

ENVIRONMENTAL STUDIES

The direct drivers of recent global anthropogenic biodiversity loss

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Effective policies to halt biodiversity loss require knowing which anthropogenic drivers are the most important direct causes. Whereas previous knowledge has been limited in scope and rigor, here we statistically synthesize empirical comparisons of recent driver impacts found through a wide-ranging review. We show that land/sea use change has been the dominant direct driver of recent biodiversity loss worldwide. Direct exploitation of natural resources ranks second and pollution third; climate change and invasive alien species have been significantly less important than the top two drivers. The oceans, where direct exploitation and climate change dominate, have a different driver hierarchy from land and fresh water. It also varies among types of biodiversity indicators. For example, climate change is a more important driver of community composition change than of changes in species populations. Stopping global biodiversity loss requires policies and actions to tackle all the major drivers and their interactions, not some of them in isolation.

INTRODUCTION

Human well-being is underpinned by ecological systems and the benefits they provide to people (1–4), so anthropogenic impacts on nature are of growing scientific, political, and societal concern (2, 5). Knowing which of the human pressures that proximally influence biodiversity—henceforth, direct drivers—are doing the most damage worldwide is a prerequisite for designing new systemic policies and action targets that can achieve major sustainability objectives such as the post-2020 global biodiversity framework of the Convention on Biological Diversity (CBD) or the Sustainable Development Goals (SDGs) of the United Nations (6–8). This is so because all the ways that human values and behaviors (the ultimate indirect drivers) cause biodiversity loss must, by definition, act through the direct

drivers (9). Thus, policies that do not mitigate the direct drivers are bound to fail, whatever effect they may have on indirect drivers earlier in the causal chain (2).

Climate change has rightly attracted attention as a recent and accelerating direct driver (5, 10, 11), but other drivers—direct exploitation of natural resources, land/sea use change, pollution, and invasive alien species—also still cause widespread biodiversity loss (12–14). Which of these direct drivers has the most impact on the various dimensions of biodiversity—from genes and species to ecosystems—surprisingly remains an open question. Previous attempts to answer it have either used expert judgment (12, 15), focused on the analysis of one or a few indicators of particular aspects of biodiversity or specific taxonomic groups (14, 16, 17), or considered only a subset of the main drivers (17, 18). None of these approaches can provide policy makers with the robust conclusions they need about which direct drivers most need mitigation.

As part of the global assessment report from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (2), we systematically reviewed natural science studies published since 2005 that compared the impacts that multiple direct drivers have had on any of a large set of indicators of the state of biodiversity (tables S1 to S4). We excluded studies that compared projected future effects of drivers. We screened the 45,162 studies (including gray literature) found by systematic database searches or suggested by a global set of experts and stakeholders involved in the external reviewing process of the IPBES report, read the most relevant 575 in full, and extracted information from the 163 studies that included nonredundant comparisons of the impacts on biodiversity of at least two of the five predefined classes of direct drivers: climate change, land/sea use change, direct exploitation of natural resources, pollution, and invasive alien species (see Materials and Methods). Focusing on these multidriver assessments is necessary to avoid simply mirroring any research biases toward investigating particular drivers (15, 18). Most of these studies did not consider impacts before 1970 (1983 was the median start year of time series analyzed in the studies). For the analyses in this paper, to estimate each driver's position in the overall dominance hierarchy even though some have been studied more than

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others (19), we converted each multidriver assessment into one or more nonredundant pairwise comparisons between drivers (see Materials and Methods). Analyzing these head-to-head comparisons (table S5) allowed us to quantify each driver’s dominance (20), using bootstrapping to test whether pairs of drivers differed significantly in their impact. Wherever possible, we also assigned each comparison to one of the four IPBES geographic regions (Africa, Americas, Asia and the Pacific, or Europe and Central Asia) (21); to the terrestrial, freshwater, or marine realm; and to one of the six broad dimensions of biodiversity represented by the classes of Essential Biodiversity Variables [EBVs; (22)]—genetic composition, species populations, species traits, community composition, ecosystem structure, and ecosystem function (table S4). This allowed us to use randomizations to test the statistical significance of differences in the driver dominance hierarchies among major regions, types of ecosystems, and dimensions of biodiversity; these groupings are still broad and heterogeneous, but biological and socioeconomic differences among them may be reflected in their driver dominance hierarchies (see Materials and Methods). Our evidence reflected large-scale geographic and taxonomic biases in knowledge, with fewer studies from Africa than from the other regions and, for those indicators relating to taxonomic groups, far more information from vertebrates than from plants or invertebrates (table S6).

RESULTS

Overall, land/sea use change was the dominant direct driver of biodiversity loss (Fig. 1A), although it was not significantly ahead of

the second-ranked driver, direct exploitation [bootstrap $P = 0.92$; all P values reported in the text have been adjusted for multiple testing (23) when appropriate]. Both land/sea use change and direct exploitation were significantly dominant over climate change (bootstrap $P = 0.034$ and $P = 0.040$, respectively) and invasive alien species ($P < 0.0001$ for both).

The dominance hierarchy of drivers differed significantly between terrestrial, freshwater, and marine realms (randomization $P < 0.0001$), with the hierarchy in the sea differing significantly from both that on land (randomization $P < 0.0001$) and that in fresh water (randomization $P = 0.018$; Fig. 1B). Land/sea use change was ranked first in terrestrial systems, significantly ahead of direct exploitation (bootstrap $P = 0.026$), and in freshwater ecosystems, ahead of pollution, but direct exploitation was the dominant driver in marine ecosystems with climate change second.

The dominance hierarchy was broadly consistent among the four IPBES regions, although land/sea use change was ranked first and direct exploitation second in Asia and the Pacific and in Europe and Central Asia (the regions with most studies), whereas these ranks were reversed in Africa and the Americas (Fig. 2). Drivers showed strong differences in dominance within Africa (steepness = 0.573, $P = 0.004$) and Asia and the Pacific (steepness = 0.501, $P = 0.001$) but not in the Americas (steepness = 0.292, $P = 0.14$) or Europe and Central Asia (steepness = 0.265, $P = 0.41$). However, these among-region differences in the dominance hierarchy of drivers were not themselves statistically significant (all four regions: randomization $P = 0.326$; planned contrast of the two most study-rich regions: randomization $P = 0.082$).

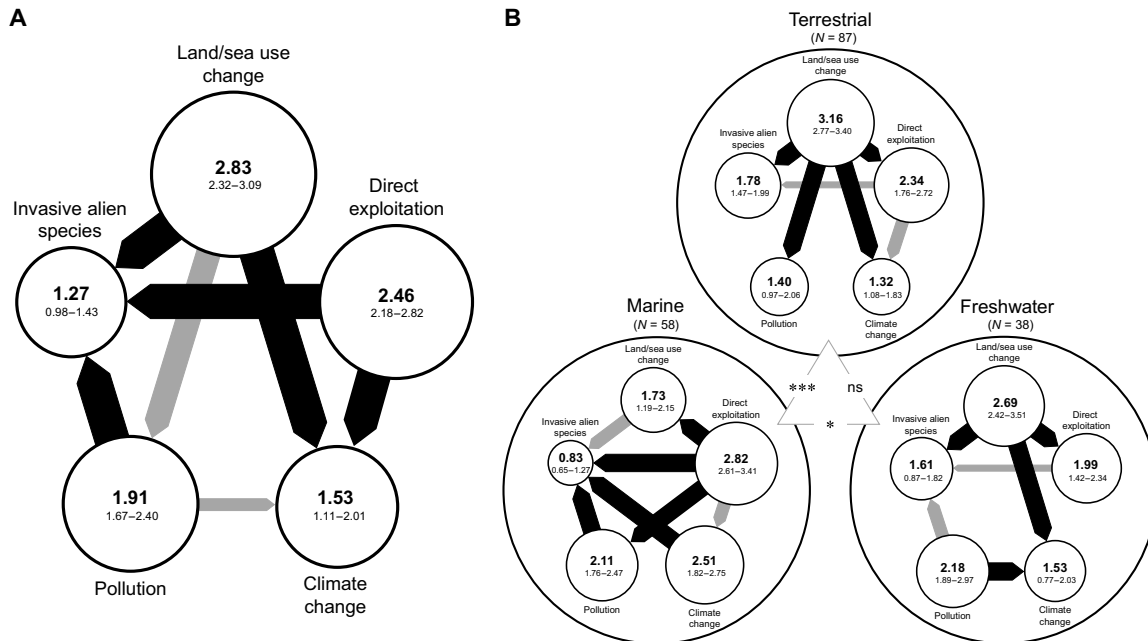


Fig. 1. Dominance hierarchies of the five studied direct drivers of biodiversity loss. (A) Overall hierarchy ($N = 154$ studies) and (B) hierarchies for terrestrial, marine, and freshwater realms. Area of the circle for each driver is proportional to its dominance score (20) (indicated inside with 95% confidence interval; possible range = 0 to 4). Arrows linking pairs of drivers show the significance of the dominance difference between them based on bootstrapping: Arrow thickness reflects unadjusted P values (thin: $P < 0.1$, intermediate: $P < 0.05$, thick: $P < 0.01$, no arrow: $P \geq 0.1$), and arrow shading reflects P values adjusted for multiple testing (black: $P < 0.05$, gray: $P \geq 0.05$). The central triangle in (B) reports the significance of differences in the among-driver dominance hierarchy between pairs of realms (***: randomization $P < 0.001$; *: $P < 0.05$; ns: $P > 0.5$). N gives numbers of studies available for the analysis within each realm. The steepness of the driver hierarchy also rejects the null hypothesis that all drivers have the same impact overall (steepness = 0.405, $P = 0.0001$), in the terrestrial realm (steepness = 0.465, $P < 0.0001$), and in the marine realm (steepness = 0.479, $P < 0.001$), but not in fresh water (steepness = 0.292, $P = 0.13$).

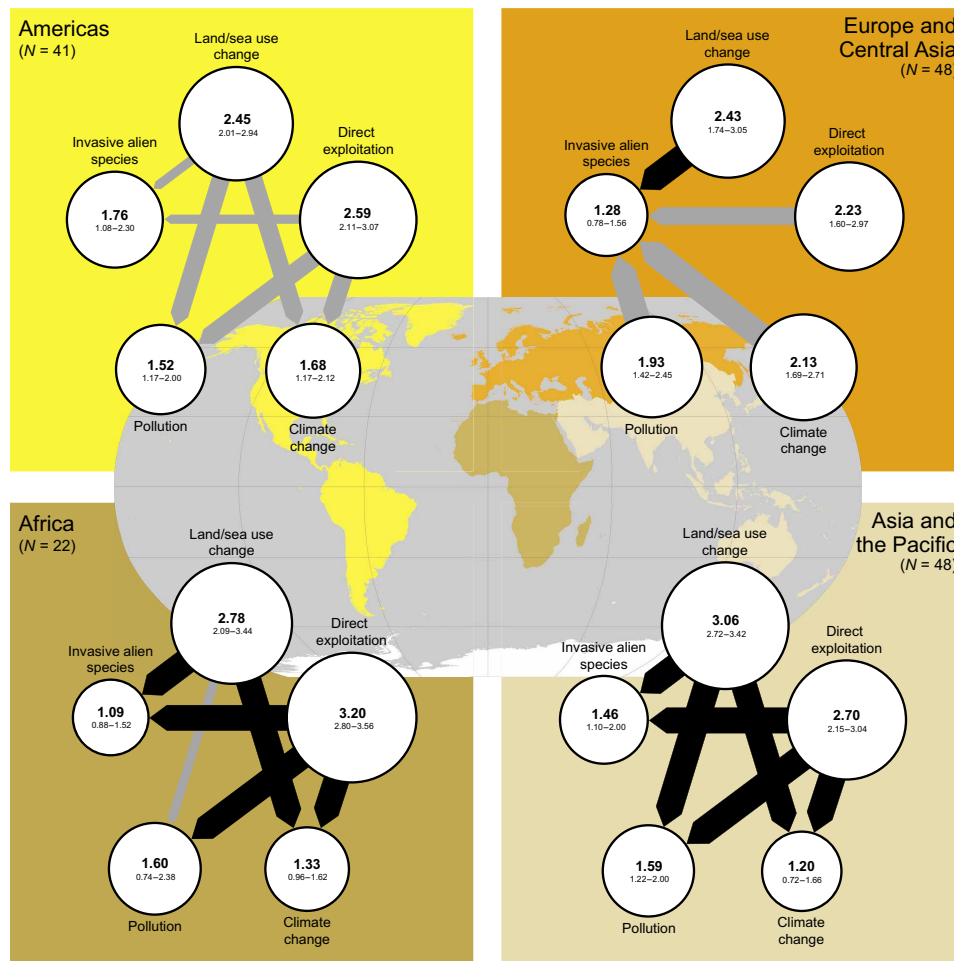


Fig. 2. Land/sea use change and direct exploitation are the main drivers in all regions. Area of the circle for each driver is proportional to its dominance score (20) (indicated inside with 95% confidence interval; possible range = 0 to 4) within each IPBES region. Arrows linking pairs of drivers show the significance of the dominance difference between them based on bootstrapping: Arrow thickness reflects unadjusted P values (thin: $P < 0.1$, intermediate: $P < 0.05$, thick: $P < 0.01$, no arrow: $P \geq 0.1$), and arrow shading reflects P values adjusted for multiple testing (black: $P < 0.05$, gray: $P \geq 0.05$). N gives numbers of studies available for the analysis within each region.

The dominance hierarchy of drivers varied significantly among the six EBV classes (randomization test: $P = 0.0004$; Fig. 3). It also differed between the two classes with most data (species populations and community composition: planned contrast randomization $P < 0.0001$). While land/sea use change was ranked first and direct exploitation second as a driver of change in species populations, they were, respectively, ranked second and fourth in community composition. Climate change ranked first among the drivers of community composition changes, but last among the drivers of species population changes. Land/sea use change was also ranked as the top driver of changes in ecosystem structure and ecosystem function. Invasive alien species were the dominant driver of changes in species traits, and, though with an extremely small dataset, climate change was the top-ranked driver of changes in genetic composition (Fig. 3). While biodiversity-focused search terms may have contributed to the shortage of comparisons of direct driver impacts for ecosystem function, the dearth of comparisons for species traits and genetic composition is a knowledge gap that highlights the lack of background information on temporal changes in these dimensions of biodiversity (24). Driver dominance varied significantly among EBV

classes in both the terrestrial (randomization $P = 0.0187$) and freshwater ($P = 0.0181$) realms, with climate change again being ranked higher as a driver for changes in community composition than for other changes. None of the four IPBES regions showed significant variation in the dominance hierarchy of drivers among the EBV classes (smallest randomization $P = 0.077$).

DISCUSSION

We have shown clearly that land/sea use change—mainly in the form of rapid expansion and intensifying management of land used for cropping or animal husbandry (9)—and direct exploitation—mostly through fishing, logging, hunting, and wildlife trade (9)—have been the two dominant drivers of global biodiversity loss overall over recent decades (Fig. 1A). Whereas previous comparisons of driver importance have been based on either very few indicators or expert judgment, our analyses have robustly synthesized scientific knowledge on the relative impacts of multiple direct drivers on an unprecedentedly wide array of indicators of the state of biodiversity (table S1). They also include tests of consistency among the main

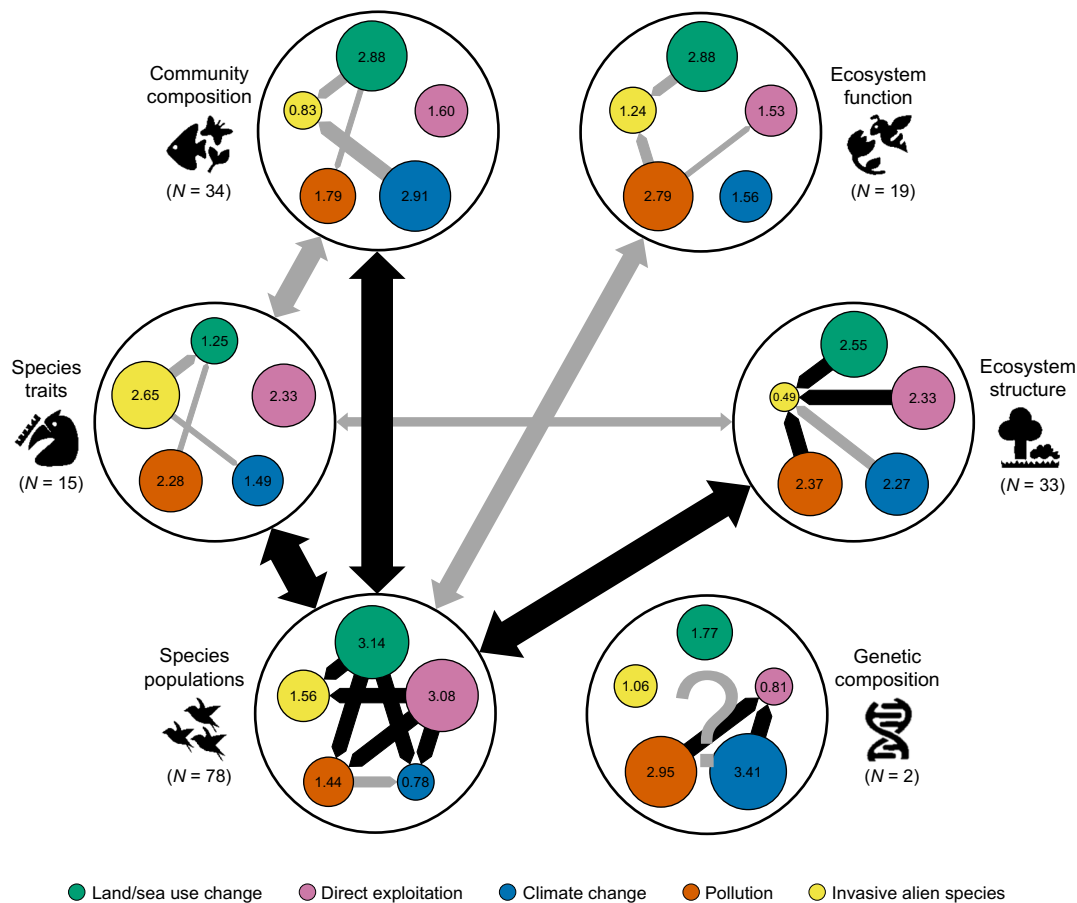


Fig. 3. The main drivers of biodiversity loss differ among the six EBV classes. Area of the circle for each driver is proportional to its dominance score (20) indicated inside the circle (possible range = 0 to 4). One-way arrows linking pairs of drivers show the significance of the dominance difference between them based on bootstrapping. Two-way arrows between EBV classes indicate significant pairwise differences in their driver dominance hierarchies based on randomization tests. For all arrows, thickness reflects unadjusted P values (thick: $P < 0.01$, intermediate: $P < 0.05$, thin: $P < 0.1$, no arrow: $P \geq 0.1$) and shading reflects P values adjusted for multiple testing (black: $P < 0.05$, gray: $P \geq 0.05$). N gives numbers of studies available for the analysis within each EBV class. The question mark indicates the very uncertain rankings for genetic composition because of small sample size. EBV class icons created by C. Gutiérrez of the Humboldt Institute (Bogotá, Colombia) for GEO BON.

geographic regions, types of ecosystems, and dimensions of biodiversity. By focusing on comparisons of two or more drivers, we have sidestepped biases caused by unequal research attention among them (18) and by underreporting of small effects (25). Climate change is probably the most rapidly intensifying threat to biodiversity, and its impacts are increasingly well quantified (26), but other threats are still doing more damage.

This finding highlights the scale of the challenge facing those who are negotiating and implementing the post-2020 global biodiversity framework of the CBD. Combating climate change alone will not be enough to prevent—or possibly even slow—the further loss of biodiversity, unless damaging land/sea use change and direct exploitation are also tackled with similar ambition and determination (14, 27). Rapidly upscaling holistic management practices that benefit both climate and biodiversity will be key (5, 28) and must be done in a manner that safeguards livelihoods and ways of life (29, 30). Actions that succeed in reversing or slowing biodiversity declines can not only considerably slow human-caused climate change (31): They can also make ecosystems more able to maintain functionality—and hence the flows of nature’s contributions to people—in the face of ongoing climatic and other environmental changes (29). Enhancing

this capability is itself a worthwhile goal, given the inevitability of ongoing climate change for at least decades, the limited state of knowledge of the complex ways it will interact with the other direct drivers, and the potential contribution of biodiversity to climate adaptation and mitigation (5, 32).

Given the need to tackle direct drivers in a holistic way, it is concerning that targets in current global environmental agreements—such as the CBD and the UN Framework Convention on Climate Change (UNFCCC)—are defined in isolation. The risk of this framing is that a narrow focus on one driver can lead to actions that overlook—and in the worst case undermine—targets on others (5). For instance, some “nature-blind” strategies for mitigating climate change include large-scale expansion of cropland bioenergy, but the resulting loss of natural habitat will directly harm biodiversity (33) and is already among the pressures with fastest-growing impacts (34). Even considering the benefit of reduced climate change, the net impact on biodiversity is likely to be negative (5, 33, 35). By contrast, nature-based solutions such as large-scale restoration of natural forest (36) and effective protection of coastal wetlands (37) not only help to mitigate climate change but also can directly provide additional benefits to biodiversity and people (5, 38).

The significantly different hierarchy in the ocean (Fig. 1B) suggests that, at the broadest scale, policies, strategies, and action targets for marine conservation need to emphasize direct exploitation and climate change more—and land/sea use change less—than their equivalents for the terrestrial and freshwater realms. The scale at which oceans are currently managed to reduce marine defaunation because of overfishing does not adequately match the great mobility of organisms at sea (39). Many of these disperse across multiple management jurisdictions, and the mean size of marine protected areas is much smaller than the home range size of most species. This mismatch may make it easier for these organisms to be affected by fishing operations, either directly when they are overfished or indirectly through bycatch. Although climate change is reshuffling marine ecological communities, high colonization potential helps many species to shift their geographical distribution across wider spatial scales than species on land (40). Climate change also has a particularly important impact on indicators of community composition on land and in fresh water (Fig. 3), but our analysis shows that changes in data-rich EBV classes are all strongly driven by land/sea use change, pointing to its major role across the various dimensions of biodiversity. The impact of direct exploitation on species populations is unsurprising but may, in part, reflect an understandable data bias toward populations and species that are being actively exploited.

Although the overall driver hierarchy is clear, exceptions are not rare: Nearly 30% of pairwise comparisons went against the overall ranking; each driver was the most important in some studies; and we provide the first robust evidence that the hierarchies differ significantly among realms (Fig. 1B) and EBV classes (Fig. 3). One obvious source of this context dependency is that all drivers show strong geographic variation in intensity, many even at quite small spatial scales (41). On land, nonclimatic drivers tend to covary positively with each other spatially but negatively with climate change such that only the temperate broadleaf and mixed forest biome faces above-average intensity of all drivers (41). This may explain why the two IPBES regions where this biome is extensive (the Americas and Europe and Central Asia) show a less strongly marked hierarchy among the drivers than elsewhere (Fig. 2). The context dependency of driver rankings has been used to argue that these rankings are at best irrelevant for conservation (42). However, far from diminishing the importance of rankings for the development of effective policies and action targets, context dependency instead emphasizes that the rankings must be based on evidence from a wide range of contexts—different realms, regions, taxa, and indicators—as we have done here, to ensure their robustness.

Our analysis provides an overview of driver hierarchies in the past few decades. Valuable next steps include adding a temporal dimension and identifying the most important interactions among drivers, for both recent changes and future projections (43). Neither is straightforward, however. Few multidriver comparisons can be partitioned into different time periods. While quantitative estimates of the impacts of climate change—the driver that is studied most often (18)—show increases over time (44, 45) that are projected to continue (5, 46, 47), similarly robust information is not yet readily available for the less studied drivers. Likewise, interactions among drivers, both in terms of nonadditive impacts on biodiversity where both are present and in terms of social-ecological feedbacks (e.g., how actions to mitigate one driver might influence the others), are not yet well understood (5). These difficulties reflect linked limitations in data and tools. Detailed spatiotemporal data have been lacking

for many drivers of change (48). Biodiversity models have largely focused on the drivers with good data, notably climate and land use, with limited, if any, exploration of interactions [e.g., (46, 49)]. Most projections of future biodiversity use scenarios that were originally developed for climate science, and which treat some of the other drivers in a much less integrated way, if at all (50, 51). The need for a clearer and more integrated picture of recent and future driver impacts is pressing. Interactions between climatic and other drivers will become more widespread as more areas experience high intensities of both. Improved data on drivers (41, 52), new approaches to modeling their interactions (53), and new scenario frameworks that better reflect the complex interplay between people and nature (54) should all help to produce a clearer picture. Understanding the effects of dynamically changing and interacting drivers is also important beyond biodiversity loss. Land-use change and direct exploitation are also both drivers of emergence of zoonotic and vector-borne diseases (55, 56); whereas current policies aim to control diseases after they have emerged, robust understanding of the driver links and feedbacks may help to develop policies that can make emergence less likely in the first place (57).

Tackling accelerating climate change and bending the curve of biodiversity loss while still producing affordable food and safe water for people will require ambitious targets, policies, and actions that are more holistic than at present (2, 5, 28, 32, 49, 58). While UNFCCC COP26 showed promising signs of the needed integration, with its recognition of the links between biodiversity and climate, its outcomes lacked the ambition required to meet the challenge. As well as mitigating the direct drivers, tackling the root causes of biodiversity loss—demographic, socioeconomic, and technological changes together with the societal values and governance structures that underpin them—requires urgent transformative change (2, 4, 5, 28, 49, 59). If we are to maximize our options for managing inevitable changes (31, 32) and widen the currently narrow (49, 60) path to a sustainable future, the results presented here show clearly that this nature-positive transformation must tackle these indirect drivers of land/sea use change and direct exploitation with as much determination as the causes of climate change.

MATERIALS AND METHODS

Overview of the literature review and synthesis

Systematic reviews of the scientific literature are key to synthesizing a large and rapidly growing body of evidence but can be time-consuming depending on the amount of studies available on the topic of interest. Rapid evidence assessments are similar to systematic reviews but with some components of the process simplified or omitted to produce information within a short period of time (61). A rapid evidence assessment was carried out as part of the IPBES Global Assessment Report on Biodiversity and Ecosystem Services to rank broad classes of anthropogenic direct drivers as causes of changes in the state of biodiversity. These broad classes—climate change, direct exploitation of natural resources, invasive alien species, land/sea use change, and pollution—are not equally represented in the literature (18, 50). To ensure that our inferences were not biased by uneven research effort, we therefore focused on the results from studies that compared the impact of two or more drivers on some facet of biodiversity. Because these comparisons were predominantly qualitative rather than quantitative, we synthesized the rankings they implied into dominance hierarchies of the direct drivers—in terms of their impacts on

major dimensions of biodiversity. Unlike the nonstatistical summary of the evidence in the IPBES Global Assessment (2, 62, 63), the analytical approach used here avoids making any assumption about the drivers not considered in each such comparison. By synthesizing driver ranks in multidriver studies, our approach also side-steps problems that could arise with estimating each driver's quantitative impact if small effect sizes are underreported in the literature (64). We have analyzed our compilation of comparisons at the global scale, within each of the four IPBES regions and within the terrestrial, freshwater, and marine realms. We also performed appropriate statistical significance tests of differences in importance within a hierarchy, and of differences between hierarchies for different subsets—realms, regions, or dimensions of biodiversity (i.e., the six classes of EBV). The assessment was organized in seven successive steps aiming at identifying, synthesizing, and analyzing adequate information from the most relevant natural science studies.

Systematic literature searching

The search of natural science studies in the literature was performed using search strings covering the two main aspects of our overarching question, i.e., the “impact of human-caused direct drivers” on the “changes in the state of biodiversity.” We elaborated partial search strings to capture (i) change in the state of biodiversity and (ii) the human-caused direct drivers of this change, and we then combined them to produce full search strings. These search strings were used in Web of Science on 5 September 2018 to find published studies based on their titles, keywords, and abstracts.

Partial search strings for changes in the state of biodiversity

Biodiversity change was captured with a series of large-scale indicators currently endorsed by global biodiversity-related initiatives, such as the CBD, Future Earth, and the IPBES (table S1). Indicators intrinsically related to a single direct driver or to a limited subset of drivers were not retained because our objective was to rank the impacts of multiple direct drivers on changes in the state of biodiversity. Partial search strings used to capture each of the indicators are reported in table S1.

Selected indicators reflected temporal changes in different dimensions of biodiversity and were classified into the six classes of EBVs (22), i.e., genetic composition, species populations, species traits, community composition, ecosystem structure, and ecosystem function (table S4). We gathered information for several indicators within EBV classes to rank drivers as comprehensively as possible (see the “Scoring driver importance” section).

Partial search strings for direct drivers

Direct drivers were classified according to five main categories representing the main human-caused proximate pressures on biodiversity (9): (i) land/sea use change, (ii) direct exploitation of natural resources, (iii) climate change, (iv) pollution, and (v) invasive alien species. Direct threats that do not fit clearly into one of the five main categories, such as fires or disturbances from recreational activities, were excluded from consideration. A list of search terms was first established on the basis of the description of each direct driver within the IPBES Global Assessment Report (2, 9). The IUCN classification of direct threats to biodiversity (65) was then used to extend the list of search terms for each driver, with further terms added from reviews of threats in freshwater (66) and marine (67) realms. Table S2 gives the partial search strings used for each driver.

To find studies that compared the impacts of at least two drivers on biodiversity, search strings from different rows in table S2 were

combined using the Boolean operator “AND” to represent each of the 10 pairwise combinations of drivers.

Full search strings for impacts of drivers on biodiversity

Each partial search string reflecting an individual indicator (table S1) was combined with each of the 10 partial search strings reflecting a pair of drivers (table S2) using the Boolean operator AND to identify studies assessing the impacts of two drivers on each indicator.

Synthetic studies that assessed and compared the impact of major drivers without mentioning them explicitly in the title, keywords, or abstract could be missed by the above approach. The following search string was therefore used to find such studies: (driver* OR factor* OR determinant* OR “driving force*” OR threat* OR “proximate cause*” OR pressure* OR stressor* OR risk* OR “global change”) AND (multi* OR quantif* OR compar* OR partition* OR rank* OR order* OR relative OR interact* OR interplay* OR synerg* OR magnitude* OR rate* OR effect* OR impact* OR influe* OR pace* OR extent OR importan*). In the same way as for the pairwise combinations of drivers, this general search string was then combined with each of the partial search strings from table S1 to identify studies assessing the impact of multiple drivers on each indicator.

Table S3 provides different examples of full search strings that were used to identify studies examining the impacts of different drivers on several dimensions of biodiversity change. After accounting for duplicates across the outcomes of different search strings, we extracted 45,162 potentially useful studies.

Inclusion of studies from additional sources

A further 138 potentially relevant studies were included manually, which fell into three categories: (i) scientific studies not captured by the search strings developed in tables S1 and S2 but considered as potentially relevant by experts and stakeholders involved in the successive phases of the external reviewing process of the IPBES report, (ii) other important studies from the gray literature (not directly available through searches in Web of Science) such as reports [e.g., CBD or Food and Agriculture Organization of the United Nations (FAO) reports], and (iii) source databases directly documenting the impact of drivers on particular indicators (i.e., Living Planet Index and Red List Index).

Screening of studies extracted from literature and other sources

Screening of abstracts, titles, and keywords

The schedule of the IPBES Global Assessment Report precluded detailed scrutiny of the entire evidence base. Our rapid evidence assessment therefore prioritized search results for consideration as follows. For each indicator, studies obtained from the 10 driver-pair searches and the broader multidriver search were pooled, with studies ordered first by the number of searches that returned them and second by recency of publication, on the grounds that more frequently returned and more recent studies were more likely to be relevant. We then screened the titles, keywords, and abstracts of the 200 top-ranked search results for each indicator; for indicators yielding fewer than 200 studies, we assessed them all. All studies included as additional source of information were also screened in the same way ($N = 138$). A total of 3822 studies were screened.

Selection of potentially suitable studies

During this screening, studies were retained for further consideration if they appeared likely to meet three initial criteria: (i) they had compared the impacts of at least two of the direct drivers, (ii)

on at least one of the indicators or one of the EBV classes, and (iii) in the past or present (rather than in the future). Reviews and meta-analyses were retained if they met these criteria. A total of 575 studies were retained as potentially suitable for further analysis.

Assessment of eligibility for inclusion in the meta-analysis

The 575 studies retained after screening were read in full to evaluate their eligibility for inclusion in the analysis based on the following attributes: (i) type of analysis: analysis of empirical data (studies using any sort of data, even if from an existing database), review (qualitative/descriptive synthesis of existing literature), and meta-analysis (quantitative synthesis of existing literature or analysis of multiple datasets from other studies); (ii) indicator(s) targeted by the analysis (table S1); (iii) EBV class(es) targeted by the analysis (table S4); (iv) assessment of temporal changes in the indicators: not applicable (studies not directly based on empirical data—e.g., reviews), not assessed (studies not reporting on observed biodiversity changes), and assessed (studies reporting on indicators with a direct or indirect estimation of temporal changes in the state of biodiversity); (v) number of drivers analyzed or assessed (table S2): between 0 and 5; (vi) assessment of the impacts of different drivers: none (impacts of drivers not compared), nominal scale (list of drivers affecting indicators without qualitative or quantitative comparison), ordinal scale (qualitative comparison, i.e., drivers ranked based on their impact), and ratio scale (quantitative comparison, i.e., impact of each driver quantified—e.g., partitioning approaches); (vii) and publication year.

Empirical studies published in/after 2005 and estimating (on at least an ordinal scale) the impacts of at least two drivers on the temporal change of biodiversity indicator(s) or EBV class(es) were considered as eligible. Reviews and meta-analyses of original studies that satisfy the aforementioned rules were also considered as eligible. Eligibility rules included the year of publication as to focus on novel information produced since the Millennium Ecosystem Assessment (68). If studies about particular indicator(s) published after 2005 were lacking, we also considered studies published before 2005 as eligible. A total of 189 studies were considered eligible and were then checked for redundancy as follows. If several studies reported on results obtained from the same source of information, only the most recent was retained for the next stage of the analysis. After this procedure, 163 studies were used to extract information on the impacts of drivers (see data S1).

Extraction of information from eligible studies

Eligible studies may report separately on the impacts of drivers on several indicators from the same or different EBV classes, in a number of regions or for different realms. They may also assess the impacts of drivers on the same indicator but for different taxonomic groups. Each of these different levels of analysis was considered as a separate assessment within the studies and, for each individual assessment, the following attributes were extracted from reading the full text and associated files: (i) spatial coverage: local (smaller than a country), regional (between a single country and several countries), continental (covering all or a representative set of countries within a continent), or global; (ii) IPBES region (21): Africa, Americas, Asia and the Pacific, Europe and Central Asia, several regions (with an option to select regions), all regions, unclear, or not specified; (iii) realm: freshwater, marine, terrestrial, several realms (with an option to select realms), all realms, unclear, or not specified; (iv) indicator (see table S1 for definitions and numbers of assessments for

each indicator); (v) EBV class (see table S4 for definitions and table S1 for numbers of assessments within each EBV class); (vi) higher taxon (see table S6; note, this is not applicable for, for example, assessments of measures of ecosystem structure); (vii) drivers (using the typology of table S2); and (viii) impact of each driver: integer to rank the impact of the drivers (starting with 1 for the driver with highest impact) on an ordinal scale (ties allowed). Too few studies compared the impacts of multiple drivers quantitatively to support an analysis of these estimates.

Scoring driver importance

We converted the driver ranks from each assessment into scores that could be synthesized to produce an overall ranking that was not affected by differences in research attention among drivers. Table S5 shows how the information contained in an assessment's ranking of multiple drivers can readily be partitioned into a set of nonredundant pairwise comparisons between drivers. In each such head-to-head comparison, the more important driver is scored as 1 and the less important driver 0; equally ranked drivers each score 0.5. This scoring is simply another representation of the original ranking, containing exactly the same information (see table S5).

We multiplied the scores from each assessment by weights to reflect two ways in which assessments vary in the amount of relevant information they contribute to an analysis, as follows:

1) Spatial coverage. Assessments encompassing a larger geographic area should contribute more information, other things being equal. Assessments within each study were therefore assigned an analysis weight based on their spatial coverage such that an assessment at a larger scale would just outweigh two assessments at the next scale down: local assessments received a "scale weight" of 1, regional assessments a scale weight of 3, continental assessments a scale weight of 7, and global assessments a scale weight of 15.

2) Representation of indicator in dataset. Because the 22 biodiversity indicators in table S1 were not equally represented within the data (either overall or within any of the subsets we analyzed), assessments of less well-represented indicators should be upweighted to avoid results being skewed by research biases toward particular indicators. For each dataset (including each bootstrap replicate) being analyzed, we first summed the scale weights for all assessments of each indicator represented within it. Each assessment was then given an "indicator weight" inversely proportional to the sum of that indicator's scale weights. The sums of the scale weights for each indicator ranged from 6 (for the area of mangrove forest cover) to 244 (for the IUCN Red List).

Each head-to-head score was multiplied by the product of its scale weight and indicator weight. Studies that considered more drivers also contribute more information to the synthesis by dint of yielding more pairwise comparisons; this reflects their greater information content without the need for any additional weighting. A consequence of this is that indicators for which more drivers tended to be compared had more total weight in each analysis. This effect was slight, however; for example, in the overall analysis (Fig. 1A), the total weight of each indicator varied only by a factor of 4.

Statistical analysis of driver scores

To infer the hierarchy of drivers for a set of assessments, we first summed the pairwise scores (weighted as above) across the assessments. From the resulting matrices, we calculated each driver's dominance as its normalized David's score (20), using the DS function in the

EloRating R package (69, 70). A feature of this measure that is desirable in this context is that a driver may have a higher dominance than another despite tending to “lose” their individual direct head-to-head comparisons, if it is more dominant against the other drivers (71). The minimum possible dominance score is 0 (for a driver that is less impactful than every other driver in every study) and the maximum, with N drivers, is $N - 1$ (for a driver that is top-ranked in every study). Confidence intervals for dominance scores were obtained by bootstrapping (10,000 replicates, selecting studies with replacement from the set of relevant studies, and recalculating indicator weights anew within each replicate). These bootstraps were also used for testing the significance of dominance differences between drivers within an inferred driver hierarchy, with P values adjusted to reflect multiple nonindependent tests (23) to control the false discovery rate. We also report the steepness of driver hierarchies; steepness is calculated from regressing drivers’ normalized David’s scores on their ranks and can range from 0 to 1 (20). As an omnibus one-tailed test of the null hypothesis that all drivers have equal impact, the steepness of each hierarchy was compared to the distribution of steepness values from 10,000 permutations of the data. Each permutation retained the structure of the original data, shuffling only the ranks of the drivers studied by each comparison.

We also constructed randomizations to test for significant differences in driver dominance between the hierarchies inferred for the four IPBES regions; those for the six EBV classes; and those for the terrestrial, freshwater, and marine realms. Although the sizes of the IPBES regions mean that each is very heterogeneous, they nonetheless show substantive differences both biogeographically (e.g., only Europe and Central Asia is entirely nontropical, while the Asia-Pacific region has a profusion of islands) and socioeconomically (e.g., Africa has by far the lowest average GDP per person), which could cause differences in driver importance. As the test statistic, we used the residual SD in a linear model predicting the normalized David’s score from driver identity, treating the subsets (e.g., regions) as replicates. The null distribution against which we compared this test statistic came from 10,000 randomization trials. Each trial pooled the comparisons for the different subsets, but randomly permuted the subset identities among comparisons, and calculated the residual SD in the same way as for the observed data. The test is one-tailed: If dominance differs significantly among subsets, the observed residual SD will be higher than that seen in the 95% of null distribution. Post hoc tests to pinpoint the significant differences between subsets were performed by conducting all pairwise comparisons, again adjusting P values for multiple nonindependent tests (23).

SUPPLEMENTARY MATERIALS

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The direct drivers of recent global anthropogenic biodiversity loss

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