# 

## RESEARCH REVIEW





## Dos and don'ts when inferring assembly rules from diversity patterns

Tamara Münkemüller<sup>1</sup>|Laure Gallien<sup>1</sup>|Laura J. Pollock<sup>1,2</sup>|Ceres Barros<sup>1,3</sup>|Marta Carboni<sup>1,4</sup>||Loïc Chalmandrier<sup>5,6,7</sup>|Florent Mazel<sup>8</sup>|Karel Mokany<sup>9</sup>|Cristina Roquet<sup>1</sup>|Jan Smyčka<sup>1,10</sup>|Matthew V. Talluto<sup>1,11,12</sup>|Wilfried Thuiller<sup>1</sup>

<sup>1</sup>University of Grenoble Alpes, CNRS, University Savoie Mont Blanc, LECA, Grenoble, France

Revised: 21 February 2020

<sup>2</sup>Department of Biology, McGill University, Montréal, Québec, Canada

<sup>3</sup>Department of Forest Resources Management, University of British Columbia, Vancouver, British Columbia, Canada

<sup>4</sup>Department of Sciences, University Roma Tre, Rome, Italy

<sup>5</sup>Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland

<sup>6</sup>Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

<sup>7</sup>Department of Botany, University of Wyoming, Laramie, Wyoming

<sup>8</sup>Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada

<sup>9</sup>CSIRO Land and Water, Canberra, Australian Capital Territory, Australia

<sup>10</sup>Center for Theoretical Study, Charles University and the Academy of Sciences of the Czech Republic, Praha, Czech Republic

<sup>11</sup>Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

<sup>12</sup>Department of Ecology, University of Innsbruck, Innsbruck, Austria

#### Correspondence

Tamara Münkemüller, Laboratoire d'Ecologie Alpine (LECA), UMR CNRS-UGA-USMB 5553, Université Grenoble Alpes, CS 40700, 38058 Grenoble cedex 9, France. Email: tamara.muenkemueller@univgrenoble-alpes.fr

#### **Funding information**

Government of Canada, Grant/Award Number: Banting postdoctoral fellowship; FP7 Ideas: European Research Council, Grant/Award Number: 281422 (TEEMBIO); LabexOSUG@2020, Grant/Award Number: ANR10 LABX56; Agence Nationale de la Recherche, Grant/Award Number: ANR-16-CE02-0009 and ANR-18-CE02-0025

Editor: Allen Hurlbert

## Abstract

**Aim:** More than ever, ecologists seek to understand how species are distributed and have assembled into communities using the "filtering framework". This framework is based on the hypothesis that local assemblages result from a series of abiotic and biotic filters applied to regional species pools and that these filters leave predictable signals in observed diversity patterns. In theory, statistical comparisons of expected and observed patterns enable data-driven tests of assembly processes. However, so far this framework has fallen short in delivering generalizable conclusions, challenging whether (and how) diversity patterns can be used to characterize and understand underlying assembly processes better.

**Methods:** By synthesizing the previously raised critiques and suggested solutions in a comprehensive way, we identify 10 pitfalls that can lead to flawed interpretations of  $\alpha$ -diversity patterns, summarize solutions developed to circumvent these pitfalls and provide general guidelines.

**Results:** We find that most issues arise from an overly simplistic view of potential processes that influence diversity patterns, which is often motivated by practical constraints on study design, focal scale and methodology. We outline solutions for each pitfall, such as methods spanning over spatial, environmental or phylogenetic scales, and suggest guidelines for best scientific practices in community ecology.

-WILEY-

A Journal of

Among key future challenges are the integration of mechanistic modelling and multitrophic interactions.

**Main conclusions:** Our conclusion is that the filtering framework still holds promise, but only if researchers successfully navigate major pitfalls, foster the integration of mechanistic modelling and multi-trophic interactions and directly account for uncertainty in their conclusions.

#### KEYWORDS

clustering, community processes, convergence, divergence, overdispersion, phylogenetic diversity, simulation model, trait diversity

## 1 | INTRODUCTION

The diversity of ecological communities is increasingly compromised by ongoing global changes (Pereira, Navarro, & Martins, 2012). Mitigation of these threats requires an understanding of the distribution of diversity along geographical, abiotic and biotic gradients and the underlying assembly processes (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Lavergne, Mouquet, Thuiller, & Ronce, 2010). A focal question is whether abiotic constraints or biotic interactions drive the taxonomic and trait structure of communities. In community ecology, this question has been addressed historically by experiments, with the limitation that these methods are typically constrained to small scales and few species. Thus, to study community assembly at large spatial scales, ecologists have assembled increasingly large community datasets spanning broad spatial extents with both trait and phylogenetic information (Diaz et al., 2016; Kunstler et al., 2016; see Figure 1a,b). Trait diversity describes the within-community variation of species' characteristics relevant for their performance, whereas phylogenetic diversity describes the evolutionary history. Combining data on distribution, traits and phylogeny in a meaningful way holds promise for a revolution in community ecology by opening the door to large-scale analyses of assembly processes (McGill, Enquist, Weiher, & Westoby, 2006; Webb, Ackerly, McPeek, & Donoghue, 2002). The idea is to harness the information on species niches contained in phylogenetic and trait data. For example, under the assumption that a set of traits represents species' niches well, we could move from a simple species-based description of communities towards a functional characterization, using community-weighted mean traits as an estimate of the community niche optimum and trait diversity as an estimate of species niche overlap (Kraft, Valencia, & Ackerly, 2008; Violle et al., 2007).

In practice, this idea has mostly been implemented through the filtering framework (Diamond, 1975; Keddy, 1992) that builds on the assumption that both abiotic (e.g., climate or land use) and biotic factors (e.g., competition) define carrying capacities and/ or growth rates of species, and thus, influence their occurrences and abundances (Figure 1d). The abiotic conditions define the environmental filters selecting species from a regional species pool, originally shaped by biogeographical history (Carstensen, Lessard, Holt, Krabbe Borregaard, & Rahbek, 2013), into the local species pool containing all species adapted to the local conditions. Then, biotic interactions influence which species from the local pool can eventually coexist in the community (Chesson, 2000; Shmida & Ellner, 1984). This deterministic view assumes that different ecological filters should lead to distinct and predictable patterns in diversity and composition. Comparison of these expected patterns with observed diversity across abiotic and biotic gradients should then allow deduction of the underlying community assembly processes, thus, moving large-scale community ecology from a purely descriptive discipline to a more process-based understanding (Leibold et al., 2004; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011; Vellend, 2010).

Relatively early on, studies that began to apply the framework used trait diversity patterns (e.g., including behavioural, life-history, morphological and physiological traits; Violle et al., 2007) and phylogenetic relatedness (Webb et al., 2002) to account for similarities in species niches. In doing so, the assumption is that measured traits are relevant for assembly processes (Mayfield, Boni, & Ackerly, 2009) and that closely related species in the phylogeny are ecologically more similar than distantly related ones (Burns & Strauss, 2011). Trait-phylogeny relationships different from these assumptions would lead to different relationships between niche similarity and phylogenetic relatedness patterns (Webb et al., 2002). To infer assembly processes, observed patterns of trait and phylogenetic diversity within a community (i.e.,  $\alpha$ -diversity) are commonly compared with null expectations (i.e., patterns under random assembly; Figure 1c). Low trait or phylogenetic  $\alpha$ -diversity is assumed to indicate ecological processes that foster the co-occurrence of species with similar niches, such as environmental filtering (Figure 1b, community A; see also Supporting Information Appendix S1). Conversely, high trait or phylogenetic  $\alpha$ -diversity can reveal ecological processes that result in limiting similarity, such as competition attributable to niche overlap (Figure 1b, community B; see also Supporting Information Appendix S1; MacArthur & Levins, 1967).

An increasingly large number of studies apply the filtering framework (see Supporting Information Appendix S2). However, first WILEY-



**FIGURE 1** Conceptual representation of the steps of the classical ecological filtering framework and related 10 common pitfalls (P1–P10; cf. left table and red points in the figure): (a) identifying research question(s) and study design, including focal organism-level, spatial and temporal scales (potential P1); (b) sampling data, specifically the choice of traits and/or phylogeny (P2); (c) choice of methodological approaches, including diversity indices, null models, species pools and statistical tests (P3–P5); and (d) drawing conclusions on the potential underlying processes, an approach with inherent problems (P6 and P7) but specific limitations in the face of complex biotic interactions (P8) and influential background factors (P9 and P10) [Colour figure can be viewed at wileyonlinelibrary.com]

reviews and meta-analyses of empirical (Emerson & Gillespie, 2008; Götzenberger et al., 2012; HilleRisLambers et al., 2012; Vamosi, Heard, Vamosi, & Webb, 2009) and simulation (Gallien, Carboni, & Münkemüller, 2014; Miller, Farine, & Trisos, 2017; Münkemüller et al., 2012) experiments have strongly dampened the enthusiasm, because they demonstrate that no simple general conclusion can be drawn from the sole observation of trait and phylogenetic diversity patterns. One prominent example is the ongoing debate on the role of competition. Although the filtering framework often fails to pinpoint signals of competition, theoretical and empirical research underscores its importance even at broad scales (for a detailed discussion, see Supporting Information Appendix S3). Seemingly, we are not much further forward than 20 years ago, when Lawton concluded that community ecology was a "mess" (Lawton, 2000). The lingering question is why the filtering framework does not provide general results despite being built on strong ecological theories (Chesson, 2000; Leibold et al., 2004).

Here, we address this question by pinpointing the major pitfalls linked to the different steps of the standard filtering approach (Figure 1). Although many of the limitations of this framework have already been pointed out in previous reviews with various foci and levels of detail, and sometimes also in combination with possible solutions (e.g., Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Lopez et al., 2016; Pontarp, Brännström, & Petchey, 2019), an overarching synthesis and a set of general guidelines for correctly applying the filtering framework is still lacking. Building on existing work, we provide a new comprehensive and structured overview of the different pitfalls and the solutions that have been developed (Table 1). We use the ongoing debate on the ecological importance of biotic interactions at large scales as an exemplary showcase (Supporting Information Appendix S3). Based on the integration of reviewed work, we then suggest step-by-step guidelines for correctly applying the filtering framework that should result in better interpretable results in community ecology.

## TABLE 1 Six solutions to pitfalls, with examples from the literature

	Pitfall	fall									
Solution	(P1) Scale choices not important	(P2) Trait and phylogenetic diversity approximate niche overlap	(P3) Diversity index is irrelevant	(P4) Species pool is obvious	(P5) Randomization is obvious	(P6) One pattern = one process	(P7) One process dominates	(P8) One type of interaction	(P9) Ignore dispersal and history	(P10) Equilibrium assumption	
(S1) Consider alternative scales of analysis $\checkmark\!\!\checkmark$											
Sample at different spatial and taxonomic scales <sup>a</sup>											
Account for temporal (e.g., seasonal) dynamics in sampling design <sup>b</sup>											
Simulate a variation of spatial and taxonomic scales with adapted null models <sup>c</sup>											
Across environmental gradients and variation <sup>d</sup>											
(S2) Measure more dynamic responses $\checkmark$											
Demographic rates as response variable <sup>b</sup>											
Set up experiments <sup>b</sup>											
Invasive species as "natural experiments" <sup>e</sup>											
Sample time series <sup>f</sup>											
(S3) Consider different biodiversity aspects and indices $\checkmark\!\!\!/$											
Traits need to be chosen and grouped adequately <sup>g</sup>				-							
Integrate trait and phylogenetic diversity <sup>h</sup>											
Weight species by their abundances <sup>i</sup>											
Incorporate intraspecific variability <sup>i</sup>											
Compare richness, regularity and divergence <sup>j</sup>											
Different indices for testing symmetric versus hierarchical competition <sup>k</sup>											
(S4) Consider alternative species pools and randomizations √√											
Use more ecologically based species pools <sup>1</sup>											
Partition diversity across evolutionary periods <sup>m</sup>											
Choose appropriate randomization algorithms <sup>n</sup>											
(S5) Validate and test the approaches applied $\checkmark$											
Undertake robustness analyses to identify mismatches between tests <sup>o</sup>											

#### TABLE 1 (Continued)

	Pitfall										
Solution	(P1) Scale choices not important	(P2) Trait and phylogenetic diversity approximate niche overlap	(P3) Diversity index is irrelevant	(P4) Species pool is obvious	(P5) Randomization is obvious	(P6) One pattern = one process	(P7) One process dominates	(P8) One type of interaction	(P9) Ignore dispersal and history	(P10) Equilibrium assumption	
Apply virtual ecologist approach, with tests of analyses using simulated data <sup>p</sup>											
Account for uncertainty in phylogenies <sup>q</sup>											
(S6) Model multiple processes jointly $\checkmark$											
Indirectly, with regressions, by accounting for nonlinear responses <sup>r</sup>											
Estimating relative importance of envronm- ental filtering, competition and dispersal <sup>s</sup>											
Explicitly account for allopatric speciation, colonization and local extinction <sup>t</sup>											
Mechanistic models with inverse parameterization based on diversity patterns <sup>u</sup>											
Note: In green the pitfall they directly address, in blue the pitfalls that they can indirectly help to solve. Ticks indicate the extent of development of the solutions.											

<sup>a</sup>Cavender-Bares et al. (2006). <sup>b</sup>Conti et al. (2018). <sup>c</sup>Münkemüller et al. (2014). <sup>d</sup>Bryant et al. (2008). <sup>e</sup>Carboni et al. (2016). <sup>f</sup>Campbell and Mandrak (2017). <sup>g</sup>Leps et al. (2006). <sup>h</sup>Cadotte et al. (2013). <sup>i</sup>Chalmandrier et al. (2015). <sup>j</sup>Raevel et al. (2012). <sup>k</sup>Kunstler et al. (2012). <sup>I</sup>Lessard et al. (2016). <sup>m</sup>Pavoine, Love and Bonsall (2009). <sup>n</sup>Hardy (2008). °Aiba et al. (2013). <sup>p</sup>Münkemüller et al. (2012). <sup>q</sup>Molina-Venegas and Roquet (2014). <sup>r</sup>Gallien et al. (2014). <sup>s</sup>Van der Plas et al. (2015). <sup>t</sup>Pigot and Etienne (2015). <sup>u</sup>Pontarp, Brännström, et al. (2019).

## 2 | COMMON PITFALLS

Application of the filtering framework requires: (a) choosing the study design with focal spatial, environmental and organism-level scales; (b) collecting information; and (c) choosing methodological approaches relevant to the research question. Finally, (d) conclusions are drawn from the results while accounting for study limitations. In the following, we review 10 different pitfalls lying in wait along these steps.

## 2.1 | Study design

The key aim of studies applying the filtering framework is to identify non-random processes in observed diversity patterns. One of the most discussed cases of non-random diversity patterns that exist despite the evident absence of directional environmental or biotic filters are neutral dynamics. Neutral theory suggests that many of the diversity patterns observed in nature may result from purely stochastic demographic processes that emerge from strong competition and dispersal limitation of functionally equivalent species, and thus, without any directional filter (Boucher, Thuiller, Davies, & Lavergne, 2014; Hubbell, 2001; Münkemüller et al., 2012). However, whether neutral dynamics lead to non-random diversity patterns depends on the focal scale of a study, and this is also true for directional assembly processes. It is thus a pitfall to assume that [pitfall (P) 1] spatial, environmental and organism-level scale choices have no influence on study results (Figure 1).

(P1) Certain processes may never be detected if we choose an inappropriate scale. First, ignoring large-scale factors, such as climate gradients, dispersal barriers, historical contingencies and evolutionary history, can mask the outcomes of small-scale processes, such as local abiotic filters and competition (Cardinale et al., 2013; Cavender-Bares, Keen, & Miles, 2006; Swenson, Enquist, Pither, Thompson, & Zimmerman, 2006; Vamosi et al., 2009). Second, ignoring small-scale factors, such as intraspecific variation in trait values (Albert et al., 2012; Siefert et al., 2015) and the fine-scale spatial arrangement of individuals (Diekmann, Law & Metz, 2000), can lead to the underlying processes being overlooked because their effects may not scale up to large-scale diversity patterns (Araujo & Rozenfeld, 2014; Thuiller et al., 2010; Turcotte & Levine, 2016). For example, it has been shown that trait plasticity increases niche differences in communities and thereby stabilizes coexistence and promotes diversity (Pérez-Ramos, Matías, Gómez-Aparicio, & Godoy, 2019). This biotic filtering mechanism would remain unnoticed when relying solely on the mean traits of species. Third, ignoring small-scale environmental variation within the community and study site may lead to high diversity in low-resolution studies and can then easily be misinterpreted as a signal of limiting similarity (Price et al., 2017).

## 2.2 | Collecting information

Trait and phylogenetic diversity are often used as proxies for niche overlap, but this common practice is often challenged (Cadotte,

-WILEY

Albert, & Walker, 2013; Gerhold et al., 2015; Li, Ives, & Waller, 2017). It is thus a pitfall to assume that (P2) trait and phylogenetic diversity are always good proxies for species niche overlap (Figure 1).

(P2) A first set of questions with regard to trait diversity is whether we are able to identify and measure the traits of ecological relevance for each (Funk et al., 2017; McGill et al., 2006), whether traits are linked closely enough to species niches (D'Andrea, Ostling, & O'Dwyer James, 2018) and whether we can avoid irrelevant traits that might confound the patterns and lead us to spurious conclusions (Kraft, Godoy, & Levine, 2015). This task is facilitated by former work (e.g., Leps, de Bello, Lavorel, & Berman, 2006) and some more recent advancements. For some clades and ecological processes, guidelines for the identification of relevant traits and database standards are now available (Diaz et al., 2016; Gravel, Albouy, & Thuiller, 2016; Luck, Lavorel, McIntyre, & Lumb, 2012; Schneider et al., 2019), open-access databases are improving (Kattge et al., 2011; Wilman et al., 2014), and trait syndromes (i.e., observed covariations in traits) can help to reduce trait space to a few relevant dimensions (Diaz et al., 2016; Wright et al., 2004). However, in many aspects, trait science still remains incomplete (Yang, Cao, & Swenson, 2018): (a) frameworks to link traits and niche dimensions are still under development for most clades (e.g., for fungi; Crowther et al., 2014); (b) even in well-studied clades, some traits are better studied than others (e.g., plant leaf traits over root traits; Funk et al., 2017); (c) it is not obvious at what level traits need to be measured (individual or population; Albert et al., 2012); and (d) the relative importance of traits can change over the life cycle (Kunstler et al., 2016). Another question is whether it is more informative to analyse each trait separately or in combination. The main argument for the former is that different traits may drive different processes and that analyses should thus be process and trait specific (Bernard-Verdier et al., 2012; Gross et al., 2013; Spasojevic, Copeland, & Suding, 2014). On the contrary, ecological niches are multidimensional and, consequently, multi-trait diversity is more likely to capture niche overlap between species across multiple niche dimensions (Kraft et al., 2015). Moreover, traits are correlated as a result of physiological trade-offs. Ignoring these trade-offs may lead to spurious conclusions (Wüest, Münkemüller, Lavergne, Pollock, & Thuiller, 2018). However, recent work shows that at least some community patterns are robust to the negligence of a relevant niche axis (D'Andrea et al., 2018).

The use of phylogenetic diversity in the filtering approach requires the assumption that phylogenetic relatedness is a good proxy for overlap in the multidimensional niche space (Anacker & Strauss, 2016; Burns & Strauss, 2011). However, phylogeny does not always represent relationships of traits that are relevant for species' niches (Blomberg, Garland, & Ives, 2003; Saito, Cianciaruso, Siqueira, Fonseca-Gessner, & Pavoine, 2016), and the phylogenetic signal of relevant traits should be tested, rather than assumed. Nonethless, this poses severe methodological problems (as discussed in detail by Gerhold et al., 2015). Moreover, relevant traits for this test are often not available, and if they are available it is not evident how they should be combined to represent species "niches" and how strong the signal should be (Mason & Pavoine, 2013). Most importantly,

if all niche-relevant traits were known and available, phylogenetic proxies would not be needed.

## 2.3 | Methodological approach

It has been demonstrated that different methodological choices can give different answers (Münkemüller et al., 2014; Perronne, Munoz, Borgya, Reboud, & Gaba, 2017). Thus, pitfalls 3, 4 and 5 are to assume that (P3) all supposedly similar diversity indices give the same results and that the construction of (P4) adequate species pools and (P5) randomization algorithms for testing deviations from expectations is obvious and straightforward (Figure 1).

(P3) A common pitfall is to assume that different diversity indices can be used interchangeably. Although some diversity indices are indeed highly redundant, others quantify different aspects of diversity (Mouchet, Villéger, Mason, & Mouillot, 2010; Tucker et al., 2017). Changing the diversity index can thus change or even invert the observed pattern of diversity (Chalmandrier, Münkemüller, Lavergne, & Thuiller, 2015; Mazel et al., 2016; Perronne et al., 2017). Indices can differ in whether they account for: (a) species abundances or not (Chao, Chiu, & Jost, 2010; Hill, 1973; Leinster & Cobbold, 2012); (b) intraspecific variability or not (Pavoine & Izsak, 2014; Violle et al., 2012); (c) different phylogenetic (e.g., species, family versus order level) or functional scales (e.g., species versus functional groups); and (d) different dimensions of the structure of assemblages, such as richness, divergence and regularity (Tucker et al., 2017; Villeger & Mouillot, 2008). Although classification schemes for available diversity metrics can be of help in the choice of an appropriate index (Pausas & Verdu, 2010; Pavoine, Vela, Gachet, de Bélair, & Bonsall, 2011; Tucker et al., 2017), it is not always evident which index is the most appropriate for a specific research question.

(P4) The species pool is generally defined as the set of all species existing in a given region that could colonize a focal community (Srivastava, 1999), but other definitions exist (Cornell & Harrison, 2014). In practice, the species pool is often the list of species in the studied dataset, which is often the result of practical constraints rather than ecological hypotheses. However, ideally, it should be defined based on the focal filtering process that the study sets out to test. Thus, it should include all species that would be selected in the community both with the focal process (filtering) and without it (randomly) but should not include any additional species resulting from another process not of interest. The choice of the species pool affects the null hypothesis associated with the null model and, consequently, can change the results of the analyses (Lessard, Belmaker, Myers, Chase, & Rahbek, 2012; Pigot & Etienne, 2015). For example, competition can be overlooked when it results in the complete exclusion of species from the pool ("dark diversity"; Pärtel, Szava-Kovats, & Zobel, 2011). In addition, the spatial extent at which the species pool is defined changes the detectability of certain assembly rules. Typically, signals of competition are prone to be overwritten by strong environmental filtering, when the study area includes steep environmental gradients (Willis et al., 2010). Importantly, not only

species richness but also trait diversity in the species pool influences patterns of diversity in local communities (Patrick & Brown, 2018).

(P5) The randomization scheme used to create a null distribution of diversity values also has a critical impact on the outcome of the analysis (Gotelli, 2000; Miller et al., 2017). Randomization breaks down patterns in the data that are caused by ecological processes. Ideally, a chosen randomization algorithm would break down only the patterns that are supposed to be generated by the process(es) of interest. However, algorithms often randomize several patterns at the same time, including those that are not of interest, and thus, test several null hypotheses simultaneously. A significant result indicates only that at least one of the null hypotheses can be rejected, but we do not know which one. For example, a high signal of phylogenetic  $\alpha$ -diversity obtained from a null model randomizing the sites can indicate competition but also that the abundance distribution in the phylogenetic tree is non-random (testing implicitly another null hypothesis; Hardy, 2008). Thus, the interpretation of a non-random pattern is not always straightforward. This problem of non-specific randomization algorithms has launched the development of more constraining algorithms (Hardy, 2008; Miller et al., 2017), often at the expense of statistical power.

## 2.4 | Drawing conclusions

The most basic shortcoming of the filtering approach is inherent to most observational studies in ecology; it is impossible to deduce a process from an observed pattern in the strict sense. However, given the complexity of nature, ecological research often uses pattern observations to formulate hypotheses or to conclude that a pattern is in (dis)agreement with hypothesized processes. The three major related pitfalls are to assume: (P6) that one pattern can emerge only from one single process; (P7) that one major process dominates the observed pattern; and (P8) that biotic interactions are simple (Figure 1).

(P6) Traditionally, clustered diversity patterns (i.e., coexisting species being in phylogenetic and trait space more similar than expected by chance) have been attributed to an environmental filter (Figure 1). However, competitive hierarchies can produce a similar pattern (Ågren & Fagerström, 1984; Kunstler et al., 2016; Mayfield & Levine, 2010; Supporting Information Appendix S1). Conversely, symmetric niche competition is assumed to produce overdispersed diversity (i.e., coexisting species being in phylogenetic and trait space more distant than expected by chance), but facilitation can also produce overdispersed diversity patterns (McIntire & Fajardo, 2014; Valiente-Banuet & Verdu, 2007; Supporting Information Appendix S1).

(P7) When multiple processes interplay, the interpretation of biodiversity patterns can be misleading (Spasojevic & Suding, 2012). This problem occurs not only when multiple processes act jointly on the same species but also if different processes drive different groups of species in the community (e.g., rare versus common species; Maire et al., 2012). For example, signals of environmental filtering are often stronger than those of competition, and thus, competition can easily be overlooked as an important driver of assembly (e.g., the overall diversity pattern is clustered, whereas environmentally binned sub-tests would reveal overdispersed diversity patterns; Chalmandrier et al., 2013; Gallien et al., 2014).

(P8) Ignoring the complex nature of biotic interactions and assuming that the only relevant biotic filter is symmetric competition is another common pitfall. After Mayfield and Levine (2010) highlighted that large parts of coexistence theory were commonly ignored, more and more contributions have developed expectations for diversity patterns structured by biotic interactions other than symmetric niche competition (Adler, Fajardo, Kleinhesselink, & Kraft, 2013; HilleRisLambers et al., 2012; Supporting Information Appendix S1). For example, for hierarchical competition, clustering of species in trait or phylogenetic space could emerge from competition for one limiting resource, because only species with adapted traits for this resource will survive (e.g., when species compete for light, only tall species will survive; Mayfield & Levine, 2010). In contrast, overdispersion is expected to emerge from competition for multiple resources when the respective adaptive traits are different for the different resources (Scheffer & van Nes, 2006). Contrasting diversity patterns are also expected to depend on the type of facilitative interactions that take place in a community (Supporting Information Appendix S1). For example, if species facilitate each other symmetrically via the same mechanism (e.g., flowers of similar colour attract common pollinators; mutualism), species with similar traits should coexist, leading to trait clustering. However, if one "benefactor" species facilitates others with different life strategies (e.g., commensalism), species with different traits could coexist, resulting in overdispersion or random patterns (Gallien, Zurell, & Zimmermann, 2018; Valiente-Banuet & Verdu, 2007). Furthermore, complex indirect interactions, such as multispecies indirect facilitation and intransitive competition (competition as in the rock-paper-scissors game, without competitive hierarchies; Gilpin, 1975; May & Leonard, 1975), may also be important drivers of community structure (Allesina & Levine, 2011; Vandermeer, 2011). For these interactions, it may be impossible to generate clear expectations for emerging diversity patterns, especially when multispecies coexistence processes are not the mere sum of their pairwise interaction outcomes (Barabas, Michalska-Smith, & Allesina, 2016; Gallien, 2017; but see Maynard et al., 2017). Moreover, multi-trophic biotic interactions have so far been largely ignored (Grilli, Barabas, Michalska-Smith, & Allesina, 2017). There are a few first example studies investigating bipartite interaction networks (Ibanez, Arène, & Lavergne, 2016; Van der Plas, Anderson, & Olff, 2012). However, the great challenge lies in extrapolating concepts of niche matching, associated trait and phylogenetic diversity patterns and cascading feedbacks from bipartite to multi-trophic communities (Levine, Bascompte, Adler, & Allesina, 2017).

Beyond these pitfalls inherent to the investigated processes, there are further pitfalls associated with unrelated processes but influential to the studied patterns, and thus, to the final conclusions. A common misconception of the filtering framework is that WILEY

we can test for a selection of ecological assembly processes while ignoring background factors. In reality, biogeography, evolution and ecological processes influence species distributions jointly (Warren, Cardillo, Rosauer, & Bolnick, 2014). Common pitfalls are to assume that (P9) dispersal and historical contingencies can be ignored and that (P10) communities are at equilibrium (Figure 1).

(P9) Although they can shape the richness and functional trait diversity of regional species pools (see also P4), diversification and historical contingencies are commonly ignored in community ecology studies (Warren et al., 2014). These processes are often thought to act at regional rather than local scales (i.e., driving the evolution of regional species pools), but long-standing evidence shows that this simplistic dichotomy of different processes acting exclusively at particular scales is fraught with exceptions in the real world (Johnson & Stinchcombe, 2007). Regional species pools and the processes that led to their establishment can sometimes be more important for local community composition than assembly processes (Chalmandrier, Albouy & Pellissier, 2017; Lawing, Eronen, Blois, Graham, & Polly, 2017; Ricklefs, 1987). In some cases, both evolutionary and ecological processes occur at the same local community scale (Pollock, Bayly, & Vesk, 2015). This problem is complicated even more by the fact that some ecological and biogeographical processes can create the same taxonomic or phylogenetic patterns. For example, from the standpoint of community ecology, "phylogenetic dispersion" in a clade can be interpreted as a sign of competitive exclusion, whereas from a biogeographical perspective, this same pattern can be interpreted as allopatric speciation (Warren et al., 2014).

(P10) The fundamental assumption that communities are at equilibrium underlies most efforts to understand community assembly (Gerhold et al., 2015). However, in the era of the Anthropocene, many observed communities are already exposed to changing environmental conditions and/or the invasion of alien species, and thus, represent a transient phase. In a transient phase, rapid changes in abiotic and biotic conditions can lead species to fill their potential range incompletely or to occur in unsuitable habitats (Ackerly, 2003). Thus, in these transient communities the current diversity patterns may not reflect ongoing assembly processes well, but instead reflect responses to past conditions (Chang & HilleRisLambers, 2016; Mittelbach & Schemske, 2015). For example, a recent study shows that climatic legacies can explain a relevant part of the variation in current community assembly (Delgado-Baquerizo et al., 2018).

## 3 | SOLUTIONS

By now it is well acknowledged that the filtering approach alone will not bring the hoped-for revolution in large-scale community ecology (Ricklefs, 2008; see also discussion on the importance of competition at large spatial scales as a showcase in Supporting Information Appendix S3). Here, we first review proposed solutions organized along the different steps commonly used in the filtering framework (comparable to the pitfall section) and point out how each of these solutions can solve (or partly solve) the different pitfalls (Table 1).

Next, we highlight new methods, theoretical advances and newly available data that could prove their utility for community assembly questions.

## 3.1 | Study design

We have seen that the filtering approach requires a number of choices and that each of these choices can affect (or even invert) the results (Münkemüller et al., 2014). It is, therefore, especially important that, at the beginning of a study, the general research question is translated into specific hypotheses and testable predictions (Figure 2). Based on these, the study design can be developed.

The scale dependence of assembly processes was recognized early on, with most studies focusing on the effects of spatial scales (Carboni et al., 2013; Kraft & Ackerly, 2010), fewer on the level of description of organisms (e.g., functional group versus species versus individual level) or different life stages (Conti et al., 2018) and very few on temporal scales (Chang & HilleRisLambers, 2016). To deal with scale dependence, studies have compared diversity patterns across different scales to test separately for signals of small- versus large-scale processes [solution (S) 1; Table 1]. A straightforward approach is a sampling design across different spatial grains and extents, levels of description of organisms and temporal scales (Cavender-Bares et al., 2006; Weithoff, Rocha, & Gaedke, 2015), including space-for-time substitutions (Bhaskar, Dawson, & Balvanera, 2014). Sampling and studying diversity patterns across several scales (using either a multiscale sampling design or a posteriori data aggregation approaches) is an obvious solution when scale choices are important but not easy to make (P1), for example when influential background factors are also scale dependent (e.g., dispersal, P9). This approach can also help to disentangle processes that create similar patterns at one scale but contrasting patterns at others (P6 and P8) and to identify the interplay of processes that act at different scales (P7). For example, for trait diversity of plant communities there is some evidence for the dominance of competitive interactions at fine spatial scales and prevalent environmental filtering at coarser scales (Carboni et al., 2013; Cavender-Bares et al., 2006).

Applying the filtering approach to dynamic response variables (S2; Table 1), such as demographic rates, is a well-known solution for several pitfalls but mostly hampered by data availability. Instead of asking, "Do species occur more often with similar or different species?", we ask, "Do species perform better with similar or different species in the neighbourhood?", thereby relating the measured performance of focal individuals to their trait and phylogenetic (dis) similarity with their neighbours. At larger spatial scales, this has been tested in systems where time series of species performance are available, such as long-term forest plots (Kunstler et al., 2012), or in systems that provide natural experiments, such as invaded communities (Carboni et al., 2016). More recently, researchers have set up experiments to test for the link between community assembly and trait or phylogenetic diversity patterns (Conti et al., 2018; Fayle, Eggleton, Manica, Yusah, & Foster, 2015). Experimental manipulation of the environmental and biotic factors that drive assembly filters allows the control of a number of influential background factors (P9 and P10) and scale dependencies (P1). In such experiments, individual



**FIGURE 2** Conceptual representation of the ongoing scientific process of generating knowledge and general theories with the ecological filtering framework. The process often starts with an experience or undirected observation (e.g., "plants in alpine meadows are often smaller than in sub-alpine meadows") that leads to further reflection about ecologically interesting questions (e.g., "why are plants smaller?"), related hypotheses (e.g., "plants might be smaller owing to environmental constraints") and testable predictions (e.g., "plant height of alpine species is a non-random selection from the mountain plant species pool"). To test these hypotheses, we suggest an interplay of studies using observations, experiments, virtual ecologist approaches (to test the logic of process-pattern-predictions and methodological approaches) and/or parameterized mechanistic models to refine, alter, expand and reject the hypotheses on ecological assembly processes. Each of the cycles can repeat many times until a hypothesis becomes so well supported that it advances community ecology as a cornerstone of a more general theory (inspired by the figure, "The scientific method as an ongoing process", developed by Theodore Garland, University of California, 2015)

success is not approximated by a single presence or abundance measure, but is captured via demographic rates at different stages (Conti et al., 2018; Li et al., 2015). Performance is often more responsive to ecological drivers than survival and might thus be more suited to measure responses in non-equilibrium situations. Moreover, long time series can reveal insights into community assembly and provide solutions for non-equilibrium situations (P9 and P10). For example, time series can be used to estimate the relative importance of environmental filtering, historical legacies and new biotic interactions in the species composition of a community in the face of past, current and future climates (Blonder et al., 2015). They can also be used to gain a better understanding of the turnover of processes during succession (Letten, Keith, & Tozer, 2014).

## 3.2 | Collection of information

Given that numerous pitfalls can bias results when focusing solely on one partial aspect of biodiversity (e.g., P2 and P3), community ecologists started early on to consider complementary facets of diversity (S3; Table 1), by comparing diversity indices between phylogenetic scales and at different levels of trait similarity, for example, close to the root versus tips in a trait-based tree (Graham, Storch, & Machac, 2018; Swenson et al., 2012), between richness, regularity and divergence components (Raevel, Violle, & Munoz, 2012), and by varying the importance of species abundances (Chalmandrier et al., 2015; Götzenberger et al., 2016) and intraspecific variability (Chalmandrier, Münkemüller, et al., 2017; Pavoine & Izsak, 2014). Guidelines for choosing the right trait and phylogenetic information come from studies from related fields. For example, studies applying the concept of trait syndromes and accounting for several traits simultaneously can aid the choice of trait combinations (Diaz et al., 2016). However, because different traits drive different processes, there is now reasonable consensus that analysis of multiple traits separately can uncover important signals in the data that would have remained undetected if all traits had been analysed together (Saito et al., 2016). Moreover, complementing trait diversity indices with community-weighted mean (CWM) traits can provide information about differences in functional strategies between communities, and thus, can allow the teasing apart of drivers that leave the same signal in trait diversity. For example, although both environmental filtering for infertile soils and hierarchical competition for light should result in clustering (Supporting Information Appendix S1), the former should select for slow-growing, small species, whereas the latter should select for fast-growing, taller species (Kunstler et al., 2012).

For phylogeny-based analyses, approaches that account for the uncertainty of the phylogeny (Rangel et al., 2015) and the uncertainty concerning the underlying trait evolution process (Gerhold et al., 2015) can aid in more correct interpretation of phylogenetic pattern analyses. Ultimately, because trait and phylogenetic information might not provide equivalent information on species niches (P2), considering them jointly probably represents the most sensible -WILEY

course of action. For example, one may complement phylogenetic measures with trait information (de Bello et al., 2017; Gianuca et al., 2017; Lopez et al., 2016; Pavoine & Bonsall, 2011) or integrate trait and phylogenetic information in a single measure in order to converge as close as possible to the multidimensional niche (Cadotte et al., 2013). In sum, moving forward from traditional single-metric analyses, a combination of different trait and phylogenetic metrics can help to disentangle processes and to detect multiple interacting processes, including different modes of competition (P6-P8) and ecological versus evolutionary processes (P9; Weinstein et al., 2014).

## 3.3 | Methodological approach

In our description of P4 and P5, we highlighted that the choice of species pools and randomization schemes can influence the outcomes of an analysis decisively (Ulrich & Gotelli, 2013). Often, different choices are (more or less) implicitly linked to different ecological hypotheses (Gotelli & Ulrich, 2012). Thus, by explicitly linking each ecological hypothesis with the correct combination of species pool and randomization, we can develop a set of tests for disentangling different ecological scenarios (S4; Table 1). This approach offers a direct solution to the methodological pitfalls (P3-P5) and can help to circumvent the challenge of disentangling patterns and processes by providing multiple-pattern comparisons (P6 and P7). For example, depending on the ecological hypothesis to be tested, it can be important to account explicitly for the dynamic nature of the species pool, recognizing that it is shaped by metacommunity dynamics in addition to speciation, extinction and dispersal (Mittelbach & Schemske, 2015). Indeed, Lessard et al. (2016) have demonstrated that the implementation of several process-based species pools, that is, species pools that already account for selected processes, and thus, can be used to test for the remaining candidates, allows the identification of otherwise hidden filters of biotic interactions. Manipulations of the species pools can also be used to simulate cross-scale sampling instead of investing the time and money to sample across different scales (Chalmandrier et al., 2013). For example, aggregating communities or cutting out smaller study areas can create ranges of spatial scales, whereas aggregating species or transforming phylogenies can create ranges of different levels of description of organisms (Münkemüller et al., 2014). Following similar logic, it is also possible to build reduced functional species pools already accounting for environmental and dispersal limitation filters at broader scales that can then be used to test simultaneously acting processes at the community scale (de Bello et al., 2012). In addition, manipulations of the randomization algorithm can be used to account for dispersal limitations by down-weighting species that do not occur in the larger surroundings (P9) and improve the detection of biotic interactions by down-weighting species for which the local environment is not suitable (Chalmandrier et al., 2013; Peres-Neto, Olden, & Jackson, 2001).

More recently, community ecologists started to validate their methods and models with the "virtual ecologist" approach, whereby

simulated data are used to mimic real species and how they are "virtually" observed and analysed (Zurell et al., 2010). This validation allows testing of the reliability and power of metrics, species pool and randomization choices (Botta-Dukat & Czucz, 2016; Miller et al., 2017; Münkemüller et al., 2012). Additionally, it allows investigation of how interacting processes and constraints (including biotic interactions, scale dependence, trait choices and confounding background factors) influence results of the filtering framework (Trisos, Petchey, & Tobias, 2014). Thus, this approach does not provide direct solutions for any pitfall, but, when using appropriate simulation models, it is a powerful tool to develop further or test the filtering approach and to interpret observed signals carefully in diversity data (S5; Table 1). The limitation of this approach inherently depends on the guality of the simulated data, and its conclusions are restricted to cases that are comparable to these virtual data (for more detail, see Zurell et al., 2010).

To avoid P7 (assuming that one process dominates the patterns), more and more approaches are being developed to model multiple processes jointly instead of testing for a single, dominant process (S6; Table 1). The range of approaches is large. Some are simple extensions of the original filtering framework. For instance, it is possible to account simultaneously for environmental filtering and symmetric competition by relying on the (strong) assumption that this should lead to a pattern, where species are not too similar (i.e., owing to competitive exclusion) and not too dissimilar (owing to environmental filtering) to each other at the same time, and by testing for this pattern (e.g., with a quadratic term in a regression model; Gallien et al., 2014). Another possibility is to build elaborate null models that allow the inclusion of multiple ecological and evolutionary processes (see also S3). Van der Plas et al. (2015) introduced static, stepwise algorithms of community assembly that simulate processes such as dispersal, environmental filtering or competition and allow the estimation of their relative importance. Pigot and Etienne (2015) developed a dynamic null model of assembly that allows the estimation of the effect of allopatric speciation, colonization and local extinction. Ultimately, the idea is to build more mechanistic, dynamic models of community assembly (Connolly, Keith, Colwell, & Rahbek, 2017; Pontarp, Brännström, et al., 2019) that are general enough to include and contrast different ecological theories and processes and can be parameterized inversely with a selection of complementary diversity patterns (Cabral, Valente, & Hartig, 2017). The logic of this inverse parameterization, in simple terms, is to run the model across the relevant parameter space, to compare simulated patterns with observed patterns using appropriate summary statistics and to choose the parameter combinations that lead to the best match between simulated and observed patterns (Grimm et al., 2005; Hartig, Calabrese, Reineking, Wiegand, & Huth, 2011). A coherent and efficient statistical method for this inverse parameterization of complex ecological and evolutionary models is approximate Bayesian computation (Csilléry, Blum, Gaggiotti, & François, 2010). Interpretation of the identified best parameter values allows quantification of the relative influence of the different ecological, biogeographical and evolutionary processes (Pontarp, Bunnefeld,

et al., 2019). Very importantly, the parameterized model could also be used to account for transient dynamics (P10) and to make predictions, so far largely unattained aims in large-scale community ecology. Examples of such mechanistic models exist already (Cazelles, Mouquet, Mouillot, & Gravel, 2016; Kalyuzhny, Kadmon, & Shnerb, 2015; Lohier, Jabot, Weigelt, Schmid, & Deffuant, 2016), but many processes and process combinations are still understudied in this young research field (Cabral et al., 2017). Interestingly, the development and application of such mechanistic models in community ecology will benefit greatly from the solutions outlined here (S1-S4) because these provide a range of partly independent diversity patterns (e.g., trait versus phylogenetic patterns, abundance weighted patterns, small versus large-scale patterns), an indispensable requisite for inverse parameterization (Grimm et al., 1996). Although this approach of jointly modelling different processes of assembly is very promising, substantial challenges remain (Cabral et al., 2017); for example, calibration and validation are data hungry, computationally demanding and require strong expert knowledge.

## 3.4 | Drawing conclusions

Observational approaches, including the filtering framework, were never meant to provide final answers to questions about ecological mechanisms and processes but to feed an ongoing scientific process of generating knowledge and general theories (Garland, 2015). Observational studies are supposed to help refine, alter, expand and test hypotheses and to inform further observations, experiments and mechanistic models (see Figure 2). In a single observational study, it is typically not possible to sample all the necessary data or to apply all the above outlined solutions. For very complex filters (e.g., complex biotic interactions that differ for different species pairs), there might not exist solutions at all. This is not a problem per se as long as these limitations are considered in the conclusions drawn from results. Ultimately, a combination of studies using observations, experiments and mechanistic models with different strengths and limitations will advance our understanding of ecological processes and their importance in realistic versus laboratory environments.

## 3.5 | Future developments and challenges

New methods, theoretical advances and newly available data offer opportunities, but also pose challenges to the study of community assembly. Their application for inferring assembly rules from diversity patterns has only started. Although broad-scale testing remains to be undertaken, we highlight here general ideas and the potential benefits to community assembly research in each of these areas:

 One strong, and certainly in most cases wrong, assumption of the filtering approach is that all species interact with each other (and based on the same underlying processes). Species distribution modelling techniques that allow the estimation of the covariation of species while modelling their response to abiotic variables may help to relax this assumption [e.g., joint species distribution models (JSDMs); Clark, Gelfand, Woodall, & Zhu, 2014; Pollock et al., 2014]. The estimated residual covariance matrices in JSDMs can result from model misspecification, influential but hidden abiotic variables, but could potentially also result from biotic interactions, and thus, be a signal of assembly rules (Ovaskainen et al., 2017; Tikhonov, Abrego, Dunson, & Ovaskainen, 2017; Zurell, Pollock Laura, & Thuiller, 2018). To gain a better understanding of the ecological meaning of these residual covariance matrices, one could test them using simulated data (Zurell et al., 2018) or one could link empirically estimated covariance matrices to trait and/or phylogenetic diversity patterns, assuming that a strong correlation would indicate ecological meaning. However, given that they rely on correlation matrices, these approaches can focus only on testing for symmetric interactions, which greatly limits their application for inferring interactions.

- 2. Recent advances in multi-trophic network theory have highlighted the links of trait (Albouy et al., 2011; Crea, Ali, & Rader, 2016) and phylogenetic relationships (Aizen et al., 2016; Peralta, 2016) with biotic interactions in the networks. Specific interactions are linked to specific trait combinations, and thus, to trait and phylogenetic diversity patterns. For example, it has been shown for plant-insect interaction networks that certain traits define sets of potentially interacting species and define clear patterns of clustering on the phylogenies of plants and insects (Ibanez et al., 2016). For food webs, Morlon, Kefi, and Martinez (2014) have suggested and applied a new framework to estimate the strength of filters of "trophic environment" versus food-mediated interspecific competition in community assembly. The framework uses trophic similarities, measured via shared predators or prey, and null models. In a similar approach, for multi-trophic tropical fish communities, it was recently highlighted that traits linked to feeding strategies or trophic level (with measurement based on stable isotope ratios) played an important role in community assembly and, accordingly, left significant signals in trait diversity (Fitzgerald, Winemiller, Sabaj, & Sousa, 2017). Advances in this direction open the door for moving from single-trophic to multitrophic community assembly (Gravel et al., 2016). Ultimately, the integration of complementary information on species differences from traits, phylogenies and interaction networks promises a better understanding of community assembly in space and time (Morlon et al., 2014).
- 3. Finally, new types of data are rapidly becoming available. One example is amplicon-based DNA analysis of environmental samples (i.e., metabarcoding data, environmental DNA; Creer et al., 2016; Taberlet et al., 2012). These data provide new information on the potential presence of organisms for calculation of diversity patterns (Calderón-Sanou, Münkemüller, Boyer, Zinger, & Thuiller, 2020; Martinez-Almoyna et al., 2019). Combined with databases or expert knowledge on functional traits, phylogenies or trophic meta-webs (containing information on all predator-prey

WILEY

interactions in a regional pool of present taxa), these diversity patterns permit better approximation of niche overlap in communities. The great advantage is the coverage of almost all prokaryote and eukaryote species present in a sample (or taxonomic units with lower resolution, depending on the reference libraries) and the integration over time (e.g., species are not missed simply because they were not visible at the sampling time). Although promising, environmental DNA data also brings new uncertainty with respect to traditional surveys, such as amplification errors, DNA degradation and contamination and barcode assignation (Taberlet et al., 2012), because reference databanks of DNA sequences that can be used to identify taxonomic units are still incomplete and impede the traditional use of diversity indices based on species concepts (Coissac et al., 2015). However, methodological advances in this area will help to address earlier limitations (e.g., data limitation for pollination networks: Pornon, Andalo, Burrus, & Escaravage, 2017; Calderón-Sanou et al., 2020) and allow the study of entirely new types of ecosystems (e.g., by combining soil metabarcoding with information from trait databases, one can study the interplay of fungi and bacteria with nematodes and plants; Anslan, Bahram, & Tedersoo, 2016; Tedersoo et al., 2016). Another promising new type of data comes from transcriptomic and meta-transcriptomic approaches (Gotelli, Ellison, & Ballif, 2012; Wang, Kong, Li, & Xie, 2016). These high-throughput methods allow the identification of proteins or genes being produced by individuals or entire communities at the time of sampling (e.g., environmental proteomics). The patterns of differential protein production and expression provide a direct assessment of physiological responses to abiotic and biotic stimuli, and thus, to the use of niches by individuals or communities. The diversity of expressed functions could help to provide insights into assembly processes that are much more tightly linked to physiological responses than the standard trait diversity measures, which are often based on "soft" traits (i.e., few easily measurable features). For example, a recent community-wide transcriptomic analysis has supported the Janzen-Connell hypothesis by demonstrating that growth rates and survival of individual trees were higher when the neighbourhood consisted of trees with dissimilar (rather than similar) defense genes (Zambrano et al., 2017). However, even more than with metabarcoding, this approach adds uncertainty with respect to traditional surveys that are linked to sampling, laboratory work and interpretation of results (Wang et al., 2016).

## 4 | GUIDELINES

Based on our critical synthesis of pitfalls and available solutions (Table 1), we suggest consideration of the following steps when applying the filtering framework:

1. Translate research question(s) into specific hypotheses and testable predictions. The expected patterns in support of each

hypothesis must be identified a priori, and each hypothesis should be tested against each of these predetermined patterns (Figure 2; S4).

- 2. Assemble all data necessary to answer the research question (across scales and diversity facets) but not more (S1 and S3). Importantly, use existing naturalist knowledge to decide on ecologically relevant traits. Inclusion of extraneous species or irrelevant traits or conducting the analysis at an inappropriate scale can obscure or distort any signal in the diversity patterns.
- 3. Measure dynamic response variables in a spatially explicit context and consider complementing this with targeted experiments if the research question and setting allow for it (S2). This seems especially important when focusing on biotic interactions or studying communities that are far from equilibrium.
- Select the diversity metrics most appropriate to the question of interest based on the conceptual framework and existing naturalist knowledge (S3).
- 5. Choose species pools and randomization techniques such that null models break only the pattern to be tested and not additional patterns (S4). If this is not possible, use a combination of tests that together allow an unbiased answer to the research question. Test the sensibleness of this methodological choice and interpret accordingly (S5).
- 6. If possible, test for the reliability and power of the chosen approach with simulated data (S5).
- 7. Test whether signals identified as significant are congruent across the relevant patterns identified a priori for each research hypothesis and always interpret them together (Figure 2; S6).
- If your research question is complex (e.g., implies a multitude of processes or is linked to evolutionary history), it may be necessary to build and parameterize a mechanistic simulation model that embraces the underlying complexity and allows disentanglement of the different drivers (S6).
- Remember that study of the causal processes in the strict sense always requires an experiment and, accordingly, report results of pattern analyses with the necessary care (Figure 2).

## 5 | CONCLUSION

If we are to exploit the filtering framework fully for a better understanding of community assembly, we need to: (a) ensure that we rely on the solutions provided for most of the known pitfalls (Table 1) and follow the guidelines suggested here for good scientific practice; (b) improve current solutions that begin to accommodate multiple confounding processes, more complex biotic interaction types and different spatial scales; and (c) integrate the rapidly accumulating types of new data (e.g., environmental metabarcoding) that represent more diverse and so far largely unknown communities (e.g., soil microbes) across an ever-increasing spatial scope. Adaptation of the filtering approach to circumvent traditional pitfalls, account for uncertainty and accommodate new data, all while retaining core fundamental ideas, holds promise to improve our understanding of the ever-widening definition of the ecological community significantly.

## ACKNOWLEDGEMENTS

The first outline of the manuscript was developed during a workshop financed by the European Research Council under the European Community's Seven Framework Program FP7/2007-2013 grant agreement no. 281422 (TEEMBIO). T.M. and W.T. acknowledge funding from the French Agence Nationale de la Recherche (ANR) through the GlobNets project (ANR-16-CE02-0009) and the GAMBAS project (ANR-18-CE02-0025). F.M. was supported by a Banting postdoctoral fellowship. The LECA is part of LabexOSUG@2020 (ANR10 LABX56).

## ORCID

Tamara Münkemüller https://orcid.org/0000-0001-9743-1322 Marta Carboni https://orcid.org/0000-0002-9348-4758 Florent Mazel https://orcid.org/0000-0003-0572-9901 Matthew V. Talluto https://orcid.org/0000-0001-5188-7332

## REFERENCES

- Ackerly, D. D. (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, 164, S165–S184.
- Adler, P. B., Fajardo, A., Kleinhesselink, A. R., & Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. *Ecology Letters*, 16, 1294–1306.
- Ågren, G. I., Fagerström, T., Agren, G. I., & Fagerstrom, T. (1984). Limiting dissimilarity in plants: Randomness prevents exclusion of species with similar competitive abilities. *Oikos*, 43, 369–375.
- Aiba, M., Katabuchi, M., Takafumi, H., Matsuzaki, S.-i. S., Sasaki, T., & Hiura, T. (2013). Robustness of trait distribution metrics for community assembly studies under the uncertainties of assembly processes. *Ecology*, 94, 2873–2885.
- Aizen, M. A., Gleiser, G., Sabatino, M., Gilarranz, L. J., Bascompte, J., & Verdú, M. (2016). The phylogenetic structure of plant-pollinator networks increases with habitat size and isolation. *Ecology Letters*, 19, 29–36.
- Albert, C. H., de Bello, F., Boulangeat, I., Pellet, G., Lavorel, S., & Thuiller,
   W. (2012). On the importance of intraspecific variability for the quantification of functional diversity. *Oikos*, 121, 116–126.
- Albouy, C., Guilhaumon, F., Villéger, S., Mouchet, M., Mercier, L., Culioli, J. M., ... Mouillot, D. (2011). Predicting trophic guild and diet overlap from functional traits: Statistics, opportunities and limitations for marine ecology. *Marine Ecology Progress Series*, 436, 17–28.
- Allesina, S., & Levine, J. M. (2011). A competitive network theory of species diversity. Proceedings of the National Academy of Sciences USA, 108, 5638–5642.
- Anacker, B. L., & Strauss, S. Y. (2016). Ecological similarity is related to phylogenetic distance between species in a cross-niche field transplant experiment. *Ecology*, 97, 1807–1818.
- Anslan, S., Bahram, M., & Tedersoo, L. (2016). Temporal changes in fungal communities associated with guts and appendages of Collembola as based on culturing and high-throughput sequencing. *Soil Biology and Biochemistry*, 96, 152–159.
- Araujo, M. B., & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *Ecography*, 37, 406–415.
- Barabas, G., Michalska-Smith, M. J., & Allesina, S. (2016). The effect of intra- and interspecific competition on coexistence in multispecies communities. *The American Naturalist*, 188, E1–E12.

- Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. (2012). Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology*, 100, 1422–1433.
- Bhaskar, R., Dawson, T. E., & Balvanera, P. (2014). Community assembly and functional diversity along succession post-management. *Functional Ecology*, 28, 1256–1265.
- Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717–745.
- Blonder, B., Nogués-Bravo, D., Borregaard, M. K., Donoghue, J. C., Jørgensen, P. M., Kraft, N. J. B., ... Enquist, B. J. (2015). Linking environmental filtering and disequilibrium to biogeography with a community climate framework. *Ecology*, *96*, 972–985.
- Botta-Dukat, Z., & Czucz, B. (2016). Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. *Methods in Ecology and Evolution*, 7, 114-126.
- Boucher, F. C., Thuiller, W., Davies, T. J., & Lavergne, S. (2014). Neutral biogeography and the evolution of climatic niches. *The American Naturalist*, 183, 573–584.
- Bryant, J. A., Lamanna, C., Morlon, H., Kerkhoff, A. J., Enquist, B. J., & Green, J. L. (2008). Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences USA*, 105, 11505–11511.
- Burns, J. H., & Strauss, S. Y. (2011). More closely related species are more ecologically similar in an experimental test. Proceedings of the National Academy of Sciences USA, 108, 5302–5307.
- Cabral, J. S., Valente, L., & Hartig, F. (2017). Mechanistic simulation models in macroecology and biogeography: State-of-art and prospects. *Ecography*, 40, 267–280.
- Cadotte, M., Albert, C. H., & Walker, S. C. (2013). The ecology of differences: Assessing community assembly with trait and evolutionary distances. *Ecology Letters*, 16, 1234–1244.
- Calderón-Sanou, I., Münkemüller, T., Boyer, F., Zinger, L., & Thuiller, W. (2020). From environmental DNA sequences to ecological conclusions: How strong is the influence of methodological choices? *Journal* of Biogeography, 47, 193–206.
- Campbell, S. E., & Mandrak, N. E. (2017). Dissecting spatiotemporal patterns of functional diversity through the lens of Darwin's naturalization conundrum. *Ecology and Evolution*, 7, 3861–3869.
- Carboni, M., Münkemüller, T., Gallien, L., Lavergne, S., Acosta, A., & Thuiller, W. (2013). Darwin's naturalization hypothesis: Scale matters in coastal plant communities. *Ecography*, 36, 560–568.
- Carboni, M., Münkemüller, T., Lavergne, S., Choler, P., Borgy, B., Violle, C., ... Thuiller, W. (2016). What it takes to invade grassland ecosystems: Traits, introduction history and filtering processes. *Ecology Letters*, 19, 219–229.
- Cardinale, B. J., Gross, K., Fritschie, K., Flombaum, P., Fox, J. W., Rixen, C., ... Wilsey, B. J. (2013). Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology*, 94, 1697–1707.
- Carstensen, D. W., Lessard, J.-P., Holt, B. G., Krabbe Borregaard, M., & Rahbek, C. (2013). Introducing the biogeographic species pool. *Ecography*, 36, 1310–1318.
- Cavender-Bares, J., Keen, A., & Miles, B. (2006). Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology*, 87, S109–S122.
- Cazelles, K., Mouquet, N., Mouillot, D., & Gravel, D. (2016). On the integration of biotic interaction and environmental constraints at the biogeographical scale. *Ecography*, 39, 921–931.
- Chalmandrier, L., Albouy, C., & Pellissier, L. (2017). Species pool distributions along functional trade-offs shape plant productivity-diversity relationships. *Scientific Reports*, *7*, 15405.

- Chalmandrier, L., Münkemüller, T., Colace, M.-P., Renaud, J., Aubert, S., Carlson, B. Z., ... Thuiller, W. (2017). Spatial scale and intraspecific trait variability mediate assembly rules in alpine grasslands. *Journal* of Ecology, 105, 277–287.
- Chalmandrier, L., Münkemüller, T., Gallien, L., de Bello, F., Mazel, F., Lavergne, S., & Thuiller, W. (2013). A family of null models to distinguish between habitat filtering and biotic interactions in functional diversity patterns. *Journal of Vegetation Science*, 24, 853–864.
- Chalmandrier, L., Münkemüller, T., Lavergne, S., & Thuiller, W. (2015). Effects of species' similarity and dominance on the functional and phylogenetic structure of a plant meta-community. *Ecology*, 96, 143–153.
- Chang, C., & HilleRisLambers, J. (2016). Integrating succession and community assembly perspectives. F1000Research, 5, 2294.
- Chao, A., Chiu, C. H., & Jost, L. (2010). Phylogenetic diversity measures based on Hill numbers. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3599–3609.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31, 343–366.
- Clark, J. S., Gelfand, A. E., Woodall, C. W., & Zhu, K. (2014). More than the sum of the parts: Forest climate response from joint species distribution models. *Ecological Applications*, 24, 990–999.
- Coissac, E., Taberlet, P., Roquet, C., Boleda, M., Gielly, L., Alberti, A., ... Lavergne, S. (2015). Towards an universal genome-based DNA barcode-The PhyloAlps project. *Genome*, 58, 206–206.
- Connolly, S. R., Keith, S. A., Colwell, R. K., & Rahbek, C. (2017). Process, mechanism, and modeling in macroecology. *Trends in Ecology and Evolution*, 32, 835–844.
- Conti, L., Block, S., Parepa, M., Münkemüller, T., Thuiller, W., Acosta, A. T. R., ... Carboni, M. (2018). Biotic resistance to the next generation of ornamental plant invaders: The roles of functional similarity and trait plasticity. *Journal of Ecology*, 106, 1607–1620.
- Cornell, H. V., & Harrison, S. P. (2014). What are species pools and when are they important? Annual Review of Ecology, Evolution, and Systematics, 45, 45–67.
- Crea, C., Ali, R. A., & Rader, R. (2016). A new model for ecological networks using species-level traits. *Methods in Ecology and Evolution*, 7, 232–241.
- Creer, S., Deiner, K., Frey, S., Porazinska, D., Taberlet, P., Thomas, W. K., ... Bik, H. M. (2016). The ecologist's field guide to sequence-based identification of biodiversity. *Methods in Ecology and Evolution*, 7, 1008–1018.
- Crowther, T. W., Maynard, D. S., Crowther, T. R., Peccia, J., Smith, J. R., & Bradford, M. A. (2014). Untangling the fungal niche: The trait-based approach. *Frontiers in Microbiology*, 5, 579.
- Csilléry, K., Blum, M. G. B., Gaggiotti, O. E., & François, O. (2010). Approximate Bayesian Computation (ABC) in practice. *Trends in Ecology and Evolution*, 25, 410–418.
- D'Andrea, R., Ostling, A., & O'Dwyer, J. P. (2018). Translucent windows: How uncertainty in competitive interactions impacts detection of community pattern. *Ecology Letters*, 21, 826–835.
- de Bello, F., Price, J. N., Münkemüller, T., Liira, J., Zobel, M., Thuiller, W., ... Pärtel, M. (2012). Functional species pool framework to test for biotic effects on community assembly. *Ecology*, 93, 2263–2273.
- de Bello, F., Smilauer, P., Diniz, J. A. F., Carmona, C. P., Lososova, Z., Herben, T., & Gotzenberger, L. (2017). Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. *Methods in Ecology and Evolution*, 8, 1200–1211.
- Delgado-Baquerizo, M., Eldridge, D. J., Travers, S. K., Val, J., Oliver, I., & Bissett, A. (2018). Effects of climate legacies on above- and belowground community assembly. *Global Change Biology*, 24, 4330-4339.
- Diamond, J. M. (1975). Assembly of species communities. In M. L. Cody, & J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342– 444). Cambridge, MA: Harvard University Press.

WILF

- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–173.
- Diekmann, U., Law, R., & Metz, J. A. J. (2000). The geometry of ecological interactions: Simplifying spatial complexity. Cambridge, UK: Cambridge University Press.
- Emerson, B. C., & Gillespie, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology* & *Evolution*, 23, 619–630.
- Fayle, T. M., Eggleton, P., Manica, A., Yusah, K. M., & Foster, W. A. (2015). Experimentally testing and assessing the predictive power of species assembly rules for tropical canopy ants. *Ecology Letters*, 18, 254–262.
- Fitzgerald, D. B., Winemiller, K. O., Sabaj, P. M. H., & Sousa, L. M. (2017). Using trophic structure to reveal patterns of trait-based community assembly across niche dimensions. *Functional Ecology*, 31, 1135–1144.
- Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., ... Wright, J. (2017). Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews*, 72, 1156–1173.
- Gallien, L. (2017). Intransitive competition and its effects on community functional diversity. *Oikos*, 126, 615–623.
- Gallien, L., Carboni, M., & Münkemüller, T. (2014). Identifying the signal of environmental filtering and competition in invasion patterns – a contest of approaches from community ecology. *Methods in Ecology* and Evolution, 5, 1002–1011.
- Gallien, L., Zurell, D., & Zimmermann, N. E. (2018). Frequency and intensity of facilitation reveal opposing patterns along a stress gradient. *Ecology and Evolution*, 8, 2171–2181.
- Garland, T. (2015). The scientific method as an ongoing process. University of California, Riverside: Institute for the Development of Educational Applications.
- Gerhold, P., Cahill, J. F., Winter, M., Bartish, I. V., & Prinzing, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, 29, 600–614.
- Gianuca, A. T., Declerck, S. A. J., Cadotte, M. W., Souffreau, C., De Bie, T., & De Meester, L. (2017). Integrating trait and phylogenetic distances to assess scale-dependent community assembly processes. *Ecography*, 40, 742–752.
- Gilpin, M. E. (1975). Limit cycles in competition communities. American Naturalist, 109, 51–60.
- Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, 81, 2606–2621.
- Gotelli, N. J., Ellison, A. M., & Ballif, B. A. (2012). Environmental proteomics, biodiversity statistics and food-web structure. *Trends in Ecology* and Evolution, 27, 436–442.
- Gotelli, N. J., & Ulrich, W. (2012). Statistical challenges in null model analysis. Oikos, 121, 171–180.
- Götzenberger, L., Botta-Dukát, Z., Lepš, J., Pärtel, M., Zobel, M., & de Bello, F. (2016). Which randomizations detect convergence and divergence in trait-based community assembly? A test of commonly used null models. *Journal of Vegetation Science*, 27, 1275–1287.
- Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., ... Pellissier, L. (2012). Ecological assembly rules in plant communities-approaches, patterns and prospects. *Biological Reviews* of the Cambridge Philosophical Society, 87(1), 111–127.
- Graham, C. H., Storch, D., & Machac, A. (2018). Phylogenetic scale in ecology and evolution. *Global Ecology and Biogeography*, 27, 175–187.
- Gravel, D., Albouy, C., & Thuiller, W. (2016). The meaning of functional trait composition of food webs for ecosystem functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 20150268.
- Grilli, J., Barabas, G., Michalska-Smith, M. J., & Allesina, S. (2017). Higherorder interactions stabilize dynamics in competitive network models. *Nature*, 548, 210–213.

- Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J., & Wissel, C. (1996). Pattern-oriented modelling in population ecology. *Science of the Total Environment*, 183, 151–166.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., ... DeAngelis, D. L. (2005). Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science*, 310, 987–991.
- Gross, N., Börger, L., Soriano-Morales, S. I., Le Bagousse-Pinguet, Y., Quero, J. L., García-Gómez, M., ... Maestre, F. T. (2013). Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. *Journal of Ecology*, 101, 637–649.
- Hardy, O. J. (2008). Testing the spatial phylogenetic structure of local communities: Statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology*, 96, 914–926.
- Hartig, F., Calabrese, J. M., Reineking, B., Wiegand, T., & Huth, A. (2011). Statistical inference for stochastic simulation models – theory and application. *Ecology Letters*, 14, 816–827.
- Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, 54, 427–432.
- HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 227–248.
- Hubbell, S. P. (2001). The unified neutral theory of biodiversity and biogeography. Princeton: Princeton University Press.
- Ibanez, S., Arène, F., & Lavergne, S. (2016). How phylogeny shapes the taxonomic and functional structure of plant-insect networks. *Oecologia*, 180, 989–1000.
- Johnson, M. T. J., & Stinchcombe, J. R. (2007). An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology and Evolution*, 22, 250–257.
- Kalyuzhny, M., Kadmon, R., & Shnerb, N. M. (2015). A neutral theory with environmental stochasticity explains static and dynamic properties of ecological communities. *Ecology Letters*, 18, 572–580.
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., ... Wirth, C. (2011). TRY – a global database of plant traits. *Global Change Biology*, 17, 2905–2935.
- Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157–164.
- Kraft, N. J. B., & Ackerly, D. D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs*, 80, 401–422.
- Kraft, N. J. B., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings* of the National Academy of Sciences USA, 112, 797–802.
- Kraft, N. J. B., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322, 580–582.
- Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., ... Westoby, M. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, *529*, 204–207.
- Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., ... Coomes, D. A. (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: Implications for forest community assembly. *Ecology Letters*, 15, 831–840.
- Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology*, *Evolution and Systematics*, 41, 321–350.
- Lawing, A. M., Eronen, J. T., Blois, J. L., Graham, C. H., & Polly, P. D. (2017). Community functional trait composition at the continental scale: The effects of non-ecological processes. *Ecography*, 40, 651–663.

- Lawton, J. H. (2000). *Community ecology in a changing world*. Oldendorf/ Luhe: Ecology Institute.
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., ... Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7, 601–613.
- Leinster, T., & Cobbold, C. A. (2012). Measuring diversity: The importance of species similarity. *Ecology*, 93, 477–489.
- Leps, J., de Bello, F., Lavorel, S., & Berman, S. (2006). Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. *Preslia*, 78, 481–501.
- Lessard, J.-P., Belmaker, J., Myers, J. A., Chase, J. M., & Rahbek, C. (2012). Inferring local ecological processes amid species pool influences. *Trends in Ecology and Evolution*, *27*, 600–607.
- Lessard, J. P., Weinstein, B. G., Borregaard, M. K., Marske, K. A., Martin, D. R., McGuire, J. A., ... Graham, C. H. (2016). Process-based species pools reveal the hidden signature of biotic interactions amid the influence of temperature. *The American Naturalist*, 187, 75–88.
- Letten, A. D., Keith, D. A., & Tozer, M. G. (2014). Phylogenetic and functional dissimilarity does not increase during temporal heathland succession. Proceedings of the Royal Society B: Biological Sciences, 281, 20142102.
- Levine, J. M., Bascompte, J., Adler, P. B., & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, 546, 56-64.
- Li, D. J., Ives, A. R., & Waller, D. M. (2017). Can functional traits account for phylogenetic signal in community composition? *New Phytologist*, 214, 607–618.
- Li, S.-P., Guo, T., Cadotte, M. W., Chen, Y.-J., Kuang, J.-L., Hua, Z.-S., ... Li, J.-T. (2015). Contrasting effects of phylogenetic relatedness on plant invader success in experimental grassland communities. *Journal of Applied Ecology*, 52, 89–99.
- Lohier, T., Jabot, F., Weigelt, A., Schmid, B., & Deffuant, G. (2016). Predicting stochastic community dynamics in grasslands under the assumption of competitive symmetry. *Journal of Theoretical Biology*, 399, 53–61.
- Lopez, B. E., Burgio, K. R., Carlucci, M. B., Palmquist, K. A., Parada, A., Weinberger, V. P., & Hurlbert, A. H. (2016). A new framework for inferring community assembly processes using phylogenetic information, relevant traits and environmental gradients. *One Ecosystem*, 1, e9501.
- Luck, G. W., Lavorel, S., McIntyre, S., & Lumb, K. (2012). Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *Journal of Animal Ecology*, 81, 1065–1076.
- MacArthur, R., & Levins, R. (1967). Limiting similarity convergence and divergence of coexisting species. *The American Naturalist*, 101, 377–385.
- Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. D. S., ... Louault, F. (2012). Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist*, 196, 497–509.
- Martinez-Almoyna, C., Thuiller, W., Chalmandrier, L., Ohlmann, M., Foulquier, A., Clément, J.-C., ... Münkemüller, T. (2019). Multi-trophic β-diversity mediates the effect of environmental gradients on the turnover of multiple ecosystem functions. *Functional Ecology*, 33, 2053–2064.
- Mason, N. W. H., & Pavoine, S. (2013). Does trait conservatism guarantee that indicators of phylogenetic community structure will reveal niche-based assembly processes along stress gradients? *Journal* of Vegetation Science, 24(5), 820–833. https://doi.org/10.1111/ jvs.12033
- May, R. M., & Leonard, W. J. (1975). Non-linear aspects of competition between 3 species. Siam Journal on Applied Mathematics, 29, 243–253.

- Mayfield, M. M., Boni, M. F., & Ackerly, D. D. (2009). Traits, habitats, and clades: Identifying traits of potential importance to environmental filtering. *The American Naturalist*, 174, E1–E22.
- Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093.
- Maynard, D. S., Bradford, M. A., Lindner, D. L., van Diepen, L. T. A., Frey,
  S. D., Glaeser, J. A., & Crowther, T. W. (2017). Diversity begets diversity in competition for space. *Nature Ecology & Evolution*, 1, 0156.
- Mazel, F., Davies, T. J., Gallien, L., Renaud, J., Groussin, M., Münkemüller, T., & Thuiller, W. (2016). Influence of tree shape and evolutionary time-scale on phylogenetic diversity metrics. *Ecography*, 39, 913–920.
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21, 178–185.
- McIntire, E. J. B., & Fajardo, A. (2014). Facilitation as a ubiquitous driver of biodiversity. *New Phytologist*, 201, 403–416.
- Miller, E. T., Farine, D. R., & Trisos, C. H. (2017). Phylogenetic community structure metrics and null models: A review with new methods and software. *Ecography*, 40, 461–477.
- Mittelbach, G. G., & Schemske, D. W. (2015). Ecological and evolutionary perspectives on community assembly. *Trends in Ecology and Evolution*, 30, 241–247.
- Molina-Venegas, R., & Roquet, C. (2014). Directional biases in phylogenetic structure quantification: A Mediterranean case study. *Ecography*, 37, 572–580.
- Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. (2011). Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, 14, 1211–1219.
- Morlon, H., Kefi, S., & Martinez, N. D. (2014). Effects of trophic similarity on community composition. *Ecology Letters*, 17, 1495–1506.
- Mouchet, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24, 867–876.
- Münkemüller, T., de Bello, F., Meynard, C. N., Gravel, D., Lavergne, S., Mouillot, D., ... Thuiller, W. (2012). From diversity indices to community assembly processes: A test with simulated data. *Ecography*, 35, 468–480.
- Münkemüller, T., Gallien, L., Lavergne, S., Renaud, J., Roquet, C., Abdulhak, S., ... Thuiller, W. (2014). Scale decisions can reverse conclusions on community assembly processes. *Global Ecology and Biogeography*, 23, 620–632.
- Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., ... Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, 20, 561–576.
- Pärtel, M., Szava-Kovats, R., & Zobel, M. (2011). Dark diversity: Shedding light on absent species. Trends in Ecology and Evolution, 26, 124–128.
- Patrick, C. J., & Brown, B. L. (2018). Species pool functional diversity plays a hidden role in generating  $\beta$ -diversity. *The American Naturalist*, 191, E159–E170.
- Pausas, J. G., & Verdu, M. (2010). The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *BioScience*, 60, 614–625.
- Pavoine, S., & Bonsall, M. B. (2011). Measuring biodiversity to explain community assembly: A unified approach. *Biological Reviews*, 68, 792-812.
- Pavoine, S., & Izsak, J. (2014). New biodiversity measure that includes consistent interspecific and intraspecific components. *Methods in Ecology and Evolution*, 5, 165–172.
- Pavoine, S., Love, M. S., & Bonsall, M. B. (2009). Hierarchical partitioning of evolutionary and ecological patterns in the organization of phylogenetically-structured species assemblages: Application to rockfish

(genus: Sebastes) in the Southern California Bight. Ecology Letters, 12, 898–908.

- Pavoine, S., Vela, E., Gachet, S., de Bélair, G., & Bonsall, M. B. (2011). Linking patterns in phylogeny, traits, abiotic variables and space: A novel approach to linking environmental filtering and plant community assembly. *Journal of Ecology*, *99*, 165–175.
- Peralta, G. (2016). Merging evolutionary history into species interaction networks. *Functional Ecology*, 30, 1917–1925.
- Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global biodiversity change: The bad, the good, and the unknown. *Annual Reviews*, 37, 25–50.
- Peres-Neto, P. R., Olden, J. D., & Jackson, D. A. (2001). Environmentally constrained null models: Site suitability as occupancy criterion. *Oikos*, 93, 110–120.
- Pérez-Ramos, I. M., Matías, L., Gómez-Aparicio, L., & Godoy, Ó. (2019). Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications*, 10, 2555.
- Perronne, R., Munoz, F., Borgya, B., Reboud, X., & Gaba, S. (2017). How to design trait-based analyses of community assembly mechanisms: Insights and guidelines from a literature review. *Perspectives in Plant Ecology Evolution and Systematics*, 25, 29–44.
- Pigot, A. L., & Etienne, R. S. (2015). A new dynamic null model for phylogenetic community structure. *Ecology Letters*, 18, 153–163.
- Pollock, L. J., Bayly, M. J., & Vesk, P. A. (2015). The roles of ecological and evolutionary processes in plant community assembly: The environment, hybridization, and introgression influence co-occurrence of *Eucalyptus*. The American Naturalist, 185, 784–796.
- Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., ... McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, *5*, 397–406.
- Pontarp, M., Brännström, Å., & Petchey, O. L. (2019). Inferring community assembly processes from macroscopic patterns using dynamic eco-evolutionary models and Approximate Bayesian Computation (ABC). Methods in Ecology and Evolution, 10, 450–460.
- Pontarp, M., Bunnefeld, L., Cabral, J. S., Etienne, R. S., Fritz, S. A., Gillespie, R., ... Hurlbert, A. H. (2019). The latitudinal diversity gradient: Novel understanding through mechanistic eco-evolutionary models. *Trends in Ecology and Evolution*, 34, 211–223.
- Pornon, A., Andalo, C., Burrus, M., & Escaravage, N. (2017). DNA metabarcoding data unveils invisible pollination networks. *Scientific Reports*, 7, 16828.
- Price, J., Tamme, R., Gazol, A., de Bello, F., Takkis, K., Uria-Diez, J., ... Pärtel, M. (2017). Within-community environmental variability drives trait variability in species-rich grasslands. *Journal of Vegetation Science*, 28, 303–312.
- Raevel, V., Violle, C., & Munoz, F. (2012). Mechanisms of ecological succession: Insights from plant functional strategies. *Oikos*, 121, 1761–1770.
- Rangel, T. F., Colwell, R. K., Graves, G. R., Fucikova, K., Rahbek, C., & Diniz, J. A. F. (2015). Phylogenetic uncertainty revisited: Implications for ecological analyses. *Evolution*, 69, 1301–1312.
- Ricklefs, R. E. (1987). Community diversity: Relative roles of local and regional processes. *Science*, 235, 167–171.
- Ricklefs, R. E. (2008). Disintegration of the ecological community. *The American Naturalist*, 172, 741–750.
- Saito, V. S., Cianciaruso, M. V., Siqueira, T., Fonseca-Gessner, A. A., & Pavoine, S. (2016). Phylogenies and traits provide distinct insights about the historical and contemporary assembly of aquatic insect communities. *Ecology and Evolution*, *6*, 2925–2937.
- Scheffer, M., & van Nes, E. H. (2006). Self-organized similarity, the evolutionary emergence of groups of similar species. Proceedings of the National Academy of Sciences USA, 103, 6230–6235.
- Schneider, F. D., Fichtmueller, D., Gossner, M. M., Güntsch, A., Jochum, M., König-Ries, B., ... Simons, N. K. (2019). Towards an ecological

trait-data standard. *Methods in Ecology and Evolution*, 10(12), 2006–2019. https://doi.org/10.1111/2041-210X.13288

- Shmida, A., & Ellner, S. (1984). Coexistence of plants with similar niches. *Vegetatio*, *58*, 29–55.
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18, 1406–1419.
- Spasojevic, M. J., Copeland, S., & Suding, K. N. (2014). Using functional diversity patterns to explore metacommunity dynamics: A framework for understanding local and regional influences on community structure. *Ecography*, 37, 939–949.
- Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*, 100, 652–661.
- Srivastava, D. S. (1999). Using local-regional richness plots to test for species saturation: Pitfalls and potentials. *Journal of Animal Ecology*, 68, 1–16.
- Swenson, N. G., Enquist, B. J., Pither, J., Thompson, J., & Zimmerman, J. K. (2006). The problem and promise of scale dependency in community phylogenetics. *Ecology*, 87, 2418–2424.
- Swenson, N. G., Erickson, D. L., Mi, X., Bourg, N. A., Forero-Montaña, J., Ge, X., ... Kress, W. J. (2012). Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. *Ecology*, 93, S112–S125.
- Taberlet, P., Prud'homme, S. M., Campione, E., Roy, J., Miquel, C., Shehzad, W., ... Coissac, E. (2012). Soil sampling and isolation of extracellular DNA from large amount of starting material suitable for metabarcoding studies. *Molecular Ecology*, 21, 1816–1820.
- Tedersoo, L., Bahram, M., Cajthaml, T., Põlme, S., Hiiesalu, I., Anslan, S., ... Abarenkov, K. (2016). Tree diversity and species identity effects on soil fungi, protists and animals are context dependent. *ISME Journal*, 10, 346–362.
- Thuiller, W., Gallien, L., Boulangeat, I., de Bello, F., Münkemüller, T., Roquet, C., & Lavergne, S. (2010). Resolving Darwin's naturalization conundrum: A quest for evidence. *Diversity and Distributions*, 16, 461–475.
- Tikhonov, G., Abrego, N., Dunson, D., & Ovaskainen, O. (2017). Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context. *Methods in Ecology and Evolution*, 8, 443–452.
- Trisos, C. H., Petchey, O. L., & Tobias, J. A. (2014). Unraveling the interplay of community assembly processes acting on multiple niche axes across spatial scales. *The American Naturalist*, 184, 593–608.
- Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., ... Mazel, F. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, 92, 698–715.
- Turcotte, M. M., & Levine, J. M. (2016). Phenotypic plasticity and species coexistence. Trends in Ecology and Evolution, 31, 803–813.
- Ulrich, W., & Gotelli, N. J. (2013). Pattern detection in null model analysis. Oikos, 122, 2–18.
- Valiente-Banuet, A., & Verdu, M. (2007). Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters*, 10, 1029–1036.
- Vamosi, S. M., Heard, S. B., Vamosi, J. C., & Webb, C. O. (2009). Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology*, 18, 572–592.
- Van der Plas, F., Anderson, T. M., & Olff, H. (2012). Trait similarity patterns within grass and grasshopper communities: Multitrophic community assembly at work. *Ecology*, 93, 836–846.
- Van der Plas, F., Janzen, T., Ordonez, A., Fokkema, W., Reinders, J., Etienne, R. S., & Olff, H. (2015). A new modeling approach estimates the relative importance of different community assembly processes. *Ecology*, 96, 1502–1515.

- Vandermeer, J. (2011). Intransitive loops in ecosystem models: From stable foci to heteroclinic cycles. *Ecological Complexity*, *8*, 92–97.
- Vellend, M. (2010). Conceptual synthesis in community ecology. The Quarterly Review of Biology, 85, 183–206.
- Villeger, S., & Mouillot, D. (2008). Additive partitioning of diversity including species differences: A comment on Hardy & Senterre (2007). *Journal of Ecology*, 96, 845–848.
- Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., ... Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology and Evolution*, 27, 244–252.
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! Oikos, 116, 882–892.
- Wang, D. Z., Kong, L. F., Li, Y. Y., & Xie, Z. X. (2016). Environmental microbial community proteomics: Status, challenges and perspectives. *International Journal of Molecular Sciences*, 17, 1275.
- Warren, D. L., Cardillo, M., Rosauer, D. F., & Bolnick, D. I. (2014). Mistaking geography for biology: Inferring processes from species distributions. *Trends in Ecology and Evolution*, 29, 572–580.
- Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. Annual Review of Ecology and Systematics, 33, 475–505.
- Weinstein, B. G., Tinoco, B., Parra, J. L., Brown, L. M., McGuire, J. A., Stiles, F. G., & Graham, C. H. (2014). Taxonomic, phylogenetic, and trait beta diversity in South American Hummingbirds. *The American Naturalist*, 184, 211–224.
- Weithoff, G., Rocha, M. R., & Gaedke, U. (2015). Comparing seasonal dynamics of functional and taxonomic diversity reveals the driving forces underlying phytoplankton community structure. *Freshwater Biology*, 60, 758–767.
- Willis, C. G., Halina, M., Lehman, C., Reich, P. B., Keen, A., McCarthy, S., & Cavender-Bares, J. (2010). Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography*, 33, 565–577.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027–2027.
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.

- Wüest, R. O., Münkemüller, T., Lavergne, S., Pollock, L. J., & Thuiller, W. (2018). Integrating correlation between traits improves spatial predictions of plant functional composition. *Oikos*, 127, 472–481.
- Yang, J., Cao, M., & Swenson, N. G. (2018). Why functional traits do not predict tree demographic rates. *Trends in Ecology and Evolution*, 33, 326–336.
- Zambrano, J., Iida, Y., Howe, R., Lin, L., Umana, M. N., Wolf, A., ... Swenson, N. G. (2017). Neighbourhood defence gene similarity effects on tree performance: A community transcriptomic approach. *Journal of Ecology*, 105, 616–626.
- Zurell, D., Berger, U., Cabral, J. S., Jeltsch, F., Meynard, C. N., Münkemüller, T., ... Grimm, V. (2010). The virtual ecologist approach: Simulating data and observers. *Oikos*, 119, 622–635.
- Zurell, D., Pollock, L. J., & Thuiller, W. (2018). Do joint species distribution models reliably detect interspecific interactions from co-occurrence data in homogenous environments? *Ecography*, 41, 1812–1819.

## BIOSKETCH

Tamara Münkemüller studies the ecological processes that drive community assembly, the resilience of communities to environmental change and feedbacks between the plant and soil compartment. Her work builds on different types of models (from mechanistic simulation models to statistical models integrating multiple species) and on different types of data (from observational data to experimental data).

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Münkemüller T, Gallien L, Pollock LJ, et al. Dos and don'ts when inferring assembly rules from diversity patterns. *Global Ecol Biogeogr.* 2020;29:1212–1229. https://doi.org/10.1111/geb.13098