UC Merced

Frontiers of Biogeography

Title

Macroecology meets IPBES

Permalink

https://escholarship.org/uc/item/93k7n8w2

Journal

Frontiers of Biogeography, 7(4)

Authors

Hof, Christian Dehling, D. Matthias Bonn, Aletta et al.

Publication Date

2015

DOI

10.21425/F5FBG28888

License

https://creativecommons.org/licenses/by/4.0/ 4.0

opinion

Macroecology meets IPBES

Christian Hof^{1*}, D. Matthias Dehling^{1,2}, Aletta Bonn^{3,4,5}, Neil D. Burgess^{6,7}, Felix Eigenbrod⁸, Michael B. J. Harfoot⁶, Thomas Hickler^{1,9}, Walter Jetz¹⁰, Elisabeth Marquard¹¹, Henrique M. Pereira^{4,12,13} and Katrin Böhning-Gaese^{1,14}

¹Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt (Main), Germany. ²School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand. ³Department of Ecosystem Services, UFZ - Helmholtz Centre for Environmental Research, Permoserstr. 15, 04318 Leipzig, Germany. ⁴Institute of Ecology, Friedrich Schiller University Jena, Dornburger -Str. 159, 07743 Jena, Germany. ⁵German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany. 6UNEP-WCMC, 219 Huntington Road, Cambridge, CB3 0DL, UK. ⁷Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, DK-2100, Copenhagen, Denmark. 8Centre for Biological Sciences, University of Southampton, Southampton SO17 1BJ, UK. 9Department of Geosciences and Geography, Goethe University, 60438 Frankfurt (Main), Germany. ¹⁰Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect Street, New Haven, Connecticut, USA. ¹¹Department of Conservation Biology, UFZ - Helmholtz Centre for Environmental Research, Permoserstr. 15, 04318 Leipzig, Germany. 12 Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany. ¹³Infraestruturas de Portugal Biodiversity Chair, CiBiO/InBIO, Universidade do Porto, 4485-661 Vairão, Portugal. ¹⁴Department of Biological Sciences, Goethe University, 60438 Frankfurt (Main), Germany

*corresponding author: phone: +49 (0) 69 7542 1804, e-mail: christian.hof@senckenberg.de, http://www.bik-f.de/root/index.php?page_id=773

Abstract. The Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES), established in 2012 to counter the biodiversity crisis, requires the best scientific input available to function as a successful science-policy interface that addresses the knowledge needs of governments for safeguarding nature and its services. For the macroecological research community, IPBES presents a great opportunity to contribute knowledge, data and methods, and to help identify and address knowledge gaps and methodological impediments. Here, we outline our perspectives on how macroecology may contribute to IPBES. We focus on three essential topics for the IPBES process, where contributions by macroecologists will be invaluable: biodiversity data, biodiversity modelling, and modelling of ecosystem services. For each topic, we discuss the potential for contributions from the macroecological community, as well as limitations, challenges, and knowledge gaps. Overall, engagement of the macroecological community with IPBES should lead to mutual benefits. Macroecologists may profit as their contributions to IPBES may strengthen and inspire them as a community to design and conduct research that provides society-relevant results. Furthermore, macroecological contributions will help IPBES become a successful instrument of knowledge exchange and uncover the linkages between biodiversity and human well-being.

Introduction

To counter the global biodiversity crisis, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) was established to facilitate the effective use of knowledge on biodiversity and ecosystem services (ESS) in decision-making at all levels. To this end, three of the most important tasks of IPBES¹ are (i) identifying and prioritizing key scientific information needed for policymakers, (ii) performing regular and timely assessments of knowledge on biodiversity and ecosystem services, and (iii) supporting policy formulation and implementation (Opgenoorth and Faith 2013). IPBES thus has the mission to provide information on issues related to biodiversity and ESS and to thereby support decision-making in these fields. To implement its work programme successfully via its conceptual framework (Díaz et al. 2015a, 2015b), IPBES needs to mobilize and engage relevant communities of scientists and other knowledge holders.

The 'scenario and modelling assessment' currently in preparation, in which several macroecologists and biogeographers are prominently involved, is providing a first window of opportunity to showcase how these expectations may play out in reality. Furthermore, and central to IPBES, a number of regional and sub-regional assessments as well as a global assessment of the status and future trends of biodiversity and ESS are now underway. These assessments additionally aim to capture how threats to biodiversity and ESS may impact human well-being and the extent to which political responses to these challenges are effective. Over the next years, these assessments within Objective 2 (see Table 1) will constitute the core body of the IPBES work program, and macroecological contributions will be essential for the success of this assessment work.

The macroecology community (which we here view in a rather inclusive way, i.e. as also including biogeographers and community ecologists) may also profit considerably from engagement with IPBES, as it may strengthen and inspire them to design and conduct research that pro-

vides society-relevant results. Thus, we see mutual benefits for IPBES and the macroecology community from engaging in the IPBES process.

In the following, we outline potential areas for particularly fruitful contributions from macroecology to IPBES (Table 1). We focus on those areas where we think macroecology will be able to make significant contributions, specifically regarding biodiversity data and the modelling of biodiversity and ESS. Furthermore, we identify the most important knowledge gaps with regard to the questions tackled by IPBES that need to be addressed by macroecologists in the near future.

Biodiversity data

Information needs

Biodiversity has many facets and properties (phenotypes, traits, functions, richness, etc.) set at different levels of organization (from genes, populations, species to communities and ecosystems) and associated ecological and evolutionary processes. The assessment of key facets of biodiversity - their basic description and their occurrence in space and time - is an essential first step to capture information vital for evaluating their conservation and sustainable use, their contribution to ESS, and their relevance for human well-being and sustainable development (Pereira et al. 2012). Species-level information on spatial occurrence and/or abundance remains a critical biodiversity data category (Jetz et al. 2012). Collected over time, this information enables tracking global conservation targets down to monitoring species at individual sites. It also provides crucial basic information to parameterize and validate any effort in model or scenario development.

Overall, quality assessed, representative, and readily accessible spatio-temporal information on species distribution and abundance is thus a key need for addressing the IPBES mission. However, to become truly relevant for the successful use within the IPBES process, the scope of required data types reaches beyond species distributions. Data on genetic diversity, species' abiotic requirements, biotic associations or co-occurrence

¹ http://www.ipbes.net/images/Functions%20operating%20principles%20and%20institutional%20arrangements%20of% 20IPBES 2012.pdf, last accessed 09/10/2015.

Table 1. Potential opportunities for contributions from macroecology to the objectives and associated deliverables of the IPBES work programme

Objectives and deliverables* **Macroecological contributions** general contributions and selected examples for contributions from macroecological work conducted in the short- and midterm future

- 1. Strengthen the capacity knowledge foundations of the sciencepolicy interface
- (d) Priority knowledge and data needs for policymaking addressed through catalysing efforts to generate new knowledge and networking
- 2. Strengthen the science-policy interface at and across subregional, regional and global levels
- (a) Guide on production and integration of assessments from and across all scales
- (b) Regional/subregional assessments on biodiversity and ecosystem services
- (c) Global assessment on biodiversity and ESS
- 3. Strengthen the science-policy interface with regard to thematic and methodological issues
- (b) Three thematic assessments: (i) land degradation and restoration; (ii) invasive alien species; (iii) sustainable use and conservation of biodiversity
- (c) Policy support tools and methodologies for scenario analysis and modelling of biodiversity and ESS
- 4. Communicate and evaluate Platform activities, deliverables and findings (b) Development of an information and
- data management plan

- Identify data needs and availability
 - identify of crucial deficits of knowledge and data; stress funding deficits for collection of primary data
 - strengthen and set up (additional) biodiversity monitoring schemes
 - improve access to and use of data from national or regional agencies
 - integrate various data types and sources via novel modelling techniques
 - engage in development of Essential Biodiversity Variables
- Identify opportunities and challenges, and provide methodological tools for linking spatial and temporal scales
 - compare performance of different models at different scales
- Provide knowledge and methods for describing and explaining the spatial and temporal variation of biodiversity and ESS on subregional, regional and global scales
 - improve links to remote sensing
 - invest more in understanding effects of biotic interactions in macroecological models
 - establish more direct links between mechanistic biodiversity models and ESS analyses
- Contribute data and methods for the three thematic assessments, especially for (ii) and (iii)
- Provide scientific foundation for the scenario and modelling assessment with provision of data and methods, as well as method development
 - find ways to improve identification and communication of uncertainties of models and scenarios
 - link different modelling types and approaches (e.g. SDMs and DGVMs)
 - establish more quantitative links among biodiversity, ecosystem functions and ESS across different scales
 - synthesize current knowledge on relationships between biodiversity and ESS
 - invest in empirical estimation of human benefits from biodiversity functions and processes
- Contribute experience with information and data sharing programs and platforms
 - improve digitization, harmonization and sharing of existing data

in communities are important for informing modelling activities. In addition, trait data may address species' roles in ecosystem functioning and ESS provision, and data on individual or population-

level genetic, trait or niche variation may provide information about the potential for adaptation and likely biodiversity responses to global change. The identification of over twenty Essential Biodi-

^{*}excerpt from the platform work programme 2014-2018 (IPBES/2/2) with relevance for macroecological contributions

versity Variables relevant for IPBES (Pereira et al. 2013) is a great advancement, but some of those variables require measurement across many species or habitats. Given these data needs, identifying avenues to prioritize efforts is paramount. One useful first step is capturing what key science communities can already provide at this point.

Data contributions: macroecological opportunities and challenges

Over the last decades, taxonomic, biogeographic, and (macro)ecological research has, together with agency and citizen science efforts, invested great effort in compiling and analysing biodiversity data. Various initiatives have increased the availability of spatial biodiversity data, such as the databases compiled as part of IUCN Red List Assessments (threat-related attributes and expert-drawn maps²), the Global Biodiversity Information Facility (GBIF; museum and other point records³) the Ocean Biogeographic Information System (OBIS, museum and other point records⁴), citizen science platforms such as eBird (Sullivan et al. 2009⁵), extensive monitoring efforts based on networks of volunteers such as the Breeding Bird Survey in North America⁶, or atlas survey efforts (such as the British Dragonfly Atlas'). Trait data has similarly seen an increase in digital availability, thanks to recent trait databases for animals (Jones et al. 2009, Foden et al. 2013, Wilman et al. 2014) or plants (Kattge et al. 2011).

However, a first challenge will be the aggregation of biodiversity information at scales relevant for the IPBES process. The coverage of most macroecological studies does not match with the areas defined for the regional assessments of IPBES, which are based rather on political than on biogeographic boundaries; the assessment for Asia and the Pacific, which includes areas from the Middle East via Australia to French Polynesia, is

probably the most extreme example. Furthermore, heavy taxonomic and regional biases in the availability of data on biodiversity distribution and change remain (Meyer et al. 2015). For instance, tropical regions with the highest diversity are largely under-sampled (Beck et al. 2012, 2014). Similarly, most invertebrate taxa, marine species, and the majority of the plant kingdom, which altogether constitute the largest portion of diversity, are poorly sampled both in terms of distribution and monitoring (Beck et al. 2012). Even though efforts for compiling data on biodiversity change are increasing (Collen et al. 2009, Hudson et al. 2014, Bowler et al. 2015, Dulle et al. 2015), such data compilations remain sparse, with only a few countries having national biodiversity monitoring systems in place (Pereira et al. 2012). Furthermore, despite first initiatives on the compilation of comprehensive trait databases (see above), such data are still lacking for most taxa.

Towards more and better data for more and better use

To increase the taxonomic and geographic coverage of the databases, incentives need to be developed for collecting (new) data in standardized and coordinated ways, for harmonizing, sharing and digitizing existing data, e.g. from museum collections, and for publishing 'raw data', e.g. in the form of descriptive studies. Here, online infrastructure such as the Map of Life (Jetz et al. 2012) can serve as catalyst by highlighting data gaps and offering collaborative tools for data integration, quality control, visualization and analysis - thus directly supporting IPBES assessment methods. Rapidly growing citizen science efforts offer great potential to help address identified data gaps and provide vast information, especially for more popular and readily identified taxa (Bonney et al. 2014). Novel modelling approaches appear to

² http://www.iucnredlist.org/, last accessed 09/10/2015

^{3 &}lt;a href="http://www.gbif.org/">http://www.gbif.org/, last accessed 09/10/2015

⁴ http://www.iobis.org/, last accessed 09/10/2015

⁵ http://www.ebird.org/, last accessed 09/10/2015

⁶ https://www.pwrc.usgs.gov/bbs/, last accessed 09/10/2015

⁷ http://www.british-dragonflies.org.uk/content/national-dragonfly-atlas/, last accessed 09/10/2015

⁸ http://www.ipbes.net/images/decisions/ipbes3/Decision_IPBES_3_1_EN.pdf (p. 36), last accessed 16/12/2015

^{9 &}lt;a href="http://mol.org/">http://mol.org/, last accessed 09/10/2015

open promising avenues for the integration and harmonization of different data types as well as correcting for collection biases (Phillips and Elith 2013, Iknayan et al. 2014, Keil and Jetz 2014, Pagel et al. 2014). Furthermore, the integration of additional data types such as information on genetic diversity or physiological traits allows a better understanding of biodiversity responses to global change impacts (Kearney and Porter 2009, Khaliq et al. 2014, 2015, Sunday et al. 2014, Fristoe et al. 2015), vital for the IPBES goal of addressing future scenarios.

Perhaps the major question is how to move forward the monitoring of biodiversity change. Macroecologists should engage in the current process of developing Essential Biodiversity Variables, helping to identify the variables that need to be measured across taxa and regions (Pereira et al. 2013). We also need to develop efficient and effective approaches for the measurement of those variables, combining in situ and remote sensing, and further developments in integrating and harmonizing existing observations (Jones et al. 2011, Pereira et al. 2013). The current limitation of resources available for data acquisition or digitization is a crucial impediment for further progress. While opportunities should not be missed to emphasize the need of mobilizing adequate funds for these efforts, it is therefore also required to use existing data, such as those collected by national or regional agencies more efficiently and to identify priorities.

Modelling of biodiversity

Information needs

Models help understand the spatial and temporal variation in biodiversity in response to both environmental variation and anthropogenic pressures. However, we are lacking biodiversity models that capture the many dimensions of biodiversity holistically, as most models deal with a geographic, taxonomic or functional subset of ecological communities. To build a picture of how biodiversity as a whole is changing, models are required that can be used in an integrated manner. Such a suite of models would be useful in an IPBES context to demonstrate the projected impacts of anthropo-

genic pressures now and in the future, under different scenarios of human development.

What information can macroecology provide at present?

Currently, macroecological modelling (which we focus on, while acknowledging that numerous other approaches of biodiversity modelling exist) can be classified into broad and largely discrete domains along several lines, including methodological approach, taxonomic coverage or intended application. Here we categorise a set of example models according to their methodological approach – correlative or mechanistic – and consider what information these models can provide in isolation and collectively.

Correlative models. Correlative models which relate the variation of biodiversity features across space and time to other factors, e.g., contemporary climatic conditions, are perhaps the most widely used approach in macroecological modelling. Correlative approaches can be further subdivided into models focusing on emergent features of species assemblages (e.g., species richness) and species distribution models (Guisan and Rahbek 2011).

'Classic' macroecological modelling mainly deals with establishing statistical relationships between diversity measures of species assemblages and the variation in environmental variables (Currie 1991, Rahbek et al. 2007, Algar et al. 2009, Dehling et al. 2010). Common diversity measures include species richness, beta-diversity, functional or phylogenetic diversity (Orme et al. 2005, Graham et al. 2009, Thieltges et al. 2011a, 2011b, Fritz and Rahbek 2012). The overarching aim is to infer general processes that govern the distribution of life in space and time, hence providing a fundament for understanding and projecting the future of biodiversity in a changing world. Over recent years, initiatives such as the GLOBIO model (Alkemade et al. 2009) or the PREDICTs framework (Hudson et al. 2014, Newbold et al. 2015) use advanced tools of correlative modelling to assess human-induced changes in biodiversity and to project potential futures of biological communities in order to inform conservation efforts.

Species distribution models (SDMs, also referred to as ecological niche models or habitat suitability models) relate occurrence (or abundance) data of single species to environmental information in space to understand species' distributions and environmental preferences, and to project species' potential distributions (Guisan and Zimmermann 2000, Elith and Leathwick 2009). While early SDM studies were simple and mostly built on climatic variables, improving data on environmental drivers, e.g., from remote sensing, new methods (machine learning, maximum entropy, etc.), enhanced computing power, as well as biodiversity data availability have led to great improvements (Elith et al. 2006, Zimmermann et al. 2010, Higgins et al. 2012). Recent studies also incorporate information on species' response mechanisms, e.g., via physiology or dispersal (Buckley et al. 2010, Jaeschke et al. 2013, Ceia-Hasse et al. 2014), or genetic information (Bálint et al. 2011). Despite several shortcomings that need to be considered (Araújo and Peterson 2012), SDMs are powerful tools to analyse and project species distributions. Thereby, SDMs, diversity models (see above) and combinations of both (Guisan and Rahbek 2011) constitute a key methodological asset from macroecology to IP-BES.

Mechanistic models. Mechanistic models are a genre of biodiversity models which aim to more closely represent or explicitly include the population dynamic, physiological, or ecological processes affecting species distributions or the spatial variation of diversity. In the macroecological context, there is a long pedigree of such models for plants, ocean microbial communities and marine ecosystems (e.g., Prentice et al. 1992, Follows et al. 2007). However, there are fewer such mechanistic models for terrestrial heterotrophs. Here we focus on mechanistic models of terrestrial biodiversity, namely on models of the plant community and models of higher trophic levels.

At the level of main tree species, plant functional types, and ecosystems, structurally very different process-based modelling approaches

have been developed. These include forest gap models (Bugmann 2001) and Dynamic Global Vegetation Models (DGVMs; for a review, see Prentice et al. 2007; for recent studies, see e.g., Scheiter and Higgins 2009, Gonzalez et al. 2010, Pavlick et al. 2012, Scheiter et al. 2013). Forest gap models simulate the population dynamics and growth of major tree species and are commonly parameterized for particular species and regions (e.g., Landsberg 2003). Based on their functional characteristics, DGVMs aggregate species into global plant functional types which compete for resources. Model outputs include the distribution of biomes, occurrence and effects of fires, vegetation structure and biogeochemical fluxes between soil, vegetation and atmosphere, and vegetation net primary productivity, some of which are closely related to ESS.

Macroecology has also been fundamental for the development of ecosystem models that include several trophic levels (e.g., Christensen and Walters 2004, Fulton et al. 2011 for marine systems). Higher trophic levels have also been included in DGVMs, which makes it possible to estimate livestock carrying capacities (Pachzelt et al. 2013, 2015). Recently, a general ecosystem model applicable globally and in all terrestrial and marine environments has been developed (Purves 2013, Harfoot et al. 2014a): the Madingley Model attempts to mechanistically represent whole ecosystems by modelling all the individual heterotrophic organisms in each ecosystem according to their functional traits and based on a set of fundamental ecological processes (Harfoot et al. 2014a).

Towards more powerful biodiversity models

To parameterize and evaluate biodiversity models, and to adjust projections of biodiversity, quantitative data on observed biodiversity change from monitoring are crucial. Underlying data are often available in different spatial resolutions, and biodiversity projections are needed at different spatial scales. The PREDICTS project which assembles data on biodiversity exposed to varying anthropogenic pressures at the local scale and which covers a large range of species, ecosystems and ecoregions (Hudson et al. 2014, Newbold et al. 2015), is

a promising approach in this regard.

More studies are needed that compare the performance of different kinds of models at different spatial scales (e.g., Thuiller et al. 2003, Elith et al. 2006). Such model verification and validation is crucial for any endeavour of biodiversity modelling and projection. The identification and communication of uncertainties and limitations is of prime importance, such as the poor predictability of important variables like fire, or the uncertainty involved with the projection into novel climates and environments (Eigenbrod et al. 2015). As another example, the now very popular concept of tipping points or planetary boundaries (Rockström et al. 2009) is inherently linked to uncertainties surrounding the definition of thresholds. Here, macroecology might help to quantify the levels of uncertainty surrounding the tipping points, as well as to reduce uncertainties by the provision of credible data. IPBES should, through its assessment work, emphasize these challenges and encourage researchers and institutions to invest more in these issues.

Currently, future projections of species distributions are often still based on simple abiotic variables. Advances could be made by incorporating other drivers into models of species distributions, such as a land cover change (Hurtt et al. 2011), changes in nitrogen availability and deposition, as well as biome shifts and changes in vegetation (driven by climate and land use change). Both forest gap models and DGVMs simulate changes in habitat characteristics, which can also be used as predictors in SDMs or population dynamics models (Triviño et al. 2011, Linder et al. 2012, Pachzelt et al. 2013). We think that such approaches of linking DGVMs and SDMs have great potential. Another promising avenue is improving the link between species distributions, species richness and various remote sensing products (Asner and Martin 2009, He et al. 2011, Pettorelli et al. 2011).

As mentioned above, models depend on the underlying data (Platts et al. 2014), and the need for more and better data and especially an in-

creased regional and taxonomic coverage of fundamental species distribution data cannot be overstressed. To link biodiversity data to ESS, models of functional diversity and ecosystem functions appear to be promising (see also below). However, to implement such models over large spatial extents, better information on species' functional traits and habitat requirements is needed (e.g., Rondinini et al. 2011). We also need research about which traits are relevant for the functions in focus (Violle et al. 2007, Dehling et al. 2014) and which may constrain or facilitate coexistence. The inclusion of biotic interactions in spatial biodiversity models remains challenging (Cooper and Belmaker 2010, Gotelli et al. 2010, Araújo et al. 2011, Kissling et al. 2012, Kissling and Schleuning 2015) and in great need of additional empirical and conceptual work.

Overall, a better exchange between different modelling communities but also between modellers and conservationists would help to identify modelling approaches relevant for the conservation of biodiversity. More generally, changes in biodiversity should be compared to changes in other sectors, e.g., agriculture, energy or health, which is currently attempted by the Inter-Sectoral Impact Model Intercomparison Project (isi-mip¹⁰; see also Harfoot et al. 2014b).

Modelling of ecosystem services

Information needs

The overarching goal when modelling ESS is to quantify the relationships between ecosystems (the potential or stocks and flows of ESS) and the different segments of human society that may (a) benefit from them and (b) help to provide ESS flows through additional human and financial capital input. Of particular interest for policy and planning is to quantify not only the current distributions of ESS, but also their capacity (Mace et al. 2015) and future trajectories (positive or negative) under different socio-economic scenarios (Reed et al. 2013). As such, ESS models are effectively models of coupled socio-ecological systems (Carpenter et al. 2009), and therefore frequently very chal-

10 https://www.pik-potsdam.de/research/climate-impacts-and-vulnerabilities/research/rd2-cross-cutting-activities/isi-mip, last accessed 09/10/2015

lenging to develop. As ESS are inherently spatial (Swetnam et al. 2011), modelling of ESS effectively means producing maps of current and future distributions of ESS at policy-relevant spatial scales.

In an IPBES context, there is recognition of the overarching question outlined above, but a particular focus on developing "... models assessing the impacts of drivers and changes in biodiversity on ESS" (IPBES/2/16/Add.4). Understanding the entirety of how changes in biodiversity affect ESS is an enormous challenge, particularly as the relationships between biodiversity, ecosystem functioning, and ESS remain relatively poorly understood (Cardinale et al. 2012). Nonetheless, models are already able to identify synergies and trade-offs of land management for different ESS. It is crucial to understand which land use or land cover changes are likely to increase or decrease which elements of biodiversity and ESS provision now and in the future, and how communities across the globe will be affected. Ideally, the models of synergies and trade-offs should be sufficiently complex to capture interactions and feedbacks between the social and ecological drivers of such land use/land cover changes and thereby to anticipate or predict indirect land use changes, too. Interactions are likely to be non-linear, complex and scale dependent (Evans et al. 2014), and IPBES assessments need to convey this complexity in an accessible manner to decision makers and clearly identify uncertainties. Overall, the feedback loops in socio-ecological systems need to be elucidated to assess synergies and trade-offs in managing for biodiversity and ESS and other societal goals. Furthermore, indicators for potential tipping points need to be identified (see also above) as well as pathways for how conservation and restoration strategies may serve to safeguard biodiversity and support the sustainable provision of ESS and thereby human well-being.

Available information and identified challenges Perhaps the single greatest challenge in ESS science remains the lack of primary data for most services in most places, and the lack of reliable

spatial proxies (Eigenbrod et al. 2010). As recently as 2008, an attempt to map all possible ESS globally resulted in only four services being mapped carbon storage and sequestration, grassland production of livestock, and water provision (Naidoo et al. 2008). Since 2008 there have been major conceptual advances (Maes et al. 2012, Martín-López et al. 2012, Crossman et al. 2013, Van der Biest et al. 2014), but progress on producing global maps of ESS has been rather slow (see e.g. Balmford et al. 2015). However, as most biodiversity-related decision making is taking place at the regional or even local level, regional models are of prime importance, and global models should have the flexibility to adapt to the special conditions of different regions. Particular challenges exist where ESS distributions are not strongly linked to readily available GIS layers (i.e., land cover, elevation) but are highly context-dependent. Such services include pollination, as well as most cultural services, whose nature and intensity differ across different cultural settings. Moreover, individual ESS models are generally not coupled, and thus future feedbacks and interactions between services cannot be identified.

Our understanding of how changes in biodiversity affect ESS is even more poorly developed. Although species richness and higher variation in species composition is thought to generally increase ESS, patterns vary by service and region, and these findings are largely based on small-scale, mostly experimental work (Cardinale et al. 2012). More global, empirical analyses, such as Maestre et al. (2012) will enable the type of large-scale understanding of the relationships among biodiversity, ecosystem functions, and ESS that are called for within IPBES (see also Midgley 2012).

Towards an integration of biodiversity and ESS models

It is likely that ESS modelling will advance sufficiently over the next years to at least partially meet the stated goals of IPBES. Modules within major ESS modelling platforms are advancing rap-

11 http://www.ipbes.net/images/documents/plenary/second/working/2_16/IPBES_2_16_Add.4_EN.pdf, last accessed 09/10/2015

idly by building on an increasing number of case studies (e.g., Ruckelshaus et al. 2015) and, crucially, by incorporating process models from different fields. Nevertheless, ESS work that is more stakeholder-oriented or social-science-based still often relies on relatively simple proxies for ecosystem services, such as land cover for erosion risk or soil organic carbon content for soil fertility (Maes et al. 2012). We think that more direct linkages between mechanistic models and ESS analyses have potential, building on recent efforts to couple biophysically-based models from different disciplines. These include DGVMs and hydrology models (e.g., Betts et al. 2007, Gerten et al. 2008), or in the case of Integrated Assessment Models, such as IMAGE 3.0 (Stehfest et al. 2014), climate, biome, biodiversity (when coupled to GLOBIO, Alkemade et al. 2009), hydrology, crop and land use models.

We need a better integration between disciplines and more incentives for inter- and transdisciplinary research. Closer collaborations between social and natural scientists as well as experts from policy and practice in research design and productions may enhance mutual understanding and developing new models. For instance, there is an emerging literature examining the full global life cycle impacts of the goods and services consumed in different countries on various natural resources (e.g., Peters et al. 2011, Holland et al. in press) and biodiversity (e.g., Lenzen et al. 2012) by using multiregional models based on trade data, such as the GTAP database¹². For example, it has been shown that within-country reductions in carbon emissions by industrialised countries were completely offset through emissions associated with the import of goods from developing countries (Peters et al. 2011). Other studies have assessed the effects of managing for carbon conservation under the REDD+ mechanism under the IPCC on other ESS (e.g. Runsten et al. 2013), including aspects of leakage effects, i.e., when conservation programmes displace adverse land use and land use change to other areas (e.g., Strassburg et al. 2012). Given the interconnected nature of the global socio-ecological system, it could be fruitful to integrate analyses of international trade patterns in IPBES assessments.

However, despite such likely future advances, large-scale ESS models will only partially be able to address what is called for in IPBES, and major uncertainties and limitations will remain. For instance, the limited availability of biodiversity data (as discussed above) limits our ability to understand relationships between biodiversity and ESS. Another major difficulty is to link biodiversity functions and processes with the estimation of their cultural, social, economic and health benefits - the final ecosystem goods (Evans et al. 2014), and how their loss will affect human well-being. This is particularly challenging as these links may vary across spatial scales, and among biome types or continents, due to their different evolutionary history. Overall, models need to move from assessing distributions of potential ESS to assessing distributions of realized ESS (Burkhard et al. 2012). Doing this at the large scales required for IPBES is extremely difficult due to the various local to regional to global scales of socio-ecological realities that drive such interactions.

In conclusion, it is unrealistic to assume that we can arrive at global models of ESS provision within a time window so that they become relevant for the first rounds of IPBES assessments. We can synthesise the current knowledge on relationship between biodiversity and ESS broadly, and we often have to rely on more regional case studies to inform stakeholders and decision makers, as well as on a combination of quantitative and qualitative methods. However, IPBES is not expected to present final answers in the near future. Its purpose is to assess and synthesize current knowledge as well as to identify knowledge gaps. Based on this, it will stimulate further research and provide suggestions for the way ahead.

Conclusions and perspectives

Adequate underlying data are indispensable for the development of more realistic scenarios of biodiversity and ESS. Incentives for closing gaps in the availability of data are therefore of paramount importance. Given the higher complexity involved in the modelling of biodiversity and ESS compared to, e.g., climate models, it is important to communicate openly any remaining uncertainties in the models. The development of sound models could greatly benefit from an increased transparency and sharing of data and methodologies, as well as from a better communication across disciplines. Probably the most ambitious, but also promising issue with regard to the goals of IPBES remains the investigation of the links between biodiversity and ESS, especially with respect to short-term and long-term feedbacks between them at different spatial scales. The final step would be the integration of scenarios and models of biodiversity and ESS into models of coupled social-ecological systems. Overall, while many challenges remain, macroecology and related disciplines have a lot to contribute to IPBES and can support it to become a successful instrument to halt the global loss of biological diversity as well as to provide a better understanding of sustainable use of natural resources for the benefit of human well-being.

Acknowledgements

This paper is the result of a workshop of the Macroecology Special Interest Group of the Ecological Society of Germany, Austria and Switzerland (GfÖ), held in Halle, Germany, funded by NeFo, the German network forum for biodiversity research (www.biodiversity.de). NeFo is a project funded by the German Federal Ministry of Education and Research (BMBF). We thank all workshop participants for inspiring discussions, and especially Julia Krohmer and the local organization team for their invaluable logistic support. We also thank Diana Bowler and Imran Khaliq for their help in documenting the discussion outcomes, and Katja Schiffers for comments on an earlier version of this manuscript. CH, DMD, TH and KB-G received support from the research funding programme "LOEWE -Landes-Offensive zur Entwicklung Wissenschaftlich -ökonomischer Exzellenz" of Hesse's Ministry of Higher Education, Research, and the Arts.

References

Algar, A.C., Kharouba, H.M., Young, E.R. & Kerr, J.T. (2009)

Predicting the future of species diversity: macroeco-

- logical theory, climate change, and direct tests of alternative forecasting methods. Ecography, 32, 22–33.
- Alkemade, R., Oorschot, M., Miles, L., Nellemann, C., Bakkenes, M. & ten Brink, B. (2009) GLOBIO3: a framework to investigate options for reducing global terrestrial biodiversity loss. Ecosystems, 12, 374–390.
- Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. Ecology, 93, 1527–1539.
- Araújo, M.B., Rozenfeld, A., Rahbek, C. & Marquet, P.A. (2011) Using species co-occurrence networks to assess the impacts of climate change. Ecography, 34, 897–908.
- Asner, G.P. & Martin, R.E. (2009) Airborne spectranomics: Mapping canopy chemical and taxonomic diversity in tropical forests. Frontiers in Ecology and the Environment, 7, 269–276.
- Bálint, M., Domisch, S., Engelhardt, C.H.M., Haase, P., Lehrian, S., Sauer, J., Theissinger, K., Pauls, S.U. & Nowak, C. (2011) Cryptic biodiversity loss linked to global climate change. Nature Climate Change, 1, 313–318.
- Balmford, A., Green, J.M.H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., Walpole, M. & Manica, A. (2015) Walk on the wild side: estimating the global magnitude of visits to protected areas. PLoS Biology, 13, e1002074.
- Beck, J., Ballesteros-Mejia, L., Buchmann, C.M., et al. (2012) What's on the horizon for macroecology? Ecography, 35, 673–683.
- Beck, J., Böller, M., Erhardt, A. & Schwanghardt, W. (2014) Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. Ecological Informatics, 19, 10–15.
- Betts, R.A., Boucher, O., Collins, M., et al. (2007) Projected increase in continental runoff due to plant responses to increasing carbon dioxide. Nature, 448, 1037–1041.
- Van der Biest, K., D'Hondt, R., Jacobs, S., Landuyt, D., Staes, J., Goethals, P. & Meire, P. (2014) EBI: An index for delivery of ecosystem service bundles. Ecological Indicators, 37, 252–265.
- Bonney, R., Shirk, J.L., Phillips, T.B., Wiggins, A., Ballard, H.L., Miller-Rushing, A.J. & Parrish, J.K. (2014) Next steps for citizen science. Science, 343, 1436–1437.
- Bowler, D.E., Haase, P, Kröncke, I., et al. (2015) A cross-taxon analysis of the impact of climate change on abundance trends in central Europe. Biological Conservation, 187, 41–50.
- Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010) Can mechanism inform species' distribution models? Ecology Letters, 13, 1041–1054.
- Bugmann, H. (2001) A review of forest gap models. Climatic Change, 51, 259–305.
- Burkhard, B., Kroll, F., Nedkov, S. & Müller, F. (2012) Mapping ecosystem service supply, demand and budgets. Ecological Indicators, 21, 17–29.
- Cardinale, B., Duffy, J. & Gonzalez, A. (2012) Biodiversity loss and its impact on humanity. Nature, 486, 59–67.
- Carpenter, S.R., Mooney, H.A., Agard, J., et al. (2009) Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. Proceedings of the National Academy of Sciences of the USA, 106, 1305– 1312.
- Ceia-Hasse, A., Sinervo, B., Vicente, L. & Pereira, H.M. (2014)

- Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. Ecography, 37, 679–688.
- Christensen, V. & Walters, C.J. (2004) Ecopath with Ecosim: Methods, capabilities and limitations. Ecological Modelling, 172, 109–139.
- Collen, B., Loh, J., Whitmee, S., McRae, L., Amin, R. & Baillie, J.E.M. (2009) Monitoring change in vertebrate abundance: the Living Planet Index. Conservation Biology, 23, 317–327.
- Cooper, N. & Belmaker, J. (2010) Habitat data resolution and the detection of species interactions. Frontiers of Biogeography, 2, 46.
- Crossman, N.D., Burkhard, B., Nedkov, S., et al. (2013) A blueprint for mapping and modelling ecosystem services. Ecosystem Services, 4, 4–14.
- Currie, D.J. (1991) Energy and large-scale patterns of animal and plant species richness. American Naturalist, 137, 27–49.
- Dehling, D.M., Hof, C., Brändle, M. & Brandl, R. (2010) Habitat availability does not explain the species richness patterns of European lentic and lotic freshwater animals. Journal of Biogeography, 37, 1919–1926.
- Dehling, D.M., Töpfer, T., Schaefer, H.M., Jordano, P., Böhning -Gaese, K. & Schleuning, M. (2014) Functional relationships beyond species richness patterns: trait matching in plant–bird mutualisms across scales. Global Ecology and Biogeography, 23, 1085–1093.
- Díaz, S., Demissew, S., Joly, C., Lonsdale, W.M. & Larigauderie, A. (2015a) A Rosetta Stone for Nature's Benefits to People. PLoS Biology, 13, e1002040.
- Díaz, S., Demissew, S., Carabias, J., et al. (2015b) The IPBES Conceptual Framework connecting nature and people. Current Opinion in Environmental Sustainability, 14, 1–16.
- Dulle, H.I., Ferger, S.W., Cordeiro, N.J., Howell, K.M., Schleuning, M., Böhning-Gaese, K. & Hof, C. (2015) Changes in abundances of forest understorey birds on Afria's highest mountain suggest subtle effects of climate change. Diversity and Distributions, DOI: 10.1111/ddi.12405
- Eigenbrod, F., Armsworth, P.R., Anderson, B.J., Heinemeyer, A., Gillings, S., Roy, D.B., Thomas, C.D. & Gaston, K.J. (2010) The impact of proxy-based methods on mapping the distribution of ecosystem services. Journal of Applied Ecology, 47, 377–385.
- Eigenbrod, F., Gonzalez, P., Dash, J. & Steyl, I. (2015) Vulnerability of ecosystems to climate change moderated by habitat intactness. Global Change Biology, 21, 275–286.
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics, 40, 677–697.
- Elith, J., Graham, C.H., Anderson, R., et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29, 129–151.
- Evans, C.D., Bonn, A., Holden, J., Reed, M.S., Evans, M.G., Worrall, F., Couwenberg, J. & Parnell, M. (2014) Relationships between anthropogenic pressures and ecosystem functions in UK blanket bogs: Linking process understanding to ecosystem service valuation. Ecosys-

- tem Services, 9, 5-19.
- Foden, W.B., Butchart, S.H.M., Stuart, S.N., et al. (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PloS One, 8, e65427.
- Follows, M.J., Dutkiewicz, S., Grant, S. & Chisholm, S.W. (2007) Emergent biogeography of microbial communities in a model ocean. Science, 315, 1843–1846.
- Fristoe, T.S., Burger, J.R., Balk, M.A., Khaliq, I., Hof, C. & Brown, J.H. (2015) Metabolic heat production and thermal conductance are mass-independent adaptations to thermal environment in birds and mammals. Proceedings of the National Academy of Sciences of the USA, 112, 15934–15939.
- Fritz, S.A. & Rahbek, C. (2012) Global patterns of amphibian phylogenetic diversity. Journal of Biogeography, 39, 1373–1382.
- Fulton, E.A., Link, J.S., Kaplan, I.C., et al. (2011) Lessons in modelling and management of marine ecosystems: The Atlantis experience. Fish and Fisheries, 12, 171– 188
- Gerten, D., Rost, S., von Bloh, W. & Lucht, W. (2008) Causes of change in 20th century global river discharge. Geophysical Research Letters, 35, L20405.
- Gonzalez, P., Neilson, R.P., Lenihan, J.M. & Drapek, R.J. (2010) Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Global Ecology and Biogeography, 19, 755–768.
- Gotelli, N.J., Graves, G.R. & Rahbek, C. (2010) Macroecological signals of species interactions in the Danish avifauna. Proceedings of the National Academy of Sciences of the USA, 107, 5030–5035.
- Graham, C.H., Parra, J.L., Rahbek, C. & McGuire, J.A. (2009) Phylogenetic structure in tropical hummingbird communities. Proceedings of the National Academy of Sciences of the USA, 106 Suppl., 19673–16678.
- Guisan, A. & Rahbek, C. (2011) SESAM a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. Journal of Biogeography, 38, 1433–1444.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. Ecological Modelling, 135, 147–186.
- Harfoot, M.B.J., Newbold, T., Tittensor, D.P., Emmott, S., Hutton, J., Lyutsarev, V., Smith, M.J., Scharlemann, J.P.W.
 & Purves, D.W. (2014a) Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. PLoS Biology, 12.
- Harfoot, M.B.J., Tittensor, D.P., Newbold, T., Mcinerny, G., Smith, M.J. & Scharlemann, J.P.W. (2014b) Integrated assessment models for ecologists: The present and the future. Global Ecology and Biogeography, 23, 124–143.
- He, K.S., Rocchini, D., Neteler, M. & Nagendra, H. (2011) Benefits of hyperspectral remote sensing for tracking plant invasions. Diversity and Distributions, 17, 381–392.
- Higgins, S.I., O'Hara, R.B. & Römermann, C. (2012) A niche for biology in species distribution models. Journal of Biogeography, 39, 2091–2095.
- Holland, R.A., Scott, K.A., Flörke, M. et al. (2015) Global impacts of energy demand on the freshwater resources

- of nations. Proceedings of the National Academy of Sciences of the USA, 112, E6707–E6716.
- Hudson, L., Newbold, T., Contu, S. & Hill, S. (2014) The PRE-DICTS database: a global database of how local terrestrial biodiversity responds to human impacts. Ecology and Evolution, 4, 4701–4735.
- Hurtt, G.C., Chini, L.P., Frolking, S., et al. (2011) Harmonization of land-use scenarios for the period 1500-2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. Climatic Change, 109, 117–161.
- Iknayan, K.J., Tingley, M.W., Furnas, B.J. & Beissinger, S.R. (2014) Detecting diversity: emerging methods to estimate species diversity., 29, 97–106.
- Jaeschke, A., Bittner, T., Reineking, B. & Beierkuhnlein, C. (2013) Can they keep up with climate change? - Integrating specific dispersal abilities of protected Odonata in species distribution modelling. Insect Conservation and Diversity, 6, 93–103.
- Jetz, W., McPherson, J.M. & Guralnick, R.P. (2012) Integrating biodiversity distribution knowledge: toward a global map of life. Trends in Ecology & Evolution, 27, 151– 159.
- Jones, J.P.G., Collen, B., Atkinson, G., et al. (2011) The why, what, and how of global biodiversity indicators beyond the 2010 target. Conservation Biology, 25, 450–457.
- Jones, K.E., Bielby, J., Cardillo, M., et al. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology, 90, 2648.
- Kattge, J., Díaz, S., Lavorel, S., et al. (2011) TRY a global database of plant traits. Global Change Biology, 17, 2905– 2935.
- Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters, 12, 334–350.
- Keil, P. & Jetz, W. (2014) Downscaling the environmental associations and spatial patterns of species richness. Ecological Applications, 24, 823–831.
- Khaliq, I., Hof, C., Prinzinger, R., Böhning-Gaese, K. & Pfenninger, M. (2014) Global variation in thermal tolerances and vulnerability of endotherms to climate change. Proceedings of the Royal Society B: Biological Sciences, 281, 20141097.
- Khaliq, I., Fritz, S.A., Prinzinger, R., Pfenninger, M., Böhning-Gaese, K. & Hof, C. (2015) Global variation in thermal physiology of birds and mammals: evidence for phylogenetic niche conservatism only in the tropics. Journal of Biogeography, 42, 2187–2196.
- Kissling, W.D. & Schleuning, M. (2015) Multispecies interactions across trophic levels at macroscales: Retrospective and future directions. Ecography, 38, 346–357.
- Kissling, W.D., Dormann, C.F., Groeneveld, J., et al. (2012) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. Journal of Biogeography, 39, 2163–2178.
- Landsberg, J. (2003) Physiology in forest models: history and the future. FBMIS, 1, 49–63.
- Lenzen, M., Moran, D., Kanemoto, K., Foran, B., Lobefaro, L. & Geschke, A. (2012) International trade drives biodiversity threats in developing nations. Nature, 486, 109– 112.

- Linder, H.P., Bykova, O., Dyke, J., et al. (2012) Biotic modifiers, environmental modulation and species distribution models. Journal of Biogeography, 39, 2179–2190.
- Mace, G.M., Hails, R.S., Cryle, P., Harlow, J. & Clarke, S.J. (2015) Towards a risk register for natural capital. Journal of Applied Ecology, 52, 641–653.
- Maes, J., Paracchini, M.L., Zulian, G., Dunbar, M.B. & Alkemade, R. (2012) Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. Biological Conservation, 155, 1–12.
- Maestre, F.T., Quero, J.L., Gotelli, N.J., et al. (2012) Plant species richness and ecosystem multifunctionality in global drylands. Science, 335, 214–218.
- Martín-López, B., Iniesta-Arandia, I., García-Llorente, M., et al. (2012) Uncovering ecosystem service bundles through social preferences. PLoS One, 7, e38970.
- Meyer, C., Kreft, H., Guralnick, R. & Jetz, W. (2015) Global priorities for an effective information basis of biodiversity distributions. Nature Communications, 6, 8221.
- Midgley, G.F. (2012) Biodiversity and Ecosystem Function. Science, 335, 174–175.
- Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R.E., Lehner, B., Malcolm, T.R. & Ricketts, T.H. (2008) Global mapping of ecosystem services and conservation priorities. Proceedings of the National Academy of Sciences USA, 105, 9495–9500.
- Newbold, T., Hudson, L.N., Hill, S.L.L., et al. (2015) Global effects of land use on local terrestrial biodiversity. Nature, 520, 45–50.
- Opgenoorth, L. & Faith, D.P. (2013) The Intergovernmental Science Policy Platform on Biodiversity and Ecosystem Services (IPBES), up and walking. Frontiers of Biogeography, 5, 207–211.
- Orme, C.D.L., Davies, R.G., Burgess, M., et al. (2005) Global hotspots of species richness are not congruent with endemism or threat. Nature, 436, 1016–1019.
- Pachzelt, A., Rammig, A., Higgins, S. & Hickler, T. (2013) Coupling a physiological grazer population model with a generalized model for vegetation dynamics. Ecological Modelling, 263, 92–102.
- Pachzelt, A., Forrest, M., Rammig, A., Higgins, S.I. & Hickler, T. (2015) Potential impact of large ungulate grazers on African vegetation, carbon storage and fire regimes. Global Ecology and Biogeography, 24, 991–1002.
- Pagel, J., Anderson, B.J., O'Hara, R.B., Cramer, W., Fox, R., Jeltsch, F., Roy, D.B., Thomas, C.D. & Schurr, F.M. (2014) Quantifying range-wide variation in population trends from local abundance surveys and widespread opportunistic occurrence records. Methods in Ecology and Evolution, 5, 751–760.
- Pavlick, R., Drewry, D.T., Bohn, K., Reu, B. & Kleidon, A. (2012)
 The Jena Diversity-Dynamic Global Vegetation Model
 (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. Biogeosciences Discussions, 9, 4627–4726.
- Pereira, H.M., Navarro, L.M. & Martins, I.S. (2012) Global biodiversity change: the bad, the good, and the unknown. Annual Review of Environment and Resources, 37, 25– 50.
- Pereira, H.M., Ferrier, S., Walters, M. et al. (2013) Essential

- Biodiversity Variables. Science, 339, 277-278.
- Peters, G.P., Minx, J.C., Weber, C.L. & Edenhofer, O. (2011) Growth in emission transfers via international trade from 1990 to 2008. Proceedings of the National Academy of Sciences of the USA, 108, 8903–8908.
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M. & Kausrud, K. (2011) The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. Climate Research, 46, 15–27.
- Phillips, S.J. & Elith, J. (2013) On estimating probability of presence from use availability or presence background data. Ecology, 94, 1409–1419.
- Platts, P.J., Garcia, R.A., Hof, C., Foden, W., Hansen, L.A., Rahbek, C. & Burgess, N.D. (2014) Conservation implications of omitting narrow-ranging taxa from species distribution models, now and in the future. Diversity and Distributions, 20, 1307–1320.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography, 19, 117–134.
- Prentice, I.C., Bondeau, A., Cramer, W., Harrison, S.P., Hickler, T., Lucht, W., Sitch, S., Smith, B. & Sykes, M.T. (2007)
 Dynamic global vegetation modelling: quantifying terrestrial ecosystem responses to large-scale environmental change. In: Terrestrial Ecosystems in a Changing World, pp. 175–192. Springer, Berlin, Heidelberg.
- Purves, D. (2013) Time to model all life on Earth. Nature, 493, 295–297.
- Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L.V.B. & Graves, G.R. (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. Proceedings of the Royal Society B: Biological Sciences, 274, 165–174.
- Reed, M.S., Hubacek, K., Bonn, A., et al. (2013) Anticipating and managing future trade-offs and complementarities between ecosystem services. Ecology and Society, 18, 5.
- Rockström, J., Steffen, W., Noone, K., et al. (2009) A safe operating space for humanity. Nature, 461, 472–475.
- Rondinini, C., Di Marco, M., Chiozza, F., et al. (2011) Global habitat suitability models of terrestrial mammals. Philosophical Transactions of the Royal Society B: Biological Sciences, 366, 2633–2641.
- Ruckelshaus, M., McKenzie, E., Tallis, H., et al. (2015) Notes from the field: Lessons learned from using ecosystem service approaches to inform real-world decisions. Ecological Economics, 115, 11–21.
- Runsten, L., Ravilious, C., Kashindye, A., et al. (2013) Using spatial information to support decisions on safeguards and multiple benefits for REDD + in Tanzania. Cambridge, UK, Dar es Salaam, Tanzania.
- Scheiter, S. & Higgins, S.I. (2009) Impacts of climate change on the vegetation of Africa: An adaptive dynamic vegetation modelling approach. Global Change Biology, 15, 2224–2246
- Scheiter, S., Langan, L. & Higgins, S.I. (2013) Next-generation dynamic global vegetation models: learning from community ecology. The New Phytologist, 198, 957–969.
- Stehfest, E., van Vuuren, D.P., Bouwman, L. & Kram, T. (2014)
 Integrated Assessment of Global Environmental

- Change with IMAGE 3.0 Model description and policy applications. PBL.
- Strassburg, B.B.N., Rodrigues, A.S.L., Gusti, M., Balmford, A., Fritz, S., Obersteiner, M., Kerry Turner, R. & Brooks, T.M. (2012) Impacts of incentives to reduce emissions from deforestation on global species extinctions. Nature Climate Change, 2, 350–355.
- Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D. & Kelling, S. (2009) eBird: A citizen-based bird observation network in the biological sciences. Biological Conservation, 142, 2282–2292.
- Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T. & Huey, R.B. (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proceedings of the National Academy of Sciences of the USA, 111, 5610– 5615
- Swetnam, R.D. et al. (2011) Mapping socio-economic scenarios of land cover change: A GIS method to enable ecosystem service modelling. Journal of Environmental Management, 92, 563–574.
- Thieltges, D.W., Hof, C., Dehling, D.M., Brändle, M., Brandl, R. & Poulin, R. (2011a) Host diversity and latitude drive trematode diversity patterns in the European freshwater fauna. Global Ecology and Biogeography, 20, 675–682
- Thieltges, D.W., Hof, C., Borregaard, M.K., Matthias Dehling, D., Brändle, M., Brandl, R. & Poulin, R. (2011b) Range size patterns in European freshwater trematodes. Ecography, 34, 982–989.
- Thuiller, W., Araújo, M.B. & Lavorel, S. (2003) Generalized models vs. classification tree analysis: Predicting spatial distributions of plant species at different scales. Journal of Vegetation Science, 14, 669-680.
- Triviño, M., Thuiller, W., Cabeza, M., Hickler, T. & Araújo, M.B. (2011) The contribution of vegetation and landscape configuration for predicting environmental change impacts on Iberian birds. PLoS One, 6, e29373.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! Oikos, 116, 882–892.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: Specieslevel foraging attributes of the world's birds and mammals. Ecology, 95, 2027.
- Zimmermann, N.E., Edwards, T.C., Graham, C.H., Pearman, P.B. & Svenning, J.-C. (2010) New trends in species distribution modelling. Ecography, 33, 985–989.

Submitted: 09 October 2015 First decision: 15 December 2015 Accepted: 24 December 2015

Edited by Joaquín Hortal and Michael N Dawson