Global land-use impacts on local terrestrial biodiversity

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- 49 Human activities, especially conversion and degradation of habitats, are causing global
- 50 biodiversity declines. How local ecological assemblages are responding is less clear a

concern given their importance for many ecosystem functions and services. We analyze a terrestrial assemblage database of unprecedented geographic and taxonomic coverage to quantify local biodiversity responses to land-use and related changes. In the worstimpacted 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 within-sample richness (by 13.6% on average), total abundance (10.7%) and rarefaction-based richness (8.1%), with changes showing marked spatial variation. Further rapid 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% reversal of past losses) 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 pollution¹. As a result, species' extinction risk increases on average while population sizes decline^{1,2}. Such assessments have usually focused on data-rich vertebrates, so might not reflect broader biodiversity³. 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 – likely depends upon local biodiversity⁴⁻⁶. Average trends in local diversity remain unclear: analyses of temporal changes in assemblages have suggested no systematic change in species richness^{7,8}, but the available times-series data might under-represent transitions between land-use types⁹ and population time series suggest sharp declines in

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vertebrate populations in recent decades³.

Spatial comparisons provide an alternative source of evidence on biodiversity impacts, assuming that differences in pressures have caused observed biodiversity differences between otherwise matched sites^{10–12}. The prevalence of published spatial comparisons makes it possible to go beyond particular taxa or regions^{11,12} 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 models¹⁰ which cannot capture all key aspects of diversity¹³.

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 pressures we consider most directly measure land use and infrastructure, but include proxies that might correlate 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 map global hindcasts of net changes in assemblages since 1500, and project future changes over this Century under different socioeconomic scenarios of land use. We then 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 based on 1,130,251 records of abundance and 320,924 of occurrence or species richness at 11,525 sites (Figure 1a) in 13 of the 14 terrestrial biomes (Extended Data Figure 1). These data, from 284 publications (see Methods), represent 26,953 species – 1.4% of the number formally described Each site was scored for six putative pressures: land use 11 and use intensity 17, land-use history 18, human population density 19, proximity to roads 20, 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.

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Human impacts 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 (Figure 1; see Supplementary Information for statistics). These results extend those of previous, geographically or taxonomically restricted, meta-analyses (e.g. refs. 11,21). Effects of other variables were weaker, but showed stronger effects in interaction with other variables (Extended Data Figure 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 (Figure 1). Differences in richness were not driven solely by differences in abundance: rarefaction-based richness²² (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 Figure 3). 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 impacted sites. Effects of pressures on vertebrate, invertebrate and plant richness were statistically indistinguishable (P > 0.05; results not shown).

The importance of secondary vegetation for conservation is hotly debated ^{11,23,24}, and is crucial because this land-use will soon become the most widespread type²⁵. 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 (Figures 1 & 2; we

caution though that not all data sources clearly distinguish mature secondary from primary vegetation). This successional rise in diversity accords with a recent meta-analysis of plant communities over time⁷.

Net changes in diversity provide an incomplete view of the effects of human impacts because they ignore replacement of original species by newcomers⁸. We therefore analysed how land use affects similarity in species composition between sites. Communities under the same land use were, unsurprisingly, the most similar (Figure 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 (Figure 2b).

Anthropogenic pressures can affect ecosystem functions and services more strongly than changes in species diversity would imply, if species' responses depend on their traits²⁶. Large size is often linked to species' declines^{27,28} and matters for some ecosystem processes²⁹. We combined abundance data with species' average sizes to calculate site-level community-weighted mean plant height and animal mass. As in local studies²⁸, 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 (Figure 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 (Figure 1d).

Models like ours that substitute space for time ignore time lags in biotic changes, which can be important³⁰. We also assume that land uses 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 impacts on local biodiversity.

Global impacts 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, we estimate the global pattern of net local changes to date in plot-level richness (we do not estimate total richness within cells; Figure 3). We estimate that human-dominated areas have lost much more local diversity than where more natural vegetation remains. The worst-affected cells showed a 31% reduction in average local richness – probably enough to impact ecosystem functioning substantially⁵. Local richness increased in 1.7% of cells (by \leq 4.8%). Total abundance and rarefied richness showed broadly similar patterns, although less pronounced in the latter case (Extended Data Figure 4).

We applied our models to global spatial estimates of how land use and human population changed from 1500-2005²⁵ (see Methods) to infer the history of local biodiversity change. 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 drivers themselves (which have not been assessed³¹) nor effects of changes in roads and accessibility, for which temporal estimates could not be obtained (they are treated as static).

Richness is estimated to have declined most rapidly in the 19th and 20th centuries (Figure 4), with other metrics showing similar responses (Extended Data Figure 4). By 2005, we estimate that human impacts had reduced local richness by an average of 13.6% (95% CI: 9.1 – 17.8%) and total abundance by 10.7% (95% CI: 3.8% gain – 23.7% reduction) compared with pre-impact times. 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 time³².

Our inferences contrast with two recent analyses of community time series^{7,8}, which suggested no overall trend in local diversity, and with the Living Planet Index³ which, based on 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 landuse types⁹. On the other hand, our approach may underestimate additions of species through climate change and species invasion (although accessibility and proximity to roads may partly capture the latter^{14,15}).

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) scenarios²⁵, which correspond to different intensities of global climate change (Table 1). Although these estimates have limitations³¹, they are the most consistent available, are widely-used³³, and are consistent with the historical estimates ²⁵. 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 (Figure 4; Extended Data Figure 4). 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 biofuels²⁵ (Table 1, Extended Data Figure 5). 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 Figure 4). 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; Extended Data Figure 5). This scenario, which has been characterised as 'business-as-usual', most closely matches recent trends in emissions and performs worst even though our projections omit direct climate impacts on local assemblages.

The global projections hide wide regional and national variation (Figure 5; Extended Data Figure 6). 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 (Figure 5a). Under this scenario, European and North American countries – typically with a high Human Development Index (HDI), 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-Sharan African countries, with more natural and semi-natural habitat, will suffer the greatest losses (Figure 5a; Extended Data Figure 6f).

Such globally inequitable outcomes might be avoidable: the best scenario for biodiversity (MiniCAM 4.5; Figure 4) yielded country-level outcomes that are relatively independent of HDI, native species richness (Figure 5b) and past changes (Extended Data Figure 6e). For local richness, outcomes under MiniCAM4.5 were better than MESSAGE 8.5 for 93% of countries worldwide (Figure 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 Figure 6). Projections

under IMAGE 2.6 are 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 impact overall on terrestrial biodiversity (Extended Data Figure 6).

Conclusions

Many assessments of the state of biodiversity have focused on global metrics such as rates of species extinction³⁶, but resilient delivery of ecosystem functions and services more likely depends on local diversity^{4–6}. 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 framework, is likely to exacerbate losses, especially under business-as-usual³⁷, although direct effects of climate change will increase local diversity in some regions⁸.

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 countries³⁸. 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-being⁵. 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.

Methods summary

We collated among-site comparisons of ecological assemblage composition from the literature³⁹. Studies compared from 2 to 360 sites (median = 15; 82% had ≥ 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).

We computed four site-level biodiversity metrics: within-sample species richness (i.e. number of species sampled at a site), total abundance, rarefaction-based richness (i.e., average number of species found by sampling a constant number of individuals) and community-weighted mean organism size (using species data for plant height and animal mass or volume). Site land use was classified from the published data sources as primary vegetation, secondary vegetation (subdivided into young, intermediate or mature), plantation forest, cropland, pasture or urban³⁹ (Extended Data Table 1); these classes were chosen to map onto those in the Representative Concentration Pathways (RCP) scenarios²⁵. Land-use intensity was scored as minimal, light or intense³⁹ (Extended Data Table 1). Land-use history was represented as the time since 30% of the 0.5° grid cell encompassing a site was converted to agricultural or urban use, above which increasingly rapid loss of biodiversity occurs⁴⁰. Estimates were taken from the HYDE model⁴¹. Human population density, proximity to the nearest road and travel time to nearest population of > 50,000 (inversely

proportional to accessibility to humans) for each site came from global datasets^{42–44}. These variables were at most weakly inter-correlated (all $R^2 < 0.31$).

Responses of site-level diversity to pressures were fitted using mixed-effects models⁴⁵, with random effects accounting for study-level differences in diversity (fitted including random slopes) and for blocks of sites within studies. Richness and rarefied richness were fitted using Poisson models, using observation-level random effects to account for overdispersion. Residuals showed little spatial autocorrelation (Extended Data Figure 7). Publication bias, which is common in datasets of this type³, would violate this assumption. There was some evidence that studies with fewer sites and less certainty in estimated coefficients were disproportionately likely to show significantly negative land-use impacts (Extended Data Figure 8). Excluding studies with few sites had little effect on most coefficients (Extended Data Figure 8), partly because our analyses use sites as data points, automatically giving less weight to such studies, and changed projections of richness by less than 1% (not shown). As with all studies based on data from the literature, we cannot incorporate unpublished data. Effects of land use on spatial turnover were estimated by averaging pairwise Sørensen community similarity²² between all pairs of land uses.

To infer temporal diversity changes, we applied the model coefficients to gridded (0.5°-resolution) historical estimates and future projections of pressure variables. Land use estimates were from HYDE and the RCP scenarios²⁵. Human population density estimates were available directly for HYDE and MESSAGE; for other scenarios we downscaled the associated region- and country-level population estimates conserving the current spatial pattern within countries⁴². Land-use intensity was inferred from statistical models relating current land-use intensity to the land use's prevalence within each cell and human population density. In the absence of global projections, proximity to roads and accessibility were assumed to be static over time. Uncertainty was estimated from model-estimated uncertainty

around the coefficients. Cross-validation (leaving out a random 10% of studies – Extended

Data Figure 3c – or one biome at a time – Extended Data Figure 3d) was used to check model

robustness. To derive global averages, we weighted grid cells by land area for community
weighted mean size; by land area and current vertebrate species richness for species richness;

and by potential terrestrial net primary production⁴⁶ for total abundance.

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- 422 **Supplementary Information** is linked to the online version of the paper at
- 423 www.nature.com/nature.

424 425 **Additional references** can be found in the Supplementary Information. 426 427 Acknowledgements 428 We thank Stuart Butchart and Birdlife International for sharing bird body-size data; Francis 429 Gilbert for hoverfly body-size data; the IMAGE, HYDE, MESSAGE and MiniCAM teams, 430 especially Rob Alkemade, Michel Bakkenes and Allison Thomson, for sharing additional 431 data from their integrated assessment models; Derek Tittensor for statistical advice; Chris 432 Sleep and Srinivas Patlola at the Natural History Museum in London for IT support with the 433 database; members of the GARD initiative (http://www.gardinitiative.org/index.html) for 434 help with estimating the reptile species richness map; Kate Jones, Jason Tylianakis, Michael 435 Crawley and E.J. Milner-Gulland for discussion, Neil Burgess for comments on a draft of the 436 paper, and all the many researchers who have made their data available to us. The study was 437 supported by the UK Natural Environment Research Council (NERC, grant number: 438 NE/J011193/1), the Biotechnology and Biological Sciences Research Council (grant number: 439 BB/F017324/1) a Hans Rausing PhD scholarship, and the TRY initiative on plant traits, 440 whose database is maintained at Max-Planck-Institute for Biogeochemistry, Jena, Germany, 441 and which is supported by DIVERSITAS, IGBP, the Global Land Project, NERC, the French 442 Foundation for Biodiversity Research, and GIS "Climat, Environnement et Société" France. 443 444 **Author contributions** 445 T.N., L.N.H., S.L.L.H., S.C., I.L., B.C., D.W.P., R.M.E., G.M.M., J.P.W.S. and A.P. 446 designed the project and this study; T.N., L.N.H., I.L., R.A.S., L.B., J.P.W.S. and A.P. 447 performed the analyses; T.N., L.N.H., S.L.L.H., S.C., D.B., A.C., B.C., J.D., A.D.P., S.E.-L., 448 M.G., M.L.K.H., T.H., D.J.I., V.K., L.K., D.L.P.C., C.M., Y.P., H.R.P.P., A.R., J.S., H.J..W.

449 and A.P. collated the assemblage composition data; T.N., L.N.H., S.L.L.H., S.C., A.D.P., 450 I.L., H.R.P.P., J.P.W.S. and A.P. designed the data-collection protocols and database; R.A.S., 451 S.D., M.E., A.F., Y.I., J.K., M.K., S.M. and E.W. made substantial contributions to the trait 452 data used in the analyses and S.T. to the site-level environmental data; R.A.S., A.F., Y.I., 453 S.M., and M.N. generated the maps of species richness used in the model projections; T.N., 454 L.N.H. and A.P. wrote the manuscript with contributions from G.M.M., L.B., D.W.P., 455 R.M.E., A.D.P., H.R.P.P., S.L.L.H., R.A.S., B.C., S.D., A.F., Y.I., J.K., M.K., S.M., J.P.W.S 456 and S.T.; T.N. and L.N.H. contributed equally to the study. 457 458 **Author information** 459 460 The authors declare no competing financial interests. Correspondence and requests for 461 material should be addressed to T.N. (Tim.Newbold@unep-wcmc.org). 462 463 **Tables** 464 465

Table 1. Key features of the four Representative Concentration Pathways (RCP) scenarios (land-use and human-population assumptions are detailed in ref. 25, energy

assumptions in refs. 47–49, and climate implications in ref. 50).

Scenario	Land use (see also	Climate and energy	Human population
	Extended Data Figure 5)		
IMAGE 2.6	Agriculture moves from	Increased energy	10.1 billion by 2100 (UN
	developed to developing	efficiency. Increased use	Medium variant, 2010)
	countries. Large increase	of carbon capture and	
	in area of biofuel	storage, nuclear,	
	plantations. Urban extent	renewable energy and	
	assumed constant.	biofuels. Approximately	
		1 °C temperature increase	
		by 2100 compared to pre-	
		industrial.	
MiniCAM 4.5	Carbon pricing leads to	Decline in overall energy	Peaks above 9 billion
	preservation of primary	use. Decreased use of	around 2065, then
	forest and expansion of	fossil fuels and increase	declines to 8.7 billion by
	secondary forest. Crop	in nuclear and renewable	2095.
	yield increases, improved	energy, and in carbon	
	agricultural efficiency	capture and storage.	
	and dietary shifts lead to	Moderate increase in use	
	decreases in cropland and	of biofuels, but limited by	
	pasture areas. Small	availability of biomass.	
	increase in area of biofuel	Approximately 1.75 °C	
	plantations. Urban extent	temperature increase by	
	assumed constant.	2100.	
AIM 6.0	Urban area increases	Approximately 2.5 °C	9.1 billion by 2100 (UN
	owing to human	temperature increase by	Medium variant, 2004)
	population growth.	2100.	

	Cropland area increases		
	to meet food demand.		
	Pasture area declines		
	strongly.		
MESSAGE 8.5	Increasing crop yields	Small improvements in	12 billion by 2100.
	and intensification	efficiency leading to high	
	account for much of the	demand for energy.	
	increased production	Conventional oil and gas	
	required, but area of	become scarce, leading to	
	cropland and, to a lesser	shift in favour of	
	extent, pasture increases	unconventional and	
	rapidly. Small increase in	carbon-intensive fossil	
	area of biofuel	fuels. Moderate increase	
	plantations. Urban area	in use of biofuels.	
	increases owing to	Approximately	
	increased population.	4 °C increase in	
		temperature by 2100.	

Figure legends

Figure 1. Locations of sites and responses of four metrics of local diversity to human pressures. a, Sites in the dataset used to model within-sample species richness. Fitted responses of three biodiversity metrics to anthropogenic variables: b, richness; c, total abundance; and e, community-weighted mean organism size – log₁₀ plant height (crosses) and log₁₀ animal mass (triangles). Error bars show 95% confidence intervals. Land use effects: Primary = primary vegetation, YSV = young secondary vegetation, ISV = intermediate secondary vegetation, MSV = mature secondary vegetation, Plantation = plantation forest. Land-use intensity: minimal (circle), light (triangle), intense (diamond), and combined light and intense (square). Continuous effects: human population density (HPD), proximity to roads (as –log(distance to nearest road); PR), and accessibility to humans (as – log(travel time to nearest major city); ACC) are shown here as modelled marginal effects for all land uses (i.e. from a model with no interactions between continuous effects and land use) at the lowest (L), median (M) and highest (H) values in the dataset.

Figure 2. Similarity in assemblage composition as a function of land use. a, Average dissimilarity of species composition (1 – Sørenson Index) between pairs of sites within and among different combinations of land use; values are expressed proportional to the average similarity between pairs of primary-vegetation sites; blue colours indicate more similar composition, and red colours less similar; more intense colours indicate more extreme values; numbers indicate numbers of studies within which comparisons could be made. b,

Dendrogram showing clustering of different land-use types based on average compositional dissimilarity; urban sites were excluded as their small sample size made their position unstable. Land-use labels as in Figure 1.

Figure 3. Net change in local richness from pre-impact times to 2000. Projections used an IMAGE reference scenario¹⁰. The pre-impact landscape was assumed to be entirely uninhabited and unused primary vegetation. Shown using a Lambert Cylindrical Equal Area projection at 0.5° resolution.

Figure 4. Projected net change in local richness from 1500 to 2095. Future projections were based on the four Representative Concentration Pathways (RCP) scenarios (Table 1). Historical (shading) and future (error bars) uncertainty is shown as 95% confidence intervals, with uncertainty rescaled to be zero in 2005 to show uncertainty in past and future change separately. The baseline for these projections is a world entirely composed of uninhabited and unused primary vegetation; thus, the value at 1500 is not constrained to be zero because non-primary land uses were present – and in some regions widespread – by that date. The global average projection for MESSAGE 8.5 does not directly join the historical reconstruction because that scenario's land use projections start in 2010 (human population estimates are available at 15-year intervals) and because human population (and thus inferred land-use intensity) and plantation-forest extent have not been harmonized among scenarios.

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 the Human Development Index (an indicator of education, life expectancy, wealth and standard of living). Colours indicate biogeographic realms; colour intensity reflects natural vertebrate species richness (more intense = higher species richness); point size 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 HDI (more intense = higher index).

Extended Data Legends

Extended Data Figure 1. Taxonomic and geographic representativeness of the dataset used. a, The relationship between the number of species represented in our data with the number estimated to have been described ¹⁶, for 47 major taxonomic groups; lines show (from bottom to top) 0.1%, 1% and 10% representation of described species in our dataset; magenta = invertebrates, red = vertebrates, green = plants, blue = fungi, and grey = all other taxonomic groups. **b,** the relationship across biomes ⁴⁰³ between the percentage of global net primary production and the number of sites in our dataset; 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, savannas and shrublands, G = Mediterranean forests, woodlands and scrub, H = deserts and xeric shrublands, J = tropical and subtropical grasslands, savannas 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 savanna biome is not represented in the dataset; grey line show 1:1 line.

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

Modelled effects (controlling for land use) 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: \mathbf{a} - \mathbf{c} , \mathbf{f} , \mathbf{g} , within-sample species richness; \mathbf{e} , \mathbf{h} , \mathbf{i} , total abundance; and \mathbf{d} , community-weighted mean vertebrate body mass. Shaded polygons in \mathbf{a} - \mathbf{d} show 95% confidence intervals. For clarity, shaded polygons in \mathbf{f} - \mathbf{i} are shown as $\pm 0.5 \times \text{SEM}$. Confidence intervals in \mathbf{e} are omitted. Rugs along the x axes in the line graphs show the values of the explanatory variables represented in the dataset 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 Figure 1.

Extended Data Figure 3. Robustness of modelled effects of human pressures. a, Effects of land use, human population density (HPD) and proximity to nearest road (PR) 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 dataset, we also show modelled effects on within-sample species richness with the same reduced dataset. 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 ten-fold 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 Figure 1 in the main text.

Extended Data Figure 4. Current, past and future projections of all metrics of local biodiversity. Net change in local diversity from pre-human times to 2000 under an IMAGE reference scenario¹⁰: **a**, richness; **b**, rarefied richness; **c**, total abundance; and **d**, community-

weighted mean plant height. 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. Hindcast and projected net change in local diversity from 1500-2095, based on estimates of land-use, land-use intensity and human population density from the four Representative Concentration Pathways (RCP) scenarios (Table 1): **e**, richness; **f**, total abundance; and **g**, community-weighted mean plant height; 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 (i.e. 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 5. Reconstructed and projected total global land-use areas under the Representative Concentration Pathways (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 6. **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 (**a**, IMAGE 2.6; **b**, MiniCAM 4.5; **c**, AIM 6.0; and **d**, MESSAGE 8.5), 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 (**e**. MiniCAM 4.5; **f**, MESSAGE 8.5), shown in relation to past change in biodiversity from the pre-impact baseline 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 = higher species richness); point size is proportional to (log) country area.

Extended Data Figure 7. Tests for spatial autocorrelation in the model residuals. For the four main modelled metrics of site-level diversity — \mathbf{a} , within-sample species richness; \mathbf{b} , total abundance; \mathbf{c} , community-weighted mean plant-height; and \mathbf{d} , community-weighted mean animal mass — histograms of P-values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for individual studies. The percentage of studies with significant spatial autocorrelation (P < 0.05; indicated by vertical red line) is shown.

Extended Data Figure 8. 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 5 sites in the land use in question (10 for secondary vegetation and plantation forest because there were more sites for these land uses and some studies with between 5 and 10 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 (i.e. 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 5 sites in that land use (10 for secondary vegetation and plantation forest).

Extended Data Table 1. Land use and land-use intensity classification definitions (from ref. 39).

Extended Data Table 2. Conversion between Global Land Systems dataset and our intensity classification for each major land-use type. To estimate proportional coverage of each intensity class for each land-use type in the 0.5° grid cells used for projection, we calculated the number of finer-resolution Global Land Systems⁴⁰¹ 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.

Methods

Data collation

Between March 2012 and April 2014 we collated data from published studies⁵¹⁻³³⁴ examining the effect of human activities on more than one named taxon. A full description of how the dataset was assembled and curated is presented elsewhere³⁹. 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 georeferenced them from maps in the papers.

The great majority of listed taxa were species-level, although many could not be given explicit species identifications (e.g. morpho-species)³⁹; henceforth we refer to distinct taxa in

our dataset as species. We matched taxonomic names given in the source paper to the Catalogue of Life 2013 Annual Checklist (COL)³³⁵, 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% as many species as are thought to have been formally described (Extended Figure 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 Figure 1b).

Site-level composition and diversity

Site-level metrics of diversity 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 density³³⁹). 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 curve³³⁶. We therefore also calculated **rarefaction-based species richness** by taking 1000 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 varied sampling effort 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, and then dividing the raw abundance measurements by this relative sampling effort. The rescaling was performed to prevent introducing additional heterogeneity in the modelled abundance values.

Community-weighted mean organism size was calculated as the arithmetic mean of logtransformed height of plants (available for 4,235 species in our dataset) or the logtransformed body mass or volume of vertebrates, beetles and hoverflies (5,236 species) present at a site, weighted by abundance³³⁷. Plant height data were taken from the TRY database³³⁸; 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 mammals³³⁹, from BirdLife International's World Bird Database for birds, and from a wide range of published and grey-literature sources for amphibians ^{340–386}. Length data for reptiles were taken from published and unpublished sources^{387,388}, and converted to estimates of body mass using published length-mass allometries ^{389,390}. Arthropod size data (beetles and hoverflies) were collated from published sources ^{391,392}. Beetle length and amphibian snoutvent 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).

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Human pressure data

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While many human pressures can impact 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 hindcasting and 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. These classes were selected to match the land-use classification adopted in the Intergovernmental Panel on Climate Change Representative Concentration Pathways scenarios²⁵ in order 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 (e.g. 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. We overlaid our sites with available global data sets to obtain site-level estimates of human population density⁴², distance to the nearest road⁴³ and estimated travel time to nearest population centre with greater than 50,000 inhabitants⁴⁴. For distance to nearest road, the roads map was first projected onto a Berhmann equal-area projection. These operations were carried out using Python code implemented using the arcpy Python module in ArcMap Version 10.0³⁹³. 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 impact. 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 model⁴¹. The 30% threshold was chosen because it has been suggested as the level of landscape conversion above which increasingly rapid loss of biodiversity occurs⁴⁰. Collinearity among variables describing

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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 1.0-5⁴⁵ in R Version 3.0.2³⁹⁴. We first compared candidate random-effects structures using the full candidate fixed-effects structure³⁹⁵. Random-intercept terms considered in all models were the identity of 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 (i.e. site identity) to account for the overdispersion present³⁹⁶. 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 AIC values.

Once the best random-effects structure had been selected, we performed backward stepwise model simplification to select the best fixed-effects structure (see 'Full Statistical Results')³⁹⁵. 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. Human population density, distance to

roads, travel time to nearest major city and time since human landscape conversion 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 prior to 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. The decision whether or not to retain terms was based on likelihood ratio tests. The coefficient estimates of the best models are shown in Figure 1b-d and Extended Figure 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 0.5-68³⁹⁷ in R; the distribution of P-values across studies was used as an indication of whether spatial autocorrelation was likely to cause a problem (Extended Data Figure 7). We used cross validation to assess the robustness of model parameter estimates, first based on dividing the studies randomly into 10 equal-sized sets and dropping each set in turn (Extended Figure 3a), and secondly based on leaving out the studies from each biome in turn (Extended Figure 3b).

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Publication bias is a potential problem for any large-scale synthesis of data from many publications. In standard meta-analyses, funnel plots³⁹⁸ can be used to test for any relationship between standard error and effect size, as a bias in effect sizes at high standard

error toward 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 meta-analysis. 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 2) 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 Figure 8). 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 Figure 8). On the other hand, study-level random slopes of human-dominated land uses tended to be more negative for studies that sampled more sites (Extended Data Figure 8). 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 Figure 8). 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).

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To model turnover of species composition between pairs of sites, we calculated average dissimilarity²² in the lists of present species (1 – 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 (i.e. 1 – similarity) matrix, using the helust function in R Version 3.0.2³⁹⁴. 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 (i.e. that secondary vegetation and plantation forests will remain closer to primary vegetation than cropland, pasture and urban habitats).

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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° resolution, using historical estimates for 1500 to 2005, and four Representative Concentration Pathways scenarios of future changes (IMAGE 2.6, MiniCAM 4.5, AIM 6.0 and MESSAGE 8.5; the names refer to the models used and the numbers to the amount of radiative forcing assumed in 2100)³⁹⁹.

Estimates of land use for both the historical reconstruction and the future scenarios were taken from the harmonized land-use data accompanying the scenarios²⁵. 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 available only 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 regions⁴⁸; 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 patterns⁴², which is the method used in other RCP-scenario land-use models lacking human population data resolved to grid cells²⁵. 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 division⁴⁰⁰, which gives the closest global predictions of future human population to those assumed by IMAGE and AIM²⁵. 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' 401, 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 dataset has a spatial resolution of 5 arc-minutes. To calculate the proportion of each 0.5° cell occupied by each land use and land-use intensity combination we calculated the proportion of 5-arc-minute cells within each 0.5° 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 (i.e. we fitted

human population density). UN sub-region data were taken from the world borders shapefile Version 0.3 (http://thematicmapping.org/downloads/world_borders.php) and converted to a 0.5° raster using ArcMap Version 10.0³⁹³. The models were developed using generalized linear models with a binomial distribution of errors, implemented in the lme4 package Version 1.0-5⁴⁵ in R Version 3.0.2³⁹⁴. 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 hindcast and forecast 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 hindcasts or forecasts, thereby assuming it to be spatially (not temporally) constant within each cell. The coefficients from the models of sitelevel 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, 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 10.0³⁹³. Data on Net Primary Production were estimates of potential NPP (i.e. in the absence of human impacts) from the Lund-Postdam-Jena (LPJ) Dynamic Global Vegetation Model⁴⁶.

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 (i.e. projections were based only on the final best model) because applying such complex mixed-effects models, based on such large datasets, 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 2.2-12⁴⁰² in R Version 3.0.2³⁹⁴. 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-economy, 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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