

Spatial predictions at the community level: from current approaches to future frameworks

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ABSTRACT

A fundamental goal of ecological research is to understand and model how processes generate patterns so that if conditions change, changes in the patterns can be predicted. Different approaches have been proposed for modelling species assemblage, but their use to predict spatial patterns of species richness and other community attributes over a range of spatial and temporal scales remains challenging. Different methods emphasize different processes of structuring communities and different goals. In this review, we focus on models that were developed for generating spatially explicit predictions of communities, with a particular focus on species richness, composition, relative abundance and related attributes. We first briefly describe the concepts and theories that span the different drivers of species assembly. A combination of abiotic processes and biotic mechanisms are thought to influence the community assembly process. In this review, we describe four categories of drivers: (i) historical and evolutionary, (ii) environmental, (iii) biotic, and (iv) stochastic. We discuss the different modelling approaches proposed or applied at the community level and examine them from different standpoints, i.e. the theoretical bases, the drivers included, the source data, and the expected outputs, with special emphasis on conservation needs under climate change. We also highlight the most promising novelties, possible shortcomings, and potential extensions of existing methods. Finally, we present new approaches to model and predict species assemblages by reviewing promising ‘integrative frameworks’ and views that seek to incorporate all drivers of community assembly into a unique modelling workflow. We discuss the strengths and weaknesses of these new solutions and how they may hasten progress in community-level modelling.

Key words: evolutionary forces, dispersal, species pool, environmental filter, biotic interactions, stochasticity, modelling framework.

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I. INTRODUCTION

Since the rise of community ecology, many theories have been proposed to explain the assembly of species diversity within communities (e.g. Hutchinson, 1959; MacArthur, 1967; Levins, 1969; May, 1975; Pacala & Tilman, 1993). A large amount of both theoretical and empirical work has provided much insight into this fundamental topic, yet some striking questions remain unanswered. To what extent can we move from descriptive and empirical data to spatial predictions of community patterns and assembly? By the same token, if environmental conditions are modified, to what extent can we predict the resulting changes in communities? The development of new approaches for predicting community responses to environmental modifications is progressing rapidly, especially considering single-species modelling (e.g. Kearney & Porter, 2009; Pearman *et al.*, 2010; Zimmermann *et al.*, 2010). However, major challenges remain in the understanding and simulation of the processes of species assembly in real, multi-species communities (Cavender-Bares *et al.*, 2009; Beck *et al.*, 2012).

In this review, we focus on those models that were developed for making spatial predictions of communities. We are specifically interested in the prediction of community attributes reflecting the number of species in a community and the evenness of species' abundances (Magurran, 1988): richness, composition, and/or relative abundance at the species level, and related attributes at larger scales such as functional, guild, and vegetation type diversity (Huston, 1994) (Fig. 1). First, we briefly describe the existing theoretical assumptions on the different forces known to shape communities. Then we present the main methods used to predict communities, focusing on their biological principles, predictive approaches, and expected outputs. In doing this we illustrate the most-promising examples, potential extensions, and possible shortcomings. As a working definition, here we consider communities as assemblages of distinct populations of species that co-occur in a given space at a given time. Given that studying all organisms across all taxonomic groups is hardly feasible by one research team, communities are often defined according to specific criteria, typically all species pertaining to a taxonomic, functional or trophic group, the choice of which depends on the research questions being asked (Begon, Harper & Townsend, 1996). We do not cover issues of species' physiology, relative abundance, or population and metapopulation dynamics. Moreover, we do not aim to review the detailed methods

of computing the models and mathematical aspects because these have been extensively treated elsewhere. Similarly, even if model evaluation is a crucial issue, assessing all the evaluation techniques for each individual model and approach is outside the scope of this review. We expect that the identified perspectives will be beneficial to conservation studies aimed at anticipating global change effects on communities.

II. DRIVERS OF COMMUNITY COMPOSITION

A large number of abiotic processes and biotic mechanisms are thought to shape the patterns of species assembly in ecological communities. Land use and other human modifications of the environment may also influence patterns of community composition through a number of processes such as local extinctions and species movements in response to these changes (Fischer & Lindenmayer, 2007). However in this review we focus on the natural drivers of community assembly, which we recognize as pertaining to four categories: (i) historical and evolutionary, (ii) environmental, (iii) biotic, and (iv) stochastic.

From the viewpoint of a long time scale, evolutionary and historical factors have been shown to influence the assemblage of species (Willis, 1922; Karr, 1976; Ricklefs & Schluter, 1993). Evolutionary processes such as speciation, extinction and adaptation determine the composition of regional species pools (i.e. the set of species that could potentially colonize by dispersal and establish within a community over large spatio-temporal scales), through spatio-temporal dynamics of species' distributions (Schluter & Ricklefs, 1993; Emerson *et al.*, 2011; Lessard *et al.*, 2012). At the local scale, evolutionary relatedness among species may set constraints on species characters to limit the ecological potential of a species and its interactions with co-occurring species (Price, 1994, 2003). A range of historical events that have modified the earth surface and the climate during geological times resulted for example in episodes of extinction, radiation or allopatric speciation that have reduced or boosted the rate of diversification over a period of time for a clade (e.g. Fedorow, 1966; Flessa, 1986). In this context, dispersal acted as a filter that determined which species in the regional source pool could have reached a given unit. Over shorter timescales, species pool richness and composition are influenced by metacommunity dynamics (Mittelbach & Schemske, 2015).

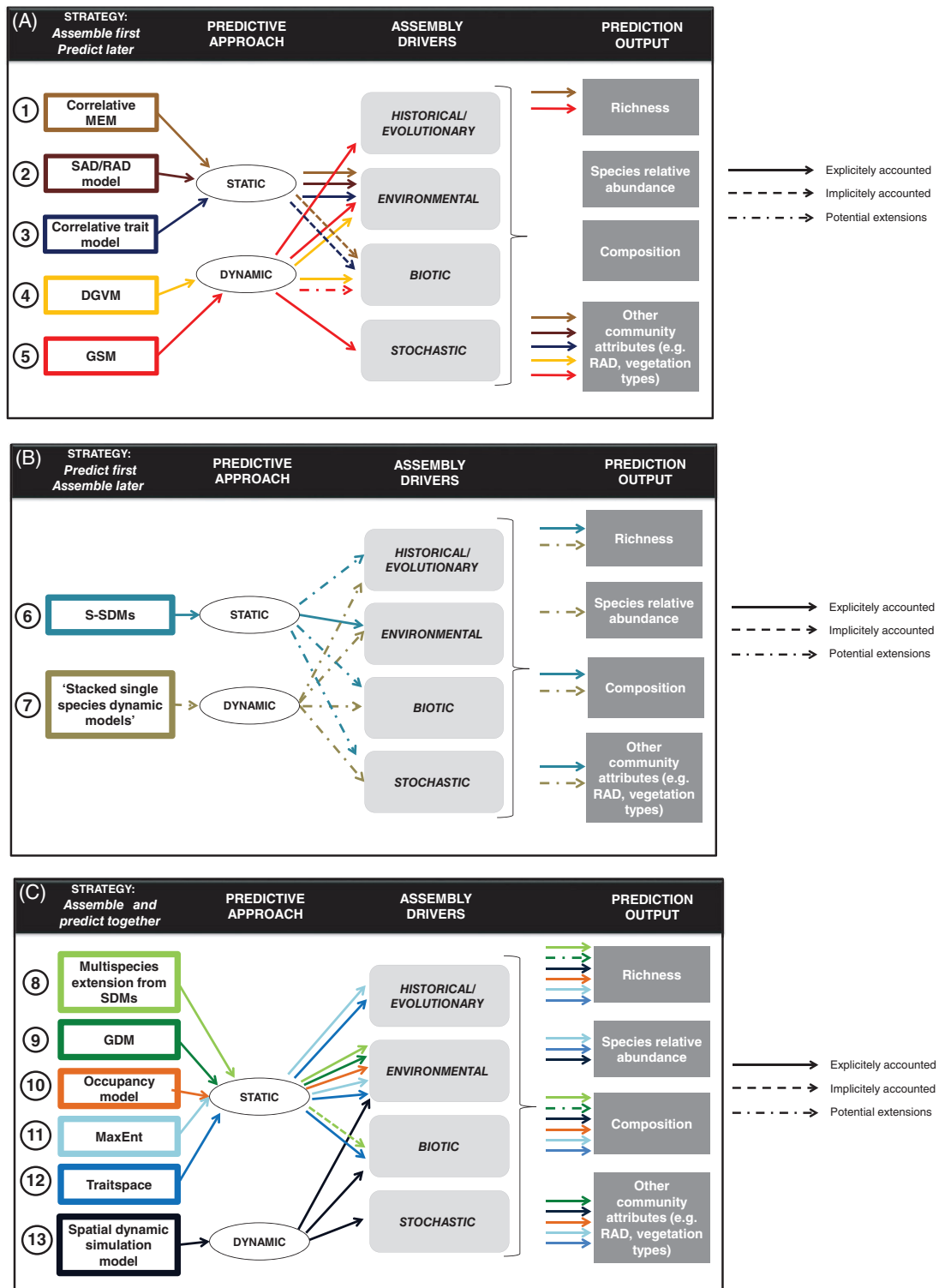


Fig. 1. Schematic illustration of the characteristics of the modelling approaches considered in this review pertaining to the strategies ‘assemble first, predict later’ (A), ‘predict first, assemble later’ (B), and ‘assemble and predict together’ (C). For each model, we indicate the predictive approach, the inclusion of different drivers of community assembly (we consider that the historical/evolutionary driver is included in the model if species’ phylogenetic relations, or origin of the species pool/dispersal limitation are considered), and the expected predictive output. In particular, we specify whether the drivers are implicitly or explicitly accounted for in the model and potential extensions anticipated by the authors. DGVM, dynamic global vegetation model; GDM, generalized dissimilarity model; GSM, general simulation model; MaxEnt, maximum entropy model; SAD, species abundance distribution; RAD, rank abundance distribution; SDM, species distribution model; S-SDM, stacked species distribution model.

Ecological mechanisms regulate the assemblage of species in a community (Lotka, 1925; Volterra, 1926; Gause, 1934; Hutchinson, 1959). According to the theory of trait-based community assembly (Keddy, 1992), the environment acts like a filter on the regional species pool including all species that lack specified combinations of functional traits (i.e. physiological and morphological properties). Support for environmental filtering typically comes from plant studies that find positive correlations between environmental gradients and community-weighted trait values (e.g. Cornwell & Ackerly, 2009; Shipley, 2010; Dubuis *et al.*, 2013) and from studies showing that trait differences generate competitive hierarchies (Freckleton & Watkinson, 2001; Kunstler *et al.*, 2012). Non-random patterns in phenotypic traits have also been documented in a wide range of animal phyla (e.g. Ricklefs & Travis, 1980; Ingram & Shurin, 2009). The abiotic environment also provides spatio-temporal heterogeneity upon which the ecological strategies of many different species can be built (Weiher & Keddy, 2001). In this sense, the environment may constrain the number of species that can actually coexist in a determined site based on available energy (Hairston, Smith & Slobodkin, 1960). The species–energy relationship, first proposed by Hutchinson (1959), has been reported for many groups and geographical settings (Connell & Orias, 1964; Brown, 1981; Wright, 1983). Theoretically, it follows that a measure of energy availability should allow the prediction of the number of species in a region (e.g. Currie, 1991). Such a measure can be seen as a rough expression of the environmental carrying capacity of a unit, determining the limits of community saturation (Loreau, 2000). However, an open question remains whether this constraint should apply to the total number of species or to the total number of individuals of all or a given combination of species in a unit.

In addition to environmental filtering and constraints, biotic interactions represent another ecological force that influences community assembly processes (e.g. Gause, 1934; MacArthur, 1964, 1965). Competition for limited resources has long been considered one of the most important species interactions in ecology (Hutchinson, 1959; MacArthur & Levins, 1967; Brown, 1981), constraining the final diversity in a community either by leading to a partitioning of resource requirements among species (driven by the limiting similarity principle), through evolutionary character displacement, or as a result of competitive exclusions among species depending on the same resources (Lack, 1947; MacArthur, 1964, 1965; Tilman, 1982; but see Andrewartha & Birch, 1954; Wiens, 1977 on the ‘variable environments’ hypothesis). However, by the early 1980s, important challenges to the limiting similarity paradigm (MacArthur & Levins, 1967) emerged, reducing the generality of its applications. The most important of these challenges was the introduction of null models in community ecology, causing ecologists to consider another view on patterns by simply asking the following: what would these patterns of species assembly look like if mechanism x (e.g. species interactions) was not in operation. Some of the patterns that were previously attributed to

interspecific competition were actually simulated by models that do not account for competitive forces (Abrams, 1975; Turelli, 1978). Moreover, other empirical and theoretical studies suggested that a great variety of different interactions can influence coexistence patterns among species across trophic levels (Hairston *et al.*, 1960; Connell, 1975; Ricklefs, 1987), but communities where local interactions are low or absent have also been observed (e.g. Strong, Lawton & Southwood, 1984), supporting the idea that real communities lie on a continuum of interactive to non-interactive processes (Cornwell & Lawton, 1992).

Environmental filtering and biotic competitive interactions stand as opposite forces regarding species traits (Zobel, 1997; Weiher & Keddy, 1999; Mayfield & Levine, 2010). Environmental filtering is observed when species in a community tend to be more similar in their ecological requirements than by chance, leading to the convergence (or clustering) of adaptive traits. On the contrary, limiting similarity is observed when species in a community tend to be less similar in their traits (i.e. trait divergence or overdispersion) than observed by chance, due to biotic interactions restricting coexistence of species with similar traits and thus similar in their resource acquisition (Raunkiaer, 1934; MacArthur & Levins, 1967; Keddy, 1992; Weiher, Clarke & Keddy, 1998). When the two controls operate at the same time, functional or phylogenetic convergence or divergence can be produced only in the relevant groups of traits associated with these diverging forces (Weiher *et al.*, 1998; Cornwell & Ackerly, 2009; Mayfield & Levine, 2010; Ndiribe *et al.*, 2013). Elucidating how these forces act based on traits, what their effects are on the community, and how they relate to ecological gradients may reveal constraints that can be used to predict community structure (Shipley, Vile & Garnier, 2006) and ecosystem function (Diaz & Rosenberg, 2008).

Even if much of the early ecological theory had mainly a deterministic basis, it has long been recognized that many patterns in nature have a stochastic component (Watt, 1947; Wiens, 1977; den Boer, 1981). However, the relative importance of stochastic *versus* deterministic processes (e.g. ecological drift *versus* selection) on community assembly is still debated (Strong *et al.*, 1984; Hubbell, 2001; Tilman, 2004; Rosindell *et al.*, 2012). Stochasticity factors can be related either to the species demographic fluctuations and genetic drift, or to external factors that reflect underlying environmental variability (e.g. extremes) and disturbances; thus, they may be important for explaining community assembly (McPeck & Gomulkiewicz, 2005). A major challenge is to determine how much the environment, history, evolutionary processes, and biotic interactions combine to explain species distributions and community assembly (Thuiller *et al.*, 2013) and how much remains unexplained by any of these factors, i.e. how much originates from purely stochastic processes (Guisan & Rahbek, 2011).

The relative importance of each driver often differs at distinct levels of observation (Rahbek & Graves, 2001;

Rahbek, 2005). In the classical view, climate is assumed to be a stronger filter at regional to continental scales (Ricklefs, 1990), whereas species interactions are often assumed to drive local assembly patterns (MacArthur, 1964, 1965; Pearson & Dawson, 2003). However, increasing evidence also show the importance of microclimates in influencing the local distribution of species and community composition and, conversely, the impact of biotic interactions in shaping species ranges at coarser resolutions and larger extents (e.g. Araujo & Luoto, 2007; Gotelli, Graves & Rahbek, 2010; Jones *et al.*, 2013). This scale dependence can also be identified in the concept of the environmental niche (Holt, 2009) and can be relevant for understanding the assembly of species into communities. Analogous with the classical partitioning of regional diversity, the ecological niche can be partitioned into α and β components (Pickett & Bazzaz, 1978). The α -niche encompasses environmental axes that vary on a scale that is smaller than the extent of the focal community, thus at the scale of the environment that is experienced by individuals, i.e. the dimension at which interactions among species occur. The β -niche characterizes larger units and varies across wider environmental gradients, and thus expresses coarser environmental filtering, generally at a regional scale. Therefore, α -niche characteristics will tend to be key for explaining species coexistence through resource partitioning and will thus tend to differ between co-occurring species, whereas β -niche characteristics will tend to be shared among co-occurring species within the same site (Ackerly, Schwilk & Webb, 2006; Silvertown *et al.*, 2006).

To encompass all of the drivers discussed above in a unique process, community ecologists often use a concept of successive filters of community assembly (Lortie *et al.*, 2004; Ferrier & Guisan, 2006; Guisan & Rahbek, 2011). Evolutionary and biogeographic history first defines the species pool for a study unit (Graves & Gotelli, 1983; Zobel, 1997). Environmental filtering then excludes from this pool those species that are physiologically unable to tolerate the physical environment (i.e. unable to establish and maintain positive population growth). Finally, positive and negative biotic interactions further influence the assembly process in complex ways (e.g. Poff, 1997; Soberon, 2007; Soberon & Nakamura, 2009). Control through macroecological constraints can act in the local communities, such as fine-scale phylogenetic relationships constraining species composition (Mayfield & Levine, 2010). Complications in reconstructing this sequence of steps originate from a number of different factors, such as (i) limits in our biological knowledge, (ii) limits in the data used for modelling, (iii) limits in the mathematical approaches behind models, and (iv) stochasticity. In particular, the latter aspect – i.e. how much stochasticity should we expect in the assembly of biological communities – is rarely addressed. Further the strength of human impacts and the spread of alien species that may disrupt the natural equilibria can be additional sources of uncertainty (Ricklefs & Schluter, 1993; see Rahbek, 2005 for a review).

III. PREDICTING COMMUNITIES IN SPACE AND TIME: EXISTING APPROACHES

For a given community, one can ask whether species number and composition are predictable, whether species are substitutable within a community (ecological equivalent or counterparts), or whether the rules that predict when such substitutions occur are discernible. In a thought-provoking paper, Ricklefs (2008) argued that community ecology, as a science, should move beyond the study of local communities as epiphenomena towards a more general understanding of interactions among populations (and species) across a continuum of spatiotemporal scales. Such an approach would provide greater explanatory and predictive power in ecology and evolution than treating communities as fixed entities. In this regard, several community-level modelling approaches to date have attempted to individuate and predict the potential mechanisms determining the assembly process, which we review here (Table 1 and Fig. 1; see online Appendix S1, for a detailed discussion of their theoretical foundations and principles, with references to the original papers for more details). We first identify the different modelling strategies, the possible approaches within them, how the different drivers are accounted for, and finally discuss the output data requirements and conservation needs under global change.

(1) Strategies

We start from the classification of community-level models into three possible ‘strategies’ suggested by Ferrier & Guisan (2006) and complement it with additional criteria. Our classification is based on the statistical procedure, conceptual basis, and expected outputs of the models.

(a) Assemble first, predict later

In this strategy, data are first assembled on the basis of some biological criteria or ordination analysis and then these community-level attributes are predicted. The output of these models is typically richness prediction or other cumulative community attributes (e.g. vegetation types), but any information on the single species. This strategy is inspired by the Clementsonian (Clements, 1916) view of communities as combinations of a fixed set of co-occurring species: the distribution of assemblages can be modelled only if the communities are stable in time and space.

(b) Predict first, assemble later

In this strategy, single species are individually modelled (e.g. with single-species distribution models) and later stacked to produce a community prediction. The application of these models allows the reconstruction of community composition and theoretically also other attributes from single species. This strategy is based on the view that communities result from the coincidental assemblage of individualistic ecological responses of species (Gleason, 1939).

Table 1. Modelling approaches considered in this review

Strategies	Model	Short description	References
Assemble first and predict later	1	Correlative macroecological models (MEM)	Fischer (1960), Currie & Paquin (1987) and Rahbek & Graves (2001); see Ferrier & Guisan (2006) for review
	2	Species abundances predictions based on SAD or RAD	Dunstan & Foster (2011); see McGill <i>et al.</i> (2007) and Ulrich, Ollik & Ugliand (2010) for a review
	3	Correlative trait models	Douma <i>et al.</i> (2012); Dubuis <i>et al.</i> (2013)
	4	Dynamic global vegetation models (DGVM)	Cramer <i>et al.</i> (2001), Stich <i>et al.</i> (2003) and Scheiter, Langan & Higgins (2013) for new extensions, e.g. deriving species composition from the functional type and the ecological processes considered
	5	General simulation model (GSM)	Rahbek <i>et al.</i> (2007) and Gotelli <i>et al.</i> (2009)
Assemble first and assemble later	6	Stacked-Species Distribution Models (S-SDMs)	Guisan & Zimmermann (2000)
	7	Stack of single-species process-based models	Only approximations. <i>Gap models</i> (Bugmann, 2001), 'mechanistic SDMs' (e.g. Buckley, 2008; Kearney & Porter, 2009; Kearney <i>et al.</i> , 2009), plant demography i.e. 'demographic SDMs' (e.g. Keith <i>et al.</i> , 2008; Schurr <i>et al.</i> , 2012) and stages of growth for plants, i.e. 'Phenologic SDMs' (e.g. Mornin, Viner & Chuine, 2008)
Predict first and assemble later	8	Multispecies extension from SDMs	De'ath (2002)
	9	Models of compositional dissimilarity (GDM)	Ferrier <i>et al.</i> (2007)
Assemble and predict together	10	Community occupancy models	Royle & Dorazio (2008)
	11	Maximum entropy (MaxEnt model)	Shipley <i>et al.</i> , (2006), Shipley, Paine & Baraloto (2012) and Shipley (2010)
	12	Traitspace	Laughlin <i>et al.</i> (2012)
	13	Spatial dynamic simulation models	Botkin, Janak & Wallis (1972), Pacala, Canham & Slander (1993), Fulton <i>et al.</i> (2004) and Lischke <i>et al.</i> (2006); see Bugmann (2001) for a review

(c) Assemble and predict together

In this strategy, all species are modelled simultaneously accounting for the entire community structure, but a final prediction can be provided for each species individually, so informing about species composition or relative abundance. This strategy reflects an intermediate theoretical view. The existence of interactions between species is recognized, so that communities are not completely fixed units (Callaway, 1997), but these interactions are only implicitly accounted for.

(2) Predictive approaches

In this review, we account for models based on predictive approaches belonging to either one of the two extremes, ‘static’ or ‘dynamic’ (i.e. when processes are explicitly modelled), as well as for those falling in the continuum defined by the extent to which processes are explicitly represented. Among classic correlative models (models 1–3, Table 1 and Fig. 1) are macroecological models, which were extensively used to evidence macroecological relationships from species-specific patterns, building on solid biological foundations (Kerr, Kharouba & Currie, 2007; Lemoine, Schaefer & Böhning-Gaese, 2007, but see Rahbek *et al.*, 2007; Rangel, Diniz-Filho & Colwell, 2007). These models are easy to use and interpret and require only a limited amount of information to predict community attributes (Ferrier & Guisan, 2006). They can thus be applied to large numbers of species even if limited information is available, a valuable characteristic for reconstructing macroecological patterns or for supporting large-scale conservation plans. However, these models also have a number of limitations discussed in recent reviews, such as the difficulty of inferring causality from observed patterns, correlated predictor variables, the loss of species’ identities, the problematic assumption of stationarity through space and time, and the difficulty of accounting mechanistically for many processes known to be important for community dynamics (e.g. Chase & Leibold, 2003; Rahbek *et al.*, 2007; Schurr *et al.*, 2012). Due to these simplifications, the reliability of macroecological models in making predictions under different environmental conditions has been questioned (e.g. Araújo & Rahbek, 2006; Zurell *et al.*, 2009; but see Kearney *et al.*, 2009; Hothorn *et al.*, 2011; Blois *et al.*, 2013).

Dynamic models are better suited to integrate some of the underlying processes shaping communities, such as demographic processes or non-equilibrium dynamics (Chave & Leigh, 2002; Travis, Brooker & Dytham, 2005; Brooker *et al.*, 2007; Kerr *et al.*, 2007), and thus to build on new conceptual developments, such as the metabolic theory (Brown *et al.*, 2004) or the stochastic niche theory (Tilman, 2004). However, dynamic models can be developed for only a few communities for which sufficient knowledge exists for the constituent species (e.g. physiology, population dynamics; see Jeltsch *et al.*, 2008), thus limiting the generality of their predictions (Thuiller *et al.*, 2008). The reduction of the number of parameters in dynamic models may increase their generality, prediction capability and applicability to higher

community levels, but such simplifications would require clear assumptions to be made about what is modelled in these systems. Examples of attempts made to tackle this duality (simplicity *versus* realism) include the *Spatial dynamic simulation model* (13 in Table 1 and Fig. 1C), which classically simulates spatial sea or forest dynamics (e.g. He & Mladenoff, 1999; Lischke *et al.*, 2006, respectively). Other approaches employ different ways and degrees of simplification, e.g. limiting the prediction to functional types (*Dynamic global vegetation model*; Cramer *et al.*, 2001, 4 in Table 1 and Fig. 1A) or using integrated simulations of multiple species with attributes of various degree of realism (*General simulation model*, Gotelli *et al.*, 2009, 5 in Table 1 and Fig. 1A).

The two predictive approaches – correlative *versus* dynamic – have complementary advantages: the generality, tractability, and applicability to large communities achieved by correlative static models and the precision and causality achieved by dynamic models (Levins, 1966; see Guisan & Zimmermann, 2000). The future development of community-level modelling is likely to see a mixing of their strengths, as has occurred for single-species predictions (semi-mechanistic or ‘hybrid’ approaches, see Thuiller *et al.*, 2013, for a review; Mokany & Ferrier, 2011). The non-mechanistic elements could include correlations between community properties or single-species predictions with environmental variables (Connor & McCoy, 1979; Sommer *et al.*, 2010), and the dynamic components may inform processes such as dispersal, biotic interactions and adaptation (Guisan & Thuiller, 2005; Thuiller *et al.*, 2008). For instance, Midgley *et al.* (2006) developed a spatially explicit approach to integrate species’ bioclimatic suitability and population-level demographic rates with simulation of landscape-level processes (dispersal, disturbance, species’ response to dynamic dominant vegetation structure). Midgley, Thuiller & Higgins (2007) linked mechanistic dispersal models with *Dynamic global vegetation models* (4 in Table 1 and Fig. 1A) to simulate migration processes of tree propagules at the leading edge of species distribution under climate change.

(3) Drivers’ inclusion and potential extensions*(a) Evolutionary and historical drivers*

Over the previous decade, evolutionary and historical components have been increasingly integrated in community modelling procedures (Emerson *et al.*, 2011; Lessard *et al.*, 2012). Defining the regional source pool of the modelled spatial units (i.e. the pool of species known to have colonized the region) may help place the study of local diversity patterns in the context of regional distribution, together with evolutionary and environmental history. A species is a member of the regional species pool if it can potentially disperse from the meta-community (a subset of the regional pool) into a local community (e.g. Sonnier, Shipley & Navas, 2010). In the absence of dispersal limitation within a study area (e.g. over small extents), all of the spatial units can be considered to share the same source species pool (e.g. D’Amen *et al.*, 2015). For analyses that cover large spatial

extents, it would be necessary to define different local species source pools from the regional source pool (Graves & Gotelli, 1993; Guisan & Rahbek, 2011). The study of source pool geometry through dispersion fields, which can be visualized as the overlap of the geographical ranges of all species that occur at a given site (Borregaard & Rahbek, 2010; Lessard *et al.*, 2012), could be useful to include dispersal limitations in the case of global studies. Moreover, Pigot & Etienne (2014) recently showed the dynamic nature of species pools over a range of temporal and spatial scales. This dynamic nature implies ecological and evolutionary feedback mechanisms from communities to the species pool that are currently lacking in the conventional model of community assembly (Mittelbach & Schemske, 2015).

Also placing phylogenetic studies in a geographic context can be valuable for studying the importance of historical processes in community assembly (see Graham *et al.*, 2009, for an example). Patterns across phylogenies (either phylogenetic clustering or overdispersion) can provide insights about the dominant ecological forces (e.g. limiting phenotypic or niche similarity) acting in the community over long time frames (Webb, 2000; Webb *et al.*, 2002). Moreover, phylogenetic structure provides information on the origin of differences in diversity between communities (Ricklefs & Schluter, 1993). Significant non-random phylogenetic structure has been evidenced in communities at multiple spatial and taxonomic scales across diverse taxa (e.g. Cavender-Bares *et al.*, 2004; Kozak *et al.*, 2005; Kembel & Hubbell, 2006). Again, as discussed by Lessard *et al.* (2012), it is important to take into account the potential effects of the available source species pool as that can significantly alter the derived patterns and results of phylogenetic predictions based on community modelling (Ndiribe, Salamin & Guisan, 2013). Many measures of phylogenetic diversity within communities have been developed (Emerson *et al.*, 2011). The first quantitative metric of phylogenetic relatedness within communities is phylogenetic diversity (PD) (Faith, 1992; Pio *et al.*, 2014), but more recent metrics have also been produced (Ferrier *et al.*, 2007; Bryant *et al.*, 2008; Prinzing *et al.*, 2008). The application of these metrics shows theoretical increasing promise to help predict community properties and responses to changing environments (see Webb, 2000, and Cavender-Bares *et al.*, 2009, for specific reviews on this topic). Moreover, detailed genetic analyses and field experiments can be useful to test for heritable variation in fitness, leading to new insights for potential adaptations of species to new conditions.

Among the techniques considered herein, evolutionary origins are simulated in *General simulation models* (Gotelli *et al.*, 2009; 5 in Table 1 and Fig. 1A) within a neutral community that can then be compared to empirical data. Similarly, Colwell & Rangel (2010) developed a geographical range-based, stochastic model that simulated speciation, anagenetic evolution, niche conservatism, range shifts and extinctions under true temperature cycles (late Quaternary) and along tropical elevation gradients. These techniques are theoretical modelling approaches, but to our

knowledge, the integration of true species phylogenies to predictive modelling at a community level is still lacking. As molecular and analytical methods became more applicable and reliable it should become increasingly easier to account for phylogenetic relationships when modelling communities (e.g. Ndiribe, Salamin & Guisan, 2013; Pellissier *et al.*, 2013). A particular challenge is to apply the knowledge gained from community phylogenetic structures to more general applications in predictive modelling of communities.

(b) *Environmental drivers*

All of the modelling approaches considered herein attribute a central role to environmental filtering in determining community attributes. Several recent studies support this choice showing that species within assemblages are functionally more similar than expected by random assembly from a regional trait pool, i.e. suggesting that processes of trait convergence (as a result of environmental filtering) are dominant over those of trait divergence (as a result of limiting similarity) at the assemblage level given the environmental variables available (e.g. Cornwell, Schilke & Ackerly, 2006). Correlative models statistically link spatial data to distribution records: environmental data are used to make inferences on species range limits and habitat suitability (e.g. S-SDMs, multispecies extension from SDMs; Dubuis *et al.*, 2011; Pottier *et al.*, 2013), on species richness or other community properties (*Correlative Macroecological Models* for richness or other community properties; e.g. Thuiller *et al.*, 2006; Dubuis *et al.*, 2011, 2013; or β -diversity models, Ferrier *et al.*, 2007) (1–3, 5, 6, 8–10 in Table 1 and Fig. 1). Mechanistic/dynamic models rely on our understanding of the dominant processes behind the pattern to be measured. Therefore these models attempt explicitly to incorporate the mechanistic links between the biological attributes (e.g. physiology) of organisms and their environment (e.g. *Dynamic global vegetation models*, *Spatial dynamic simulation models*, Cramer *et al.*, 2001; Midgley *et al.*, 2010, 4, 13 in Table 1 and Fig. 1A, C). In both cases, the objects of the models are individuals or single species, or community aggregated properties (Dubuis *et al.*, 2011).

Another approach to account for environmental filtering is to focus on species traits (e.g. Grime, 1977; Connell, 1978). Traits can be modelled by classical correlative approaches (e.g. Dubuis *et al.*, 2013) under the 'Assemble first, predict later' strategy (*Correlative trait models*, 3 in Table 1 and Fig. 1A). These approaches are applicable to a range of systems because they are taxon independent and because traits can be linked directly to the environment, thus facilitating prediction across environmental gradients (McGill *et al.*, 2006; Westoby & Wright, 2006). The drawback is the risk of a high level of abstractness that strongly limits their usefulness in climate change predictions (Thuiller *et al.*, 2008). In recent years, trait databases and trait-based ecology have improved our predictive ability (e.g. Dawson *et al.*, 2013) so that outcomes of trait models are increasingly informative (i.e. relative abundance of the component species of the community; Shipley *et al.*, 2006; Webb *et al.*, 2010; Laughlin & Laughlin, 2013), but on the other hand remain very demanding in

terms of source data [e.g. the *Traitspace* model of Laughlin *et al.* (2012) requires measures of traits for all individuals to derive the biotic term in his computation, so that it can be applied only to small, well-surveyed communities] (11, 12 in Table 1 and Fig. 1C).

(c) Biotic drivers

In a few cases, biotic interactions are accounted for in community-level models in an explicit fashion. Two examples can be found among the approaches considered here. The *Spatial dynamic simulation models* (13 in Table 1 and Fig. 1C) consider in the simulation process species' interactions, where inter- or intraspecific competition for light (or space, water, or nitrogen) are modelled *via* empirical or physiology-based mathematical functions describing resource competition, growth and demographic processes of establishment and mortality (see Cramer *et al.*, 2001; Sitch *et al.*, 2003). In the *Traitspace* model, competition is modelled by allowing single individuals to overlap in trait space (Laughlin *et al.*, 2012, 12 in Table 1 and Fig. 1C). Most often the effect of biotic interactions is accounted for indirectly by considering as the response variable synthetic community attributes, spatial species dissimilarity indices or interspecific covariation in species ranges (e.g. Ferrier *et al.*, 2007), or traits dependent on biotic interactions (Norberg *et al.*, 2001). Using surrogates is necessary because the study of pairwise interactions in highly diverse communities is virtually impossible. However, some alternative solutions were proposed, e.g. by indirect measures of non-consumable environmental conditions that mediate interactions, *interaction currencies* [as described in Kissling *et al.*, 2012 and implemented in food-web models and in *Spatial dynamic simulation models* (Fulton *et al.*, 2004; Lischke *et al.*, 2006, 13 in Table 1 and Fig. 1C)] or by latent variables (Pellissier *et al.*, 2013). Alternatively, the interactions of each individual with a community background could be quantified, e.g. the *interaction milieu* (McGill *et al.*, 2006). An example could be competition for light in a forest, where the light is the resource, the height of individual plants at given site are an approximation of a *competition milieu*, and the frequency distribution of heights of all plants is the community background.

Another promising approach to include biotic drivers into predictive community models is their integration through network analysis (Gilman *et al.*, 2010; Araújo *et al.*, 2011; Gravel *et al.*, 2013). As this approach may require extensive data, complex food webs can be reduced using tractable smaller 'community modules' of species that interact strongly and share the same type of interaction (Gilman *et al.*, 2010) before integrating them within community models. Food-web models are generally not spatially explicit, but a few spatialization attempts were recently made (Naisbit *et al.*, 2012, but see Massol *et al.*, 2011). For instance, Jabot & Bascompte (2012) integrated a spatial meta-community structure into food-web network approaches by studying a bitrophic plant–pollinator interaction, and Pellissier *et al.* (2013) used interaction links between species inferred from food-web models as predictor variables in stacked species distribution models. Moreover, as interactions effects are

also mediated by the environmental context in which species coexist, an increasing number of macroecological analyses correlated networks metrics with environmental conditions at the sites (e.g. Dalsgaard *et al.*, 2011, 2013; Trøjelsgaard & Olesen, 2013). A potential shortcoming of current network analyses is that they are built upon taxonomically resolved interactions so requiring species-specific source data that limit their application to large scales. Incorporating traits effects in multispecies interactions could be a way to increase their generality (Kissling & Schleuning, 2014).

One route to address the lack of data to characterize biotic interactions (Araújo *et al.*, 2011; Gravel *et al.*, 2013; Wisz *et al.*, 2013) could be the analysis of patterns of geographic overlap in the distributions of species. Using matrices of species spatial co-occurrences associated with a null model approach, potential broad-scale interactions could be derived (e.g. Diamond, 1975; Gotelli & Graves, 1996; Gotelli *et al.*, 2010). Precautions should be taken before inferring the cause of the observed overlap in distribution (Diamond, 1975). For instance, controlling for species habitat requirements in null models could increase the chances to discriminate between environmental influences and biotic interactions (e.g. Gotelli, Buckley & Wiens, 1997; Peres-Neto, Olden & Jackson, 2001). There are many indices available to summarize patterns in species distribution from matrices of spatial co-occurrence (e.g. Stone & Roberts, 1992; Gotelli, 2000) and some recent papers explored their use in the context of explanatory community modelling studies (e.g. Boulangeat, Gravel & Thuiller, 2012; Kissling *et al.*, 2012).

(d) Stochasticity

Purely stochastic processes can be of a different nature, being related to species demography fluctuations and genetic drift (Hubbell, 2001; Keith *et al.*, 2008), or to external factors reflecting underlying environmental variability (Guisan & Zimmermann, 2000). Their effects further depend on many non-stochastic factors, for instance the specific process that is affected, e.g. birth, death, competition, or predation, or the species attributes, e.g. body size (Farjalla *et al.*, 2012). Finally, the scale can influence the effect of stochastic processes both within and among biogeographic regions, e.g. for instance, stochasticity may lead to a poorer predictability of species composition in smaller species pools, i.e. in fine-resolution analyses (Shipley, 2010; Pellissier *et al.*, 2012; Pottier *et al.*, 2013). Due to this variability, the importance given to stochasticity in planning any community model should be strictly related to the system under study and questions being addressed.

An extreme view on the role of stochasticity in community assembly is represented by the popular neutral metacommunity model arising from the Hubbell's neutral theory for community assembly (Hubbell, 2001). The neutral community theory explains species coexistence as a stochastic balance between immigration and extinction on a local level, and between speciation and extinction on a regional level, with all individuals being expected to have exactly the same biological traits (Etienne & Alonso, 2006).

Models based on the neutrality principle often produce relative-abundance patterns that are indistinguishable from those derived from niche theory (e.g. Bell, 2001; Hubbell, 2001; Volkov *et al.*, 2007). Among the community-level models previously described, the *General Simulation Model* has a very strong stochastic component as it simulates stochastic origin, spread, and extinction of species geographical ranges in a heterogeneous landscape (Rahbek *et al.*, 2007; Gotelli *et al.*, 2009, 5 in Table 1 and Fig. 1A). Also *Spatial dynamic simulation models* (13 in Table 1 and Fig. 1C) incorporate stochastic elements in demographic processes such as individual tree establishment and mortality, so that patch dynamics is partially Bayesian as a stochastic process. The other approaches usually only acknowledge the existence of, but do not simulate explicitly, stochastic factors, so that the predictive ability of the models rests on the relative importance of the deterministic drivers *versus* other stochastic forces influencing community assembly (Shipley *et al.*, 2006; Guisan & Rahbek, 2011).

A different approach to consider stochasticity in community modelling could be to address its consequences *a posteriori*. Evidence suggests that in most cases, community assembly can lead to multiple stable equilibria (e.g. Luh & Pimm, 1993; Pottier *et al.*, 2013), which could happen due to assembly history when a stochastic variation in colonization influences more-deterministic priority effects and consequently the final assemblage composition (Chase, 2003) or due to shorter-time stochastic processes, e.g. random dispersal and demography (Chase & Myers, 2011; Weiher *et al.*, 2011). To depict the uncertainty associated with community prediction in every studied unit, Pellissier *et al.* (2013) applied a probabilistic approach to S-SDMs and provided a variability map along with the prediction outcome (6 in Table 1 and Fig. 1B).

(4) Data requirements and conservation needs under global change

As the success in dealing with environmental change emerges from our anticipative capacity (Bellard *et al.*, 2012; Guisan *et al.*, 2013), providing predictive tools is a crucial challenge for ecologists and conservation planners. The modelling approaches considered herein can provide information about the potential distribution of specific diversity, with variable degrees of accuracy according to their characteristics and the available initial data. Data availability often hampers the possibility to predict communities, and this limitation is even more severe for dynamic models that require more detailed information (e.g. physiology, demographic parameters, and dispersal ability). In the case of incomplete data for many regions and taxonomic groups (e.g. Dunn, 2005; D'Amen *et al.*, 2013), especially for large-scale conservation plans, modelling the emergent patterns of species diversity directly seems to be the most straightforward solution (Myers *et al.*, 2000). Only count data are required and the sampling effort is relatively low. Moreover, all available data across species can be used regardless of the number of records per species [models from the 'Assemble first and predict later' strategy (1–5 in Table 1 and Fig. 1A)]. However,

even the simplest count data could be biased in many ways: counts of species are challenging for many taxonomic groups, geographic locations, and ecosystems, and differences in sampling effort should be considered before comparisons can be made (Fleishman, Noss & Noon, 2006). Other synthetic community properties can be of particular interest for conservation (Dubuis *et al.*, 2013). For instance, community phylogenetic diversity can inform conservation managers about the communities' capacity to respond to environmental changes, a larger phylogenetic diversity being indicative of a higher evolutionary potential and resilience (Faith, 1992; Thuiller *et al.*, 2011). Functional properties of communities can provide information about future impacts on ecosystem goods and services (Dubuis *et al.*, 2013).

Species richness has often been assumed to be an indicator of conservation value related to the protection of multiple levels of biodiversity (e.g. Meir, Anelmann & Possingham, 2004), but it alone provides no information on species identity or the functional roles of individual species and their population attributes. Complementary measures based on species composition can overcome some of these limitations (Margules & Pressey, 2000). Compositional information allows attribution of differential conservation value to the species and estimation of indices such as complementarity and irreplaceability for maximizing the total number of species to be represented in a set of conservation areas (Margules & Pressey, 2000). Often, the specific data employed are readily available (e.g. samples from museum collections) and are typically incomplete (Rondinini *et al.*, 2006). In these cases, precautions should be taken because models based on these data could be biased, and this error could propagate in the planned system of protected areas. Community composition is the natural outcome for the models pertaining to the 'Predict first, assemble later' strategy (6, 7 in Table 1 and Fig. 1B). Many studies based on *stacked species distribution modelling* proposed their results to identify priority areas for natural protection (e.g. D'Amen *et al.*, 2011; Faleiro, Machado & Loyola, 2013; Leach, Zalut & Gilbert, 2013; Mateo *et al.*, 2013), notwithstanding, examples of real application of these S-SDM outcomes to guide conservation planning are still scarce in the literature (Guisan *et al.*, 2013). Composition is also predicted by most of the approaches in the 'Assemble and predict together' strategy (8–13 in Table 1 and Fig. 1C). Among these approaches, *models of compositional dissimilarity* (GDM) are especially promising for conservation planning in data-poor regions because they can extrapolate community-specific information by modelling turnover in community composition (9 in Table 1 and Fig. 1C) (Ferrier & Guisan, 2006; Ferrier *et al.*, 2007). Some limitations in predicting species composition should be highlighted. Filtering and sorting processes can constrain community assembly and make some assemblages less likely to persist than others, without reaching a unique equilibrium. This fact along with the neutral processes influencing species assembly, make a fixed species composition hardly predictable (Weiher *et al.*, 2011).

Another important criterion to consider in conservation planning is to maximize the probability of persistence of

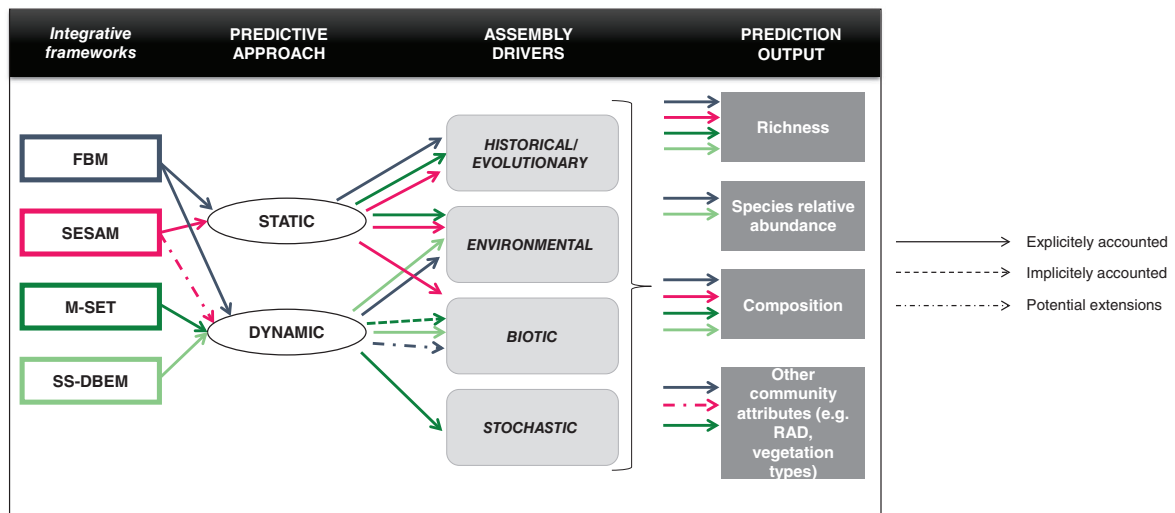


Fig. 2. Schematic illustration of the characteristics of the integrative frameworks considered in this review. For each framework, we indicate the predictive approach, the inclusion of different drivers of community assembly (we consider that the historical/evolutionary driver is included in the model if species' phylogenetic relations or origin of the species pool/dispersal limitation are considered), and the expected predictive output. In particular, we specify whether the drivers are implicitly or explicitly accounted for in the model and potential extensions anticipated by the authors. FBM, first-principles Bayesian multilevel model; M-SET, dynamic metacommunity model; SESAM, spatially explicit species assemblage modelling; SS-DBEM, size-spectrum dynamic bioclimate envelope model.

viable populations. Attempts have been made to maximize persistence across multiple species using occurrence data only (Araújo & Williams, 2000). Other reserve selection methods use species relative abundance or density as proxies for population viability (Pearce & Ferrier, 2002). However, one of the problems with abundance data is that it requires a high sampling effort, and it may be difficult to compare among different areas (Araújo & Williams, 2000). Some modelling approaches reviewed here provide predictions of the relative abundance of species (e.g. trait-based models and dynamic ones, 11–13 in Table 1 and Fig. 1C), but it usually comes at the cost of high data demand for parameterization (see Section III.2). Dynamic forest models often have been used to optimize sustainable management planning (e.g. Shifley *et al.*, 2006; Zollner *et al.*, 2008) and to forecast changes in wildlife habitat suitability (Shifley *et al.*, 2008). A few examples of species abundance predictions exist also from the 'Predict first and assemble later' strategy, e.g. hybrid SDMs (combination of static SDMs with dynamics landscape and/or population models) have been stacked to forecast the impacts of environmental change on population viability in communities (e.g. Bonnot, Thompson & Millsbaugh, 2011).

IV. NEW SOLUTIONS AND PERSPECTIVES: INTEGRATIVE FRAMEWORKS

A solution to manage the complexity of factors and processes leading to community assembly could be that instead of searching for a universal formula to apply, work should be carried out in a case-specific setting

within a general conceptual and methodological framework. Ideally, this framework should be general enough to incorporate in separate but interconnected steps (here called 'modules') all of the drivers that can potentially influence community assembly. A pre-analytical step should first identify which drivers are important to switch 'on' or 'off' the relevant modules of the framework, such as the integrative framework. Thus, the 'integrative framework' may represent an answer to the need to encompass all of the drivers of community modelling in a unique approach. This approach is expected to progress quickly in the field of community modelling because it may, in principle, resume in its structure the current knowledge of community assembly process and should be flexible enough to accommodate promptly any technical improvement coming from new theoretical advances. Moreover, the different modules can be implemented with pre-existing modelling approaches, taking advantage of their strengths and correcting their identified pitfalls, e.g. it allows the integration of static and dynamic approaches. A highly challenging perspective from both the theoretical and technical points of view would be to link the different modules. The exact procedures for such linking need further development, but some community modelling studies can be found in the most recent literature, which proposed a framework structure (here called 'integrative frameworks'). Below, we provide an overview of these newer implementations to portray the range of views regarding how to combine different approaches (Fig. 2).

Webb *et al.* (2010) proposed a theoretical framework that attempted to revise and unify conceptual and technical advances in trait-based ecology. The framework is based on three elements: (i) a trait distribution from the pool

of possible traits of all organisms (individual level); (ii) a performance filter defining the fitness of traits in different environments; (iii) a dynamic projection of the performance filter along environmental gradients to make predictions. The three elements are integrated into series of modules that can be applied sequentially or alternatively, according to the study system, the information content of the trait data, and the biological questions. The framework is exemplified by applying Bayesian multilevel models (Gelfand *et al.*, 2005; Latimer *et al.*, 2006), along with dynamic system models that can be projected outside the original data range to obtain predictions (Norberg *et al.*, 2001; Loreau, Mouquet & Gonzales, 2003; Savage, Webb & Norberg, 2007). The resulting model (first-principles Bayesian multilevel model, FBM) is expected to be used for mechanistic exploration of systems or for predictions across time or space. In the reported conceptual example, the output of the model consists of predictions of the temporal trajectories in biomass for each combination of trait values as well as richness and species information under given climate change scenarios. The conceptual foundation of this framework is extremely appealing and the generality of the formulation is achieved by focusing on trait types that are independent from any particular species within the target group, and can thus be linked directly to the environment (Grime, 1977; Keddy, 1992; McGill *et al.*, 2006; Shipley *et al.*, 2006; Cornwell & Ackerly, 2009). Considering intraspecific variability in traits, biotic drivers can be taken into account (Laughlin *et al.*, 2012), allowing us to discern between the effects of habitat filtering *versus* limiting similarity. The addition of the dynamic dimension should allow improving predictions outside the measured range of parameters. However, the framework does not overcome the need for a large amount of information evidenced previously for many trait-based models. Moreover, building realistic filters based on species performance under a set of conditions requires a deep understanding of the nature of the trait–environment relationship, based on species eco-physiological knowledge.

Guisan & Rahbek (2011) proposed a framework (SESAM – ‘spatially explicit species assemblage modelling’) for predicting spatio-temporal patterns of species assemblages. This framework aims at reconstructing species assemblages by four successive steps: (i) designing the species pool (the candidate species); (ii) applying abiotic filter based on species’ ecological niche; (iii) applying macroecological constraints to set the limit of coexisting species number (e.g. species–energy or metabolic theory; Brown *et al.*, 2004); (iv) applying biotic rules for selecting among the potential species from step ii, those actually able to coexist in the modelled community. Each of these modules can be implemented with different modelling options and assessed independently. The authors exemplify the SESAM framework by coupling *Stacked-species distribution models* (6 in Table 1 and Fig. 1B) (in step ii) to apply the abiotic filter, with *Macroecological models* (1 in Table 1 and Fig. 1A) (in step iii) to define a macroecological constraint for each modelled unit. Each step of the SESAM framework is anchored in robust and tested bodies

of ecological theory and its formulation allows a broad applicability to different study cases. A comprehensive application of this framework has the potential to provide synthesis of the joint effects of biogeographical and community-level processes on the diversity and structure of local communities. Both static and dynamic techniques can be used to implement different steps of the framework, so that this structure is particularly suited to build hybrid approaches. For instance, more dynamic approaches (Keith *et al.*, 2008) to predict distribution ranges may be included in the framework by stacking new-generation SDMs accounting for dispersal (Hortal *et al.*, 2012), and more mechanistic (e.g. fundamental niche; Kearney & Porter, 2009) approaches to mapping species distribution could be tested. Macroecological models not based on correlative statistics can also be included explicitly to incorporate the mechanisms responsible for the observed distributions (e.g. Gotelli *et al.*, 2009). To date the SESAM framework has been tested on plant and insect communities in the Swiss Alps combining S-SDMs, macroecological models (also based on species traits) and different approaches to set biotic rules, based either on a ranking of probability of presence or on co-occurrence analyses. The SESAM application improved the community predictions when the simple ‘predict first and assemble later’ approach using SDMs is not able alone to depict the community structure (D’Amen *et al.*, 2015; D’Amen, Pradervand & Guisan, 2015).

The Dynamic FOAM model (dynamic framework for occurrence allocation in metacommunities), proposed by Mokany *et al.* (2011), combines correlative richness (α -diversity) models and models of compositional turnover (β -diversity) (1 and 9 in Table 1 and Fig. 1A, C). The model then generates compositional data for metacommunities and γ -diversity, and predicts species distributions consistently with known community diversity patterns. This output forms the initial conditions to apply the new spatially explicit, dynamic metacommunity model (M-SET, Mokany *et al.*, 2011) that incorporates stochastic dispersal processes. M-SET predicts compositional changes for each community over time, consistent with the predicted changes in α - and β -diversity under climate change: the overall loss or gain of species is calculated to maximize the richness of the community without exceeding the potential richness calculated by the α -diversity model, and the resulting turnover is adjusted on the basis of the predictions from the β -model. M-SET is a general model that can be applied to any taxonomic group. It is technically well resolved in the links among the framework modules, especially concerning the integration of α - and β -diversity models. The approach has the potential to reduce neutrality if incorporating attributes for individual species or functional groups, such as specifying different dispersal kernels for each species. However, no step has been devoted to explicitly include the effect of biotic interactions, which are only indirectly accounted for in α - and β -diversity models. Mechanistic models of either α - or β -diversity could equally be applied in the different steps, to make this framework more process-based.

More recently, Fernandes *et al.* (2013) proposed a framework based on stacking dynamic bioclimate envelope models (DBEM) that explicitly consider population dynamics, dispersal (larval and adult) and ecophysiology, used so far to project changes in marine species distribution, abundance, and body size (Cheung *et al.*, 2008, 2013). An improved framework called size-spectrum DBEM (SS-DBEM) allows coupling these models with a size-based spectrum model to account for biotic interactions. The size-based spectrum model describes the energy transfer from primary producers to consumers as a log–log relationship between abundance and body size and estimates the total abundance of individuals from all species that can be supported in any defined body-size class (Dickie, Kerr & Boudreau, 1987). The integration of the two approaches allows SS-DBEM to (i) estimate the potential biomass supported by the system, (ii) predict habitat suitability, and (iii) model species interactions. This framework is a successful example of the integration of correlative and dynamic dimensions to predict changes in growth and other life-history traits in response to changes in temperature and oxygen concentration (Cheung *et al.*, 2013). The model also simulates spatial and temporal changes in relative abundance within a cell based on the carrying capacity of a cell, density-dependent population growth, larval dispersal, and adult migration (Cheung *et al.*, 2008).

All of these integrative frameworks make use of previous modelling techniques and can potentially integrate static and dynamic approaches, resulting in predictions of increasing ecological realism, although a good equilibrium between complexity and generality is still not achieved. For instance, the complete implementation of the Webb *et al.* (2010) framework has a good predictive potential but needs a high amount of input. A simplified version was proposed that approximates individual-level with species-level trait data, suggesting that data sets coming from different sources can represent a valid substitute to *ad hoc* experiments estimating species' physiological requirements. Interestingly, most of the integrative frameworks include a macroecological model to estimate changes in how many species/biomass may be supported in each location over time. This approach implies the concept of community saturation (Elton, 1950) used in different contexts but referring here to niche saturation of species richness in the community (MacArthur, 1972; Cody & Diamond, 1975) or to saturation of any measure of community-level performance related to resource use (Loreau, 2000). Specifically, both M-SET and the SESAM frameworks limit species richness in each site by an α -diversity model (but see D'Amen *et al.*, 2015a). In this case, saturation is viewed in relation to the saturation of niche spaces. Instead, SS-DBEM is based on the concept of maximum potential biomass supported by the system in any defined body class size, which limits the number and the abundance of species that can be supported in each geographical unit. In this latter case, the saturation is relative to a community-level performance measure (i.e. biomass) to indicate the saturation of available energy up

to the environmental carrying capacity. The assumption of community saturation is still matter of debate in ecology, i.e. whether communities or regions can become saturated with species and how to assess this process, with a recent shift of focus to the more general relations among assembly processes at local and regional scales (e.g. Loreau, 2000; Mouquet *et al.*, 2003; Freestone & Harrison, 2006).

Among the integrative frameworks, only one (Webb, 2000) is explicitly based on traits. However, as models based on traits alone could miss the influence of important drivers of community assembly, such as environmental filter and biotic interactions, the integration of trait analyses in frameworks accounting for multiple drivers could represent a promising advance. Yet, few attempts have been made. For instance, in the SESAM framework predictions of different trait community values were used to filter, from the species predicted by S-SDM, those occurring in each modelled community (D'Amen *et al.*, 2015a,b). The use of traits data holds promise to increase our mechanistic understanding of biological responses and to allow the prediction of species distributions based on the traits that each species possesses without prior knowledge of the aggregated trait values of the community. However, it should be noted that trait models can become taxon/system specific, thus allowing few cross-taxa applications and comparisons. To face climate change, particular focus should be placed on those traits that could be good predictors of species adaptation or vulnerability (e.g. diet specialists) (Guisan, 2014), which could facilitate the prediction of novel communities under climate change (Lurgi, Lopez & Montoya, 2012). In addition, connections between traits and phylogeny could be particularly useful as the variation in trait states could be related not only to environmental filters but also to phylogeny (Desvignes *et al.*, 2003; see Pavoine & Bonsall, 2011 for a review).

V. CONCLUSIONS

(1) The community assembly process is highly complex because usually more than one mechanism is acting with varying importance according to the case study, and these multiple processes interact with each other. We believe that a promising solution to manage this complexity and obtain more reliable community predictions could be the integration of multiple drivers in a unique modelling framework. Here, we define 'modelling frameworks' as methodological procedures made of a series of sequential analytical and/or modelling steps. This structure should be anchored in a solid theoretical background, still allowing the implementation of case-specific settings according to the case study. The steps can use pre-existing methods independently developed to predict communities or incorporate new technical advances and include static and dynamic models to make the most of their respective strengths. In the most recent literature, some proposed solutions agree with the framework structure, and in describing these approaches,

we exemplify the range of views on how to combine different steps into a comprehensive modelling workflow. Further development is still needed to test the proposed framework under different conditions and applications. In particular, the complexity of the frameworks should be constrained as much as possible in order to maintain a good predictive power (see e.g. Merow *et al.*, 2014).

(2) By analysing the most recent solutions for community-level modelling, it emerges that understanding the complexity of interspecific interactions remains a major challenge (Kissling *et al.*, 2012; Wisz *et al.*, 2013). Interspecific interactions are often indirectly addressed in the analyses, but substantial evidence at a range of spatial scales supports the view that incorporating the biotic drivers is an advance over models that do not account for species interactions (e.g. Leathwick & Austin, 2001; Meier *et al.*, 2010; Fernandes *et al.*, 2013). It should be noted that many models assuming no spatial interaction have been very successful at making predictions about macroecological species richness patterns (McGill, 2010), and a recent review paper showed that non-random co-occurrence of plant species is still difficult to uncover in meta-analyses due to high heterogeneity of the methods used (Götzenberger *et al.*, 2012). This difficulty does not mean that biotic drivers have negligible importance in shaping species in communities, but the above observations can be the result of statistical arguments (McGill, 2010). In considering large communities, the number of possible pairwise interactions becomes very high and few may be strong enough to have predictive value. An absence of strong interactions in a community would validate the assumption of independence among species and allow accurate community predictions without interactions. Thus, the importance of explicitly taking into account biotic interactions is highly dependent on the ecosystem under study.

(3) The threat of human impacts on biodiversity makes the need for reliable predictions of species communities pressing (Nogués-Bravo & Rahbek, 2011). Modelling currently provides the most comprehensive and flexible approach to generate projections of community change under predicted global change. We have shown many alternative solutions and what their expected outputs can teach us in the context of current and future conditions. Here we focused on the natural processes of assembly, but complementary studies could be valuable in reviewing how the different modelling approaches are able to address these socio-economic components. Notwithstanding all of the possible advances in theoretical model formulations, the type and quality of distributional data available will often constrain what can be accomplished analytically (Dawson *et al.*, 2013). Many situations of sparse or biased biological data exist, with species' presence/absence or abundance, which could perhaps be overcome by simulation approaches, but most often real data are needed when the results are intended to inform conservation managers to help reduce or minimize climate change impacts on biodiversity. In addition, even with improved availability of distribution data, we would still have limited ability to use them if we do

not also have better insights on the processes involved, which is better obtained through experimentation. Finding ways to cope with the availability of data, manage the complexity of the relevant processes and maintain tractability of the modelling process, will likely challenge future research in community ecology and spatial modelling.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Description of the modelling approaches analysed in the text.

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Supporting Information

Appendix S1. Description of the modelling approaches analysed in the text

The ‘Assemble first, predict later’ strategy

Examples of the ‘Assemble first, predict later’ strategy are the traditional correlative-based macroecological models that can identify changes in how many species may be supported in each location over time. Macroecologists have devoted decades of study to spatial patterns of diversity (e.g. Fischer, 1960; Currie & Paquin, 1987; Rahbek & Graves, 2001), this research leading to the development of empirical theory. If the observed links between environmental characteristics and species richness (or other measures of biodiversity) are causal, then spatial models based on macroecological theory should accurately predict temporal species richness trends as the environment changes (White & Kerr, 2006). Thus, this discipline offers a theoretical basis to build models for biodiversity predictions, demonstrating high relevance for improving conservation decisions under global change (Kerr, Kharouba & Currie, 2007).

According to the response variable utilized, e.g. community types or richness, the prediction could inform if current community types will or will not be able to persist at their present locations, or if the expected number of species will be able to coexist in a site, respectively. Community-level properties, such as interspecific interactions and community assembly, are implicitly included in the predictions. A number of models have been proposed to describe patterns of species abundance distributions (SADs), based on the log-normal distribution or some variant of it (see McGill *et al.*, 2007 and Ulrich, Ollik & Ugland, 2010, for a review), or more recently its related measure rank abundance distribution (RAD; Foster & Dustan, 2010; Dunstan & Foster, 2011). Other approaches use classification or ordination techniques to create assemblages of species as analytical units (e.g. Ferrier *et al.*, 2007, and Ferrier & Guisan, 2006, for a review). A recent implementation of this strategy is the *Species archetypes model* (SAD; Dustan & Foster, 2011) that predicts communities using a finite mixture of regression models on the basis of common responses to environmental gradients. Community types have also been created and modelled on the basis of species’ traits, mainly for plants, i.e. characterizing organisms in terms of their multiple biological attributes such as physiological, morphological, or life-history traits. This category includes both static models (e.g. Douma *et al.*, 2012; Dubuis *et al.*, 2013) and dynamic approaches [e.g. *Dynamic global vegetation models* (DGVMs); Cramer *et al.*, 2001; Sitch *et al.*, 2003; see Scheiter, Langan & Higgins, 2013, for new extensions]. These DGVMs simulate the behaviour of plant functional traits to reproduce biogeochemical processes and ecosystem structure and allow for competition. Generally DGVMs treat

vegetation cover as a fractional representation consisting of different types (Cramer *et al.*, 2001), thus in their main application they predict changes in only vegetation distribution, without allowing identification of single species: for this reason they are listed in this first category. Potentially, extension from DGVMs can derive species composition from the functional type and the ecological processes considered.

To overcome many limitations of correlative macroecological models evidenced in recent years, a new class of predictive macroecological models was introduced by Rahbek *et al.* (2007). These were spatially explicit Monte Carlo models of the placement of geographical ranges in an environmentally heterogeneous landscape, which mechanistically simulates species richness patterns. The approach was subsequently discussed and advocated by Gotelli *et al.* (2009), who named them *General simulation models* (GSMs). A typical *General simulation model* could expand the approach of Rahbek *et al.* (2007) by also simulating the occurrence of similar but not identical species with a small number of parameters, and incorporating key processes, e.g. speciation, dispersal, and extinction. Because the *General simulation model* predicts community attributes, as species richness, from the overlap of species ranges, and in the original formulation does not account for biotic interactions, operatively it could be seen as part of the ‘Predict first and assemble later’ strategy. However, as for the macroecological models mentioned above, its main result is species richness, and it cannot provide information on the community constituent species, as they are only simulated. All patterns simulated by the *General simulation model* can be directly compared to empirical patterns providing a direct goodness-of-fit test of the model being tested or simulated. For this reason we place it in this first strategy. In fact, the original aim is to explain (not to predict) observed patterns of species richness. Extensions of the model are possible, by appointing different degrees of realistic attributes to species (e.g. species assigned to different functional groups, up to a theoretical species-specific attribute) and adding biotic terms. Future implementations could also allow projection of species richness under climate change (Gotelli *et al.*, 2009).

The ‘Predict first, assemble later’ strategy

Following the strategy of ‘Predict first, assemble later’, *Stacked Species Distribution Models* (S-SDMs) derive community properties from the stacking of individual species’ distributions predicted by bioclimatic species distribution models (SDMs; Guisan & Zimmermann, 2000). Species distribution models are essentially a form of sophisticated curve-fitting algorithms developed to project species distributions from correlations between occurrence and environmental conditions in a static fashion (Guisan & Thuiller, 2005). In these models processes are implicit and the explanatory variables employed are expected to represent as many as possible causal mechanisms (Austin, 2002; Dormann *et al.*, 2012). In recent years many improvements and extensions have been proposed for species distribution models, making explicit assumption about dispersal (e.g. Midgley *et al.*, 2006;

Engler & Guisan, 2009) or incorporating processes such as extinction and stochastic population models (e.g. De Marco, Diniz-Filho & Bini, 2008; Keith *et al.*, 2008). Such new implementations could in turn improve the *Stacked single-species distribution models* making them more dynamic by including data on dispersal, population dynamics or other relevant processes (Guisan & Thuiller, 2005, Thuiller *et al.*, 2008).

Potentially also species-level predictions derived from pure dynamic models can be used in the ‘Predict first, assemble later’ strategy, if interaction processes are ignored in the simulation, i.e. community properties resulting from the sum of individual species’ dynamics. Typically, species-specific dynamic models predict the response of a population to environmental conditions by explicitly incorporating biological processes calibrated with observations on individuals in natural populations, e.g. integrated metabolic rate or energy uptake from animal physiology, i.e. ‘Mechanistic SDMs’ (e.g. Buckley, 2008; Kearney & Porter, 2009), plant demography i.e. ‘Demographic SDMs’ (e.g. Keith *et al.*, 2008; Schurr *et al.*, 2012) and stages of growth for plants, i.e. ‘Phenologic SDMs’ (e.g. Morin, Viner & Chuine, 2008, see Morin & Thuiller, 2009, Dormann *et al.*, 2012, for a discussion on process-based models for single species, and a comparison with correlative models). However, to our knowledge, pure-dynamic models for real species have never been stacked across a whole species pool to reconstruct community attributes, probably due to parameterization difficulty for the large number of community constituent species. Gap models (Bugmann, 2001) go some way in this direction but usually only include the dynamics of a few dominant species.

The ‘Assemble and predict together’ strategy

Many widely used static approaches in single-species modelling have been extended to model assemblages using data on all species simultaneously to obtain an overall view of the community (e.g. Glonek & McCullagh, 1995; Hastie & Tibshirani, 1996; De’ath, 2002; see Table 1 of the main paper). Their main output is the predicted distribution for each species, but these applications generally fail to show in detail how the relationship between environmental covariates and the species community builds up from species-specific responses (Ferrier & Guisan, 2006). These approaches remain static and thus projections to different environmental conditions (e.g. in the future) will nevertheless implicitly consider the fitted biotic interactions to remain fixed. Other classical models belonging to this strategy are those predicting β -diversity patterns (Legendre, Borcard & Peres-Neto, 2005). For instance, the *Generalized dissimilarity model* (GDM; Ferrier *et al.*, 2007) predicts the compositional dissimilarity observed between pairs of surveyed locations as a continuous non-linear function of the relative position of these sites along multiple environmental gradients. This model does not assume fixed community types (in that it does not fit in the ‘Assemble first and predict later’ strategy), while it assumes that emergent rates of spatial turnover along environmental gradients under current climatic conditions can act as a reliable surrogate for temporal turnover given changing conditions (Fitzpatrick

et al., 2011). Finally, traditional *Landscape simulation models* also fall in this strategy. Dynamic forest models simulate single-species dynamics considering in the process intraspecific interactions i.e. at least intra- and interspecific competition for light (Botkin, Janak & Wallis, 1972; Pacala & Tilman, 1993; Lischke *et al.*, 2006; see Bugmann, 2001, for a review). These models can differ for the parameterization but in general the level of ecological and environmental detail is very high, and their predictions simulate species composition, abundance, and potentially other community-level attributes (forest dynamics). Similarly, the marine environment simulation models, spatially resolved in three dimensions, track nutrient (usually N and S) flows through the main biological groups in the system. Many ecological processes are modelled: consumption, production, waste production, migration, predation, recruitment, habitat dependency, and mortality. These models usually connect the biophysical world with fisheries to manage marine living resources (e.g. Atlantis model; Fulton *et al.*, 2004).

The ‘Assemble and predict together’ strategy may also encompass a number of highly varied approaches developed in the last decade (e.g. Dorazio & Royle, 2005; Shipley, Vile & Garnier, 2006; Laughlin *et al.*, 2012), although some are hard to classify. An original starting point for assessing community composition is the occupancy criterion (Zipkin, DeWan & Royle, 2009): by using occupancy data the *Community occupancy model* links within a hierarchical (or multi-level) Bayesian model individual species occurrence models (Gelman & Hill, 2007; Royle & Dorazio, 2008). In this way it accounts for both species-level effects as well as aggregated effects of landscape/habitat on the community as a whole (MacKenzie *et al.*, 2003). Rooted in trait-based community assembly theory, is the Shipley *et al.* (2006) *MaxEnt* model (Maximum entropy model; Shipley *et al.*, 2011; Shipley, Paine & Baraloto, 2012). *MaxEnt* treats community development as a sorting process involving species that are ecologically equivalent except with respect to particular functional traits, where the relative abundance of each species follows a general exponential distribution as a function of its traits. *MaxEnt* predicts the distribution of relative abundances for every species in a regional pool on the basis of species’ mean trait values (Shipley *et al.*, 2011). The main weakness of this approach is that it ignores competition for limiting resources that tends to limit the functional similarity of co-occurring species. The two opposite forces of trait convergence and divergence are reconciled in the other trait-based approach recently proposed by Laughlin *et al.* (2012), *Traitspace*. *Traitspace* extends the *MaxEnt* formulation incorporating intraspecific trait variation as a quantification of species niches, thus it requires a data set of trait measurements from individual plants growing under known environmental conditions. It predicts relative abundances using a Bayesian framework. Both of these trait-based models are generalizable to any ecosystem and can theoretically accommodate any number of species, traits, and environmental conditions (see Laughlin & Laughlin, 2013, for a detailed comparison between these trait-based models).