

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 international challenge. Here, we present the Sustainable Ecology and Economic Development (SEED) framework, which includes plants, animals, and microbes and consolidates multiple dimensions of biodiversity (genetic, species, and ecosystems) into a single measure of biocomplexity at a given location relative to a comparable, minimally-disturbed ‘reference’ ecosystem. We demonstrate the utility of the SEED framework and highlight its features using a novel measure of ecosystem structural intactness and the first-generation SEED 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

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 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 economy¹, most saliently distilled in the Kunming-Montreal Global Biodiversity Framework (GBF)². 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)³. 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 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 wellbeing⁸. 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)⁹. 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^{10,11}. 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 structure¹² and connectivity¹³. To align monitoring efforts, GEO BON has identified the Essential Biodiversity Variables (EBVs)¹⁴ and established guidelines for EBV estimation using both ground-sourced and remote-sensed data¹⁵. 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; impact, dependencies, and risk 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 the first generation of an integrative framework, 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 into 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 product 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^{16,17}. 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 Database¹⁸. While there are good insights about genetic variation for certain plant¹⁹ and animal species^{18,20,21}, 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 habitat²² leaving threatened species with low genetic diversity²³ 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 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 maps²⁴, floras²⁵, and taxonomic monographs as data sources²⁶. Generally, these observed data are interpolated or extrapolated – using either machine learning²⁷, species distribution modeling²⁸, or process-based models²⁹ – based on correlations with remotely-sensed and modeled environmental variables (e.g. temperature, precipitation, topography, geology, etc.) to generate spatially continuous models of diversity³⁰. 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 do not aim 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 species³¹ and functional diversity refers to the range and distribution of organismal traits and life history strategies across species within a system³². Because trait expression is a byproduct of evolutionary history, functional diversity is often closely related to phylogenetic diversity, 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 phylogeny³³ or a functional-trait matrix³⁴ 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)³⁵. Phylogenetic and functional richness are typically highly correlated with species richness and thus encode little additional information³⁶. By reflecting the uniformity of species in functional or phylogenetic space, evenness metrics have especially linked to ecosystem function and the biodiversity-productivity relationship³⁷. 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 species³⁸. Whereas a species-rich community may be composed of evolutionarily and functionally redundant species, other less species-rich 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.

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 function³⁷ 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^{39,40} 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^{18,20,41-43}. This is changing due to recent advances in high-throughput sequencing technologies that enable us to observe and quantify microscopic and otherwise cryptic species⁴⁴, 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, ecosystem-level metrics provide a more up-to-date view of current conditions because they are predominantly measured and modeled from satellite imagery (e.g., radar and multispectral imaging). A wealth of global-scale remote sensing products have been designed to capture information about human modifications⁴⁵, land use change⁴⁶, canopy cover⁴⁷, canopy height⁴⁸, above and belowground biomass⁴⁹, habitat heterogeneity⁵⁰, leaf area index⁵¹, ecosystem connectivity^{52,53}, net primary productivity⁵⁴ and ecological resilience^{55,56}. We group all ecosystem-level products that measure some aspect of biodiversity into one of three broad categories: ecosystem structure, function¹⁴, 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 feed back to affect the environment. These ecosystem properties provide a direct link to measures of ecosystem services^{57,58}. The three-dimensional structure of an ecosystem characterizes the environmental context in which species coexist. Structural diversity has been shown to improve ecosystem function¹² and stability⁵⁹. 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 decrease with habitat loss and

fragmentation, but both connectivity and fragmentation indices can provide unique insights into the ecological functionality at the landscape-scale⁶⁰.

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)⁶¹ by the United Nations Environment Programme World Conservation Monitoring Centre, the Biodiversity Intactness Index (BII)^{62,63} by the Natural History Museum in London, and the Mean Species Abundance (MSA)⁶⁴ 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)⁴⁵; ecosystem function is measured by the ratio of actual to potential net primary productivity⁵⁴; and ecosystem composition is measured by the BII^{62,65}. 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. 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 MSA index is conceptually similar to the BII but focuses exclusively on species abundance, includes additional human-related pressures, and estimates an average intactness value that is weighted by the fraction of each land use type that is present in each pixel.

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. All three indices are primarily based on the PREDICTS database⁶⁶, which is valuable for quantifying the impact of human disturbance on biodiversity in different regions of the globe. However, at present, the data coverage 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^{66,67}. Given that each of these different organismal groups respond differently to human disturbance and show unique global distribution patterns^{68,69}, 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 among-species level diversity and, except for the EII, do not include ecosystem level properties that emerge from the web of interactions among species and their environment. Finally, the BII and MSA both reflect the proportion of natural biodiversity rather than real values of biodiversity.

3. A framework for observing the biological complexity on Earth

With this 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 represent exciting new opportunities for our understanding of biodiversity across the planet. The development of conceptual frameworks will be essential to ingest and interpret this growing body of information to generate a holistic understanding of global biocomplexity. Our global understanding of biocomplexity will never be fully complete, as emerging scientific assessments will always 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 first generation of a holistic ecological framework (hereafter referred to as SEED). By combining datasets on the major levels of biodiversity, SEED generates both a framework for evaluating multiple dimensions of biodiversity and a globally-standardized index (ranging from zero and one) to estimate the similarity between the current state of biocomplexity of an ecosystem relative to 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.”⁷⁰ 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 main 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 BON¹⁴.

For interpretability, a single biocomplexity value can be estimated for any area of interest on a standardized scale. To aid comprehension and facilitate action-impact assessments, the SEED biocomplexity index can be separated to its primary axes of variation. A sample site can be summarized in the style of a radar plot (Figure 2), whereby the current values for each axis (yellow) are plotted alongside values for the potential natural state (white). The mean similarity between the current and potential measures 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. After combining all relevant available layers within each of the biodiversity dimensions (Figure 2), these nine axes are consolidated into a single biocomplexity index using a multivariate Gaussian kernel estimator⁷¹.

$$K(\mathbf{x}, \bar{\mathbf{x}}_r) = \exp[-\delta(\mathbf{x} - \bar{\mathbf{x}}_r)^T \mathbf{C}_r^{-1}(\mathbf{x} - \bar{\mathbf{x}}_r)] \quad (\text{Eq. 1})$$

Here \mathbf{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 Gaussian kernel, K , measures the similarity between each row of \mathbf{x} and the mean values for the reference area $\bar{\mathbf{x}}_r$, while accounting

for the covariance structure, \mathbf{C}_r , which is estimated in the reference area. At the heart of this kernel is the Mahalanobis distance, which is essentially the Euclidean distance weighted by the covariation matrix⁷². Replacing the covariation matrix in equation 1 with the identity matrix would result in a Gaussian kernel⁷². We optimized the scaling parameter, δ , to maximize the relationship between K and the HMI in each landcover-ecoregion combination (see Supplement X). This allows the biocomplexity index to measure the intactness of nature as the overall similarity between a focal and reference area when considering all biodiversity axes with equal weighting.

To avoid weighting any one dimension of biocomplexity over another, we give equal weight to each of the nine biodiversity axes by scaling them to range from zero to one. First, we ensure equitability among all species within each taxonomic group, i.e., plants, animals, and microbes. That is, each species counts as one regardless of size, rarity, or charisma. We then transform genetic, phylogenetic, functional, and species diversity) using the natural logarithm and divide by the global maximum value. Genetic, phylogenetic, functional, and species diversity are all positive valued metrics, whereby higher values indicate higher biodiversity. Scaling in this way converts the range to zero (no species present) and one (the global maximum estimated diversity) in each group. One key result from this is that plants, animals, and microbes are equitable as opposed to the 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.

Ecosystem level dimensions require a different approach than the genetic- and species- level datasets because the contributing variables have non-uniform properties, which prevents simple addition or averaging of layers. Not only do these variables differ in magnitude and range, but they also may align along entirely different scales, whereby higher values could have opposing implications in different regions. Ecosystem structure, for example, is currently composed of six metrics: forest canopy cover⁴⁷, vegetation height⁴⁸, leaf area index⁵¹, above and belowground biomass⁴⁹, and habitat heterogeneity⁵⁰. We expect differences in canopy cover, height, and LAI between forest and non-forest cover classes. A useful measure of structure will characterize the unique combination of features that distinguish different land cover classes. We therefore scale all ecosystem variables to range from zero to one, then calculate the similarity to the reference area

using Equation 1. Ecosystem structure in the reference area defines the target values for each component metric, against which the values at each site are compared. While the average value can still be informative (see Figure 3), similar average values may falsely indicate similarity in cases where the underlying values of different metrics counterbalance each other.

3.2. Reference area versus a counterfactual landscape

Measuring the level of biocomplexity intactness 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 Hemisphere⁷³. 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 estimate⁷⁴.

Specifically, we developed an algorithm that uses the HMI⁴⁵, land-cover⁴⁶, and potential natural vegetation (PNV)⁴⁶ to select reference areas for each land-cover type within each of the 846 delineated ecoregions⁷⁵ 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 the fifth percentile of HMI scores as an upper limit (Figure 3.a). This threshold is set just high enough to ensure a sufficiently large area, enabling representative and robust estimates (Figure 3.a). This *least-impacted area* serves as the reference area for all areas of the same land cover type within that ecoregion (e.g., Figure 3.b,d). All artificial land use classes in the land-use/land-cover map are updated with the predicted land cover from the PNV (Figure 3.c). All comparisons for the biocomplexity index are then guided by the land cover class of the focal and reference area within each 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 landscape⁷⁶. 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 practices¹⁴.

3.3. Illustration of the SEED biocomplexity framework

The first generation of this biocomplexity index was developed using a comprehensive list of the most up-to-date maps of genetic, species, and ecosystem diversity. To illustrate the capabilities of the framework, we first show the viability of our dimensionality reduction calculation and reference area approach using ecosystem structure as an example. We then analyze the biocomplexity index using the available layers for ecosystem structure, ecosystem function, plant diversity⁷⁷, and animal diversity⁷⁸ (see Section 2). Currently, most genetic, phylogenetic, and functional diversity maps are too coarse and unrepresentative of the true conditions on the landscape for us to include. To account for the fact that species diversity maps do not explicitly incorporate the effects of human impact (Figure 1), we scaled the available measures of plant and animal diversity by the MSA intactness index. We then compare this prototype with other biodiversity estimators (EII, BII, and MSA) and provide an analysis of Gabon as a case study. These comparisons serve as a calibration of divergent patterns between the SEED index and other measures of biodiversity intactness (see section 2.4).

Based on our dimensional reduction calculation and reference area approach, we find that 17% of the earth's terrestrial land area remains relatively intact (i.e., in the lower fifth percentile of HMI per land cover class and ecoregion). According to our reference area algorithm, a large majority of this unmodified land area lies in the northern boreal and tundra biomes (Figure 3.a & S2). Using the ecosystem structure values for these reference areas for each land cover in each ecoregion, we estimate the intactness of every terrestrial pixel (e.g., Figure 3.b and 3.d). Similar to other intactness/integrity measures, our analysis identifies area of notably low structural intactness in a

narrow band across the savannas of sub-Saharan West Africa and in previously forested areas in northern India, Eastern China, and the Midwestern United States (Figure 3.e).

The Saharan and Saudi Arabian deserts stand out as highly intact landscapes (Figure 3.e) despite also having low ecosystem structure on average (Figure 3.f). This important distinction illustrates the difference between a quantity and its intactness, defined as the similarity between observed and reference quantities. It is important to have both measures available to distinguish sites that have high quantity values from sites with high intactness values. On average, ecosystem structure is high in forests, low in grasslands, and intermediate in savannas and shrublands (Figure 3.f). Within shrublands, ecosystem structure values are bimodally distributed, potentially reflecting open and closed shrublands.

The value in our biocomplexity framework lies in its ability to integrate multiple dimensions of diversity. Even with only four dimensions (plant and animal diversity, ecosystem structure and function) of our target of nine dimensions included in this version of SEED, the index offers a more comprehensive view of nature's state than existing indices (Figure 4.a). Incorporating these dimensions of biodiversity into the SEED index leads to several notable differences in global patterns, relative to indices that reflect ecosystem or compositional intactness. Specifically, our index appears to be more conservative than MSA and BII (waiting for EII comparison). SEED was systematically lower than BII and diverged from MSA in a less predictable manner (i.e., producing higher or lower estimates; Figure 4.b). The distribution of MSA values is bimodal compared with the unimodal BII and the intermediate SEED index (Figure S1, S3). This means that MSA may more commonly characterize an ecosystem as 'pristine' or 'highly degraded', while SEED would more commonly characterize the same ecosystem as 'moderately intact'.

At its core, SEED is an intactness index, which aims to detect changes in biocomplexity intactness on a standardized scale across the globe. However, 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 compositional diversity for a subset

of taxa, and the EII adds only net primary productivity and HMI compositional intactness. 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.

Box 1. Case study of SEED Biocomplexity in Gabon

To demonstrate the current utility of the SEED index, we illustrate emergent properties of biocomplexity for Gabon. Gabon is a global leader in the exploration of financial and policy mechanisms that incentivize sustainable forest management and nature conservation⁷⁹. Our analysis shows that urban/built-up areas score lowest overall, followed by grasslands and savannas, which both exist mostly in either a degraded state (i.e., with a peak at low SEED index) or a relatively intact state (Figure 4.d). Forests and wetlands showed similar bimodalities, but sites in these cover classes more commonly scored as relatively intact (Figure 4.d). Shrublands exhibit a range of intactness values, but they are most commonly in a degraded state. These findings are in line with reported patterns in biodiversity and levels of human modification. For example, the bimodality in forests and wetlands could result from regulations protecting a majority of Gabonese forests and resulting in high intactness values, while a fraction has been converted to palm-oil plantations^{80,81} with low intactness. Similarly, a large proportion of wetlands are close to the coast where they are susceptible to human degradation, while the rest may consist of more intact flooded forests and grassland⁸².

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 rules⁸³ and correlations in species occurrences⁸⁴. 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 diversity⁸⁵, 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^{86,87} are also expected to provide valuable data to assess how plant species and functional biodiversity respond to different practices⁸⁸. Overall, we gain a more complete spatial coverage from remote sensing than would be possible from field with more reliable information than extrapolating models⁸⁹. Remote sensing can provide the means for both direct and indirect biodiversity monitoring⁹⁰. 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^{44,92}, bioacoustics⁹³, and camera traps – may prove to be essential for scaling data collection in a cost-effective manner⁹⁴. 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

Any political and financial mechanisms to distribute the wealth of our planet towards the local efforts that promote biodiversity depend fundamentally on the ability to measure the integrity of ecological systems across the globe. As policy frameworks and markets are developed to promote and protect biodiversity, there is a growing need for a holistic assessment of the state of nature and ecological impacts of human activity across the globe. Such an integrative metric is needed to evaluate progress toward climate change and land protection pledges (e.g. the GBF, Bonn Challenge⁹⁵, and UN Sustainable Development Goals⁹⁶), bring transparency to policy frameworks, and to encourage corporate accountability (under the Taskforce for Nature-related Financial Disclosures (TNFD)⁹⁷ and Science-Based Targets for Nature (SBTN)⁹⁸).

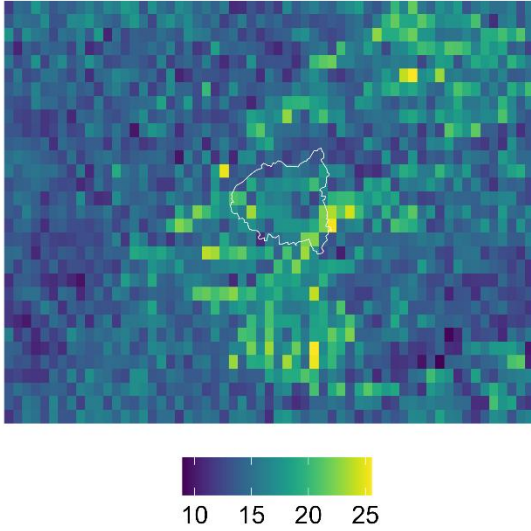
The SEED framework consolidates the three primary dimensions of biodiversity (genetic, species and ecosystem diversity) to produce a standardized and comprehensible measure of biocomplexity. This framework is fundamentally collaborative, incorporating biodiversity assessments and models from biodiversity experts across the globe, and 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 first generation of the SEED index captures coarse scale changes in biodiversity (Figure 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 policy- and 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

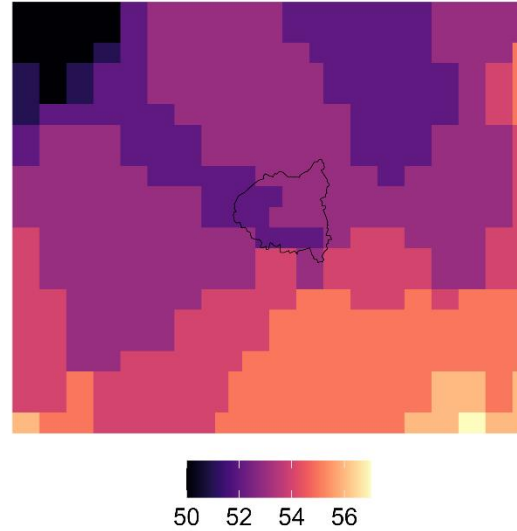
experts, including ecologists, remote-sensing specialists, and others from around the globe. Leveraging the latest scientific and technological breakthroughs, we aim to enhance and refine the biocomplexity index, thus fostering better outcomes for ecosystem protection and restoration.

Figures

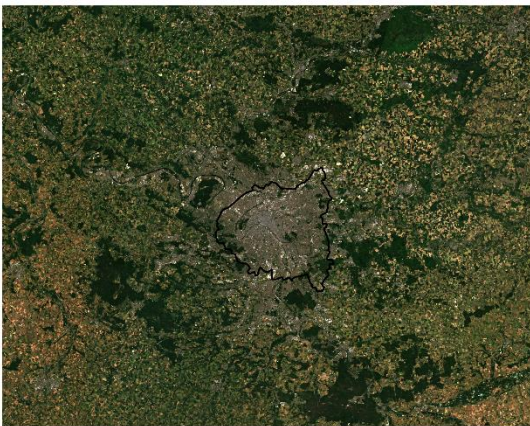
a) Plant Richness



b) Mammal Richness



c) Aerial View



d) Human Modification Index

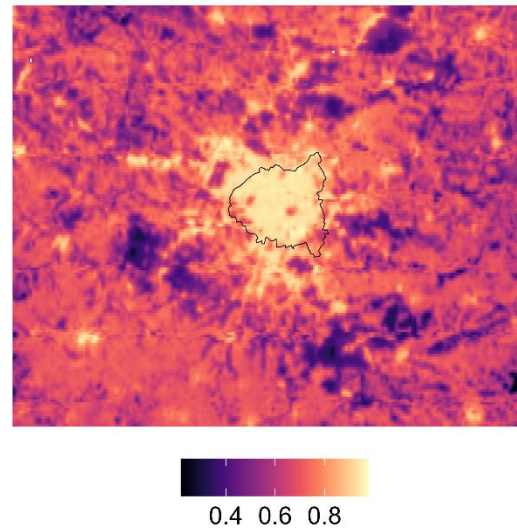


Figure 1. Performance of species richness maps in human modified landscapes. This figure illustrates how maps of species richness, e.g., (a) plant⁷⁷ and (b) mammals⁷⁸, may not reflect the true impacts of humans, which can be seen here in (c) the aerial view from Sentinel-2⁹⁹ and (d) the human modification index⁴⁵. These maps all focus on Paris (outline) and the surrounding landscape.

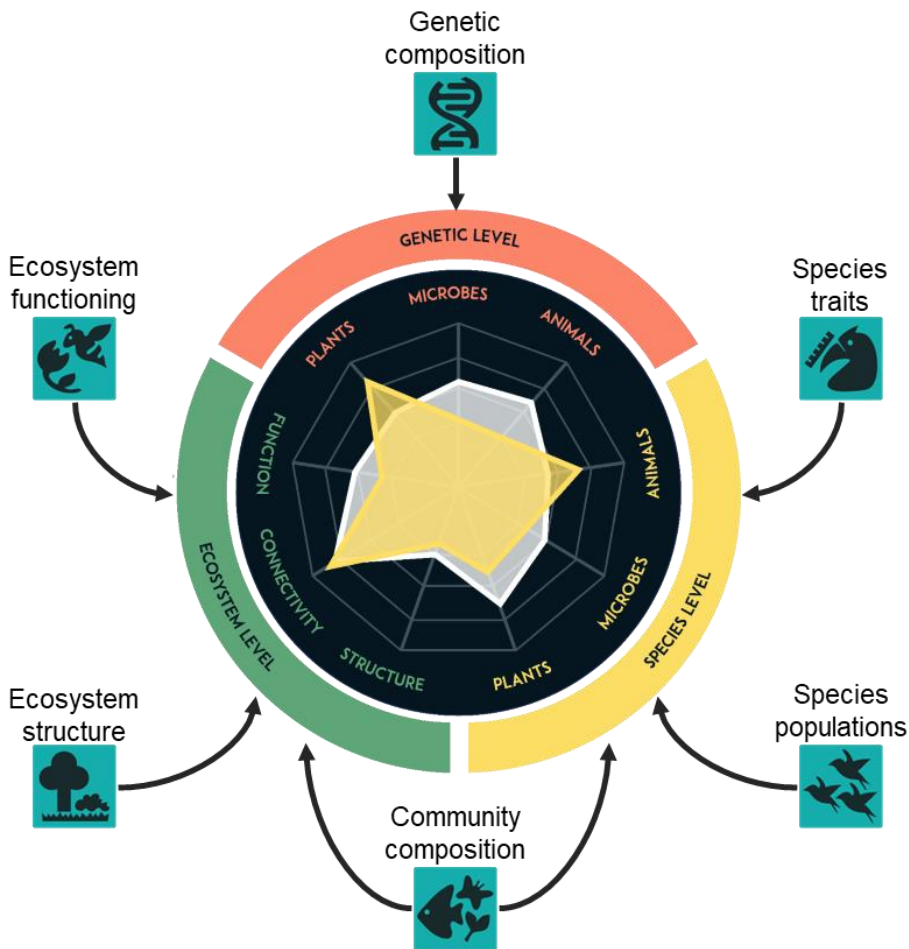


Figure 2. SEED biocomplexity index. Example visualization of the SEED framework for an area of interest, showing the dimensionality-reduced values across three axes for each of the three scales of variation (genetic, species, and ecosystems). For each axis, the visualization shows the difference between the current state (yellow), and the potential natural state based on a comparable, minimally-disturbed ecosystem (white). The distance between the current and potential measures creates a score – the SEED biocomplexity index. Arrows indicate the relationships between the three scales of variation and the Essential Biodiversity Variables (EBVs)¹⁴.

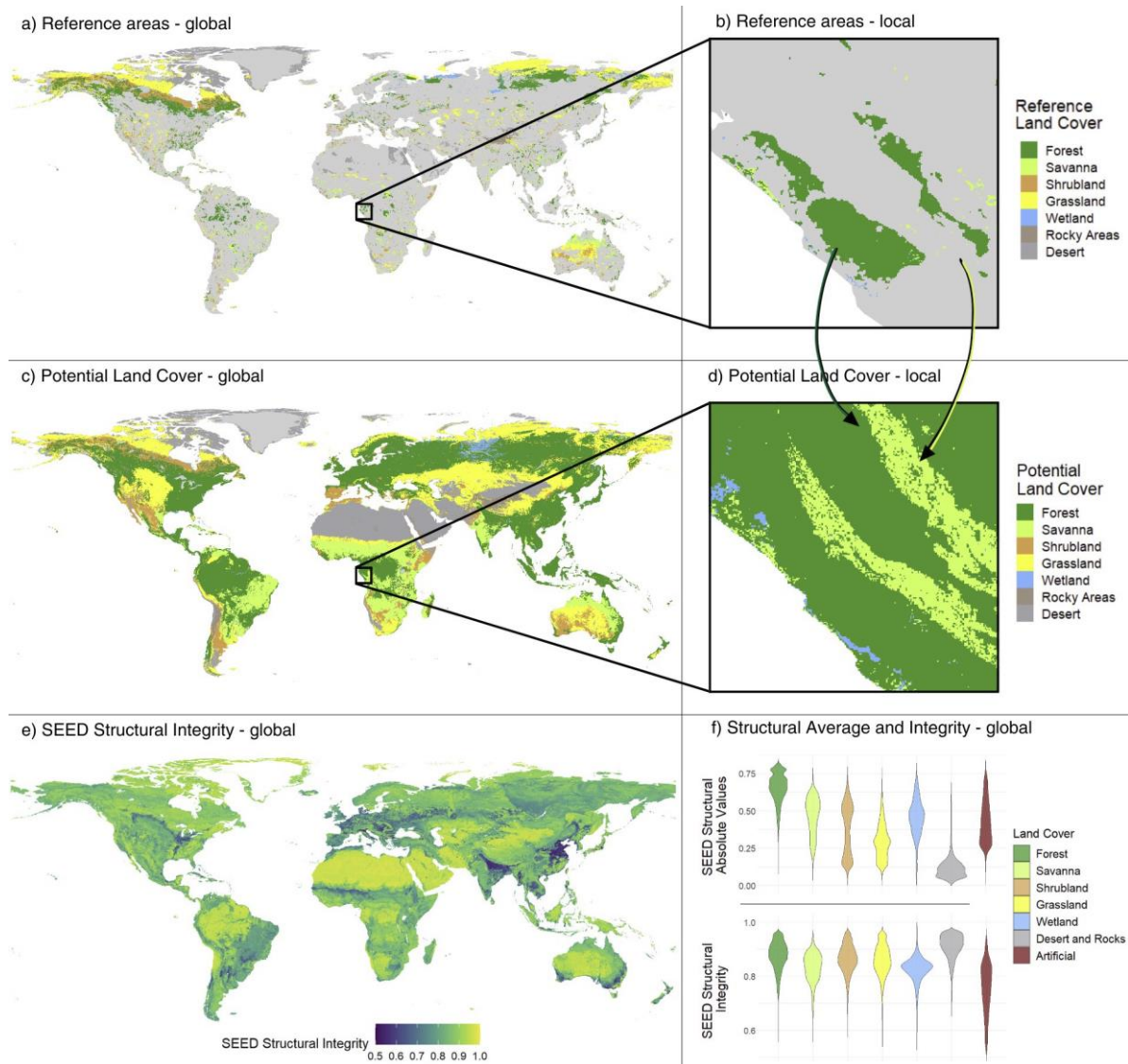


Figure 3. Assessing the potential state of ecosystems through the identification of relevant reference areas. a) and b) Reference areas representing the 5% least disturbed areas within each combination of ecoregion and land cover type. c) Potential land cover obtained from⁴⁶, substituting artificial ecosystems with the potential layer from the same study. The artificial class is composed of plantations, arable land, pasture, urban areas, and rural gardens. d) Potential land cover types at a local scale in Gabon, indicating which reference areas from (b) are used to calculate biodiversity values for those areas. e) Ecosystem structural intactness, obtained by comparing ecosystems with their reference. Structural components include canopy height, homogeneity, LAI, and forest cover, above-ground, and below-ground biomass. f) Violin plots of SEED structural absolute values and intactness across different land-use categories.

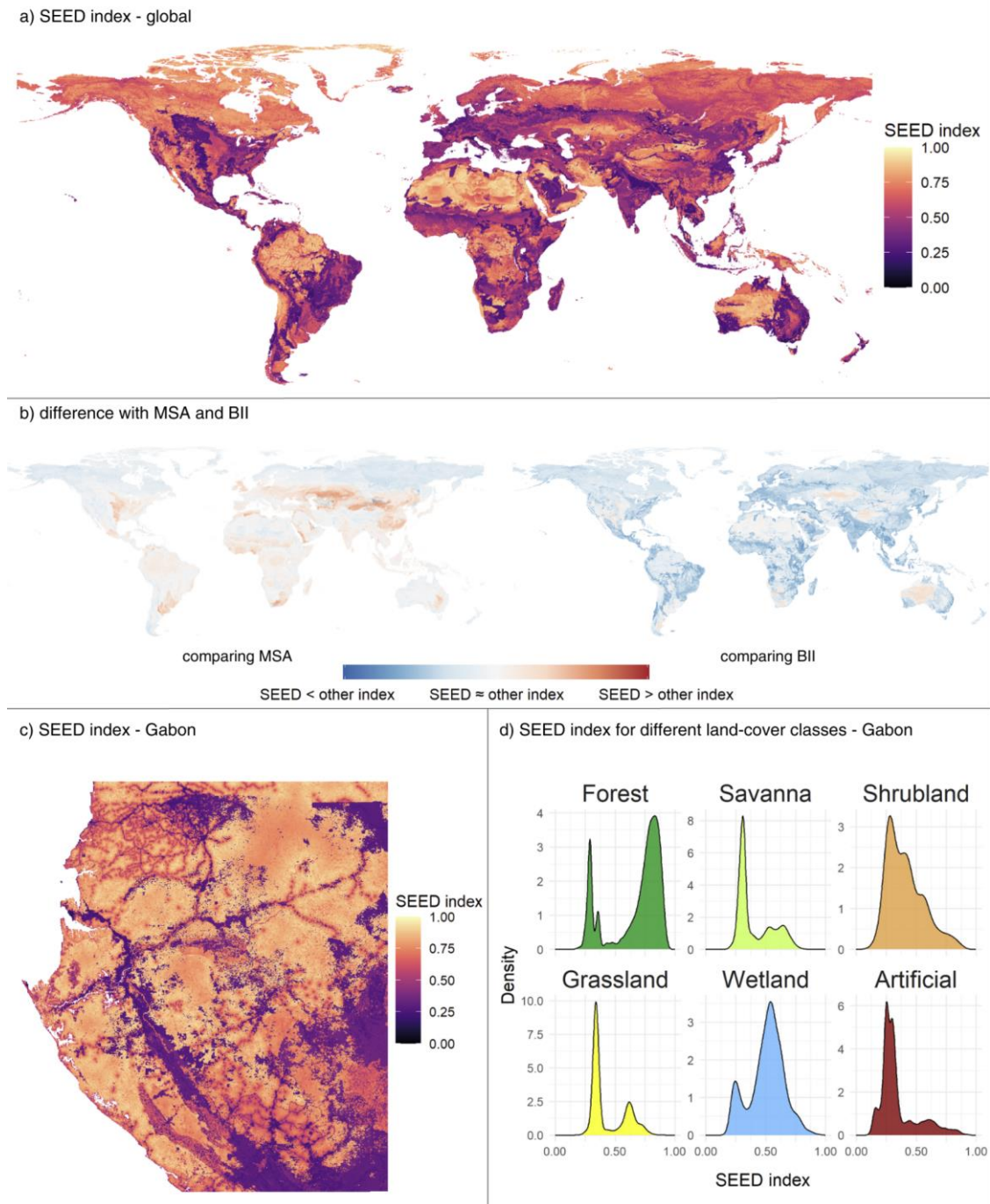


Figure 4. Comparative analysis of the SEED Index. a) Global representation of the SEED index. b) Comparisons between the SEED index and MSA (left) or BII (right). c) The SEED index in the country of Gabon and surrounding areas. d) SEED index densities across six land cover classes in Gabon. The artificial class is composed of plantations, arable land, pasture, urban areas, and rural gardens.

Supplemental information:

Document S1: Figures S1-4

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Author contributions:

This work was conceptualized by TWC, DM, JvdH, TE, RMM, and CFL. RMM, CFL, TWC, and JvdH developed the methodology and CFL, RMM, JvdH composed the software. Data curation, formal analyses, and validation were performed by CFL and RMM with assistance from 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, except Figure 2 was created by RM and IB. 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.

Declaration of Generative AI and AI-assisted technologies in the writing process:

During the preparation of this work the author CFL used ChatGPT to improve readability and language during the first steps of the draft. After using this tool, the authors completely rewrote all this content and take full responsibility for the content of the publication.

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Supplementary Figures

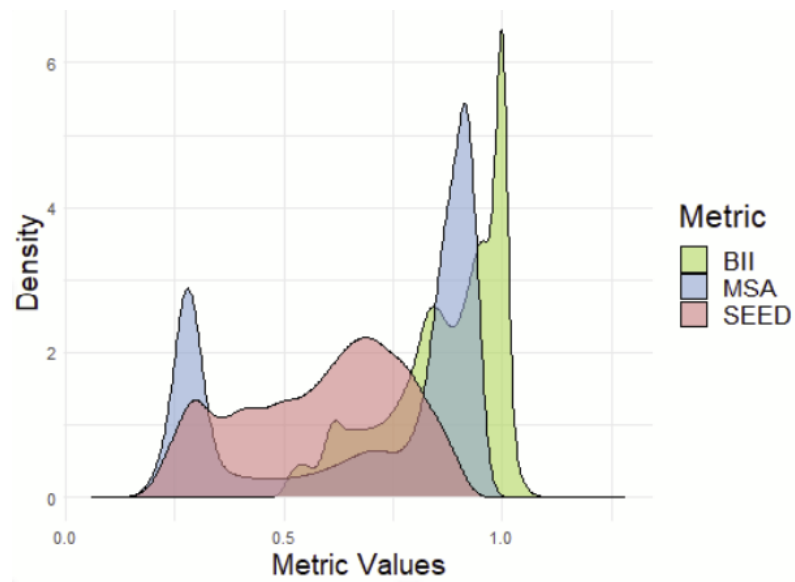


Figure S1. Density plot displaying the distribution of the first generation of the SEED index in relation to MSA and BII at a global scale.

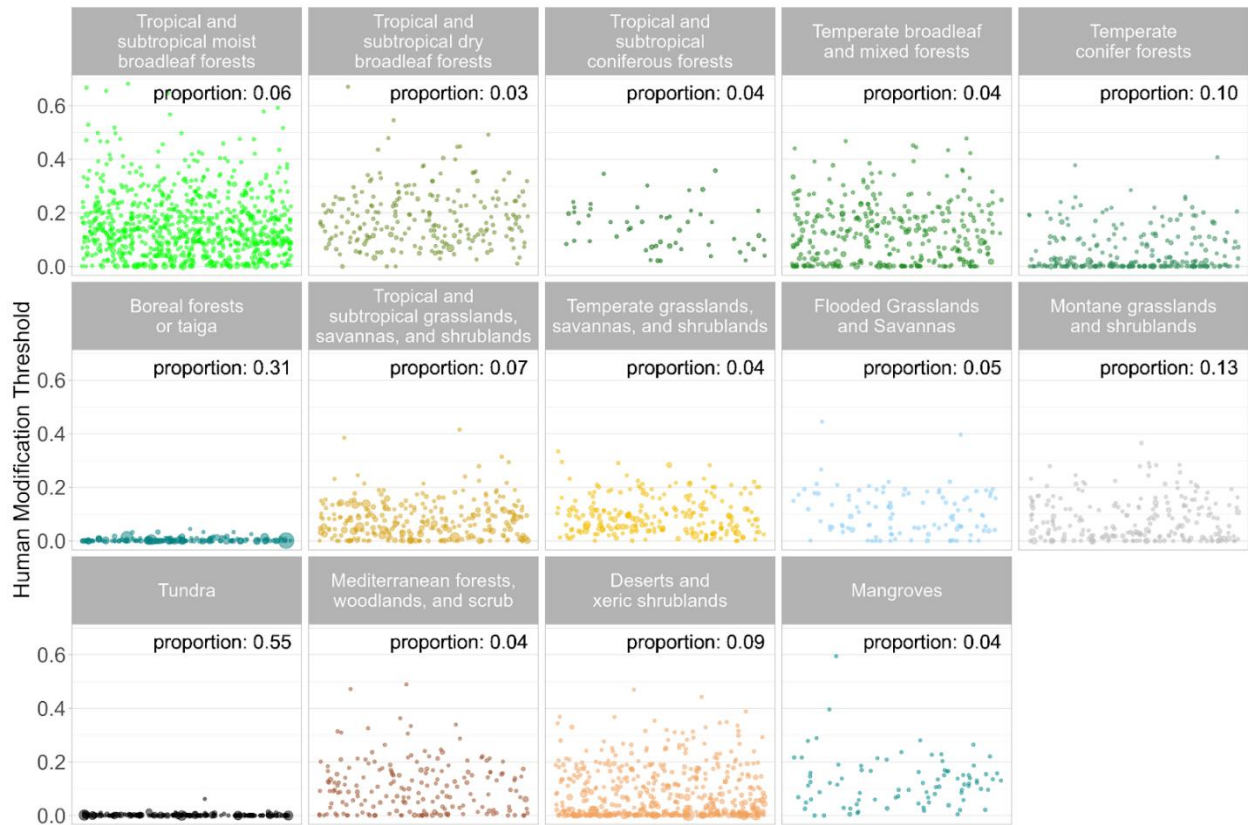
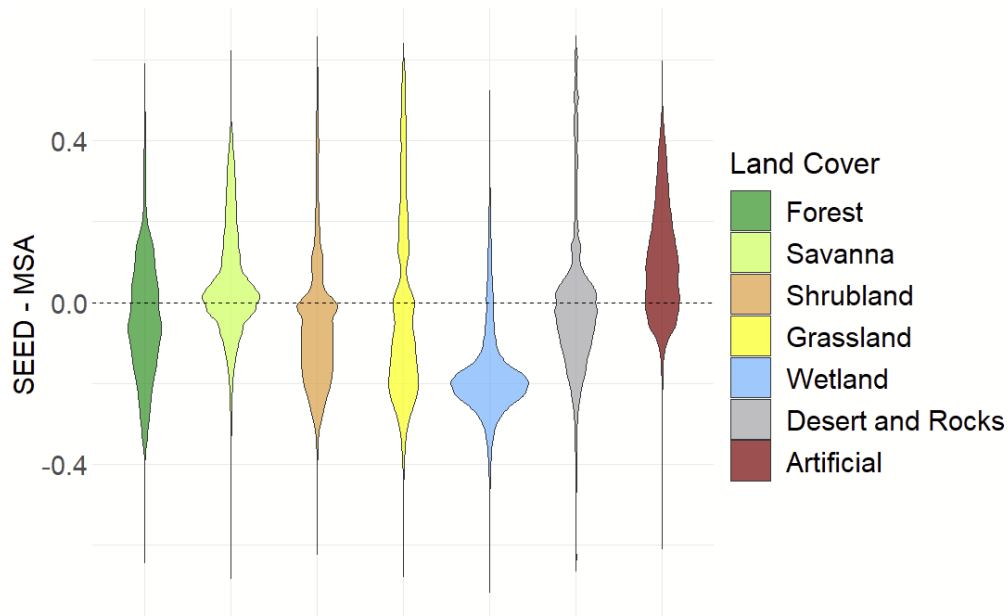


Figure S2. Distribution of human modification index (HMI) thresholds identified in the reference area approach, for each combination of land-cover and ecoregion, summarized for each biome⁷⁵. The proportion of land identified as a reference in each biome compared to the total area is plotted on the top-right. In very intact areas, the HMI may be close to zero in most of its extent, resulting in more than 5% of the area being considered as a reference. In boreal forests and tundra, which are largely unmodified biomes, 31% and 55% of their respective areas will serve as reference points.

a)



b)

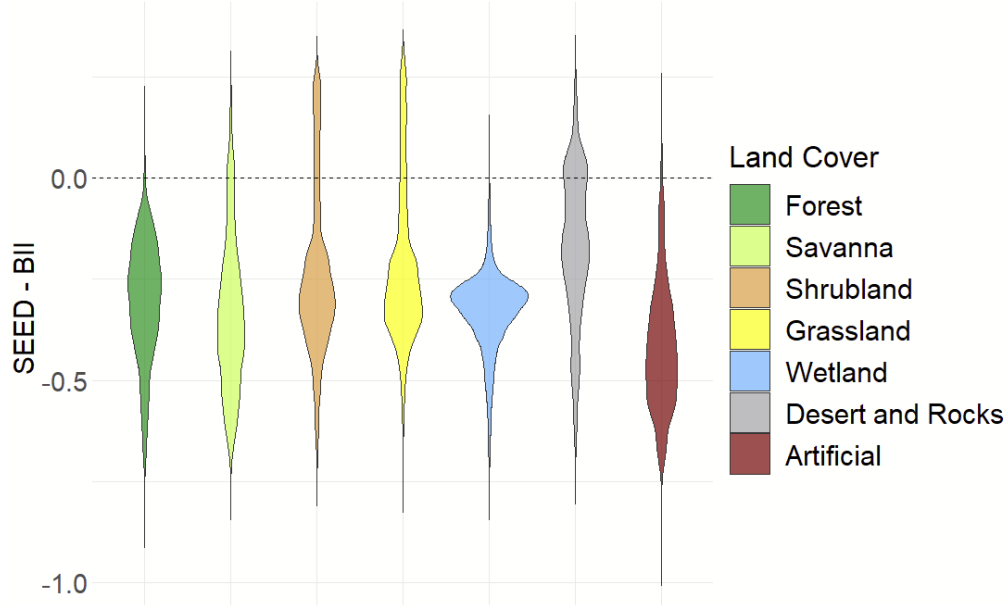


Figure S3. Violin plots illustrating the distribution of differences between the first generation of the SEED index and a) MSA, and b) BII, across different land-cover classes.

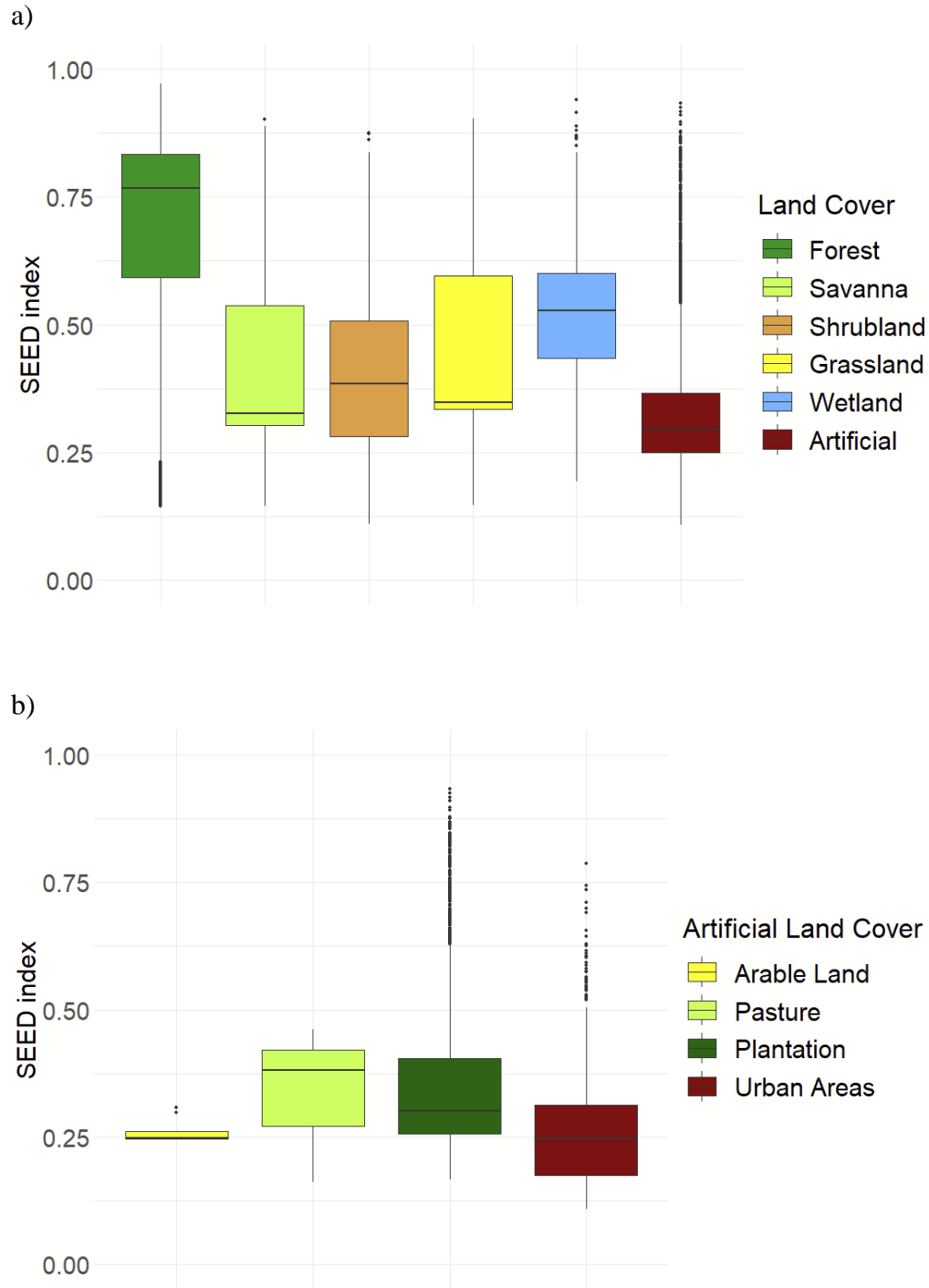


Figure S4. Boxplots illustrating the distribution of the first generation of the SEED index: a) across different land-cover classes in the Gabon region, and b) specifically within different artificial land-cover classes.