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Opinion

Biodiversity Models: What If Unsaturation Is the Rule?

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Improving biodiversity predictions is essential if we are to meet the challenges posed by global change. As knowledge is key to feed models, we need to evaluate how debated theory can affect models. An important ongoing debate is whether environmental constraints limit the number of species that can coexist in a community (saturation), with recent findings suggesting that species richness in many communities might be unsaturated. Here, we propose that biodiversity models could address this issue by accounting for a duality: considering communities as unsaturated but where species composition is constrained by different scale-dependent biodiversity drivers. We identify a variety of promising advances for incorporating this duality into commonly applied biodiversity modelling approaches and improving their spatial predictions.

Taking a Modelling Perspective on an Old Debate: Are Communities Saturated?

A recent debate [1,2] has revived an old discussion in ecology: are communities 'saturated'? Is there a limit to the number of species that a **community** (see Glossary) can support? Whether **saturation** plays a role in shaping communities remains a fundamental issue widely assessed in ecology and evolution, but no formal consensus has been reached (see Figure I in Box 1). If saturation occurs, is it caused by ecological limits or by geographic area? In particular, are communities constrained by an '**environmental carrying capacity**' (ECC) that limits the number of coexisting species?

Answering this overarching saturation question is not only crucial from a fundamental perspective, but also constitutes a major challenge for the **biodiversity models** used to predict current and future patterns of species composition and richness. Here, we do not intend to continue or solve the saturation debate *per se*, but we aim instead to assess the key implications that this question has for modelling communities (see Outstanding Questions), particularly taking a spatial and temporal perspective.

Explicitly considering potential for unsaturation or saturation in biodiversity models can have drastic effects on their predictions as well as on their interpretation, yet this issue is rarely addressed. Predictions under global change or following biological invasions might differ markedly depending on the approaches applied and whether saturation is assumed or not. This is especially important if we consider that, under global change, the flux of species in and out of communities (i.e., the species turnover) is likely to increase [3]. The level to which communities are saturated is therefore likely to have a very large influence on the potential for species to shift their distributions and track changing climates, given inertia in the composition of communities, founder priority effects, and limits on space resources [4,5]. Hence, improving our capacity to predict **species richness** and community composition by considering saturation or unsaturation is key for using models to produce more reliable conservation strategies in response to global environmental change [6].

Trends

The majority of biodiversity modelling approaches do not explicitly address the question of saturation.

Theoretical and methodological implications of saturation or unsaturation in biodiversity modelling.

Addressing saturation or unsaturation is vital to produce more reliable conservation strategies.

Integrative community modelling frameworks may be the way forward.

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Biodiversity Modelling and Community Saturation

Tremendous effort has been expended to explain biodiversity patterns [7], including high-profile theories [8] (Box 2) and an increasing number of spatiotemporal biodiversity modelling techniques [9] (Table 1, Key Table). These theories and models focus on different questions, biodiversity drivers, contexts, and scales, with corresponding variety in the ways in which community saturation is considered. Here, we focus primarily on modelling approaches developed for constructing spatially explicit predictions of species richness and community composition across large regions and over changing environmental conditions. We emphasize correlative modelling approaches (and not stochastic ones, like neutral models; see [9] and references therein) because they are the techniques most commonly applied to address conservation issues [10] and predict future patterns of biodiversity in the face of global change [6], such as for global biodiversity assessments [11].

Two commonly applied biodiversity modelling approaches [12] crystallize the debate on saturation when taken from a modelling perspective, predicting for instance similar or distinct patterns under future climate [13]. The first approach to predicting community composition and diversity has been to model the distributions of many individual species and combine the projected occurrences or probabilities – that is, **stacked species distribution models** (S-SDM); 'predict-first, assemble later' in [14]. This S-SDM approach implicitly assumes unsaturated communities [12], and has been used in situations such as reconstructing patterns of plant diversity along elevation [15]. It has been suggested that the implicit assumption made by S-SDMs of unsaturated communities could help explain their observed tendency to overpredict species richness [12,15] (but see [16]). One proposed solution is to stack the original probabilistic predictions rather than converting them to binary ones [12,17].

The second alternative approach, **macroecological models** (MEMs) [12], predicts the number of species (i.e., species richness) directly as a function of various hypothesized environmental drivers ('assemble first, predict later' in [14]), thus assuming species–energy, species–area, and other richness–environment relationships (Box 2) to implicitly define limits to the expected number of species based on some ECC (Box 2) [12].

A variety of other biodiversity modelling approaches also lie in-between these two extremes, which correlate the whole species composition to environmental factors based on the covariance of species, thus allowing simultaneous predictions of the occurrences of multiple species. These approaches thus better incorporate the effect of biotic interactions, but usually do not consider saturation explicitly. Typical examples include ordination-based modelling approaches such as canonical correspondence analysis [18], multivariate regression trees [19], constrained additive ordination [20], or approaches directly accounting for interactions in SDMs, for example, the recent joint SDMs (J-SDMs) [21]. Constrained additive ordination and J-SDMs are, however, currently technically limited to relatively small suites of species, usually a subset of all the species of a taxonomic group present in a region.

Very recently, whole integrative community modelling frameworks have been proposed [9]. For example, the spatially explicit species assemblage modelling (SESAM) [22] approach can (or not) use MEM predictions (in such case assuming saturation), but also other information, such as biotic interactions and **regional species pools**, to constrain S-SDMs predictions [22]. The recent linked approaches of DynamicFOAM [23] and the M-SET metacommunity model [24] more explicitly consider beta-diversity patterns (which SESAM does not), and also include saturation explicitly [9] (Table 1). While these new approaches have been successful in improving predictions of community composition and diversity [16], the question of the saturation assumption remains crucial, especially if these approaches are to be harnessed for projecting changes into the future.

Glossary

Biodiversity models: here, we consider biodiversity models that use data from most or all the species in a taxonomic group to generate information about the spatial patterns in the distribution of diversity at the community level. The outputs from these biodiversity models comprise predictive mapping of species richness or gradients of compositional variation [14].

Community: an assemblage of species that co-occur in a location at a given time.

Community assembly: mechanisms (drivers) that determine the species composition of a community.

Dark biodiversity: portion of the regional species pool that is absent from the local community [49]. In other words, the species present at a regional scale that can potentially colonize the local community but are absent from it. This concept provides valuable information for conservation applications and for improving knowledge of community assembly processes [49].

Environmental carrying capacity (ECC) of a community: 'steady-state level of richness specific to a particular site or local ecosystem that is set by resource availability and other local conditions and is maintained despite changes in species composition' [90]. Here it thus refers to a carrying capacity for the number of species in a community, not to be misled with the ECC that traditionally refers to the number of individuals that a population of a single species can sustain in a given environment.

Macroecological models: biological data are first classified or aggregated to produce community-level data (e.g., species richness data) that are then modelled as such in relation to environmental predictors. These models have been described as 'assemble first, predict later' models by Ferrier and Guisan [14].

Regional species pool: set of species present in a region that could potentially colonize a local site or community based on the suitability of local ecological conditions.

Saturation: in a saturated community, local richness exhibits a maximal level that depends on

A range of mechanistic models have also been used to make spatial predictions of communities [8,24]. Mechanistic models of single species (e.g., mechanistic SDMs) [25] are typically only applicable to a small number of species for which the required input parameters are available [26,27]. By contrast, mechanistic models of whole communities or ecosystems often apply to a specific taxonomic or functional group, and those able to predict composition usually only apply to a defined region and limited number of species (e.g., dominant trees and shrubs in forest gap models) [28]. The latter typically assume unsaturated communities, and let species richness and composition emerge from the component processes (e.g., resource use, competition). However, mechanistic models applicable to large spatial extents are usually not informative of species composition and cannot always predict richness, for example, dynamic vegetation models of intermediate complexity (dynamic global vegetation models) [26], and hence do not provide a simple solution in themselves for considering (un)saturation in biodiversity modelling of whole flora and fauna. However, more mechanisms could be added to the modelling of communities by coupling or incorporating dynamic global vegetation models with or into one of the integrative community modelling frameworks (Table 1) – for example, as additional community constraints.

Identifying a Duality: Unsaturation and Constraints in Biodiversity Modelling

Studies that have examined the evidence for or against saturation have yielded contrasting results, and no unanimous conclusion has emerged [1,2]. Yet, one major advance is that unsaturation is increasingly considered a valid and likely assumption. Although certainly not valid for all cases (e.g., not at very fine scale where physical space becomes limiting; Box 1), it might apply to a large majority of communities, especially towards larger resolutions (Box 1). Therefore, biodiversity modelling frameworks [9] should at least partially incorporate an unsaturated perspective, allowing some flexibility in the number of species occurring in a community. Yet, the multitude of MEM predicting species richness from its direct correlation with environmental factors has also shown that variations in richness follow, at least in part, the variations in environmental conditions (Box 2). And accordingly, the mean or maximum number of species in a given location can, in many cases, be predicted with reasonable accuracy from limits in available area, energy, resources, or heterogeneity [29] (Box 2).

This contradiction represents the key challenge for biodiversity modelling stemming from the ongoing saturation debate [1,2]. Here, we suggest that this apparent contradiction underlies a duality: all communities might be unsaturated and yet inherently constrained in their composition by various drivers (i.e., ecological, evolutionary, historical, or biological; Box 3). Biodiversity

ecological or areal constraints or limits.
Species richness: number of species present in a community or area. This concept is equivalent to α-diversity.
Stacked species distribution models: individual species are modelled separately as a function of environmental variables; the model predictions are then stacked to produce a potential richness map. These models have been described as 'predict first, assemble later' models by Ferrier and Guisan [14].

Box 1. Are Communities Saturated?

In the past, a large body of literature aimed at identifying the ecological limits of species richness concluded that strong control is exerted by environmental factors, especially climate conditions and environmental heterogeneity [29,61] (and references therein). In this context, a central method used has been the regression of local on regional richness [62]; saturating or nonlinear functions indicate that an upper limit of local diversity has been set by ecological limits [63]. However, important methodological limitations, such as pseudoreplication, limit the use of this graphical approach [30,64]. More recently, ecological analyses of seed addition experiments [65,66], contemporary biotic exchanges [66], fossil records [67], invasion processes [66,68–70], the packing and filling of functional space considering functional trait data [71] (but see [72]), diversification models [73], and molecular phylogenies [1,39,74] have suggested that ecological systems might rarely be saturated and instead remain open to new species (Figure I).

The relevance of saturation might therefore be relative to the scale [31,34,75]. Thus, some authors suggest that communities might not be saturated [76] or might only be saturated at very small scales (e.g., <1 m² for plant communities [69]). At such scales, stochasticity (e.g., disturbances such as fires, neutral processes) [7,50] is an important element in understanding biodiversity, with purely physical parameters becoming more important, such as how many individuals can occupy the total area. At coarser resolutions, according to several authors [1,66], communities are dynamic in space and time and are virtually always accessible to new species (with speciation and migration occurring more often than extinction), and community diversity is not set by ecological limits. Nevertheless, richness would remain correlated with variables that are related to productivity or energy within a geographic space [77], though this correlation might be explained by alternative hypotheses [1,38] (Boxes 2 and 3).

Although we take into consideration that communities might be unsaturated, at local scales and for high values of richness, the invasion of a community by new species is likely to become progressively more arduous [66]. This resistance might result from more intense biotic interactions at a higher species richness [66] and the inhibitory properties of established species [50]. Therefore, at fine spatial resolution, locally dominant species, organism body size, and disturbances are important factors [7].

	Saturated community	**Unsaturated community**
Local assemblage	**Local realized species**	
	- Community at equilibrium - Speciations and immigrations are equal to extinctions - Ecological limits set a limit to the number of species - Equilibrium community close to new species	- Dynamic community in space and time - Speciations and immigrations can be greater than extinctions - Maximum number of species is only driven by the regional species pool - Community open to new species
Regional species pool	**Regional species pool**	
	- Regional species pool set by ecological limits - Region with more stable climates and greater inputs of energy exhibit greater species richness because of a greater environmental carrying capacity	- Regional species pool driven by different mechanisms: diversification rate, immigration, speciation, regional age, etc. - Regions with more stable climates and greater inputs of energy exhibit greater species richness because of higher diver-fiction rates (leading to a larger species pool)
Continental species pool	**Continental species pool**	
	- Number of species explained by *species–area, species–energy,* and other ecological limits theories - Environmental drivers represents a fixed carrying capacity	- Nº of species explained by *niche conser-vative,* faster *diversification, or other theoriest* - No maximum continental species pool - Environmental drivers influence on the rates of immigration, extinction, and speciation

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Figure I. Main Theoretical Implications for Saturation and Unsaturation. The main theoretical differences and implications in community ecology assuming communities as saturated or unsaturated.

modelling approaches therefore need to deal with these two dimensions – unsaturation and constraints – simultaneously.

Communities are assembled by biodiversity drivers that operate over a variety of temporal and spatial scales [30–34] (Box 3). And although scale can be a complicating factor, an increasing number of hierarchical approaches are now emerging that should allow integrating scale within modelling frameworks [35]. More importantly, most correlative biodiversity modelling approaches have neglected important theoretical advances, especially from evolutionary biology [33,36,37]. Diversification rates (Box 3), in particular, are expected to be major processes influencing the biodiversity found in a site [33,36,38], with major effects on two important aspects: (i) the size of the regional species pool, which also depends on the dispersal history of taxa [39], and (ii) the size of the 'habitat' species pool, nested within the regional pool, as defined in [22], that is, the number of species that could successfully evolve adaptations to particular environments [39]. Incorporating constraints such as these into biodiversity model-ling, within an unsaturated community perspective, therefore requires a range of innovative modelling solutions.

Box 2. Towards a Reinterpretation of Some Macroecological Theories?

The relationship between available energy and biodiversity is well known [78]. This species–energy relationship was suggested by Hutchinson [79] and has been interpreted by some authors as a limit on the number of species based on the available energy [80]. Consequently, fifty years ago, many ecologists assumed that communities were saturated [34]. Later, Currie [29] theorized that a measure of energy availability ought to enable the species richness in a region to be predicted [2]. This measure is interpreted by some authors as the ECC of a unit and defines the boundaries of community saturation [81,82].

Nevertheless, the macroecological theories of a direct association between current climate and biodiversity, such as the 'species–energy' theory [78], 'species–area' theory [83], or 'ecological limit' hypothesis [2], have not led to an adequate description of all the drivers of species richness patterns [47,77]; for example, they do not consider evolutionary history factors [47]. At least three alternative theories [1,7,38,39], the 'niche conservative' [84], the 'faster diversification', and the 'metabolic' theories [85], have been proposed in an attempt to explain this correlation between species richness and energy (and habitat heterogeneity) without placing a limit on the number of species. These theories predict that greater values of biodiversity are observed not because of greater energy or space availability, but because more species in the regional species pool are adapted to the ecological conditions in the area. These theories are the most promising for explaining diversity patterns because they are integrative and consider a combination of drivers that affect the fundamental processes underlying species richness patterns (evolution, immigration, extinctions, and ecological interactions), rather than only the influence of environmental variables [7]. For example, these theories note that time and diversification rates, as well as adaptive traits, are important drivers of biodiversity patterns [86] and that mutualistic interactions promote diversification in some groups [73]. More studies might still be needed to explain the role of evolutionary history in community assembly [33,87].

Recently, Cornell [38] proposed the new 'damped increase hypothesis', which attempts to reconcile two opposing hypotheses (saturated vs. unsaturated). Cornell's theory further predicts that 'biodiversity generally increases through the time but that its rate of increase is often slowed by ecological constraints'. Under this point of view, the regional species pool remains an important concept, recalling the importance of scale in community assembly (Box 3).

Confronting the Duality: Accounting for Unsaturation and Constraints in Biodiversity Modelling

Here, we propose that advancing biodiversity modelling requires accounting for the duality of unsaturated communities where species composition is constrained by a variety of scale-dependent biodiversity drivers. An important core requirement in developing more robust biodiversity models under this perspective would be to improve our basic ecological understanding of saturation, and the ways in which drivers and constraints influence **community assembly** processes at different scales [40,41]. These empirical investigations will however be especially informative where applied at the local community (e.g., 30–1000 m) and regional (e.g., 100–5000 km) extents that match those typical of biodiversity models.

The development of improved biodiversity models should thus benefit from incorporating new information from the increasing number of macroecological studies on systematics, phylogenetics, biogeography, palaeontology, and other approaches [42], which all represent biodiversity drivers and potential constraints on community assemblages. For example, phylogenetic

Box 3. On the Significance of Scale for Biodiversity Drivers

Communities are assembled by drivers that operate over a variety of temporal and spatial scales [31] (Figure I). Local species richness has been reported to be limited or driven by local factors, such as available energy [78] and some authors state that saturation is only possible at this local scale (Box 1). In this view, local environmental factors (mainly energy and habitat heterogeneity) constitute important controls on species richness (Box 2). Other studies and theories have suggested that achieving a comprehensive understanding of biodiversity patterns at local scale also requires information on regional and historical drivers (Box 2). Under this perspective communities are not saturated; local assemblages would not only be governed by local ecological limits, but also by processes at larger scale (e.g., historical contingencies, evolution) [88]. In addition, biotic and abiotic filters [89] might interact to downgrade regional species composition in local sites [89]. Following this reasoning, saturation would not be possible at regional and continental scales. The regional species pool would be mainly shaped by speciation, immigration, range extension, diversification rates, and regional age [38,39]. Diversification rates can potentially be driven by climatic stability, time available for diversification, climatic age, time available for immigration, ambient energy, the size of the regional area, productivity, and habitat heterogeneity [38,39]. Areas with stable climates and greater inputs of energy should exhibit greater species numbers, not because of a greater ECC [90], but because they present higher diversification rates and, consequently, larger regional species pools [38]. At the continental scale, richness patterns are shaped mainly by biogeographical drivers (rates of speciation, immigration and extinction of lineages, and historical processes) and dispersal limitations [39].

To summarize, the maximum species richness at a local site might be more strongly influenced by the regional species pool than by some ECC. Thus, to understand the drivers of local richness, the drivers of regional and continental biodiversity must first be known [76]. An improved understanding of biodiversity drivers is key to building a more robust theory that would improve our ability to predict biodiversity.
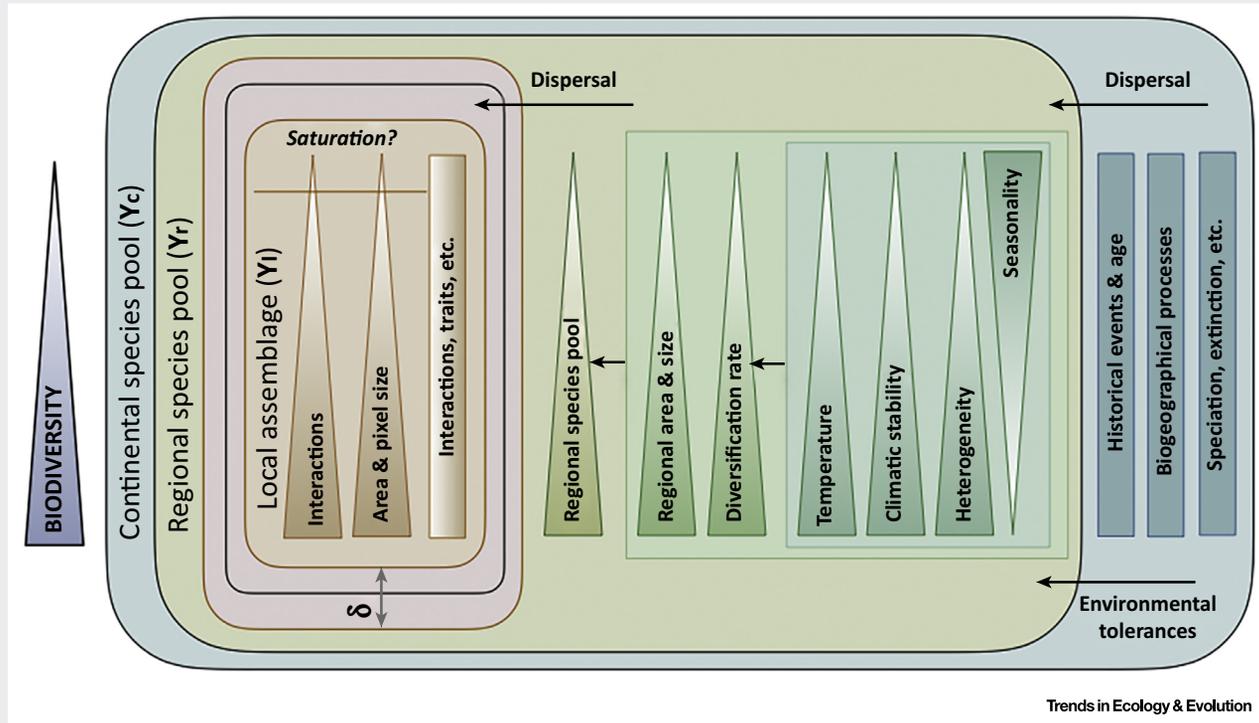
Figure I. Main Biodiversity Drivers across Scales. The main drivers influencing species diversity (purple) across scales, considering theories that reflect communities as unsaturated at local (brown), regional (green), and continental (blue) scales. Triangles express the magnitude of the relationship (the wider part reflects greater magnitude) between the driver and the biodiversity. Integrated biodiversity modelling frameworks could be used to consider the final predicted composition or species richness as a probability distribution (δ), whose properties (i.e., mean and variance) depend on the different drivers and processes at different scales (γ_l, γ_r, γ_c).

community ecology (ecophylogenetics) [43] is an emerging field that uses phylogenetics to test hypotheses about how ecological communities are assembled by providing temporal and evolutionary dimensions to community ecology [33,44,45]. New perspectives are also offered by evolutionary models simulating speciation and extinction events through time, or by operationalizing trait-based environmental filtering knowledge into predictive modelling techniques [46]. It would also be important to provide flexibility such that these models could consider complementary or alternative theories than the current mainstream theories (e.g., 'species–energy'), such as the 'faster diversification or metabolic' theories (Box 2), and could include complementary spatial information (i.e., not strictly related to ECC), such as the location of endemism centres, patterns of beta-diversity, species phylogenies, phylogeographical patterns, and species traits. Innovative, more mechanistic approaches [47,48] will thus be needed to incorporate key processes with generic, easily applicable correlative modelling techniques, including multiple interacting attributes of species (e.g., environmental suitability, functional traits), local properties of assemblages (e.g., resource availability, co-occurrence patterns, disturbance), and regional (e.g., species pool, dispersal barriers) and continental (historical factors, speciation) contexts.

Key Table

Table 1. Biodiversity Modelling Approaches[a,b]

Modelling approach	Predictions and model type	Saturation assumption	Taxonomic scope	Complexity	Methodological solution
S-SDM [15]	SC and SR from stacked correlative SDMs	No	All except rare species (e.g., <10 occurrences)	Low	Incorporate constraints as predictors to avoid overpredicting richness
Mechanistic S-SDM [25]	SC and SR from stacked mechanistic SDMs	No	Groups with physiological data for all species	High	Need to incorporate processes of interspecific interactions and other ecological constraints
Joint-SDM [21]	SC and SR from a multispecies correlative model	Yes (implicitly)	Small communities (computational limits)	High	Same as S-SDM but including interactions and allowing rare species
Correlative MEM [29]	Only SR (or other whole community properties) from correlative model	Yes (explicitly)	Total richness based on all species (no limitation), no composition	Low	Implicitly assume saturation New, multiscale and probabilistic solutions will be needed to account for unsaturation
Simulation MEM [47]	Only SR from MEM based on (non-niche-based) range simulations	No	Total richness based on all species (no limitation), no composition	High	Through individual range simulations, theoretically includes solutions to account for unsaturation, i.e., account for biogeographic legacies
SESAM [22]	SC and SR from integrating correlative S-SDMs, correlative MEMs, species pools, and assembly rules	Flexible	All except rare species (e.g., <10 occurrences)	Moderate	Saturation can or not be enforced. Possibility of probabilistic SR predictions. Switching 'on' or 'off' of various eco-evolutionary filters/constraints at different scales
DynamicFOAM [23]	SC from correlative MEM and dissimilarity model	Yes (explicitly)	All species	High	Possibility of probabilistic SR predictions. Predictions can be tuned by different drivers and constrains at different scales
M-SET [24]	Metacommunity model. SC from processes as well as correlative MEM	Yes (explicitly)	All species	High	Possibility to switch 'off' saturation, and to incorporate additional drivers constraining richness without assuming saturation
Hierarchical Bayesian [35]	SR using a flexible-scale hierarchical Bayesian framework	No	All species, no composition	High	Explicitly incorporate probability distribution of SR, whose properties depend on different drivers at different scales
DVM [28]	Dominant tree and shrub species at local scale from forest dynamic gap models, and thus SR or SC for these species	Not strictly	Suite of dominant species with known ecodemographic parameters	High	Saturation implicitly assumed by the number of species parameterized in the model. Could be alleviated by adding any new species entering the system if parameters available
DGVM [26]	Mainly functional plant composition from mechanistic model at large scales. Possibility for some DGVM to model some dominant species	Not really applicable	Plant functional groups, dominant plant species	High	Not a solution directly applicable. Could be coupled with or incorporated into one of the integrative community modelling frameworks (see above) to set constraints (e.g., to available water for the community)

[a]The table presents identified methodological solutions when considering unsaturation and biodiversity constraints in different modelling approaches to predict SR and SC. The complexity (need for data and computational time) and the taxonomic scope of the model are also provided.
[b]Abbreviations: DGVM, dynamic global vegetation models; DVM, dynamic vegetation model; SC, species composition; SR, species richness.

For the widely applied S-SDM approach, we see that it appropriately considers communities as unsaturated, but it ignores many important constraints on community composition (see below), hence it bears the risk of overpredicting the number of species in a location [22]. However, as a way forward, it could be useful here to view the species that are overpredicted as the '**dark biodiversity**' [49] of the unsaturated local assemblage, or a set of species that could potentially

invade the community [50]. Additional constraints could be incorporated into S-SDMs, such as through new multiscale (and potentially more mechanistic) spatial (i.e., remote sensing) layers [51] in the component SDMs that better encapsulate some of the nonabiotic constraints to species occurrence, such as known size of the regional species pool, historical events, site accessibility, or biotic interactions. Regarding the later, further development of J-SDMs or other similar approaches might be beneficial in deriving SDMs that incorporate some elements of interspecific interactions as community constraints [52]. In this regard, an explicit way to incorporate these additional constraints into S-SDMs could involve application of the SESAM approach, which integrates species-level and community-level modelling and information to account for biotic interactions (see below) [53].

By contrast, correlative curve-fitting MEMs can capture spatial and environmental constraints in predicting species richness, with accurate predictions under present conditions (Box 2). However, because these models implicitly tend to consider communities as saturated, their predictions of species richness into the future, under global change and shifting species distributions, are likely to be far less reliable. As with S-SDMs, there could be opportunities for accounting for unsaturation in correlative MEMs through incorporating scalers modifying spatially explicit richness predictions as predictors in the models. Layers describing the likely regional species richness around every grid cell (either now, or in the future; e.g., focal windows approaches) could be used for such a purpose, enabling the predictions of MEMs to be 'corrected' by the neighbourhood, for example, in areas likely to experience substantial influx of range-shifting species. Pattern-oriented modelling approaches could also be an interesting alternative [54], where it is possible to use correlative MEMs conceptually based on theories that do not assume saturation (Box 2). An initial set of relevant explanatory variables – not only energy-related, and not assuming saturation – could be used from which to define competing models that best encompass and predict species richness patterns at the targeted scale. For example, Mateo *et al.* [55] employed a multimodel inference approach within an MEM frame-work for this purpose. Provided all explanatory variables are spatially explicit, model averaging can then be used to derive spatial predictions. Following this procedure, MEMs would not just limit the number of species by energy drivers, but would represent the statistical correlation between different biodiversity drivers (e.g., historical climatic stability, annual climatic stability, geographical and spatial gradients, historical aspects, evolutionary history, vegetation types, human impact) and species richness patterns, potentially involving other processes than saturation to predict biodiversity patterns.

One recurrent problem of the simple correlative approaches previously described (e.g., one single model for richness or a simple stacking of species models) is that they cannot account explicitly for processes, but can only fit and predict patterns. This limits the capacity for these approaches to fully account for the duality of unsaturated communities where composition is constrained by different drivers. Here, we propose instead that if models have to account for this duality, they should be able to incorporate the different mechanisms behind biodiversity drivers (i.e., ecological, historical, and evolutionary processes) operating across multiple scales. There is thus a challenge to develop modelling approaches incorporating more process-based drivers in generic, easily transferable, and applicable ways.

One way forward is to further develop the new integrative community modelling frameworks, like SESAM [22] and DynamicFOAM [24], or M-SET [56], by enabling these to use mechanistic knowledge as much as possible, relying less on empirically measured (i.e., observed) corre-lations. In particular, D'Amen *et al.* [9] suggested the use of such frameworks in a way that different modelling modules are not only more mechanistic but can also be switched 'on' or 'off' after identifying the importance of different drivers. This could be the perfect setting to account for both unsaturation and constraints in biodiversity modelling. For instance, within the SESAM

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framework based on stacking predictions from individual species models [16], unsaturation could be simply enforced by not constraining the stack of species predictions by a separate richness prediction model (MEM) while using eco-evolutionary models to define the regional and habitat species pools. The individual species models could then be based on mechanistic approaches (e.g., [25]), and experimentally based (rather than empirical) biotic interactions (e. g., [57]) could, for instance, be used to determine which species might ultimately coexist. Where environmental constraints are particularly strong (e.g., small pixel size at local scale, with tight richness–environment relationships), application of the SESAM, DynamicFOAM, or M-SET frameworks (or the simpler MEM) might then be used as currently.

Finally, a further promising development in such integrated frameworks could be to consider the final predicted composition or species richness as a probability distribution, whose properties (i.e., mean and variance) depend on the different processes at different scales (see Figure I in Box 3). As an unsaturated community does not have a fixed number of species, the probability distribution of species richness values would define the flexibility to capture and predict the composition and species richness at a local scale. One approach to develop such analysis is a Bayesian hierarchical modelling approach [35], where each driver could be considered as a different component in the modelling framework [9,24]. A Bayesian hierarchical approach allows a conceptual approximation and incorporation of different model components, and inclusion of diverse information sources from empirical ecological studies [58,59], for example, the regional species pool. Bayesian hierarchical modelling offers a flexible approach to incorporate drivers that operate over a variety of temporal and spatial scales (Box 3), though development of generic, easily transferable, and applicable models requires further attention. We suggest exploring the implementation of different hierarchical Bayesian methods frequently applied to spatial–temporal clinical data, for example 'Joint Models' [60], and represent useful starting points to develop methodological solutions for the spatial modelling of communities and biodiversity.

Concluding Remarks

Our understanding of community saturation or unsaturation is far from complete, and the ways in which drivers influence community assembly processes at different scales remain one of the most important challenges in ecology and biogeography [40,41]. Substantial effort, including new methodological and conceptual approaches, will be needed in the future to illuminate this research area. These studies should be considered as important conceptual bases for improving biodiversity models that have typically ignored, or insufficiently addressed, the saturation concept to date. Here, we have proposed a number of practical solutions to accounting for a duality of unsaturated communities in biodiversity models, where species richness is constrained by scale-dependent biodiversity drivers, where the final predicted composition or species richness is a probability distribution, whose properties depend on the different processes at different scales.

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