independent scorer blind to each duckling's imprinting condition and to the study's hypothesis. Ducklings that were inactive during testing (fewer than five approaches) were excluded from analysis. Preferences were assessed via sign test, with sample size being the number of individual ducklings. Ducklings making more than half of their approaches toward a given stimulus were scored as having preferred it (see the methods in the supplementary materials). Video of sample trials (movie S1) is available in the supplementary materials.

Figure 3 shows the preference results. In experiment 1, out of a total of 47 active ducklings, 32 preferred the pair bearing their imprinted shape relation (two-tailed binomial test, $P = 0.02$). In experiment 2, out of 66 active ducklings, 45 preferred the stimulus pairs bearing their imprinted color relation (two-tailed binomial test, $P = 0.004$). Combining both results, out of 113 active ducklings, 77 preferred the relational concept, same or different, upon which they had imprinted (two-tailed binomial test, $P < 0.0001$).

The accuracy of our ducklings was comparable to, or better than, reinforced relational concept discrimination in primates ([24]) and crows ([1]). This finding supports a richer emerging view of the representation of information in the animal brain than is presently prevalent, in which even relatively simple learning systems do not process information just through the content of sensory signals but also by encoding higher-level, abstract aspects of stimulus analyses, already the target of neural network models designed to simulate such cognitive function ([25]). The ducklings' performance indicates that their brains may be prepared, not just to respond differentially to certain visual inputs, such as scrambled objects containing species-specific elements like legs or heads or virtual points that move in a biologically plausible coordination ([20]), but also to pick up abstract relational properties between elements of their sensory input and those elements' characteristics.

For young precocious birds, having this competence makes biological sense. For a duckling critically dependent on proximity to its mother and siblings, defining the attachment stimulus configuration as a library of sensory inputs and logical rules increases the likelihood that the mother and sibling group will be identified with high fidelity in spite of considerable variations in how they are perceived. The rules that may define the imprinted attachment target are likely to extend beyond properties of a single object such as color, shape, or symmetry, to include properties of object assemblies such as their informational entropy ([26]).

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BIODIVERSITY

Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment

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Land use and related pressures have reduced local terrestrial biodiversity, but it is unclear how the magnitude of change relates to the recently proposed planetary boundary ("safe limit"). We estimate that land use and related pressures have already reduced local biodiversity intactness—the average proportion of natural biodiversity remaining in local ecosystems—beyond its recently proposed planetary boundary across 58.1% of the world's land surface, where 71.4% of the human population live. Biodiversity intactness within most biomes (especially grassland biomes), most biodiversity hotspots, and even some wilderness areas is inferred to be beyond the boundary. Such widespread transgression of safe limits suggests that biodiversity loss, if unchecked, will undermine efforts toward long-term sustainable development.

Land use and related pressures have been the main drivers of terrestrial biodiversity change ([1]) and are increasing ([2]). Biodiversity has already experienced widespread large net losses ([3]), potentially compromising its contribution to resilient provision of ecosystem functions and services, such as biomass production and pollination, that underpin human well-being ([4]–[7]). Species-removal experiments suggest that loss of ecosystem function accelerates with ongoing species loss ([5]), implying that there may be thresholds beyond which human intervention is needed to ensure adequate local ecosystem function ([8], [9]). The loss of 20% of species—which affects ecosystem productivity as strongly as other direct drivers ([5])—is one possible threshold, but it is unclear by which

mechanism species richness affects ecosystem function and whether there are direct effects or only effects on resilience of function (6, 7). Whereas this proposed safe limit comes from studies of local ecosystem health, the Planetary Boundaries framework (8, 9) considers longer-term maintenance of function over much larger (biome to global) scales. At these temporal and spatial scales, the maintenance of function depends on functional diversity—the ranges and abundances of the functional traits of the species present (8, 10). Because direct functional trait data are lacking, the Biodiversity Intactness Index [BII; the average abundance of originally present species across a broad range of species, relative to abundance in an undisturbed habitat (11)] is suggested as the best metric (8, 9). The safe limit is placed at a precautionary 10% reduction in BII, but it might be as high as a 70% reduction (9).

A key uncertainty when estimating safe limits concerns the value of species not present in the undisturbed ecosystem. Such species could benefit ecosystem functioning, have no effect (as assumed by the BII), or even impair it (12–15). Most models estimating net human impacts on biodiversity (3, 16) treat novel and originally present species as functionally equivalent, whereas experimental studies manipulate species originally present (17).

Given the possibly severe consequences of transgressing safe biodiversity limits, global assessments of relevant metrics are needed urgently. Data limitations have hampered efforts to date; BII has so far only been estimated, from expert opinion, for seven southern African countries (11). More recently, we combined global models linking land-use pressures to local biodiversity with global land-use maps. We estimated that net reductions in local species richness exceeded 20% across 28% of the world's land surface by 2005, whereas 48.7% of land had seen net reductions in total abundance of ≥10% (3). However, our projections of net effects did not account for any reductions of originally present diversity that were offset by an influx of novel species (18), as well as being at too coarse a scale (~50 km^2) to be relevant for local ecosystem functioning and decision-making. Furthermore, we did not analyze the spatial distribution of the transgression of proposed safe limits.

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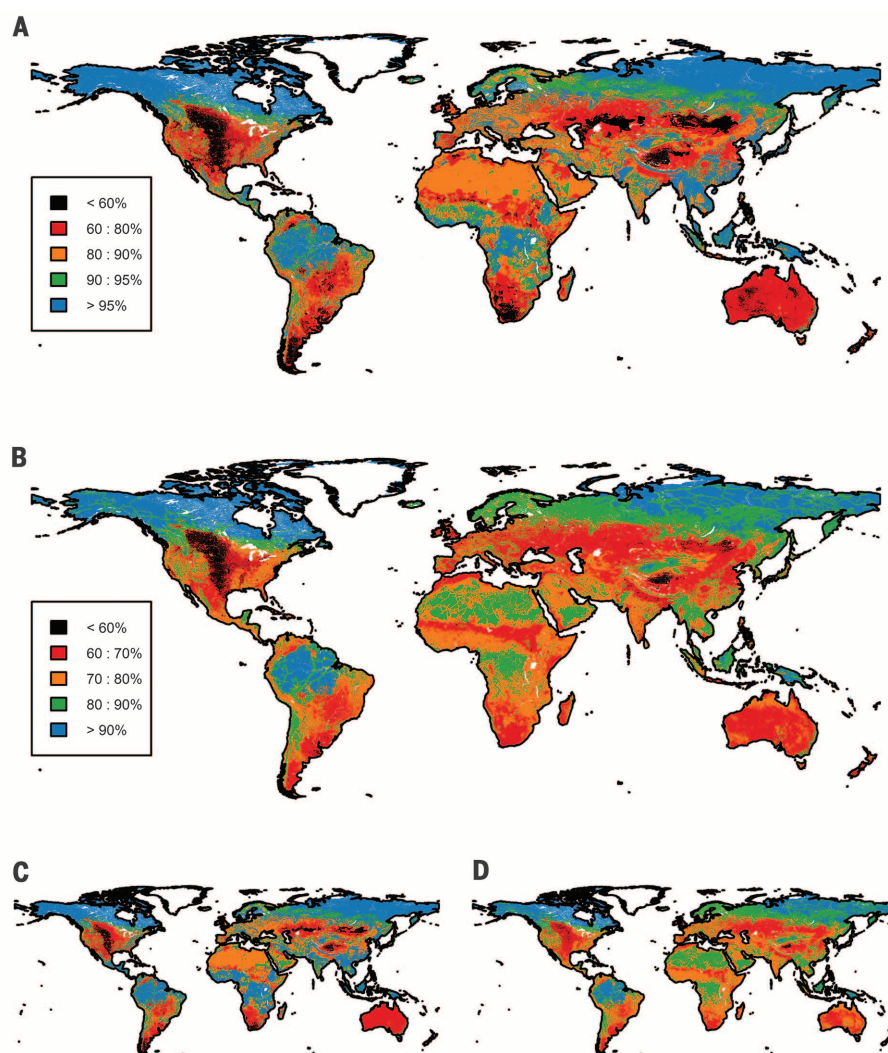
Fig. 1. Biodiversity intactness of ecological assemblages. (**A**) Total abundance of species occurring in primary vegetation (BII). (**B**) Richness of species occurring in primary vegetation. (**C**) and (**D**) correspond to (A) and (B), respectively, and have the same legend values but include species not present in primary vegetation.
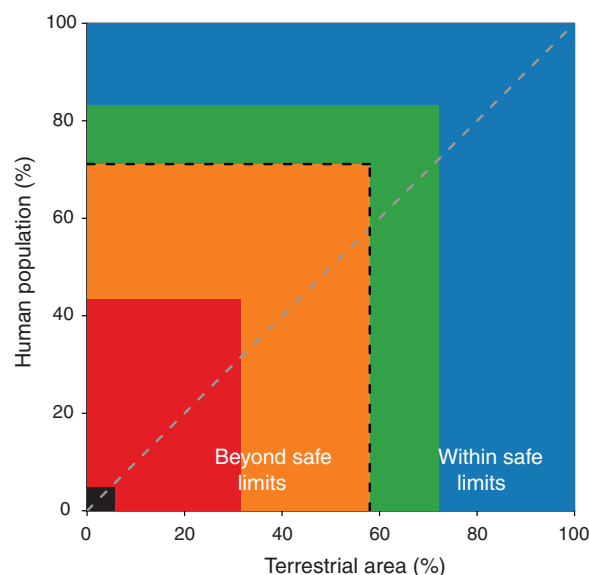
Fig. 2. Terrestrial area and human population at different levels of BII. Biodiversity intactness increases from bottom left to top right and has the same color scheme as that of Fig. 1. The dashed black line shows the position of the planetary boundary (9): Only areas to the right and human population above this line (shaded green and blue) are within the proposed safe operating space. If human population were distributed randomly with respect to BII, the corners of the boxes would align with the dashed gray line; the extent to which the corners lie above this line indicates the strength of the bias in human populations toward less intact areas.
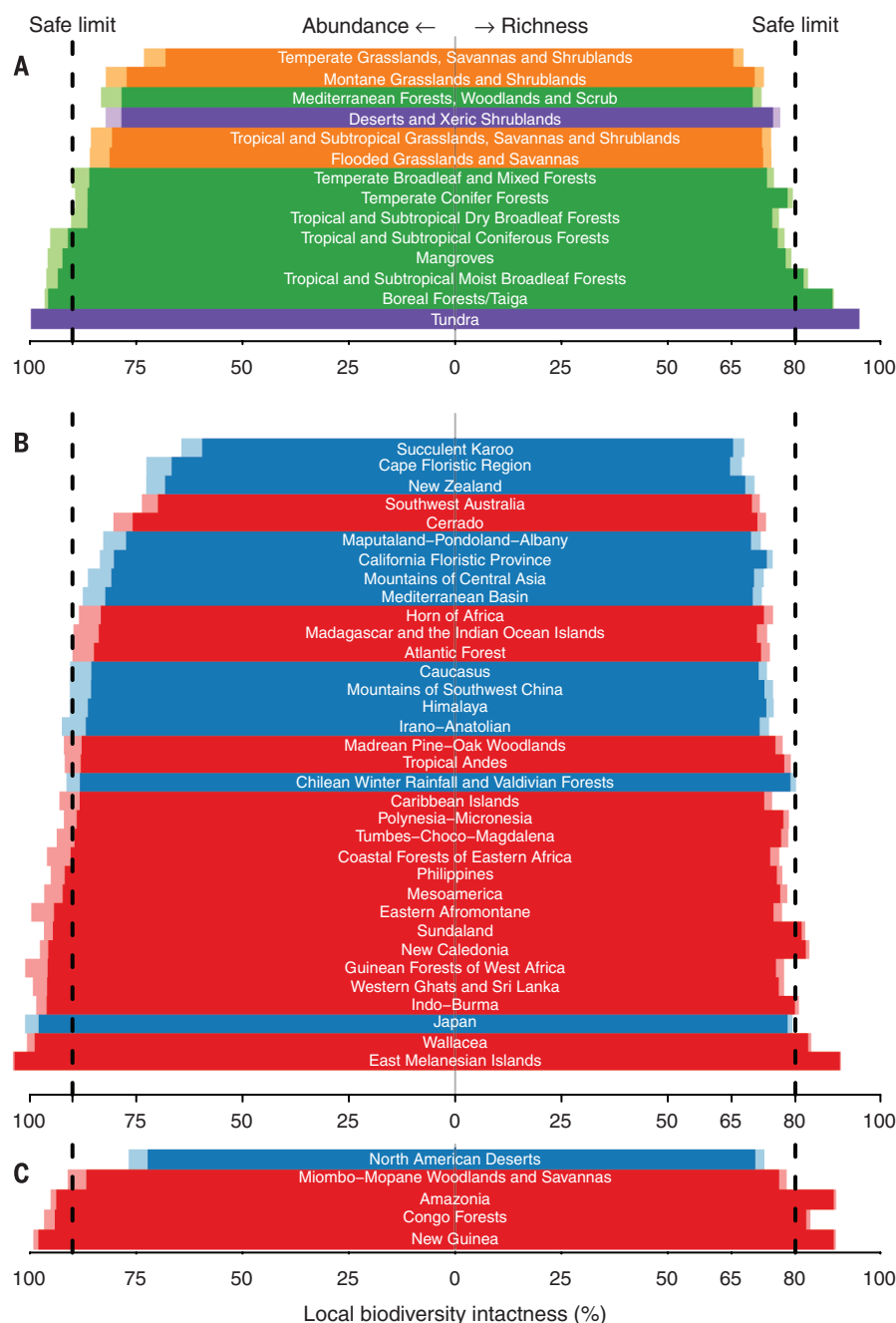
Fig. 3. Biodiversity intactness for biomes, biodiversity hotspots, and high biodiversity wilderness areas. (A to C) Biodiversity intactness in terms of total abundance (BII; solid bars on left) and species richness (solid bars on right) in each of (A) 14 terrestrial biomes, (B) 34 biodiversity hotspots, and (C) five high biodiversity wilderness areas. Translucent bars indicate the corresponding relative biodiversity values if novel species are treated as equivalent to those originally present (these numbers can surpass 100% because gains may outnumber losses). Bars in (A) are colored by major biome type (orange, grasslands; green, forests; purple, other), whereas bars in (B) and (C) are colored according to whether they are in the temperate (blue) or tropical (red) realms.

Here, we present fine-scale (~1 km²) global estimates of how land-use pressures have affected the numbers of species and individuals found in samples from local terrestrial ecological assemblages (19). To explore different assumptions about novel species, we estimated both overall net change (correct if novel species contribute fully to ecosystems) and—using estimates of species turnover among land uses to exclude novel species—change in species originally present (correct if novel species play no role). We asked how much of the Earth's land surface is already "biotically compromised" (exceeds the boundaries of 10% loss of abundance or 20% loss of species). We focused on results for the relative abundance of originally present species (BII) because this is the measure suggested in the Planetary Boundaries framework (9). We estimated average losses per biome because of the suggested importance of biomes for the functioning of the whole Earth system (8, 9), and to assess possible consequences for people—assuming that many biodiversity-regulated ecosystem services operate locally—we quantified the geographical congruence between biodiversity reduction and human population. We also assessed the biotic integrity of areas identified as particularly important for conservation (although the proposed planetary boundary in terms of BII may not always be relevant for areas much smaller than biomes and probably needs to vary depending on the sensitivity of the biota). First, Conservation International's "biodiversity hotspots"—areas rich in endemic species but with high levels of habitat loss—have been suggested as urgent conservation priorities (20). Because these areas were identified reactively (20) with a criterion of 70% loss of primary vegetation, we expect them to have lower biodiversity intactness than average. For comparison, we also estimated the biodiversity intactness of Conservation International's high biodiversity wilderness areas, which also meet the criterion of high species endemism but retain 70% of their natural habitat, and so present more opportunity for proactive conservation (20).

We modeled how sampled richness and abundance respond to land-use pressures using data from the PREDICTS (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems) database (21). These data consisted of 2,382,624 records (fig. S1) [nearly twice as many as our earlier, coarser-scale analyses (3)] of the abundance (1,888,784 records) or else presence/absence of 39,123 species at 18,659 sites. The hierarchical mixed-effects models we used considered four pressure variables—land use, land-use intensity, human population density, and proximity to the nearest road—as fixed effects (figs. S2 and S3), whereas random effects accounted for among-study differences in sampling (methods, effort, and focal taxonomic groups) and for the spatial arrangement of sampled sites within studies (supplementary materials, materials and methods). We had insufficient data to fit separate models for each biome or clade. Responses may vary taxonomically or geographically, although our earlier analyses showed no significant differences among plants, invertebrates, and vertebrates and suggested limited variation among biomes (3). As more data become available, future analyses will be better able to reflect any differences in response. We combined the models of species richness and total abundance with models of species turnover among land uses [based on (22), but adapted to reflect asymmetric differences among land uses] to discount the fraction of species absent in nonprimary habitat (supplementary materials, materials and methods). To map modeled responses, we used global pressure data for the year 2005 at a resolution of 30 arc sec (~1 km²). We used land-use estimates for 2005 (23) and estimated land-use intensity as in (3); human

population (for the year 2000) came from (*24*), and proximity to nearest road came from (*25*). Values of the response variables are always expressed relative to an intact assemblage undisturbed by humans and therefore do not rely on estimates of absolute abundance or species richness, which vary widely among biomes and taxa.

Our map of terrestrial BII (Fig. 1A and fig. S4) suggests that the average local abundance of originally present species (*11*) globally has fallen to 84.6% [95% confidence interval (CI), 82.2 to 91.6%] of its value in the absence of human land-use effects, which is probably below the value (90%) proposed as a safe limit (*9*). Considering net changes in abundance, as in (*3*), assuming that novel species contribute fully to ecosystem function, global average abundance has fallen to 88.0% (95% CI, 83.5 to 94.8%) of its value before human effects.

Assuming that only originally present species contribute to ecosystem function, most of the world's land surface is biotically compromised in terms of BII (58.1% of terrestrial area; 95% CI, 40.4 to 70.2%) (Fig. 1A) and within-sample richness of originally present species (62.4%; 95% CI, 20.0 to 72.7%) (Fig. 1B). If the proposed boundaries are broadly correct, ongoing human intervention may be needed to ensure delivery of ecosystem functions across most of the world (*5*). The proposed planetary boundary for BII (*9*) had uncertainty ranging from 30 to 90%; the proportion of the land surface exceeding the boundary varies widely across this range (fig. S5), highlighting the urgent need for better understanding of how BII relates to Earth-system functioning (*9*). Assuming that novel species contribute as much to ecosystems as originally present species, we estimate the safe limit for total abundance to have been crossed in 48.4% (95% CI, 30.9 to 66.5%) of land (Fig. 1C) and that for within-sample species richness in 58.4% (95% CI, 21.8 to 75.0%) (Fig. 1D). If novel species impair ecosystem function (rather than benefit it or have no effects), then all of these estimates will be too optimistic. Most people (71.4%) live in biotically compromised areas, as judged with BII (Fig. 2), although uncertainty in this result was high (95% CI, 8.7 to 92.4%). There is growing evidence that access to high-biodiversity areas benefits people's physical and psychological well-being (*26*, *27*), although uncertainty remains over which aspects of biodiversity are important.

The biodiversity impact of land-use pressures varies among biomes (Fig. 3A and table S2): grasslands are most affected, and tundra and boreal forests are least affected. Our BII estimates suggest 9 of the 14 terrestrial biomes (95% CI, 4 to 12) have on average transgressed safe limits for biodiversity (Fig. 3A), although this number drops to seven (95% CI, 1 to 12) if novel species are included. The BII limit has been crossed in 22 of 34 terrestrial biodiversity hotspots (95% CI, 7 to 31) (Fig. 3B and table S3) (*28*); this figure falls to 12 (95% CI, 5 to 32) if novel species are included, again highlighting the need to understand their effects on ecosystem function. Given that bio-

diversity hotspots were identified partly on the basis of widespread historical habitat loss (*20*), their low average BII is unsurprising, although our results suggest that at least some hotspots might stay within safe ecological limits if future land conversion is reduced. In contrast, three out of the five high biodiversity wilderness areas, which were identified for conservation proactively because the habitat is still relatively intact (*20*), have not experienced average losses of local biodiversity (BII) that cross the planetary boundaries (95% CI, 2 to 4) (four out of five if novel species are included; 95% CI, 2 to 5) (Fig. 3C and table S4). Results concerning which areas have crossed proposed planetary boundaries were generally consistent between the richness- and abundance-based biodiversity measures (Fig. 3 and tables S2 to S4).

Our models suggest a generally smaller impact of land use on BII than that in a previous study (*11*). This might reflect differences in taxonomic coverage, but there are also two reasons why our results may overestimate BII. First, we ignore lagged responses. Second, our models use sites in primary vegetation as a baseline because historical data are so rare (*3*, *11*); these sites will often have experienced some human impact. Nevertheless, because our models are global, their baseline is not biome- or region-specific and they do not rely on data from minimally affected land use from heavily modified landscapes, where such conditions do not exist. Our data have good coverage of taxa and biomes (fig. S1), but the density of sampling is inevitably uneven. Biomes that are particularly underrepresented, relative to their global ecosystem productivity, are boreal forests, tundra, flooded grasslands, and savannas and mangroves (fig. S1), meaning that less confidence can be placed in the results for these biomes. The data probably also underrepresent soil and canopy species. The estimate of land area biotically compromised in terms of species richness is much higher than our previous assessment (58.4 versus 28.4%, although the CIs overlap), but the estimates based on total abundance are almost identical (48.4 versus 48.7%) (*3*). The discrepancy for species richness is because of a stronger modeled interaction here between land use and human population density (fig. S3) and because we include the effect of roads and the interaction between roads and land use, which were omitted from the projections in (*3*).

The Sustainable Development Goals adopted in September 2015 (*29*) aim to improve human well-being while protecting, restoring, and sustainably using terrestrial ecosystems. Our results highlight the magnitude of the challenge. Exploitation of terrestrial systems has been vital for human development throughout history (*30*), but the cost to biosphere integrity has been high. Slowing or reversing the global loss of local biodiversity will require preserving the remaining areas of natural (primary) vegetation and, so far as possible, restoring human-used lands to natural (secondary) vegetation. Such an outcome would be beneficial for biodiversity, ecosystems, and—at least in the long term—human well-being.

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