

# Global effects of land use on local terrestrial biodiversity

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

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

Spatial comparisons provide an alternative source of evidence on how human pressures affect biodiversity, assuming that differences in pressures have caused observed biodiversity differences between otherwise matched sites<sup>10–12</sup>. The prevalence of published spatial comparisons makes it possible to go beyond particular taxa or regions<sup>11,12</sup> to develop global, taxonomically representative models. Furthermore, the willingness of

many researchers to share their raw data makes it possible to consider multiple aspects of biodiversity, rather than the single, simple metrics of most existing models<sup>10</sup>, which cannot capture all key aspects of diversity<sup>13</sup>.

We present the most geographically and taxonomically representative models to date of how several aspects of the composition and diversity of terrestrial assemblages respond to multiple human pressures. The explanatory variables in our models most directly measure land use and infrastructure, but might correlate<sup>14,15</sup> with two other important pressures, harvesting and invasive species, for which comparable high-resolution spatial data are unavailable globally. We exclude climate change effects because they are not captured well by spatial comparisons. We use our models to infer past net changes in assemblages since the year 1500, project future changes over this century under different socioeconomic scenarios of land use, and relate projected national changes in local biodiversity to socioeconomic variables and natural biodiversity.

Our models of local within-sample species richness (hereafter 'richness'), rarefaction-based species richness (hereafter 'rarefied richness'), total abundance, compositional turnover and average organism size are

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based on among-site comparisons of ecological assemblage composition collated from the literature as part of the PREDICTS project<sup>16</sup>. The data set consisted of 1,130,251 records of abundance and 320,924 of occurrence or species richness at 11,525 sites (2–360 sites per study, median 15; Fig. 1a). These data, from 284 publications (see Methods), represent 26,953 species (1.4% of the number formally described<sup>17</sup>) and 13 of the 14 terrestrial biomes (Extended Data Fig. 1). Each site was

scored for six putative pressures: land use<sup>11</sup> and use intensity<sup>18</sup>, land-use history<sup>19</sup>, human population density<sup>20</sup>, proximity to roads<sup>21</sup> and accessibility from the nearest large town. Random effects in our models accounted for study-level differences in response variables and sampling methods, and for the within-study spatial arrangement of sites.

## Effects of pressure on site-level diversity

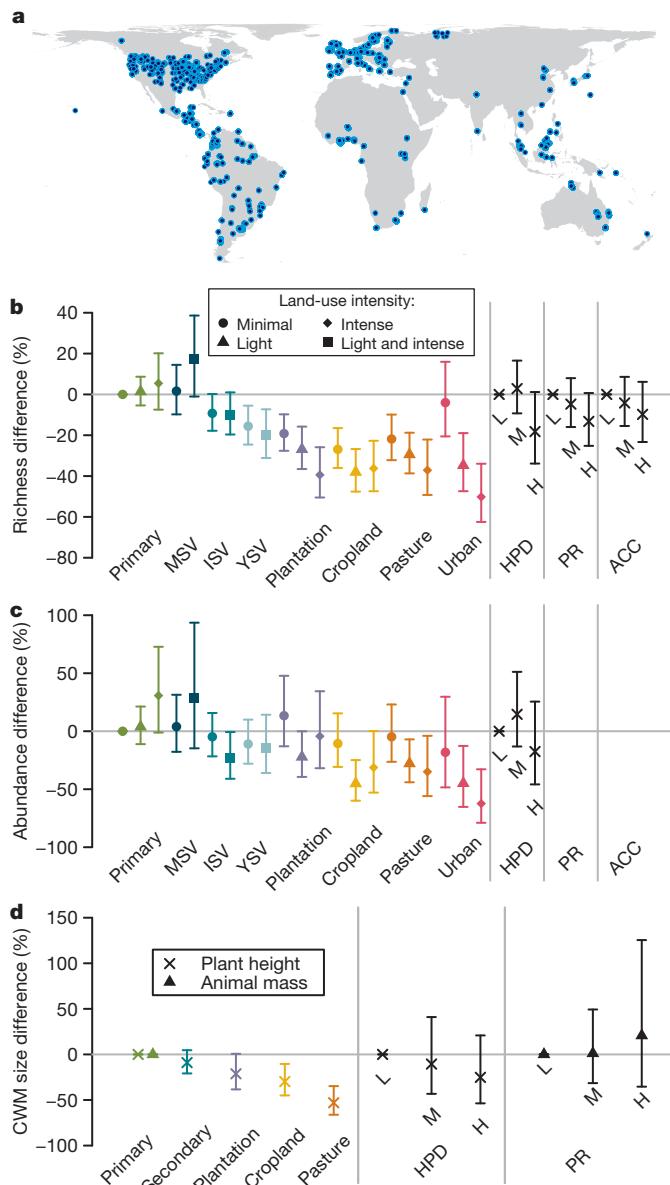
Local richness, rarefied richness and total abundance were most strongly influenced by land use and land-use intensity: they were substantially lower in most other land-use types than in primary vegetation, especially in intensively used areas (Fig. 1; see Supplementary Information for statistics and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

The importance of secondary vegetation for conservation is a hotly debated topic<sup>11, 24, 25</sup>, and an important one, given that this land use will soon become the most widespread type<sup>26</sup>. We find that the answer depends strongly on the secondary vegetation's maturity: early-stage communities tend to be less diverse than those in primary vegetation and are compositionally distinct, but these differences are much reduced in mature secondary vegetation (Figs 1 and 2; we caution though that not all data sources clearly distinguished mature secondary from primary vegetation). This successional rise in diversity accords with a recent meta-analysis of plant communities over time<sup>7</sup>.

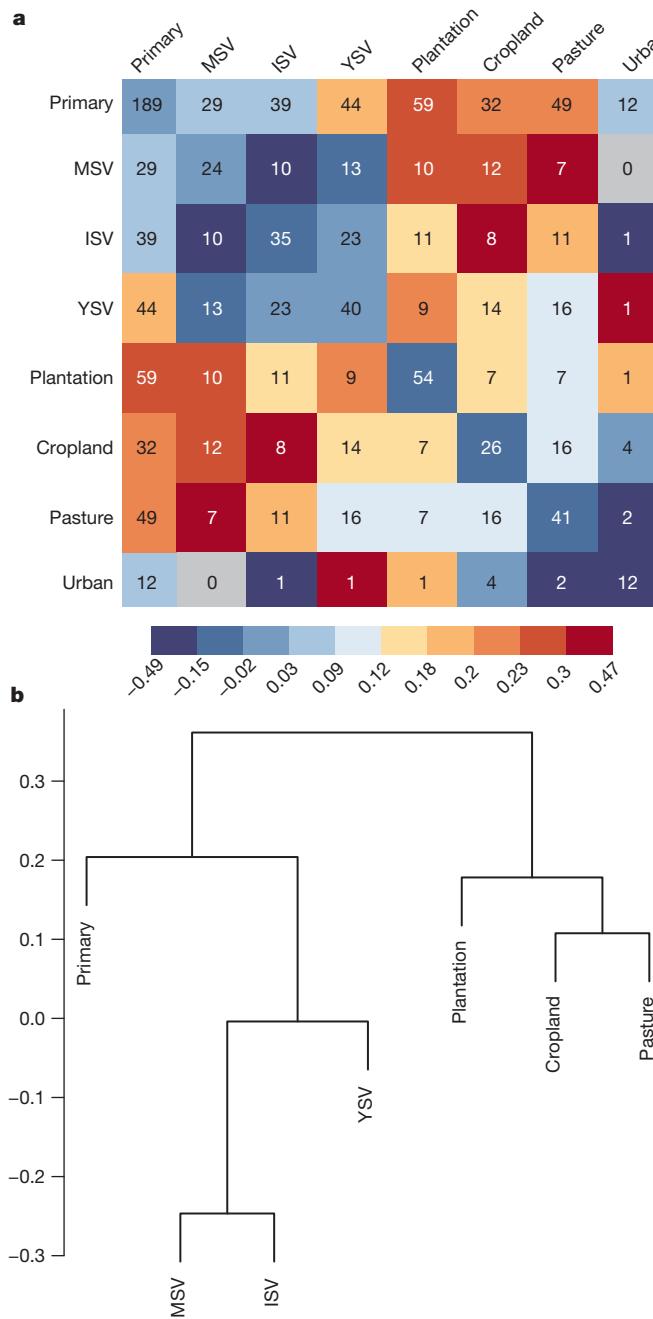
Net changes in diversity provide an incomplete view of the effects of human activities on biodiversity because they ignore the replacement of original species by newcomers<sup>8</sup>. We therefore analysed how land use affects similarity in species composition between sites. Communities under the same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

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

Models like ours that substitute space for time ignore time lags in biotic changes, which can be important<sup>31</sup>. We also assume that land uses



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



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

### Global effects on local diversity to date

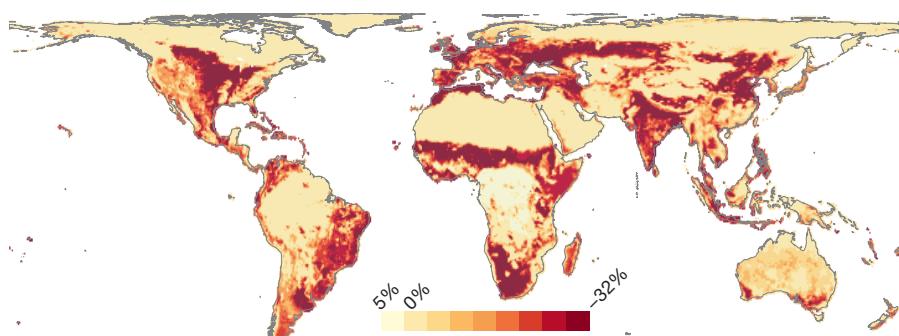
By applying our model for within-sample species richness—the most widely used and understood biodiversity measure—to maps of current pressure variables<sup>10</sup>, we estimated the global pattern of net local changes to date in plot-level richness (Fig. 3; we did not estimate total richness within the  $0.5^\circ \times 0.5^\circ$  grid cells). Human-dominated areas are inferred to have lost much more local diversity than have regions where more natural vegetation remains. The worst-affected cells showed a 31% reduction in average local richness—probably enough to alter ecosystem functioning substantially<sup>4</sup>. Local richness increased in 1.7% of cells (by  $\leq 4.8\%$ ). Total abundance and, less strongly, rarefied richness showed broadly similar patterns (Extended Data Fig. 6).

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

Richness is estimated to have declined most rapidly in the 19th and 20th centuries (Fig. 4), with other metrics showing similar responses (Extended Data Fig. 6). By 2005, we estimate that land use and related pressures had reduced local richness by an average of 13.6% (95% confidence interval (CI): 9.1–17.8%) and total abundance by 10.7% (95% CI: 3.8% gain to 23.7% reduction) compared with what they would have been in the absence of human effects. Approximately 60% of the decline in richness was independent of effects on abundance; average rarefied richness has fallen by 8.1% (95% CI: 3.5–12.9%). Although these confidence limits omit uncertainty in the projections of land use and other pressures, there is less uncertainty in estimates of current pressure levels than in changes over time<sup>33</sup>.

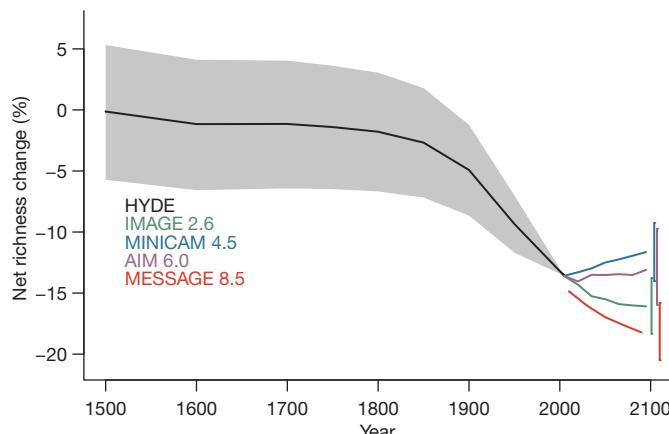
Our inferences contrast with two recent analyses of community time series<sup>7,8</sup>, which suggested no overall trend in local diversity, and with the Living Planet Index<sup>3</sup>, which, based on vertebrate population time series, reports a much more rapid decline in abundance than we infer.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

are situated randomly within studies relative to sites' intrinsic suitability for biodiversity. Adding global data on other important pressures as they become available, and also incorporating climate change, will give a more complete picture of human effects on local biodiversity.



**Figure 3 | Net change in local richness caused by land use and related pressures by 2000.**

Projections used an IMAGE reference scenario<sup>10</sup>. The baseline landscape was assumed to be entirely uninhabited, unused primary vegetation. Shown using a Lambert Cylindrical Equal-Area projection at  $0.5^\circ \times 0.5^\circ$  resolution.



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

## Global and national projections to 2095

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

Projected net changes in average local diversity to 2095 vary widely among scenarios (Fig. 4 and Extended Data Fig. 6). The scenario with the least climate change (IMAGE 2.6) yields the second-worst outcome for biodiversity, because it assumes rapid conversion of primary vegetation, especially in the tropics, to crops and biofuels<sup>26</sup> (Table 1 and Extended Data Fig. 7). These projections do not imply that low-emission

scenarios must entail large losses of biodiversity, but instead reflect that scenario's mitigation strategy. Indeed, in MiniCAM 4.5 (where mitigation is through carbon markets, crop improvements and diet shifts, Table 1) average richness is projected to increase (though other diversity metrics respond more weakly, Extended Data Fig. 6). The worst biodiversity outcomes arise from the scenario with most climate change (MESSAGE 8.5) in which rapid human population growth drives widespread agricultural expansion (Table 1 and Extended Data Fig. 7). This scenario, which has been characterized as 'business-as-usual'<sup>35</sup>, most closely matches recent trends in emissions<sup>36</sup> and gives the worst outcomes even though our projections omit direct climate effects on local assemblages.

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

Such globally inequitable outcomes might be avoidable. The best scenario for biodiversity (MiniCAM 4.5; Fig. 4) yielded country-level outcomes that are relatively independent of Human Development Index, native species richness (Fig. 5b) and past changes (Extended Data Fig. 8e). For local richness, outcomes under MiniCAM4.5 were better than MESSAGE 8.5 for 93% of countries worldwide (Fig. 5c).

Under AIM 6.0, most Afrotropical countries are projected to gain in local richness but heavy losses are inferred for the Indo-Malay region (Extended Data Fig. 8). Projections under IMAGE 2.6 are spatially similar to those under MESSAGE 8.5. The land-use change caused by the biofuels-based strategy in IMAGE 2.6 is projected to have a major negative effect overall on terrestrial biodiversity (Extended Data Fig. 8).

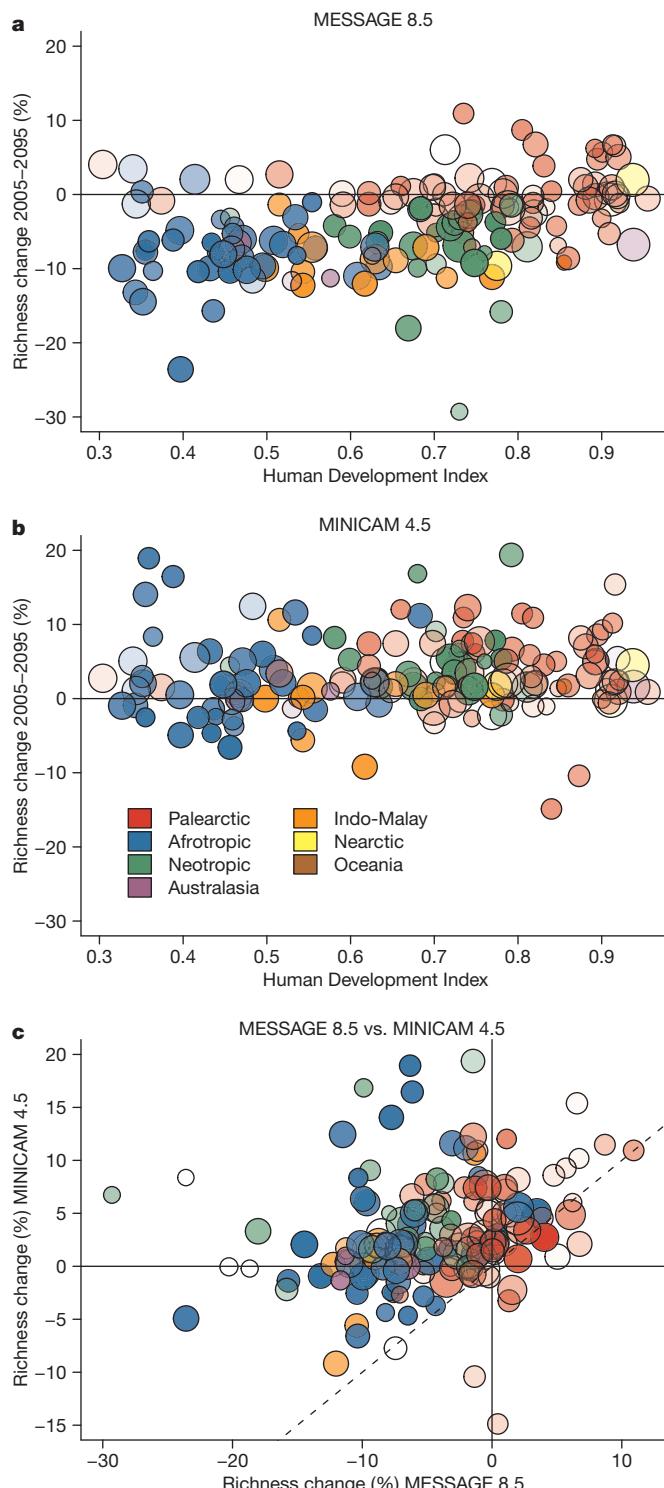
## Conclusions

Many assessments of the state of biodiversity have focused on global metrics such as rates of species extinction<sup>37</sup>, but resilient delivery of ecosystem functions and services is more likely to depend on local diversity<sup>4–6</sup>. Our models suggest land-use changes and associated pressures strongly reduce local terrestrial biodiversity, and we estimate global average reductions to date of 13.6% in within-sample species richness, 10.7% in total abundance and 8.1% in rarefaction-based species richness (Figs 3 and 4). Climate change, which we could not include in our

**Table 1 | Key features of the four RCP scenarios**

Scenario	Land use (see also Extended Data Fig. 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.

Land-use and human population assumptions are detailed in ref. 26, energy assumptions in refs 40–42, and climate implications in ref. 43.



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

framework, is likely to exacerbate losses, especially under business-as-usual<sup>38</sup>, although direct effects of climate change will increase local diversity in some regions<sup>8</sup>.

It is important to remember that the habitat conversion and associated changes that reduced local biodiversity had largely positive consequences for people; agricultural intensification underpinned many countries' development. However, benefits have not been shared equally among or within countries<sup>39</sup>. Losses of local species richness exceeding 20% are likely to substantially impair the contribution of biodiversity to ecosystem function and services, and thus to human well-being<sup>4</sup>. We estimate that reductions in average plot-level species richness currently exceed this level for 28.4% of grid cells, increasing to 41.5% of cells by 2095 under business-as-usual (note that we do not estimate or project total richness across the cell). Importantly, our projections suggest that such widespread large losses are not inevitable. With concerted action and the right societal choices, global sustainability of local biodiversity may be an achievable goal.

**Online Content** Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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## METHODS

**Data collation.** Between March 2012 and April 2014 we collated among-site comparisons of ecological assemblage composition from published studies (or from unpublished datasets where the methods have been published) examining the effect of human activities on more than one named taxon. A full description of how the data set was assembled and curated is presented elsewhere<sup>16</sup>. We define sites to be in the same study if they were sampled using the same methodology and the data were reported in the same paper; therefore, some publications contain multiple studies. After six months of broad searching, we targeted efforts towards under-represented taxa, habitat types, biomes and regions. We accepted data only from published or in-press papers, or data collected using a published methodology, and we required that the data providers agreed to our making their data publicly available at the end of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project in 2015. We accepted data only where abundance, occurrence or richness had been measured at two or more sampling locations and/or times, and where all sites were sampled using the same sampling procedure and with either the same effort or site-specific data on effort. We used geographical coordinates preferentially from the paper or supplied by data providers; but where coordinates were not thus available, we geo-referenced them from maps in the papers. The final data set came from 378 studies<sup>18–329</sup> and two unpublished datasets (M. E. Hanley, 2005 and 2011) that were collected with published methods<sup>146</sup>.

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

The great majority of listed taxa were species level, although many could not be given explicit species identifications (for example, morpho-species)<sup>16</sup>; henceforth we refer to distinct taxa in our data set as species. We matched taxonomic names given in the source paper to the Catalogue of Life 2013 Annual Checklist (COL)<sup>330</sup>, obtaining the full taxonomic classification. In order to relate the taxonomic names to species-level trait databases, we generated, for each taxon, a ‘best-guess’ Latin binomial as: (a) the taxon name from COL if the COL query returned a species-level identification; (b) the first two words of the text returned by the COL query if this was a sub-species designation; (c) the first two words of the taxon name in the source publication if the COL query returned neither a species or sub-species name, and the taxon name in the source publication contained two or more words. Taxa that met none of these criteria were not matched to trait data, but were included in the calculation of richness and total abundance, and for estimating turnover in community composition among sites.

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

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

Within-sample species richness was calculated as the number of differently-named taxa recorded at a given site in a standardised sampling unit (a measure also known as species density<sup>331</sup>). We gave precedence to the author’s classification of species, even where a search of global databases revealed potential synonymies, because only certain taxonomic groups could be reliably matched to accepted taxonomies.

This measure of richness is appropriate for conservation questions but among-site differences could be due to effects on numbers of individuals as well as to changes in the shape of the species accumulation curve<sup>331</sup>. We therefore also calculated rarefaction-based species richness by taking 1,000 random samples of  $n$  individuals from each site, where  $n$  is the smallest total number of individuals recorded at any site within its study, and calculating the mean species richness across samples. This index could only be calculated for sites where, in addition to the criteria above being met, abundance was recorded as number of individuals. Rarefied species richness was rounded to the nearest integer for analysis with Poisson errors.

Total abundance was calculated as the sum of the measures of abundance of all taxa at a site; we were thus unable to estimate abundance for sites where only species occurrence or overall richness or diversity had been recorded (17% of sites). Some abundance metrics—those not reported as densities per unit time, distance, area or volume sampled—were sensitive to sampling effort. When a study reported any

of these metrics and sampling effort varied among sites within a study, we corrected the raw abundance measurements for the sampling effort expended at each sampling location and time. This was done by rescaling the sampling efforts within each study so that the most heavily sampled site had a value of one (to prevent introducing additional heterogeneity into the modelled values), and then dividing the raw abundance measurements by this relative sampling effort.

Community-weighted mean organism size was calculated as the arithmetic mean of log-transformed height of plants (available for 4,235 species in our data set) or the log-transformed body mass or volume of vertebrates, beetles and hoverflies (5,236 species) present at a site, weighted by abundance<sup>332</sup>. Plant height data were taken from the TRY database<sup>333</sup>; for 61 species where plant vegetative height data were unavailable, we estimated it from generative height from a regression across the 2,554 species with estimates of both traits ( $R^2 = 0.91$ ). Data on vertebrate body mass were taken from the PanTHERIA database for mammals<sup>334</sup>, from BirdLife International’s World Bird Database for birds, and from a wide range of published and grey-literature sources for amphibians<sup>335–381</sup>. Length data for reptiles were taken from published<sup>382,383</sup> and unpublished (S. Meiri and A. Feldman, unpublished data) sources, and converted to estimates of body mass using published length-mass allometries<sup>384,385</sup>. Arthropod size data (beetles and hoverflies) were collated from published sources<sup>386,387</sup>. Beetle length and amphibian snout-vent length values were raised to the power three so that they had the same dimensionality as the other animal size measures. For both plant height and vertebrate body mass, missing values were interpolated as the average values for congeners, since both of these traits are strongly conserved phylogenetically (Pagel’s  $\lambda = 0.98, 0.997, 0.93, 0.89$  for plant height, vertebrate body mass, beetle body length and hoverfly thorax volume, respectively).

**Human pressure data.** While many human pressures can affect local biodiversity, we focus on those that can be obtained for sites around the world and for which, as far as possible, spatiotemporal data are available for 1500–2095; this focus enables us to use our statistical models as a basis for projecting responses through time. Each site was assigned to one of eight land-use classes based on the description of the habitat given in the source paper (see Extended Data Table 1 for definitions): primary vegetation, secondary vegetation (subdivided into mature, intermediate or young secondary vegetation), plantation forest, cropland, pasture and urban<sup>16</sup>. These classes were selected to match the land-use classification adopted in the Intergovernmental Panel on Climate Change Representative Concentration Pathways scenarios<sup>26</sup> to facilitate the projection of our models onto these scenarios. Sites were also assigned to a level of human intensity of use (minimal, light or intense) within each major land-use class, also based on the description of the habitat in the source paper (see Extended Data Table 1 for definitions). The factors that determined this level depended on the land-use class (for example, bushmeat extraction and limited logging in primary and secondary vegetation, or stocking density and chemical inputs in pasture; Extended Data Table 1). Sites that could not be classified for land-use and use intensity were excluded from the analyses. The final dataset contained the following numbers of sites in each land use and land-use intensity level: primary vegetation, minimal use, 1,546 (from 183 studies); light use, 860 (76 studies); intense use, 449 (33 studies); mature secondary vegetation, minimal use, 198 (52 studies); light/intense use, 213 (23 studies); intermediate secondary vegetation, minimal use, 404 (55 studies); light/intense use, 269 (30 studies); young secondary vegetation, minimal use, 431 (50 studies); light/intense use, 331 (34 studies); plantation forest, minimal use, 356 (47 studies); light use, 402 (42 studies); intense use, 238 (29 studies); cropland, minimal use, 427 (45 studies); light use, 632 (43 studies); intense use, 703 (36 studies); pasture, minimal use, 525 (43 studies); light use, 434 (52 studies); intense use, 174 (23 studies); and urban, minimal use, 174 (23 studies); light use, 244 (26 studies); intense use, 195 (18 studies).

We overlaid our sites with available global data sets to obtain site-level estimates of human population density<sup>45</sup>, distance to the nearest road<sup>46</sup> and estimated travel time to nearest population centre with greater than 50,000 inhabitants<sup>47</sup>. For distance to nearest road, the map of roads was first projected onto a Berghmann equal-area projection. These operations were carried out using Python code implemented using the arcpy Python module in ArcMap version 10.0 (ref. 388). In the main figures, the inverses of distance to roads and travel time to major population centre (proximity to roads and accessibility) were presented so that high values corresponded to higher hypothesized human effect. To estimate the history of human use of the landscapes within which sites were located, we calculated the number of years since the 30-arc-second grid cell containing each site became 30% covered by human land uses (cropland, pasture and urban), according to the HYDE model<sup>389</sup>. Co-linearity among variables describing anthropogenic change was low; the highest correlation was between land use and human population density (Pearson  $R^2 = 0.31$ ).

**Modelling site-level diversity, composition and turnover.** The response of site-level diversity to the measures of anthropogenic change was modelled using generalized linear mixed effects models, implemented in the lme4 package version

1.0–5 (ref. 44) in R version 3.0.2 (ref. 390). We first compared candidate random-effects structures using the full candidate fixed-effects structure<sup>391</sup>. Random-intercept terms considered in all models were the identity of the study from which data were taken, to account for study-level differences in the response variables and sampling methods used, and—within study—the spatial block in which the site was located, to account for the spatial arrangement of sites. For models of species richness (within-sample and rarefied), we also fitted an observation-level random effect (that is, site identity) to account for the overdispersion present<sup>392</sup>. We also considered random slopes, with respect to study, of each of the main fixed effects (land use, land-use intensity, human population density, distance to nearest road, travel time to nearest major city and time since the landscape was majority converted to human uses). Random effects were retained or discarded based on the models' Akaike Information Criterion values.

Once the best random-effects structure had been selected, we performed backward stepwise model simplification to select the best fixed-effects structure (see Supplementary Information)<sup>391</sup>. Human population density, distance to roads, travel time to nearest major city and time since major human use of the landscape were log transformed in the analyses, with a value of 1 added to human population density, travel time to nearest major city and time since major landscape conversion to deal with zero values. These four variables were fitted as continuous effects, with quadratic polynomials for human population, distance to roads and travel time to nearest major city, and as a linear effect for time since human landscape conversion. For variables fitted as quadratic polynomials, we also tested linear effects during the backward stepwise model selection. All continuous variables were rescaled before analysis so that values ranged between zero and one. Interaction terms were tested first, and then removed to test the main effects. All main effects that were part of significant interaction terms were retained in the final models regardless of their significance as main effects. For the model of community-weighted mean body mass and plant height, because the number of sites with data was smaller than for the other metrics, only land use (excluding urban sites, which were few), human population density and distance to roads, and no interactions, were fitted (for the model of plant height, sample sizes in each land use were: primary vegetation, 634 sites; secondary vegetation, 851 sites; plantation forest, 222 sites; cropland, 72 sites; pasture, 412 sites; and for the model of animal mass: primary vegetation, 1728 sites; secondary vegetation, 805 sites; plantation forest, 602 sites; cropland, 641 sites; pasture, 440 sites). The decision whether or not to retain terms was based on likelihood ratio tests. The coefficient estimates of the best models are shown in Fig. 1b–d and Extended Data Fig. 2, and the formulae and statistical results are shown in the Supplementary Information. To test for spatial autocorrelation in the residuals of the final best models, we calculated Moran's *I* values and associated *P* values, separately for each study considered in the models, using the spdep package version 0.5–68 (ref. 393) in R; the distribution of *P* values across studies was used as an indication of whether spatial autocorrelation was likely to cause a problem. This revealed that the residuals showed little spatial autocorrelation (Extended Data Fig. 5). We used cross validation to assess the robustness of model parameter estimates, first based on dividing the studies randomly into ten equal-sized sets and dropping each set in turn (Extended Data Fig. 3c), and second based on leaving out the studies from each biome in turn (Extended Data Fig. 3d).

Publication bias is a potential problem for any large-scale synthesis of data from many publications. In standard meta-analyses, funnel plots<sup>394</sup> can be used to test for any relationship between standard error and effect size, as a bias in effect sizes at high standard error towards more positive or more negative effects indicates a likely effect of publication bias. Creating funnel plots for our data was more complicated because ours was a site-level analysis of raw diversity estimates rather than a traditional meta-analysis. Instead we generated individual models relating diversity to land use for each study that sampled at least two sites within each of at least two land-use types. We focused on land use because: (a) there were a small number of sites included in most within-study models; and (b) the original studies focused on effects of land use, not generally on land-use intensity, human population density or distance to roads, and thus any effect of publication bias would likely be seen in the land-use coefficients. Funnel plots were generated by plotting, for each land-use type, the estimated model coefficients against the associated standard errors (Extended Data Fig. 4). There were some indications of an effect of publication bias, with less certain coefficient estimates tending to have more negative estimates for some of the land uses (Extended Data Fig. 4). However, study-level random slopes of human-dominated land uses tended to be more negative for studies that sampled more sites (Extended Data Fig. 4). It is important to emphasize that in a site-level analysis like ours, studies with fewer sites have less weight in the models. Modelled coefficient estimates were generally robust to the removal of these studies (Extended Data Fig. 4). Basing projections on coefficient estimates from models where small studies were excluded led to a less than 1% change in the estimated global richness values (results not shown). As with all studies based on data from the literature, we underrepresent unpublished data.

To model turnover of species composition between pairs of sites, we calculated average dissimilarity<sup>23</sup> in the lists of present species ( $1 - \text{Sørensen index}$ ) between all pairs of sites within each study. For this analysis, we were only able to consider studies with more than one site in at least one of the land-use types considered. Once compositional similarity had been calculated for every pair of sites within each study, the average compositional similarity was calculated for every pair of land-use types considered within each study (including comparisons between sites in the same land-use type). Finally, the average compositional similarity was calculated for each pair of land-use types across all studies. To visualize the clustering of different land-use types in terms of community composition, we performed a hierarchical complete-linkage cluster analysis on the compositional dissimilarity (that is,  $1 - \text{similarity}$ ) matrix, using the hclust function in R version 3.0.2 (ref. 390). To test whether differences in the average geographic distance between pairs of sites in different land-use combinations affected these results, we correlated average compositional similarity with average distance between sites, for all pairwise combinations of land use (including comparisons of a land-use type with itself). Correlations between average distance and average community similarity were only very weakly negative ( $R^2 = 0.001$ ), suggesting they do not strongly distort the comparisons of community composition. However, the fact that some land uses tend to occur more closely together than others could influence the diversity patterns seen in our models, if some land uses are typically close to high-diversity habitats and so are more likely to benefit from dispersal. For example, sites in secondary vegetation and plantation forest were closer, on average, to primary vegetation sites than were those in cropland, pasture and urban (average distances to sites in primary vegetation were: other primary vegetation sites = 7.38 km; mature secondary vegetation = 4.4 km; intermediate secondary vegetation = 3.9 km; young secondary vegetation = 6.9 km; plantation forest = 4.2 km; cropland = 16.4 km; pasture = 10.1 km; and urban = 11.4 km). Accounting for distance in such already complex models is not computationally tractable. In making the projections, we therefore implicitly assume that the average distances will not change (that is, that secondary vegetation and plantation forests will remain closer to primary vegetation than cropland, pasture and urban habitats).

**Projecting the models onto spatial estimates of anthropogenic variables.** We projected the best overall models of richness (within-sample and rarefied), abundance and community-weighted mean organism size onto estimates of land use, land-use intensity and human population density at  $0.5^\circ \times 0.5^\circ$  resolution, using historical estimates for 1500 to 2005, and four RCP scenarios of future changes (IMAGE 2.6, MiniCAM 4.5, AIM 6.0 and MESSAGE 8.5; the names refer to the integrated assessment models used and the numbers to the amount of radiative forcing assumed in 2100)<sup>395</sup>. In the absence of global projections, proximity to roads and accessibility were omitted from our projections.

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

Gridded temporal estimates of human population density were directly available for the HYDE historical scenario and MESSAGE future scenario. Human population trajectories in the MiniCAM model were resolved only to the level of United Nations regions<sup>41</sup>; we therefore downscaled these to grid cells assuming no temporal change in the spatial pattern of relative population density within regions compared to present day patterns<sup>45</sup>, which is the method used in other RCP-scenario land-use models lacking human population data resolved to grid cells<sup>26</sup>. Gridded estimates of human population from the MESSAGE model were downloaded from <http://www.iiasa.ac.at/web-apps/ggi/GgiDb/>. For the scenarios for which human population projections were not available (IMAGE and AIM), we used country-level estimates from the 'medium' scenario of the United Nations population division<sup>396</sup>, which gives the closest global predictions of future human population to those assumed by IMAGE and AIM<sup>26</sup>. These country-level estimates were downscaled to grid cells using the same method as for MiniCAM's regional projections.

Land-use intensity was an important explanatory variable in our models, but global maps of land-use intensity are not available. We therefore generated global

estimates of current land-use intensity based on a map of 'Global Land Systems'<sup>397</sup>, which divides coarse land-use types into sub-categories based on levels of cropland intensity, livestock densities and human population density. We mapped each Global Land Systems class onto one or more relevant combinations of our classes of land use and land-use intensity (Extended Data Table 2). The Global Land Systems data set has a spatial resolution of 5 arcmin. To calculate the proportion of each  $0.5^\circ \times 0.5^\circ$  cell occupied by each land use and land-use intensity combination we calculated the proportion of 5-arcmin cells within each  $0.5^\circ \times 0.5^\circ$  cell containing matching Global Land Systems categories (see legend of Extended Data Table 2 for details).

To generate past and future estimates of land-use intensity, we modelled the current proportion of each land-use type estimated to be under minimal, light or intense levels of intensity within each grid cell (one model for each intensity level), as a function of the prevalence of the land-use type within each cell and human population density, with the relationships allowed to vary among the 23 United Nations (UN) sub-regions (that is, we fitted interaction terms between UN sub-region and both the prevalence of each land-use type and human population density). UN sub-region data were taken from the world borders shapefile version 0.3 ([http://thematicmapping.org/downloads/world\\_borders.php](http://thematicmapping.org/downloads/world_borders.php)) and converted to a  $0.5^\circ \times 0.5^\circ$  raster using ArcMap version 10.0 (ref. 388). The models were developed using generalized linear models with a binomial distribution of errors, implemented in the lme4 package version 1.0-5 (ref. 44) in R version 3.0.2 (ref. 390). The resulting models explained between 30.6% and 76.7% of the deviance in estimated current levels of intensity. Past and future land-use intensities were estimated by applying the models to the same past and future estimates of land use and human population density as above.

The scenarios gave the proportion of each grid cell estimated to be occupied by each combination of land use and land-use intensity. We did not attempt to resolve human population density within grid cells for our historical estimates or forecasts, thereby assuming it to be spatially (but not temporally) constant within each cell. The coefficients from the models of site-level diversity were thus applied to each combination of land use and intensity within each cell, with the same human population density estimate across all combinations. All predictions were expressed as a percentage net change compared with a baseline before human land-use effects on biodiversity, in which all land use was assumed to be primary vegetation of minimal intensity of use, and with a human population density of zero. Each cell's average value of net biodiversity change was calculated as the area-weighted mean value across all land uses and intensities. Global average values were calculated as mean values across all cells, weighted by cell area and an appropriate weighting factor to account for the fact that cells have different baseline levels of diversity. The weighting factors applied were: terrestrial vertebrate species richness in the case of richness, and net primary production (NPP) in the case of total abundance. No weighting factor was applied for projections of community-weighted mean plant height. Terrestrial vertebrate species richness was estimated by overlaying extent-of-occurrence range maps for mammals, birds, amphibians and reptiles, using Python code written by ourselves and implemented in ArcMap version 10.0 (ref. 388). Data on NPP were estimates of potential NPP (that is, in the absence of human effects) from the Lund-Postdam-Jena (LPJ) Dynamic Global Vegetation Model<sup>398</sup>.

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

To estimate average biodiversity change in individual countries, we intersected the gridded projections with the world borders shapefile (see above) using the extract function in the raster package version 2.2-12 (ref. 399) in R version 3.0.2 (ref. 390). Mean values across the cells associated with each country were calculated, weighted by cell area. To interpret the outcomes for countries in terms of their natural biodiversity, we related the country-level projections to estimates of average natural vertebrate species richness (see above). To interpret the outcomes for countries in terms of their socio-economic status, we related the projections to estimates of the Human Development Index, which is an indicator of education, life expectancy, wealth and standard of living (<https://data.undp.org/>).

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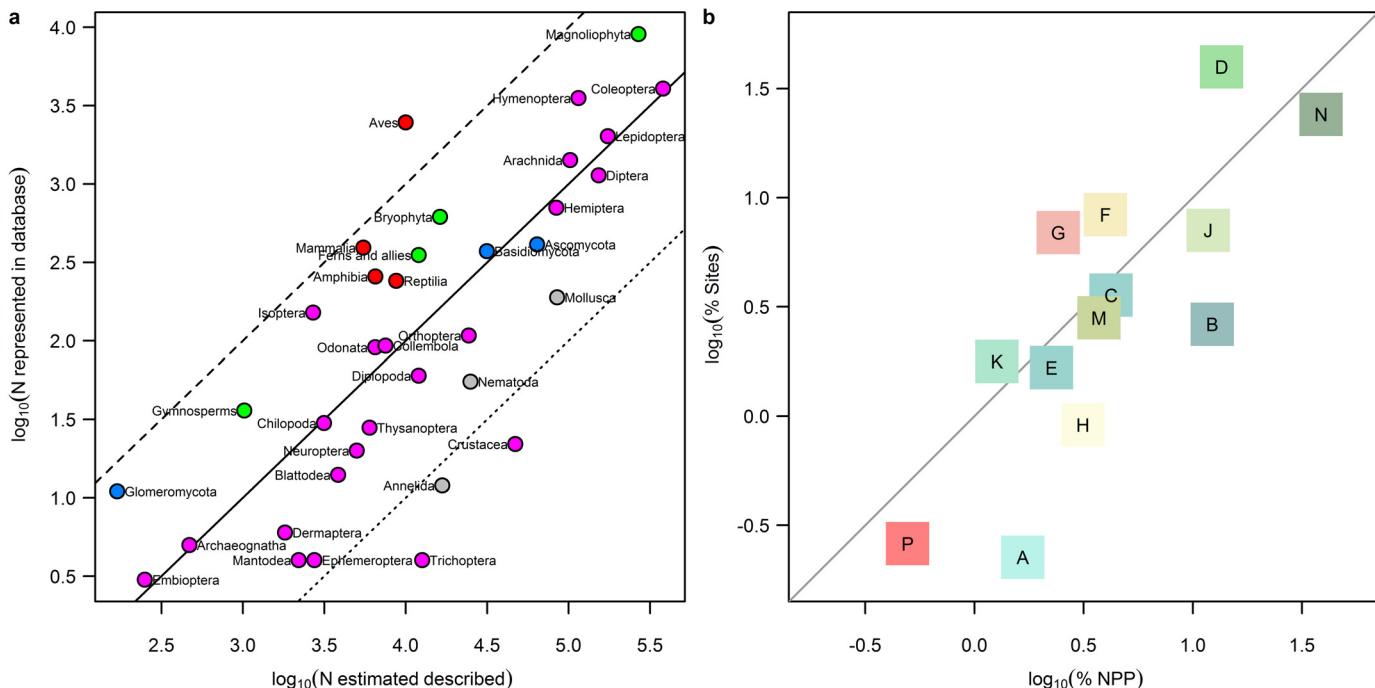
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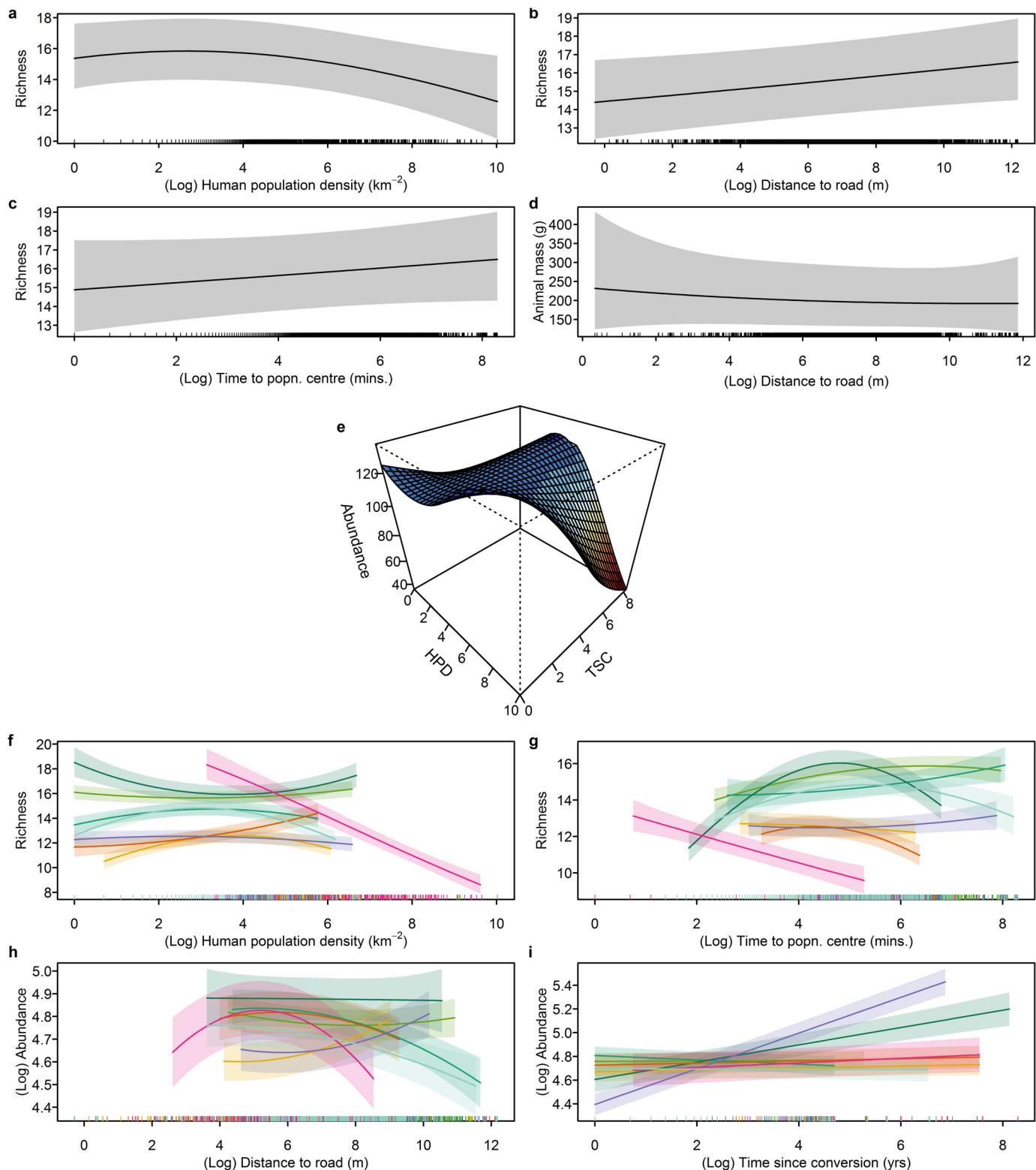
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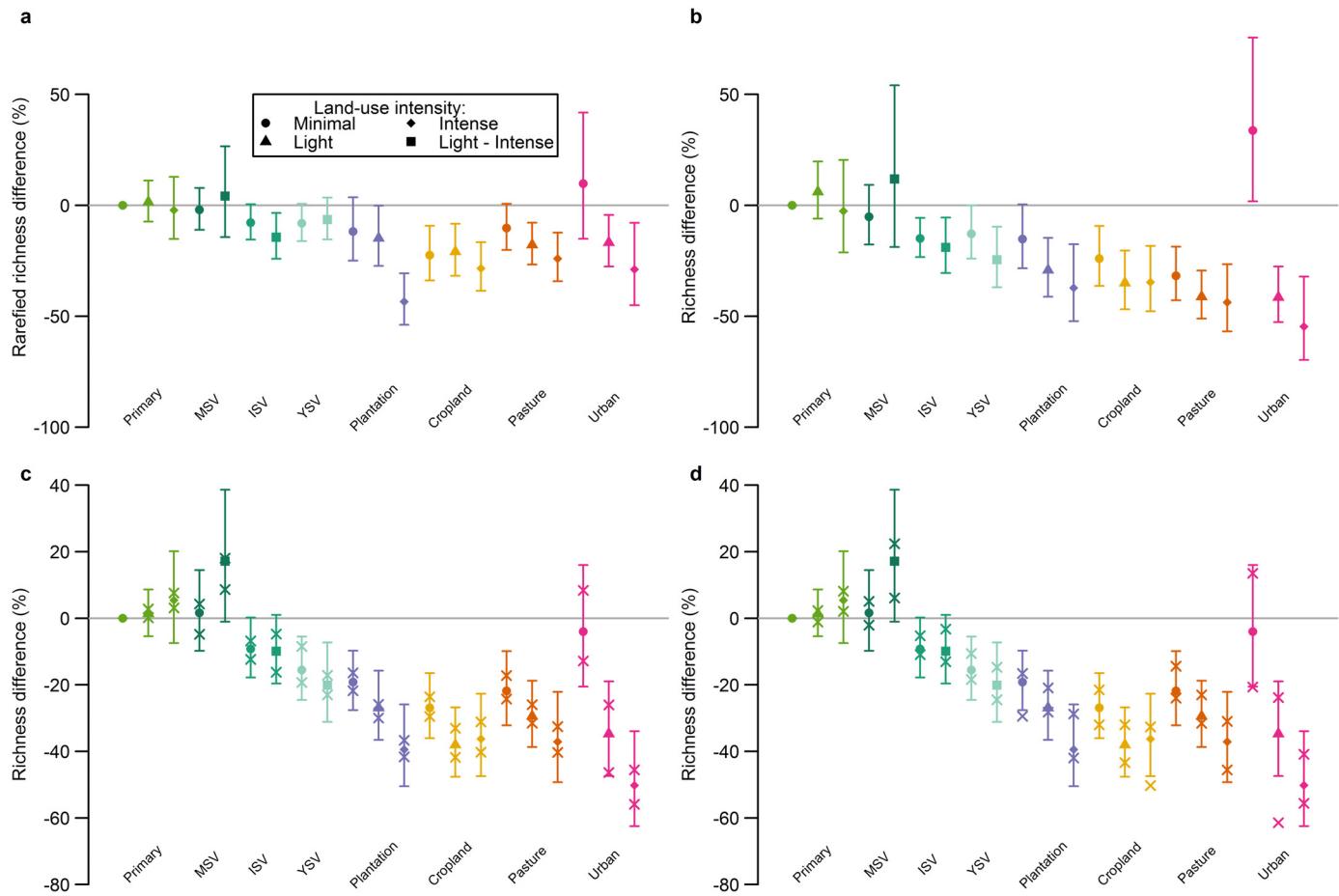
**Extended Data Figure 1 | Taxonomic and geographic representativeness of the data set used.** **a**, The relationship between the number of species represented in our data and the number estimated to have been described<sup>17</sup> for 47 major taxonomic groups. Lines show (from bottom to top) 0.1%, 1% and 10% representation of described species in our data set; magenta, invertebrates; red, vertebrates; green, plants; blue, fungi; and grey, all other taxonomic groups. **b**, The relationship across biomes<sup>400</sup> between the percentage of global terrestrial net primary production and the number of sites in our data set; A, tundra; B, boreal forests and taiga; C, temperate conifer forests; D, temperate

broadleaf and mixed forests; E, montane grasslands and shrublands; F, temperate grasslands, savannahs and shrublands; G, Mediterranean forests, woodlands and scrub; H, deserts and xeric shrublands; J, tropical and subtropical grasslands, savannahs and shrublands; K, tropical and subtropical coniferous forests; M, tropical and subtropical dry broadleaf forests; N, tropical and subtropical moist broadleaf forests; P, mangroves; note that the flooded grasslands and savannah biome is not represented in the data set; grey line shows a 1:1 relationship.



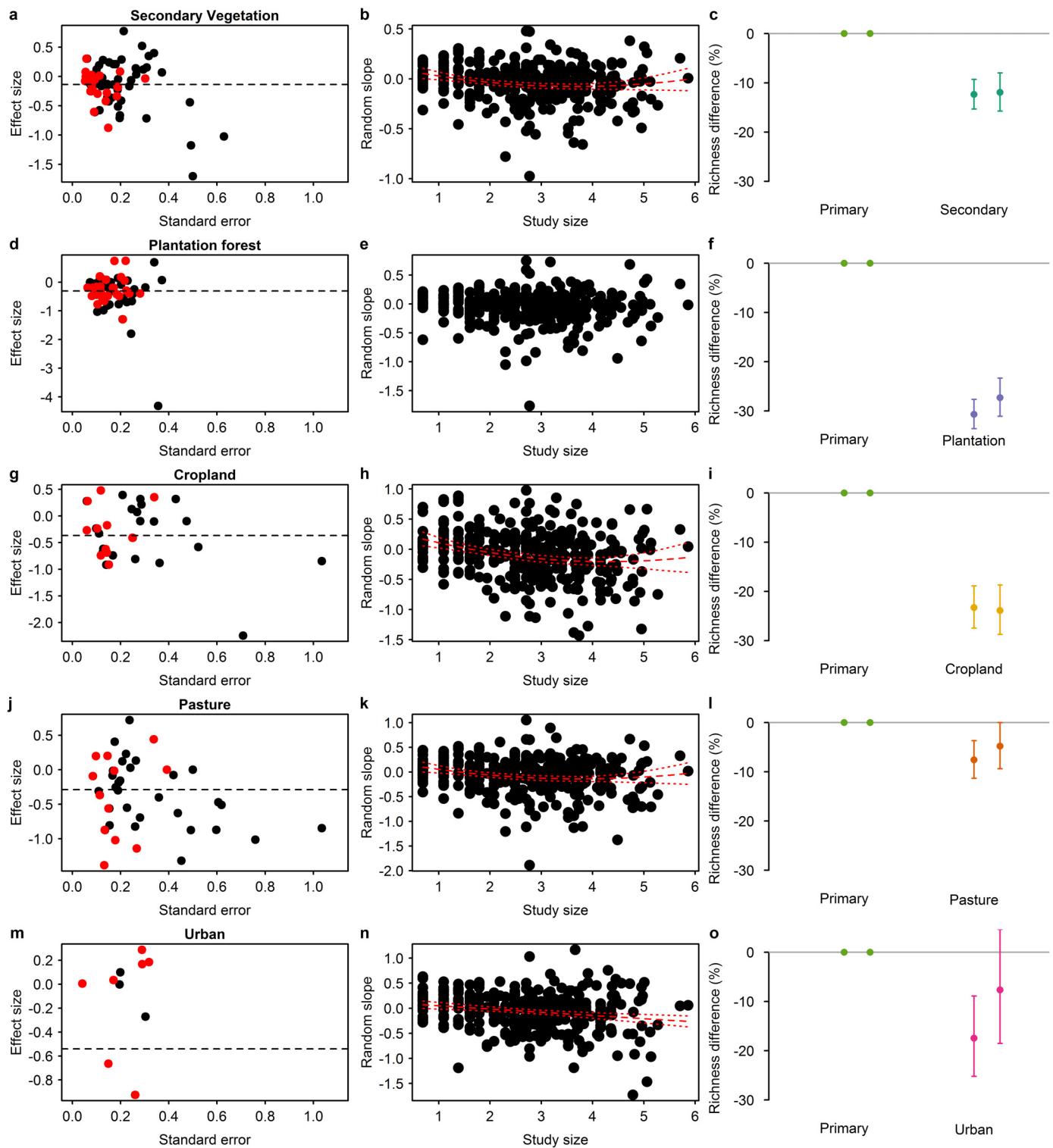
**Extended Data Figure 2 | Detailed response of local diversity to human pressures.** **a–i**, Modelled effects (controlling for land use and land-use intensity) of human population density (HPD), distance to nearest road, time since 30% conversion of a landscape to human uses (TSC) and time to nearest population centre with greater than 50,000 inhabitants (**a–d**), interactions between pairs of these variables (**e**), and interactions between these variables and land use (**f–i**) on site-level diversity. **a–c**, **f**, **g**, Within-sample species richness; **e**, **h**, **i**, total abundance; and **d**, community-weighted mean vertebrate body mass. Shaded polygons in **a–d** show 95% confidence intervals. For clarity,

shaded polygons in **f–i** are shown as  $\pm 0.5 \times \text{s.e.m.}$  Confidence intervals in **e** are omitted. Rugs along the  $x$  axes in the line graphs show the values of the explanatory variables represented in the data set used for modelling. Only significant effects are shown. Note that distance to nearest road and travel time to major population centre measures are the raw (log-transformed) values fitted in the models rather than the proximity to roads and accessibility values (obtained as 1 minus the former values) presented in Fig. 1. Sample sizes are given in full in the Methods.



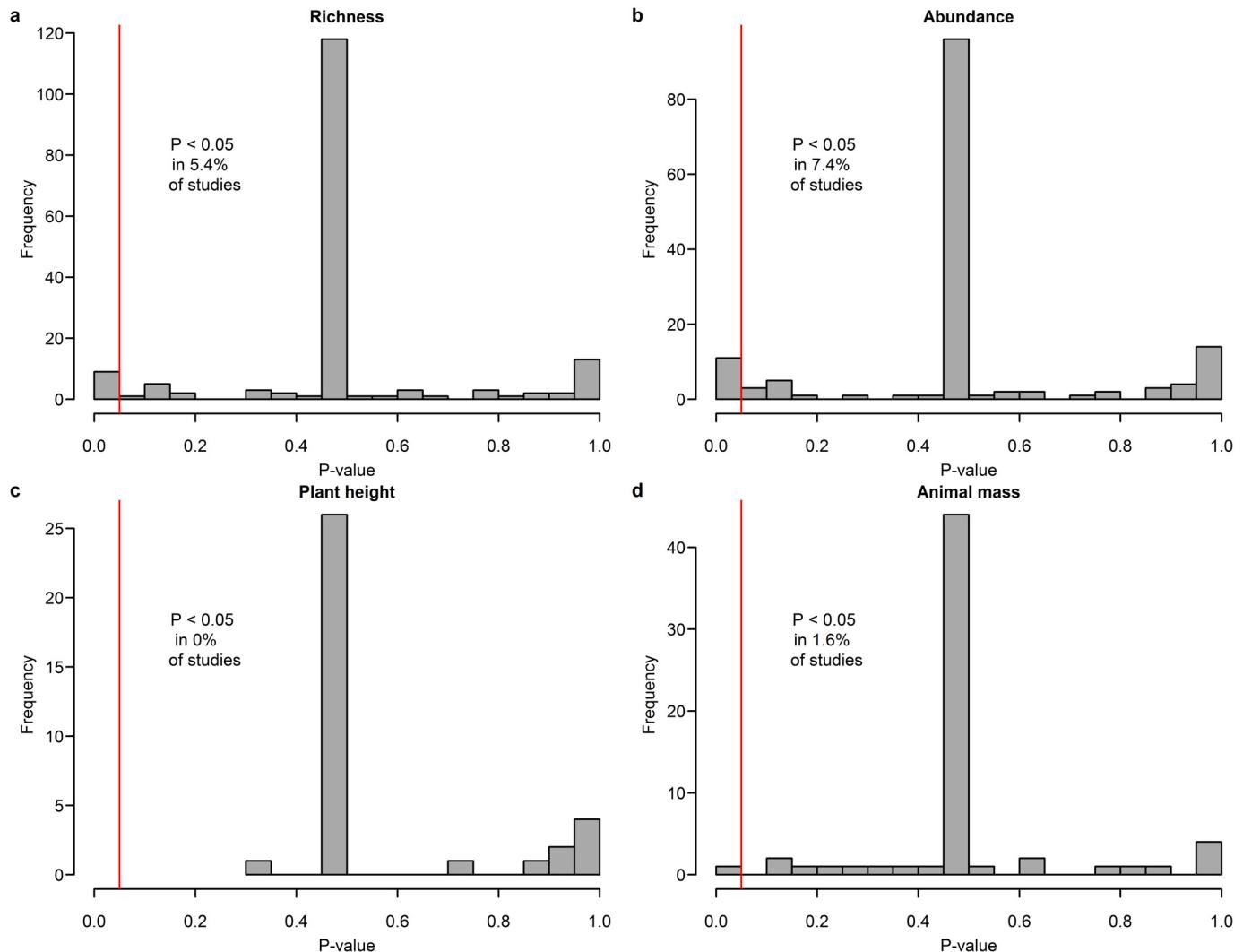
**Extended Data Figure 3 | Robustness of modelled effects of human pressures.** **a**, Effects of land use and land-use intensity on rarefaction-based species richness. **b**, To test that any differences between these results and the results for within-sample species richness presented in the main manuscript were not because rarefied species richness could only be calculated with a smaller data set, we also show modelled effects on within-sample species richness with the same reduced data set. **c, d**, Cross-validated robustness of

coefficient estimates for land use and land-use intensity. Crosses show 95% confidence intervals around the coefficient estimates under tenfold cross-validation, excluding data from approximately 10% of studies at a time (**c**), and under geographical cross-validation, excluding data from one biome at a time (**d**); colours, points, error bars and land-use labels are as in Fig. 1 in the main text. Sample sizes are given in full in the Methods.



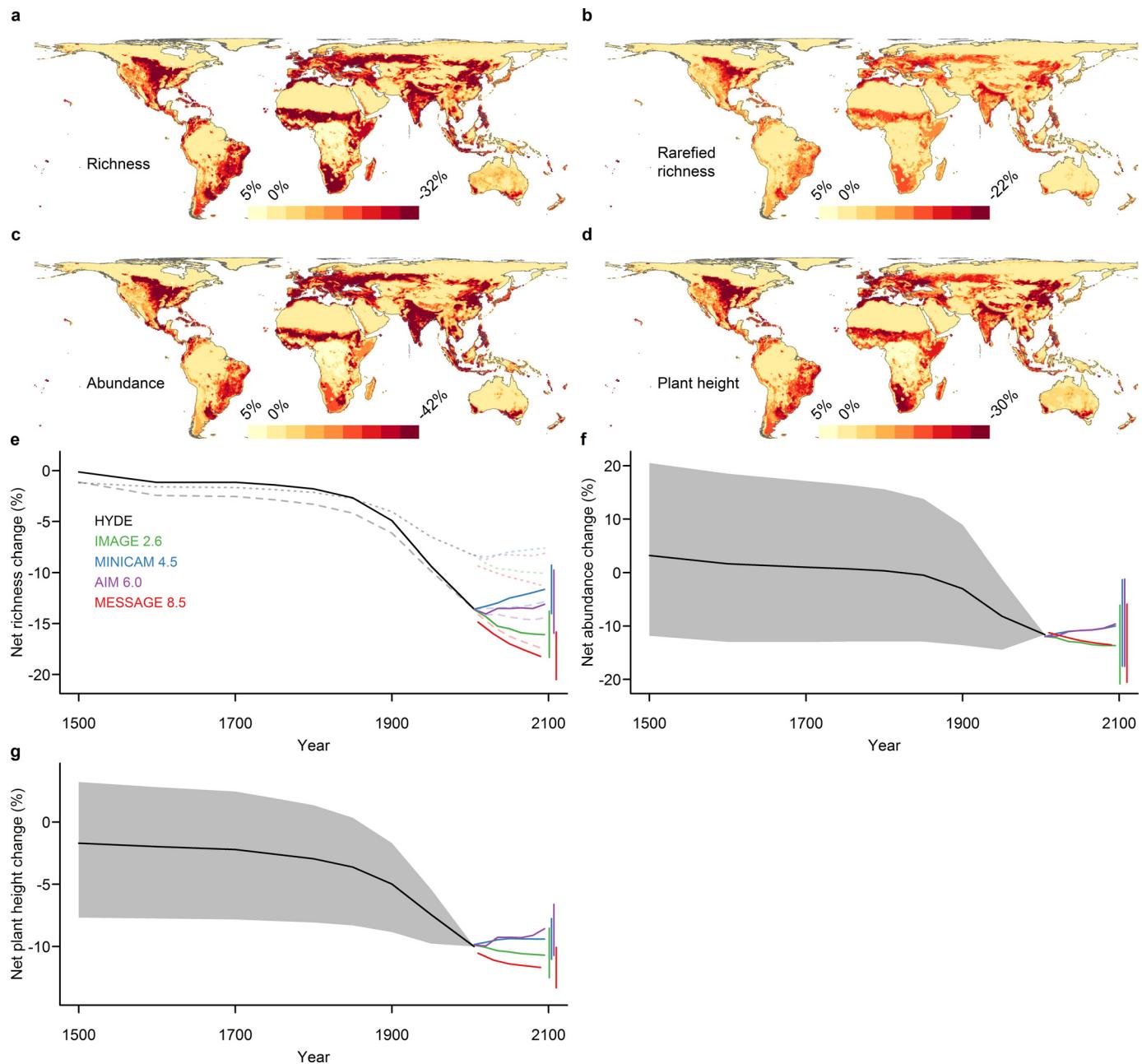
**Extended Data Figure 4 | Tests of the potential for publication bias to influence the richness models and projections.** Left-hand panels (a, d, g, j, m) show funnel plots of the relationship between the standard error around coefficient estimates (inversely related to the size of studies) and the coefficient estimates themselves for each coarse land-use type; there is evidence for publication bias with respect to some of the land-use types, as indicated by an absence of points on one or other side of zero for studies with large standard errors (but note that small studies are down-weighted in the model). Red points show studies with more than five sites in the land use in question (ten for secondary vegetation and plantation forest because there were more sites for these land uses and some studies with between five and ten sites showed variable responses); horizontal dashed lines show the modelled coefficients for each land use. Central panels (b, e, h, k, n) show the relationship between study

size (log-transformed total number of sites) and the random slope of the land use in question with respect to study identity, from a random-slopes-and-intercepts model. Where a significant relationship was detected using a linear model, fitted values and 95% confidence intervals are shown as a red dashed line and red dotted lines, respectively. Conversely to what would be expected if publication bias was present, where significant relationships between study size and random slopes were detected, these were negative (that is, larger studies detected more negative effects). Right-hand panels (c, f, i, l, o) show the robustness of modelled coefficients to removal of studies with few sites in a given land use (black points in the left-hand panels). Left-hand error bars show coefficient estimates for all studies and right-hand error bars show coefficient estimates for studies with more than five sites in that land use (ten for secondary vegetation and plantation forest).



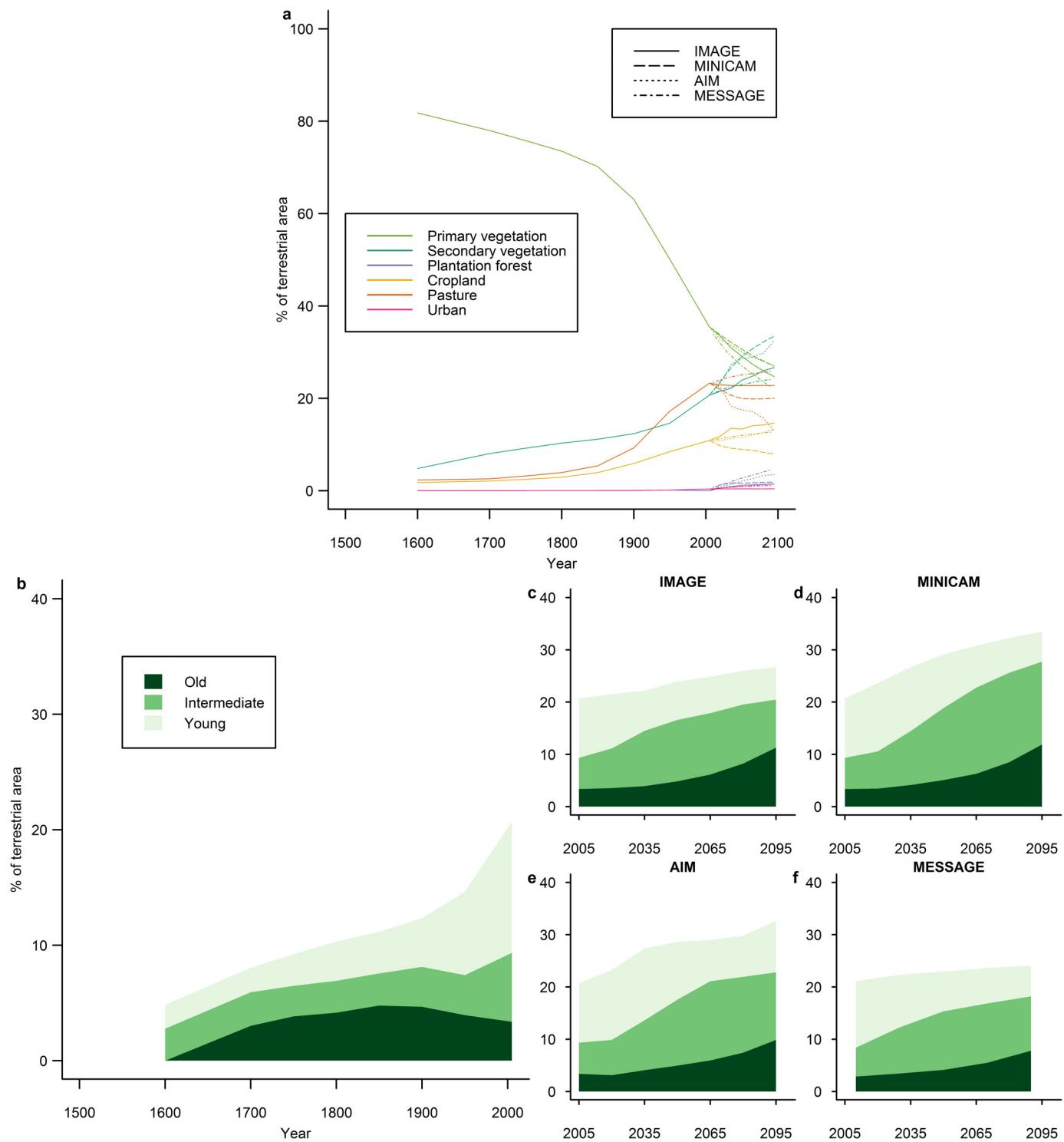
**Extended Data Figure 5 | Tests for spatial autocorrelation in the model residuals.** **a–d**, For the four main modelled metrics of site-level diversity—within-sample species richness (**a**), total abundance (**b**), community-weighted mean plant-height (**c**) and community-weighted mean animal mass

(**d**)—histograms of  $P$  values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for individual studies are shown. The percentage of studies with significant spatial autocorrelation ( $P < 0.05$ ; indicated by a vertical red line) is shown.

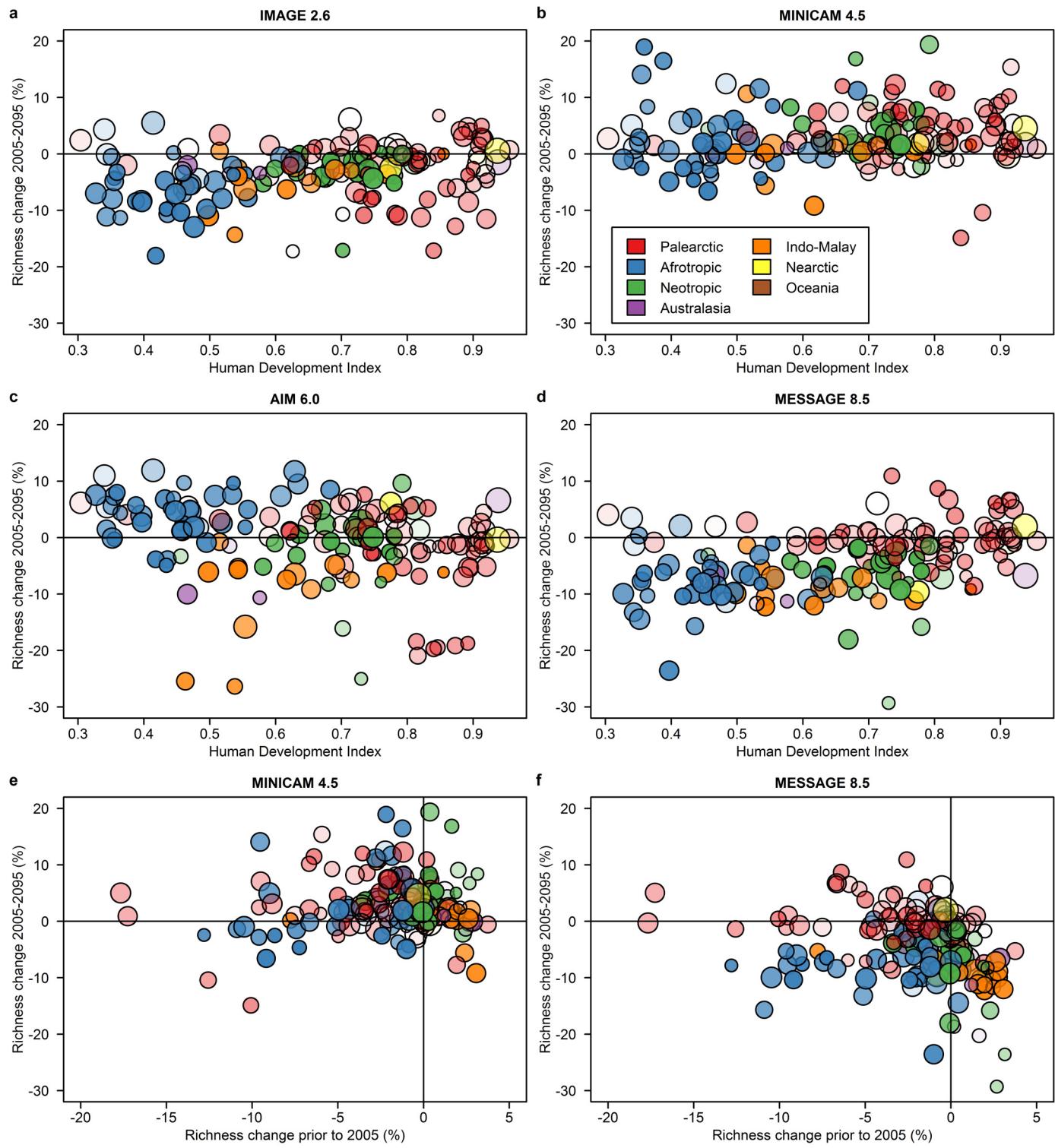


**Extended Data Figure 6 | Current, past and future projections of all metrics of local biodiversity.** **a–d**, Net change in local diversity caused by land use and related pressures by 2000 under an IMAGE reference scenario<sup>10</sup>. Changes in richness (a), rarefied richness (b), total abundance (c) and community-weighted mean plant height (d) are shown. Note that the values used to divide the colours are the same in all panels, but that the maximum and minimum values are different, as indicated in the legends. **e–g**, Historical and future estimates of net change in local diversity from 1500–2095, based on estimates of land-use, land-use intensity and human population density from the four RCP scenarios (Table 1). Net changes in richness (e), total abundance (f) and community-weighted mean plant height (g) are shown. Historical (shading)

and future (error bars) uncertainty shown as 95% confidence intervals, with uncertainty rescaled to be zero in 2005 to show uncertainty in past and future change separately. The global average projection for the MESSAGE scenario does not directly join the historical reconstruction because projections start in 2010 (human population estimates are available at 15-year intervals) and because human population (and thus land-use intensity) and plantation forest extent have not been harmonized among scenarios. In panel e, the dashed line shows projected diversity change under land-use change only (that is, without land-use intensity and human population density, the projections of which involved simplifying assumptions), and the dotted line shows projections of rarefaction-based species richness.



**Extended Data Figure 7 | Reconstructed and projected total global land-use areas under the RCP scenarios.** **a**, Estimated total area of the major land-use types. **b–f**, Estimated total area of secondary vegetation in different stages of recovery.



#### Extended Data Figure 8 | Biodiversity projections at the country level.

**a–d**, Country-level projections of net change in local richness between 2005 and 2095 under the four RCP scenarios (IMAGE 2.6 (**a**), MiniCAM 4.5 (**b**), AIM 6.0 (**c**) and MESSAGE 8.5 (**d**)), shown in relation to the Human Development Index (an indicator of education, life expectancy, wealth and standard of living in the most recent year for which data are available). **e, f**, Country-level projections of net change in local richness between 2005 and 2095 under the

best- and worst-performing RCP scenarios in terms of biodiversity (MiniCAM 4.5 (**e**) and MESSAGE 8.5 (**f**), respectively), shown in relation to past change in biodiversity from a baseline with no human land-use effects to 2005 according to the HYDE land-use reconstruction. Colours indicate biogeographic realms (key in **b**); colour intensity reflects native vertebrate species richness (more intense colour represents higher species richness); point size is proportional to (log) country area.

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

Level 1 Land Use	Predominant Land Use	Minimal use	Light use	Intense use
No evidence of prior destruction of the vegetation	<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.
Recovering after destruction of the vegetation	<b>Mature Secondary Vegetation</b>			
	<b>Intermediate Secondary Vegetation</b>			
	<b>Young Secondary Vegetation</b>			
	<b>Secondary Vegetation (indeterminate age)</b>			
Human use (agricultural)	<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).
Human use (urban)	<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.

**Extended Data Table 2 | Conversion between Global Land Systems data set and our intensity classification for each major land-use type**

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

To estimate proportional coverage of each intensity class for each land-use type in the  $0.5^\circ \times 0.5^\circ$  grid cells used for projection, we calculated the number of finer-resolution Global Land Systems<sup>397</sup> cells with a matching intensity class for the land-use type in question, as a proportion of Global Land Systems cells matching any intensity class for the land-use type in question. For example, to calculate the proportion of urban land that is under intense use, we divided the number of cells with a Global Land Systems classification of 'urban' by the number of cells classified as 'urban' or 'peri-urban and villages'. None of the Global Land Systems classes could inform about the intensity of plantation forest, and so we assumed that any plantation forest was composed of equal proportions under minimal, light and intense use.