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LETTER

Reconciling Biodiversity Indicators to Guide Understanding

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Introduction

Concerns over the global loss of biodiversity and the degradation of ecosystem goods and services have led to international commitments aimed at preventing further declines. For example, the parties to the Convention on Biological Diversity (CBD) committed to the Strategic Plan for Biodiversity 2011-2020, supported by 20 Aichi Biodiversity Targets to be met by 2020, which calls for effective and urgent action during this decade to tackle biodiversity loss. These targets are echoed in the United Nations' newly approved Sustainable Development Goals (SDGs) and, in particular, their goals 14 and 15 concerning the conservation of seas and terrestrial ecosystems respectively. It is critical both to be able to measure progress against these targets and to identify the most effective policies and interventions for achieving them. However, there are a number of difficulties associated with both these needs. We highlight five of the most pressing.

First, biodiversity is a complex concept and no single indicator can effectively summarize its status or trend. Many different metrics of biodiversity are used for reporting trends although most are based upon the number of species or individuals present. Some aspects of biodiversity, such as phylogenetic and functional diversity, are rarely assessed despite their potential

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Abstract

Many metrics can be used to capture trends in biodiversity and, in turn, these metrics inform biodiversity indicators. Sampling biases, genuine differences between metrics, or both, can often cause indicators to appear to be in conflict. This lack of congruence confuses policy makers and the general public, hindering effective responses to the biodiversity crisis. We show how different and seemingly inconsistent metrics of biodiversity can, in fact, emerge from the same scenario of biodiversity change. We develop a simple, evidence-based narrative of biodiversity change and implement it in a simulation model. The model demonstrates how, for example, species richness can remain stable in a given landscape, whereas other measures (e.g. compositional similarity) can be in sharp decline. We suggest that linking biodiversity metrics in a simple model will support more robust indicator development, enable stronger predictions of biodiversity change, and provide policy-relevant advice at a range of scales.

relevance (Diaz *et al.* 2013; Mace *et al.* 2014; Steffen *et al.* 2015). A framework for essential biodiversity variables (EBVs) (Pereira *et al.* 2013) is now gaining support and providing a basis for collaboration (see http://geobon.org/essential-biodiversity-variables/ebv-

classes-2/) but is still far from being streamlined, with six classes of metrics and 22 categories of measurement (Pereira et al. 2013). Furthermore, being based on ecological principles, the EBVs may not easily link to decisions or policies designed to achieve the CBD targets (Jones et al. 2011; Nicholson et al. 2012) or even to the targets themselves (Tittensor et al. 2014). Even when considering a single target, several different metrics may be in use. For example, Aichi Target 12 calls for the prevention of extinctions and progress is currently assessed using three indicators: the Red List Index that measures change in the number of threatened species since the previous assessment, the Living Planet Index that assesses changes in abundance within populations of vertebrates since 1970, and the Wildlife Picture Index that uses modeled changes in species occupancy of birds and mammals in 16 sites since 2007. In addition to the differing metrics of change used by such indicators, different indicators may give different results because they sample different places or taxa, or because they calculate change from different baselines.

Second, most indicators of global biodiversity are extrapolated or modeled from local observations at a particular time and place. However, the processes of biodiversity change (e.g., migration and local extinction) interact and vary across scales of space and time, so that global trends are not a simple function of local or regional trends (Sax & Gaines 2003; Thomas 2013). This complicates the description of global trends (McGill *et al.* 2015) and confounds efforts to extrapolate and forecast future changes.

Third, there are substantial gaps in data and observations due to the accessibility, popularity, measurability, and even fundamental knowledge of different components of biodiversity. Observations sourced for the most widely used indicators are inevitably biased; generally toward recent decades, large-bodied and charismatic species, in terrestrial, temperate, economically-developed, and easily-accessible environments (Boakes *et al.* 2010; Hudson *et al.* 2014; Pimm *et al.* 2014; Geijzendorffer *et al.* 2015; Meyer *et al.* 2015; Newbold *et al.* 2015; Gonzalez *et al.* 2016). Certain areas of significant biodiversity, such as soils and oceans, especially involving invertebrate and microscopic organisms, are extremely poorly known and weakly sampled (Mora *et al.* 2011).

Fourth, the system within which biodiversity loss is observed is not well understood. Often, including for the Aichi targets, the drivers-pressure-state-impactresponse (DPSIR) framework is used (Han *et al.* 2014; Marques *et al.* 2014). However, the framework linkages are assumed rather than evidence-based, and the metrics of biodiversity are rather weak proxies for global metrics, being based on available data but without evidence of causal associations or knowledge of the dynamic relationships involved. Developing linked indicator sets, based on established cause-effect and feedback relationships, has been recognized as important (Sparks *et al.* 2011), espe-

cially considering the different Aichi targets that are heterogeneous in intent and unlikely all to be achievable simultaneously (Perrings *et al.* 2011; Joppa *et al.* 2013; Di Marco *et al.* 2016).

Lastly, it has proven difficult to link biodiversity change into models of socioeconomic and environmental change, with the result that biodiversity is at best weakly involved in integrated assessment models (IAMs), and often only as a response metric (van Vuuren *et al.* 2006), rather than in the system dynamics (Harfoot *et al.* 2014a).

As a consequence of all these factors it is difficult to present a summary of biodiversity loss that is comprehensive and consistent. Recent studies indicating that there is no recent loss of local species richness or diversity (Vellend et al. 2013; Dornelas et al. 2014) have been challenged due to systematic biases in the data (Gonzalez et al. 2016). But other recent reports state the following suite of conclusions: a sixth global mass extinction is already underway (Ceballos et al. 2015), global species survival measured by the Red List Index could fall by about 0.2 by 2020 (Tittensor et al. 2014), species extinction rates are about 100 times background rates (Pimm et al. 2014), land-use pressures have reduced average local terrestrial species richness by about 14% (Newbold et al. 2015), vertebrate populations have declined by 52% (WWF 2014), terrestrial vertebrate populations have declined by about 25%, and invertebrate populations by about 45% (Dirzo et al. 2014). Can all these be true, and if so what explains the differences?

Here, we develop a simple narrative of global biodiversity change drawing upon current knowledge as well as experts' understandings of the system. We implement this in a stylized spatially-explicit simulation of a hypothetical region and show how commonly used biodiversity metrics might be expected to respond to anthropogenic impacts in human-modified landscapes over different spatial scales. We measure biodiversity indicators in the modeled system. We suggest that this approach, as well as being a useful heuristic device, has practical and applied value for refining global biodiversity metrics in order to 1) measure the most influential changes, 2) identify key points for intervention within the system, and 3) reconcile apparent conflicts between biodiversity indicators.

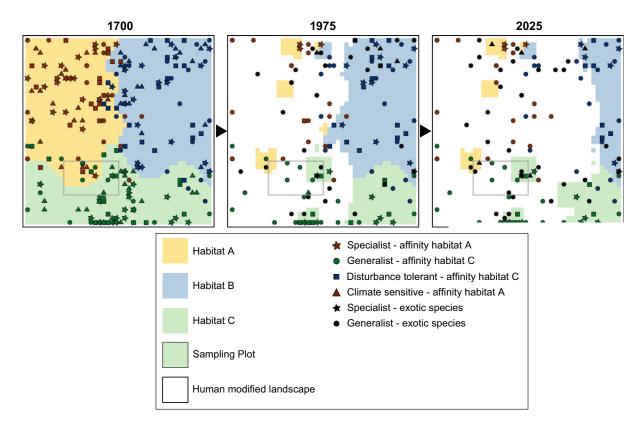


Figure 1 Regional landscape and community composition at three time points along a trajectory of human disturbance, starting from a pristine state in 1700 and running forward to 2100, as simulated by the idealized biodiversity response model. Pristine areas are indicated by coloured regions and human-dominated areas by white regions. A set of species exist in this landscape, each with an affinity for a particular habitat type (indicated by the color of the symbol) and with traits indicated by the symbol shape. In the first 275 years, 55% of the pristine habitat in the landscape was converted to human-modified matrix, while the ambient temperature increased by 2.75 °C. In the last 125 years, a further 25% of the pristine habitat is converted, while temperature increases by 1.25 °C.

Methods

Constructing the narrative

Our first step was to develop a picture of the current state of understanding of global biodiversity change and the most well-established causes and effects. We invited 26 biodiversity specialists, representing five countries, employed within academia, nongovernmental organizations, and private companies, to state what they considered to be the most important changes taking place to biodiversity (causes, states, and foci) based on their expert knowledge (see Section S1 for details). To assess the evidence base for these changes, we asked them to state also their level of confidence in each statement by indicating its comprehensiveness (taxonomic, geographic and across disciplines, and the extent of scientific consensus among experts). This information was used to construct the narrative that formed the basis for the simulation. The narrative guided our selection of anthropogenic impacts and provided the baseline of current state with which to test the simulation's results.

Exploring and visualizing the narrative through a simulation

The information gathered in the "Constructing the narrative" section was sufficiently complete to create a representation of a hypothetical terrestrial landscape. A stylized, spatially-explicit agent-based model of ecosystem change in response to anthropogenic impacts was constructed (Reconciling Biodiversity Indicatorshttp://reconciling-biodiversity-indicators.unep-wcmc. org) using the graphic language Processing (see Fry, B. & Reas, C. Processing URL https://processing.org/). The model simulates the time dynamics of individuals belonging to a set of 14 hypothetical species (see Table S1), living in a randomly generated landscape initially comprising three contiguous habitat types and a set of protected areas (Figure 1). The region is initialized in a pseudorandom pristine state. The extent and configuration of each habitat is generated randomly from defined spatial ranges, while the location of protected areas is drawn randomly and the configuration determined randomly within a defined range. The species agents are subsequently distributed randomly within habitat types. The region is then subjected to habitat conversion, climate change, and species invasions.

There are four native species types within the model: habitat specialists, habitat generalists, disturbance tolerants, and climate sensitives. Each species type has an affinity for its native habitat (Figure 1). Habitat specialists can exist only inside their native habitat, while other types can persist in other natural habitats or in the converted matrix if other criteria are met. Assuming that resources are more limiting in the matrix (Felton et al. 2003), only a limited density of conspecific generalists can be supported in the matrix, while disturbance-tolerant species can only exist within a threshold distance of their native habitat. There was no density dependence in native habitats. Climate-sensitive organisms can exist anywhere as long as the climatic conditions are within their tolerance range. Each natural habitat is initialized with 20 individuals of each species type. The model also incorporates two additional species types: exotic generalists and exotic climate-sensitive organisms. These are not present in the initial model landscape but are probabilistically introduced following anthropogenic change. The simulation moves forward in time intervals of 25 years, and at each step, habitat is converted following a random walk from a randomly chosen start location at a rate of 0.2% per year, approximately equivalent to the global rate of conversion of pristine habitat to human-dominated area documented in the HYDE reconstruction of land-use change (Goldewijk 2001) and observed in global land conversion data (Balmford et al. 2003). The ambient temperature of the region increases at a rate of 0.01 °C per year. Source code for the model can be obtained from https://github.com/mikeharfoot/Reconciling-Biodi versity-Indicators

The model was used to generate biodiversity metrics comparable to those most often used to characterize biodiversity (see above): species richness, population abundance, and extinction rates. Richness and abundance were measured over time at two different spatial scales: a local scale comparable to a single plot (which was sited randomly) and a regional scale (i.e., across the whole landscape) such as may be targeted for national, regional, or ecosystem-wide assessments. Extinction rate was only measured at the regional scale since it has little meaning at the plot scale. We also calculated a metric of compositional similarity through time-Bray Curtis similarity, which takes into account both species identities and their abundances (Bray & Curtis 1957)-to measure the overall similarity of the regional community at each time step to the initial state. A value of 1 indicates that the community has a composition of species in identical relative abundances to that of the initial state, and a value of 0 indicates that no initial species are present in the current community. The necessary data are seldom available to calculate compositional similarity for real ecosystems.

Full details of the model are provided in Section S2.

Results

The narrative

Most experts described change to global biodiversity in terms of loss of species (extinctions), loss of species abundance, and spatial changes due to invasions, loss of habitat, geographic range shifts, and homogenization processes (see Table 1). Experts were more confident when making statements at a global scale than at regional or local scales, and were more confident about the state of biodiversity than the causes of change, with particularly high uncertainty over how anthropogenic pressures interact and the consequences for ecosystems. Experts were more confident when making statements about vertebrates, and identified gaps in knowledge concerning invertebrates, some plants, and microbes (see Section S3 for details).

The key threats (habitat degradation and loss, climate change, and invasive species) were identified as affecting species differentially so that the simulation included species with differing sensitivities (see Methods section). Protected areas were identified as a key response and were therefore included within the simulation landscape.

The simulation results

Figure 2 shows how the four metrics (species richness (a), species abundance (b), extinction rate (c), and compositional similarity (d)) respond over a 400-year period. Regional richness increases in the early stages of the simulation due to the introduction of exotic species to the region while native specialists persist. Regional richness shows a clearer response than the plot-based metrics that are subject to sampling variation across the landscape. After around 1900, however, many habitat specialists and climate-sensitive species are extirpated leading to rapid declines in regional richness and increases in extinction rate. Plot-level richness declines monotonically throughout these simulations as species are lost from the sites faster than exotics establish. Both regional and plot-level abundances decline but asymptote once all sensitive species are filtered out. Because the original assemblage is known precisely in these simulations (as opposed to in real life), we can also track change in compositional similarity to the starting condition over time. Unlike other metrics, compositional similarity has declined sharply, linearly, and continuously.

 Table 1
 Summary of major findings from the survey of experts used to create the narrative. Details of the questions posed and answers given are provided in the Sections S1 and S3, respectively

Main generalizations	Further comments
There are widespread global	We are more certain of the status of vertebrates than other taxonomic groups
losses in species abundance	All species, including common species, may be impacted
and range size	Large-bodied mammal populations are rebounding from a very low baseline in North America and northerr Europe.
	Large predators and all medium-sized animals are declining in Africa and other developing nations outside protected areas due to persecution and hunting
	Large-bodied mammals have declined (on average) in the past 50 years
	Freshwater species are faring worse than other groups, everywhere and including most taxa
	The marine environment is really suffering in nearshore parts of Africa due to intensive fishing.
Many species are threatened	Invertebrates are just as threatened as vertebrates
with extinction and the situation is not improving	Specialist species are worse off than generalist species
Local species richness is not declining	Locally, across sites at plot scale, there is no overall change in species richness over time for plant communities
	In time series, there is no overall loss of species richness within sites
	This may be temporary and due to extinction debt or introduced species
Local species richness is declining	Selected species are being removed from ecosystems
Homogenization is occurring	Invasions of nonnative species are very significant in this process
 species communities are becoming more similar 	This can lead to losing diversity globally but not locally
Climate change is set to	Species ranges are moving consistent with climate change
further impact biodiversity	Climate change is already affecting species in the oceans and at high latitudes on land
	As climate change increases in scope and severity, it will affect susceptible species and those subject to other threats
	We do not understand how pressures from climate change will interact with other pressures such as hunting and land conversion
Invasive species pose a threat	Currently, this is especially evident on islands and increasingly in continental areas
to native species	Invasive species are greatly underreported in Africa and the tropics
The establishment of protected areas is preventing species loss in some places	The rate of habitat loss has increased over the past 50 years—this has been the primary driver of wildlife decline
Biodiversity has been	Reduction of area of natural habitats causes "overcrowding" of habitat specialists, causing an extinction
detrimentally impacted by	debt of unknown size and duration
loss and degradation of habitat, human presence, and harvesting	We need ecosystem-level analyses of how these pressures interact

Discussion

While the narrative is simplistic and the simulation stylized, we suggest that the coupling of these approaches is valuable in a number of different ways. First, our approach acts as a heuristic tool. The narrative of change derived from expert judgment can be encoded in a simulation model that can be used by biodiversity experts, policy makers, and general public to better understand how responses emerge. As a result, our approach provides a straightforward means to explain and even enhance the messages derived from the suite of biodiversity metrics, which may be confusing to policy makers and the general public, or even be interpreted as conflicting. For example, evidence that there is no local loss of diversity on average (Vellend *et al.* 2013; Dornelas *et al.* 2014) may seem to be inconsistent with evidence for overall loss of abundance (Dirzo *et al.* 2014) (though see Gonzalez *et al.* 2016). However, our simulation shows that short-term stability in species richness can be consistent with significant decreases in abundance (Figure 2). Similarly, greatly elevated global extinction rates (Barnosky *et al.* 2011; Pimm *et al.* 2014) are consistent with much lower levels of net loss—or even gain—in local species richness, both of

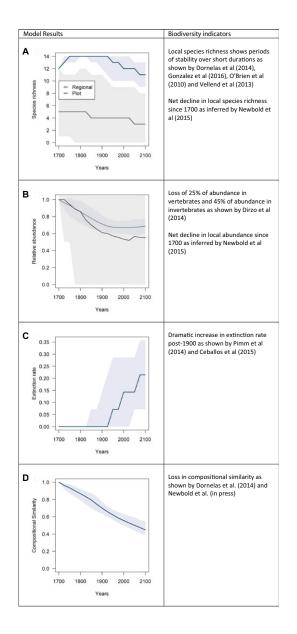


Figure 2 Comparison of time series of biodiversity metrics emerging from an ensemble of 125 simulations of the stylized biodiversity model with recent biodiversity indicators. Dark lines on plots indicate median responses and shaded regions show minimum and maximum ranges. (a) Species richness is a count of the number of species in the entire region (blue) or measured at the plot scale (black). (b) Abundance is the total number of individuals—irrespective of species—in the entire region (blue) or measured at the plot scale (black). (c) Extinction rate is the proportion of all species present at the start of the simulation that have been lost, recorded across the entire region. (d) Compositional similarity between the ecological community in the simulation at each time step and its initial state. The compositional similarity index has a value of 1 when the community composition is the same as the initial state and zero when none of the same species are present, and is based on 125 simulations with the line showing the median result and the shaded regions indicating maximum and minimum observed values.

the net outcomes of local invasions and homogenization, and because of the longer term stabilization. The failure of commonly used diversity metrics, such as local species richness and abundance, (Figures 2a and b) to capture fully the rapid ongoing degradation in the composition of the ecological assemblage (Figure 2d) is a worrying feature for indicators that might be used as a basis for policy decisions. However, the ability to present a consensus view based upon evidence from a variety of indicators, capturing differing aspects of biodiversity, is advantageous when communicating with policy makers, and it is encouraging that we did not observe any metrics that diverged from the narrative.

Second, the simulation results demonstrate that, with recognition of cause and effect, it is possible to link biodiversity indicators dynamically. Though currently poorly understood, these relationships can be improved dynamically as we gain more ecological understanding. Future knowledge may support functional or even phylogenetic diversity metrics that could underpin the development of more efficient and informative indicators providing information better linked to decisions (Jones *et al.* 2011), for example, when comparing community changes resulting from two different patterns of habitat loss (Keil *et al.* 2015).

Third, a more comprehensive dynamic framework would permit more meaningful integration of biodiversity models into 1) decision-analysis tools, for example, to demonstrate the consequence of climate change affecting only the most sensitive species, or the conservation interventions that might best mitigate the impacts of a particular anthropogenic pressure on biodiversity, and 2) IAMs to demonstrate biodiversity feedback to socioeconomic futures. This would allow robust and evidencebased biodiversity goals to be produced. Until such integration takes place, it is hard to see how biodiversity can be mainstreamed into the development agenda.

There are many candidate models to support such developments, such as those that are being reviewed for the IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, see http://www.ipbes.net/) guide for scenario analysis and modeling of biodiversity and ecosystem services. Here, for illustration, we focus on the potential benefits of integration across two particular types of model that lie at opposite ends of the pattern- to process-based model continuum and differ in the characteristic units of ecological representation: taxonomic-versus functional-trait based. The PREDICTS model is a statistical model that currently focuses on land-use change, and allows various biodiversity metrics to be predicted based on a global compilation of studies of local ecological communities (Hudson

et al. 2014; Newbold et al. 2015). Already PREDICTS can be used to illustrate how different metrics of local biodiversity may behave under different extrinsic forces at different scales (Newbold et al. in press; Newbold et al. 2015). However, PREDICTS contains no ecological processes, it is entirely empirical based on a large number of observations, and currently cannot be used to predict changes in regional or global biodiversity. Spatial and temporal dynamics relevant to real ecological systems are most directly incorporated through process-based models, such as the Madingley model (Harfoot et al. 2014b) or the Ecosim model (Walters et al. 2002); such models have the additional advantage that they can report directly on some aspects of ecosystem function and services, such as biomass production or aspects of ecosystem dynamics such as stability or resilience, but do not currently report on the species-based biodiversity variables that are used to calculate currently mainstream indicators.

By coordinating these different modeling approaches, it will be possible to substantially strengthen simulations that establish cause and effect through the DPSIR framework. This could refine the process of indicator production, from focusing data collection toward key metrics, to defining and implementing indicators that more comprehensively describe the changing state of the system. As a whole, this development would allow the conservation community to more strategically and effectively evaluate how the biodiversity and ecosystem targets of the SDGs can be met simultaneously with those for socioeconomic development.

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Author contributions

The project was designed by GM, DP, and AP; MH and DP developed the simulation; and SH and GM developed the narrative. GM, SH, and MH led the writing of the article with contributions from all authors.

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