup>,  
118 proximity to roads<sup>21</sup>, and accessibility from the nearest large town. Random effects in our  
119 models accounted for study-level differences in response variables and sampling methods,  
120 and for the within-study spatial arrangement of sites.

121

#### 122 *Effects of pressures on site-level diversity*

123

124 Local richness, rarefied richness and total abundance were most strongly influenced by land  
125 use and land-use intensity: they were substantially lower in most other land-use types than in  
126 primary vegetation, especially in intensively-used areas (Figure 1; see Supplementary  
127 Information for statistics and coefficient estimates). These results extend those of previous,  
128 geographically or taxonomically restricted, meta-analyses (e.g. refs. 11,22). Other variables  
129 were weaker as main effects, but showed stronger effects in interaction (Extended Data  
130 Figure 2) and were often significant overall (see Supplementary Information). Richness and  
131 total abundance tended to be slightly lower at the highest human population densities, and  
132 richness was lower nearer to roads and in more accessible sites (Figure 1). Differences in  
133 richness were not driven solely by differences in abundance: rarefied richness<sup>23</sup> (see Methods  
134 for details) showed weaker but mostly similar patterns, although the effects of variables other  
135 than land use and land-use intensity were not significant (Extended Data Figure 3a,b). Under  
136 the worst combinations of pressures, our models estimated richness, rarefied richness and  
137 total abundance to be 76.5%, 40.3% and 39.5% lower, respectively, than in minimally  
138 impacted sites. Effects of pressures on vertebrate, invertebrate and plant richness were  
139 statistically indistinguishable ( $P > 0.05$ ; results not shown). The modelled coefficients were  
140 robust to efforts to correct for publication bias (Extended Data Figure 4). As with all studies  
141 based on data from the literature, unpublished data are almost unrepresented. Coefficients  
142 were also robust under cross-validation (Extended Data 3c,d), and the model residuals  
143 showed little spatial autocorrelation (Extended Data Figure 5).

144 The importance of secondary vegetation for conservation is hotly debated<sup>11,24,25</sup>, and is  
145 crucial because this land-use will soon become the most widespread type<sup>26</sup>. We find that the  
146 answer depends strongly on the secondary vegetation’s maturity: early-stage communities  
147 tend to be less diverse than those in primary vegetation and are compositionally distinct, but  
148 these differences are much reduced in mature secondary vegetation (Figures 1 & 2; we  
149 caution though that not all data sources clearly distinguished mature secondary from primary

150 vegetation). This successional rise in diversity accords with a recent meta-analysis of plant  
151 communities over time<sup>7</sup>.

152 Net changes in diversity provide an incomplete view of the effects of human activities  
153 on biodiversity because they ignore replacement of original species by newcomers<sup>8</sup>. We  
154 therefore analysed how land use affects similarity in species composition between sites.  
155 Communities under the same land use were, unsurprisingly, the most similar (Figure 2a).  
156 Across land uses, communities in primary vegetation were most like those in secondary  
157 vegetation, while plantation forest, pasture and cropland communities formed a different,  
158 human-dominated, cluster (Figure 2b).

159 Anthropogenic pressures can affect ecosystem functions and services more strongly  
160 than changes in species diversity would imply, if species' responses depend on their traits<sup>27</sup>.  
161 Large size is often linked to species' declines<sup>28,29</sup> and is important for some ecosystem  
162 processes<sup>30</sup>. We combined abundance data with species' average sizes to calculate site-level  
163 community-weighted mean plant height and animal mass. As in local studies<sup>29</sup>, mean plant  
164 height was lower in human-dominated land uses than in primary and secondary vegetation,  
165 and tended to decline with increasing human population density (Figure 1d). Most field  
166 studies focused on particular plant taxa, so this difference does not simply reflect tree  
167 removal. Average animal mass did not change consistently with land use or human  
168 population density, but increased with proximity to roads (Figure 1d).

169 Models like ours that substitute space for time ignore time lags in biotic changes,  
170 which can be important<sup>31</sup>. We also assume that land uses are situated randomly within studies  
171 relative to sites' intrinsic suitability for biodiversity. Adding global data on other important  
172 pressures as they become available, and also incorporating climate change, will give a more  
173 complete picture of human impacts on local biodiversity.

#### 174 *Global effects on local diversity to date*

175  
176  
177 By applying our model for within-sample species richness – the most widely used and  
178 understood biodiversity measure – to maps of current pressure variables, we estimate the  
179 global pattern of net local changes to date in plot-level richness (Figure 3; we did not estimate  
180 total richness within the  $0.5^\circ \times 0.5^\circ$  grid cells). Human-dominated areas are inferred to have  
181 lost much more local diversity than have regions where more natural vegetation remains. The  
182 worst-affected cells showed a 31% reduction in average local richness – probably enough to  
183 impact ecosystem functioning substantially<sup>5</sup>. Local richness increased in 1.7% of cells (by  $\leq$   
184 4.8%). Total abundance and rarefied richness showed broadly similar patterns, although less  
185 pronounced in the latter case (Extended Data Figure 6).

186 We applied our models to global spatial estimates of how land use and human  
187 population changed from 1500-2005<sup>26</sup> (see Methods) to infer the global history of local  
188 biodiversity change. We focus on within-sample species richness because of its wide use and  
189 easy interpretation. Our inferences incorporate uncertainty in model parameter estimates, but  
190 not in the trajectories of the drivers themselves (which have not been assessed<sup>32</sup>) nor effects  
191 of changes in roads and accessibility, for which temporal estimates could not be obtained.

192 Richness is estimated to have declined most rapidly in the 19<sup>th</sup> and 20<sup>th</sup> centuries  
193 (Figure 4), with other metrics showing similar responses (Extended Data Figure 6). By 2005,  
194 we estimate that land use and related pressures had reduced local richness by an average of  
195 13.6% (95% CI: 9.1 – 17.8%) and total abundance by 10.7% (95% CI: 3.8% gain – 23.7%  
196 reduction) compared with what they would have been in the absence of human effects.  
197 Approximately 60% of the decline in richness was independent of effects on abundance:  
198 average rarefied richness has fallen by 8.1% (95% CI: 3.5 – 12.9%). Although these

199 confidence limits omit uncertainty in the projections of land use and other pressures, there is  
200 less uncertainty in estimates of current pressure levels than in changes over time<sup>33</sup>.

201 Our inferences contrast with two recent analyses of community time series<sup>7,8</sup>, which  
202 suggested no overall trend in local diversity, and with the Living Planet Index<sup>3</sup> which, based  
203 on vertebrate population time series, reports a much more rapid decline in abundance than we  
204 infer. Although time series potentially provide a more direct view of temporal trends than our  
205 space-for-time approach, the available data might under-represent transitions between land-  
206 use types<sup>9</sup>. On the other hand, our approach may underestimate additions of species through  
207 climate change and species invasion (although accessibility and proximity to roads may  
208 partly capture the latter<sup>14,15</sup>).

209

### 210 *Global and national projections to 2095*

211 Global changes in local diversity from 2005 to 2095 were projected using estimated land use  
212 and human population from the four Intergovernmental Panel on Climate Change  
213 Representative Concentration Pathway (RCP) scenarios<sup>26</sup>, which correspond to different  
214 intensities of global climate change (Table 1). Although these estimates have limitations<sup>32</sup>,  
215 they are the most consistent available, are widely-used<sup>34</sup>, and are consistent with the  
216 historical estimates<sup>26</sup>. However, they – like all other global land-use projections – include no  
217 estimate of uncertainty; therefore, each of our projections must be viewed as the predicted  
218 biodiversity outcome under one particular set of land-use assumptions.

219 Projected net changes in average local diversity to 2095 vary widely among scenarios  
220 (Figure 4; Extended Data Figure 6). The scenario with the least climate change (IMAGE 2.6)  
221 yields the second-worst outcome for biodiversity, because it assumes rapid conversion of  
222 primary vegetation – especially in the tropics – to crops and biofuels<sup>26</sup> (Table 1, Extended  
223 Data Figure 7). These projections do not imply that low-emission scenarios must entail large  
224 losses of biodiversity, but instead reflect that scenario's mitigation strategy. Indeed, in  
225 MiniCAM 4.5 (where mitigation is through carbon markets, crop improvements and diet  
226 shifts: Table 1), average richness is projected to increase (though other diversity metrics  
227 respond more weakly: Extended Data Figure 6). The worst biodiversity outcomes arise from  
228 the scenario with most climate change – MESSAGE 8.5 – in which rapid human population  
229 growth drives widespread agricultural expansion (Table 1; Extended Data Figure 7). This  
230 scenario, which has been characterised as 'business-as-usual'<sup>35</sup>, most closely matches recent  
231 trends in emissions<sup>36</sup> and gives the worst outcomes even though our projections omit direct  
232 climate impacts on local assemblages.

233 The global projections hide wide regional and national variation (Figure 5; Extended  
234 Data Figure 8). Projections for 2095 under 'business-as-usual' (MESSAGE 8.5) are strongly  
235 inequitable, presenting serious challenges for both sustainable development and global  
236 conservation of biodiversity (Figure 5a). Under this scenario, European and North American  
237 countries – typically with a high Human Development Index (HDI), low native biodiversity  
238 and widespread historical land conversion – are mostly projected to gain in local richness by  
239 2095. More naturally biodiverse but less economically developed Southeast Asian and  
240 especially sub-Saharan African countries, with more natural and semi-natural habitat, will  
241 suffer the greatest losses (Figure 5a; Extended Data Figure 8f).

242 Such globally inequitable outcomes might be avoidable: the best scenario for  
243 biodiversity (MiniCAM 4.5; Figure 4) yielded country-level outcomes that are relatively  
244 independent of HDI, native species richness (Figure 5b) and past changes (Extended Data  
245 Figure 8e). For local richness, outcomes under MiniCAM4.5 were better than MESSAGE 8.5  
246 for 93% of countries worldwide (Figure 5c).

247 Under AIM 6.0, most Afrotropical countries are projected to gain in local richness but  
248 heavy losses are inferred for the Indo-Malay region (Extended Data Figure 8). Projections

249 under IMAGE 2.6 are spatially similar to those under MESSAGE 8.5. The land-use change  
250 caused by the biofuels-based strategy in IMAGE 2.6 is projected to have a major negative  
251 impact overall on terrestrial biodiversity (Extended Data Figure 8).

252

### 253 *Conclusions*

254 Many assessments of the state of biodiversity have focused on global metrics such as rates of  
255 species extinction<sup>37</sup>, but resilient delivery of ecosystem functions and services is more likely  
256 to depend on local diversity<sup>4–6</sup>. Our models suggest land-use changes and associated  
257 pressures strongly reduce local terrestrial biodiversity, and we estimate global average  
258 reductions to date of 13.6% in within-sample species richness, 10.7% in total abundance and  
259 8.1% in rarefaction-based species richness (Figs. 3 and 4). Climate change, which we could  
260 not include in our framework, is likely to exacerbate losses, especially under business-as-  
261 usual<sup>38</sup>, although direct effects of climate change will increase local diversity in some  
262 regions<sup>8</sup>.

263 It is important to remember that the habitat conversion and associated changes that  
264 reduced local biodiversity had largely positive consequences for people: agricultural  
265 intensification underpinned many countries' development. However, benefits have not been  
266 shared equally among or within countries<sup>39</sup>. Losses of local species richness exceeding 20%  
267 are likely to substantially impair the contribution of biodiversity to ecosystem function and  
268 services, and thus to human well-being<sup>5</sup>. We estimate that reductions in average plot-level  
269 species richness currently exceed this level for 28.4% of grid cells, increasing to 41.5% of  
270 cells by 2095 under 'business-as-usual' (note that we do not estimate or project total richness  
271 across the cell). Importantly, our projections suggest that such widespread large losses are not  
272 inevitable. With concerted action and the right societal choices, global sustainability of local  
273 biodiversity may be an achievable goal.

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385  
386 **Supplementary Information** is linked to the online version of the paper at  
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388  
389 **Additional references** can be found in the Supplementary Information.

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412

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422 Y.I., S.M., and M.N. generated the maps of species richness used in the model projections;  
423 T.N., L.N.H. and A.P. wrote the manuscript with contributions from G.M.M., L.B., D.W.P.,  
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425 and S.T.; T.N. and L.N.H. contributed equally to the study.  
426

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431

#### 432 **Tables**

433

434

435 **Table 1. Key features of the four Representative Concentration Pathways (RCP)**  
 436 **scenarios** (land-use and human-population assumptions are detailed in ref. 26, energy  
 437 assumptions in refs. 40–42, and climate implications in ref. 43).

Scenario	Land use (see also Extended Data Figure 7)	Climate and energy	Human population
IMAGE 2.6	Agriculture moves from developed to developing countries. Large increase in area of biofuel plantations. Urban extent assumed constant.	Increased energy efficiency. Increased use of carbon capture and storage, nuclear, renewable energy and biofuels. Approximately 1 °C temperature increase by 2100 compared to pre-industrial.	10.1 billion by 2100 (UN Medium variant, 2010)
MiniCAM 4.5	Carbon pricing leads to preservation of primary forest and expansion of secondary forest. Crop yield increases, improved agricultural efficiency and dietary shifts lead to decreases in cropland and pasture areas. Small increase in area of biofuel plantations. Urban extent assumed constant.	Decline in overall energy use. Decreased use of fossil fuels and increase in nuclear and renewable energy, and in carbon capture and storage. Moderate increase in use of biofuels, but limited by availability of biomass. Approximately 1.75 °C temperature increase by 2100.	Peaks above 9 billion around 2065, then declines to 8.7 billion by 2095.
AIM 6.0	Urban area increases owing to human population growth. Cropland area increases to meet food demand. Pasture area declines strongly.	Approximately 2.5 °C temperature increase by 2100.	9.1 billion by 2100 (UN Medium variant, 2004)
MESSAGE 8.5	Increasing crop yields and intensification account for much of the increased production required, but area of cropland and, to a lesser extent, pasture increases rapidly. Small increase in area of biofuel plantations. Urban area increases owing to increased population.	Small improvements in efficiency leading to high demand for energy. Conventional oil and gas become scarce, leading to shift in favour of unconventional and carbon-intensive fossil fuels. Moderate increase in use of biofuels. Approximately 4 °C increase in temperature by 2100.	12 billion by 2100.

438  
439

440 **Figure legends**

441

442 **Figure 1. Locations of sites and responses of four metrics of local diversity to human**  
443 **pressures. a**, Sites used in the models. Responses<sup>44</sup> of richness, **b**, total abundance, **c**, and  
444 community-weighted mean organism size – plant height (crosses) and animal mass  
445 (triangles), **d**, to anthropogenic variables. Error bars show 95% confidence intervals. Primary  
446 = primary vegetation, YSV = young secondary vegetation, ISV = intermediate secondary  
447 vegetation, MSV = mature secondary vegetation, Plantation = plantation forest. Land-use  
448 intensity: minimal (circle), light (triangle), intense (diamond), and combined light and intense  
449 (square). HPD = human population density<sup>45</sup>, PR = proximity to roads<sup>46</sup> (as  $-\log(\text{distance to}$   
450  $\text{nearest road})$ ), ACC = accessibility to humans<sup>47</sup> (as  $-\log(\text{travel time to nearest major city})$ )  
451 are shown as fitted effects from a model with no interactions between continuous effects and  
452 land use, at the lowest (L), median (M) and highest (H) values in the dataset. Sample sizes are  
453 given in full in the Methods (Table S2).

454

455 **Figure 2. Similarity in assemblage composition as a function of land use. a**, Average  
456 dissimilarity of species composition ( $1 - \text{Sørensen Index}$ ) between pairs of sites within and  
457 among land uses (shown relative to the similarity between pairs of primary-vegetation sites);  
458 blue and red colours indicate, respectively, more and less similar composition; numbers  
459 indicate numbers of studies within which comparisons could be made. **b**, Clustering of land-  
460 use types based on average compositional dissimilarity; urban sites were excluded owing to  
461 the small sample size. Land-use labels as in Figure 1.

462

463 **Figure 3. Net change in local richness caused by land use and related pressures by 2000.**  
464 Projections used an IMAGE reference scenario<sup>10</sup>. The baseline landscape was assumed to be  
465 entirely uninhabited, unused primary vegetation. Shown using a Lambert Cylindrical Equal-  
466 Area projection at  $0.5^\circ \times 0.5^\circ$  resolution.

467

468 **Figure 4. Projected net change in local richness from 1500 to 2095.** Future projections  
469 were based on the four RCP scenarios (Table 1). Historical (shading) and future (error bars)  
470 uncertainty is shown as 95% confidence intervals, rescaled to zero in 2005. The baseline for  
471 projections is a world entirely composed of uninhabited, unused primary vegetation; thus, the  
472 value at 1500 is not constrained to be zero because by then non-primary land uses were  
473 present – and in some regions widespread. The global average projection for MESSAGE 8.5  
474 does not join the historical reconstruction because that scenario's human-population  
475 projections start in 2010 and because human population and plantation-forest extent have not  
476 been harmonized among scenarios.

477

478 **Figure 5. Biodiversity projections at the country level. a-b**, Country-level projections of  
479 average net local richness change between 2005 and 2095 under the worst (**a**, MESSAGE  
480 8.5) and best (**b**, MiniCAM 4.5) RCP scenarios for biodiversity, shown in relation to the  
481 Human Development Index. Colours indicate biogeographic realms; colour intensity reflects  
482 natural vertebrate species richness (more intense = higher richness); point size is proportional  
483 to (log) country area. **c**, Correlation between projected richness changes under the MiniCAM  
484 4.5 and MESSAGE 8.5 scenarios, with dashed line showing equality; colours as in **a and b**;  
485 colour intensity is proportional to the HDI (more intense = higher index).

486

487 **Methods**

488

489 *Data collation*

490

491 Between March 2012 and April 2014 we collated among-site comparisons of ecological  
492 assemblage composition from published studies (or from unpublished datasets where the  
493 methods have been published) examining the effect of human activities on more than one  
494 named taxon. A full description of how the dataset was assembled and curated is presented  
495 elsewhere<sup>16</sup>. We define sites to be in the same study if they were sampled using the same  
496 methodology and the data were reported in the same paper; therefore, some publications  
497 contain multiple studies. After six months of broad searching, we targeted efforts towards  
498 under-represented taxa, habitat types, biomes and regions. We accepted data only from  
499 published or in-press papers, or data collected using a published methodology, and we  
500 required that the data providers agreed to our making their data publicly available at the end  
501 of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial  
502 Systems) project in 2015. We accepted data only where abundance, occurrence or richness  
503 had been measured at two or more sampling locations and/or times, and where all sites were  
504 sampled using the same sampling procedure and with either the same effort or site-specific  
505 data on effort. We used geographical coordinates preferentially from the paper or supplied by  
506 data providers; but where coordinates were not thus available, we georeferenced them from  
507 maps in the papers. The final dataset came from 378 studies<sup>49-332</sup> and two unpublished  
508 datasets (M. E. Hanley, 2005 and 2011) that were collected with published methods<sup>146</sup>.

509 Studies compared from 2 to 360 sites (median = 15; 82% had  $\geq 5$  sites); most sampled  
510 species from multiple families but fewer than half sampled multiple orders. Over 70% of sites  
511 were from studies that sampled entire communities within a taxonomic group rather than a  
512 target list of species. Removing studies having a target list did not substantially alter model  
513 coefficients (results not shown) and increased the projected global net average loss of local  
514 species richness until 2005 by 0.6%. Sites varied in the maximum linear extent sampled  
515 (median 106 m; interquartile range 50 m to 354 m). Model coefficients for the approximately  
516 50% of studies that reported maximum linear extent were robust to its inclusion in the models  
517 (results not shown).

518 The great majority of listed taxa were species-level, although many could not be given  
519 explicit species identifications (e.g. morpho-species)<sup>16</sup>; henceforth we refer to distinct taxa in  
520 our dataset as species. We matched taxonomic names given in the source paper to the  
521 Catalogue of Life 2013 Annual Checklist (COL)<sup>333</sup>, obtaining the full taxonomic  
522 classification. In order to relate the taxonomic names to species-level trait databases, we  
523 generated, for each taxon, a 'best-guess' Latin binomial as: a) the taxon name from COL if  
524 the COL query returned a species-level identification; b) the first two words of the text  
525 returned by the COL query if this was a sub-species designation; c) the first two words of the  
526 taxon name in the source publication if the COL query returned neither a species or sub-  
527 species name, and the taxon name in the source publication contained two or more words.  
528 Taxa that met none of these criteria were not matched to trait data, but were included in the  
529 calculation of richness and total abundance, and for estimating turnover in community  
530 composition among sites.

531 The resulting data set contained data for 26,953 species at 11,525 sites. For many high-  
532 diversity taxa, the database contains data for more than 1% of the number of species thought  
533 to have been formally described (Extended Figure 1a). The distribution of sites among major  
534 biomes is roughly proportional to the amount of terrestrial net primary productivity (NPP)  
535 fixed within each biome (Extended Figure 1b).

536

537 *Site-level composition and diversity*

538

539 We computed four site-level biodiversity metrics: within-sample species richness, total  
540 abundance, rarefaction-based richness and community-weighted mean organism size. These  
541 were calculated as follows.

542

543 **Within-sample species richness** was calculated as the number of differently-named taxa  
544 recorded at a given site in a standardised sampling unit (a measure also known as species  
545 density<sup>334</sup>). We gave precedence to the author's classification of species, even where a search  
546 of global databases revealed potential synonymies, because only certain taxonomic groups  
547 could be reliably matched to accepted taxonomies.

548 This measure of richness is appropriate for conservation questions but among site-  
549 differences could be due to effects on numbers of individuals as well as to changes in the  
550 shape of the species accumulation curve<sup>334</sup>. We therefore also calculated **rarefaction-based**  
551 **species richness** by taking 1000 random samples of  $n$  individuals from each site, where  $n$  is  
552 the smallest total number of individuals recorded at any site within its study, and calculating  
553 the mean species richness across samples. This index could only be calculated for sites  
554 where, in addition to the criteria above being met, abundance was recorded as number of  
555 individuals. Rarefied species richness was rounded to the nearest integer for analysis with  
556 Poisson errors.

557

558 **Total abundance** was calculated as the sum of the measures of abundance of all taxa at a  
559 site; we were thus unable to estimate abundance for sites where only species occurrence or  
560 overall richness or diversity had been recorded (17% of sites). Some abundance metrics –  
561 those not reported as densities per unit time, distance, area or volume sampled – were  
562 sensitive to sampling effort. When a study reported any of these metrics and sampling effort  
563 varied among sites within a study, we corrected the raw abundance measurements for the  
564 sampling effort expended at each sampling location and time; this was done by rescaling the  
565 sampling efforts within each study, so that the most heavily sampled site had a value of one,  
566 and then dividing the raw abundance measurements by this relative sampling effort. The  
567 rescaling was performed to prevent introducing additional heterogeneity in the modelled  
568 abundance values.

569

570 **Community-weighted mean organism size** was calculated as the arithmetic mean of log-  
571 transformed height of plants (available for 4,235 species in our dataset) or the log-  
572 transformed body mass or volume of vertebrates, beetles and hoverflies (5,236 species)  
573 present at a site, weighted by abundance<sup>335</sup>. Plant height data were taken from the TRY  
574 database<sup>336</sup>; for 61 species where plant vegetative height data were unavailable, we estimated  
575 it from generative height from a regression across the 2,554 species with estimates of both  
576 traits ( $R^2 = 0.91$ ). Data on vertebrate body mass were taken from the PanTHERIA database  
577 for mammals<sup>337</sup>, from BirdLife International's World Bird Database for birds, and from a  
578 wide range of published and grey-literature sources for amphibians<sup>338–384</sup>. Length data for  
579 reptiles were taken from published<sup>385,386</sup> and unpublished (S. Meiri & A. Feldman,  
580 unpublished data) sources, and converted to estimates of body mass using published length-  
581 mass allometries<sup>387,388</sup>. Arthropod size data (beetles and hoverflies) were collated from  
582 published sources<sup>389,390</sup>. Beetle length and amphibian snout-vent length values were raised to  
583 the power three so that they had the same dimensionality as the other animal size measures.  
584 For both plant height and vertebrate body mass, missing values were interpolated as the  
585 average values for congeners, since both of these traits are strongly conserved  
586 phylogenetically (Pagel's  $\lambda = 0.98, 0.997, 0.93, 0.89$  for plant height, vertebrate body mass,  
587 beetle body length and hoverfly thorax volume, respectively).

588

589 *Human pressure data*

590

591 While many human pressures can impact local biodiversity, we focus on those that can  
592 be obtained for sites around the world and for which, as far as possible, spatiotemporal data  
593 are available for 1500-2095; this focus enables us to use our statistical models as a basis for  
594 projecting responses through time. Each site was assigned to one of eight land-use classes  
595 based on the description of the habitat given in the source paper (see Extended Data Table 1  
596 for definitions): primary vegetation, secondary vegetation (subdivided into mature,  
597 intermediate or young secondary vegetation), plantation forest, cropland, pasture and urban<sup>16</sup>.  
598 These classes were selected to match the land-use classification adopted in the  
599 Intergovernmental Panel on Climate Change Representative Concentration Pathways  
600 scenarios<sup>26</sup> in order to facilitate the projection of our models onto these scenarios. Sites were  
601 also assigned to a level of human intensity of use – minimal, light or intense – within each  
602 major land-use class, also based on the description of the habitat in the source paper (see  
603 Extended Data Table 1 for definitions). The factors that determined this level depended on  
604 the land-use class (e.g. bushmeat extraction and limited logging in primary and secondary  
605 vegetation; or stocking density and chemical inputs in pasture; Extended Data Table 1). Sites  
606 that could not be classified for land-use and use intensity were excluded from the analyses.  
607 The final dataset contained the following numbers of sites in each land use and land-use  
608 intensity level: Primary vegetation, minimal use – 1546 (from 183 studies), light use – 860  
609 (76 studies), intense use – 449 (33 studies); mature secondary vegetation, minimal use – 198  
610 (52 studies), light/intense use – 213 (23 studies); intermediate secondary vegetation, minimal  
611 use – 404 (55 studies), light/intense use – 269 (30 studies); young secondary vegetation,  
612 minimal use – 431 (50 studies), light/intense use – 331 (34 studies); plantation forest,  
613 minimal use – 356 (47 studies), light use – 402 (42 studies), intense use – 238 (29 studies);  
614 cropland, minimal use – 427 (45 studies), light use – 632 (43 studies), intense use – 703 (36  
615 studies); pasture, minimal use – 525 (43 studies), light use – 434 (52 studies), intense use –  
616 174 (23 studies); and urban, minimal use – 174 (23 studies), light use – 244 (26 studies),  
617 intense use – 195 (18 studies).

618 We overlaid our sites with available global data sets to obtain site-level estimates of  
619 human population density<sup>45</sup>, distance to the nearest road<sup>46</sup> and estimated travel time to nearest  
620 population centre with greater than 50,000 inhabitants<sup>47</sup>. For distance to nearest road, the map  
621 of roads was first projected onto a Berhmann equal-area projection. These operations were  
622 carried out using Python code implemented using the arcpy Python module in ArcMap  
623 Version 10.0<sup>391</sup>. In the main figures, the inverses of distance to roads and travel time to major  
624 population centre (proximity to roads and accessibility) were presented so that high values  
625 corresponded to higher hypothesized human impact. To estimate the history of human use of  
626 the landscapes within which sites were located, we calculated the number of years since the  
627 30-arc-second grid cell containing each site became 30% covered by human land uses  
628 (cropland, pasture and urban), according to the HYDE model<sup>48</sup>. Collinearity among variables  
629 describing anthropogenic change was low: the highest correlation was between land use and  
630 human population density (Pearson  $R^2 = 0.31$ ).

631

632

633 *Modelling site-level diversity, composition and turnover*

634

635 The response of site-level diversity to the measures of anthropogenic change was  
636 modelled using generalized linear mixed effects models, implemented in the lme4 package  
637 Version 1.0-5<sup>44</sup> in R Version 3.0.2<sup>392</sup>. We first compared candidate random-effects structures  
638 using the full candidate fixed-effects structure<sup>393</sup>. Random-intercept terms considered in all

639 models were the identity of study from which data were taken, to account for study-level  
640 differences in the response variables and sampling methods used, and – within-study – the  
641 spatial block in which the site was located, to account for the spatial arrangement of sites. For  
642 models of species richness (within-sample and rarefied), we also fitted an observation-level  
643 random effect (i.e. site identity) to account for the overdispersion present<sup>394</sup>. We also  
644 considered random slopes, with respect to study, of each of the main fixed effects (land use,  
645 land-use intensity, human population density, distance to nearest road, travel time to nearest  
646 major city and time since the landscape was majority converted to human uses). Random  
647 effects were retained or discarded based on Akaike Information Criterion values.

648 Once the best random-effects structure had been selected, we performed backward  
649 stepwise model simplification to select the best fixed-effects structure (see ‘Full Statistical  
650 Results’)<sup>393</sup>. Human population density, distance to roads, travel time to nearest major city  
651 and time since major human use of the landscape were log transformed in the analyses, with a  
652 value of 1 added to human population density, travel time to nearest major city and time since  
653 major landscape conversion to deal with zero values. These four variables were fitted as  
654 continuous effects, with quadratic polynomials for human population, distance to roads and  
655 travel time to nearest major city, and as a linear effect for time since human landscape  
656 conversion. For variables fitted as quadratic polynomials, we also tested linear effects during  
657 the backward stepwise model selection. All continuous variables were rescaled prior to  
658 analysis so that values ranged between zero and one. Interaction terms were tested first, and  
659 then removed to test the main effects. All main effects that were part of significant interaction  
660 terms were retained in the final models regardless of their significance as main effects. For  
661 the model of community-weighted mean body mass and plant height, because the number of  
662 sites with data was smaller than for the other metrics, only land use (excluding urban sites,  
663 which were few), human population density and distance to roads, and no interactions, were  
664 fitted (for the model of plant height, sample sizes in each land use were: primary vegetation –  
665 634 sites, secondary vegetation – 851 sites, plantation forest – 222 sites, cropland – 72 sites,  
666 pasture – 412 sites; and for the model of animal mass: primary vegetation – 1728 sites,  
667 secondary vegetation – 805 sites, plantation forest – 602 sites, cropland – 641 sites, pasture –  
668 440 sites). The decision whether or not to retain terms was based on likelihood ratio tests.  
669 The coefficient estimates of the best models are shown in Figure 1b-d and Extended Data  
670 Figure 2, and the formulae and statistical results are shown in the Supplementary  
671 Information. To test for spatial autocorrelation in the residuals of the final best models, we  
672 calculated Moran’s I values and associated P-values, separately for each study considered in  
673 the models, using the *spdep* package Version 0.5-68<sup>395</sup> in R; the distribution of P-values  
674 across studies was used as an indication of whether spatial autocorrelation was likely to cause  
675 a problem. This revealed that the residuals showed little spatial autocorrelation (Extended  
676 Data Figure 5). We used cross validation to assess the robustness of model parameter  
677 estimates, first based on dividing the studies randomly into 10 equal-sized sets and dropping  
678 each set in turn (Extended Data Figure 3c), and secondly based on leaving out the studies  
679 from each biome in turn (Extended Data Figure 3d).

680 Publication bias is a potential problem for any large-scale synthesis of data from many  
681 publications. In standard meta-analyses, funnel plots<sup>396</sup> can be used to test for any  
682 relationship between standard error and effect size, as a bias in effect sizes at high standard  
683 error toward more positive or more negative effects indicates a likely effect of publication  
684 bias. Creating funnel plots for our data was more complicated because ours was a site-level  
685 analysis of raw diversity estimates rather than a traditional meta-analysis. Instead we  
686 generated individual models relating diversity to land use for each study that sampled at least  
687 two sites within each of at least two land-use types. We focused on land use because: a) there  
688 were a small number of sites included in most within-study models; and 2) the original

689 studies focused on effects of land use – not generally on land-use intensity, human population  
690 density or distance to roads – and thus any effect of publication bias would likely be seen in  
691 the land-use coefficients. Funnel plots were generated by plotting, for each land-use type, the  
692 estimated model coefficients against the associated standard errors (Extended Data Figure 4).  
693 There were some indications of an effect of publication bias, with less certain coefficient  
694 estimates tending to have more negative estimates for some of the land uses (Extended Data  
695 Figure 4). On the other hand, study-level random slopes of human-dominated land uses  
696 tended to be more negative for studies that sampled more sites (Extended Data Figure 4). It is  
697 important to emphasize that in a site-level analysis like ours, studies with fewer sites have  
698 less weight in the models. Modelled coefficient estimates were generally robust to the  
699 removal of these studies (Extended Data Figure 4). Basing projections on coefficient  
700 estimates from models where small studies were excluded led to a less than 1% change in the  
701 estimated global richness values (results not shown). As with all studies based on data from  
702 the literature, we under-represent unpublished data.

703 To model turnover of species composition between pairs of sites, we calculated average  
704 dissimilarity<sup>23</sup> in the lists of present species (1 – Sørensen index) between all pairs of sites  
705 within each study. For this analysis, we were only able to consider studies with more than one  
706 site in at least one of the land-use types considered. Once compositional similarity had been  
707 calculated for every pair of sites within each study, the average compositional similarity was  
708 calculated for every pair of land-use types considered within each study (including  
709 comparisons between sites in the same land-use type). Finally, the average compositional  
710 similarity was calculated for each pair of land-use types across all studies. To visualize the  
711 clustering of different land-use types in terms of community composition, we performed a  
712 hierarchical complete-linkage cluster analysis on the compositional dissimilarity (i.e. 1 –  
713 similarity) matrix, using the hclust function in R Version 3.0.2<sup>392</sup>. To test whether differences  
714 in the average geographic distance between pairs of sites in different land-use combinations  
715 affected these results, we correlated average compositional similarity with average distance  
716 between sites, for all pairwise combinations of land use (including comparisons of a land-use  
717 type with itself). Correlations between average distance and average community similarity  
718 were only very weakly negative ( $R^2 = 0.001$ ), suggesting they do not strongly distort the  
719 comparisons of community composition. However, the fact that some land uses tend to occur  
720 more closely together than others could influence the diversity patterns seen in our models, if  
721 some land uses are typically close to high-diversity habitats and so are more likely to benefit  
722 from dispersal. For example, sites in secondary vegetation and plantation forest were closer,  
723 on average, to primary vegetation sites than were those in cropland, pasture and urban  
724 (average distances to sites in primary vegetation were: other primary vegetation sites = 7.38  
725 km, mature secondary vegetation = 4.4 km, intermediate secondary vegetation = 3.9 km,  
726 young secondary vegetation = 6.9 km, plantation forest = 4.2 km, cropland = 16.4 km,  
727 pasture = 10.1 km, and urban = 11.4 km). Accounting for distance in such already-complex  
728 models is not computationally tractable. In making the projections, we therefore implicitly  
729 assume that the average distances will not change (i.e. that secondary vegetation and  
730 plantation forests will remain closer to primary vegetation than cropland, pasture and urban  
731 habitats).

### 732 733 *Projecting the Models onto Spatial Estimates of Anthropogenic Variables*

734  
735 We projected the best overall models of richness (within-sample and rarefied),  
736 abundance and community-weighted mean organism size onto estimates of land use, land-use  
737 intensity and human population density at  $0.5^\circ \times 0.5^\circ$  resolution, using historical estimates  
738 for 1500 to 2005, and four Representative Concentration Pathways scenarios of future



739 changes (IMAGE 2.6, MiniCAM 4.5, AIM 6.0 and MESSAGE 8.5; the names refer to the  
740 integrated assessment models used and the numbers to the amount of radiative forcing  
741 assumed in 2100)<sup>397</sup>. In the absence of global projections, proximity to roads and accessibility  
742 were omitted from our projections.

743 Estimates of land use for both the historical reconstruction and the future scenarios  
744 were taken from the harmonized land-use data accompanying the scenarios<sup>26</sup>. Estimates of  
745 the stage of secondary vegetation (young, intermediate or mature) are not available directly in  
746 the RCP land-use data. However, these data contain estimates of the transition each year  
747 between secondary vegetation and all other land-use types. To convert this into an estimate of  
748 the proportion of secondary vegetation in each of the stages of maturity, we considered any  
749 transition to secondary vegetation to result in secondary vegetation of age zero. Each year,  
750 this age was then incremented by one. In the absence of better information, any transitions  
751 from secondary vegetation to any other land-use type were assumed to be drawn evenly from  
752 the ages currently represented. For the purposes of the projections, secondary vegetation was  
753 considered to be young until an age of 30 years, intermediate between 30 years and 100  
754 years, and mature thereafter. We developed C# code to convert land-use transitions into  
755 estimates of the stage structure of secondary vegetation.

756 Gridded temporal estimates of human population density were directly available for the  
757 HYDE historical scenario and MESSAGE future scenario. Human population trajectories in  
758 the MiniCAM model were resolved only to the level of United Nations regions<sup>41</sup>; we  
759 therefore downscaled these to grid cells assuming no temporal change in the spatial pattern of  
760 relative population density within regions compared to present day patterns<sup>45</sup>, which is the  
761 method used in other RCP-scenario land-use models lacking human population data resolved  
762 to grid cells<sup>26</sup>. Gridded estimates of human population from the MESSAGE model were  
763 downloaded from <http://www.iiasa.ac.at/web-apps/ggi/GgiDb/>. For the scenarios for which  
764 human population projections were not available (IMAGE and AIM), we used country-level  
765 estimates from the ‘medium’ scenario of the United Nations population division<sup>398</sup>, which  
766 gives the closest global predictions of future human population to those assumed by IMAGE  
767 and AIM<sup>26</sup>. These country-level estimates were downscaled to grid cells using the same  
768 method as for MiniCAM’s regional projections.

769 Land-use intensity was an important explanatory variable in our models, but global  
770 maps of land-use intensity are not available. We therefore generated global estimates of  
771 current land-use intensity based on a map of ‘Global Land Systems’<sup>399</sup>, which divides coarse  
772 land-use types into sub-categories based on levels of cropland intensity, livestock densities  
773 and human population density. We mapped each Global Land Systems class onto one or  
774 more relevant combinations of our classes of land use and land-use intensity (Extended Data  
775 Table 2). The Global Land Systems dataset has a spatial resolution of 5 arc-minutes. To  
776 calculate the proportion of each 0.5° cell occupied by each land use and land-use intensity  
777 combination we calculated the proportion of 5-arc-minute cells within each 0.5° cell  
778 containing matching Global Land Systems categories (see legend of Extended Data Table 2  
779 for details).

780 To generate past and future estimates of land-use intensity, we modelled the current  
781 proportion of each land-use type estimated to be under minimal, light or intense levels of  
782 intensity within each grid cell (one model for each intensity level), as a function of the  
783 prevalence of the land-use type within each cell and human population density, with the  
784 relationships allowed to vary among the 23 United Nations (UN) sub-regions (i.e. we fitted  
785 interaction terms between UN sub-region and both the prevalence of each land-use type and  
786 human population density). UN sub-region data were taken from the world borders shapefile  
787 Version 0.3 ([http://thematicmapping.org/downloads/world\\_borders.php](http://thematicmapping.org/downloads/world_borders.php)) and converted to a  
788 0.5° × 0.5° raster using ArcMap Version 10.0<sup>391</sup>. The models were developed using

789 generalized linear models with a binomial distribution of errors, implemented in the lme4  
790 package Version 1.0-5<sup>44</sup> in R Version 3.0.2<sup>392</sup>. The resulting models explained between  
791 30.6% and 76.7% of the deviance in estimated current levels of intensity. Past and future  
792 land-use intensities were estimated by applying the models to the same past and future  
793 estimates of land use and human population density as above.

794 The scenarios gave the proportion of each grid cell estimated to be occupied by each  
795 combination of land use and land-use intensity. We did not attempt to resolve human  
796 population density within grid cells for our historical estimates or forecasts, thereby assuming  
797 it to be spatially (not temporally) constant within each cell. The coefficients from the models  
798 of site-level diversity were thus applied to each combination of land use and intensity within  
799 each cell, with the same human population density estimate across all combinations. All  
800 predictions were expressed as a percentage net change compared with a baseline before  
801 human land-use impacts on biodiversity, in which all land use was assumed to be primary  
802 vegetation of minimal intensity of use, and with a human population density of zero. Each  
803 cell's average value of net biodiversity change was calculated as the area-weighted mean  
804 value across all land uses and intensities. Global average values were calculated as mean  
805 values across all cells, weighted by cell area and an appropriate weighting factor to account  
806 for the fact that cells have different baseline levels of diversity. The weighting factors applied  
807 were: terrestrial vertebrate species richness in the case of richness, and net primary  
808 production (NPP) in the case of total abundance. No weighting factor was applied for  
809 projections of community-weighted mean plant height. Terrestrial vertebrate species richness  
810 was estimated by overlaying extent-of-occurrence range maps for mammals, birds,  
811 amphibians and reptiles, using Python code written by ourselves and implemented in ArcMap  
812 Version 10.0<sup>391</sup>. Data on Net Primary Production were estimates of potential NPP (i.e. in the  
813 absence of human impacts) from the Lund-Postdam-Jena (LPJ) Dynamic Global Vegetation  
814 Model<sup>400</sup>.

815 The 95% confidence intervals around the projected values of biodiversity for each  
816 combination of pressure variables were estimated based on uncertainty in the modelled  
817 coefficients. We were unable to conduct multi-model averaging to account for uncertainty in  
818 the structure of the models (i.e. projections were based only on the final best model) because  
819 applying such complex mixed-effects models, based on such large datasets, to multiple  
820 scenarios of human pressure at a global scale was intractable both in terms of time and  
821 computer-memory requirements. We were also unable to account for uncertainty in the  
822 trajectories of the human pressure variables, because uncertainty estimates are not available  
823 for any of the variables considered.

824 To estimate average biodiversity change in individual countries, we intersected the  
825 gridded projections with the world borders shapefile (see above) using the extract function in  
826 the raster package Version 2.2-12<sup>401</sup> in R Version 3.0.2<sup>392</sup>. Mean values across the cells  
827 associated with each country were calculated, weighted by cell area. To interpret the  
828 outcomes for countries in terms of their natural biodiversity, we related the country-level  
829 projections to estimates of average natural vertebrate species richness (see above). To  
830 interpret the outcomes for countries in terms of their socio-economy, we related the  
831 projections to estimates of the Human Development Index, which is an indicator of  
832 education, life expectancy, wealth and standard of living (<https://data.undp.org/>).

### 833 834 **Extended Data Legends**

835  
836 **Extended Data Figure 1. Taxonomic and geographic representativeness of the dataset**  
837 **used. a,** The relationship between the number of species represented in our data and the  
838 number estimated to have been described<sup>17</sup>, for 47 major taxonomic groups; lines show (from

839 bottom to top) 0.1%, 1% and 10% representation of described species in our dataset; magenta  
840 = invertebrates, red = vertebrates, green = plants, blue = fungi, and grey = all other taxonomic  
841 groups. **b**, the relationship across biomes<sup>402</sup> between the percentage of global terrestrial net  
842 primary production and the number of sites in our dataset; A = tundra, B = boreal forests and  
843 taiga, C = temperate conifer forests, D = temperate broadleaf and mixed forests, E = montane  
844 grasslands and shrublands, F = temperate grasslands, savannas and shrublands, G =  
845 Mediterranean forests, woodlands and scrub, H = deserts and xeric shrublands, J = tropical  
846 and subtropical grasslands, savannas and shrublands, K = tropical and subtropical coniferous  
847 forests, M = tropical and subtropical dry broadleaf forests, N = tropical and subtropical moist  
848 broadleaf forests, P = mangroves; note that the flooded grasslands and savanna biome is not  
849 represented in the dataset; grey line show 1:1 line.

850

851 **Extended Data Figure 2. Detailed response of local diversity to human pressures.**

852 Modelled effects (controlling for land use) of human population density (HPD), distance to  
853 nearest road, time since 30% conversion of a landscape to human uses (TSC) and time to  
854 nearest population centre with greater than 50,000 inhabitants (**a-d**), interactions between  
855 pairs of these variables (**e**), and interactions between these variables and land use (**f-i**) on site-  
856 level diversity: **a-c, f, g**, within-sample species richness; **e, h, i**, total abundance; and **d**,  
857 community-weighted mean vertebrate body mass. Shaded polygons in **a-d** show 95%  
858 confidence intervals. For clarity, shaded polygons in **f-i** are shown as  $\pm 0.5 \times \text{SEM}$ .  
859 Confidence intervals in **e** are omitted. Rugs along the x axes in the line graphs show the  
860 values of the explanatory variables represented in the dataset used for modelling. Only  
861 significant effects are shown. Note that distance to nearest road and travel time to major  
862 population centre measures are the raw (log-transformed) values fitted in the models rather  
863 than the proximity to roads and accessibility values (obtained as 1 minus the former values)  
864 presented in Figure 1. Sample sizes are given in full in the Methods.

865

866 **Extended Data Figure 3. Robustness of modelled effects of human pressures.** **a**, Effects  
867 of land use, human population density (HPD) and proximity to nearest road (PR) on  
868 rarefaction-based species richness. **b**, To test that any differences between these results and  
869 the results for within-sample species richness presented in the main manuscript were not  
870 because rarefied species richness could only be calculated with a smaller dataset, we also  
871 show modelled effects on within-sample species richness with the same reduced dataset. **c-d**,  
872 Cross-validated robustness of coefficient estimates for land use and land-use intensity:  
873 crosses show 95% confidence intervals around the coefficient estimates under ten-fold cross-  
874 validation, excluding data from approximately 10% of studies at a time (**c**), and under  
875 geographical cross-validation, excluding data from one biome at a time (**d**); colours, points,  
876 error bars and land-use labels are as in Figure 1 in the main text. Primary, primary vegetation;  
877 YSV, young secondary vegetation; ISV, intermediate secondary vegetation; MSV, mature  
878 secondary vegetation; plantation, plantation forest. Sample sizes are given in full in the  
879 Methods.

880

881 **Extended Data Figure 4. Tests of the potential for publication bias to influence the**  
882 **richness models and projections.** Left-hand panels (**a, d, g, j, m**) show funnel plots of the  
883 relationship between the standard error around coefficient estimates (inversely related to the  
884 size of studies) and the coefficient estimates themselves for each coarse land-use type; there  
885 is evidence for publication bias with respect to some of the land-use types, as indicated by an  
886 absence of points on one or other side of zero for studies with large standard errors (but note  
887 that small studies are down-weighted in the model); red points show studies with more than 5  
888 sites in the land use in question (10 for secondary vegetation and plantation forest because

889 there were more sites for these land uses and some studies with between 5 and 10 sites  
890 showed variable responses); horizontal dashed lines show the modelled coefficients for each  
891 land use. Central panels (**b, e, h, k, n**) show the relationship between study size (log-  
892 transformed total number of sites) and the random slope of the land use in question with  
893 respect to study identity, from a random-slopes-and-intercepts model; where a significant  
894 relationship was detected using a linear model, fitted values and 95% confidence intervals are  
895 shown as a red dashed line and red dotted lines, respectively; conversely to what would be  
896 expected if publication bias was present, where significant relationships between study size  
897 and random slopes were detected, these were negative (i.e. larger studies detected more  
898 negative effects). Right-hand panels (**c, f, i, l, o**) show the robustness of modelled coefficients  
899 to removal of studies with few sites in a given land use (black points in the left-hand panels);  
900 left-hand error bars show coefficient estimates for all studies and right-hand error bars show  
901 coefficient estimates for studies with more than 5 sites in that land use (10 for secondary  
902 vegetation and plantation forest).

903

904 **Extended Data Figure 5. Tests for spatial autocorrelation in the model residuals.** For the  
905 four main modelled metrics of site-level diversity — **a**, within-sample species richness; **b**,  
906 total abundance; **c**, community-weighted mean plant-height; and **d**, community-weighted  
907 mean animal mass — histograms of P-values from sets of Moran's tests for spatial  
908 autocorrelation in the residuals of the best models for individual studies. The percentage of  
909 studies with significant spatial autocorrelation ( $P < 0.05$ ; indicated by vertical red line) is  
910 shown.

911

912 **Extended Data Figure 6. Current, past and future projections of all metrics of local**  
913 **biodiversity.** Net change in local diversity caused by land use and related pressures by 2000  
914 under an IMAGE reference scenario<sup>10</sup>: **a**, richness; **b**, rarefied richness; **c**, total abundance;  
915 and **d**, community-weighted mean plant height. Note that the values used to divide the  
916 colours are the same in all panels, but that the maximum and minimum values are different,  
917 as indicated in the legends. Historical and future estimates of net change in local diversity  
918 from 1500-2095, based on estimates of land-use, land-use intensity and human population  
919 density from the four Representative Concentration Pathways (RCP) scenarios (Table 1): **e**,  
920 richness; **f**, total abundance; and **g**, community-weighted mean plant height; historical  
921 (shading) and future (error bars) uncertainty shown as 95% confidence intervals, with  
922 uncertainty rescaled to be zero in 2005 to show uncertainty in past and future change  
923 separately; the global average projection for the MESSAGE scenario does not directly join  
924 the historical reconstruction because projections start in 2010 (human population estimates  
925 are available at 15-year intervals) and because human population (and thus land-use intensity)  
926 and plantation-forest extent have not been harmonized among scenarios. In panel **e**, the  
927 dashed line shows projected diversity change under land-use change only (i.e. without land-  
928 use intensity and human population density, the projections of which involved simplifying  
929 assumptions), and the dotted line shows projections of rarefaction-based species richness.

930

931 **Extended Data Figure 7. Reconstructed and projected total global land-use areas under**  
932 **the Representative Concentration Pathways (RCP) scenarios.** **a**, estimated total area of  
933 the major land-use types. **b-f**, estimated total area of secondary vegetation in different stages  
934 of recovery.

935

936 **Extended Data Figure 8. Biodiversity projections at the country level.** **a-d**, Country-level  
937 projections of net change in local richness between 2005 and 2095 under the four RCP  
938 scenarios (**a**, IMAGE 2.6; **b**, MiniCAM 4.5; **c**, AIM 6.0; and **d**, MESSAGE 8.5), shown in

939 relation to the Human Development Index (an indicator of education, life expectancy, wealth  
940 and standard of living) in the most recent year for which data are available. **e-f**, Country-level  
941 projections of net change in local richness between 2005 and 2095 under the best- and worst-  
942 performing RCP scenarios in terms of biodiversity (**e**. MiniCAM 4.5; **f**, MESSAGE 8.5),  
943 shown in relation to past change in biodiversity from a baseline with no human land-use  
944 effects to 2005 according to the HYDE land-use reconstruction. Colours indicate  
945 biogeographic realms (key in **b**); colour intensity reflects native vertebrate species richness  
946 (more intense = higher species richness); point size is proportional to (log) country area.

947  
948  
949

950 **Extended Data Table 1. Land use and land-use intensity classification definitions (from**  
951 **ref. 16).**

952

953 **Extended Data Table 2. Conversion between Global Land Systems dataset and our**  
954 **intensity classification for each major land-use type.** To estimate proportional coverage of  
955 each intensity class for each land-use type in the  $0.5^\circ \times 0.5^\circ$  grid cells used for projection, we  
956 calculated the number of finer-resolution Global Land Systems<sup>399</sup> cells with a matching  
957 intensity class for the land-use type in question, as a proportion of Global Land Systems cells  
958 matching any intensity class for the land-use type in question. For example, to calculate the  
959 proportion of urban land that is under intense use, we divided the number of cells with a  
960 Global Land Systems classification of ‘urban’ by the number of cells classified as ‘urban’ or  
961 ‘peri-urban and villages’. None of the Global Land Systems classes could inform about the  
962 intensity of plantation forest, and so we assumed that any plantation forest was composed of  
963 equal proportions under minimal, light and intense use.

964

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966

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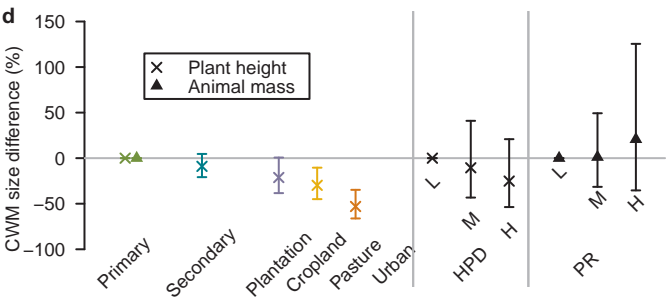
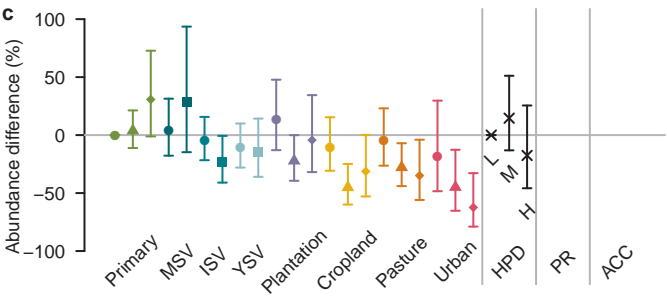
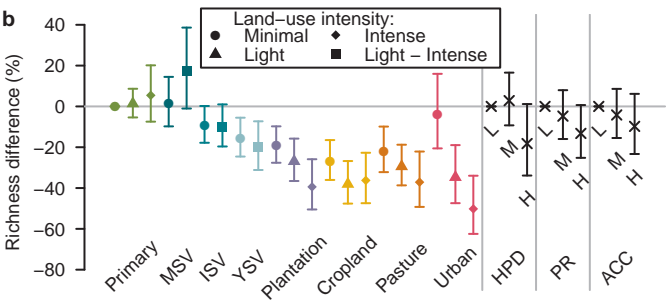
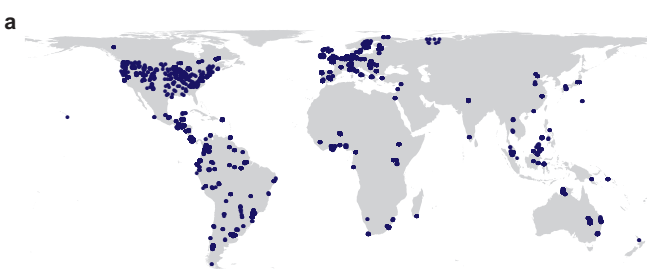
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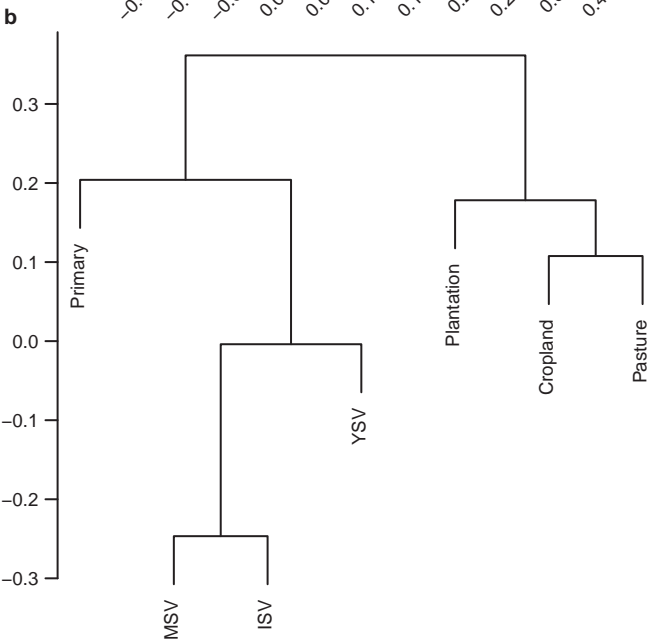
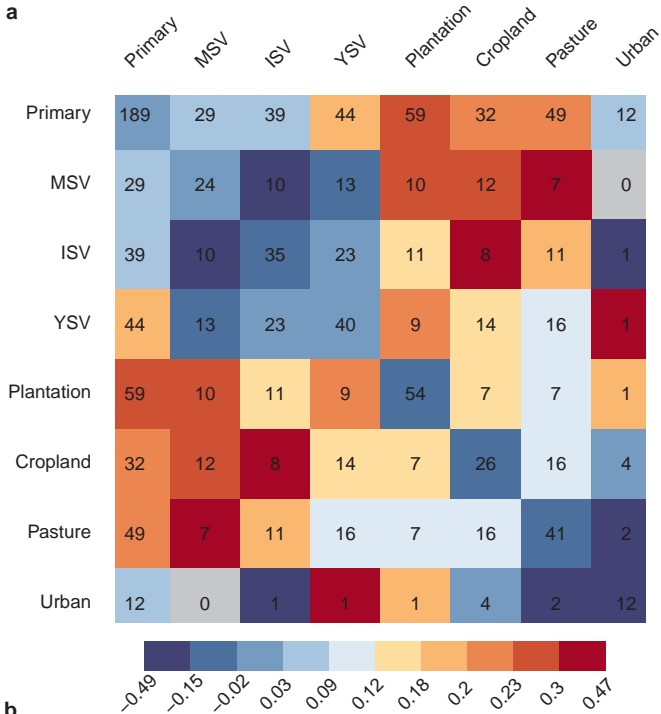


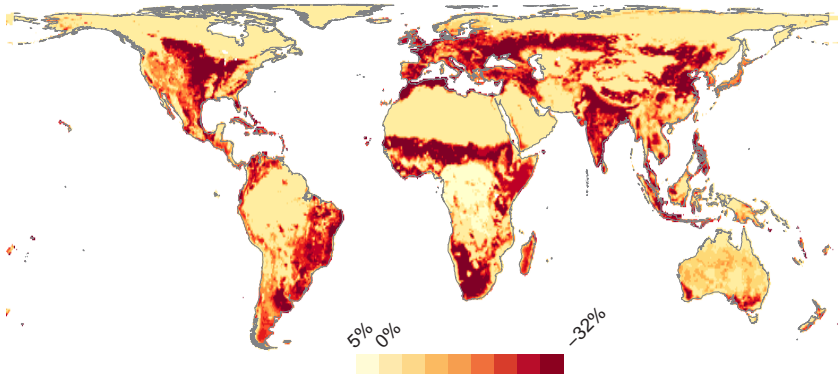
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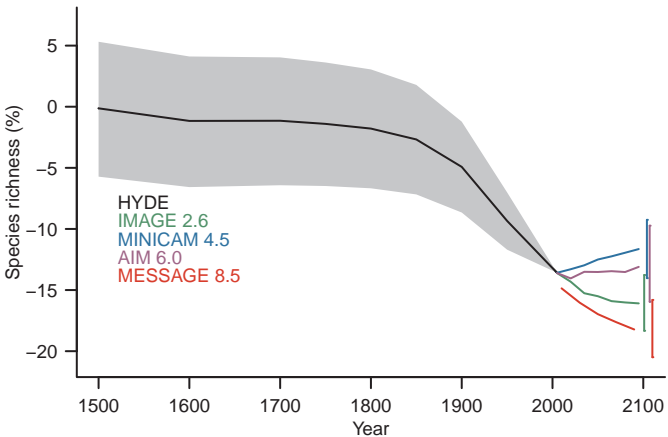
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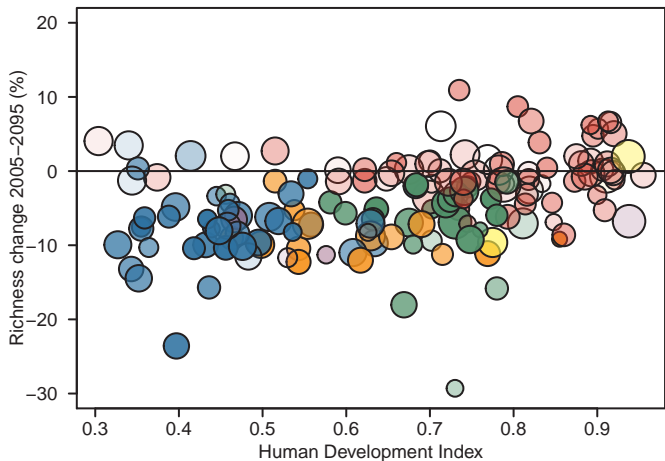
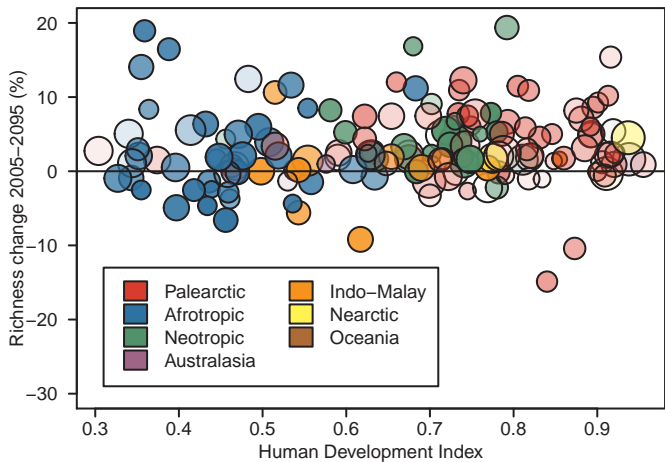
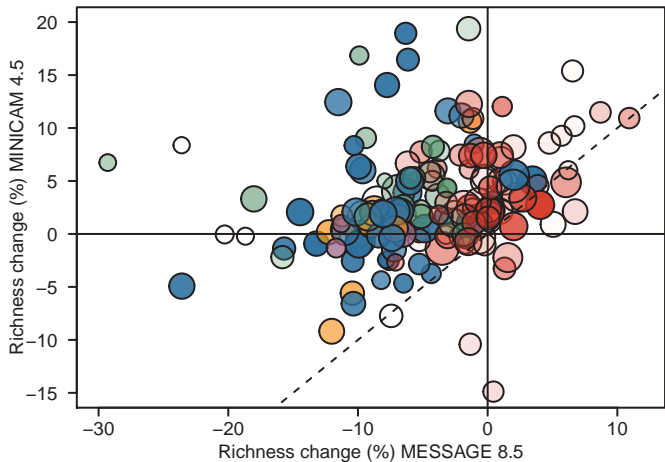
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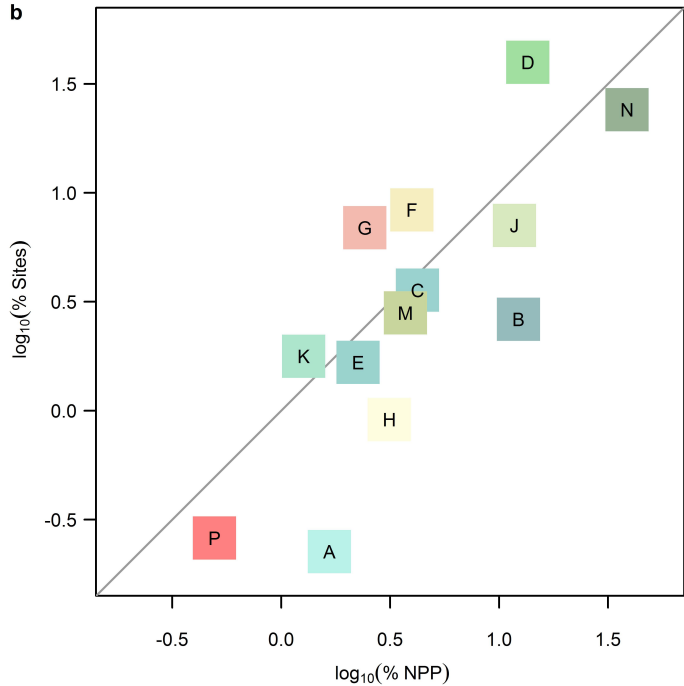
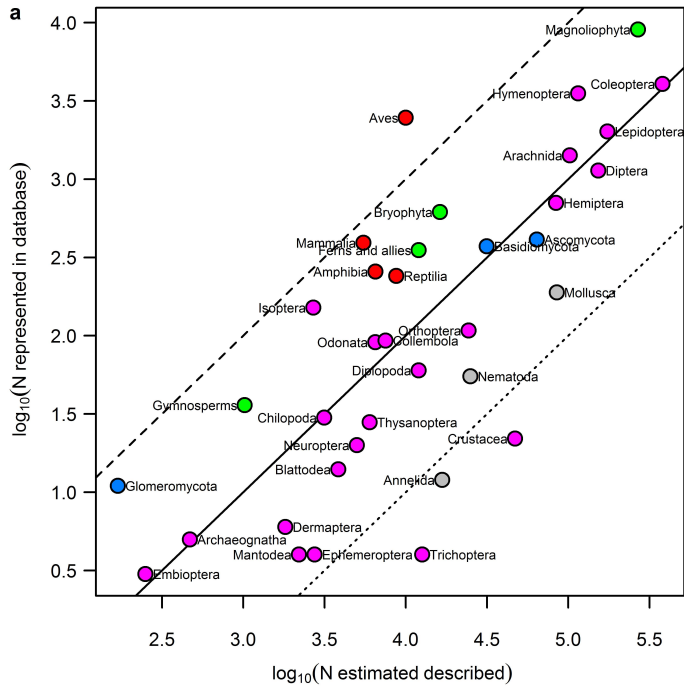


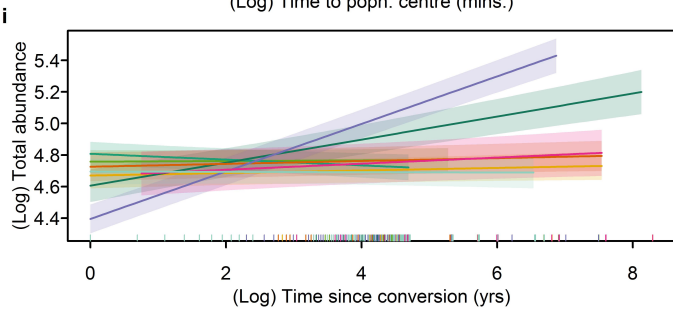
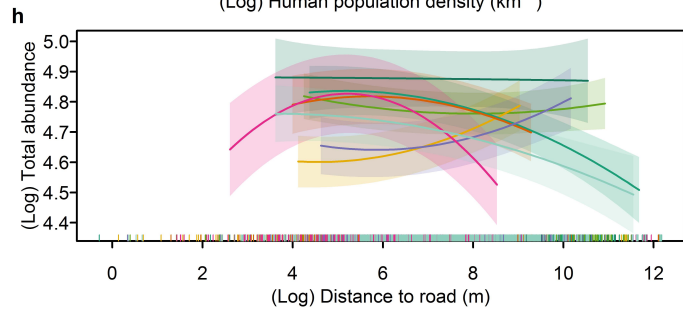
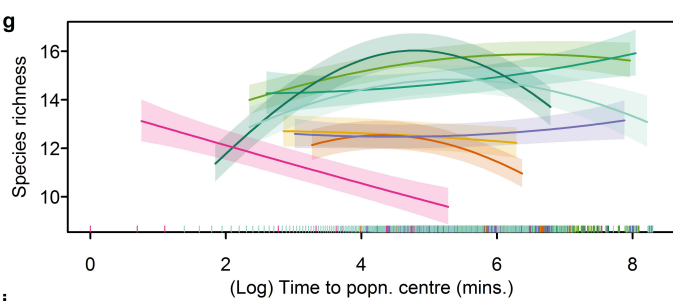
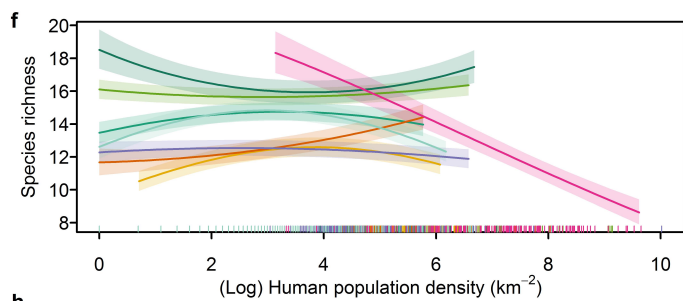
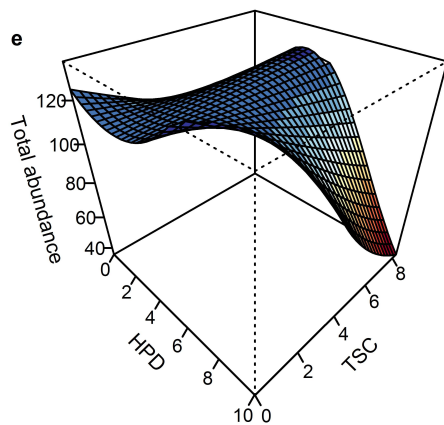
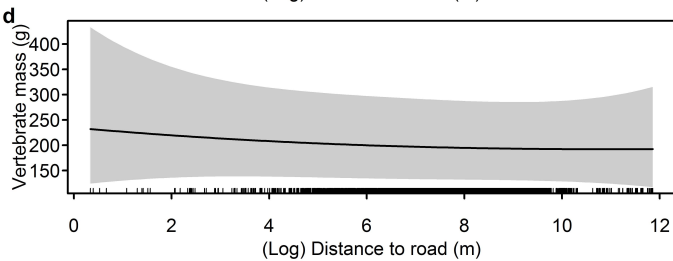
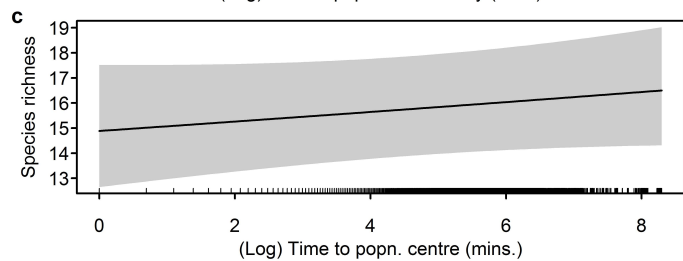
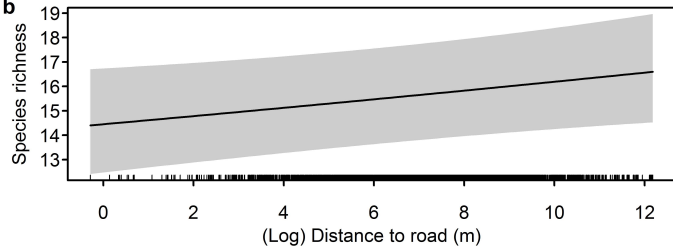
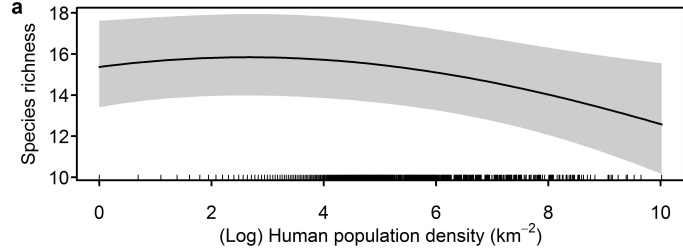


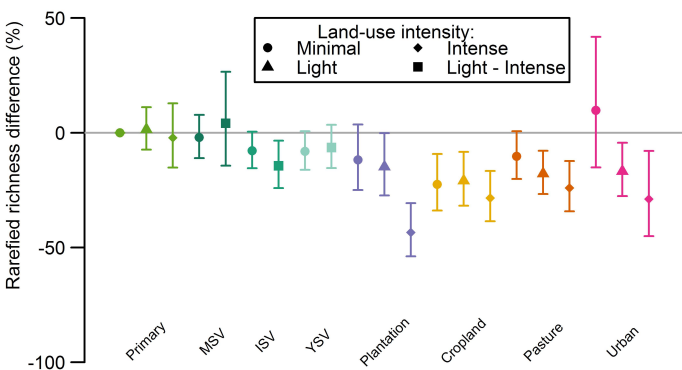
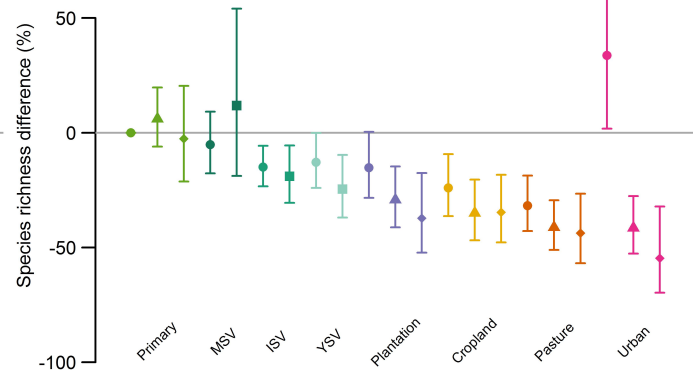
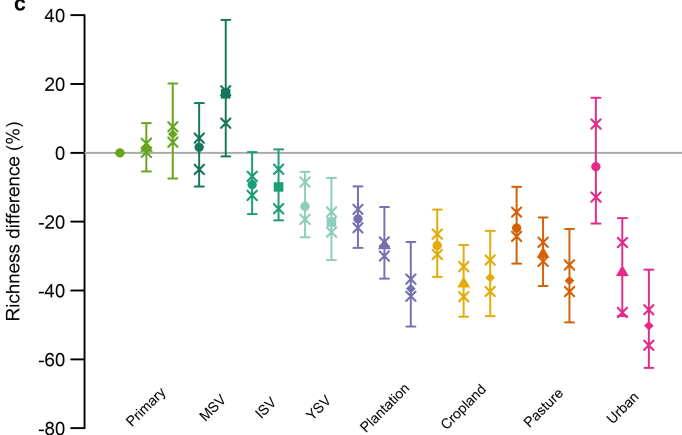
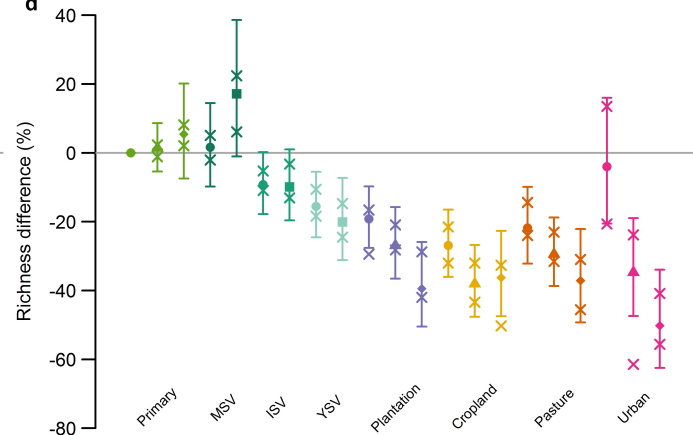


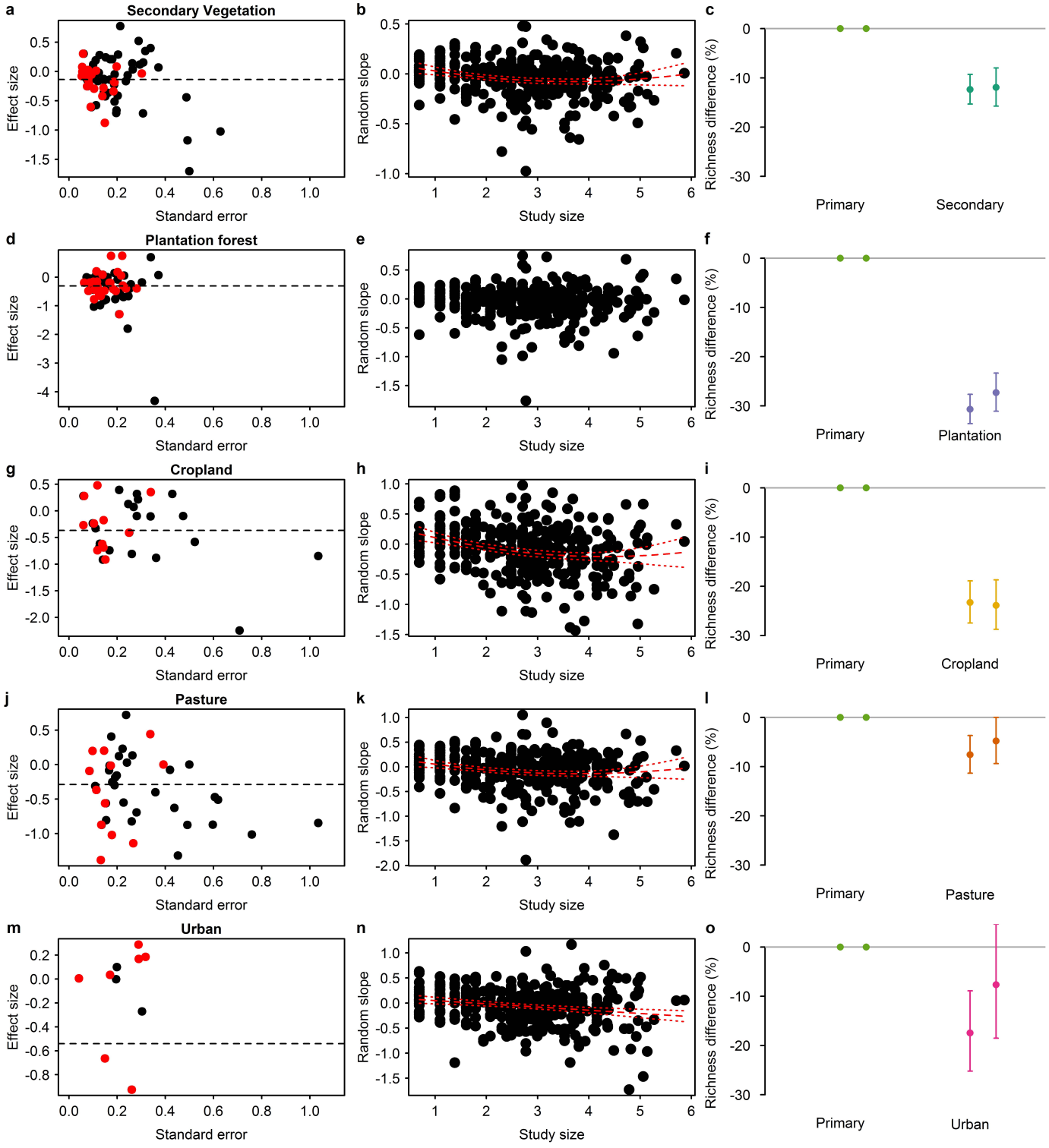
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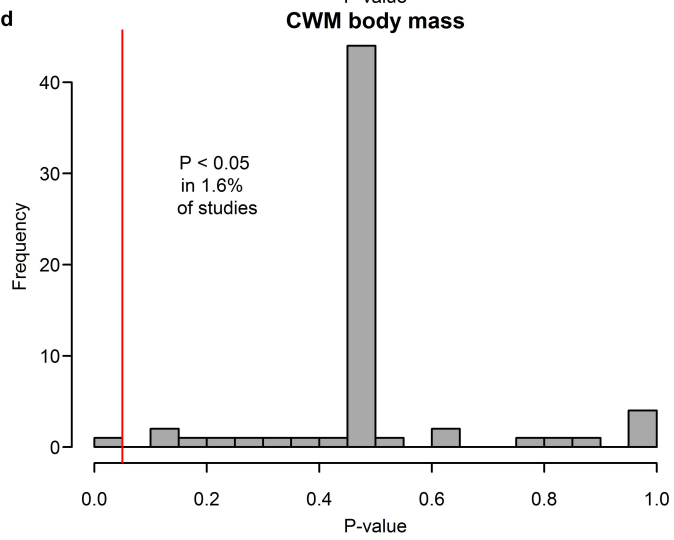
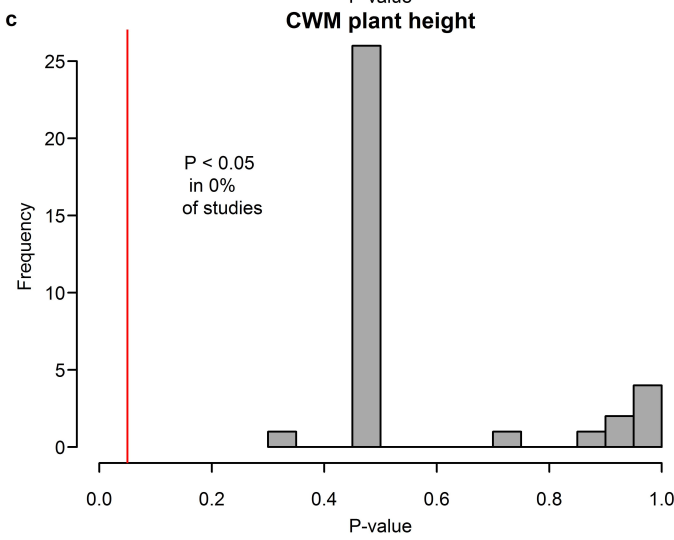
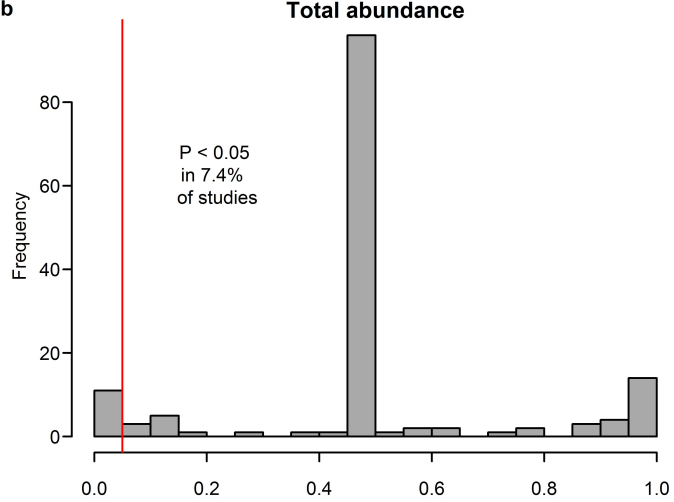
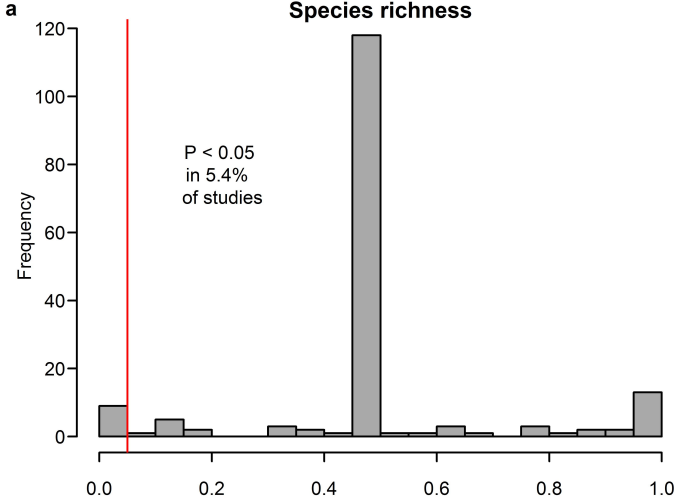


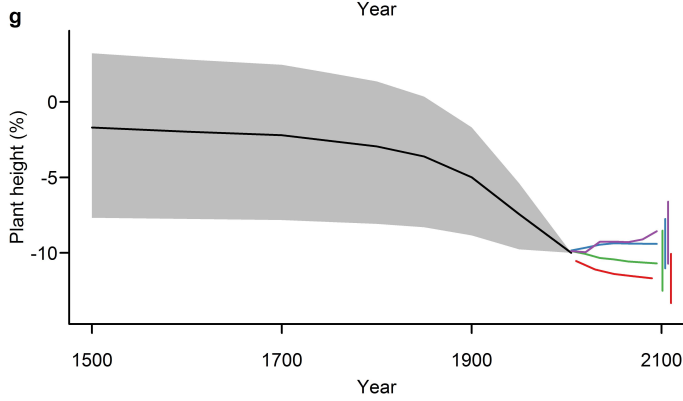
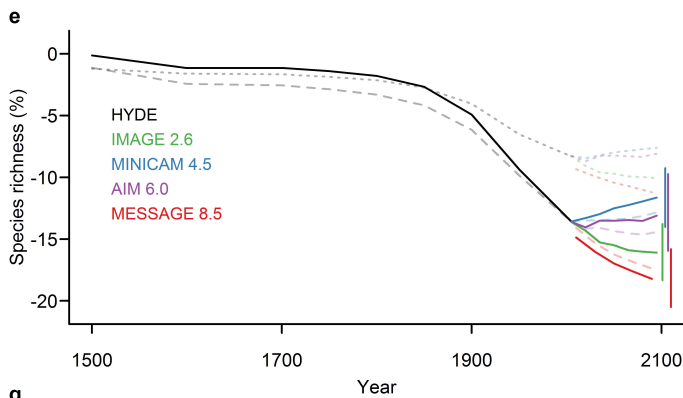
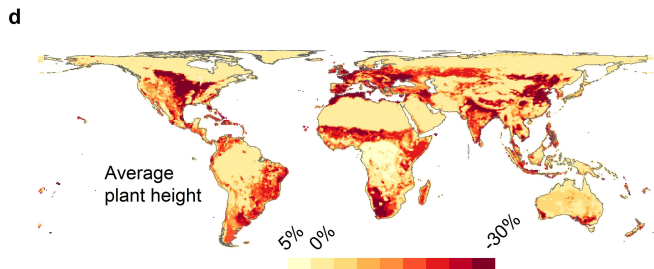
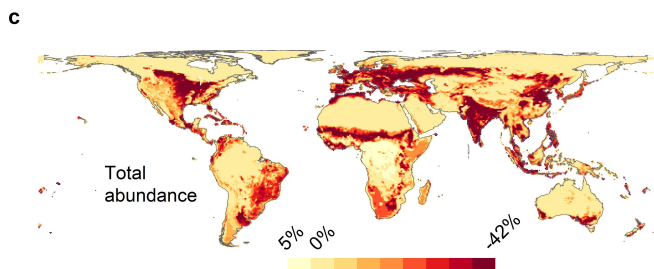
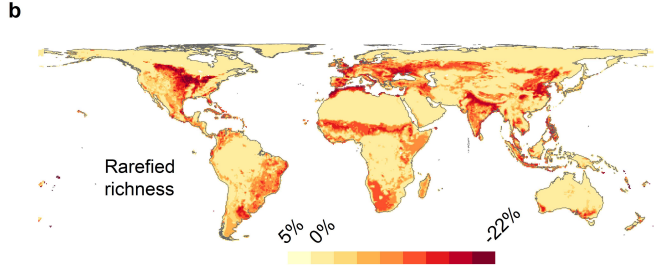
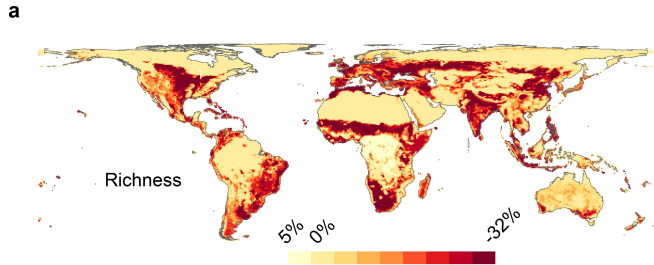


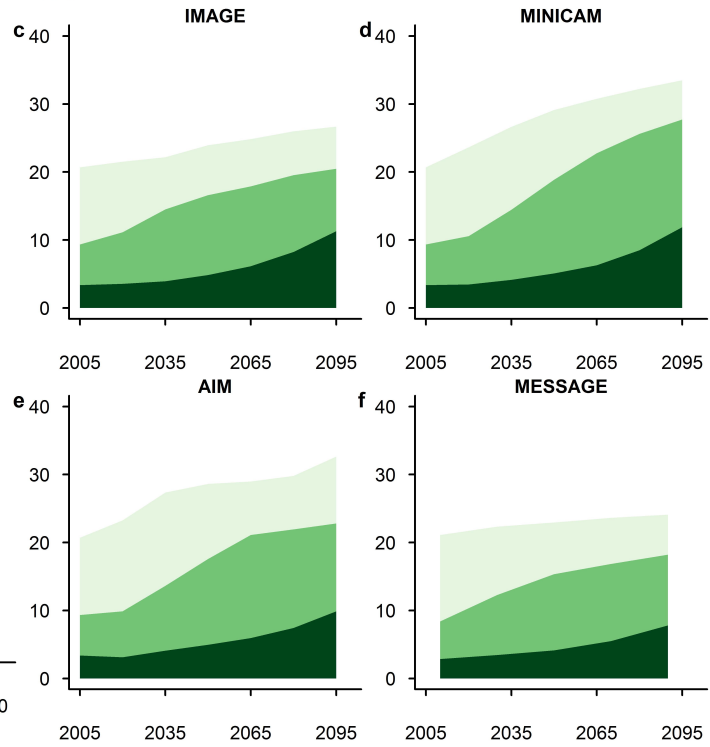
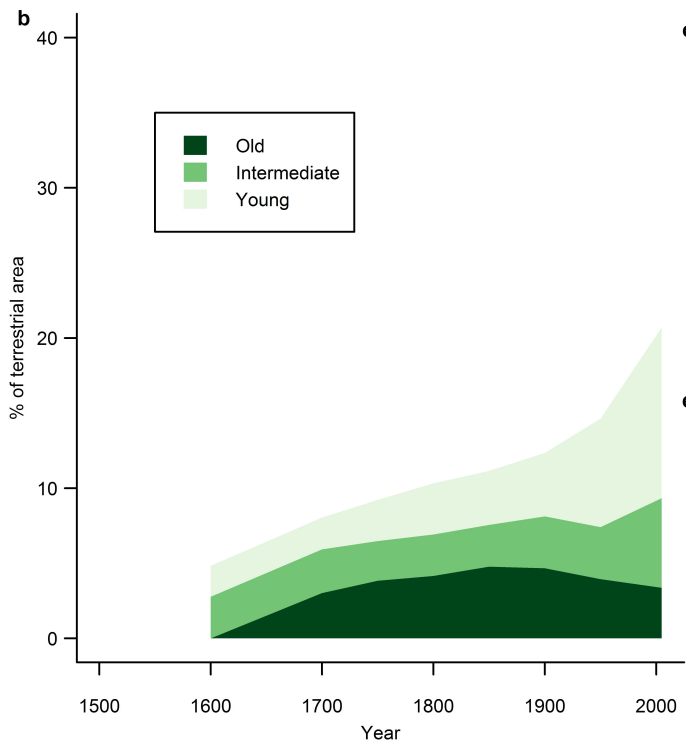
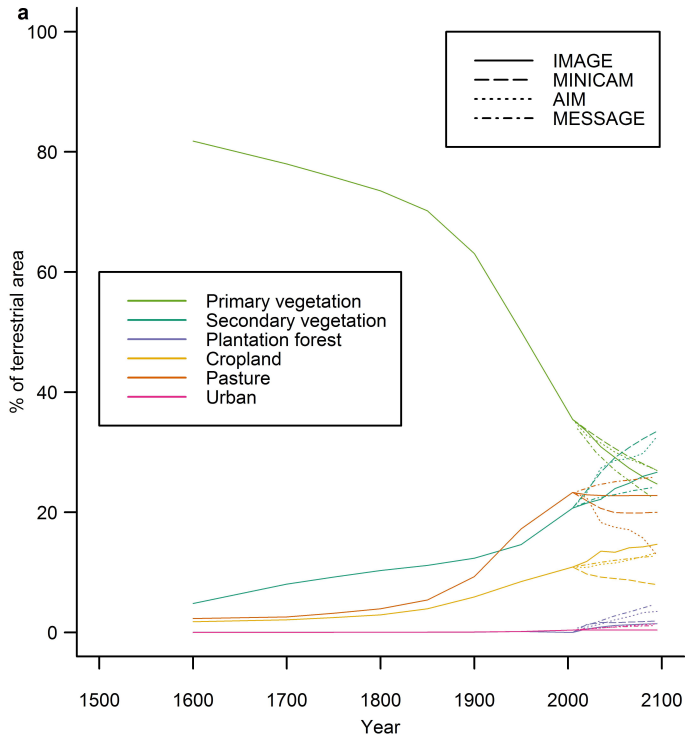


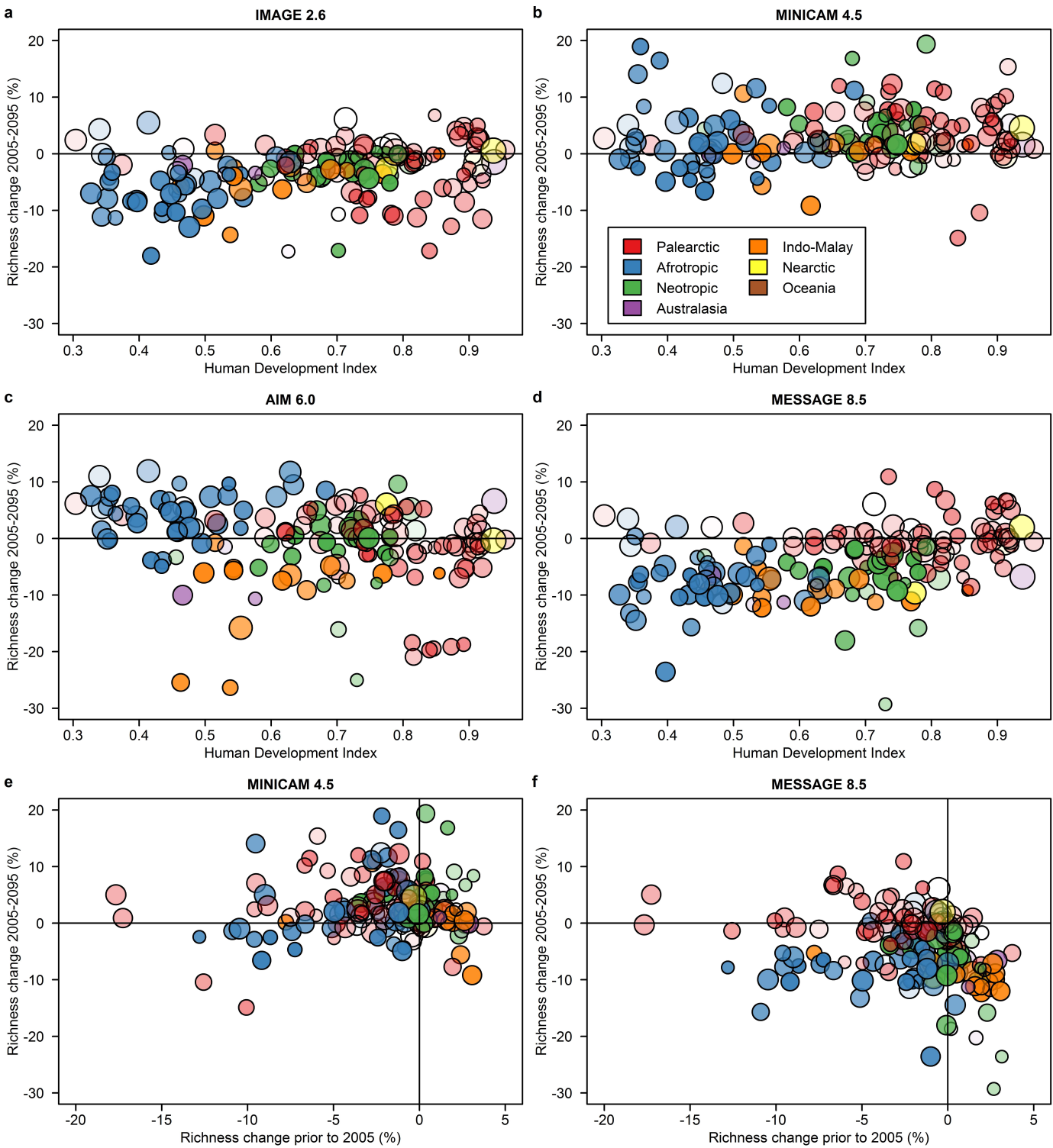
**a****b****c****d**













Level 1 Land Use	Predominant Land Use	Minimal use	Light use	Intense use
<b>No evidence of prior destruction of the vegetation</b>	<b>Primary Vegetation</b>	Any disturbances identified are very minor (e.g., a trail or path) or very limited in the scope of their effect (e.g., hunting of a particular species of limited ecological importance).	One or more disturbances of moderate intensity (e.g., selective logging) or breadth of impact (e.g., bushmeat extraction), which are not severe enough to markedly change the nature of the ecosystem. Primary sites in suburban settings are at least Light use.	One or more disturbances that are severe enough to markedly change the nature of the ecosystem; this includes clear-felling of part of the site too recently for much recovery to have occurred. Primary sites in fully urban settings should be classed as Intense use.
<b>Recovering after destruction of the vegetation</b>	<b>Mature Secondary Vegetation</b>			
	<b>Intermediate Secondary Vegetation</b>			
	<b>Young Secondary Vegetation</b>			
	<b>Secondary Vegetation (indeterminate age)</b>			
<b>Human use (agricultural)</b>	<b>Plantation forest</b>	Extensively managed or mixed timber, fruit/coffee, oil-palm or rubber plantations in which native understorey and/or other native tree species are tolerated, which are not treated with pesticide or fertiliser, and which have not been recently (< 20 years) clear-felled.	Monoculture fruit/coffee/rubber plantations with limited pesticide input, or mixed species plantations with significant inputs. Monoculture timber plantations of mixed age with no recent (< 20 years) clear-felling. Monoculture oil-palm plantations with no recent (< 20 years) clear-felling.	Monoculture fruit/coffee/rubber plantations with significant pesticide input. Monoculture timber plantations with similarly aged trees or timber/oil-palm plantations with extensive recent (< 20 years) clear-felling.
	<b>Cropland</b>	Low-intensity farms, typically with small fields, mixed crops, crop rotation, little or no inorganic fertiliser use, little or no pesticide use, little or no ploughing, little or no irrigation, little or no mechanisation.	Medium intensity farming, typically showing some but not many of the following: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, no crop rotation, mechanisation, monoculture crop. Organic farms in developed countries often fall within this category, as may high-intensity farming in developing countries.	High-intensity monoculture farming, typically showing many of the following features: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, mechanisation, no crop rotation.
	<b>Pasture</b>	Pasture with minimal input of fertiliser and pesticide, and with low stock density ( <i>not</i> high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture either with significant input of fertiliser or pesticide, or with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture with significant input of fertiliser or pesticide, <i>and</i> with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).
<b>Human use (urban)</b>	<b>Urban</b>	Extensive managed green spaces; villages.	Suburban (e.g. gardens), or small managed or unmanaged green spaces in cities.	Fully urban with no significant green spaces.

Global Land Systems classification	Primary	Secondary	Cropland	Pasture	Urban
Cropland, extensive with few livestock	NA	NA	minimal	light	NA
Cropland, extensive with bovines, goats & sheep	NA	NA	minimal	intense	NA
Cropland, extensive with pigs & poultry	NA	NA	minimal	intense	NA
Cropland, medium intensive with few livestock	NA	NA	light	light	NA
Cropland, medium intensive with bovines, goats & sheep	NA	NA	light	intense	NA
Cropland, medium intensive with pigs & poultry	NA	NA	light	intense	NA
Cropland, intensive with few livestock	NA	NA	intense	light	NA
Cropland, intensive with bovines, goats & sheep	NA	NA	intense	intense	NA
Cropland, intensive with pigs & poultry	NA	NA	intense	intense	NA
Mosaic cropland and grassland with bovines, goats and sheep	NA	NA	intense	intense	NA
Mosaic cropland and grassland with pigs & poultry	NA	NA	intense	intense	NA
Mosaic cropland (extensive) and grassland with few livestock	NA	NA	minimal	light	NA
Mosaic cropland (medium intensive) and grassland with few livestock	NA	NA	light	light	NA
Mosaic cropland (intensive) and grassland with few livestock	NA	NA	intense	light	NA
Mosaic cropland and forest with pigs & poultry	NA	NA	intense	intense	NA
Mosaic cropland (extensive) and forest with few livestock	NA	NA	minimal	light	NA
Mosaic cropland (medium intensive) and forest with few livestock	NA	NA	light	light	NA
Mosaic cropland (intensive) and forest with few livestock	NA	NA	intense	light	NA
Dense forest	minimal	minimal	NA	NA	NA
Open forest with few livestock	light	light	NA	light	NA
Open forest with pigs & poultry	intense	intense	NA	intense	NA
Mosaic grassland and forest	minimal	minimal	NA	NA	NA
Mosaic grassland and bare	minimal	minimal	NA	NA	NA
Natural grassland	minimal	minimal	NA	NA	NA
Grassland with few livestock	NA	NA	NA	light	NA
Grassland with bovines, goats and sheep	NA	NA	NA	intense	NA
Bare	NA	NA	NA	NA	NA
Bare with few livestock	NA	NA	NA	light	NA
Peri-urban and villages	NA	NA	NA	NA	minimal
Urban	NA	NA	NA	NA	intense

## Statistical Model Structure

In the following section, we give the R formula for the final best model (i.e. after stepwise variable selection) of each site-level diversity metric. Response variables are SR (species richness), LA ( $\log_e$  total abundance), PH (community-weighted mean  $\log_{10}$  plant height) and AM (community-weighted mean  $\log_{10}$  animal body mass). Random intercepts considered were SS (study identity, nested within source publication; a source could have multiple studies where sampling methods differed e.g. for different taxonomic groups); SSB (spatial block nested within study nested within source) and – for models with Poisson errors, to control for overdispersion – SSBS (site nested within spatial block nested within study nested within source). Note that when random intercepts are strictly nested, the following two ways of specifying the random-effects structure are exactly equivalent: (1|SS) + (1|SSB) + (1|SSBS) and (1|SS/SSB/SSBS). Explanatory variables considered (fitted as fixed effects) were: LU (land use), UI (land-use intensity), LUI (land use in interaction with land-use intensity), HPD ( $\log_e$  human population density), DR ( $\log_e$  distance to nearest road), DP ( $\log_e$  distance to nearest major population centre and TSC (time since 30% conversion of a landscape to human uses – cropland, pasture and urban).

```
SModel<-glmer(SR ~ LUI + poly(HPD,2) + poly(DR,1) + poly(DP,2) + LU:poly(HPD,2) +  
LU:poly(DP,2) + (1+LU+UI|SS) + (1|SSB) +  
(1|SSBS),family="poisson",control=glmerControl(optimizer="bobyqa"))
```

```
AModel<-lmer(LA ~ LUI + poly(HPD,2) + poly(DR,2) + poly(TSC,1) + LU:poly(DR,2) +  
LU:poly(TSC,1) + poly(HPD,2):poly(TSC,1) + (1+LU+UI|SS) + (1|SSB),  
lmerControl(optimizer="bobyqa"))
```

```
PHModel<-lmer(PH ~ LU + poly(HPD,1) + (1+LU|SS), lmerControl(optimizer="bobyqa"))
```

```
AMModel<-lmer(AM ~ poly(DR,2) + (1+LU+poly(DR,2)|SS) + (1|SSB),  
lmerControl(optimizer="bobyqa"))
```

## Full Statistical Results

The four types of diversity metric that we analyzed (within-sample species richness, rarefaction-based richness, total abundance, average organism size) are not completely independent of one another. If we were to assume that they were entirely dependent on each other (which is not the case) and correct for multiple testing, we would apply a threshold P-value of 0.0125 instead of 0.05. In the following, we indicate with an \* those effects that would not be significant with the more stringent threshold, thus identifying overall the most and least restrictive putative outcomes. The final structure of the model that was used to make the main spatial and temporal projections of species richness would not have changed had the more stringent threshold been applied: accessibility to humans and its interaction with land use were the only terms that would have been dropped from the final models, but these variables were not included in the projections owing to a lack of past and future estimates of accessibility.

For **within-sample species richness**, there was a significant effect of the interaction between land use and land-use intensity ( $\chi^2_{18, 113} = 89.0$ ;  $P < 0.001$ ;  $\Delta AIC = -52.3$ ), and of land use ( $\chi^2_{7, 71} = 58.3$ ;  $P < 0.001$ ;  $\Delta AIC = -38.3$ ) and intensity ( $\chi^2_{2, 71} = 14.1$ ;  $P < 0.001$ ;  $\Delta AIC = -9.47$ ) separately. Human population density ( $\chi^2_{1, 71} = 5.71$ ;  $P = 0.017^*$ ;  $\Delta AIC = -3.85$ ), distance to roads ( $\chi^2_{1, 71} = 5.68$ ;  $P = 0.017^*$ ;  $\Delta AIC = -7.29$ ) and accessibility to humans ( $\chi^2_{1, 71} = 4.82$ ;  $P = 0.028^*$ ;  $\Delta AIC = +0.14$ ) had significant effects on species richness, with a quadratic polynomial supported for human population density, but only linear terms for proximity to roads and accessibility. Note that the effect of

accessibility was weak with inclusion causing a slight increase in the model's AIC value. Human population density ( $\chi^2_{14, 113} = 34.0$ ;  $P = 0.0020$ ;  $\Delta AIC = -6.08$ ) and accessibility ( $\chi^2_{14, 113} = 24.5$ ;  $P = 0.040^*$ ;  $\Delta AIC = +2.91$ ) also had significant effects in interaction with land use, although the latter was a weak effect whose inclusion led to an increase in AIC. Human population density, distance to roads and accessibility to humans did not show any significant two-way interactions, nor did distance to roads interact significantly with land use ( $P > 0.05$ ;  $\Delta AIC > +1.74$ ). Time since substantial conversion to human land use did not have a significant effect on species richness alone, or in interaction with any other variable ( $P > 0.05$ ;  $\Delta AIC > +0.36$ ).

For **rarefaction-based species richness**, there was a significant effect of land use ( $\chi^2_{7, 47} = 16.2$ ;  $P = 0.023^*$ ;  $\Delta AIC = -2.21$ ), land-use intensity ( $\chi^2_{2, 47} = 13.5$ ;  $P = 0.001$ ;  $\Delta AIC = -9.46$ ) and their interaction ( $\chi^2_{11, 65} = 24.6$ ;  $P = 0.011$ ;  $\Delta AIC = -2.55$ ), but not of any of the continuous variables ( $P > 0.05$ ;  $\Delta AIC > 0.919$ ). We did not consider any interaction terms except for that between land use and intensity owing to the much smaller number of sites for which rarefaction-based richness could be calculated.

Land use and land-use intensity in interaction also had a significant effect on **total abundance** ( $\chi^2_{18, 108} = 43.6$ ;  $P < 0.001$ ;  $\Delta AIC = -21.4$ ). Land-use intensity also had a significant effect alone ( $\chi^2_{2, 13} = 13.7$ ;  $P = 0.0011$ ;  $\Delta AIC = -9.67$ ), but land use did not ( $\chi^2_{7, 69} = 8.76$ ;  $P = 0.27$ ;  $\Delta AIC = +3.28$ ). Human population density had a significant effect alone ( $\chi^2_{1, 13} = 5.90$ ;  $P = 0.015$ ;  $\Delta AIC = -3.90$ ), and in interaction with time since substantial human conversion of the landscape ( $\chi^2_{2, 108} = 11.0$ ;  $P = 0.0041$ ;  $\Delta AIC = -6.76$ ). Time since human conversion of the landscape also had a significant effect on total abundance in interaction with land use ( $\chi^2_{7, 108} = 29.4$ ;  $P < 0.001$ ;  $\Delta AIC = -13.5$ ), but not alone ( $\chi^2_{1, 70} = 3.12$ ;  $P = 0.077$ ;  $\Delta AIC = +0.837$ ). Proximity to roads did not have a significant effect on total abundance alone ( $\chi^2_{1, 74} = 0.045$ ;  $P = 0.83$ ;  $\Delta AIC = +1.80$ ) or in interaction with any other variable ( $P > 0.05$ ;  $\Delta AIC > +0.610$ ).

Land use ( $\chi^2_{4, 22} = 19.6$ ;  $P < 0.001$ ;  $\Delta AIC = -11.6$ ) and human population density (linear term only:  $\chi^2_{1, 22} = 3.9$ ;  $P = 0.048^*$ ;  $\Delta AIC = -1.90$ ) had significant effects on **community-weighted mean plant height**, but distance to roads ( $\chi^2_{1, 25} = 2.77$ ;  $P = 0.096$ ;  $\Delta AIC = -0.765$ ) and accessibility ( $\chi^2_{1, 27} = 1.74$ ;  $P = 0.19$ ;  $\Delta AIC = +1.80$ ) did not. Only proximity to nearest road ( $\chi^2_{4, 11} = 41.7$ ;  $P < 0.001$ ;  $\Delta AIC = -33.7$ ) had a significant effect on **community-weighted mean animal body mass** (all other variables,  $P > 0.05$ ;  $\Delta AIC > +0.706$ ). We did not consider land-use intensity, time since substantial human conversion of the landscape, or any interactions between variables in these models, because the datasets were much smaller for these metrics than for those reported above.

## Estimated Effect Sizes

**Table S1. Relative biodiversity values at each level of each modelled human pressure.** Values are shown relative to an un-impacted baseline (primary vegetation, minimal intensity of use, zero human population density, and maximum observed distance to roads and travel time to major city. Variables other than that presented were held at their reference levels for factors (land use = primary vegetation; land-use intensity = minimal) or at the median observed values of the continuous pressure variables. First numbers give modelled mean estimates and numbers in brackets the 95% confidence limits. Land-use intensity was not considered for mean plant height and mean animal mass, so a single value is given for each land use.

Pressure level	Species richness	Total abundance	Rarefaction-based richness	Mean plant height	Mean animal mass
Primary vegetation (Minimal use)	100	100	100	100	
Primary vegetation (Light use)	101.4 (94.6 - 108.6)	103.8 (88.9 - 121.3)	101.5 (92.6 - 111.1)		
Primary vegetation (Intense use)	105.4 (92.5 - 120.1)	130.7 (98.9 - 172.8)	97.8 (84.8 - 112.8)		
Mature secondary vegetation (Minimal use)	101.6 (90.2 - 114.5)	104.0 (82.2 - 131.4)	97.9 (88.9 - 107.8)	96.0 (90.4 - 102.0)	NS
Mature secondary vegetation (Light/intense use)	117.1 (99.0 - 138.6)	128.5 (85.3 - 193.6)	104.1 (85.6 - 126.6)		
Intermediate secondary vegetation (Minimal use)	90.8 (82.2 - 100.2)	95.2 (78.3 - 115.7)	92.2 (84.6 - 100.4)		
Intermediate secondary vegetation (Light/intense use)	90.1 (80.4 - 101.0)	76.6 (59.0 - 99.3)	85.6 (75.9 - 96.5)		
Young secondary vegetation (Minimal use)	84.4 (75.4 - 94.5)	89.0 (72.0 - 110.0)	91.9 (83.9 - 100.6)		
Young secondary vegetation (Light/intense use)	79.9 (68.8 - 92.7)	85.5 (64.0 - 114.2)	93.6 (84.6 - 103.5)		
Plantation forest (Minimal use)	80.8 (72.4 - 90.2)	113.4 (87.0 - 147.8)	88.2 (75.0 - 103.6)	90.2 (81.0 - 100.3)	NS
Plantation forest (Light use)	73.1 (63.4 - 84.2)	77.8 (60.6 - 99.9)	85.2 (72.7 - 99.8)		
Plantation forest (Intense use)	60.6 (49.5 - 74.1)	95.7 (68.1 - 134.5)	56.6 (46.2 - 69.3)		
Cropland (Minimal use)	73.1 (64.0 - 83.5)	89.4 (69.2 - 115.4)	77.5 (66.1 - 90.8)	85.8 (77.2 - 95.3)	NS
Cropland (Light use)	61.9 (52.4 - 73.2)	54.9 (40.1 - 75.1)	79.1 (68.2 - 91.6)		
Cropland (Intense use)	63.7	68.7	71.5		

use)	(52.6 - 77.3)	(47.1 - 100.2)	(61.4 - 83.4)		
Pasture (Minimal use)	78.2 (67.8 - 90.1)	95.2 (73.6 - 123.1)	89.7 (79.9 - 100.7)	72.0 (62.5 - 83.1)	NS
Pasture (Light use)	70.6 (61.3 - 81.2)	72.2 (56.0 - 93.0)	82.2 (73.3 - 92.1)		
Pasture (Intense use)	62.9 (50.8 - 77.9)	65.1 (44.1 - 96.0)	76.0 (65.8 - 87.7)		
Urban (Minimal use)	96.0 (79.4 - 116.0)	81.8 (51.6 - 129.7)	109.7 (84.9 - 141.8)	Not estimated	NS
Urban (Light use)	65.3 (52.6 - 81.0)	55.1 (34.8 - 87.3)	83.2 (72.4 - 95.6)		
Urban (Intense use)	49.8 (37.5 - 66.0)	37.6 (21.1 - 67.2)	71.1 (54.9 - 92.1)		
Human population density (minimum)	100	100	NS	100	NS
Human population density (median)	102.8 (90.7 - 116.6)	114.6 (86.9 - 151.2)	NS	95.3 (78.2 - 116.1)	NS
Human population density (maximum)	81.8 (66.1 - 101.2)	82.5 (54.2 - 125.5)	NS	88.2 (71.6 - 108.6)	NS
Distance to nearest road (furthest)	100	NS	NS	NS	100
Distance to nearest road (median)	95.2 (84.0 - 108.0)	NS	NS	NS	100.5 (84.8 - 119.0)
Distance to nearest road (closest)	86.8 (74.8 - 100.7)	NS	NS	NS	108.5 (82.7 - 142.3)
Travel time to nearest city (longest)	100	NS	NS	Not estimated	Not estimated
Travel time to nearest city (median)	95.8 (84.5 - 108.6)	NS	NS	Not estimated	Not estimated
Travel time to nearest city (shortest)	90.2 (76.7 - 106.2)	NS	NS	Not estimated	Not estimated

**Table S2. Sample size in each land-use and use-intensity combination.** Numbers of sites in each combination and numbers of studies in which a given combination is sampled are given.

Land-use—Use-intensity combination	Number of sites	Number of studies
Primary vegetation (Minimal use)	1546	183
Primary vegetation (Light use)	860	76
Primary vegetation (Intense use)	449	33
Mature secondary vegetation (Minimal use)	198	52
Mature secondary vegetation (Light/intense use)	213	23
Intermediate secondary vegetation (Minimal use)	404	55
Intermediate secondary vegetation (Light/intense use)	269	30

Young secondary vegetation (Minimal use)	431	50
Young secondary vegetation (Light/intense use)	331	34
Plantation forest (Minimal use)	356	47
Plantation forest (Light use)	402	42
Plantation forest (Intense use)	238	29
Cropland (Minimal use)	427	45
Cropland (Light use)	632	43
Cropland (Intense use)	703	36
Pasture (Minimal use)	525	43
Pasture (Light use)	434	52
Pasture (Intense use)	174	23
Urban (Minimal use)	174	23
Urban (Light use)	244	26
Urban (Intense use)	195	18

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