

Assessing the multidimensional complexity of biodiversity using a globally standardized approach

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Highlights

1. The value of nature lies in its complexity.
2. We define a global framework for a holistic measure of the state of nature.
3. Inclusion of microbes and invertebrates is crucial to evaluate biodiversity.
4. Human activity consistently reduces and homogenizes biodiversity worldwide.

Summary

Quantifying biodiversity across the globe is critical for transparent reporting and assessment under the Kunming-Montreal Global Biodiversity Framework. Understanding the complexity of biodiversity requires consideration of the variation of life across genes, species, and ecosystems. Achieving this in a standardized way remains a key challenge for creating an equitable nature positive future. Here, we present the Sustainable Ecology and Economic Development (SEED) framework, which assesses the dimensions that structure biodiversity patterns worldwide (genetics, species, and ecosystems) across plants, animals, and microbial taxa, and consolidates this into a single measure of biocomplexity at every location, relative to a ‘reference’ ecosystem with minimal human disturbance. We describe the SEED methodology and highlight its features, which include numerous datasets collapsed into nine novel dimensions of biodiversity intactness that are integrated into the SEED biocomplexity index. SEED will continuously integrate new datasets and maps to provide up-to-date estimates of local biocomplexity across the planet, providing a tool for decision makers to assess and improve the global state of nature.

Keywords

Biocomplexity; biodiversity monitoring; biodiversity intactness; state of nature; genetic diversity; species diversity; ecosystem diversity

Abbreviations

SEED	Sustainable Ecology and Economic Development
GBF	Kunming-Montreal Global Biodiversity Framework
GEO BON	Group on Earth Observations Biodiversity Observation Network
EBV	Essential Biodiversity Variable
IUCN	International Union for Conservation of Nature
EII	Ecosystem Integrity Index
BII	Biodiversity Intactness Index
MSA	Mean Species Abundance
HMI	Human Modification Index
PNV	Potential Natural Vegetation

1. Introduction

Every species depends on other species to survive. This vast interdependence means biological diversity is critical for the maintenance of life as we know it. However, humans have historically valued the components of nature we can use for food, timber, and medicine over others^{1,2}. The development of markets for these products has incentivized their mass propagation at the expense of other components of biodiversity, driving the oversimplification of biological systems and the loss of the ecosystem services on which we depend³.

As nature positive policy frameworks and nature markets emerge, it is critical that we learn from past challenges. Mechanisms that value a single aspect of nature – such as carbon sequestration – risk driving the oversimplification of the system⁴⁻⁷. This can lead to potentially counterproductive outcomes, like the creation of monocultures of exotic tree species at the expense of local biodiversity⁷ and human wellbeing⁸. If political and financial structures are to promote the conservation of natural biodiversity, they must be underpinned by robust, globally standardized monitoring that reflects the full dimensionality of life, across genetic, species and ecosystem levels.

The most prominent guidelines for biodiversity monitoring are described within the Kunming-Montreal Global Biodiversity Framework (GBF)⁹, which sets a series of global targets to halt and reverse nature loss by 2030. Key targets in the GBF include protecting areas of high biodiversity importance (Target 1), restoring 30% of degraded areas by 2030 (Target 2), and the headline ‘30x30’ target that aims to conserve 30% of the Earth’s surface by 2030 (Target 3). In the financial sector, the GBF requires businesses to disclose their impacts on biodiversity (Target 15), and the Taskforce on Nature-related Financial Disclosures was assembled to provide guidance and outline best practices for nature-related disclosures. At the heart of nature-related disclosures is a measure of the “state of nature” against which impacts, dependencies, risks, and opportunities may be measured¹⁰. However, it is not yet clear what constitutes a suitable measure of the state of nature.

Over the past decade, a growing number of metrics have been developed to measure and monitor biodiversity across the globe. Biodiversity metrics generally fall into one of two categories based on their dataset and scope: local ground-sourced data (e.g. plot surveys, eDNA, bioacoustics monitors and camera traps), and global remotely-sensed data (e.g. radar and multispectral imagery

from satellites)¹¹. Local ground-sourced data provide detailed insights into the diversity of organisms, but the scalability of these assessments are challenging^{12,13}. Conversely, remotely-sensed data provide globally-standardized assessments of ecosystem-scale characteristics like forest structure¹⁴ and connectivity¹⁵, but not all aspects of nature can be measured directly from satellites. Many global biodiversity metrics incorporate both ground-sourced and remote-sensed data to offer a balance between local relevance and global scope. To align monitoring efforts, the Group on Earth Observations Biodiversity Observation Network (GEO BON) recently proposed a worldwide system of observation networks¹⁶ and established guidelines for 16 Essential Biodiversity Variables (EBVs)^{17,18}. However, we lack a coherent method to consolidate these EBVs and all other biodiversity metrics to derive a unified perspective of the state of nature.

To address the need for a unified, globally standardized measure of biodiversity across all its dimensions, we first review existing global biodiversity metrics that are used to measure the current state of nature and highlight their strengths and weaknesses (Section 2). We then present a new integrative framework (the Sustainable Ecology and Economic Development (SEED) framework) which is designed to consolidate the three primary hierarchical levels that underpin biodiversity – genetic, species, and ecosystem – into a single globally standardized measure of biodiversity intactness, which we call biocomplexity (Section 3). Nature is inherently complex, and biocomplexity is defined as the emergent properties from multiple, often hierarchical levels of interacting factors that “affect, sustain, or are modified by living organisms, including humans”¹⁹. Recognizing this complexity, we designed the SEED framework so that it can integrate numerous global biodiversity maps and include new maps as they become available. This ensures that policy and market tools will have the most up-to-date information on the state of nature.

2. Current state of global biodiversity measurement

Spatially-explicit biodiversity data products consist of a heterogeneous mix of calculations, model predictions, metrics (standard of measure), and indices (aggregation of multiple indicators). Given our exclusive focus on data products mapped over the globe, we hereafter refer to these products in general as ‘maps’. We grouped existing maps into three main organizational levels of ecological systems: within-species genetic diversity, among-species diversity, and ecosystem diversity. Global maps at each level reflect different dimensions of diversity that are essential for a holistic

understanding of biocomplexity across the globe. Although some global maps correspond to a given EBV²⁰, the EBVs do not consist of a set of spatially-explicit global maps²¹. Their main purpose is to identify the key variables and provide standards on how to measure them¹⁷. Rather than discussing this detail in depth, we identify the strengths and weaknesses of existing maps and the considerations for including them in a unified measure of biodiversity. We conclude this section with a brief description of a fourth group of maps that represent standardized measures of biodiversity.

2.1 Genetic (within-species) diversity

Genetic diversity (heritable variation) represents variation in the genetic composition of individuals within a species and among populations and is the source for adaptive responses to environmental change^{22,23}. There are few global measures of genetic diversity and these are estimated from mitochondrial DNA sequences stored in the National Centre for Biotechnology Information GenBank and the Barcode of Life Database^{24–26}. While there are good insights about genetic variation for certain plant²⁷ and animal species^{24–26}, we currently lack global predictions of genetic variation for most species on the planet. Among the few taxonomic groups that have been studied, loss of genetic diversity is often correlated with the loss of suitable habitat²⁸ and reduced abundance²⁹. This may suggest that we could use measures of population declines to generate proxy measures of decline in genetic diversity, but this population timeseries data is lacking for the vast majority of organismal groups, except for the 5,200+ species in the Living Planet Database³⁰. However, with modern advancements in genetic sequencing technology and widespread usage of barcoding and metabarcoding³¹, new data are continually becoming available that will enable the global measurement of genetic diversity across taxonomic groups²³.

2.2 Species, phylogenetic, and functional diversity

Global biodiversity research has traditionally focused on emergent patterns of species richness (the number of unique taxa). However, species diversity also includes phylogenetic (i.e., a measure of evolutionary history³²) and functional diversity, which can provide a more in-depth understanding of diversity patterns across the globe. Species richness maps are generally created by overlaying several species range maps then summing the number of species per pixel^{33–35}, which in some cases

are then modeled against a set of predictor variables before predicting richness^{36–38}. Phylogenetic and functional diversity are calculated using a phylogeny³⁹ or a functional-trait matrix⁴⁰ to quantify the unique contributions from each of the species present at each locality and thus provide information about phylogenetic and functional components of diversity. Whereas a species-rich community may be composed of evolutionarily and functionally redundant species, other species-poor communities may (or may not) have more evolutionarily and functionally divergent species that may contribute unique functions to the community. Therefore, highlighting those communities with particularly rich evolutionary roots and functional traits is key for a holistic measure of biodiversity.

Species diversity maps inherit biases from their underlying data sources, which affect their applicability. All global biodiversity databases over-represent some regions and under-represent others, typically with a bias toward developed nations⁴¹. There are also considerable disparities in taxonomic coverage, with a bias toward larger and more charismatic organisms. For example, the IUCN database, which is the source of many biodiversity maps^{24,25,42–45}, contains distribution data for over 80% of described vertebrate species and 14% of vascular plants, but only 2% of invertebrate species, which represent the vast majority of animal species diversity. In addition, microbes represent 88% to 99% of all species on Earth^{46,47} but are vastly underrepresented, with only 0.4% of known fungi and protists included in the IUCN database. This pattern is now changing due to recent advances in high-throughput sequencing technologies that enable us to observe and quantify microscopic and otherwise cryptic species⁴⁸, and the availability of microbial biodiversity maps is expanding exponentially^{49–52}.

Species diversity maps are also limited by their original scope and the underlying models. Until now, most global maps of species diversity were not designed to capture fine-scale patterns in species composition, or the effects of local human disturbance. With a focus on broad-scale biogeographic trends, species diversity models use climatic, edaphic, and topographic variables to predict diversity patterns across environmental gradients. The general lack of human influence in early models may be due in part to the recent emergence of global human modification maps^{53–56} and also due to a paucity of biodiversity data in both heavily degraded and intact landscapes. As a result, species diversity maps have low predictive accuracy for quantifying the impacts of human

disturbance (Figure 1). Furthermore, species diversity maps tend to be temporally static, calculated as an average of observations that can span decades. Additionally, sampling methodologies are taxon and/or habitat specific and may also differ by region and discipline or agency. These complexities make it difficult to harmonize available data and generate well-rounded estimates that scale in space and change over time in response to shifting conditions on the ground.

2.3 Ecosystem diversity

In contrast to genetic and species diversity, which rely heavily on ground-sourced data, ecosystem-level maps provide a more up-to-date view of current conditions because they can be measured directly from satellite imagery, or modeled based on spectral imagery (e.g., radar and multispectral imaging). A wealth of global-scale remote sensing products have been designed to capture information about human modifications⁵⁵, land use change⁵⁷, canopy cover⁵⁸, canopy height⁵⁹, above and belowground biomass^{60,61}, soil respiration⁶², habitat heterogeneity⁶³, leaf area index⁶⁴, ecosystem connectivity^{65,66}, net primary productivity⁶⁷ and ecological resilience^{68,69}. These ecosystem-level maps can be grouped into three broad categories of biodiversity: ecosystem structure, function¹⁷, or connectivity.

Ecosystem structure, function, and connectivity are emergent properties that arise from the combination of species, landscape physiognomy, climate, and human modifications. For example, the occurrence and extent of mangroves⁷⁰ and peatlands^{71,72} result from a specific set of conditions, and their structural features are critical to their functional roles. The interplay between living organisms and their environment are also key ecosystem properties, perhaps best exemplified by plant-disperser and plant-fungal associations. Global maps of plant-disperser associations or species interaction networks are not currently available, but progress in this field indicates potential for such maps in the future⁷³. The field of plant-fungal associations has produced numerous global maps, which predict such functional features as the relative proportions of nitrogen fixing and arbuscular mycorrhizal or ectomycorrhizal associated plants⁷⁴ and the densities of plant fine roots⁷⁵ across landscapes, which may affect the intensity of mycorrhizal colonization⁷⁵, soil moisture⁷⁶ and decomposition rates⁷⁷. These ecosystem properties provide a direct link to measures of ecosystem services^{78,79}. Just as the three-dimensional structure of an ecosystem characterizes the environmental context in which species coexist, the spatial arrangement of habitat fragments and

species-specific dispersal abilities and limitations determine ecosystem connectivity. Ecosystem connectivity tends to decrease with habitat loss and fragmentation, and both connectivity⁸⁰ and fragmentation⁸¹ indices can provide unique insights into the ecological functionality at the landscape-scale⁸².

2.4 Standardized measures of biodiversity

Given the challenges of capturing dynamic changes in ecological diversity at a global scale, few analyses estimate how far the ecological community has diverged from its natural state. Using a database from targeted experiments and local studies spanning disturbance gradients, it is possible to identify how land use changes affect ecological diversity and use these relationships to predict ecological intactness across the globe. Three commonly used global indices are the Ecosystem Integrity Index (EII)⁸³ by the United Nations Environment Programme World Conservation Monitoring Centre, the Biodiversity Intactness Index (BII)^{84,85} by the Natural History Museum in London, and the Mean Species Abundance (MSA)⁸⁶ index by the Netherlands Environmental Assessment Agency.

The EII includes three components: structure, function, and composition. Ecosystem structure is based on the human modification index (HMI)⁵⁵; ecosystem function is measured by the ratio of actual to potential net primary productivity⁶⁷; and ecosystem composition is measured by the BII^{84,87}. For a given location, the EII uses the lowest score of the three components to predict the extent to which any ecosystem has been impacted or altered from its original state. The BII uses a linear model of the impacts of land use and related pressures on two aspects of biodiversity, species abundances and compositional similarity, to estimate the intactness of a community of plants, vertebrates, and invertebrates. The MSA index is conceptually similar to the BII but focuses mainly on species abundance, includes additional human-related pressures, and estimates an average intactness value that is weighted by the land use type and its associated human pressures.

The MSA, BII, and EII represent the current state-of-the-art in global biodiversity modeling. Yet, there are two key aspects of diversity that these indices do not capture. First, these indices are fairly limited in taxonomic scope. The BII and EII (and to some degree MSA) are primarily based on the PREDICTS database (Projecting Responses of Ecological Diversity In Changing Terrestrial

Systems)⁸⁸, which is valuable for quantifying the impact of land use on biodiversity in different regions of the globe. However, at present, the data coverage of PREDICTS represents a relatively limited taxonomic range, including less than 10% of the described species for most large taxonomic groups like vascular plants and invertebrate animals, and a far smaller proportion for microbes^{88,89}. Given that these taxa respond differently to human disturbance and show unique global distribution patterns^{90,91}, the underrepresentation of important taxa may therefore bias global biodiversity assessments. Second, these indices focus exclusively on species level diversity and do not include genetic diversity or, except for the EII, ecosystem level properties that emerge from the web of interactions among species and their environment.

3. A framework for observing biological complexity on Earth

With the increasing combination of ground-sourced and remotely-sensed data, we are at the beginning of a data revolution in global ecology^{92,93}. The exponential growth of global ecological datasets and maps across genetic, species, and ecosystem levels represents exciting new opportunities for our understanding of biodiversity across the planet. Conceptual frameworks that integrate and interpret this growing body of information are essential to generate a holistic understanding of global biocomplexity. Our global understanding of biocomplexity will never be fully complete, as emerging scientific assessments continue to capture novel information. Therefore, it is important to establish flexible and dynamic frameworks that can incorporate new and emerging information as it becomes available.

A key element in new nature-related disclosure frameworks is a vaguely defined measure of the state of nature¹⁰, which would presumably represent the full multidimensional complexity of nature, but for which there is currently no agreed upon metric. To address the need for a unified state of nature metric, we present a more holistic ecological framework (hereafter referred to as SEED) that is designed to represent the multidimensionality of nature by defining nine axes of variation, nested within the three hierarchical levels of diversity: genetics, species (including phylogenetic and functional diversity), and ecosystems (Figure 2). Within the genetic and species levels of variation, we include plants, animals, and microbes. The grouping of microbes to include archaea, bacteria, protists, and fungi could be disaggregated in the future as more information becomes available. Within ecosystems, we distinguish three axes: structure, function, and connectivity.

The SEED framework was designed to be a flexible ‘living’ index, which is poised to incorporate any new map layers relating to any component of biodiversity as they become available. Thus, the SEED index will continually improve as missing data gaps are filled in and technological advancements improve. Currently, the SEED framework leverages 85 global genetics, species, and ecosystem maps (Figure 2a; Table S1) from the global scientific community. Analogous to an ensemble model, this approach minimizes the risk of relying on a single dataset and associated model output to provide a more robust accounting of global biodiversity patterns. The framework generates summary indices for nine axes of biodiversity, and also provides a unified biocomplexity index score that represents the intactness of biocomplexity. We apply the term biocomplexity¹⁹ to set it apart from measures of single biodiversity components, and to highlight the inclusion of multiple hierarchical levels of diversity, which emerge not just from the complex interplay between biological life and the environment, but also from the billions of years of physical and biological evolution on Earth.

To generate truly standardized estimates of biocomplexity across the globe, we estimate the similarity (ranging from zero to one) between the current state of an ecosystem and its potential natural state. We defined the natural state empirically using the HMI to mask our set of biodiversity maps. We then summarize the sets of values in these areas by ecoregion and vegetation type and link these summaries to all pixels of the same ecoregion and vegetation type (Figure 2a-c; Section 3.2). Against this empirical counterfactual landscape, the SEED framework summarizes the intactness (i.e., similarity to natural state) of the multiple underlying biodiversity features in each axis and calculates the mean intactness for all nine axes combined to create a unified score: the SEED biocomplexity index (Figure 2e; Section 3.1). All intactness values range between zero and one, where values near zero represent the near absence of biocomplexity (e.g., an open pit mine or paved area), and one represents an area that is equal to a counterfactual reference state (i.e., a minimally-disturbed ecosystem). The SEED framework therefore offers both a single standardized biocomplexity value for any area of interest and nine intactness indices for each axis of biodiversity, thus allowing the user to unpack this information.

3.1 Integrating dimensions of biodiversity

Consolidating the multiple hierarchical levels of biodiversity into a single value is a critical feature that makes our biocomplexity index generalizable and comprehensible. All available global maps are combined within each of the relevant biodiversity axes (Figure S1), using a multivariate kernel estimator⁹⁴ (Eq. 1), and then the mean of these nine axes consolidates this information into a single biocomplexity index.

$$K(\mathbf{z}, \mathbf{z}_r) = \exp[-\delta \|\mathbf{w} \circ (\mathbf{z} - \mathbf{z}_r)\|_1] \quad (\text{Eq. 1})$$

Here, \mathbf{z} is a n -dimensional data vector for a given location, where n represents the number of input maps involved in the calculation. The term $\|\mathbf{w}(\mathbf{z} - \mathbf{z}_r)\|_1$ represents the Manhattan distance, (or ℓ^1 distance), between the data vector \mathbf{z} and the mean values for the corresponding reference areas \mathbf{z}_r after elementwise multiplication (\circ) by the n -dimensional vector, \mathbf{w} , which contains the normalized weight for each input map. The resulting distance value is then converted into a similarity value, which is bounded by zero and one, by applying the kernel function, K , where δ represents a scaling parameter.

Sensitivity of similarity is set by the scaling parameter, δ , which we set for each biodiversity axis according to two criteria. First, δ must be strictly positive to ensure that the kernel values are bound between zero and one. Second, the similarity values measured by K capture the intactness of nature and should span the full range between zero and one. We set δ to the lowest value that met these criteria, given that increasing values simply shifted the distribution further to the left toward zero intactness (see Supplement S1).

The weight of information is the final key consideration in our kernel estimator. We designed this framework to integrate numerous biodiversity maps, and we test it here with 85 maps (Figure S1; Table S2) – ecosystem structure (29), function (13), and connectivity (1); species diversity of plants (11), microbes (13), and animals (13); and genetic diversity of microbes (2), and animals (2). We reprojected all maps to a common projection (epsg:4326) and spatial resolution (30 arc-seconds, ~926 meters at the equator) using a nearest-neighbor algorithm. The maps we reviewed vary in several aspects: coverage extent, spatial resolution, non-independence from other maps, extrapolation across regional data gaps, and in the degree to which satellite imagery or other

measures of local conditions were integrated. To help control for these differences, we developed a dynamic weighting system to define the normalized weight of each map in a set, represented by w (defined above). We grouped non independent layers to share equal weight, resulting in a short hierarchical structure. We also applied a confidence score and associated decreasing confidence with decreasing weight (see Supplement Table S1 for details). Although we found no global maps of the genetic diversity of plants, we filled in a blank map to test the full framework and set the weight of this map to a very small nonzero number.

We structured the integration of the nine biodiversity axes to be an even-weighted average of the intactness in each dimension. This places genetic, species, and ecosystem level diversity on equal grounds in the integrated index. SEED also offers an index for each biodiversity axis for independent use alongside the integrated index. Even weighting of all dimensions ensures equitability within genetic and species diversity among plants, animals, and microbes, which deviates strongly from the more common case wherein smaller, more cryptic taxa are overlooked in favor of more visible or personable taxa. However, if evidence emerges to suggest a different weighting scheme is more ecologically relevant, our method can be adapted in accordance with the evolving scientific landscape.

In practice, a key challenge is that the availability and quality of available maps is not balanced among axes, which resulted in some axes having higher relative weight and therefore more influence on the overall biocomplexity index (See Supplement S1 for details on how confidence scores affect the relative weights among axes). Identifying the optimal weighting for various levels of biodiversity information remains a key challenge for future biodiversity research as our theoretical understanding of ecological systems evolves.

3.2. Reference area as an empirical counterfactual landscape

To measure the intactness of biocomplexity requires establishing a baseline potential state that can be used for comparison. Here, we used an empirical approach to identify the counterfactual baseline potential state for all biodiversity axes and underlying layers. Specifically, we developed an algorithm that uses the HMI⁵⁵ and potential natural vegetation (PNV)⁵⁷ to select reference areas for each land cover class within each of the 846 ecoregions⁹⁵ on Earth (Figure 2b; Supplement

S1.1). This was done separately for each ecoregion to ensure ecologically relevant comparisons. For each ecoregion, we identify the least impacted areas for each land cover class (from the PNV), using a dynamically-defined upper-limit HMI threshold to ensure a sufficiently large area, enabling representative and robust estimates (see Figure 2 and Supplement S1.1). The mean value \pm one standard deviation for each biodiversity feature layer within this *least-impacted area* is used as the estimate of \mathbf{z}_r in equation 1, forming the basis for comparing all feature values in all pixels of the same vegetation class within each ecoregion. The maximum allowable upper-limit HMI threshold that was used to identify the counterfactual reference community was defined as areas with a HMI < 0.05 .

Although a natural landscape with minimal anthropogenic disturbance is not a universal goal in all scenarios, this minimal-disturbance baseline provides an objective, and replicable benchmark for measuring the state of nature. For example, food security and financial wellbeing are the primary considerations in agricultural settings, while restoration targets in conservation settings may deviate from a fully natural state due to a myriad of ecological and socioeconomic factors and needs, as well as previous alterations to the landscape⁹⁶. Management practices and targets will vary depending on the local situation, and progress toward these targets can be evaluated against local minimal-disturbance benchmarks and other landscapes in similar settings. In these contexts, the SEED index provides a useful tool to benchmark local achievement against a globally-standardized biodiversity metric and enables a standardized assessment of biodiversity improvement in response to management practices¹⁷.

We chose to use minimally modified areas as our counterfactual ‘intact’ reference community because it involves few a priori assumptions and best reflects our current understanding of diversity patterns across the nine defined dimensions of biocomplexity. As such, this approach provides a contemporary benchmark of the current state of nature. Although a ‘historic baseline’ approach could also be theoretically used, it raises several philosophical challenges, including the recognition that systems are inherently dynamic and non-static⁹⁷. It also poses significant data limitations, with few existing historic baseline maps for most of the nine dimensions of diversity. While historic reference conditions are the most appropriate for certain scientific inquiries, such as assessing nitrogen deposition or climate change, they become less applicable for evaluating more direct

human impacts like mining or agriculture, or for informing conservation and restoration efforts. In such cases, the concept of a historic 'natural' state is more ambiguous. Given these challenges, the counterfactual reference community approach provides a robust and practical framework for characterizing biocomplexity. It avoids overreliance on incomplete historical data and allows for a more comprehensive representation of current diversity across multiple dimensions.

3.3. Illustration of the SEED biocomplexity framework

The biocomplexity framework was developed using a comprehensive list of the most up-to-date global-scale maps of genetic, species, and ecosystem diversity (see Supplement Figure S1 and Table S2). Although, our framework is designed to integrate nine biodiversity axes, the current lack of global maps to represent the genetic diversity of plants limits the current index to eight functioning axes. To illustrate the capabilities of the framework, we first show the viability of our dimensionality reduction calculation (equation 1) and reference area (Figure 2) approach to calculate the intactness of nine biodiversity axes (Figure 3a-h). Combined, these intactness layers generate a unified measure of the intactness of nature, the SEED biocomplexity index (Figure 4a). We show how SEED can be aggregated across ecological boundaries and at various spatial scales to summarize biocomplexity in total and along each biodiversity axis (Figure 4b-c). Finally, we conduct a cursory comparison of SEED against the leading biodiversity intactness indices (Figure S2).

Among the eight (out of nine) biodiversity intactness indices that we calculated, we identified broad global patterns where the indices unanimously show similar levels of intactness (Figure 3). High intactness is nearly universally indicated across tundra, northern boreal forests, deserts, and the Amazon basin – areas that have not experienced extensive human development. Low intactness is indicated in Central and Eastern North America, Brazil's Atlantic Forest, narrow bands along the West African coast and Sub-Saharan Africa, temperate forests across Europe and east across Asia toward Siberia, Northern India, the western edge of Southeast Asia, Northeastern China, and the eastern and southwestern coasts of Australia.

There is also notable divergence among these indices. While the intactness of ecosystem structure (Figure 3b) and ecosystem function (Figure 3d) are larger similar in some regions, these indices

strongly diverge from plant diversity, e.g., parts of North America (northeast and Appalachia) and the Brazilian Cerrado. Within these regions, high intactness of ecosystem function and structure were associated with low intactness of plant diversity. While the factors underpinning these differences remain unclear – it does highlight that examining single components of biodiversity can lead to a skewed perspective when evaluating a system’s intactness. This highlights the benefit in using an integrative approach, such as SEED, that combines these axes of diversity into a single measure of biocomplexity; minimizing the risk of valuing some aspects of diversity over others (e.g., ecosystem function versus plant diversity).

The intactness of plant, animal, and microbial species diversity (Figure 3h) also diverge in many regions of the world, with the most prominent differences between the intactness of microbial diversity relative to both plant and animal diversity. While the mechanisms underpinning this emergent pattern remain unclear, it does suggest a decoupling in the intactness of these components of diversity and highlight an exciting avenue for future research.

Ecosystem connectivity (Figure 3c) also appears to form a unique pattern relative to the other indices. However, the SEED connectivity index is highly sensitive to fragmentation⁸¹, and therefore scores land area as either highly intact or highly degraded, highlighting the need for improvements in fragmentation maps. The genetic diversity of animals (Figure 3e) also shows a unique pattern, but this is likely because we have only two genetic diversity maps with very coarse resolution (~380-km)²⁵. This, along with the absence of global models for plant genetic diversity, emphasizes the need for future research to prioritize global genetic diversity assessments before they can be equally represented within biocomplexity assessments.

The value in our biocomplexity framework is twofold; it integrates information regarding multiple hierarchical levels of diversity and numerous maps within each level, and it can be aggregated to provide summary statistics at the desired scale. The integrated SEED biocomplexity index represents a single measure of the state of nature for terrestrial land areas across the globe (Figure 4a). This suggests that, on average, the Earth is currently at approximately 60% of its natural ecological state across the three major dimensions of biodiversity (Figure 4b). By aggregating

within administrative boundaries⁹⁸, we can evaluate the state of nature at a level where local policies may directly affect the mechanisms governing the direct human impacts on nature (Figure 4c).

In comparison to existing global biodiversity indices, SEED (Figure 4) offers a more comprehensive view of nature's state due to its inclusion of 85 global biodiversity maps, while also offering disaggregated information in the form of nine intactness sub-indices (Figure 3a-h). Existing global intactness indices (BII, and MSA) exclusively represent species level diversity for a subset of taxa. SEED expands the taxa represented with a wealth of microbial datasets (including fungi, bacteria, and archaea), while also expanding in scope to include multiple ecosystem attributes that capture landscape dynamics and ecological feedback. Their inclusion in SEED may account for differences between SEED and the other intactness indices (Figure S2). For example, SEED may indicate low ecosystem intactness where satellite imagery detects ecosystem fragmentation, while models predicting species composition may not register a change in species intactness. Given the global coverage and high temporal resolution of satellite imagery, the inclusion of remote-sensed ecosystem characteristics not only adds dimensionality to biodiversity estimates, but it also improves the spatial and temporal resolution of biodiversity intactness predictions.

While the SEED framework offers the most holistic estimate of biocomplexity to date—drawing on the most comprehensive set of genetic, species, and ecosystem-level data layers—several important caveats remain. These include limited data on the genetic diversity of plants, animals, and microbes, as well as propagated uncertainty of species diversity maps due to unbalanced sampling efforts in under-studied regions of the world. We emphasize that these limitations represent both major conceptual challenges and key opportunities for future research. Addressing these knowledge gaps will improve our understanding of nature's biocomplexity, which is essential for guiding global biodiversity policy and ensuring financial accountability of market-based nature impacts.

3.4. Spatial and temporal scalability and next steps

There is a growing demand for spatial and temporal scalability in global biodiversity monitoring but achieving this remains a central challenge for ecology. Determining how biodiversity scales in space and time has been the focus of countless investigations, and one general result is that

outcomes are highly context dependent. Meeting the demand for scalability will require reimagining our approach to biodiversity modeling. Work by Map of Life⁹⁹ in association with GEO BON exemplifies the scalable biodiversity models of the future. Map of Life provides a catalog of species distributions predicted over space and time, generated using the most up-to-date remote sensing technologies and species distribution models²⁰. Bringing these maps together, we can reevaluate species richness, phylogenetic and functional diversity, and genetic diversity via declines in species ranges; and we can generate time series for these biodiversity metrics in high spatial resolution. As these new products emerge, they will be fed directly into the SEED framework to update the biocomplexity index and improve the spatial and temporal resolution of the index to allow for more fine-scale assessments of biodiversity and dynamic changes over time.

The integration of remote sensing in biodiversity modeling will be the key distinguishing factor that transforms novel approaches from simply predicting general patterns to the prediction of local conditions and the actual state of nature. Overall, we gain more complete spatial coverage from remote sensing than would be possible from field observation, with more reliable information than extrapolation of models¹⁰⁰. Remote sensing can provide the means for both direct – many trees and large animals are visible from space – and indirect biodiversity monitoring via the coupling of remote sensing products with ecological models¹⁰¹. Future advances in remote sensing such as hyper-spectral imaging^{102,103} are expected to provide valuable additional information, which may help assess how plant species and functional biodiversity respond to different practices¹⁰⁴.

Global biodiversity monitoring undoubtedly requires a combination of ground-sourced and remote-sensed approaches. Future on-the-ground sampling in under-sampled regions of the planet and for under-sampled taxa like invertebrates is urgently needed to fill in key gaps and narrow the uncertainty in global genetic and species diversity models. The emergence of new technologies – such as eDNA^{48,105}, bioacoustics¹⁰⁶, and camera traps – will likely be essential for filling in these core data gaps in a cost-effective manner¹⁰⁷.

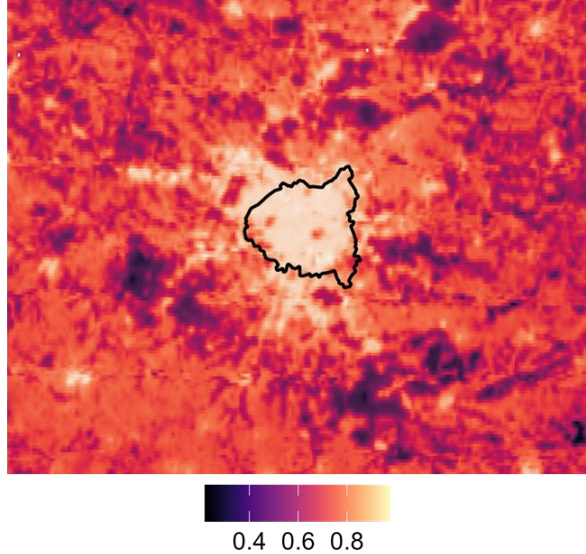
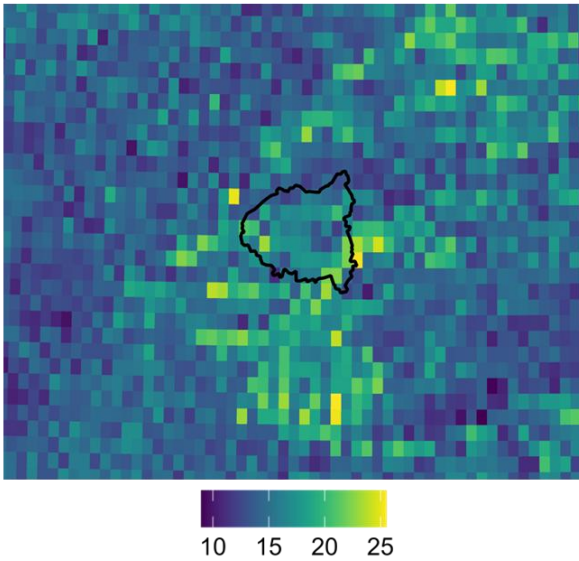
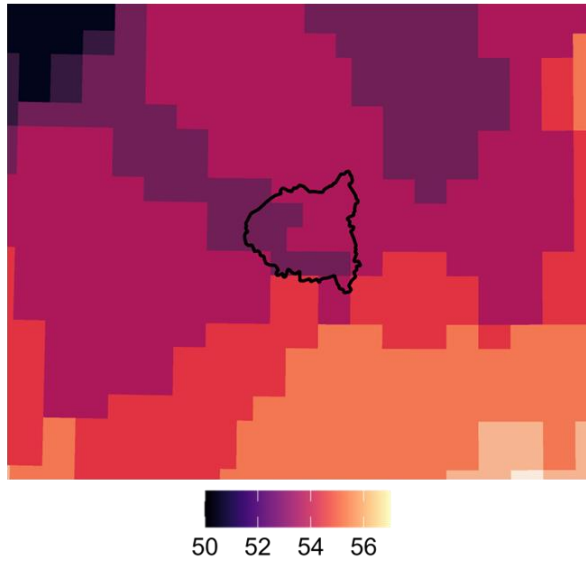
4. Conclusion and outlook

There is growing recognition that we need both the political and financial mechanisms to distribute wealth towards local efforts that promote biodiversity¹⁰⁸. To support this transition to equitable

biodiversity protection, we require globally standardized assessments of ecological intactness that can detect change over time and are available to everyone, everywhere. Given the expansion of global datasets, across various dimensions of biodiversity including plants, animals, and microbes, frameworks for integrating this information are now within our grasp. The resulting global assessments of biocomplexity are necessary to evaluate progress toward climate change and land protection pledges (e.g. the GBF, Bonn Challenge¹⁰⁹, and UN Sustainable Development Goals¹¹⁰) to bring transparency to policy frameworks, and to encourage corporate accountability (e.g., under the Taskforce for Nature-related Financial Disclosures (TNFD)¹⁰ and Science-Based Targets for Nature (SBTN)¹¹¹).

The SEED framework consolidates the three broadest dimensions of biodiversity to produce a single, standardized and comprehensible measure of biocomplexity across the globe. This framework is fundamentally collaborative, incorporating biodiversity assessments and models from a diverse range of biodiversity experts. In addition, it is flexible, allowing for a dynamic index that evolves alongside the development of new map products and scientific advancements. We demonstrate that the SEED framework captures multidimensional changes in biodiversity along nine distinct axes (Figures 3) and provides a unified understanding of the state of nature at multiple scales (Figure 4). Yet, there are several key challenges that need to be addressed to improve the resolution of our index at finer spatial and temporal scales. Most notably, the development of models that integrate remote sensing data products into maps of species richness and genetic diversity will greatly improve the spatial and temporal resolution of our index.

To ensure that the most high-integrity and up-to-date ecological information is available to policy- and decision-makers, we invite the wider scientific community to collaborate on the continual advancement of this biocomplexity index (www.seed-index.com). We believe that for this biodiversity index to lead to positive outcomes, its satellite-based predictions must accurately represent the actual biodiversity at a site. Achieving this level of accuracy presents a scientific challenge that requires the collaboration of a diverse team of experts, including ecologists, remote-sensing specialists, and others from around the globe. Leveraging the latest scientific and technological breakthroughs, we aim to enhance and refine the biocomplexity index, thus fostering better outcomes for ecosystem protection and restoration.

497 **Figures****a. Aerial View****b. Human Modification Index****c. Plant Richness****d. Mammal Richness**

498

499 **Figure 1. Poor performance of species richness maps in human modified landscapes.** The
 500 impacts of human activities – as is shown here for Paris (outline) and the surrounding landscape (a)
 501 in satellite imagery¹¹² and (b) in the human modification index⁵⁵ – were not included in the
 502 development of most maps of species richness, e.g., (c) plant¹¹³ and (d) mammals³⁴.

503

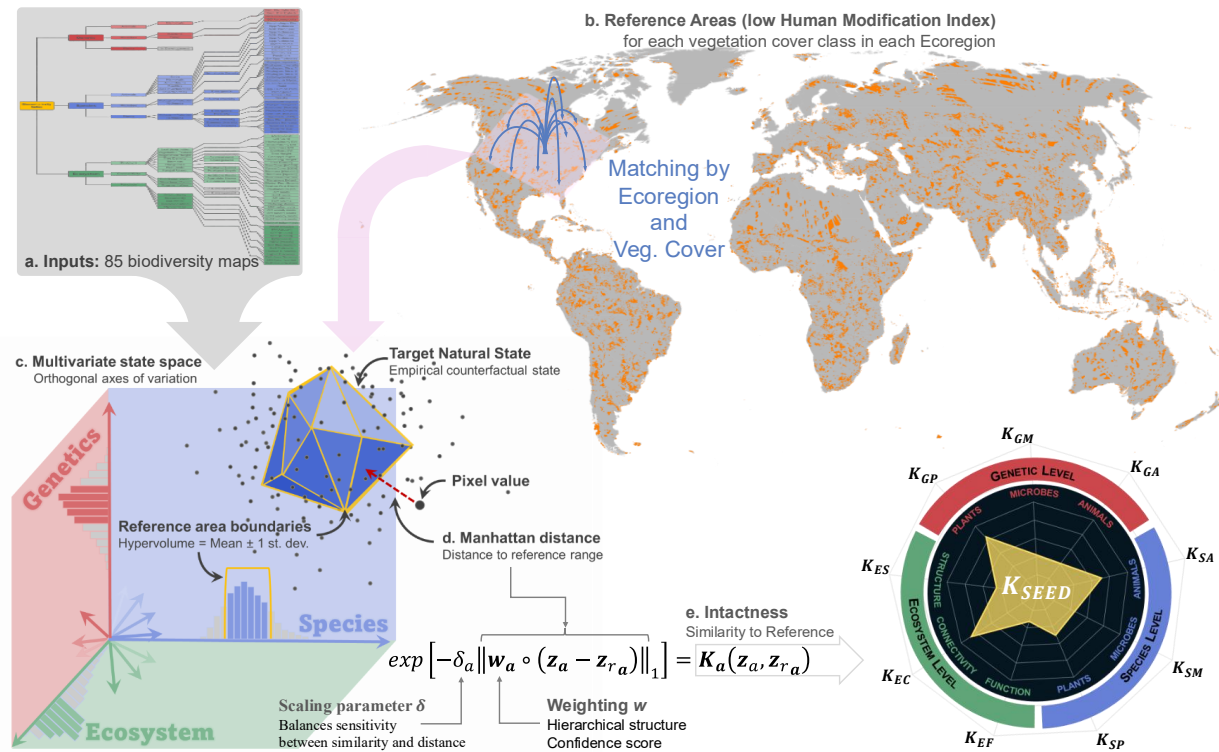


Figure 2. SEED framework methodology. (a) We defined a hierarchy to guide the flow of data from 85 biodiversity input layers to each of the nine dimensions of biocomplexity (Figure S1). (b) Using minimally human modified areas to serve as reference points, we linked all pixels to a reference area with matching ecoregion and vegetation class. (c) In a multivariate context, we calculate the bounds for each input as the mean \pm one standard deviation. (d) Within each dimension we calculate the Manhattan distance between each pixel and the bounds of the reference area values. (e) The kernel function converts distance to similarity for each of nine dimensions (a E (GP, GM, GA, SP, SM, SA, ES, EC, EF). Similarity to natural reference state indicates intactness, which can be visualized together in the radar plot in yellow. The weighted sum of the nine kernels yields a single biocomplexity intactness index.

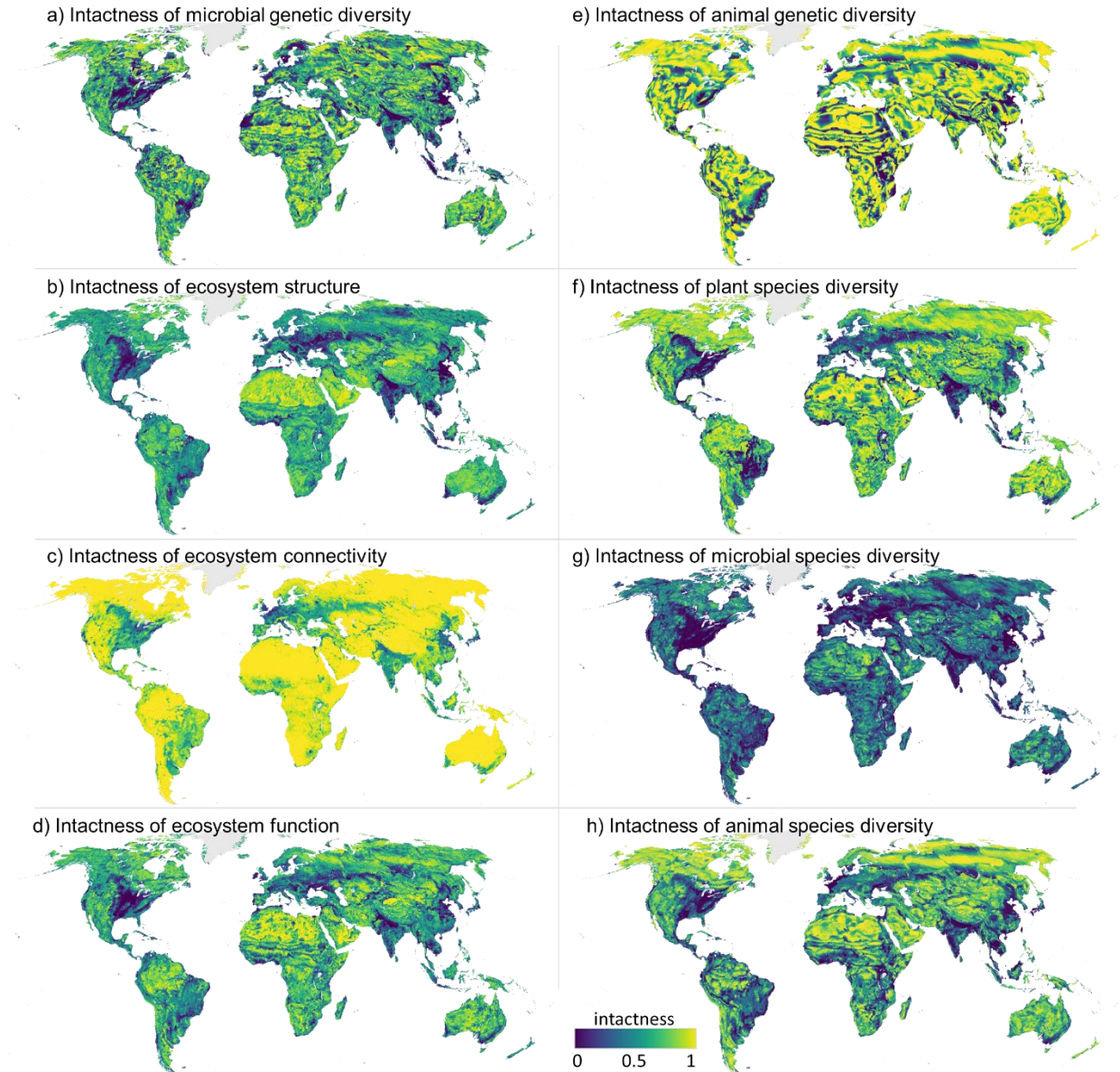
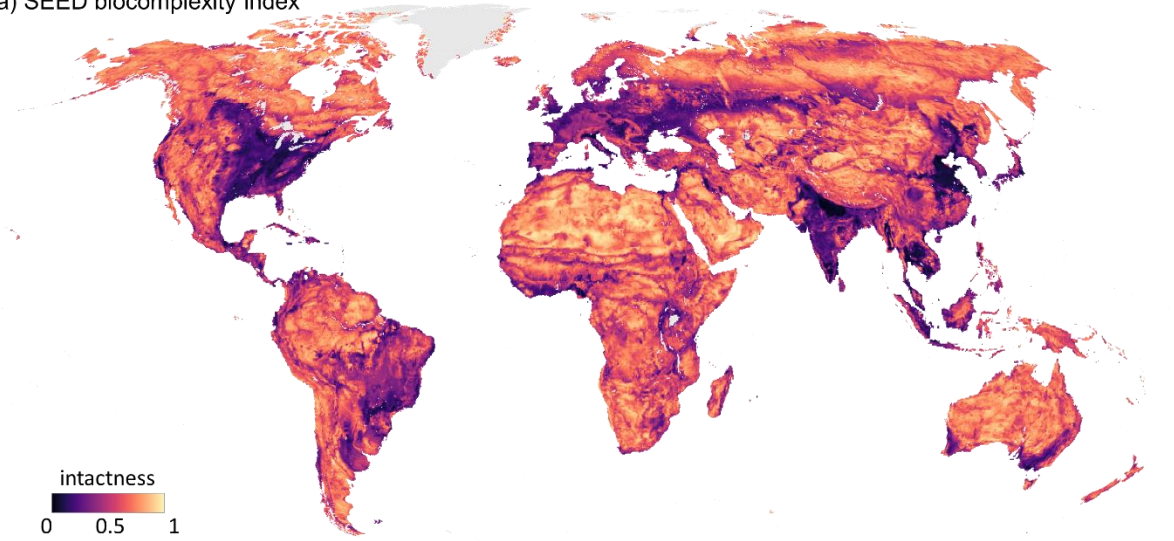
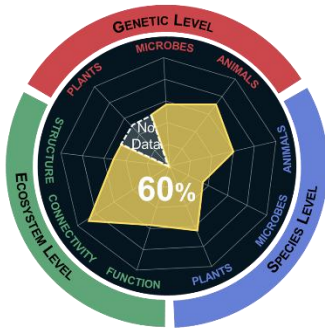


Figure 3. Intactness along each axis of biodiversity. Series of maps showing the intactness – relative to minimally impacted reference areas – of diversity along each biodiversity axis: genetic diversity of (a) microbes and (e) animals; ecosystem (b) structure, (c) connectivity, and (d) function; and species diversity of (f) plants, (g) microbes, and (h) animals.

a) SEED biocomplexity index



b) Global SEED analysis



c) Mean biocomplexity at administrative level 1

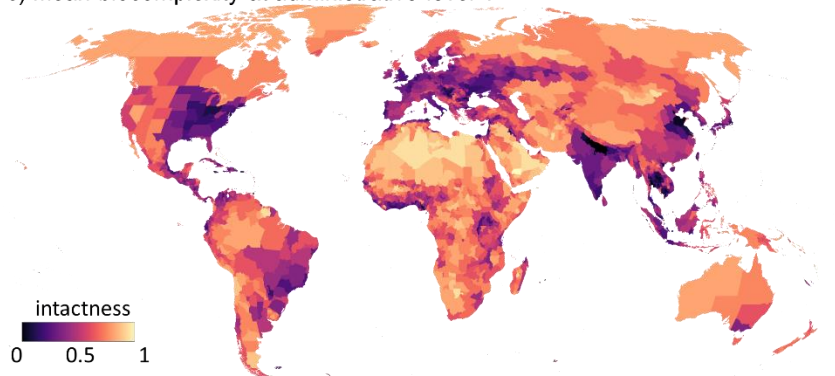


Figure 4. Global analysis of biocomplexity. Map of the (a) SEED biocomplexity index, which measures the intactness of biodiversity for every 1-km of pixel of land. SEED can be aggregated across ecological boundaries, as is demonstrated with (b) a global analysis and (c) the summaries by administrative boundaries.

Resource availability

Lead contact: Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Robert McElderry (robert.mcelerry@usys.ethz.ch).

Materials availability: All unique biodiversity indices generated in this study may be accessed at <https://doi.org/10.5281/zenodo.13799961>

Data and code availability: This paper analyzes existing, publicly available data. We compiled a list of the sources where these data may be accessed [[See Excel file](#)]. All original code is currently unavailable.

Acknowledgements:

This work was supported by DOB Ecology, the Bernina Initiative, and Nestlé. CSD was supported by SNSF Postdoctoral fellowship TMPFP3_209925. DHD and LKW were supported by a Google Carbon Removal Research award. We also thank Jelle P. Hilbers for reviewing our manuscript and offering several useful suggestions.

Author contributions:

This work was conceptualized by TWC, DM, JvdH, TE, RMM, and CFL. RMM, CFL, CEL, FS, PC, TWC, and JvdH developed the methodology while CEL, FS, PC, RMM, TL, CFL, and JvdH composed the software. Data curation, formal analyses, and validation were performed by RMM and CFL with assistance from CEL, SM, PC, JvdH and TL. Resources were curated by TL, CFL, CEL, PC, and RMM. The original draft was composed by TWC, RMM, CFL, and IB, followed by revisions by all authors. Visuals were envisioned by TWC, RMM, and IB, and created by CFL and RMM. TWC and RMM supervised this work, and funding was acquired by TWC, TWE, RMM, LKW, and IB.

Declaration of interests:

Restor (Restor Eco AG) is a non-profit spin-out from the Crowther Lab at ETH Zurich and is wholly owned and financed by the Restor Foundation. None of the authors own any shares in Restor. TWE is the CEO of Restor and TCW is the President of the Council of the Restor Foundation and a member of Restor's Science Advisory Council.

Supplemental information:

Document S1. Materials and methods, Table S1-2, and Figure S1-2

Table S2. Citations and details for the list of layers incorporated in SEED. [See Excel file.](#)

Web-based map viewer. <https://robertmcelderry.users.earthengine.app/view/seed-biocomplexity-global-beta>

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Supplement S1. Materials and methods

1. Reference Area Methodology

We developed an approach that offers a contemporary baseline in which all global biodiversity maps may be evaluated. Our algorithm uses the human modification index (HMI)⁵⁵ and potential natural vegetation (PNV)⁵⁷ to create a reference area mask that delineates the relatively pristine areas on the globe. The combination of PNV classes and 846 delineated ecoregions⁹⁵ then guides the assignment of reference areas to all non-reference pixels having the same ecoregion-PNV class. Due to the large variations in the extent of human modification among different ecoregion landcover combinations, we designed a dynamic decision tree for selecting a threshold HMI to define reference pixels and then to link reference to non-reference pixels to obtain the reference mask.

We targeted reference pixels with minimal human modification which we defined as follows. For each PNV class, v , within each ecoregion, e , we calculated the 5th and 3rd percentile of the HMI, $P_{0.05}(HMI_{e,v})$ and $P_{0.03}(HMI_{e,v})$. The reference threshold value, $r_{e,v}$ was then set to the maximum of either $P_{0.05}(HMI_{e,v})$ or $P_{0.03}(HMI_{e,v})$ if they were less than 0.05, or 0.05 (See equation S1 below).

$$r_{e,v} = \begin{cases} P_{0.05}(HMI_{e,v}) & \text{if } P_{0.05}(HMI_{e,v}) \leq 0.05 \\ P_{0.03}(HMI_{e,v}) & \text{if } P_{0.05}(HMI_{e,v}) > 0.05 \text{ and } P_{0.03}(HMI_{e,v}) \leq 0.05 \\ 0.05 & \text{if } P_{0.05}(HMI_{e,v}) > 0.05 \text{ and } P_{0.03}(HMI_{e,v}) > 0.05 \end{cases} \quad \text{Equation S1}$$

Within relatively unmodified ecoregions, we set more restrictive criteria to refine and focus the selected reference areas to include only pixels with very low HMI. In more thoroughly modified ecoregions, we loosened the criteria for more inclusion in selected reference areas, but only to the point of an HMI equal to 0.05. With the threshold defined for each ecoregion-PNV class, we selected reference areas as all pixels less than $r_{e,v}$. If an ecoregion-PNV class had fewer than five pixels, we stepped down the reference threshold – from the $P_{0.05}(HMI_{e,v})$ to $P_{0.03}(HMI_{e,v})$, or from $P_{0.03}(HMI_{e,v})$ to $0.05(x_{e,v}, y_{e,v})$. If $r_{e,v}$ was 0.05, and the ecoregion-PNV class still possessed fewer than five reference pixels, then we looked beyond the ecoregion boundary and included all reference pixels of the same PNV class within the same biome.

2. Delta calculation

To calculate the delta value for each axis (subindex) of the seed index, we use the following formula:

$$K = e^{-\delta D}$$

where K is the kernel, δ is the delta parameter and D is the maximum Manhattan distance of the axis for all the pixel points. δ mediates the translation of distance to similarity, effectively mapping the highest possible distance to the lowest kernel value ($K > 0$). Tuning δ shifts the balance between similarity and dissimilarity. Balance in our case was achieved by equating the highest distance to the lowest similarity, a kernel value of 0.001, and solving for the δ value for each of the axis. We then substitute this delta value in the equation to calculate the kernel for the world of each axis. The SEED index is then calculated based on the weighted average of the individual axes.

3. Weighting system

We considered two points of information in calculating the normalized weight for each map layer: the hierarchical structuring of data layers into groups and our confidence in each individual layer. Similar types of data were paired evenly at each level of the hierarchy (Figure S1) to ensure both averaging of duplicate information and equal weighting among components at the same level.

We ranked our confidence in each map layer based on several features: underlying predictive layers, quality of validation data (including spatial coverage), spatial resolution, and perceived error at SEED's 1-km resolution. We defined five rank classes associated with percent scores (Table S1). The scores associated with each ranking are tunable parameters. We opted for skewed mid-level scores, with medium high scoring 90% and medium low scoring 10%.

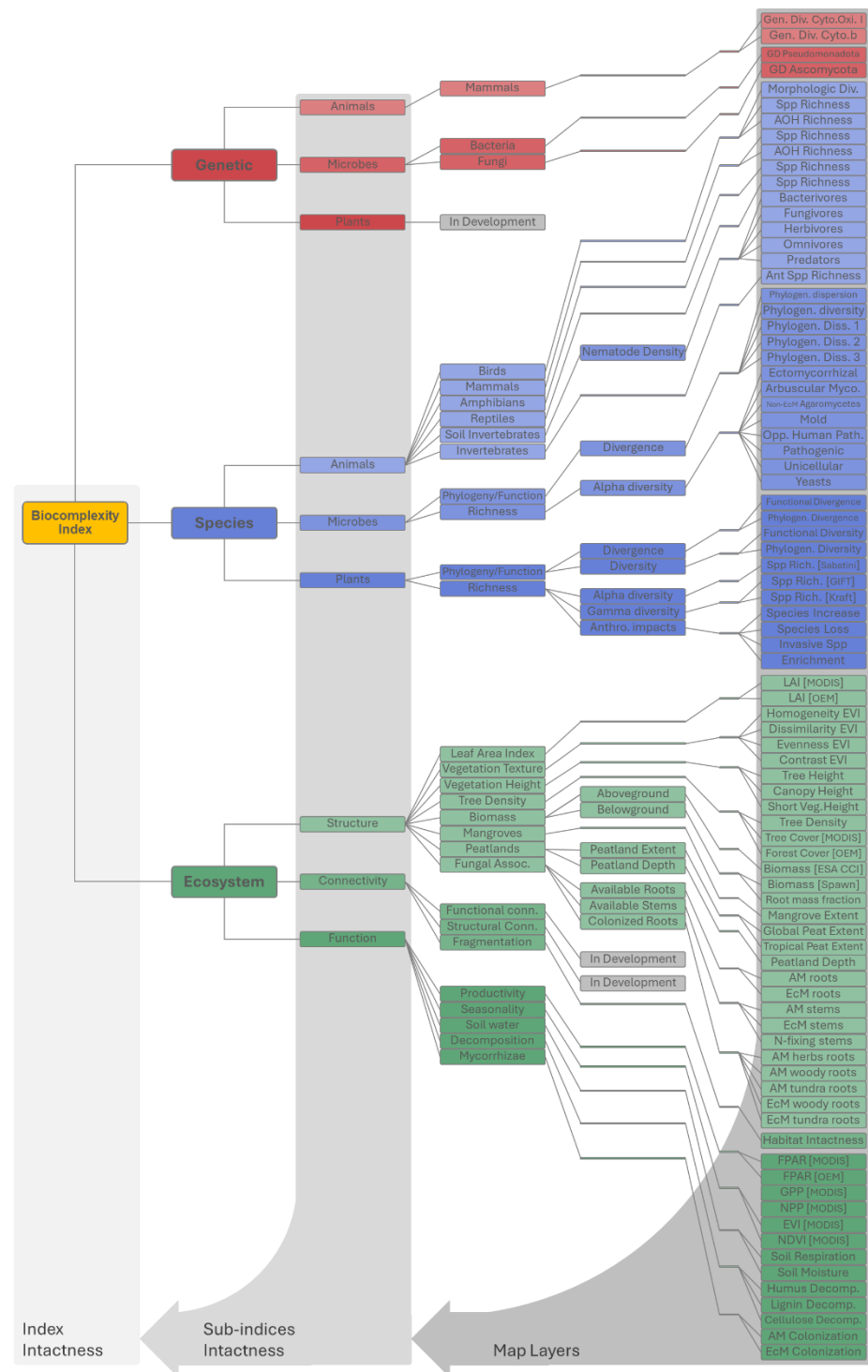


Figure S1. Hierarchy of information. Hierarchy of global biodiversity map layers (branch tips) that feed into the nine sub-indices (Figure 2) and then into the headline biocomplexity index. Details for each map are listed in supplemental Table S2.

979 **Table S1.** Table of scores, weights, and a description of the criteria guiding our judgment in rating
 980 the quality of information contained with each map that we incorporated in SEED.

Confidence Score	Weight	Description
5	100	Fully validated model representing on the ground conditions with at least 1-km resolution
4	90	Partially validated model representing on the ground conditions with at least 1-km resolution
3	50	Model predicting on the ground conditions with at least 5-km resolution, requires validation
2	10	Model predicting general diversity patterns with some human impacts considered
1	1	Model of general diversity patterns. Does not represent human impacts on nature.

981

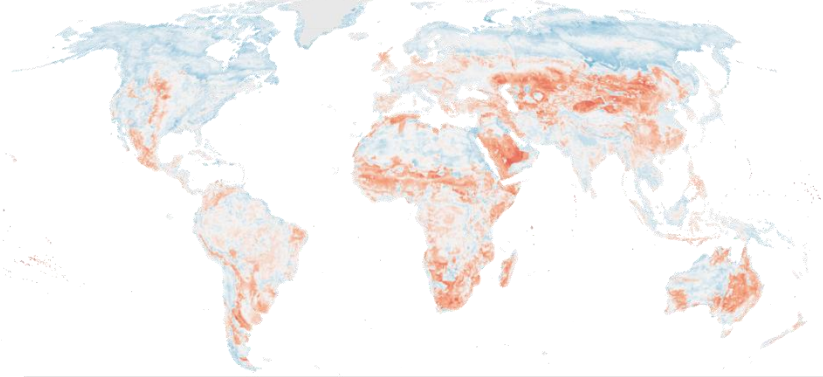
Table S2. List of global biodiversity maps alongside their unique details (resolution, units, and citations) our confidence scores and the normalized weights. For interactive links see [online table](#)

[illegible]

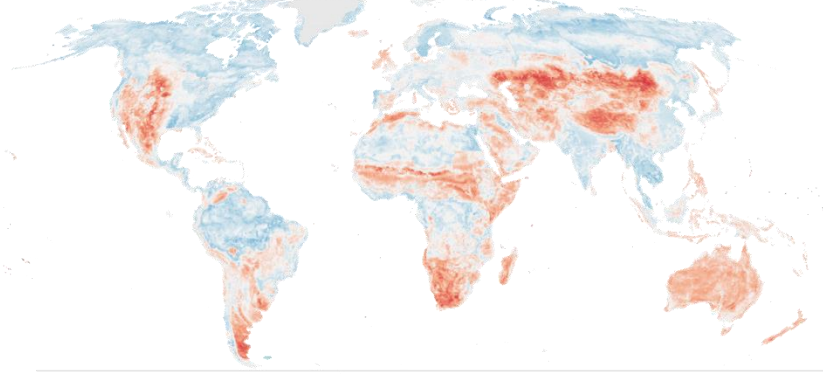
4. Comparison with similar global indices

To compare SEED with three of the most widely used global indices, we computed the difference between SEED and the MSA from GLOBIO⁸⁶, the BII from the Natural History Museum¹¹⁴, and a second BII (which we will call BDI) produced with a less recent version of the same core methodology^{84,115}. The broad scale differences in our index indicate that SEED may be more conservative than MSA and BII (Figure S2a-b) in boreal and desert regions, while SEED estimates higher intactness across temperate regions, sub-Saharan Africa, South Africa, and parts of Australia (Figure S2a-b). SEED was consistently lower than the BDI globally (Figure S2c). Underlying these differences, the distribution of MSA and BII values are bimodal compared with the BDI and SEED, which are unimodal. This means that MSA and BII may more commonly characterize an ecosystem as either highly intact or not very intact, while SEED would more commonly characterize the same ecosystem as moderately intact.

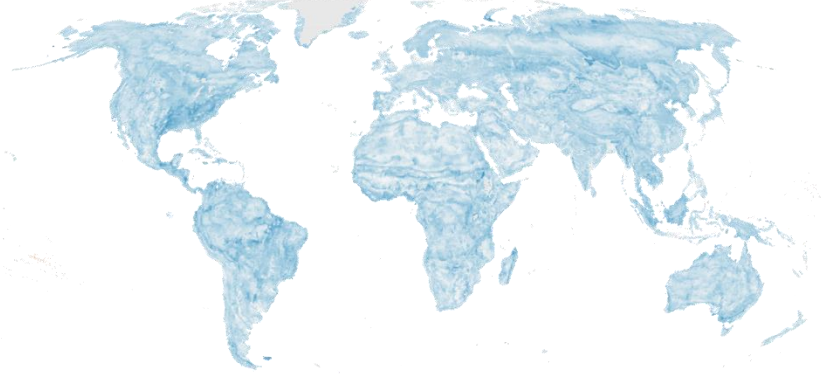
a) Mean Species Abundance (GLOBIO)



b) Biodiversity Intactness Index (Natural History Museum)



c) Biodiversity Intactness Index (Impact Observatory and Vizzuality)



SEED < BII or MSA Equal SEED > BII or MSA

Figure S2. Comparison between the leading global biodiversity models. These global maps illustrate differences between SEED and (a) MSA⁸⁶, (b) BII from NHM¹¹⁴, and (c) BDI, which was created independently from the BII while using the same model¹¹⁵.