# 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. Human activity consistently reduces and homogenizes biodiversity.
- 3. We define a global framework for a holistic measure of the state of nature.
- 4. Inclusion of microbes and invertebrates is crucial to evaluate biodiversity.

#### 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 genetic, species and ecosystem levels. Achieving this in a globally standardized way remains a key challenge for achieving an equitable nature positive future. Here, we present the Sustainable Ecology and Economic Development (SEED) framework, which assesses multiple dimensions of biodiversity (genetic, 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 disturbance. We demonstrate the utility of the SEED framework and highlight its features which include seven novel measures of biodiversity intactness that are integrated into the SEED biocomplexity index. As new information emerges, the SEED framework continuously integrates state-of-the-art datasets and maps to provide up-to-date estimates of local biocomplexity across the planet for decision makers who strive to improve the global state of nature.

#### Keywords

Biocomplexity; biodiversity monitoring; biodiversity intactness; genetic diversity; species diversity; ecosystem diversity

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
BII MSA HMI PNV	Biodiversity Intactness Index Mean Species Abundance Human Modification Index Potential Natural Vegetation

#### Abbreviations

## **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 certain components of nature (i.e., the parts we can use for food, timber, medicines etc.) over others. The development of markets for these products has incentivized their mass propagation at the expense of all other components of biodiversity, driving the oversimplification of biological systems and the loss of the ecosystem services on which we depend.

In recent years, there has been a growing appreciation for the role that biodiversity plays in the global economy<sup>1</sup>, most saliently distilled in the Kunming-Montreal Global Biodiversity Framework (GBF)<sup>2</sup>. The most prominent 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). To coordinate monitoring, a worldwide system of observation networks has recently been proposed by the Group on Earth Observations Biodiversity Observation Network (GEO BON)<sup>3</sup>. In the financial sector, the GBF also sets a requirement for businesses to disclose their impacts on biodiversity (Target 15) and promotes a substantial increase in funding for nature conservation and restoration from all sectors, including through payments for ecosystem services and biodiversity credits (Target 19).

As policy frameworks and nature markets emerge with the potential to promote biodiversity, it is critical that we learn from challenges of the past. Mechanisms that value a single aspect of nature – such as carbon sequestration – risk driving the oversimplification of the system<sup>4–7</sup>. This can lead to potentially counterproductive outcomes, like the creation of monocultures of exotic tree species at the expense of local biodiversity<sup>7</sup> and wellbeing<sup>8</sup>. If political and financial structures are to promote the maintenance of natural biodiversity, they must be underpinned by robust scientific monitoring that reflects the full dimensionality of life, across genetic-, species- and ecosystem-levels. At present, countless biodiversity metrics have been developed to support biodiversity monitoring, and these are based on datasets that generally fall into two categories: (i) ground-sourced data (e.g. plot surveys, eDNA, bioacoustics monitors and camera traps), and (ii) remotely-sensed data (e.g. radar and multispectral imagery from satellites)<sup>9</sup>. While ground-sourced data are critical for providing detailed insights into the diversity of organisms in any specific study area,

their insights are limited outside of the local study sites<sup>10,11</sup>. By contrast, remotely-sensed data can provide globally-standardized assessments that are widely available, but these are generally more coarse, and limited to spectral information relating to ecosystem-scale characteristics like forest structure<sup>12</sup> and connectivity<sup>13</sup>. To align monitoring efforts, GEO BON has identified the Essential Biodiversity Variables (EBVs)<sup>14</sup> and established guidelines for EBV estimation using both groundsourced and remote-sensed data<sup>15</sup>. Currently, there is still no single measure of biodiversity that incorporates available information across spatial scales to fully evaluate the state of nature.

A standardized measure of biodiversity across all taxa and scales of variation is critically needed to help inform nature-related policy and market tools (e.g., GBF target monitoring; impacts, dependencies, and risks assessments; nature capital accounting; and measurement, reporting, and validation). To address this growing demand, we first review existing global biodiversity metrics and highlight their strengths and weaknesses in measuring the current state of nature (Section 2). We then present a new integrative framework, SEED, which is designed to consolidate three primary dimensions of biodiversity – genetics, species, and ecosystems – into a measure of biocomplexity, which we apply to every terrestrial location on Earth (Section 3). To ensure policy and market tools have the most up-to-date information on the state of nature, SEED is designed to be flexible. This allows us to incorporate novel scientific advancements and data as they become available.

#### 2. Current state of global biodiversity mapping

Spatially explicit biodiversity data products generally cover four main dimensions of ecological systems: genetic (within-species) diversity, species (among-species) diversity, ecosystem diversity, and ecosystem intactness. Genetic and species diversity metrics measure the diversity within and among biological organisms, whereas ecosystem diversity metrics quantify ecosystem properties such as productivity, vegetation cover, biomass, or habitat heterogeneity. Ecosystem intactness – sometimes called ecosystem integrity – metrics estimate the similarity of an area to an estimate of how it would look if it were not affected by humans. Each of these levels of global data products reflect different dimensions of diversity that are essential for a holistic understanding of biocomplexity across the globe. Here we discuss these four levels of global ecological datasets, and the considerations for their inclusion into a holistic framework.

## 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<sup>16,17</sup>. Global measures of genetic diversity are currently estimated from mitochondrial DNA sequences stored in the National Centre for Biotechnology Information GenBank and the Barcode of Life Database<sup>18</sup>. While there are good insights about genetic variation for certain plant<sup>19</sup> and animal species<sup>18,20,21</sup>, we currently lack global predictions about genetic variation within most of the ~1 trillion species on the planet. Among the few taxonomic groups that have been studied, loss of genetic diversity is often correlated with loss of suitable habitat<sup>22</sup> leaving threatened species with low genetic diversity<sup>23</sup> and hence low adaptability. To generate a proxy measure of genetic diversity, it is possible to use the estimates of effective population size, but this information is lacking for the vast majority of organismal groups. Moreover, this narrow view of genetic diversity is problematic for microbes (including archaea, bacteria, and fungi), for which genetic variation is often the sole basis for division of operational taxonomic units (OTUs) in the absence of information that delineates taxonomic groups. A broader view of genetic diversity across species would also include among species phylogenetic variation, for which there is a growing number of global products, particularly focusing on plants and animals (discussed in section 2.2).

## 2.2 Species, phylogenetic, and functional diversity

A large part of the explosion in global biodiversity research has focused on modeling species richness (the number of unique taxa) across plant, animal, and microbial taxa. These global assessments are generally created from ground-sourced datasets that may contain plot-level measures of species composition, georeferenced point occurrences, or both. Some may also utilize regional checklists, range maps<sup>24</sup>, floras<sup>25</sup>, and taxonomic monographs as data sources<sup>26</sup>. Generally, these observed data are interpolated or extrapolated – using either machine learning<sup>27</sup>, species distribution modeling<sup>28</sup>, or process–based models<sup>29</sup> – based on correlations with remotely-sensed and modeled environmental variables (e.g. temperature, precipitation, topography, geology, etc.) to generate spatially continuous models of diversity<sup>30</sup>. While these approaches provide differing levels of predictive accuracy and causal inference, most global models of species diversity focus on broad-

scale biogeographic trends. As such, until now, most products have not aimed to capture fine-scale patterns in species composition, or the effects of local human disturbance.

Phylogenetic (i.e., evolutionary) and functional novelty add variety to the form and function of a natural community. Phylogenetic diversity is a measure of the evolutionary history represented by a set of species<sup>31</sup> and functional diversity refers to the range and distribution of organismal traits and life history strategies across species within a system<sup>32</sup>. Because trait expression is a byproduct of evolutionary history, functional diversity is often closely related to phylogenetic diversity<sup>33</sup> but can deviate substantially due to processes such as convergent evolution. Phylogenetic and functional diversity metrics combine information about both species composition and either evolutionary history (phylogeny) or trait variation. In practice, the list of species present at each locality are coupled with a phylogeny<sup>34</sup> or a functional-trait matrix<sup>35</sup> to provide information about phylogenetic and functional components of diversity.

Numerous functional and phylogenetic diversity metrics exist, each measuring a different aspect of evolutionary or trait space. Three groups can be categorized based on whether they capture: richness (or spread), evenness (or regularity/uniformity), and divergence (or uniqueness)<sup>36</sup>. Phylogenetic and functional richness are typically highly correlated with species richness and thus encode little additional information<sup>37</sup>. By reflecting the uniformity of species in functional or phylogenetic space, evenness metrics have been especially linked to ecosystem function and the biodiversity-productivity relationship<sup>38</sup>. Divergence on the other hand is indicative of the evolutionary or functional differences among species. It is largely independent of species richness and quantifies the redundancy of species<sup>39</sup>. Whereas a species-rich community may be composed of evolutionarily and functionally redundant species, other less 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.

While global maps of genetic, species, phylogenetic, and functional diversity provide important insights to improve our fundamental understanding of ecology, they are not typically aimed at isolating the effects of anthropogenic change on diversity patterns. The predominance of modeled

climate, edaphic and topographic variables in the construction of these maps results in high predictive accuracy of diversity patterns across environmental gradients, but the general lack of human influences in these models leads to low predictive accuracy for quantifying the impacts of human disturbance (Figure 1). This may be due to a paucity of biodiversity data in both heavily degraded and intact landscapes, and across a sufficient range of land use types and intensities. Furthermore, these maps are just now beginning to include high-resolution remote-sensed information that can help reveal local ecosystem structure and function<sup>38</sup> to enable a resolution more indicative of on-the-ground conditions. It is increasingly important for us to move beyond simply understanding patterns of global biodiversity and build maps of species, phylogenetic, and functional diversity that provide an accurate estimation of biodiversity at fine spatial scales.

Another inherent challenge facing global biodiversity products is incomplete data coverage. Most global biodiversity databases over-represent some regions and under-represent other regions, due to disparities in financing and accessibility, which often drive a bias toward developed nations. Similarly, the climate layers, which are fundamental to biodiversity mapping, also unevenly represent areas around the globe. On top of the geographic gaps in data coverage, there are also considerable disparities in taxonomic coverage. For example, larger, and more charismatic organisms tend to be over-represented in biodiversity assessments. The IUCN database contains distribution data for over 80% of described vertebrate species and 14% of vascular plants, but only 2% of invertebrate species are represented despite invertebrates representing the majority of animal species. In addition, microbes represent 88% to 99% of all species on Earth<sup>40,41</sup> but are vastly underrepresented, with only 0.4% of known fungi and protists included in the IUCN database, which is the source of many biodiversity maps<sup>18,20,42–44</sup>. This is changing due to recent advances in high-throughput sequencing technologies that enable us to observe and quantify microscopic and otherwise cryptic species<sup>45</sup>, and the availability of microbial biodiversity maps is expanding exponentially.

Finally, global maps of genetic, species, phylogenetic, and functional diversity tend to be temporally static and coarsely resolved. Biodiversity databases include information over several years at least, but often also include decades-old observations. Maps generated from these databases therefore represent an average of the dates of observations. Additionally, the relevant databases for

a particular map may involve different sampling methods and encompass different spatial and temporal scales. Sampling methodologies are taxon and/or habitat specific and may also differ by region and discipline or agency. Altogether, this makes 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, ecosystemlevel metrics 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 modifications<sup>46</sup>, land use change<sup>47</sup>, canopy cover<sup>48</sup>, canopy height<sup>49</sup>, above and belowground biomass<sup>50</sup>, habitat heterogeneity<sup>51</sup>, leaf area index<sup>52</sup>, ecosystem connectivity<sup>53,54</sup>, net primary productivity<sup>55</sup> and ecological resilience<sup>56,57</sup>. We group all ecosystemlevel products that measure some aspect of biodiversity into one of three broad categories: ecosystem structure, function<sup>14</sup>, or connectivity.

Ecosystem structure, function, and connectivity are emergent properties that arise from the combination of species, landscape physiognomy, climate, and human modifications. It is the interplay between living organisms and their environment that generates these ecosystem properties and contributes to carbon, water, and nutrient cycling dynamics, which then feedback to affect the environment. These ecosystem properties provide a direct link to measures of ecosystem services<sup>58,59</sup>. The three-dimensional structure of an ecosystem characterizes the environmental context in which species coexist. Structural diversity has been shown to improve ecosystem function<sup>12</sup> and stability<sup>60</sup>. Ecosystem function captures the ecological processes that occur within an ecosystem, including primary and secondary productivity, decomposition, nutrient cycling, and the natural disturbance regime. Similarly, ecosystem connectivity describes both the spatial arrangement of habitat fragments (structural component) and species-specific dispersal abilities and limitations (functional component). Connectivity is commonly measured using graph theory, which divides the landscape into edges and nodes, and it may also evaluate the resistance of flow of organisms and energy between nodes. Ecosystem connectivity tends to decrease with habitat loss

and fragmentation, but both connectivity and fragmentation indices can provide unique insights into the ecological functionality at the landscape-scale<sup>61</sup>.

#### 2.4 Ecosystem intactness

Given the challenges of capturing dynamic changes in ecological diversity at a global scale, a few analyses estimate how far the ecological community has diverged from its natural state. Using experiments or local gradient studies, it is possible to identify how land use changes affect ecological diversity, and then use those relationships to predict ecological intactness across the globe. The three most prominent of these global indices are the Ecosystem Integrity Index (EII)<sup>62</sup> by the United Nations Environment Programme World Conservation Monitoring Centre, the Biodiversity Intactness Index (BII)<sup>63,64</sup> by the Natural History Museum in London, and the Mean Species Abundance (MSA)<sup>65</sup> 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)<sup>46</sup>; ecosystem function is measured by the ratio of actual to potential net primary productivity<sup>55</sup>; and ecosystem composition is measured by the BII<sup>63,66</sup>. For a given location, the EII uses the lowest score of the three components to predict the scale 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 a few 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<sup>67</sup>, 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, covering less than 10% of the described species for most large taxonomic groups of vascular plants, invertebrate animals, and a far smaller proportion

for microbes<sup>67,68</sup>. Given that each of these different organismal groups respond differently to human disturbance and show unique global distribution patterns<sup>69,70</sup>, the underrepresentation of important taxa may therefore bias global biodiversity assessments. Second, uneven data availability among regions can lead to considerable bias and uncertainty in under-represented regions. Third, these indices all 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 the 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. The exponential growth of global ecological datasets across genetic, species, and ecosystem levels represents exciting new opportunities for our understanding of biodiversity across the planet. The development of conceptual frameworks will be essential to integrate and interpret this growing body of information into evolving biodiversity frameworks to generate a holistic understanding of global biocomplexity. Our global understanding of biocomplexity will never be fully complete, as emerging scientific assessments will continue to capture more information. Therefore, it is important to establish dynamic frameworks that can incorporate new and emerging information as it becomes available.

To address the need for a standardized measure of the state of nature, we present the beta version of a holistic ecological framework (hereafter referred to as SEED). By combining datasets representing each of three hierarchical levels of biodiversity (genetic, species and ecosystem levels), SEED generates a framework for evaluating multiple dimensions of biodiversity. To globally-standardize this index we estimate the similarity (ranging from zero and one) between the current state of biocomplexity of an ecosystem and its native state, i.e., in comparison to reference areas where nature has only been subjected to minimal human disturbance.

Biocomplexity has been defined as the "properties emerging from the interplay of behavioral, biological, chemical, physical, and social interactions that affect, sustain, or are modified by living organisms, including humans."<sup>71</sup> The current state of genetic, species, and ecosystem diversity and each of their subcomponents are all properties that 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. Our biocomplexity index is designed to represent the multidimensionality of nature by defining nine primary axes of variation, which are nested within the three hierarchical levels of variation that define biodiversity: genetics, species (including phylogenetic and functional diversity), and ecosystems (Figure 2). Within the genetic and species levels of variation, we distinguish three primary taxonomic groups (i.e., axes): plants, animals, and microbes (bacteria and fungi). Within ecosystems, we distinguish three axes: structure, function, and connectivity. These axes could represent or incorporate components already identified as EBVs by GEO BON<sup>14</sup>.

For simplicity and interpretability, SEED offers a single standardized biocomplexity value for any area of interest, but the SEED framework also allows the user to unpack this information. Each axis summarizes the intactness (i.e., similarity to native state) of multiple underlying biodiversity features, and these axes may be viewed separately to aid comprehension and facilitate action-impact assessments. This information can be summarized in the style of a radar plot (Figure 2), whereby the intactness values for each axis at a site are plotted on scale from zero to one. The mean similarity between the current and potential natural state for all nine axes combined creates a score: the SEED biocomplexity index, which ranges between zero and one, where values near zero represents the near absence of biocomplexity (e.g., an open pit mine or paved area), and one represents an area that is equal to its potential natural state (i.e., a minimally-disturbed ecosystem).

#### 3.1 Integrating dimensions of biodiversity

Consolidating the multiple dimensions of biodiversity into a single value is a critical feature that makes our biocomplexity index generalizable and comprehensible. All available global map layers are combined within each of the relevant biodiversity dimensions (Figure 2), using a multivariate kernel estimator<sup>72</sup> (Eq. 1), and then the mean of these nine axes (currently seven) consolidates this information into a single biocomplexity index.

$$K(\boldsymbol{x}, \overline{\boldsymbol{x}}_r) = exp[-\delta \boldsymbol{w} \| \boldsymbol{x} - \overline{\boldsymbol{x}}_r \|] \quad \text{(Eq. 1)}$$

Here x is a data matrix with a biodiversity metric in each column and each of n rows representing the set of values for a unique pixel or location. This multivariate kernel, K, measures the similarity

between each row of x and the mean values for the reference area  $\overline{x}_r$ . We estimated a kernel, and hence similarity for each biodiversity dimension. At the heart of each kernel is the Manhattan distance, which is essentially the sum of the distance between two points along each dimension in multidimensional space. In order of equation complexity, the Manhattan distance is simpler than Euclidean and the Mahalanobis, but the latter two distances we found to be too discriminatory for our purposes (leading to strong bimodality in our tests), and the Manhattan distance provided a nice gradient from intact to not intact.

Sensitivity of similarity is set by the scaling parameter,  $\delta$ , which we set for each dimension according to two criteria. First,  $\delta$  must be strictly positive to ensure that the kernel values are bound between zero and one. Second, the similarity values measured by *K* indicate the intactness of nature and should span the full range between zero and one. We set  $\delta$  to the lowest 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, perhaps hundreds of biodiversity maps, and we test it here with 75 maps – ecosystem structure (25), function (12), and connectivity (1); species diversity of plants (11), microbes (13), and animals (11); and genetic diversity of plants (0), microbes (0), and animals (2). The maps we reviewed vary in several aspects: coverage extent, spatial resolution, nonindependence from other maps, extrapolation across regional data gaps, and in the degree to which satellite imagery or other measures of local conditions were integrated. We developed a dynamic weighting system to define the normalized weight of each map layer in a set, represented by w. We grouped non independent layers to share equal weight, which resulted in a short hierarchical structure. We applied a confidence score and associated decreasing confidence with decreasing weight (see Supplement Table S1 for details).

We structured the integration of the nine biodiversity dimensions to be an even-weighted average of the intactness of each dimension. This places genetic, species, and ecosystem level diversity on equal grounds in the integrated index, but SEED also offers each dimensional index for independent use alongside the integrated index. Even weighting also 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. If, however, evidence emerges which suggests that a different weighting scheme is warranted, this method can be adapted to keep up with the evolving scientific landscape. In practice, however, the availability and quality of available maps is not even among dimensions, which resulted in some dimensions having higher relative weight and therefore more influence on the overall biocomplexity index. Identifying the optimal weighting for different levels of biodiversity information remains a key challenge for future biodiversity research as our theoretical understanding of ecological systems evolves.

## 3.2. Reference area versus a counterfactual landscape

Measuring the intactness of biocomplexity requires establishing a baseline potential state that can be used for comparison. Estimating this baseline state poses several philosophical questions regarding the non-static nature of natural systems. It also poses data limitations for regions of the world that have been heavily degraded and thus lack 'pristine' potential states, such as large regions of the Northern Hemisphere<sup>73</sup>. Thus, we opt for a more direct approach than estimating a potential natural state for all biodiversity dimensions and underlying layers. We identify minimally modified areas as points of reference with a procedure that involves few assumptions, considers the full suite of biodiversity together, and allows for a contemporary definition of natural as opposed to a historical estimate<sup>74</sup>.

Specifically, we developed an algorithm that uses the HMI<sup>46</sup> and potential natural vegetation (PNV)<sup>47</sup> to select reference areas for each vegetation class within each of the 846 delineated ecoregions<sup>75</sup> on Earth. This was done separately for each ecoregion to ensure ecologically relevant comparisons. In each ecoregion, we identify the least-impacted areas for each land cover class, using an upper limit HMI threshold is set just high enough to ensure a sufficiently large area, enabling representative and robust estimates (see Figure 3h and Supplement S1). The mean value for each biodiversity feature layer within this *least-impacted area* estimates  $\bar{x}_r$  in equation 1 and is the basis for comparing all feature values in all pixels of the same vegetation class within that ecoregion.

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. Of course, different targets will be appropriate in different settings. 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 as well as previous alterations to the landscape<sup>76</sup>. 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 enable a standardized assessment of biodiversity improvement in response to management practices<sup>14</sup>.

#### 3.3. Illustration of the SEED biocomplexity framework

The beta release of this biocomplexity index was developed using a comprehensive list of the most up-to-date maps of genetic, species, and ecosystem diversity (see Supplement Table S2). To illustrate the capabilities of the framework, we first show the viability of our dimensionality reduction calculation (equation 1) and reference area (Figure 3a) approach in calculating the intactness of seven of the nine biodiversity dimensions (Figure 3b-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 any scale to summarize biocomplexity in total and in each dimension (Figure 4b-c). Finally, we conduct a cursory comparison of SEED against the leading biodiversity intactness metrics (Figure 5).

Among the seven biodiversity intactness metrics that we calculated, we identified a few broad global patterns where the metrics 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 historically not seen extensive human development. Low intactness is indicated in the temperate grasslands and savannas of North America, Brazil's Atlantic forests, 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 ends of Australia.

There is also notable diverge among these metrics. While the intactness of plant and microbial species show very similar patterns (Figure 3e-f), and to some degree also with ecosystem structure (Figure 3a), ecosystem function (Figure 3c) shows divergent patterns in some regions, e.g., central North America, Western Ghats and Central Deccan Plateau. Ecologically, we know very well that plants and microbes share special linkages and that ecosystem structure and function result from the local communities of plants, microbes, and animals. The intactness of animal species diversity (Figure 3g) is also divergent and highlights the Andes and Appalachian Mountain ranges as having particularly low intactness relative to the other metrics. In the Indo-Gangetic Plains, animal species intactness remains relatively high while other metrics predict low intactness. Ecosystem connectivity (Figure 3b) shows a largely unique pattern. It is highly sensitive to fragmentation, which is a feature of a large proportion of land globally, and therefore either highly intact or not at all. The genetic diversity of animals (Figure 3d) also shows a unique pattern, but this likely stems from its two lone data layers with very coarse resolution (10-km)<sup>20</sup>. This along with the absence of global models for plant and microbial genetic diversity emphasizes the need for more work in global modeling of genetic diversity.

The value in our biocomplexity framework is twofold; it integrates information regarding multiple dimensions of diversity, and it can be aggregated to provide summary statistics at the desired scale. The beta SEED biocomplexity index currently integrates seven biodiversity dimensions to represent a single measure of the state of nature for all land area across the globe (Figure 4a). Overall, this shows that the terrestrial earth is currently at 68% of its natural state (Figure 4b). Aggregating by administrative boundaries<sup>77</sup>, 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 metrics (Figure 5), the beta version of SEED (Figure 4) offers a more comprehensive view of nature's state due to its inclusion of 75 global biodiversity maps, while also offering the seven intactness sub-metrics (Figure 3a-g). We computed the difference between SEED and the MSA from GLOBIO<sup>65</sup>, the BII from the Natural History Museum<sup>78</sup>, and a second BII (which we will call BDI) produced with the same core methodology<sup>79</sup>. The broad scale differences in our metrics indicate that SEED may be more conservative than MSA and BII (Figure 5a-b) in boreal and desert regions, while SEED estimates higher intactness across

temperate regions, sub-Saharan Africa, South Africa, and parts of Australia (Figure 5a-b). SEED was consistently lower than the BDI (Figure 5c). Underlying these differences, the distribution of MSA and BII values are bimodal compared with the BDI and SEED, which are unimodal (Figure S1). This means that MSA and BII may more commonly characterize an ecosystem as 'pristine' or 'highly degraded', while SEED would more commonly characterize the same ecosystem as 'moderately intact'.

These differences between SEED and the other intactness indices may arise from the inclusion of multiple structural and functional ecosystem attributes, as well as a greater focus on the wealth of microbial datasets (including fungi, bacteria and archaea), which are rapidly emerging in the scientific literature. Existing global intactness indices (EII, BII, and MSA) represent the intactness of species level diversity for a subset of taxa. SEED includes the variation in many ecosystem characteristics (aggregated within ecosystem connectivity, structure, and function), which will capture landscape dynamics and ecological feedbacks that operate at broader spatial and temporal scales. For example, according to existing global intactness measures degradation is characterized as diminished species diversity. However, the SEED index would immediately identify a loss of ecological integrity if satellite imagery detected ecosystem fragmentation, even if the subsequent change of species composition was not detected yet. Given that satellite imagery provides full global coverage, the inclusion of ecosystem-level characteristics can provide an additional opportunity to improve the spatial and temporal resolution of intactness predictions.

#### 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. Building on classic correlative models of species occurrence/richness in response to climatic and physiographic properties, new models are starting to include conceptual routines that mimic species assemblage rules<sup>80</sup> and correlations in species occurrences<sup>81</sup>. In support of such models, satellite imagery offers high resolution data with global coverage and sometimes spanning multiple decades. Hybrid biodiversity models will emerge

soon that link biodiversity data with remote sensing products such as spectral diversity<sup>82</sup>, leaf traits, vegetation height, density, and other structure components. 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.

Advances in remote sensing such as hyper-spectral imaging<sup>83,84</sup> are also expected to provide valuable data to assess how plant species and functional biodiversity respond to different practices<sup>85</sup>. Overall, we gain a more complete spatial coverage from remote sensing than would be possible form field with more reliable information than extrapolating models<sup>86</sup>. Remote sensing can provide the means for both direct and indirect biodiversity monitoring<sup>87</sup>. Many trees and large animals are visible from space and may therefore be directly monitored from space, while less visible components may be indirectly monitored via the coupling of remote sensing products with biodiversity models, e.g., species distribution models.

Future on-the-ground sampling is urgently needed in under-sampled regions of the planet, in order to fill in key gaps and narrow the uncertainty in global genetic and species diversity models. The emergence of next-generation technologies – such as eDNA<sup>45,88</sup>, bioacoustics<sup>89</sup>, and camera traps – may prove to be essential for scaling data collection in a cost-effective manner<sup>90</sup>. Ultimately, large-scale monitoring of ecological integrity will undoubtedly require a combination of such ground-sourced and global-scale approaches. Incorporation of these emerging technologies into the SEED framework will continually improve the resolution of the index (currently at 1 km), allowing for more fine-scale assessments (aiming for 30 meters resolution) of biodiversity and dynamic changes over time. A core aim in the continual development and fine-tuning of the SEED index is to incorporate emerging methods and technologies, to ensure the best possible estimation of biodiversity.

## 4. Conclusion and outlook

With growing recognition for the need for political and financial mechanisms to distribute the wealth of our planet towards the local efforts that promote biodiversity, there is an urgent need for globally standardized assessments of ecological intactness. To facilitate equitable biodiversity protection, such ecological assessments must be available to everyone, everywhere. Given the

expansion of global datasets reflecting various dimensions of biodiversity across plants, microbes and animals, 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 Challenge<sup>91</sup>, and UN Sustainable Development Goals<sup>92</sup>), bring transparency to policy frameworks, and to encourage corporate accountability (under the Taskforce for Nature-related Financial Disclosures (TNFD)<sup>93</sup> and Science-Based Targets for Nature (SBTN)<sup>94</sup>).

The SEED framework consolidates the three primary dimensions of biodiversity (genetic, species and ecosystem diversity) to produce a 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 data products and scientific advancements. Here, we demonstrate that the beta release of the SEED index captures coarse scale changes in biodiversity (Figures 3,4), providing a multidimensional understanding of the state of nature at the national scale. 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 phylogenetic divergence 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 policyand decision-makers, we invite the wider scientific community to collaborate on the continual advancement of this biocomplexity index. We believe that, for this biodiversity index to lead to positive outcomes, it must accurately represent "on-the-ground" biodiversity. 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.

# Figures

a. Aerial View







Figure 1. Performance of species richness maps in human modified landscapes. The impacts of human activities – as is shown here for Paris (outline) and the surrounding landscape (a) in satellite imagery<sup>95</sup> and (b) in the human modification index<sup>46</sup> – were not included in the development of most maps of species richness, e.g., (a) plant<sup>96</sup> and (b) mammals<sup>97</sup>.



**Figure 2**. **SEED biocomplexity index.** Example visualization of the SEED framework for an area of interest, showing the dimensionality-reduced intactness scores across the nine dimensions of biodiversity. Along each axis the yellow line measures the intactness, the similarity of the current state and the potential natural state based on a comparable, minimally-disturbed ecosystem. For this area of interest, the average of these values, weighted by the quality of the data, yields the SEED biocomplexity index and indicates the total intactness of nature. Arrows trace the relationships between SEED's biodiversity dimensions and the Essential Biodiversity Variables (EBVs)<sup>14</sup>.



**Figure 3. A reference area approach to measuring intactness of seven dimensions of biodiversity.** Series of maps showing the intactness of diversity along seven of the nine biodiversity dimensions: ecosystem (a) structure, (b) connectivity, and (c) function, genetic diversity of (d) animals, and species diversity of (e) plants, (f) microbes, and (g) animals. Intactness was measured against (h) minimally impacted reference areas (colored by ecoregion<sup>75</sup>).



**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.



**Figure 5. Comparison with leading global biodiversity models.** Global showing the difference between SEED and (a) MSA<sup>65</sup>, (b) BII from NHM<sup>78</sup>, and (c) BDI, which was created independently from the BII while using the same model<sup>79</sup>.

## Supplemental information:

Document S1: Additional methods and Tables S1-2

Web-based map viewer: https://robertmcelderry.users.earthengine.app/view/seed-biocomplexityglobal-beta

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## 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. 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, TE, RMM, and IB.

#### **Declaration of interests:**

The Restor platform (Restor Eco AG) was founded by and spun 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. TCW is the President of the Council of the Restor Foundation and a member of Restor's Science Advisory Council.

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## Supplement S1

#### **Reference Area Methodology**

We developed an approach that offers a contemporary baseline which all global biodiversity maps may be evaluated. Our algorithm uses the human modification index (HMI)<sup>46</sup> and potential natural vegetation (PNV)<sup>47</sup> to create a reference area mask that delineates the relatively pristine areas on the globe. The combination of PNV classes and 846 delineated ecoregions<sup>75</sup> 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 5<sup>th</sup> and 3<sup>rd</sup> 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 the minimum of either  $P_{0.05}(HMI_{e,v})$ ,  $P_{0.03}(HMI_{e,v})$ , or 0.05. We set these criteria to focus the reference areas in relative unmodified ecoregions, while allowing a more inclusion in reference where needed, but only to the point 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.

#### **Delta calculation**

For calculating the delta value of each axis of the seed index, we use the following formula:

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

where K is the kernel,  $\delta$  is the delta parameter and D is the maximum Manhattan distance of the axis for all the pixel points. This effectively maps the highest possible distance of the layers of the

axis to the lowest kernel value of the axis possible. In this case we define this lowest kernel value as 0.001. By solving for  $\delta$  parameter as other values in the equation are known we can get the delta 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.

Table S1.	Table of scores,	weights, a	nd a de	escription	of the	criteria	guiding	our jud	lgment	in rat	ting
the quality	of information	contained v	with ea	ich map la	ayer tha	at we in	corporat	ed in S	EED.		

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.

Table S2. List of layers incorporated in SEED. See Excel file.