

Opinion

Protecting Biodiversity (in All Its Complexity):
New Models and Methods

Laura J. Pollock,^{1,2,*} Louise M.J. O'Connor,² Karel Mokany,³ Dan F. Rosauer,⁴ Matthew V. Talluto,^{5,6} and Wilfried Thuiller²

We are facing a biodiversity crisis at the same time as we are acquiring an unprecedented view of the world's biodiversity. Vast new datasets (e.g., species distributions, traits, phylogenies, and interaction networks) hold knowledge to better comprehend the depths of biodiversity change, reliably anticipate these changes, and inform conservation actions. To harness this information for conservation, we need to integrate the largely independent fields of biodiversity modeling and conservation. We highlight new developments in each respective field, early examples of how they are being brought together, and ideas for a future synthesis such that conservation decisions can be made with fuller awareness of the biodiversity at stake.

We Need Greater Diversity in Biodiversity Conservation

Aside from a small fraction of well-known species that have established conservation status, most of the world's biodiversity is poorly integrated into conservation efforts. Even for iconic clades such as birds and mammals, only a subset of species are considered in conservation despite continuously refined understanding of the ecology and evolution of these clades [1,2]. Lesser-known taxa are nearly always overlooked [3], even those that are most at risk of extinction [4]. First, we need to expand the focus of biodiversity in conservation programs to consider more of the tree of life, even taxa without names [5,6], especially because increasing evidence suggests that 'invisible' diversity is important to ecosystem functioning [7]. Second, we must consider the role of species in ecosystems [8]. Biodiversity is not simply the mere sum of species, but includes complex interaction networks with fluxes of energy and nutrients [9,10]. Even conservation efforts for focal charismatic species would benefit from considering the other species that enable their existence. Biodiversity losses impact all facets of biodiversity (species, genetic diversity, **functional diversity**, and **phylogenetic diversity**, see [Glossary](#)) and on spatial extents ranging from local assemblages to the global pool of biodiversity. Considering these dimensions is essential to prevent widespread biodiversity loss.

Conservation Evaluation Often Falls Short for Under-Represented Biodiversity Simplified Metrics Likely Miss Many Types of Biodiversity

Despite scientific recognition of the widespread importance of biodiversity, most planning and on-the-ground conservation programs still focus on a simplified representation of biodiversity such as the amount or quality of habitat. Habitat-based metrics are used more often in conservation than in ecology [11], and are often the basis of conservation offsetting, wetland mitigation, conservation easements, conservation, and management of listed species (alongside population abundances, connectivity, and threat information when available), and are used at a regional extent in coordinated reserve designs (e.g., Natura 2000, https://ec.europa.eu/environment/nature/natura2000/index_en.htm). Reliance on habitat metrics can overlook important biodiversity that falls outside commonly held notions of high-quality habitat [12], and

Highlights

The world's biodiversity is complex, but we are rapidly making progress in understanding its distribution, breadth, and dimensionality.

Very little of this total biodiversity is currently considered in applied conservation programs.

The fields of statistical modeling of biodiversity and conservation planning are developing along similar lines, using increasingly similar datasets and techniques, but are doing so independently.

Integration of these fields could lead to conservation of a much broader set of taxa by improving the process of conservation evaluation and extending it to the many different facets of biodiversity that are important to ecosystems and to us.

¹Department of Biology, McGill University, 1205 Dr. Penfield Avenue, Montréal, Québec H3A 1B1, Canada

²Université Grenoble Alpes and Université Savoie Mont Blanc, Centre National de la Recherche Scientifique (CNRS), Laboratoire d'Écologie Alpine (LECA), F-38000 Grenoble, France

³Commonwealth Scientific and Industrial Research Organisation (CSIRO), PO Box 1700, Canberra, ACT 2601, Australia

⁴Research School of Biology, Australian National University, Acton, Canberra, ACT 2601, Australia

⁵Department of Ecohydrology, Leibniz Institute for Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany

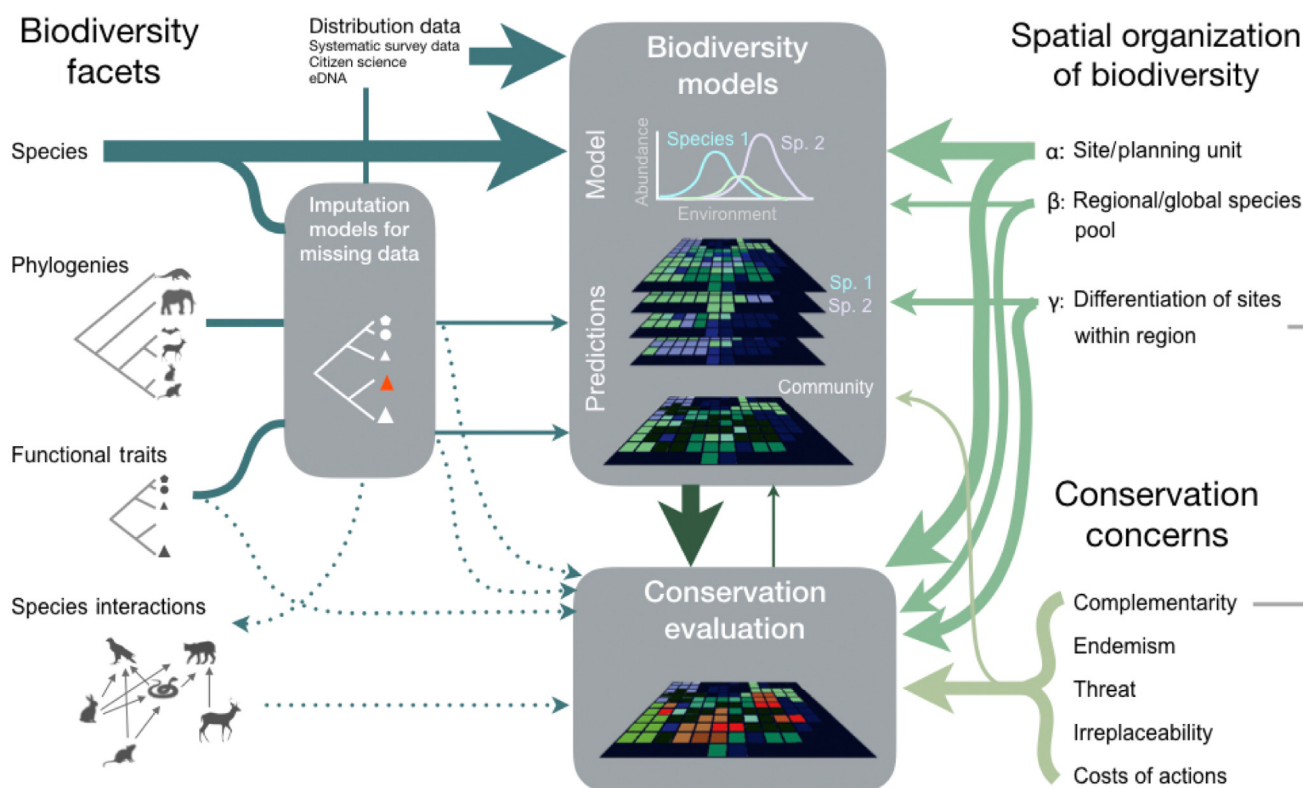


these metrics do not necessarily represent population persistence [11]. Although the use of habitat metrics certainly has follow-on benefits for some aspects of diversity, its surrogacy value for even well-known species is unclear [13], and is unknown for many taxa and for different **biodiversity facets**.

In cases where multiple species are considered together in applied conservation, they are most often represented as species richness (the count of species in areas) [11]. The use of species richness cannot address the known biases in extinction risk towards particular clades (e.g., amphibians [14]) and functional types (e.g., top predators). Although species richness and other species-based metrics can be an effective surrogate for phylogenetic diversity [10] or functional diversity [15], their surrogacy value depends on the conservation scenario [16] and tends to decrease in scenarios where resources are limited (i.e., few sites available for protection) [17]. We have very limited evidence for the surrogacy value of different biodiversity facets outside iconic animal groups (e.g., does aboveground animal richness relate to soil microbial diversity?). Finally, how species interact within ecosystems is almost never considered in applied conservation, despite links to the important conservation goals of ecosystem functioning and resilience [9].

⁶Department of Ecology, University of Innsbruck, Innrain 52, AT-6020 Innsbruck, Austria

*Correspondence: laura.pollock@mcgill.ca (L.J. Pollock).



Trends in Ecology & Evolution

Figure 1. How Biodiversity Facets, Different Scales of Biodiversity, and Conservation Concerns Factor into Biodiversity Modeling and Conservation Evaluation. Modeling and evaluation generally involve particular target species rather than other facets of diversity (e.g., evolutionary history, species interactions). Most biodiversity models focus on ecological processes instead of explicitly considering conservation concerns, although many models are built for threatened species or species of conservation interest, resulting in a mostly unidirectional flow of information from models to evaluation. In the case of spatial conservation planning, both models and evaluation use similar data inputs and spatial organization of biodiversity. Both have a local scale (or planning units) and a regional or global scale. In particular, the use of metrics or algorithms to differentiate sites from one another (β -diversity in modeling, complementarity in conservation planning) are treated similarly in modeling and planning. Abbreviations: eDNA, environmental DNA; Sp., species.

Independent Conservation Efforts Fail to Protect the World's Biodiversity

Safeguarding multiple facets of biodiversity, especially for the purposes of preventing extinction, protecting our biological heritage, and retaining future options for society, requires an understanding of the global biodiversity pool, arguably more than for other conservation aims (e.g., managing local ecosystems or protecting ecosystem services) [18]. Nevertheless, conservation actions are typically local or regional, and this can lead to unintended outcomes for global biodiversity [19]. First, species are declining globally [20], but not necessarily locally [21–23], leading to homogenization of biodiversity where different areas have increasingly similar biodiversity [20]. Second, conservation priorities established for local species assemblages [16], or even for species at a national scale [19], differ from global biodiversity priorities [16,19]. Lastly, the emphasis on protecting large patches and connected habitats (e.g., species corridor initiatives), which is based on research on metapopulations and conservation genetics, risks overlooking important biodiversity (e.g., endemic species, highly functional communities) that occur in small and isolated habitat patches [24]. A more spatially coordinated approach is needed that recognizes how local conservation efforts impact the regional and global biodiversity pool.

The Potential to Bring Together Biodiversity Modeling and Conservation

The fields of ecology and conservation planning already consider the spatial extents necessary for this coordination, but they do so in slightly different ways. In systematic conservation planning (SCP), biodiversity features (e.g., species distributions) are considered in planning units. Planning units are compared across the entire area of interest using the principles of spatial **complementarity** and **irreplaceability**. In ecology, a similar hierarchy can be found in the delineation of **α-diversity** (within-site or within-ecosystem diversity), **β-diversity** (differentiation of sites in a region; e.g., compositional turnover), and **γ-diversity** (diversity of the entire region). We refer to **γ-diversity** as the total set of biodiversity in the area of interest, which could have a regional or global extent, to better align with conservation planning. Both fields are progressing independently toward a multi-scale, multi-faceted view of biodiversity (Figure 1). Now is the time to integrate these fields to rapidly expand the amount of biodiversity data that reaches conservation practice (Figure 2).

Advances in Biodiversity Models

Although steady progress has been made on addressing the major biodiversity shortfalls through increased data collection (e.g., citizen science [25] and environmental DNA) and global initiatives to compile data on species occurrences (e.g., Group on Earth Observations–Biodiversity Observation Network (GEO-BON) initiative, geobon.org; Global Biodiversity Information Facility, gbif.org), traits (e.g., TRY Plant Trait Database, www.try-db.org), genetic and phylogenetic data (e.g., GenBank), and species interaction data (e.g., GloBI, globalbioticinteractions.org), major shortfalls remain [26]. **Biodiversity models** are essential tools to rapidly overcome these shortfalls. We consider biodiversity models to be any model that makes predictions for biodiversity (including species occurrences or abundances, traits, phylogenetic placements, and species interactions). We highlight here two classes of models: (i) **imputation models** for missing biodiversity data and (ii) **spatial biodiversity models** for predicting taxa or other biodiversity facets for unsampled locations, which often serve as an input for conservation planning (Figure 1).

Imputation Models

Imputation models are necessary to fill in the many gaps in biodiversity datasets. For example, they can generate missing trait values for taxa [27], which can be estimated from phylogenies, assuming that traits have a general pattern of conserved evolution [28], or through multivariate imputation that does not rely on phylogenies [29]. Increasingly sophisticated approaches are

Glossary

α-Diversity: quantifies local diversity, usually species richness or the effective number of species (Shannon exponent).

β-Diversity: quantifies the dissimilarity or turnover between locations in terms of composition. Can be pairwise between locations, global (average dissimilarity across the region), or reflect the distinctiveness of a location compared to all others in the region.

γ-Diversity: quantifies the total diversity across locations for an entire area of interest, which could be at a regional or global scale depending on the study.

Biodiversity facets: categories of biodiversity that describe relevant taxonomic or ecological information to support biodiversity evaluation, and that apply to and can be (relatively) easily measured for all or most taxa. Examples include taxonomic diversity, phylogenetic diversity, genetic diversity, trait/functional diversity, and network diversity.

Biodiversity models: statistical or process-based models that are used to make inferences and predictions about the effect of the environment on biodiversity, accounting for ecological processes explicitly or implicitly. Biodiversity can be represented in units ranging from individuals to entire communities, and additionally represent attributes of those taxa (e.g., abundances, functional traits, phylogenetic position, threat).

Complementarity: in conservation planning, complementarity quantifies the difference between locations in terms of species or features represented within them (two locations are fully complementary if their pairwise β-diversity is equal to 1). By contrast, in ecology, two species are complementary if they fill different roles in an ecosystem or use resources differently.

Functional diversity: the diversity of functional forms in a species set (or community) measured by a variety of metrics that use dendrograms or representations in multidimensional space.

Imputation model: a model that estimates values for missing datapoints in biodiversity datasets (e.g., trait values for a particular taxa).

Irreplaceability: the extent to which a location or species is distinct from all others (opposite of redundancy). For example, a location where an endemic

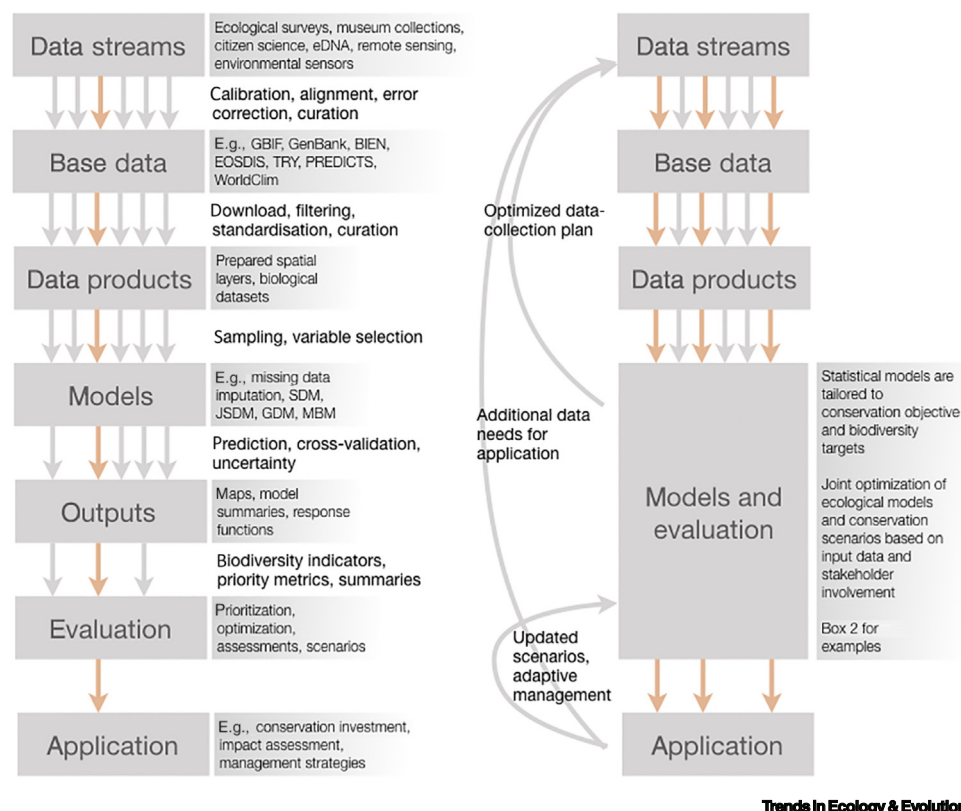


Figure 2. The Steps and Information Flow in a Typical Data-Implementation Pipeline (Left) and a Streamlined Version (Right) That Combines Models and Evaluation in One Step. We expect that more biodiversity information would reach the application stage (orange arrows) with a unified instead of disconnected method of evaluating biodiversity from the data products to their use in conservation applications, and that the combined approach requires increasing transparency and additional communication between biodiversity scientists and stakeholders. Abbreviations: BIEN, Botanical Information and Ecology Network; eDNA, environmental DNA; EOSDIS, Earth Observing System Data and Information System; GBIF, Global Biodiversity Information Facility; GDM, generalized dissimilarity model; JSMD, joint species distribution model; MBM, macroecological model; PREDICTS, Predicting the Future of Biodiversity; SDM, species distribution model; TRY, Plant Trait Database; WorldClim, Global Climate Data.

also being used to generate phylogenies when some gene sequences are missing [30], and to combine multiple datasets into aggregated phylogenies either based on the phylogenies themselves ('supertrees') or preferably from a combined gene matrix [31]. There is also growing interest in predicting interactions between species based on their trait attributes (e.g., predator–prey trait matching [32]) and spatial co-occurrence data [33]. Predicting species interactions across many species or at multiple locations is difficult with severely limited data, but can be addressed by combining empirical data and expert knowledge [34].

Although imputation models are greatly expanding the coverage of biodiversity datasets, challenges remain. Data collection is systematically geographically and taxonomically biased, and this could bias predictions, especially for rare taxa. We are increasingly relying on the same datasets for different types of analyses, hence there is also a danger of circularity if these analyses are later combined (e.g., using the phylogeny to predict trait values and later combining phylogeny and traits in spatial models). We need more robust tests for the impact of these biases, and must ensure that uncertainty is propagated from the original data sources to all subsequent analyses. A partial solution is to integrate methods and create a transparent and documented

species occurs is irreplaceable; an irreplaceable species has a unique position in its community (in terms of function or interactions, i.e., distinctive) or in the phylogeny.

Macroecological model (MEM): a biodiversity model that uses a top-down approach to model α - or β -diversity directly instead of modeling the distributions of the component taxa.

Phylogenetic diversity: the evolutionary diversity represented by sets of taxa, where the most common metric (Faith's phylogenetic diversity) is the branch length of the minimum spanning tree connecting a set of species in a phylogeny [51] (sets of species can be from a single area or multiple areas combined).

'Sideways' biodiversity models: models that predict the distribution of biodiversity with a combination of bottom-up (i.e., single-taxon predictions) and top-down (i.e., models of the properties of an assemblage or community of taxa) approaches.

Spatial biodiversity models: biodiversity models that are explicitly spatial, and where inferences and predictions are made for biodiversity in particular locations (e.g., planning units or grid cells).

Spatial prioritization: a form of systematic conservation planning (SCP) that selects a set of areas that maximize conservation value given other constraints (e.g., cost, protected areas, feasibility).

Weighted endemism: the ratio between a species local range of occurrence and its total range. Note: this is different from the definition of endemism; the extent to which a species range is restricted to a particular location.

pipeline of analyses (Figure 2), but we must still address the underlying causes of bias and use this knowledge to guide future collection.

Spatial Biodiversity Models

The Wallacean shortfall (inadequate knowledge of geographic distributions) greatly hinders progress in identifying conservation priorities [26]. This shortfall is particularly problematic at local scales; it is easier to define a regional or national set of species than to pinpoint the precise distributions of species at fine spatial scales [26]. Biodiversity models are essential tools to address this shortfall. In many cases, they can provide continuous coverage of species distributions at a resolution relevant for conservation purposes [35]. The most common examples are single-species distribution models (i-SDMs; see Figure 1 in Box 1) that have been and will continue to be invaluable tools for conservation applications [35]. Advanced models can additionally accommodate multiple facets (e.g., traits and phylogenies) and integrate elements of α - and β -diversity (Box 1). A notable advance is the ability to combine a top-down approach focused on an entire species assemblage with a bottom-up approach focused on single species ('sideways' biodiversity models; Boxes 1 and 2). One such model, joint species distribution models (j-SDMs, reviewed in [36]), offers potential improvements by modeling all species simultaneously [37,38], enabling conditional predictions [39–41], and has a flexible hierarchy amenable to adding other information such as traits [37], phylogenies [42], geographic space [43], temporal data [44], and detection bias [45] which impact multifaceted biodiversity estimates [46]. Models that can account for species interactions [47] are an exciting arena for future developments.

A key advantage of these advanced biodiversity models is their ability to process highly multidimensional datasets (e.g., many taxa, sites, and environmental variables). Combining multiple, large biodiversity datasets can quickly result in a computationally intractable problem. Solutions include dimensionality reduction in a Bayesian framework [36,48] or via machine learning [49]. However, what these approaches gain in flexibility may come at a cost in terms of generality, and the relationships derived between explanatory variables and diversity metrics are often empirical with little to no grounding in ecological theory. An important future research avenue will be to rigorously test new biodiversity models to evaluate their capacity to aid ecological inference and to make predictions for new situations (e.g., novel climates or altered ecosystems).

Advances in Conservation Evaluation of Multifaceted Biodiversity

Although the methods described previously could offer a richer representation of biodiversity and improved predictive abilities, identifying conservation solutions requires more than mere predictions. These predictions must be translated to meaningful outputs that can be used to meet defined objectives (e.g., protected area targets) or provide forecasts for decision makers. In systematic conservation planning (SCP) [50], priorities are established that efficiently meet goals for representation of biodiversity under a range of spatial or other constraints (e.g., in a **spatial prioritization**). Targets can be set for diversity (e.g., 10% of each species range protected [17]) or approaches without targets, such as algorithms based on **weighted endemism** [16,19]. Although i-SDMs are commonly used as inputs to spatial prioritization, more advanced biodiversity models are rarely used (Box 2 for exceptions). Multiple biodiversity facets are also rarely considered in conservation despite decades of recognized conservation benefit in, for example, phylogenetic diversity [51]. However, in recent years methodological advances [52–54] have enabled the use of phylogenies and functional diversity [16,53] in conservation planning studies at regional [6,52] and global [16,17] scales, and initiatives such as EDGE (evolutionarily distinct and globally endangered; edgeofexistence.org) are promoting

Box 1. Modeling Biodiversity from Top-Down, Bottom-Up, and Sideways

Biodiversity models can be defined by their 'response objectives' and internal structure (particularly the response variable; what is being predicted). These response objectives can be represented with axes that describe whether the objective is a top-down versus bottom-up, or a within- versus between-site, depiction of biodiversity (Figure I). Current modeling approaches can be mapped onto this space, and the potentially most information-rich approaches (gray circle in Figure I) crosslink biodiversity facets (traits and phylogenies) while jointly predicting community composition (e.g., species abundance or occurrence), within-site community diversity, and between-site turnover.

In the top-down approach, known as a **macroecological model** (MEM), α -diversity is itself the response (e.g., species richness or phylogenetic diversity) and the input data are a site versus diversity matrix. β -Diversity models (e.g., GDMs, generalized dissimilarity models [73]; and MBMs, multi-faceted biodiversity models [49]) estimate turnover in species or phylogenetic diversity [74] between sites as a function of differences in environmental and geographic distances.

Bottom-up approaches, where individual species are the response variables (single-species distribution model, i-SDM), are by far the most common type of biodiversity model used. Note that α -diversity can also be derived by aggregating models of individual species together in a stacked species distribution model (s-SDM). This feature is important for conservation planning because both the species pool of a set of sites and diversity metrics for entire species assemblages can be calculated (e.g., endemism-based metrics). However, the resulting diversity metrics are simply the sum of the parts, there is no information on species associations or community-level attributes.

'Sideways' methods are methods that combine top-down and bottom-up approaches: joint species distribution models (j-SDMs), the multi-species version of i-SDMs that model effects of individual species and communities [39,40], can include shared responses between species and can include other information such as phylogeny and traits in a hierarchical framework, as well as spatial and temporal dynamics [66]; also dynamic framework for occurrence allocation in metacommunities (DynamicFOAM) [75], that balances richness and turnover to predict occurrences for all species; and SESAM (spatially explicit species assemblage modeling [76]), that adjusts combined s-SDM predictions based on those of macroecological models.

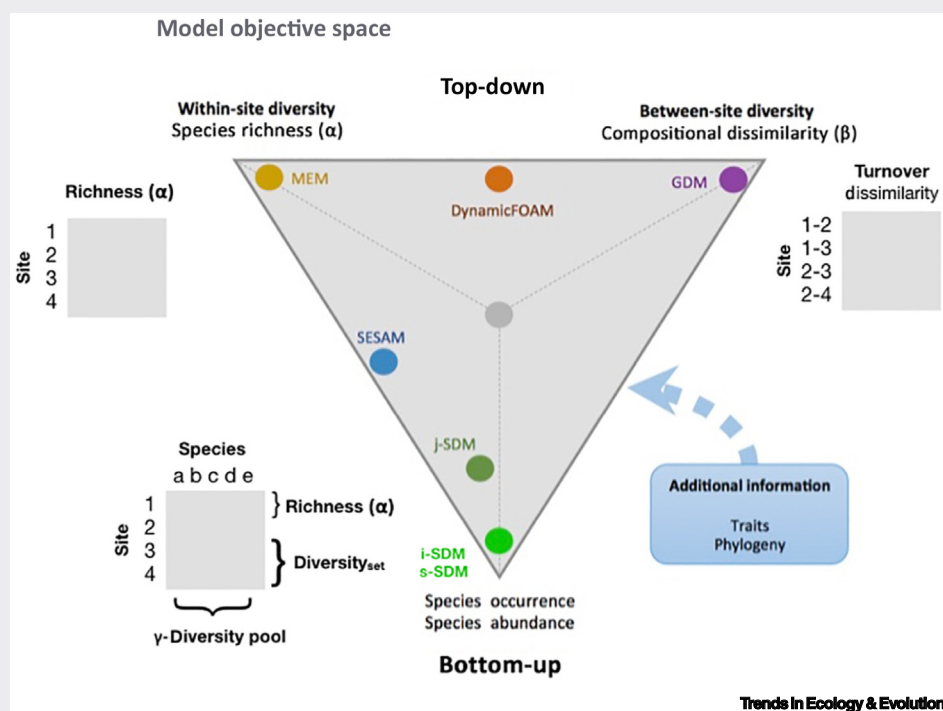


Figure I. The Dimensions of Recent Biodiversity Models. Models can have different types of response objectives: within-site models, between-site models, and models of individual species. These response objectives fall along two axes: (i) top-down approaches where α -diversity or other diversity metrics are the focus, versus bottom-up approaches where individual species are the focus (vertical axis), and (ii) whether the focus is on predicting biodiversity within sites or between sites (horizontal axis).

Box 2. Hybrid Approaches for Integrating Advanced Biodiversity Models and Conservation Decisions

We have emphasized the need for models that join different spatial and taxonomic dimensions of biodiversity that can be combined with conservation evaluation. We provide examples from two classes of advanced biodiversity models (Box 1) that directly address applied conservation questions. There is much scope for building upon and extending these early examples.

(i) Macroecological Models

For taxa for which there are no abundance or time-series data, models based on α - and β -diversity (Box 1) can also be used to directly design, predict, and compare conservation scenarios. For example, β -diversity models can summarize the expected effects on future biodiversity of changes to habitat condition, extent, or management as a change in effective habitat area [77]. With sophisticated models of environmental or land-use change, for example new protected areas, habitat loss [78] or degradation, and climate change [79], scenarios can be planned for the most beneficial effect on biodiversity even at global extents [77], and can also be used with phylogenetic [74] or functional [49] β -diversity.

(ii) 'Sideways' Biodiversity Models

Multi-species models that contain a species-level and community (or ecosystem)-level hierarchy (Box 1) are widely relevant to conservation applications because they can simultaneously estimate ecological processes that are relevant to individual species and larger-scale attributes (e.g., ecosystem properties). Perhaps the best example of this approach has been for evaluating management strategies in fisheries, in which models of fish species (or sets of species) are combined with ecosystem-level attributes [64]. In this way, important ecological and ecosystem constraints can be considered (e.g., population dynamics in response to habitat or predators) together with management scenarios (harvest controls) [57]. Recent versions allow evaluation of harvest impacts, survey designs, and protection scenarios for finescale habitats in a changing climate [66]. Although these more elaborate designs are only possible for a subset of well-studied taxa, this will be increasingly possible with ever-improving sampling and imputation models.

the conservation of multiple biodiversity facets. Species interactions are even more rarely considered, although emerging examples show how interactions can be used to evaluate ecological network collapse [55], and set spatial priorities [56] and management scenarios that account for predators and their prey [57].

The Way Forward: Integrating Biodiversity Models and Conservation Evaluation

Modeling has a crucial but underappreciated role in conservation planning and practice, especially with respect to setting and achieving global conservation targets (Aichi targets for threatened species, habitat loss, and protected areas) in the Strategic Plan for Biodiversity 2011–2020 and the post-2020 global biodiversity framework [58]. Models that predict the distribution of species in space and time are crucial for these global initiatives, and i-SDMs are already widely used in conservation [35]. We believe that the more advanced biodiversity models have vast potential for representing not only species but also entire communities, clades, or functional roles (early examples are given in Box 2), but they first must be better integrated into conservation efforts.

The advantages of this integration are many. First, a combined approach retains the unique strengths of each individual approach. Conservation planning would benefit from having access to the most advanced statistical machinery including model calibration, model validation, and the propagation of uncertainty. Such models can also incorporate more flexible hierarchical structures that account for biases in sampling biodiversity, different sources of inputs (e.g., museum location data with community-based sampling of environmental DNA), different extents (α - and β -diversity), and different resolutions of input data. They can take advantage of new data types (e.g., tracking data [59]) as they become available. Conversely, the field of biodiversity modeling would benefit from tailoring predictions for use in tangible conservation scenarios and targets.

Second, an integrated approach reduces any redundancies that arise from using similar datasets and approaches in an unsynchronized manner. The potential for redundancy becomes greater

the larger and the more complex the representation of biodiversity becomes. Redundancy could be reduced on two fronts; the raw data inputs and the methodological similarities (e.g., by combining modeling and conservation optimization algorithms, as discussed in the following text).

Finally, this synthesis would make the pipeline of data implementation more efficient and likely to result in a better representation of under-represented biodiversity in conservation. Recent calls to streamline analytical pipelines in ecology [60–62] point to increased efficiency [63] of readily available technological solutions, such as user-friendly interfaces (e.g., R Shiny and Dash). Importantly, the integration of conservation goals, targets, and scenarios into modeling would require stakeholder input into the modeling decisions [64], which could lead to increased coordination, trust, and uptake of these models, thus decreasing the ‘black box’ problem of biodiversity models [60]. It would engage biodiversity scientists beyond academia to understand the needs of stakeholders and provide more tailored conservation guidance.

Steps Forward

We recommend three related areas of focus to speed integration of biodiversity models and conservation: (i) adapting biodiversity models to accommodate conservation goals and scenarios, (ii) combining biodiversity models and conservation optimization algorithms, and (iii) re-evaluating model validation in light of conservation goals and scenarios. Recent examples show that this integration is indeed possible (Box 2).

In many cases, statistical methods are already available to adapt biodiversity models for use in conservation. For example, management actions (or management history) could be included as model predictors, which could then be used to make predictions for different future actions. More complex methods of scenario-building are also possible by altering various model parameters [65,66] (Box 2) or even by adding submodels of ecological processes (e.g., population viability). Previously collected ‘prior’ information (information on species threat or response to management action) can be combined with newly collected data to refine model estimates [67]. The challenge will be to find the best data and models for the conservation question at hand [68], and this will require close collaboration between modelers and conservation practitioners [65].

Combining conservation optimization algorithms with biodiversity models is another important step (Figure 2) that will enable relevant ecological processes to be directly considered in the conservation alternatives [65]. This integration will require some methodological developments, but will benefit from the similarities in data types (Figure 1), especially when definitions are synchronized (e.g., α -diversity is equivalent to diversity in planning units, β -diversity to complementarity [69], and γ -diversity to the total set of biodiversity). In particular, β -diversity could be used in ecological models with scenarios (Box 2) or within optimization algorithms, thus streamlining methods and opening the possibility of evaluating the conservation value of biodiversity that is not represented in a single-species approach (e.g., ecological interaction networks [70]).

Finally, model evaluation, although always a crucial step in biodiversity modeling, is especially important for conservation scenarios that are often extrapolations to new situations (e.g., different environmental conditions, alternative restoration scenarios, poorly known taxa). Model evaluation will help to address questions such as which type of model to use. For some conservation applications, a highly flexible and accurate model is likely to be appropriate (e.g., predicting the current distribution of a threatened species). For others, it might be preferable

to have models that are more closely aligned with ecological theory (e.g., when predicting to novel environments such as climate change, or when the conservation question depends on a particular variable; e.g., the properties of a connectivity corridor). Although there are examples that evaluate the ability of advanced biodiversity models to predict rare species [71] and their interactions [72], very few studies have tested how well models extrapolate to new conditions with independent datasets, or whether they predict realistic conservation outcomes. Much more research will be necessary to understand how biodiversity models will perform in an applied setting.

Concluding Remarks

We urgently need to understand how biodiversity loss impacts critical ecosystem functioning and prunes the tree of life. We propose an integration of advanced biodiversity models with conservation goals, targets, assessments, and practice. This integration would improve the ability to rapidly evaluate biodiversity data, make predictions, and recommend conservation action for taxa, communities, and ecosystems. The backbone of this integration already exists because of recent developments in biodiversity modeling and conservation. Early examples show that this integration is possible, could be extended to several other conservation efforts, and could be used to address unresolved questions of how to best protect the world's biodiversity (see [Outstanding Questions](#)).

Acknowledgments

L.J.P. was supported by a Marie Skłodowska-Curie Fellowship (Conserving the Legacy of Evolution into the Future; AMD-659422-1). This work received funding from the European Research Area Network (ERA-Net) BiodIVERSa, Belmont Forum, in conjunction with the national funder Agence National pour la Recherche (FutureWeb: ANR-18-EBI4-0009).

References

1. Jetz, W. *et al.* (2012) The global diversity of birds in space and time. *Nature* 491, 444–448
2. Mazel, F. *et al.* (2017) Global patterns of β -diversity along the phylogenetic time-scale: the role of climate and plate tectonics. *Glob. Ecol. Biogeogr.* 26, 1211–1221
3. Eisenhauer, N. *et al.* (2019) Recognizing the quiet extinction of invertebrates. *Nat. Commun.* 10, 50
4. Davies, T. *et al.* (2018) Popular interest in vertebrates does not reflect extinction risk and is associated with bias in conservation investment. *PLoS One* 13, e0203694
5. Asmyhr, M.G. *et al.* (2014) Systematic conservation planning for groundwater ecosystems using phylogenetic diversity. *PLoS One* 9, e115132
6. Rosauer, D.F. *et al.* (2018) Real-world conservation planning for evolutionary diversity in the Kimberley, Australia, sidesteps uncertain taxonomy. *Conserv. Lett.* 11, e12438
7. Delgado-Baquerizo, M. *et al.* (2016) Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nat. Commun.* 7, 10541
8. Violle, C. *et al.* (2017) Functional rarity: the ecology of outliers. *Trends Ecol. Evol.* 32, 356–367
9. Harvey, E. *et al.* (2017) Bridging ecology and conservation: from ecological networks to ecosystem function. *J. Appl. Ecol.* 54, 371–379
10. Thompson, R.M. *et al.* (2012) Food webs: reconciling the structure and function of biodiversity. *Trends Ecol. Evol.* 27, 689–697
11. Marshall, E. *et al.* (2020) What are we measuring? A review of metrics used to describe biodiversity in offsets exchanges. *Biol. Conserv.* 241, 108250
12. Hobbs, R.J. (2016) Degraded or just different? Perceptions and value judgements in restoration decisions. *Restor. Ecol.* 24, 153–158
13. Beier, P. *et al.* (2015) A review of selection-based tests of abiotic surrogates for species representation. *Conserv. Biol.* 29, 668–679
14. González-del-Piiego, P. *et al.* (2019) Phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. *Curr. Biol.* 29, 1557–1563
15. Rapacciolo, G. *et al.* (2019) Species diversity as a surrogate for conservation of phylogenetic and functional diversity in terrestrial vertebrates across the Americas. *Nat. Ecol. Evol.* 3, 53–61
16. Pollock, L.J. *et al.* (2017) Large conservation gains possible for global biodiversity facets. *Nature* 546, 141–144
17. Rosauer, D.F. *et al.* (2017) Phylogenetically informed spatial planning is required to conserve the mammalian tree of life. *Proc. R. Soc. B* 284, 20170627
18. Pearson, R.G. (2016) Reasons to conserve nature. *Trends Ecol. Evol.* 31, 366–371
19. Pouzols, F.M. *et al.* (2014) Global protected area expansion is compromised by projected land-use and parochialism. *Nature* 516, 383–386
20. Di Marco, M. *et al.* (2018) Changes in human footprint drive changes in species extinction risk. *Nat. Commun.* 9, 4621
21. Sax, D.F. and Gaines, S.D. (2003) Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* 18, 561–566
22. Vellend, M. *et al.* (2013) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proc. Natl. Acad. Sci. U. S. A.* 110, 19456–19459
23. Cardinale, B.J. *et al.* (2018) Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. *Biol. Conserv.* 219, 175–183
24. Wintle, B. *et al.* (2018) Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proc. Natl. Acad. Sci.* 116, 201813051
25. Kobori, H. *et al.* (2016) Citizen science: a new approach to advance ecology, education, and conservation. *Ecol. Res.* 31, 1–19
26. Hortal, J. *et al.* (2015) Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 46, 523–549
27. Wilman, H. *et al.* (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* 95, 2027
28. Swenson, N.G. (2014) Phylogenetic imputation of plant functional trait databases. *Ecography* 37, 105–110
29. Penone, C. *et al.* (2014) Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods Ecol. Evol.* 5, 961–970

Outstanding Questions

What aspects of biodiversity are we overlooking because of the focus on charismatic and threatened species? What biodiversity is being overlooked because of the focus on protecting large and continuous habitat?

What is the surrogacy value of different facets of biodiversity in a range of different conservation applications?

For which taxa, which facets, and in which situations will advanced biodiversity models make better predictions? How will we accurately evaluate extrapolation to new situations?

How can we best integrate models and conservation planning? Do we focus on the models and bring in conservation objectives and scenarios, or do we focus on the conservation planning algorithms and integrate some elements of the models such as uncertainty?

How can we encourage communication between biodiversity modelers and conservation practitioners to facilitate integration of these fields?

30. Bhattacharjee, A. and Bayzid, Md.S. (2020) Machine learning based imputation techniques for estimating phylogenetic trees from incomplete distance matrices. *BMC Genomics* 21, 497
31. von Haeseler, A. (2012) Do we still need supertrees? *BMC Biol.* 10, 13
32. Gravel, D. *et al.* (2013) Inferring food web structure from predator-prey body size relationships. *Methods Ecol. Evol.* 4, 1083–1090
33. Morales-Castilla, I. *et al.* (2015) Inferring biotic interactions from proxies. *Trends Ecol. Evol.* 30, 347–356
34. Braga, J. *et al.* (2019) Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe. *Glob. Ecol. Biogeogr.* 28, 1636–1648
35. Guisan, A. *et al.* (2013) Predicting species distributions for conservation decisions. *Ecol. Lett.* 16, 1424–1435
36. Warton, D.I. *et al.* (2015) So many variables: joint modeling in community ecology. *Trends Ecol. Evol.* 30, 766–779
37. Pollock, L.J. *et al.* (2012) The role of functional traits in species distributions revealed through a hierarchical model. *Ecography* 35, 716–725
38. Ovaskainen, O. and Soininen, J. (2011) Making more out of sparse data: hierarchical modeling of species communities. *Ecology* 92, 289–295
39. Clark, J.S. *et al.* (2014) More than the sum of the parts: forest climate response from joint species distribution models. *Ecol. Appl.* 24, 990–999
40. Pollock, L.J. *et al.* (2014) Understanding co-occurrence by modelling species simultaneously with a joint species distribution model (JSDM). *Methods Ecol. Evol.* 5, 397–406
41. Ovaskainen, O. *et al.* (2010) Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. *Ecology* 91, 2514–2521
42. Ives, A.R. and Helmus, M.R. (2011) Generalized linear mixed models for phylogenetic analyses of community structure. *Ecol. Monogr.* 81, 511–525
43. Ovaskainen, O. *et al.* (2016) Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. *Methods Ecol. Evol.* 7, 428–436
44. Schliep, E.M. *et al.* (2018) Joint species distribution modelling for spatio-temporal occurrence and ordinal abundance data. *Glob. Ecol. Biogeogr.* 27, 142–155
45. Tobler, M.W. *et al.* (2019) Joint species distribution models with species correlations and imperfect detection. *Ecology* 100, e02754
46. Jarzyna, M.A. and Jetz, W. (2016) Detecting the multiple facets of biodiversity. *Trends Ecol. Evol.* 31, 527–538
47. Staniczenko, P.P.A. *et al.* (2017) Linking macroecology and community ecology: refining predictions of species distributions using biotic interaction networks. *Ecol. Lett.* 20, 693–707
48. Taylor-Rodríguez, D. *et al.* (2017) Joint species distribution modeling: dimension reduction using Dirichlet processes. *Bayesian Anal.* 12, 939–967
49. Talluto, M.V. *et al.* (2018) Multifaceted biodiversity modelling at macroecological scales using Gaussian processes. *Divers. Distrib.* 24, 1492–1502
50. Margules, C.R. and Pressey, R.L. (2000) Systematic conservation planning. *Nature* 405, 243–252
51. Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10
52. Pollock, L.J. *et al.* (2015) Phylogenetic diversity meets conservation policy: small areas are key to preserving eucalypt lineages. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 370, 20140007
53. Strecker, A.L. *et al.* (2011) Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. *Ecol. Appl.* 21, 3002–3013
54. Hanson, J.O. *et al.* (2020) prioritizr: systematic conservation prioritization in R. Available at <https://CRAN.R-project.org/package=prioritizr>
55. McDonald-Madden, E. *et al.* (2016) Using food-web theory to conserve ecosystems. *Nat. Commun.* 7, 10245
56. Decker, E. *et al.* (2017) Incorporating ecological functions in conservation decision making. *Ecol. Evol.* 7, 8273–8281
57. Punt, A.E. *et al.* (2016) Exploring the implications of the harvest control rule for Pacific sardine, accounting for predator dynamics: a MICE model. *Ecol. Model.* 337, 79–95
58. Nicholson, E. *et al.* (2019) Scenarios and models to support global conservation targets. *Trends Ecol. Evol.* 34, 57–68
59. Hays, G.C. *et al.* (2019) Translating marine animal tracking data into conservation policy and management. *Trends Ecol. Evol.* 34, 459–473
60. Rapacciuolo, G. (2019) Strengthening the contribution of macroecological models to conservation practice. *Glob. Ecol. Biogeogr.* 28, 54–60
61. Golding, N. *et al.* (2018) The zoon r package for reproducible and shareable species distribution modelling. *Methods Ecol. Evol.* 9, 260–268
62. White, E.P. *et al.* (2019) Developing an automated iterative near-term forecasting system for an ecological study. *Methods Ecol. Evol.* 10, 332–344
63. Lowndes, J.S.S. *et al.* (2017) Our path to better science in less time using open data science tools. *Nat. Ecol. Evol.* 1, 160
64. Plagányi, É.E. *et al.* (2014) Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish* 15, 1–22
65. Scroggie, M.P. *et al.* (2019) Optimizing habitat management for amphibians: from simple models to complex decisions. *Biol. Conserv.* 236, 60–69
66. Thorson, J.T. *et al.* (2019) Spatio-temporal models of intermediate complexity for ecosystem assessments: a new tool for spatial fisheries management. *Fish* 20, 1083–1099
67. Morris, W.K. *et al.* (2015) The neglected tool in the Bayesian ecologist's shed: a case study testing informative priors' effect on model accuracy. *Ecol. Evol.* 5, 102–108
68. Guillera-Aroita, G. *et al.* (2015) Is my species distribution model fit for purpose? Matching data and models to applications. *Glob. Ecol. Biogeogr.* 24, 276–292
69. Bush, A. *et al.* (2016) Current uses of beta-diversity in biodiversity conservation: a response to Socolar *et al.* *Trends Ecol. Evol.* 31, 337–338
70. Ohlmann, M. *et al.* (2019) Diversity indices for ecological networks: a unifying framework using Hill numbers. *Ecol. Lett.* 22, 737–747
71. Zhang, C. *et al.* (2020) Improving prediction of rare species' distribution from community data. *Sci. Rep.* 10, 12230
72. Flores-Tolentino, M. *et al.* (2020) Distribution and conservation of species is misestimated if biotic interactions are ignored: the case of the orchid *Laelia speciosa*. *Sci. Rep.* 10, 9542
73. Ferrier, S. *et al.* (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers. Distrib.* 13, 252–264
74. Rosauer, D.F. *et al.* (2014) Phylogenetic generalised dissimilarity modelling: a new approach to analysing and predicting spatial turnover in the phylogenetic composition of communities. *Ecography* 37, 21–32
75. Mokany, K. *et al.* (2011) Combining α - and β -diversity models to fill gaps in our knowledge of biodiversity: filling gaps in biodiversity knowledge. *Ecol. Lett.* 14, 1043–1051
76. Guisan, A. and Rahbek, C. (2011) SESAM – a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *J. Biogeogr.* 38, 1433–1444
77. Hoskins, A.J. *et al.* (2019) Supporting global biodiversity assessment through high-resolution macroecological modelling: Methodological underpinnings of the BILBI framework. *Environ. Model. Softw.* 132, 104806
78. Alnutt, T.F. *et al.* (2008) A method for quantifying biodiversity loss and its application to a 50-year record of deforestation across Madagascar. *Conserv. Lett.* 1, 173–181
79. Prober, S.M. *et al.* (2012) Combining community-level spatial modelling and expert knowledge to inform climate adaptation in temperate grassy eucalypt woodlands and related grasslands. *Biodivers. Conserv.* 21, 1627–1650