

# Scaling the linkage between environmental niches and functional traits for improved spatial predictions of biological communities

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## Funding information

FP7 People: Marie-Curie Actions, Grant/Award Number: 327987 (SESAM-ZOOL); H2020 European Research Council, Grant/Award Number: 678841; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 31003A-1528661 (SESAM'ALP) CR2312-162754 (INTEGR)

Editor: Arndt Hampe

## Abstract

**Issue:** Approaches to predicting species assemblages through stacking individual niche-based species distribution models (S-SDMs) need to account for community processes other than abiotic filtering. Such constraints have been introduced by implementing ecological assembly rules (EARs) into S-SDMs, and can be based on patterns of functional traits in communities. Despite being logically valid, this approach has led to a limited improvement in prediction, possibly because of mismatches between the scales of measurement of niche and trait data.

**Evidence:** S-SDM studies have often related single values of a species' traits to environmental niches that are captured by abiotic conditions measured at a much finer spatial scale, without accounting for intraspecific trait variation along environmental gradients. Many pieces of evidence show that omitting intraspecific trait variation can hinder the proper inference of EARs from trait patterns, and we further argue that it can therefore also affect our capacity to spatially predict functional properties of communities. In addition, estimates of environmental niches and trait envelopes may vary depending on the scale at which environmental and trait measurements are made.

**Conclusion:** We suggest that to overcome these limitations, surveys sampling both niche and trait measurements should be conducted at fine scales along wide environmental gradients, and integrated at the same scale to test and improve a new generation of spatial community models and their functional properties.

## KEYWORDS

ecological assembly rules, environmental gradients, fine-scale sampling, microhabitat, multivariate envelope, stacked species distribution models

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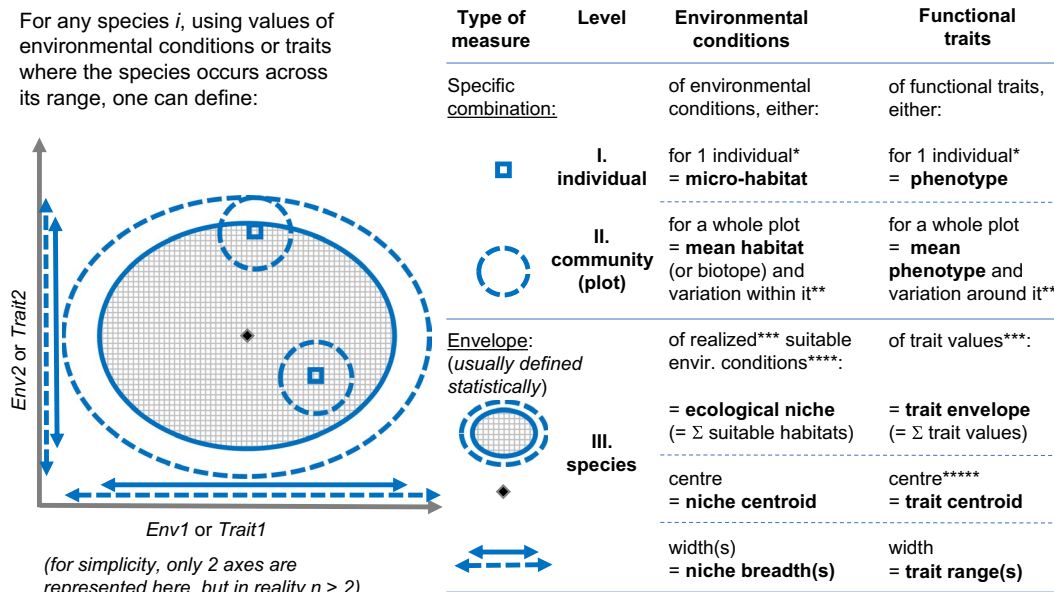
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# 1 | STATING THE CHALLENGES

Species assemblages are commonly modelled in geographic space (D'Amen, Rahbek, Zimmermann, & Guisan, 2017) by stacking predictions of individual species distribution models (hereafter S-SDMs; Ferrier & Guisan, 2006; Guisan & Rahbek, 2011; Hortal, Marco, Santos, & Diniz-Filho, 2012; see Guisan, Thuiller & Zimmermann, 2017) based on estimates of species' realized abiotic environmental niches (i.e., the multidimensional envelope of abiotic requirements occupied by a species in the field, sensu Hutchinson; e.g., Soberon & Nakamura, 2009; see Figure 1 and Kearney, 2006). S-SDMs have already been applied to various taxonomic groups (e.g., plants, birds, insects, amphibians; see review by D'Amen et al., 2017, and Calabrese, Certain, Kraan, & Dormann, 2014) and to model different properties of assemblages, such as their phylogenetic, functional or taxonomic diversity (D'Amen, Mateo, et al., 2018). However, these models can overestimate local species richness or yield inaccurate community predictions when they ignore assembly mechanisms such as dispersal processes, biotic interactions and community carrying capacities (Mateo, Mokany, & Guisan, 2017; Soberon & Nakamura, 2009; Wisz et al., 2013). Dispersal is a component that is increasingly being considered in species distribution predictions (Zurell et al., 2016), and the

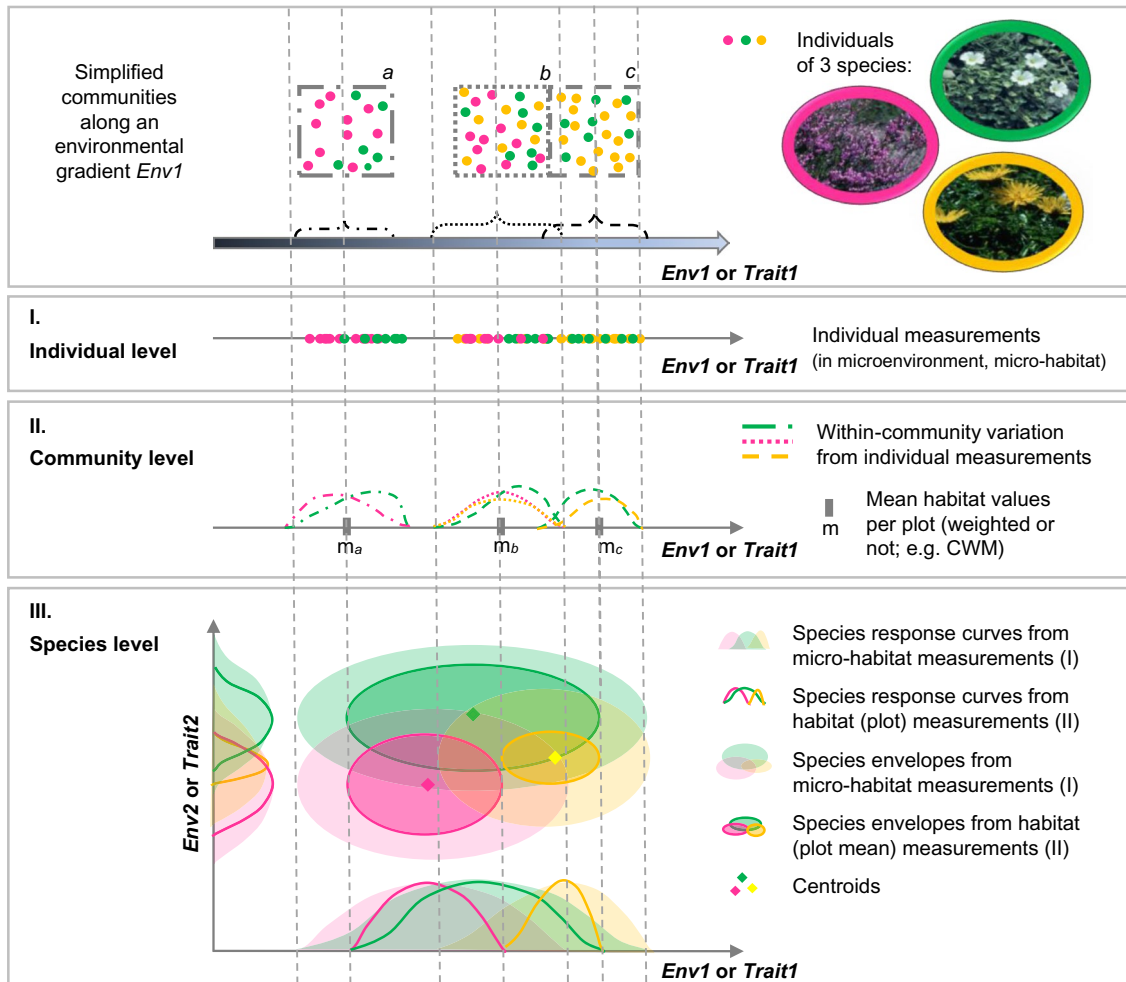
use of community carrying capacity is still debated (Mateo et al., 2017). Meanwhile, the incorporation of biotic ecological assembly rules (EARs; Gotzenberger et al., 2012) into S-SDM building holds much promise (Kissling et al., 2012; Wisz et al., 2013), yet is still in its infancy (D'Amen, Mod, Gotelli, & Guisan, 2018).

How should biotic assembly rules be defined? One way is to use trait-based approaches (Ackerly & Cornwell, 2007; McGill, Enquist, Weiher, & Westoby, 2006) to infer them, as derived from the distribution of a few to multiple functional traits (i.e., species characteristics representing ecological strategies and adaptations to local environments; Cornelissen et al., 2003; Laughlin & Messier, 2015; Diaz et al., 2016) within and among species in a community (Fitzpatrick & Keller, 2015; Laughlin, 2014; Moran, Hartig, & Bell, 2016), and especially across assemblages along environmental gradients (Figure 2; Blonder et al., 2018; Cadotte, Arnillas, Livingstone, & Yasui, 2015; Levine, 2016; Scherrer et al., 2019). The logic behind this is that observed non-random patterns of trait variation (e.g., convergence versus divergence) within assemblages reflect community assembly rules (Gotzenberger et al., 2012), including the role of interspecific competition (Funk & Wolf, 2016; Gaudet & Keddy, 1988; Kunstler et al., 2016) and trophic interactions (Morales-Castilla, Matias, Gravel, & Araújo, 2015). In particular, in homogenous habitats (as variations



\* or ramet in the case of clonal plants  
 \*\* and sub-envelope of micro-habitats or phenotypes  
 \*\*\* if the physiological conditions would be considered instead of the observed ones (only possible experimentally), then the fundamental environmental niche would be defined, which is larger and includes the realized environmental niche  
 \*\*\*\* from micro-habitat/single phenotype measurements (dashed arrows and ellipse) or from habitat-level/mean phenotype measurements (plain arrows and ellipse)  
 \*\*\*\*\* means of different traits

**FIGURE 1** Definitions of specific combinations or envelope (and their centre and width) of environmental conditions and traits associated with a given species *i*, which allow definition of specific (micro-)habitat, realized niche, niche breadth, trait combination (phenotype), trait envelope ("functional niche"), mean trait (mean phenotype) and trait range. The definition of environment, niche and habitat follows Kearney (2006), although here the niche is always the realized niche (not the fundamental niche). Note that, as shown in the figure, trait or micro-habitat variation within a community can also yield an envelope at the community level (e.g., Carmona et al., 2016 for traits) [Colour figure can be viewed at wileyonlinelibrary.com]

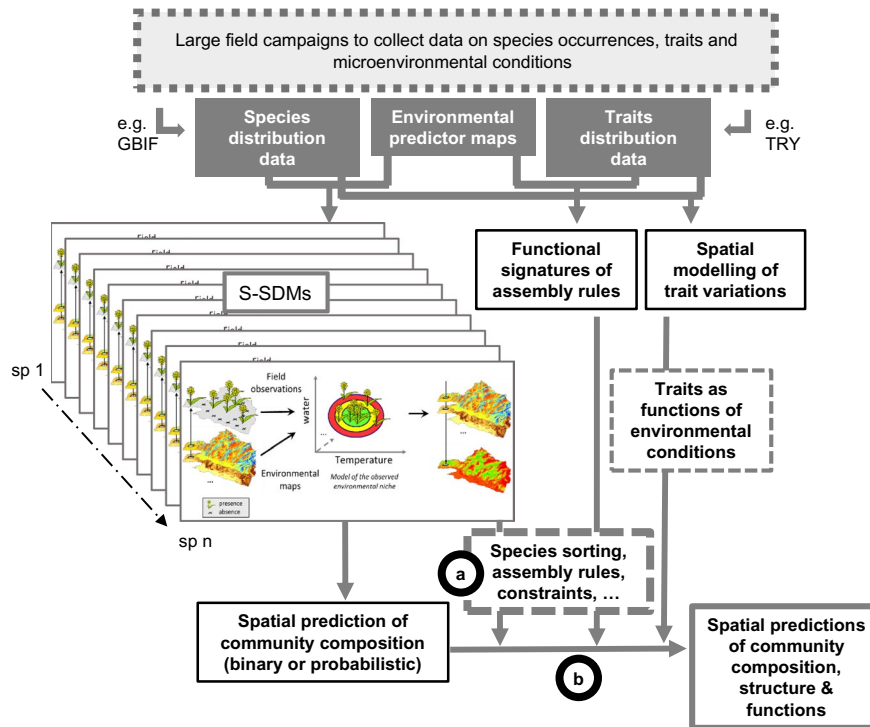


**FIGURE 2** Illustration of the measurement levels of species' environmental conditions (niche) and functional traits in a simplified situation with maximum three species (here plants) sampled in three plots (a, b, c) along one or two environmental gradients Env1 and Env2. Provided the three plots are sufficient to sample all possible conditions for the three species, three levels of measurements of environmental conditions and traits can be defined for each species: (I) the individual level, measured for each individual within a community (or plot); (II) community level, mean environmental conditions or mean trait values along environmental or trait gradients, with associated response curves displayed to illustrate within-plot variation; and (III) species level, values measured across the whole range of a species. To represent a simplified multidimensional niche or trait space for the whole-species level, a second variable was added (Env2). As shown in Figure 1, several measures can be used at the whole-species level: envelope, response curves, centroid and breadth. Trait–environment (niche and lower levels) relationships are best assessed at the same level (I, II or III). CWM = weighted means of community properties

in habitat heterogeneity could also lead to trait variations), a constraint that demands greater trait variation than expected by chance (i.e., trait divergence or overdispersion as driven by limiting similarity) could be used to infer competitive effects, while trait convergence (or underdispersion) could be used to account both for environmental filtering (i.e., selection for similar adaptations to the abiotic environment) and exclusion of inferior competitors (i.e., selection for traits conferring high competitive ability) (Cadotte & Tucker, 2017; Kraft, Godoy, & Levine, 2015; Mason, Bello, Dolezal, & Leps, 2011; Mayfield & Levine, 2010). These deviations from random expectations indicate trait-based EARs (e.g., combination of traits) that could theoretically be used to constrain niche-based S-SDMs (e.g., D'Amen et al., 2015), be it through single traits or trait combinations (Kraft et al., 2015), thus combining niche

and trait information to improve spatial predictions of communities (D'Amen et al., 2017; Laughlin, 2014). The power of combining niche and trait information is further supported by accumulating evidence that relationships exist, for a given species, between traits (or combinations of traits) and particular features of its environmental niche (Hawkins, Rueda, Rangel, Field, & Diniz-Filho, 2014; Kuhner & Kleyer, 2008; Rueda, Godoy, & Hawkins, 2017, 2018; Siefert, 2012; Thuiller, Albert, Dubuis, Randin, & Guisan, 2010). Therefore, traits can explain the outcome of interactions between species (Kraft et al., 2015; Mason et al., 2011) and ultimately explain their coexistence (Chesson, 2000).

However, most studies attempting to infer assembly rules from patterns of functional traits within communities across environmental gradients (e.g., D'Amen, Mateo, et al., 2018; de Bello et al., 2013;



**FIGURE 3** A framework for incorporating trait distributions into the spatial modelling of biological communities. As species distribution data coupled with environmental predictors allow predictions from stacked species distribution models (S-SDMs), and thus community composition (binary or probabilistic), the newly gathered data on variation of species traits sampled in geographic space could also be coupled with environmental maps to obtain spatial predictions of trait values per species. The original or modelled trait distribution data could then be used to either: (a) develop or refine rules of species interactions, or quantify the strength of biotic interactions along gradients, to be used as assembly rules in S-SDMs; or (b) be combined with stacked species distribution predictions (probability of occurrence) to predict functional or structural patterns of communities spatially. See main text for explanations. Parts of the figure inspired by graphs taken from Guisan et al. (2017) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Pottier et al., 2013; Scherrer et al., 2019; Spasojevic & Suding, 2012) have used single values per trait (e.g., the average of a few measurements) and per species, ignoring the large intraspecific trait variation (ITV; Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Bolnick et al., 2011; Moran et al., 2016) that is observed along many environmental gradients (Albert et al., 2012; Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Midolo, Frenne, Hölzel, & Wellstein, 2019; Read, Henning, & Sanders, 2017). Here we argue that ignoring this variation can have profound effects on the spatial predictions of communities and should thus not be done naively. It has been shown that ITV can influence measures of functional diversity (Albert et al., 2012; Carmona, Bello, Mason, & Lepš, 2016), community assembly (Carmona, Rota, Azcarate, & Peco, 2015; Chalmandrier et al., 2017; Siefert, 2012) and community predictions (Laughlin, Joshi, Bodegom, Bastow, & Fule, 2012; Moran et al., 2016; Read et al., 2017). It is thus expected that a single value for species-level trait information is insufficient to correctly capture community assembly processes constraining local species richness and trait distributions (Carmona et al., 2016). The next challenge to fully exploit the linkage between environmental niches and functional traits for improved spatial predictions of communities is thus to use trait values corresponding to the environmental conditions prevailing at each observation site.

The choice of the scale of trait and niche measurements is particularly important and will depend on the goal of the analysis. Each spatial resolution potentially carries different information about species and their assemblages (de Bello et al., 2013; Carmona et al., 2015; Messier, McGill, Enquist, & Lechowicz, 2017; see next section and Figure 2), and scale mismatches between measurements of niche and traits have been shown to potentially affect the detection of species assembly processes (Carmona et al., 2016; Chalmandrier et al., 2017; Hart, Schreiber, & Levine, 2016; Scherrer et al., 2019; Thuiller, Pollock, Gueguen, & Münkemüller, 2015). Here, we address two challenges related to such niche-trait scale mismatches and the need to account for ITV when complementing niche-based S-SDMs by trait-based EARs (Figure 3): (a) deriving trait-based EARs from field-measured data on species' occurrences (and ideally abundance) and species' traits within communities, thus accounting for ITV (Figure 3a); and (b) predicting trait distributions in space and along environmental gradients, and using these through the previously developed trait-based EARs to constrain, and thus improve, the raw S-SDM predictions of functional and structural properties of communities in space (Figure 3b). We argue that, to tackle these challenges, we must: (a) collect fine-scale data on species assemblages, species traits (for all co-occurring species or at least the dominants) and abiotic (micro-)habitat characteristics along key environmental

gradients, and (b) harmonize scales (or levels) between environmental niche and trait measurements for subsequent analyses.

## 2 | DIFFERENT SPATIAL MEASUREMENT SCALES FOR SPECIES' NICHES AND TRAITS

Using common definitions of environmental niches and functional traits (Figure 1), three key scales can be described that are most often used in ecological research (Figure 2). Firstly, at the finest scale, point measurements can be made of the traits of individuals within a plot and of the microenvironmental conditions where those individuals precisely occur («*individual level*» in Figures 1 and 2-I; see e.g., Blonder et al., 2018; Carmona et al., 2015, 2016). This level is still rarely considered in community analyses and modelling (but see Taylor et al., 2014; Thuiller, Gallien, et al., 2010 and references in table 1 of Silvertown, 2004). Secondly, mean values of traits and environmental conditions – or other summary statistics (e.g., median, variance or envelope) – can be calculated per plot (as sampling units; «*community level*» in Figures 1 and 2-II). This is the level of a community that allows comparison of mean traits and conditions in plots (or other summary statistics) along wide environmental gradients. For environmental niche measurement in modelling studies over large spatial extents, these are thus expected to be the values associated with each pixel in raster environmental maps (e.g., mean annual temperature for the pixel). Defining traits at this level would require calculating a mean (or other metric) value from multiple within-plot measurements across many spatial locations, but this is not commonly done (but see Albert et al., 2012; Carmona et al., 2015). Thirdly, measures of niches and traits can be aggregated across whole species' ranges (or possibly subspecies or ecotypes) («*species level*» in Figures 1 and 2-III), yielding an envelope of values (e.g., environmental niche or trait envelope), a central value (e.g., niche centroid, mean trait) or a range of value (niche breadth, trait range) (Figure 1; note that all these can similarly be calculated within a plot at the community level; see Carmona et al., 2016).

In many studies to date, there is a scale mismatch in the availability of niche and trait data. The environmental measures used to depict species niches are often derived from spatial layers (or plot level measures of abiotic conditions) with a specific resolution matching the spatial accuracy of occurrence records (e.g., climatic information at 25-m resolution; D'Amen et al., 2015), and are thus mainly based on habitat measurements, that is, mean community level environmental conditions. For trait envelopes, however, although intraspecific trait measures across species ranges or environmental gradients are rapidly accumulating (Albert et al., 2012; Anderegg et al., 2018; Bolnick et al., 2011; Carmona et al., 2015; Chalmandrier et al., 2017; Read et al., 2017; Siefert, 2012), most large-scale trait databases (e.g., Kattge et al., 2011) only provide a single value (or a few values) per trait and per species (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Carmona et al., 2016, 2015). This is problematic, because these single trait values may be based on observations made outside the area of interest or covering only a part of the values observed

for the species along the studied/modelled environmental gradients, potentially biasing estimations of trait–niche relationships. In the next section, we provide two examples of such scale mismatches between niche and trait measurements using functional traits to constrain (through deriving EARs) or predict species assemblages (Laughlin et al., 2012; but see Read et al., 2017).

## 3 | EVIDENCE OF SCALE MISMATCHES BETWEEN TRAIT AND ENVIRONMENTAL NICHE MEASURES

A first example of niche–trait scale data mismatches comes from studies attempting to detect functional signatures and unravel processes driving community assembly (e.g., Gotzenberger et al., 2012; Scherrer et al., 2019; Spasojevic & Suding, 2012), especially biotic interactions (Morales-Castilla et al., 2015), along environmental gradients without accounting for ITV (Carmona et al., 2016; Hart et al., 2016; Jung et al., 2010). Many studies in functional ecology have analysed trait dispersion patterns within plots based on single trait values per species (i.e., without accounting for ITV; e.g., D'Amen et al., 2015; Pottier et al., 2013; Spasojevic & Suding, 2012; see Violle et al., 2012). If these trait values differ from the locally expressed trait patterns (under given environmental conditions), conclusions about the underlying assembly process are inaccurate (Carmona et al., 2016; D'Andrea & Ostling, 2016). Instead, mean trait values per species in a community, or even better a probability distribution function derived from all individual measurements per species within a plot, should be obtained to infer trait patterns at the community scale (Figure 2; Carmona et al., 2015), and the latter be used to identify EARs and infer community assembly processes (Hart et al., 2016). Omission of ITV (and thus of measurements of trait variation at the individual/microhabitat or community/habitat scale) could help explain the failure of the few early attempts to use traits to refine S-SDM-based community predictions across large gradients that used a single value per trait and per species (e.g., D'Amen et al., 2015).

A second, closely related way in which scale mismatches in niche–trait data can bias community analyses is associated with spatial predictions of functional properties of communities (D'Amen, Mateo, et al., 2018; Ferrier & Guisan, 2006; Figure 3b). The previously reported failures to quantify local trait patterns from species-level trait values may lead to large uncertainty in the relationship between community functional patterns and environmental factors, and therefore ultimately affect niche-based predictions of functional properties (Figure 3b). Spatial predictions of community trait variation, such as functional diversity (FD) indices or weighted means of community properties (CWM), can be based on a single value per species and per trait (applied to all plots), or on local trait estimates per plot conditional on the specific environmental conditions. A mismatch arises when single trait values measured at the species level are related to community- or plot-level niche estimates. As a result, most S-SDM studies that tested the use of species traits to detect assembly rules (e.g., Pottier et al., 2013) or predict the outcome of

biotic interactions and community properties (e.g., D'Amen et al., 2015; D'Amen, Mateo, et al., 2018) without accounting for ITV are likely to have improperly estimated trait distributions (e.g., mean, variance, skewness, kurtosis) within and between communities along environmental gradients (Carmona et al., 2015; Read et al., 2017). Furthermore, this problem likely worsens when using such models to predict spatial patterns of community properties under future global change (Moran et al., 2016). Indeed, neglecting ITV was already shown to increase the risk of overestimating future community changes under changing environments (Bolnick et al., 2011), and could also impact future spatial predictions of trait distributions under climate change (as e.g., in Dubuis et al., 2013).

#### 4 | A RELATED SCALE ISSUE: QUANTIFYING NICHE OR TRAIT ENVELOPES WITH INDIVIDUAL- OR COMMUNITY-LEVEL MEASUREMENTS

A related scale issue may also affect trait and niche perception, and therefore community predictions. Research into species environmental niches has typically focused so far on the representation of niche envelopes at the whole species level (see Figures 1 and 2) from field observations measuring the mean value of environmental conditions in each plot or modelling unit (Guisan et al., 2017). While such representations are applicable for modelling and predicting species distributions, there has been little assessment so far of whether niche envelopes (or even the full trait space, as in Diaz et al., 2016) based on finer measurements at the individual level might provide a more accurate picture of species requirements and a better linkage with traits (e.g., to compare niche and trait envelopes; Blonder, 2017; Blonder et al., 2018; Figure 2). For example, species could occupy distinct microhabitats within a given plot (i.e., habitat), which might in some cases display as much variability in microclimatic conditions across relatively short distances as variability observed along environmental gradients across larger distances (e.g., Scherrer & Körner, 2011), and could thus promote within-plot species coexistence and impact community assembly inference (Scherrer et al., 2019). This therefore also depends on the size of the sampling unit and where its surface lies along a species–area curve for the type of habitat or ecosystem considered. Reducing the size of the sampling and modelling units down to presumably homogenous habitats (i.e., where all individuals experience the same conditions) may reduce the need for individual-level measurements. Evaluation of the predictive power gained from small-scale characterization of niches is thus needed, not only to provide insight into how scale influences niche quantification (Moran et al., 2016), and detection of biotic interactions (Araujo & Rozenfeld, 2014; Scherrer et al., 2019), but also to assess how it could affect spatial predictions of species and communities. For example, in attempts to estimate species sensitivity to climate changes, niches fitted from community-level (habitat) measurements (i.e., the approach currently used in the large majority of cases) could be different from niches estimated from individual-level

(microhabitat) measures, which could in turn affect community predictions. The same could apply to trait envelopes, whose shapes and sizes could vary depending on whether the envelope is quantified from microhabitat measures (within plots) or community (plot) mean trait measurements, although examples are more difficult to find given the scarcity of studies including trait envelope quantifications (Blonder, 2017).

#### 5 | RESOLVING THE MISMATCHES: PREDICTING BIOLOGICAL COMMUNITIES WITH TRAITS AND ENVIRONMENTAL NICHE MEASUREMENTS AT THE SAME SCALE

Taken together, one major impediment in integrating niches and traits to better predict the spatial distribution of communities from S-SDMs is the difficulty of gathering *individual* and/or *community* level measurements for both the abiotic environment and traits within the same plots across broad environmental gradients (Carmona et al., 2015; Enquist et al., 2017). In the published literature, original data are usually aggregated prior to storage and analysis (Violle et al., 2012) and, as a result, individual-level data are typically not publicly available, although intraspecific trait information is increasingly being added to trait databases (e.g., TRY; Kattge et al., 2011). This development would need to be expanded to include local measures of environmental data (i.e., micro-environments) and to store both types of data, traits and niche (as in studies such as Blonder et al., 2018), together with accurate geographic positions (e.g., in the Global Biodiversity Information Facility database; see Anderson et al., 2016). The issue of scale mismatches we identified thus also calls into question studies that still combine species-level traits (i.e., ignoring trait variation) with community-level habitat measurements, and raises the question whether other or complementary types of data and/or analyses should be used in such cases (e.g., accounting for estimates of trait variation from other sources, running sensitivity analyses).

One way to obtain the data necessary to improve the niche–trait linkage in the context of improving communities' spatial predictions would be to design large field surveys jointly sampling intraspecific niche and trait variation at the finest level (i.e., individuals) spanning a wide range of distinct environmental conditions. This becomes increasingly within reach, as shown by the increasing number of studies sampling intraspecific trait measurements along wide environmental gradients (Carmona et al., 2015; Chalmandrier et al., 2017; see Moran et al., 2016), which will allow quantification of trait envelopes and associated central and variance measures (Rosenfeld, 2002; Violle & Jiang, 2009) analogous to what has been done so far for the environmental niche (see Blonder, 2017; Figure 1). With such intraspecific trait measurements sampled more systematically along wide environmental gradients, it will then become possible to test whether niche and trait envelopes differ if quantified from individual versus community measurements (Figure 2), and if community predictions from

S-SDMs could be refined with EARs obtained from individual and/or site level trait patterning. A key challenge thus remains to define which dimensions of environmental niches and species traits should be jointly measured in the field. In this regard, approaches to assess the minimal dimensionality in traits are very useful, and some categories of traits (e.g., below-ground traits for plants) might require novel field approaches (Laughlin, 2014). Similarly, novel approaches will be required (ideally including experiments) to select the most optimal descriptors of species' environmental niches (Mod, Scherrer, Luoto, & Guisan, 2016; Scherrer & Guisan, 2019). This will also require a better understanding of which trait relates to which environmental niche dimension, and thus which multi-trait phenotype is found where across dynamic landscapes and complex environmental gradients (Laughlin & Messier, 2015).

Finally, although we mainly discussed ITV as an evolutionary component of species that needs to be accounted for through new sampling strategies when analysing and predicting community patterns in space and time, ITV also has an ecological component that can modulate population dynamics and therefore buffer potential extinctions in the context of future climate or other environmental change (Bolnick et al., 2011), and therefore also has implications for predicting future community patterns, deserving future investigations.

## ACKNOWLEDGMENTS

We are grateful to C. Moritz, H. M. Pereira, Y. Hautier, L. Pellissier, I. R. Sanders, D. Birtele and anonymous referees for their helpful insights and discussion on earlier versions of the manuscript. MD received funding from the People Programme (Marie Curie Actions) of the European Union's Seventh Framework Programme (FP7/2007-2013) under grant agreement no. 327987 (SESAM-ZOOL). AG received funding from the Swiss National Science Foundation (SESAM'ALP project, grant 31003A-1528661 and IntegrAlp project, grant CR23I2-162754). JMA received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement no. 678841.

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## BIOSKETCHES

**Antoine Guisan, Manuela D'Amen, Heidi K. Mod and Daniel Scherrer** were part of the ECOSPAT Spatial Ecology Lab at the University of Lausanne (<http://www.unil.ch/ecospat>) at the time of this study. ECOSPAT is specialized in modelling species, communities and ecosystems in space and time, with a particular focus on impacts of climate and land use changes, biological invasion and mountain ecosystems.

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**How to cite this article:** Guisan A, Mod HK, Scherrer D, et al. Scaling the linkage between environmental niches and functional traits for improved spatial predictions of biological communities. *Global Ecol Biogeogr.* 2019;28:1384–1392. <https://doi.org/10.1111/geb.12967>