

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 biocomplexity.
3. We define a globally standardized measure of the state and intactness of nature.
4. Inclusion of microbes, fungi 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 full 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 for biodiversity monitoring efforts. Here, we present the Sustainable Ecology and Economic Development (SEED) framework, which consolidates multiple dimensions of biodiversity into a single measure of biocomplexity as a holistic estimate of the current state of nature at a given location. The SEED framework continuously integrates state-of-the-art datasets and maps of the biological variation in plants, microbes, animals, and ecosystems to estimate the local biocomplexity across the planet relative to a comparable, minimally-disturbed ‘reference’ ecosystem. The SEED framework allows an assessment of ecological health in response to positive and negative human impacts, and informs 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
MSA	Mean Species Abundance
EBV	Essential Biodiversity Variable
EII	Ecosystem Integrity Index
BII	Biodiversity Intactness Index
IUCN	International Union for Conservation of Nature
GBF	Kunming-Montreal Global Biodiversity Framework
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. A system that effectively monitors changes in biodiversity over time is required to meet numerous prominent targets in the GBF, including 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). The role of business and financial sectors is also addressed in the GBF, which 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 that have the potential to promote biodiversity, it is critical that we learn from the challenges of the past. Mechanisms that value any single aspect of nature – such as carbon sequestration – risk driving the oversimplification of the system³⁻⁶. This can lead to potentially counterproductive outcomes, like the creation of monocultures of exotic tree species at the expense of local biodiversity⁶ and wellbeing⁷. 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 complexity 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)⁸. 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^{9,10}. 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 structure¹¹ and connectivity¹². 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 the three primary dimensions of biodiversity – genetics, species, and ecosystems – into a measure of biocomplexity to evaluate the state of nature for 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. (Challenge framing) Current state of global biodiversity mapping

Spatially-explicit biodiversity data products generally fall into four main categories: genetic (within-species) diversity, species (among-species) diversity, ecosystem diversity, and intactness. Genetic and species diversity metrics measure the diversity of within and among biological organisms, whereas ecosystem diversity metrics quantify ecosystem properties such as productivity, vegetation cover, biomass, or habitat heterogeneity. Intactness, sometimes called integrity, measures the similarity of an area to an estimate of how it would look if it were not affected by humans. We review the benefits and shortcomings of each of these biodiversity data products before proposing a framework to synthesize and build upon these to provide a holistic measure that includes multiple dimensions of biodiversity.

2.1 Genetic and functional diversity

Genetic diversity (heritable variation) represents variation in the genetic composition of individuals within a species and is the source for adaptive responses to environmental change^{13,14}. Functional diversity refers to the range and distribution of organismal traits and life history strategies across species within a system. Because trait expression is a byproduct of evolutionary history, functional diversity is often closely related to genetic diversity, but can deviate substantially due to processes such as convergent evolution. Functional diversity is therefore more directly linked to ecosystem function, elemental cycling rates, resilience, and stability than genetic variation per se.

While there are currently good insights about genetic and functional variation for some plant and animal species¹⁵, we lack global predictions about genetic/functional variation within most of the ~1 trillion species on the planet¹⁶⁻¹⁹. At best, one could use the estimates of effective population size to generate a proxy measure of genetic richness, 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. Given these data limitations, we focus our discussion on existing measures of phylogenetic and functional divergence, represented by among-species metrics, which are more widely available.

Phylogenetic (i.e., evolutionary) and functional novelty give rise to variety in the form or function of a natural community. Whereas a species-rich community may be composed of evolutionarily and functionally redundant species, highlighting those communities with particularly rich evolutionary roots and functional traits is key for a holistic measure of biodiversity. Phylogenetic and functional diversity metrics therefore combine information about both species composition and genetic/trait expression. The list of species present at each locality are coupled with a phylogeny²⁰ or a functional-trait matrix²¹ to provide information about functional and phylogenetic components of diversity, or even ecosystem services²². There are numerous functional and phylogenetic diversity metrics, each measuring a different aspect of evolutionary or trait space, but these are generally categorized into three groups based on whether they capture: richness (or spread), divergence (or uniqueness), and evenness (or regularity/uniformity). Phylogenetic and functional

richness are typically highly correlated with species richness, and generally encode relatively little additional information. Divergence on the other hand, indicative of the evolutionary or functional differences among species, is largely independent of species richness and quantifies the redundancy of species. By reflecting the uniformity of species in functional or phylogenetic space, evenness metrics have especially linked to ecosystem function and the biodiversity-productivity relationship²³.

2.2 Species diversity

A large part of the explosion in global biodiversity research has focused on modeling species richness (the number of unique taxa) across plant, microbial and animal 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. A common theme is that observed data are interpolated or extrapolated – using either machine learning²⁷, species distribution modeling²⁸, or process-based models²⁹ – according to correlations with remotely-sensed and modeled environmental variables (e.g. temperature, precipitation, topography, geology, etc.)³⁰.

2.3 Global estimates of diversity

While global species diversity maps 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. While the predominance of modeled environmental variables—and general lack of human influences—in the construction of these maps results in high predictive accuracy of diversity patterns across environmental gradients, this also 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 often exclude remote-sensed information that can help reveal ecosystem and habitat structure, which are well known to indicate and be influenced by local species composition²³. These maps of species diversity and phylogenetic/functional divergence have improved our understanding of global biodiversity

patterns but, critically, they do not 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 generally over-represent some regions and under-represent other regions, due to disparities in financing and accessibility, which often drive a bias toward developed nations. 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 vast majority of animal species. In addition, microbes represent 88% to 99% of all species on Earth^{31,32} 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 maps³³⁻³⁷. This is changing due to recent advances in high-throughput sequencing technologies that enable us to observe and quantify microscopic and otherwise cryptic species³⁸, and the availability of microbial biodiversity maps is expanding exponentially.

Finally, maps of species diversity and phylogenetic/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 time frame 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 generally 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.

2.4 Ecosystem diversity

In contrast to genetic and species diversity, 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 variety of products exist, including maps of human

modifications, land use and land cover, tree cover, canopy height, above and belowground biomass, habitat heterogeneity, leaf area index, and net primary productivity, for which satellite imagery are the primary inputs. We focus on the subset of these products that measure some aspect of biodiversity, i.e., ecosystem structure, function³⁹, and connectivity^{40,41}.

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 both living organisms and their environment. These ecosystem properties provide a direct link to measures of ecosystem services^{42,43}.

The three-dimensional structure of an ecosystem characterizes the environmental context in which species coexist. Structural diversity has been shown to improve ecosystem function¹¹ and stability⁴⁴. 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, 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 between nodes.

2.4. Ecosystem intactness

Given the challenges of capturing dynamic changes in diversity at a global scale, a widely used proxy is the degree to which the current landscape resembles the potential natural state. The two most prominent of these so-called intactness metrics are the Ecosystem Integrity Index (EII) by the United Nations Environment Programme World Conservation Monitoring Centre⁴⁵, and the Mean Species Abundance (MSA) metric by the Netherlands Environmental Assessment Agency⁴⁶.

The EII includes three components: structure, function, and composition. Ecosystem structure is based on the human modification index (HMI)⁴⁷; ecosystem function is measured by the ratio of actual to potential net primary productivity⁴⁸; and ecosystem composition is measured by the Biodiversity Intactness Index (BII)⁴⁹. The BII estimates the intactness of a community of plants,

vertebrates, and relatively few invertebrates by scaling species richness and community abundance according to the impacts of land use, land use intensity, human population density, and distance to roads. For a given location, the EII uses the lowest score of the three components. The MSA metric is conceptually similar to the BII, but estimates an average intactness value that is weighted by the fraction of each land use type per pixel.

The MSA and EII represent the current state-of-the-art in global biodiversity modeling. Yet, there are several aspects of diversity that these metrics do not capture that are critical components of biodiversity. First, both metrics are primarily based on the PREDICTS database^{50,51}, which is valuable for quantifying the impact of human disturbance on biodiversity, but under-represents several large taxonomic groups including non-vascular plants, invertebrate animals, and microbes. Each of these groups respond differently to human disturbance and show unique global distribution patterns^{52,53} (Liu 2020, Prober 2014). The underrepresentation of these important taxa may therefore bias global biodiversity assessments. Second, it is difficult to know how impacts may differ by region, given uneven data availability among regions. While global patterns are critical for making standardized assessments, there are some contexts in which region- and taxon-specific models may be more appropriate. Third, BII and MSA are measures of the proportion of natural biodiversity rather than absolute values of biodiversity. A quantification of biodiversity such as species composition would be a useful input for other models such as phylogenetic and functional divergence, but this is not extractable from either intactness metric. Even with these caveats, these are currently the best metrics available for realistic biodiversity estimates, and new versions with additional features are in development.

3. (Solution) A framework for observing the biological complexity on Earth

A truly integrative and holistic measure of biodiversity that is globally relevant and locally accurate will require a wealth of information, and it will never be fully complete, as emerging scientific assessments will continue to generate more information. However, 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 yet comprehensible framework (hereafter referred to as SEED) that generates a globally-standardized index between 0 and 1 and represents the similarity between the current state

of biocomplexity of an ecosystem relative to its native state. This quantitative framework can be used to estimate both current biocomplexity in the real landscape, and potential biocomplexity according to reference areas where nature has only been subjected to minimal human disturbance.

Our biocomplexity metric 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, and ecosystems (Figure 2). Within the (phylo)genetic and species levels of variation, we distinguish three primary taxonomic groups: animals, plants, and microbes (bacteria and fungi). Within ecosystems, we distinguish structure, function, and connectivity. These axes could represent or incorporate components already identified as Essential Biodiversity Variables (EBVs) in the GEO BON framework³⁹.

For simplicity, 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 0 and 1, where 0 represents a complete absence of biocomplexity (e.g. an open pit mine or paved area), and 1 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 Gaussian kernel estimator.

$$K(X_f, X_r) = \exp \left[-\frac{\|X_f - X_r\|^2}{2\sigma^2} \right] \quad (\text{Eq. 1})$$

The Gaussian kernel, K , is used in machine learning classification algorithms and is a nonlinear transformation of the Euclidean distance, $\left\|X_f - X_r\right\|^2$ that measures the similarity between values for the focal area, X_f , and the reference area, X_r . The tuning parameter, σ , allows user control of the distance-similarity relationship. We explored various values of σ and settled on $\sigma^2 = 0.2$ to produce a final index that is near zero in highly degraded landscapes ($HMI \cong 1$) and near one in minimally impacted landscapes (Figure S1). This allows the index to represent a complete range of habitat degradation over the globe. Thus, the biocomplexity value measures the intactness of nature as the average intactness among nine biodiversity dimensions with equal weighting.

So as not to award importance to one dimension over another, we give equal weight to each of the nine biodiversity dimensions by scaling them to range from zero to one. First, we ensure equitability among all species within each taxonomic group, i.e., animals, plants, and fungi/microbes. That is, each species counts as one regardless of size, rarity, or charisma. Then, we divide the total species richness (or phylogenetic/functional divergence) by its global maximum value. Species richness, phylogenetic and functional divergence are all positive valued metrics, whereby higher values indicate higher biodiversity. Scaling in this way converts the range to zero (no species present, or no divergence) and one (the global maximum estimated richness/divergence) in each group. One key result from this is that animals, plants, 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 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 different scales, whereby higher values may or may not be ideal for a given location. Ecosystem structure, for example, is currently composed of six metrics: forest canopy cover⁵⁴, vegetation height⁵⁵, leaf area index⁵⁶, above and belowground biomass⁵⁷, and habitat heterogeneity⁵⁸. 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 using Equation 1, rather than calculating the average. While the average value can still be informative (see Figure 3), similar mean focal and reference values may falsely be obtained if the values of each layer counterbalance each other.

3.2. Reference area versus a counterfactual landscape

Measuring the level of biocomplexity degradation 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 lack ‘pristine’ potential states, such as large regions of the Northern Hemisphere⁵⁹. Thus, we opt for a more direct approach than estimating a potential natural state for all biodiversity dimensions and underlying layers. Specifically, 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 estimate⁶⁰. To ensure ecologically relevant comparisons, we developed an algorithm that uses the 846 delineated ecoregions⁶¹, the HMI⁴⁷, a map of land-cover⁶², and a map of potential natural vegetation (PNV)⁶² to select reference areas for each land-cover type within each ecoregion. 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 disturbance is not a universal goal, this minimal-disturbance baseline is the most appropriate benchmark for measuring the state of nature. We fully acknowledge that 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 landscape⁶³. 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 practices³⁹.

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 phylogenetic, 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 diversity⁶⁴, and animal diversity⁶⁵ (see Section 2). 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 animal and plant diversity by the Mean Species Abundance intactness metric. We then compare this prototype with other biodiversity estimators (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 biodiversity estimates that are based on 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. A large majority of this unmodified land area – according to our reference area algorithm – 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 integrity of every terrestrial pixel (e.g., Figure 3.b and 3.d). In analyzing the integrity of ecosystem structure alone, we show some features similar to other intactness/integrity measures. Notable areas of low structural integrity include a narrow band across the savannas of sub-Saharan West Africa and 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 very low ecosystem structure on average (Figure 3.f). This important distinction illustrates the difference between quantity and integrity, defined as the ratio 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 integrity 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 (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 metrics (Figure 4.a). Incorporating these dimensions of biodiversity into the SEED index leads to several notable differences in global patterns, relative to metrics based on ecosystem intactness. Specifically, our index appears to be more conservative than MSA and BII. SEED was systematically lower than BII and diverged from MSA in a less predictable manner (i.e., generally producing higher or lower estimates; Figure 4.b). The distribution of MSA values is bimodal compared with the unimodal BII and the somewhat 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'.

The differences between SEED and the other metrics may arise from the inclusion of both structural and functional ecosystem attributes. Both the MSA and BII represent the intactness of species diversity and do not include ecosystem level measures. Degradation according to MSA and BII is therefore characterized as diminished species diversity. However, diminished diversity may occur in an area that possesses considerable structural integrity or productivity, leading to a moderate rating on the SEED index.

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 conservation⁶⁶. 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^{67,68} 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 grassland⁶⁹.

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 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, species-area relationships, and successional dynamics (including recovery and degradation type responses). 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, 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 new 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 analysis are also expected to provide valuable data to assess how plant species and functional biodiversity respond to different practices⁷⁰. Indeed, remote sensing capabilities will soon be extended with the deployment of hyperspectral satellites, such as the Surface Biology and Geomorphology (SBG) satellite by NASA⁷¹ (launching in 2027) and the Copernicus Hyperspectral Imaging Mission for the Environment (CHIME) satellite by the European Space Agency⁷² (launching in 2028).

Future on-the-ground sampling could focus on under-sampled regions to fill in key gaps and narrow the uncertainty in global diversity maps. These new datasets can be collected using the standard methodologies (e.g. habitat surveillance, plot surveys⁷³). Additionally, a number of next-generation technologies have emerged – such as eDNA^{38,74}, bioacoustics⁷⁵, and data collected by low-flying drones – have the potential to scale data collection in a cost-effective manner⁷⁶.

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 future outlook

As new policy frameworks and nature markets are developed to promote and protect biodiversity, the key challenge for ecologists is to produce a realistic estimate of the state of nature that is valid on both local and global scales and can reliably inform these developing policies and markets. Such an integrative metric is needed to evaluate progress toward climate change and land protection pledges (e.g. the GBF, Bonn Challenge⁷⁷, and UN Sustainable Development Goals⁷⁸), bring transparency to policy frameworks, and to encourage corporate accountability (under the Taskforce for Nature-related Financial Disclosures (TNFD)⁷⁹ and Science-Based Targets for Nature (SBTN)⁸⁰).

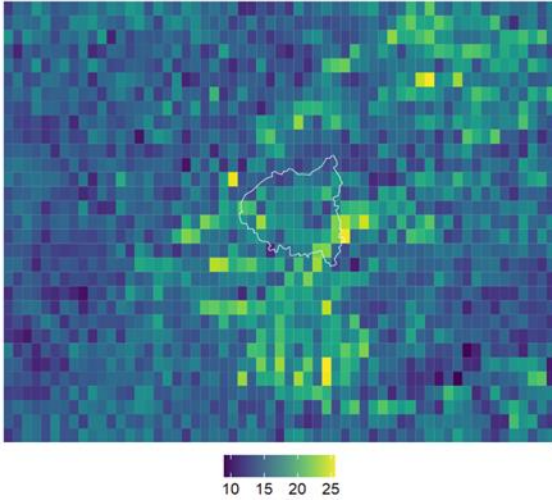
We present the SEED framework that consolidates the primary dimensions of biodiversity to produce a standardized and comprehensible measure of biocomplexity. Our framework is flexible, allowing for a dynamic index that evolves alongside the development of new data products and

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 metric at finer spatial and temporal scales. Toward this goal, we have already begun building models that integrate remote sensing data products into maps of species richness and phylogenetic divergence that will improve the spatial and temporal resolution of our index.

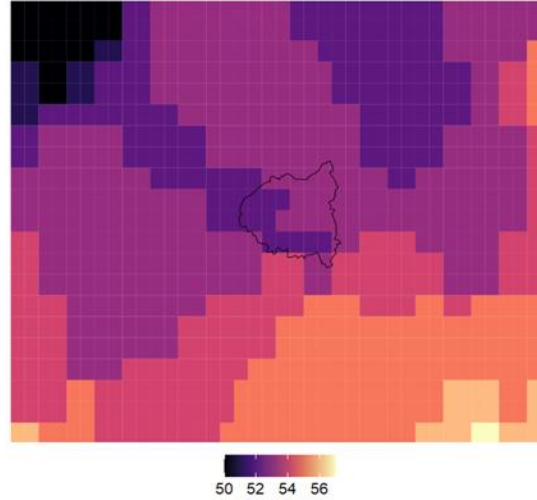
To ensure that the most high-integrity and up-to-date ecological information is available to policy- and decision-makers, we invite the wider scientific community to collaborate on the continual advancement of this biocomplexity metric. We strongly believe that for this biodiversity metric to lead to 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 metric, thus fostering better outcomes for ecosystem protection and restoration.

Figures

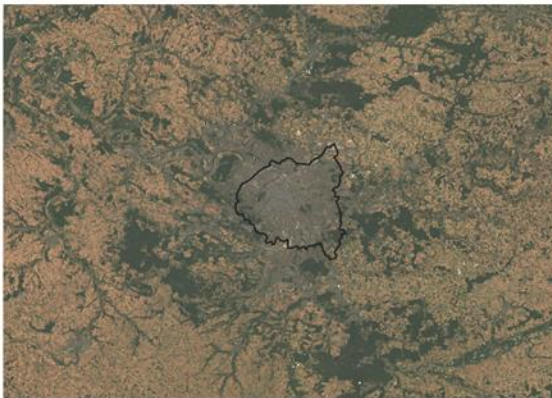
a) Plant Richness



b) Mammal Richness



c) Aerial View



d) Human Modification Index

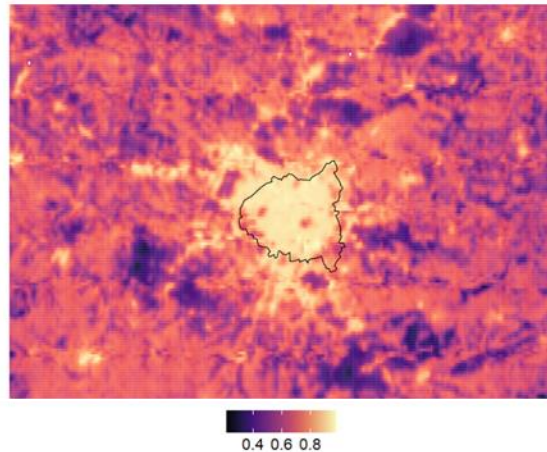


Figure 1. Performance of species richness maps in human modified landscapes. This figure illustrates how maps of species richness, e.g., (a) plant⁶⁴ and (b) mammals⁶⁵, may not reflect the true impacts of humans, which can be seen here in (c) the aerial view from Sentinel-2⁸¹ and (d) the human modification index⁴⁷. These maps all focus on Paris (outline) and the surrounding landscape.

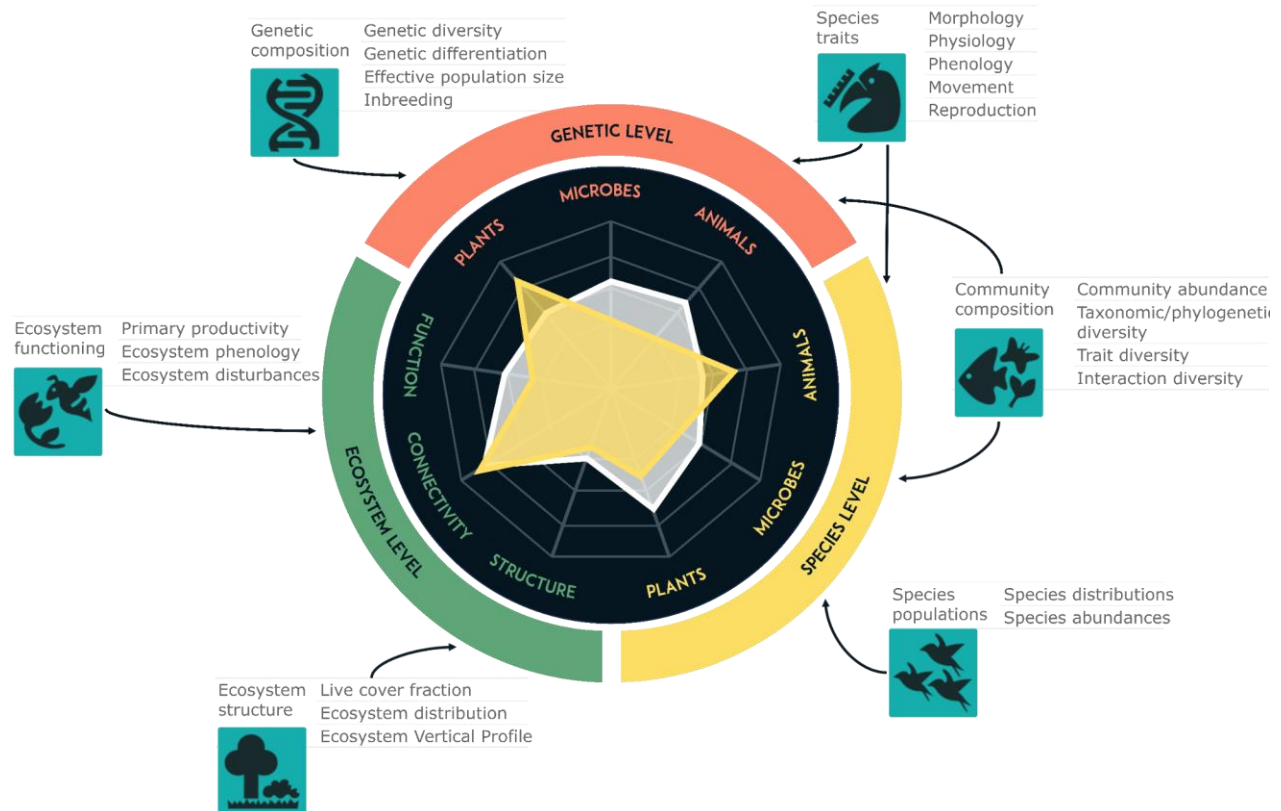


Figure 2. SEED biocomplexity index. Example visualization of the SEED framework for an area of interest, showing the dimensionality-reduced values across 3 axes for each of the 3 scales of variation (genetic, species, and ecosystems). For each axis, the visualization shows the difference between the 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 – which ranges from 0 and 1, where 0 represents a complete absence of biocomplexity, and 1 represents an area that is equivalent in complexity to its potential natural state. Arrows indicate the relationships between the three scales of variation and the Essential Biodiversity Variables (EBVs).

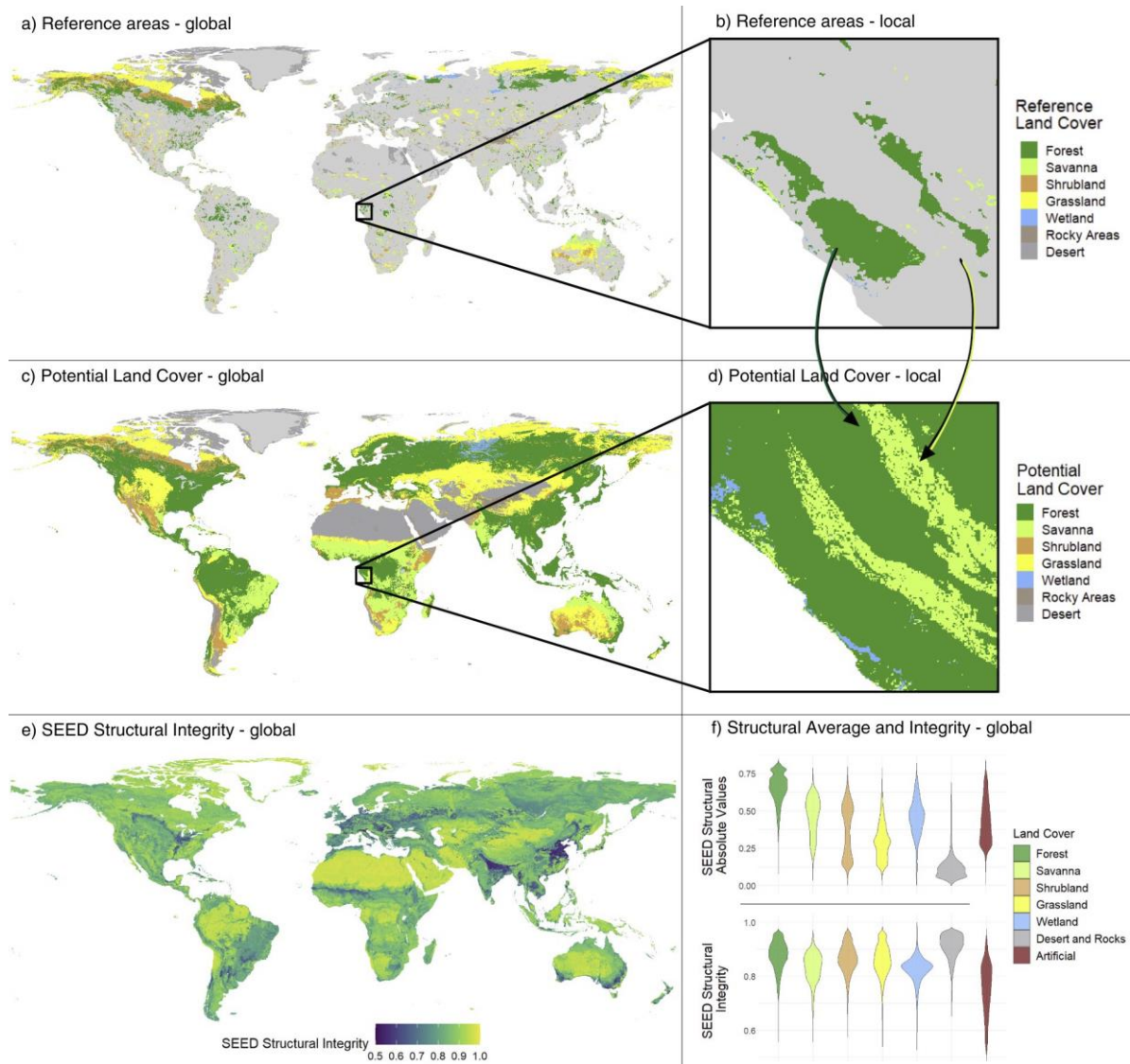


Figure 3. Assessing the potential state of ecosystems through the identification of relevant reference areas. a) and b) Reference areas representing the 5% least disturbed areas within each combination of ecoregion and land cover type. c) Potential land cover obtained from ⁶², substituting artificial 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 integrity, 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 integrity across different land-use categories.

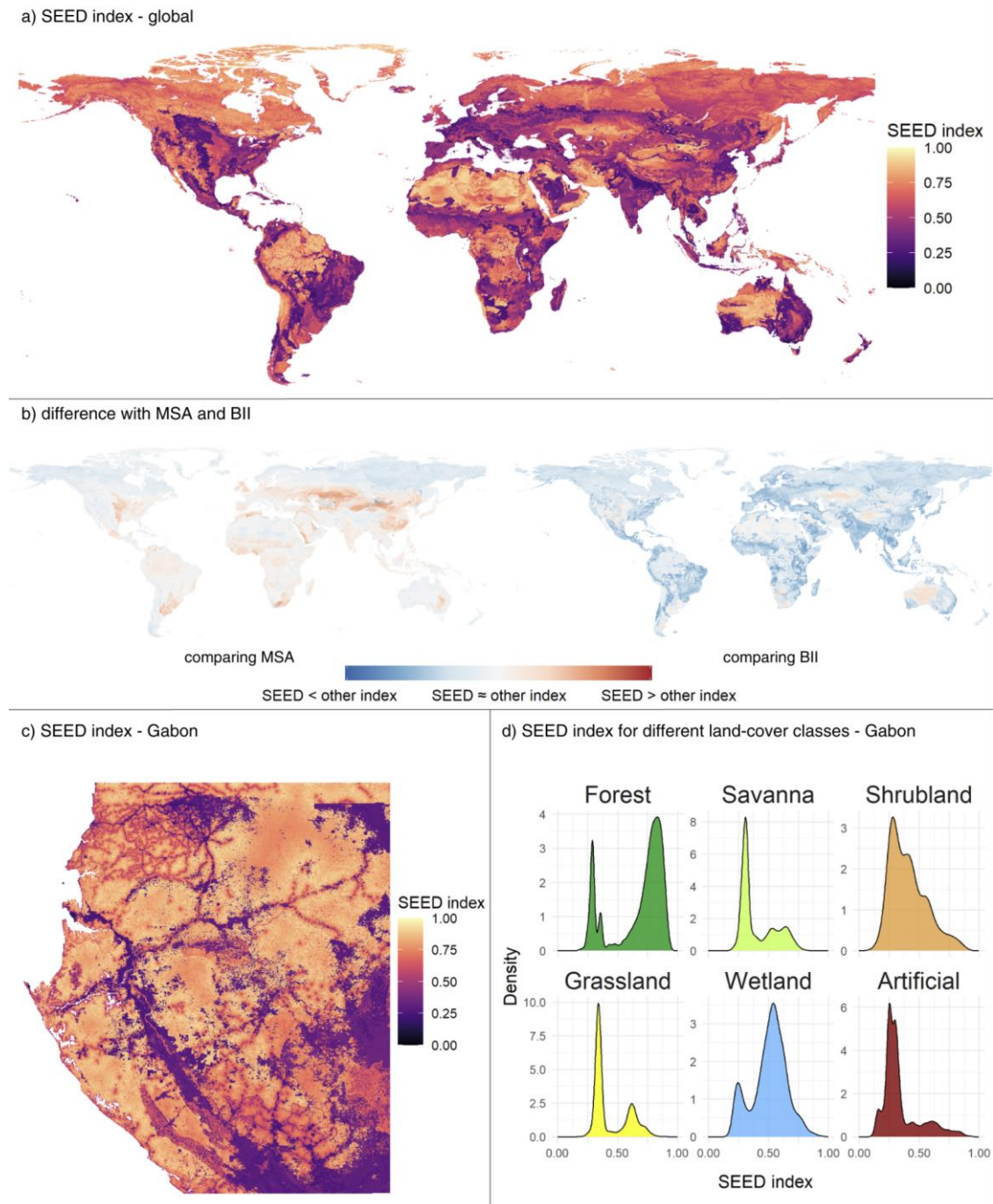


Figure 4. Comparative analysis of the SEED Index. a) Global representation of the SEED index. b) Comparisons between the SEED index and MSA (left) or BII (right). c) The SEED index in the country of Gabon and surrounding areas. d) SEED index densities across six land cover classes in Gabon. The artificial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

Supplemental information:

Document S1: Figures S1-4

Acknowledgements:

This work is supported by DOB Ecology and the Bernina Initiative. On behalf of all co-authors, we would like to extend our sincere gratitude to Alexa Firmenich for their invaluable contributions to conceptual development and funding acquisition. We also sincerely thank Felix Specker for coding assistance.

Author contributions:

This work was conceptualized by TWC, DM, JvdH, 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 (Figures 1, 3, 4 and Supplementary Figures) and IB (Figure2). TWC and RMM supervised this work and funding was acquired by TWC, 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 in order to improve readability and language during the first steps of the draft. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

6. References

1. Dasgupta, P. (2021). The Economics of Biodiversity: The Dasgupta Review.
2. Conference of the Parties to the Convention on Biological Diversity (2022). Decision 15/4.
3. Bremer, L.L., and Farley, K.A. (2010). Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodivers. Conserv.* *19*, 3893–3915. 10.1007/s10531-010-9936-4.
4. Armenteras, D., Rodríguez, N., and Retana, J. (2015). National and regional relationships of carbon storage and tropical biodiversity. *Biol. Conserv.* *192*, 378–386. 10.1016/j.biocon.2015.10.014.
5. Lima, T.A., and Vieira, G. (2013). High plant species richness in monospecific tree plantations in the Central Amazon. *For. Ecol. Manag.* *295*, 77–86. 10.1016/j.foreco.2013.01.006.
6. Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., et al. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc. Natl. Acad. Sci.* *104*, 18555–18560. 10.1073/pnas.0703333104.
7. Hulvey, K.B., Hobbs, R.J., Standish, R.J., Lindenmayer, D.B., Lach, L., and Perring, M.P. (2013). Benefits of tree mixes in carbon plantings. *Nat. Clim. Change* *3*, 869–874. 10.1038/nclimate1862.
8. Geller, G.N., Halpin, P.N., Helmuth, B., Hestir, E.L., Skidmore, A., Abrams, M.J., Aguirre, N., Blair, M., Botha, E., and Colloff, M. (2017). Remote sensing for biodiversity. In *The GEO handbook on biodiversity observation networks* (Springer International Publishing), pp. 187–210.
9. Witmer, G.W. (2005). Wildlife population monitoring: some practical considerations. *Wildl. Res.* *32*, 259–263. 10.1071/WR04003.
10. Adam, E., Mutanga, O., and Rugege, D. (2010). Multispectral and hyperspectral remote sensing for identification and mapping of wetland vegetation: a review. *Wetl. Ecol. Manag.* *18*, 281–296. 10.1007/s11273-009-9169-z.
11. LaRue, E.A., Fahey, R.T., Alvshere, B.C., Atkins, J.W., Bhatt, P., Buma, B., Chen, A., Cousins, S., Elliott, J.M., Elmore, A.J., et al. (2023). A theoretical framework for the ecological role of three-dimensional structural diversity. *Front. Ecol. Environ.* *21*, 4–13. 10.1002/fee.2587.
12. Bishop-Taylor, R., Tulbure, M.G., and Broich, M. (2018). Evaluating static and dynamic landscape connectivity modelling using a 25-year remote sensing time series. *Landsc. Ecol.* *33*, 625–640. 10.1007/s10980-018-0624-1.
13. O’Brien, D., Laikre, L., Hoban, S., Bruford, M.W., Ekblom, R., Fischer, M.C., Hall, J., Hvilson, C., Hollingsworth, P.M., Kershaw, F., et al. (2022). Bringing together approaches to reporting on within species genetic diversity. *J. Appl. Ecol.* *59*, 2227–2233. 10.1111/1365-2664.14225.
14. Hoban, S., Archer, F.I., Bertola, L.D., Bragg, J.G., Breed, M.F., Bruford, M.W., Coleman, M.A., Ekblom, R., Funk, W.C., Grueber, C.E., et al. (2022). Global genetic diversity status and trends: towards a suite of Essential Biodiversity Variables (EBVs) for genetic composition. *Biol. Rev.* *97*, 1511–1538. 10.1111/brv.12852.
15. Wesse, C., Welk, E., Hurka, H., and Neuffer, B. (2021). Geographical pattern of genetic

- diversity in *Capsella bursa-pastoris* (Brassicaceae)—A global perspective. *Ecol. Evol.* *11*, 199–213. 10.1002/ece3.7010.
16. Guo, W.-Y., Serra-Diaz, J.M., Schrodte, F., Eiserhardt, W.L., Maitner, B.S., Merow, C., Violle, C., Anand, M., Belluau, M., Bruun, H.H., et al. (2022). High exposure of global tree diversity to human pressure. *Proc. Natl. Acad. Sci.* *119*, e2026733119. 10.1073/pnas.2026733119.
 17. Hughes, E.C., Edwards, D.P., Bright, J.A., Capp, E.J.R., Cooney, C.R., Varley, Z.K., and Thomas, G.H. (2022). Global biogeographic patterns of avian morphological diversity. *Ecol. Lett.* *25*, 598–610. 10.1111/ele.13905.
 18. Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armour-Marshall, K., and Diniz-Filho, J.A.F. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. *Philos. Trans. R. Soc. B Biol. Sci.* *366*, 2536–2544. 10.1098/rstb.2011.0024.
 19. Rosauer, D.F., and Jetz, W. (2015). Phylogenetic endemism in terrestrial mammals. *Glob. Ecol. Biogeogr.* *24*, 168–179. 10.1111/geb.12237.
 20. Fritz, S.A., and Rahbek, C. (2012). Global patterns of amphibian phylogenetic diversity. *J. Biogeogr.* *39*, 1373–1382. 10.1111/j.1365-2699.2012.02757.x.
 21. Wolf, S., Mahecha, M.D., Sabatini, F.M., Wirth, C., Bruehlheide, H., Kattge, J., Moreno Martínez, Á., Mora, K., and Kattenborn, T. (2022). Citizen science plant observations encode global trait patterns. *Nat. Ecol. Evol.* *6*, 1850–1859. 10.1038/s41559-022-01904-x.
 22. Numbere, A.O. (2018). Mangrove species distribution and composition, adaptive strategies and ecosystem services in the Niger River Delta, Nigeria. In *Mangrove ecosystem ecology and function* (IntechOpen London), pp. 17–40.
 23. Zheng, Z., Schmid, B., Zeng, Y., Schuman, M.C., Zhao, D., Schaepman, M.E., and Morsdorf, F. (2023). Remotely sensed functional diversity and its association with productivity in a subtropical forest. *Remote Sens. Environ.* *290*, 113530. 10.1016/j.rse.2023.113530.
 24. Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M., and Brooks, T.M. (2006). The value of the IUCN Red List for conservation. *Trends Ecol. Evol.* *21*, 71–76. 10.1016/j.tree.2005.10.010.
 25. Cai, L., Kreft, H., Taylor, A., Denelle, P., Schrader, J., Essl, F., van Kleunen, M., Pergl, J., Pyšek, P., Stein, A., et al. (2023). Global models and predictions of plant diversity based on advanced machine learning techniques. *New Phytol.* *237*, 1432–1445. 10.1111/nph.18533.
 26. König, C., Weigelt, P., Schrader, J., Taylor, A., Kattge, J., and Kreft, H. (2019). Biodiversity data integration—the significance of data resolution and domain. *PLOS Biol.* *17*, e3000183. 10.1371/journal.pbio.3000183.
 27. Tuia, D., Kellenberger, B., Beery, S., Costelloe, B.R., Zuffi, S., Risse, B., Mathis, A., Mathis, M.W., van Langevelde, F., Burghardt, T., et al. (2022). Perspectives in machine learning for wildlife conservation. *Nat. Commun.* *13*, 792. 10.1038/s41467-022-27980-y.
 28. Zimmermann, N.E., Edwards Jr, T.C., Graham, C.H., Pearman, P.B., and Svenning, J.-C. (2010). New trends in species distribution modelling. *Ecography* *33*, 985–989. 10.1111/j.1600-0587.2010.06953.x.
 29. Kearney, M., and Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* *12*, 334–350. 10.1111/j.1461-0248.2008.01277.x.
 30. Turner, D.P. (2011). Global vegetation monitoring: toward a sustainable technobiosphere. *Front. Ecol. Environ.* *9*, 111–116. 10.1890/090171.

31. Locey, K.J., and Lennon, J.T. (2016). Scaling laws predict global microbial diversity. *Proc. Natl. Acad. Sci.* *113*, 5970–5975. 10.1073/pnas.1521291113.
32. Larsen, B.B., Miller, E.C., Rhodes, M.K., and Wiens, J.J. (2017). Inordinate Fondness Multiplied and Redistributed: the Number of Species on Earth and the New Pie of Life. *Q. Rev. Biol.* *92*, 229–265. 10.1086/693564.
33. Miraldo, A., Li, S., Borregaard, M.K., Flórez-Rodríguez, A., Gopalakrishnan, S., Rizvanovic, M., Wang, Z., Rahbek, C., Marske, K.A., and Nogués-Bravo, D. (2016). An Anthropocene map of genetic diversity. *Science* *353*, 1532–1535. 10.1126/science.aaf4381.
34. Theodoridis, S., Fordham, D.A., Brown, S.C., Li, S., Rahbek, C., and Nogués-Bravo, D. (2020). Evolutionary history and past climate change shape the distribution of genetic diversity in terrestrial mammals. *Nat. Commun.* *11*, 2557. 10.1038/s41467-020-16449-5.
35. Howard, C., Flather, C.H., and Stephens, P.A. (2020). A global assessment of the drivers of threatened terrestrial species richness. *Nat. Commun.* *11*, 993. 10.1038/s41467-020-14771-6.
36. Hughes, A.C., Orr, M.C., Yang, Q., and Qiao, H. (2021). Effectively and accurately mapping global biodiversity patterns for different regions and taxa. *Glob. Ecol. Biogeogr.* *30*, 1375–1388. 10.1111/geb.13304.
37. Jung, M., Arnell, A., de Lamo, X., García-Rangel, S., Lewis, M., Mark, J., Merow, C., Miles, L., Ondo, I., Pironon, S., et al. (2021). Areas of global importance for conserving terrestrial biodiversity, carbon and water. *Nat. Ecol. Evol.* *5*, 1499–1509. 10.1038/s41559-021-01528-7.
38. Ruppert, K.M., Kline, R.J., and Rahman, M.S. (2019). Past, present, and future perspectives of environmental DNA (eDNA) metabarcoding: A systematic review in methods, monitoring, and applications of global eDNA. *Glob. Ecol. Conserv.* *17*, e00547. 10.1016/j.gecco.2019.e00547.
39. Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford, M.W., Brummitt, N., Butchart, S.H.M., Cardoso, A.C., et al. (2013). Essential Biodiversity Variables. *Science* *339*, 277–278. 10.1126/science.1229931.
40. Cisneros-Araujo, P., Goicolea, T., Mateo-Sánchez, M.C., García-Viñás, J.I., Marchamalo, M., Mercier, A., and Gastón, A. (2021). The Role of Remote Sensing Data in Habitat Suitability and Connectivity Modeling: Insights from the Cantabrian Brown Bear. *Remote Sens.* *13*, 1138. 10.3390/rs13061138.
41. Cisneros-Araujo, P., Ramirez-Lopez, M., Juffe-Bignoli, D., Fensholt, R., Muro, J., Mateo-Sánchez, M.C., and Burgess, N.D. (2021). Remote sensing of wildlife connectivity networks and priority locations for conservation in the Southern Agricultural Growth Corridor (SAGCOT) in Tanzania. *Remote Sens. Ecol. Conserv.* *7*, 430–444. 10.1002/rse2.199.
42. Assis, J.C., Hohlenwerger, C., Metzger, J.P., Rhodes, J.R., Duarte, G.T., da Silva, R.A., Boesing, A.L., Prist, P.R., and Ribeiro, M.C. (2023). Linking landscape structure and ecosystem service flow. *Ecosyst. Serv.* *62*, 101535. 10.1016/j.ecoser.2023.101535.
43. Baude, M., and Meyer, B.C. (2023). Changes in landscape structure and ecosystem services since 1850 analyzed using landscape metrics in two German municipalities. *Ecol. Indic.* *152*, 110365. 10.1016/j.ecolind.2023.110365.
44. Mitchell, J.C., Kashian, D.M., Chen, X., Cousins, S., Flaspohler, D., Gruner, D.S., Johnson, J.S., Surasinghe, T.D., Zambrano, J., and Buma, B. (2023). Forest ecosystem properties emerge from interactions of structure and disturbance. *Front. Ecol. Environ.* *21*, 14–23. 10.1002/fee.2589.
45. Hill, S.L.L., Fajardo, J., Maney, C., Harfoot, M., Harrison, M., Guaras, D., Jones, M., Oliva,

- M.J., Danks, F., Hughes, J., et al. (2022). The Ecosystem Integrity Index: a novel measure of terrestrial ecosystem integrity with global coverage. 2022.08.21.504707. 10.1101/2022.08.21.504707.
46. Schipper, A.M., Hilbers, J.P., Meijer, J.R., Antão, L.H., Benítez-López, A., de Jonge, M.M.J., Leemans, L.H., Scheper, E., Alkemade, R., Doelman, J.C., et al. (2020). Projecting terrestrial biodiversity intactness with GLOBIO 4. *Glob. Change Biol.* 26, 760–771. 10.1111/gcb.14848.
 47. Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S., and Kiesecker, J. (2019). Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Glob. Change Biol.* 25, 811–826. 10.1111/gcb.14549.
 48. Running, S.W., and Zhao, M. Daily GPP and Annual NPP (MOD17A2/A3) Products NASA Earth Observing System MODIS Land Algorithm.
 49. Scholes, R.J., and Biggs, R. (2005). A biodiversity intactness index. *Nature* 434, 45–49. 10.1038/nature03289.
 50. Hudson, L.N., Newbold, T., Contu, S., Hill, S.L.L., Lysenko, I., De Palma, A., Phillips, H.R.P., Senior, R.A., Bennett, D.J., Booth, H., et al. (2014). The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. *Ecol. Evol.* 4, 4701–4735. 10.1002/ece3.1303.
 51. Hudson, L.N., Newbold, T., Contu, S., Hill, S.L.L., Lysenko, I., De Palma, A., Phillips, H.R.P., Alhusseini, T.I., Bedford, F.E., Bennett, D.J., et al. (2017). The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project. *Ecol. Evol.* 7, 145–188. 10.1002/ece3.2579.
 52. Liu, L., Zhu, K., Wurzburger, N., and Zhang, J. (2020). Relationships between plant diversity and soil microbial diversity vary across taxonomic groups and spatial scales. *Ecosphere* 11, e02999. 10.1002/ecs2.2999.
 53. Prober, S.M., Leff, J.W., Bates, S.T., Borer, E.T., Firn, J., Harpole, W.S., Lind, E.M., Seabloom, E.W., Adler, P.B., Bakker, J.D., et al. (2015). Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. *Ecol. Lett.* 18, 85–95. 10.1111/ele.12381.
 54. Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., et al. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* 342, 850–853. 10.1126/science.1244693.
 55. Simard, M., Pinto, N., Fisher, J.B., and Baccini, A. (2011). Mapping forest canopy height globally with spaceborne lidar. *J. Geophys. Res. Biogeosciences* 116. 10.1029/2011JG001708.
 56. Myneni, R., Knyazikhin, Y., and Park, T. (2021). MODIS/Terra+Aqua Leaf Area Index/FPAR 4-Day L4 Global 500m SIN Grid V061. 10.5067/MODIS/MCD15A3H.061.
 57. Spawn, S.A., Sullivan, C.C., Lark, T.J., and Gibbs, H.K. (2020). Harmonized global maps of above and belowground biomass carbon density in the year 2010. *Sci. Data* 7, 112. 10.1038/s41597-020-0444-4.
 58. Tuanmu, M.-N., and Jetz, W. (2015). A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Glob. Ecol. Biogeogr.* 24, 1329–1339. 10.1111/geb.12365.
 59. Gallagher, R., and Carpenter, B. (1997). Human-Dominated Ecosystems. *Science* 277, 485–485. 10.1126/science.277.5325.485.

60. Balaguer, L., Escudero, A., Martín-Duque, J.F., Mola, I., and Aronson, J. (2014). The historical reference in restoration ecology: Re-defining a cornerstone concept. *Biol. Conserv.* *176*, 12–20. 10.1016/j.biocon.2014.05.007.
61. Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., et al. (2017). An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *BioScience* *67*, 534–545. 10.1093/biosci/bix014.
62. Jung, M., Dahal, P.R., Butchart, S.H.M., Donald, P.F., De Lamo, X., Lesiv, M., Kapos, V., Rondinini, C., and Visconti, P. (2020). A global map of terrestrial habitat types. *Sci. Data* *7*, 256. 10.1038/s41597-020-00599-8.
63. Suding, K.N. (2011). Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. *Annu. Rev. Ecol. Evol. Syst.* *42*, 465–487. 10.1146/annurev-ecolsys-102710-145115.
64. Sabatini, F.M., Jiménez-Alfaro, B., Jandt, U., Chytrý, M., Field, R., Kessler, M., Lenoir, J., Schrodtt, F., Wisser, S.K., Arfin Khan, M.A.S., et al. (2022). Global patterns of vascular plant alpha diversity. *Nat. Commun.* *13*, 4683. 10.1038/s41467-022-32063-z.
65. Jenkins, C.N., Pimm, S.L., and Joppa, L.N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl. Acad. Sci.* *110*, E2602–E2610. 10.1073/pnas.1302251110.
66. Lyons-White, J., Mikolo Yobo, C., Ewers, R.M., and Knight, A.T. (2022). Understanding zero deforestation and the High Carbon Stock Approach in a highly forested tropical country. *Land Use Policy* *112*, 105770. 10.1016/j.landusepol.2021.105770.
67. Shapiro, A.C., Grantham, H.S., Aguilar-Amuchastegui, N., Murray, N.J., Gond, V., Bonfils, D., and Rickenbach, O. (2021). Forest condition in the Congo Basin for the assessment of ecosystem conservation status. *Ecol. Indic.* *122*, 107268. 10.1016/j.ecolind.2020.107268.
68. Austin, K.G., Lee, M.E., Clark, C., Forester, B.R., Urban, D.L., White, L., Kasibhatla, P.S., and Poulsen, J.R. (2017). An assessment of high carbon stock and high conservation value approaches to sustainable oil palm cultivation in Gabon. *Environ. Res. Lett.* *12*, 014005. 10.1088/1748-9326/aa5437.
69. Aldous, A., Schill, S., Raber, G., Paiz, M.-C., Mambela, E., and Stévant, T. (2021). Mapping complex coastal wetland mosaics in Gabon for informed ecosystem management: use of object-based classification. *Remote Sens. Ecol. Conserv.* *7*, 64–79. 10.1002/rse2.161.
70. Cavender-Bares, J., Gamon, J.A., Hobbie, S.E., Madritch, M.D., Meireles, J.E., Schweiger, A.K., and Townsend, P.A. (2017). Harnessing plant spectra to integrate the biodiversity sciences across biological and spatial scales. *Am. J. Bot.* *104*, 966–969. 10.3732/ajb.1700061.
71. Cawse-Nicholson, K., Townsend, P.A., Schimel, D., Assiri, A.M., Blake, P.L., Buongiorno, M.F., Campbell, P., Carmon, N., Casey, K.A., Correa-Pabón, R.E., et al. (2021). NASA’s surface biology and geology designated observable: A perspective on surface imaging algorithms. *Remote Sens. Environ.* *257*, 112349. 10.1016/j.rse.2021.112349.
72. European Space Agency (2020). Chime (Copernicus Hyperspectral Imaging Mission for the Environment) - eoPortal. <https://www.eoportal.org/satellite-missions/chime-copernicus#eo-quick-facts-section>.
73. Walters, M., and Scholes, R.J. (2017). *The GEO handbook on biodiversity observation networks* (Springer Nature).
74. Deiner, K., Bik, H.M., Mächler, E., Seymour, M., Lacoursière-Roussel, A., Altermatt, F., Creer, S., Bista, I., Lodge, D.M., de Vere, N., et al. (2017). Environmental DNA

- metabarcoding: Transforming how we survey animal and plant communities. *Mol. Ecol.* 26, 5872–5895. 10.1111/mec.14350.
75. Sueur, J., and Farina, A. (2015). Ecoacoustics: the Ecological Investigation and Interpretation of Environmental Sound. *Biosemiotics* 8, 493–502. 10.1007/s12304-015-9248-x.
 76. Buřivalova, Z., Yoh, N., Butler, R.A., Chandra Sagar, H.S.S., and Game, E.T. (2023). Broadening the focus of forest conservation beyond carbon. *Curr. Biol.* 33, R621–R635. 10.1016/j.cub.2023.04.019.
 77. The Bonn Challenge | Bonchallenge <https://www.bonnchallenge.org/>.
 78. THE 17 GOALS | Sustainable Development <https://sdgs.un.org/goals>.
 79. TNFD – Taskforce on Nature-related Financial Disclosures TNFD. <https://tnfd.global/>.
 80. Science Based Targets Network Sci. Based Targets Netw. <https://sciencebasedtargetsnetwork.org/>.
 81. European Space Agency (2022). Copernicus Sentinel-2 (processed by ESA), 2022, MSI Level-2A BOA Reflectance Product. Collection 1.

Supplementary Figures

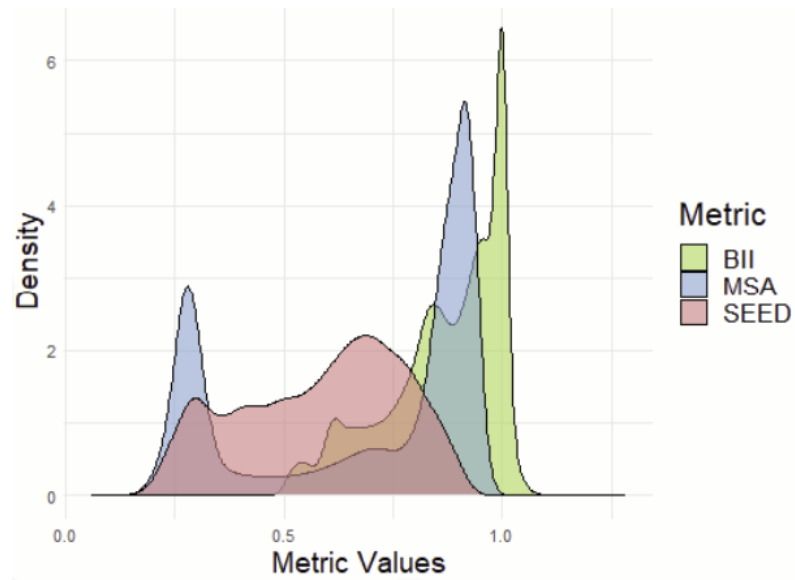


Figure S1. Density plot showcasing the distribution of the first generation of the SEED index in relation to MSA and BII at a global scale.

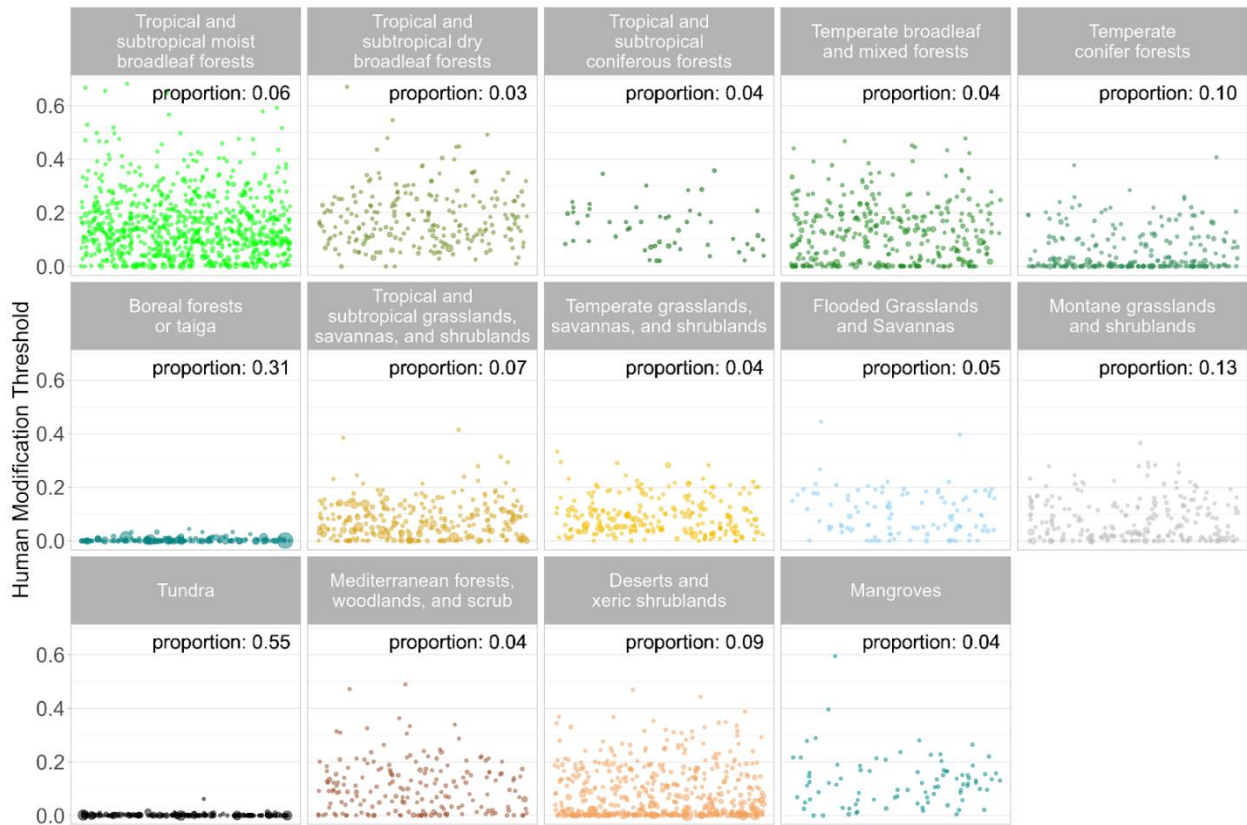
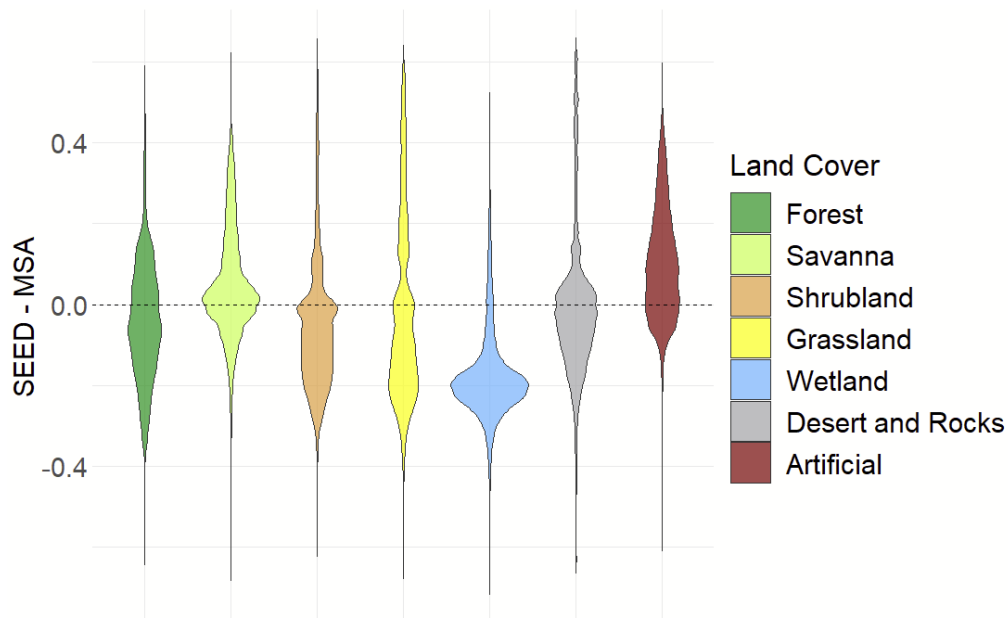


Figure S2. Distribution of human modification index (HMI) thresholds identified in the reference area approach, for each combination of land-cover and ecoregion, summarized for each biome (Dinerstein et al., 2017). The proportion of land identified as a reference in each biome compared to the total area is plotted on the top-right. In very intact areas, the HMI may be close to 0 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)

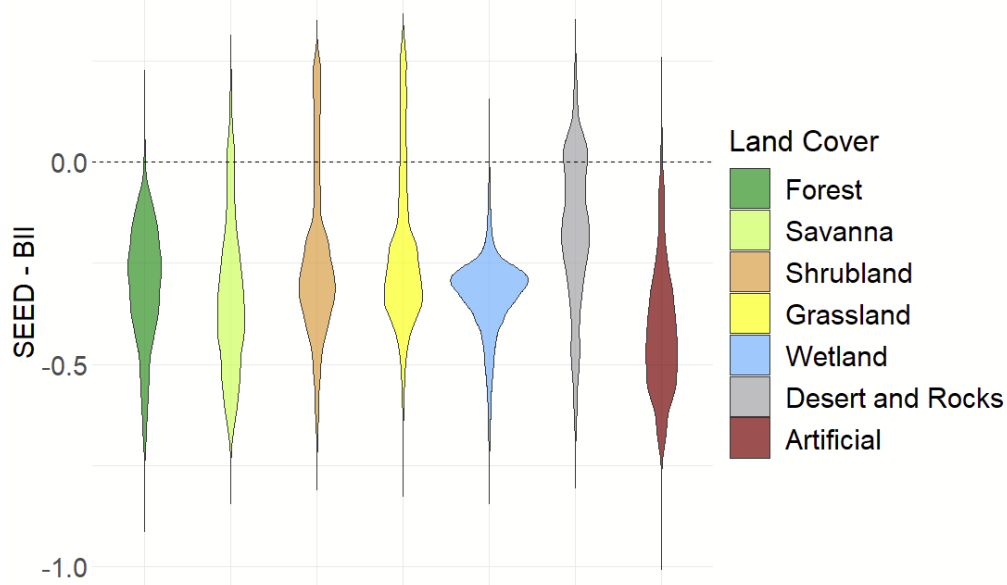


Figure S3. Violin plots illustrating the distribution of differences between the first generation of the SEED index and a) MSA, and b) BII, across different land-cover classes.

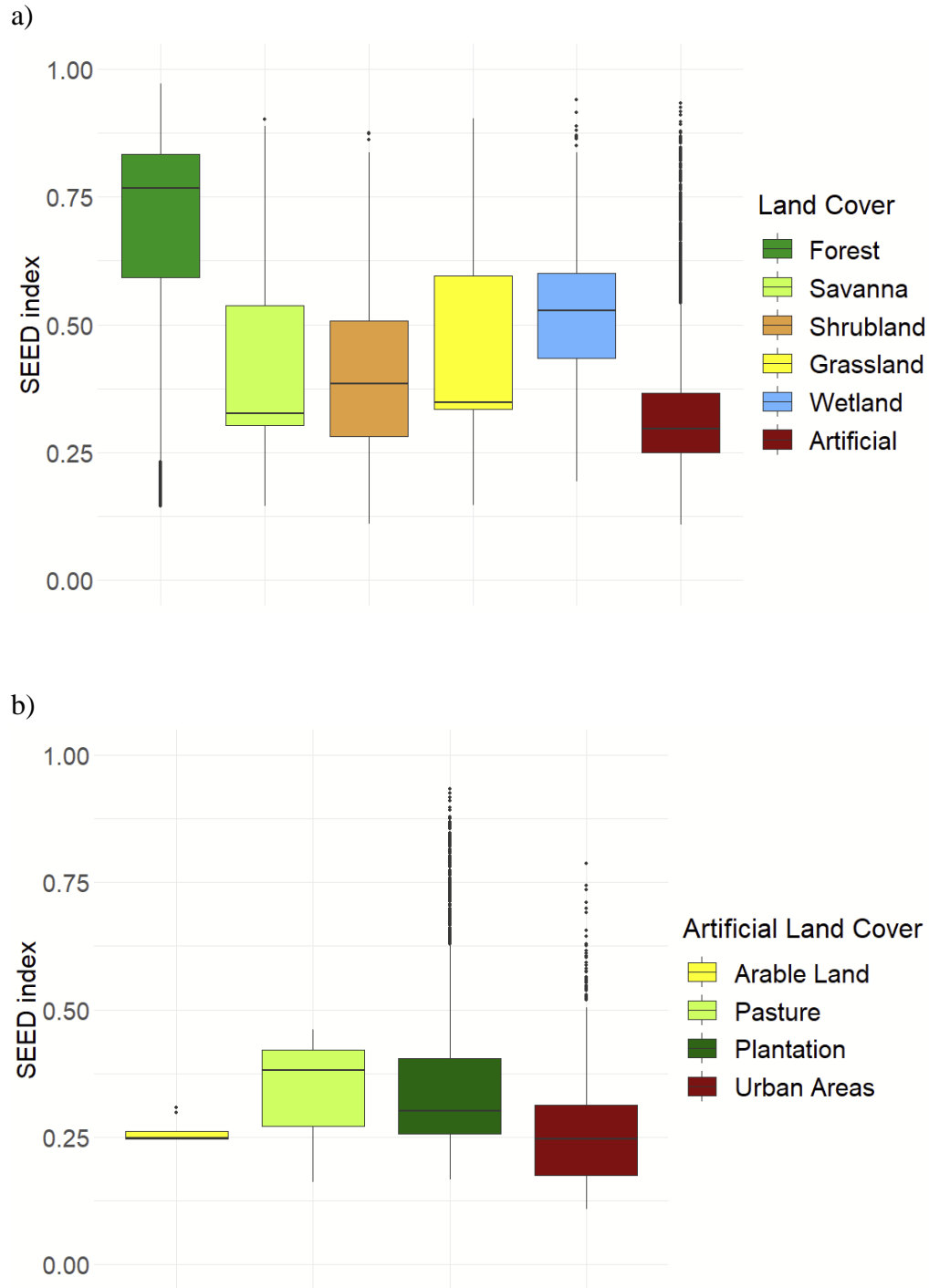


Figure S4. Boxplots illustrating the distribution of the first generation of the SEED index: a) across different land-cover classes in the Gabon region, and b) specifically within different artificial land-cover classes.

References:

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E. C., Jones, B., Barber, C. V., Hayes, R., Kormos, C., Martin, V., Crist, E., ... Saleem, M. (2017). An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *BioScience*, 67(6), 534–545. <https://doi.org/10.1093/biosci/bix014>