

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

Tamara Münkemüller, Laure Gallien, Laura Pollock, Ceres Barros, Marta Carboni, Loïc Chalmandrier, Florent Mazel, Karel Mokany, Cristina Roquet, Jan Smyčka, et al.

## ▶ To cite this version:

Tamara Münkemüller, Laure Gallien, Laura Pollock, Ceres Barros, Marta Carboni, et al.. Do's and don'ts when inferring assembly rules from diversity patterns. Global Ecology and Biogeography, 2020, 29 (7), pp.1212-1229. 10.1111/geb.13098 . hal-02617926

## HAL Id: hal-02617926 https://hal.science/hal-02617926

Submitted on 25 Jun 2020

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31	Acknowledgements
32	The first outline of the manuscript was developed during a workshop financed by the European
33	Research Council under the European Community's Seven Framework Program FP7/2007-2013 Grant
34	Agreement no. 281422 (TEEMBIO). TM and WT acknowledge funding from the French Agence
35	Nationale de la Recherche (ANR) through the GlobNets project (ANR-16-CE02-0009) and the
36	GAMBAS project (ANR-18-CE02-0025). F.M. was supported by a Banting postdoctoral fellowship.
37	The LECA is part of LabexOSUG@2020 (ANR10 LABX56).

## 38 Biosketch

- 39 Tamara Münkemüller studies the ecological processes that drive community assembly, the resilience
- 40 of communities to environmental change and feedbacks between the plant and soil compartment. Her
- 41 work builds on different types of models (from mechanistic simulation models to statistical models
- 42 integrating multiple species) and on different types of data (from observational data to experimental
- 43 data).
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- 45

#### 46 Abstract

Aim: More than ever, ecologists seek to understand how species are distributed and have 47 assembled into communities using the 'filtering framework'. This framework hypothesizes that 48 49 local assemblages result from a series of abiotic and biotic filters applied to regional species 50 pools, and that these filters leave predictable signals in observed diversity patterns. In theory, 51 statistical comparisons of expected and observed patterns enable data-driven tests of assembly 52 processes. However, so far this framework has fallen short in delivering generalizable 53 conclusions, challenging whether (and how) diversity patterns can be used to better characterize 54 and understand underlying assembly processes.

55 **Methods:** By synthesizing the previously raised critiques and suggested solutions in a 56 comprehensive way, we identify ten pitfalls that can lead to flawed interpretations of  $\alpha$ -diversity 57 patterns, summarize solutions developed to circumvent these pitfalls and provide general 58 guidelines.

59 Results: We find that most issues arise from an overly simplistic view of potential processes 60 that influence diversity patterns, that is often motivated by practical constraints on study design, 61 focal scale and methodology. We outline solutions for each pitfall, such as methods spanning 62 over spatial, environmental or phylogenetic scales, and suggest guidelines for best scientific 63 practices in community ecology. Among key future challenges are the integration of 64 mechanistic modeling and multi-trophic interactions.

65 Conclusion: Our conclusion is that the filtering framework still holds promise, but only if 66 researchers successfully navigate major pitfalls, foster the integration of mechanistic modelling 67 and multi-trophic interactions and directly account for uncertainty in their conclusions.

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Keywords: Community processes, overdispersion, clustering, convergence, divergence, trait
diversity, phylogenetic diversity, simulation model.

## 71 **1. Introduction**

72 The diversity of ecological communities is increasingly compromised by ongoing global changes (Pereira, Navarro & Martins, 2012). Mitigating these threats requires to understand the 73 74 distribution of diversity along geographic, abiotic and biotic gradients and the underlying 75 assembly processes (Lavergne, Mouquet, Thuiller & Ronce, 2010; HilleRisLambers, Adler, Harpole, Levine & Mayfield, 2012). A focal question is whether abiotic constraints or rather 76 77 biotic interactions drive the taxonomic and trait structure of communities. In community 78 ecology, this question has historically been addressed by experiments, with the limitation that 79 these methods are typically constrained to small scales and few species. Thus, to study 80 community assembly at large spatial scales, ecologists have assembled increasingly large 81 community datasets spanning broad spatial extents with both trait and phylogenetic information 82 (Diaz, Kattge, Cornelissen, Wright, Lavorel et al., 2016; Kunstler, Falster, Coomes, Hui, 83 Kooyman et al., 2016, see Fig. 1a, b). Trait diversity describes the within-community variation 84 of species' characteristics relevant for their performance, while phylogenetic diversity describes the evolutionary history. Combining data on distribution, traits and phylogeny in a meaningful 85 way holds promise for a revolution in community ecology by opening the door to large-scale 86 87 analyses of assembly processes (Webb, Ackerly, McPeek & Donoghue, 2002; Mc Gill, Enquist, 88 Weiher & Westoby, 2006). The idea is to harness the information on species niches contained 89 in phylogenetic and trait data. For example, under the assumption that a set of traits represents 90 species' niches well, we could move from a simple species-based description of communities 91 towards a functional characterization, using community weighted mean traits as an estimate of 92 the community niche optimum, and trait diversity as an estimate of species niche overlap (see 93 below for more detail, Violle, Navas, Vile, Kazakou, Fortunel et al., 2007; Kraft, Valencia & 94 Ackerly, 2008).

In practice, this idea has mostly been implemented through the filtering framework 95 96 (Diamond, 1975; Keddy, 1992) that builds on the assumption that both abiotic (e.g. climate or 97 land use) and biotic factors (e.g. competition) define species' carrying capacities and/or growth 98 rates and thus influence their occurrences and abundances (Fig. 1d). The abiotic conditions 99 define the environmental filters selecting species from a regional species pool, originally shaped 100 by biogeographical history (Carstensen, Lessard, Holt, Krabbe Borregaard & Rahbek, 2013), 101 into the local species pool containing all species adapted to the local conditions. Then, biotic 102 interactions influence which species from the local pool can eventually coexist in the 103 community (Shmida & Ellner, 1984; Chesson, 2000). This deterministic view assumes that 104 different ecological filters should lead to distinct and predictable patterns in diversity and 105 composition. Comparing these expected patterns with observed diversity across abiotic and 106 biotic gradients should then allow for deducing underlying community assembly processes, 107 thus moving large-scale community ecology from a purely descriptive discipline to a more 108 process-based understanding (Leibold, Holyoak, Mouquet, Amarasekare, Chase et al., 2004; 109 Vellend, 2010; Morin, Fahse, Scherer-Lorenzen & Bugmann, 2011).

110 Relatively early on, studies that began to apply the framework used trait diversity patterns 111 (e.g. including behavioural, life-history, morphological and physiological traits, Violle et al., 112 2007) and phylogenetic relatedness (Webb et al., 2002) to account for species' niche 113 similarities. Doing so assumes that measured traits are relevant for assembly processes 114 (Mayfield, Boni & Ackerly, 2009) and that closely related species in the phylogeny are 115 ecologically more similar than distantly related ones (Burns & Strauss, 2011). Trait-phylogeny 116 relationships different from these assumptions would lead to different relationships between 117 niche similarity and phylogenetic relatedness patterns (Webb et al., 2002). To infer assembly 118 processes, observed patterns of trait and phylogenetic diversity within a community (i.e.  $\alpha$ -119 diversity) are commonly compared to null expectations (i.e. patterns under random assembly,

Fig. 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 (Fig. 1b, community A, see also Appendix S1 in Supporting Information). Conversely, high trait or phylogenetic  $\alpha$ -diversity can reveal ecological processes that result in limiting similarity, such as competition due to niche overlap (Fig. 1b, community B, see also Appendix S1, Mac Arthur & Levins, 1967).

126 An increasingly large number of studies apply the filtering framework (see Appendix S2). 127 However, first reviews and meta-analyses of empirical (Emerson and Gillespie 2008, Vamosi 128 et al. 2009, Götzenberger et al. 2012, HilleRisLambers et al. 2012) and simulation experiments 129 (Münkemüller, de Bello, Meynard, Gravel, Lavergne et al., 2012; Gallien, Carboni & 130 Münkemüller, 2014; Miller, Farine & Trisos, 2017) have strongly dampened the enthusiasm, 131 as they demonstrate that no simple general conclusion can be drawn from the sole observation 132 of trait and phylogenetic diversity patterns. One prominent example is the ongoing debate on 133 the role of competition: While the filtering framework often fails to pinpoint signals of 134 competition, theoretical and empirical research underscores its importance even at broad scales 135 (see Appendix S3 for a detailed discussion). Seemingly, we are not much further than 20 years 136 ago when Lawton concluded that community ecology is a 'mess' (Lawton, 2000). The lingering 137 question is why the filtering framework does not provide general results even though it is built 138 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 (Fig. 1). While 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, Burgio, Carlucci, Palmquist, Parada et al., 2016; Pontarp, Brännström & Petchey, 2019), an overarching synthesis and a set of general guidelines for correctly 145 applying the filtering framework is still lacking. Building on existing work, we provide a novel 146 comprehensive and structured overview of the different pitfalls and the solutions that have been 147 developed (Tab. 1). We use the ongoing debate on the ecological importance of biotic 148 interactions at large scales as an exemplary showcase (Appendix S3). Based on the integration 149 of reviewed work we then suggest step-by-step guidelines for correctly applying the filtering 150 framework that should result in better interpretable results in community ecology.

151

## 152 **2.** Common Pitfalls

Applying the filtering framework requires (1) choosing the study design with focal spatial, environmental and organism-level scales, (2) collecting information and (3) choosing methodological approaches relevant to the research question. Finally, (4) 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.

158

## 159 2.1 Study design

160 The key aim of studies applying the filtering framework is to identify non-random processes in 161 observed diversity patterns. One of the most discussed cases of non-random diversity patterns 162 that exist despite the evident absence of directional environmental or biotic filters are neutral 163 dynamics. Neutral theory suggests that many of the diversity patterns observed in nature may 164 result from purely stochastic demographic processes that emerge from strong competition and 165 dispersal limitation of functionally equivalent species and thus without any directional filter 166 (Hubbell, 2001; Münkemüller et al., 2012; Boucher, Thuiller, Davies & Lavergne, 2014). 167 However, whether neutral dynamics lead to non-random diversity patterns depends on the focal 168 scale of a study, and this is true for directional assembly processes as well. It is thus a pitfall to assume that: (P1) spatial, environmental and organism-level scale choices have no influence onstudy results (Fig. 1).

(P1) Certain processes may never be detected if we chose an inappropriate scale. First, 171 ignoring large-scale factors, such as climate gradients, dispersal barriers, historical 172 173 contingencies and evolutionary history can mask outcomes of smaller-scale processes such as 174 local abiotic filters and competition (Cavender-Bares, Keen & Miles, 2006; Swenson, Enquist, 175 Pither, Thompson & Zimmerman, 2006; Vamosi, Heard, Vamosi & Webb, 2009; Cardinale, 176 Gross, Fritschie, Flombaum, Fox et al., 2013). Second, ignoring small-scale factors, such as 177 intraspecific variation in trait values (Albert, de Bello, Boulangeat, Pellet, Lavorel et al., 2012; 178 Siefert, Violle, Chalmandrier, Albert, Taudiere et al., 2015) and the fine scale spatial 179 arrangement of individuals (Diekmann, Law & Metz, 2000), can lead to overlooking the 180 underlying processes as their effects may not scale up to large-scale diversity patterns (Thuiller, 181 Gallien, Boulangeat, de Bello, Munkemuller et al., 2010; Araujo & Rozenfeld, 2014; Turcotte 182 & Levine, 2016). For example, it has been shown that trait plasticity increases niche differences 183 in communities and thereby stabilize coexistence and promote diversity (Pérez-Ramos, Matías, 184 Gómez-Aparicio & Godoy, 2019). This biotic filtering mechanism would remain unnoticed 185 when relying solely on species' mean traits. Third, ignoring small-scale environmental variation 186 within the community and study site may lead to high diversity in low-resolution studies and 187 can then be easily misinterpreted as a signal of limiting similarity (Price, Tamme, Gazol, Bello, 188 Takkis et al., 2017).

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## 190 2.2 Collecting information

191 Trait and phylogenetic diversity are often used as proxies for niche overlap, yet this common
192 practice is often challenged (Cadotte, 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 alwaysgood proxies for species niche overlap (Fig. 1).

195 (P2) A first set of questions with regard to trait diversity is whether we are able to identify 196 and measure the traits of ecological relevance for each (Mc Gill et al., 2006; Funk, Larson, 197 Ames, Butterfield, Cavender-Bares et al., 2017), whether traits are closely enough linked to 198 species niches (D'Andrea, Ostling & O'Dwyer James, 2018) and whether we can avoid 199 irrelevant traits that might confound the patterns and lead us to spurious conclusions (Kraft, 200 Godoy & Levine, 2015). This task is facilitated by former work (e.g. Leps, de Bello, Lavorel 201 & Berman, 2006) and some more recent advancements: For some clades and ecological 202 processes, guidelines for the identification of relevant traits and database standards are now 203 available (Luck, Lavorel, McIntyre & Lumb, 2012; Diaz et al., 2016; Gravel, Albouy & 204 Thuiller, 2016; Schneider, Jochum, Le Provost, Ostrowski, Penone et al., 2018), open-access 205 databases are improving (Kattge, Díaz, Lavorel, Prentice, Leadley et al., 2011; Wilman, 206 Belmaker, Simpson, de la Rosa, Rivadeneira et al., 2014), and trait syndromes (i.e. observed 207 covariations in traits) can help to reduce trait space to a few relevant dimensions (Wright, Reich, Westoby, Ackerly, Baruch et al., 2004; Diaz et al., 2016). However, in many aspects, trait 208 209 science still remains incomplete (Yang, Cao & Swenson, 2018): (i) frameworks to link traits 210 and niche dimensions are still under development for most clades (e.g. for fungi, Crowther, 211 Maynard, Crowther, Peccia, Smith et al., 2014), (ii) even in well-studied clades, some traits are 212 better studied than others (e.g. plant leaf traits over root traits, Funk et al., 2017), (iii) it is not 213 obvious at what level traits need to be measured (individual or population, Albert et al., 2012), 214 and (iv) the relative importance of traits can change over the life cycle (Kunstler et al., 2016). 215 Another question is whether it is more informative to analyse each trait separately or in 216 combination. The main argument for the former is that different traits may drive different 217 processes, and that analyses should thus be process and trait specific (Bernard-Verdier, Navas, 218 Vellend, Violle, Fayolle et al., 2012; Gross, Boerger, Soriano-Morales, Le Bagousse-Pinguet, 219 Quero et al., 2013; Spasojevic, Copeland & Suding, 2014). On the other hand, ecological niches 220 are multidimensional and, consequently, multi-trait diversity is more likely to capture niche 221 overlap between species across multiple niche dimensions (Kraft et al., 2015). Moreover, traits 222 are correlated as a result of physiological trade-offs. Ignoring these trade-offs may lead to 223 spurious conclusions (Wüest, Münkemüller, Lavergne, Pollock & Thuiller, 2018). However, 224 recent work shows that at least some community patterns are robust to the negligence of a 225 relevant niche axis (D'Andrea et al., 2018).

226 Using phylogenetic diversity in the filtering approach assumes that phylogenetic relatedness 227 is a good proxy for overlap in the multidimensional niche space (Burns & Strauss, 2011; 228 Anacker & Strauss, 2016). However, phylogeny does not always represent relationships of traits 229 that are relevant for species' niches (Blomberg, Garland & Ives, 2003; Saito, Cianciaruso, 230 Siqueira, Fonseca-Gessner & Pavoine, 2016), and phylogenetic signal of relevant traits should 231 be tested, rather than assumed. Yet, this poses severe methodological problems (as discussed 232 in detail in Gerhold et al., 2015). Moreover, relevant traits for this test are often not available 233 and if they are available it is not evident how they should be combined to represent species 234 'niches' and how strong the signal should be (Mason & Pavoine 2013). Most importantly, if all 235 niche-relevant traits were known and available, phylogenetic proxies would not be needed.

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### 237 2.3 Methodological approach

It has been demonstrated that different methodological choices can give different answers (Münkemüller, Gallien, Lavergne, Renaud, Roquet et al., 2014; Perronne, Munoz, Borgya, Reboud & Gaba, 2017). Thus, pitfalls three, four and five 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 obviousand straightforward (Fig. 1).

244 (P3) A common pitfall is to assume that different diversity indices can be used interchangeably. While some diversity indices are indeed highly redundant, others quantify 245 246 different aspects of diversity (Mouchet, Villéger, Mason & Mouillot, 2010; Tucker, Cadotte, 247 Carvalho, Davies, Ferrier et al., 2017). Changing the diversity index can thus change or even 248 invert the observed pattern of diversity (Chalmandrier, Münkemüller, Lavergne & Thuiller, 249 2015; Mazel, Davies, Gallien, Groussin, Münkemüller et al., 2016; Perronne et al., 2017). 250 Indices can differ in whether they account for (i) species abundances or not (Hill, 1973; Chao, 251 Chiu & Jost, 2010; Leinster & Cobbold, 2012), (ii) intraspecific variability or not (Violle, 252 Enquist, McGill, Jiang, Albert et al., 2012; Pavoine & Izsak, 2014) (iii) different phylogenetic 253 (e.g. species, family vs. order level) or functional scales (e.g. species vs. functional groups), 254 and (iv) different dimensions of the structure of assemblages, such as richness, divergence and regularity (Villeger & Mouillot, 2008; Tucker et al., 2017). While classification schemes for 255 256 available diversity metrics can help choose an appropriate index (Pausas & Verdu, 2010; Pavoine, Vela, Gachet, de Bélair & Bonsall, 2011; Tucker et al., 2017), it is not always evident 257 258 which index is the most appropriate for a specific research question.

259 (P4) The species pool is generally defined as the set of all species existing in a given region 260 that could colonize a focal community (Srivastava, 1999), but other definitions exist (Cornell 261 & Harrison, 2014). In practice, the species pool often is the list of species in the studied dataset, 262 often the result of practical constraints rather than ecological hypotheses. However, ideally, it 263 should be defined based on the focal filtering process that the study sets out to test. Thus, it 264 should include all species that would be selected in the community both with the focal process 265 (filtering) and without it (randomly), but should not include any additional species resulting 266 from another process not of interest. The choice of the species pool affects the null hypothesis

267 associated with the null model and consequently can change the results of the analyses (Lessard, 268 Belmaker, Myers, Chase & Rahbek, 2012; Pigot & Etienne, 2015). For example, competition 269 can be overlooked when it resulted in the complete exclusion of species from the pool ("dark 270 diversity", Pärtel, Szava-Kovats & Zobel, 2011). In addition, the spatial extent at which the 271 species pool is defined changes the detectability of certain assembly rules. Typically, signals of 272 competition are prone to be overwritten by strong environmental filtering when the study area 273 includes steep environmental gradients (Willis, Halina, Lehman, Reich, Keen et al., 2010). 274 Importantly, not only species richness but also trait diversity in the species pool influences 275 patterns of diversity in local communities (Patrick & Brown, 2018).

276 (P5) The randomization scheme used to create a null distribution of diversity values also has 277 a critical impact on the outcome of the analysis (Gotelli, 2000; Miller et al., 2017). 278 Randomization breaks down patterns in the data that are caused by ecological processes. 279 Ideally, a chosen randomization algorithm would only break down the patterns that are 280 supposed to be generated by the process(es) of interest. However, algorithms often randomize 281 several patterns at the same time, including those that are not of interest, and thus test several 282 null hypotheses simultaneously. A significant result indicates only that at least one of the null 283 hypotheses can be rejected, but we do not know which one. For example, a high signal of 284 phylogenetic  $\alpha$ -diversity obtained from a null model randomizing the sites can indicate 285 competition but also that the abundance distribution in the phylogenetic tree is non-random 286 (testing implicitly another null hypothesis, Hardy, 2008). Thus, the interpretation of a non-287 random pattern is not always straightforward. This problem of non-specific randomization 288 algorithms has launched the development of more constraining algorithms (Hardy, 2008; Miller 289 et al., 2017), often at the expense of statistical power.

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#### 291 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 only emerge from one single process, (P7) that one major process dominates the observed pattern and (P8) that biotic interactions are simple (Fig. 1).

299 (P6) Traditionally, clustered diversity patterns (i.e. coexisting species being in phylogenetic 300 and trait space more similar than expected by chance) have been attributed to an environmental 301 filter (Fig. 1). However, competitive hierarchies can produce a similar pattern (Ågren & 302 Fagerström, 1984; Mayfield & Levine, 2010; Kunstler et al., 2016, Appendix S1). Conversely, symmetric niche competition is assumed to produce overdispersed diversity (i.e. co-existing 303 304 species being in phylogenetic and trait space more distant than expected by chance), but 305 facilitation can also produce overdispersed diversity patterns (Valiente-Banuet & Verdu, 2007; 306 McIntire & Fajardo, 2014, Appendix S1).

307 (P7) When multiple processes interplay, interpreting biodiversity patterns can be misleading 308 (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 309 310 community (e.g. rare vs. common species, Maire, Gross, Börger, Proulx, Wirth et al., 2012). 311 For example, signals of environmental filtering are often stronger than those of competition and 312 thus competition can be easily overlooked as an important driver of assembly (e.g. the overall 313 diversity pattern is clustered while environmentally binned sub-tests would reveal 314 overdispersed diversity patterns, Chalmandrier, Münkemüller, Gallien, de Bello, Mazel et al., 315 2013; Gallien et al., 2014).

316 (P8) Ignoring the complex nature of biotic interactions and assuming that the only relevant 317 biotic filter is symmetric competition is another common pitfall. After Mayfield and Levine 318 (2010) highlighted that large parts of coexistence theory were commonly ignored, more and 319 more contributions have developed expectations for diversity patterns structured by biotic 320 interactions other than symmetric niche competition (HilleRisLambers et al., 2012; Adler, 321 Fajardo, Kleinhesselink & Kraft, 2013, Appendix S1). For example, for hierarchical 322 competition, clustering of species in trait or phylogenetic space could emerge from competition 323 for one limiting resource because only species with adapted traits for this resource will survive 324 (e.g. when species compete for light only tall species will survive, Mayfield & Levine, 2010). 325 In contrast, overdispersion is expected to emerge from competition for multiple resources when 326 the respective adaptive traits are different for the different resources (Scheffer & van Nes, 327 2006). Contrasting diversity patterns are also expected to depend on the type of facilitative 328 interactions that take place in a community (Appendix S1). For example, if species facilitate 329 each other symmetrically via the same mechanism (e.g. flowers of similar colour attract 330 common pollinators; mutualism), species with similar traits should coexist, leading to trait 331 clustering. However, if one "benefactor" species facilitates others with different life strategies 332 (e.g. commensalism), species with different traits could coexist, resulting in overdispersion or 333 random patterns (Valiente-Banuet & Verdu, 2007; Gallien, Zurell & Zimmermann, 2018). 334 Furthermore, complex indirect interactions, such as multi-species indirect facilitation and 335 intransitive competition (competition as in the rock-paper-scissors game, without competitive 336 hierarchies; Gilpin, 1975; May & Leonard, 1975), may also be important drivers of community 337 structure (Allesina & Levine, 2011; Vandermeer, 2011). For these interactions it may be 338 impossible to generate clear expectations for emerging diversity patterns, especially when 339 multispecies coexistence processes are not the mere sum of their pairwise interaction outcomes (Barabas, Michalska-Smith & Allesina, 2016; Gallien, 2017; but see Maynard, Bradford, 340

Lindner, van Diepen, Frey et al., 2017). Moreover, multi-trophic biotic interactions are so far largely ignored (Grilli, Barabas, Michalska-Smith & Allesina, 2017). There are a few first example studies investigating bipartite interaction networks (Van der Plas, Anderson & Olff, 2012; Ibanez, Arene & Lavergne, 2016). 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).

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349 Beyond these pitfalls inherent to the investigated processes, there are further pitfalls 350 associated to unrelated processes but influential to the studied patterns and thus to the final 351 conclusions. A common misconception of the filtering framework is that we can test for a 352 selection of ecological assembly processes while ignoring background factors. In reality, 353 biogeography, evolution and ecological processes jointly influence species' distributions (Warren, Cardillo, Rosauer & Bolnick, 2014). Common pitfalls are to assume that (P9) 354 355 dispersal and historical contingencies can be ignored and that (P10) communities are at 356 equilibrium (Fig. 1).

357 (P9) While they can shape the richness and functional-trait diversity of regional species pools (see also P4), diversification and historical contingencies are commonly ignored in 358 359 community ecology studies (Warren et al., 2014). These processes are often thought to act at 360 regional rather than local scales (i.e. driving the evolution of regional species pools), but long-361 standing evidence shows that this simplistic dichotomy of different processes acting exclusively 362 at particular scales is fraught with exceptions in the real world (Johnson & Stinchcombe, 2007). 363 Regional species pools and the processes that led to their establishment can sometimes be more 364 important for local community composition than assembly processes (Ricklefs, 1987; 365 Chalmandrier, Albouy & Pellissier, 2017; Lawing, Eronen, Blois, Graham & Polly, 2017). In some cases, both evolutionary and ecological processes occur at the same local community scale (Pollock, Bayly & Vesk, 2015). This problem is even more complicated by the fact that some ecological and biogeographical processes can create the same taxonomic or phylogenetic patterns. For example, from a community ecology standpoint, 'phylogenetic dispersion' in a clade can be interpreted as a sign of competitive exclusion, while from a biogeographic perspective, this same pattern can be interpreted as allopatric speciation (Warren et al., 2014).

372 (P10) The fundamental assumption that communities are at equilibrium underlies most 373 efforts to understand community assembly (Gerhold et al., 2015). However, in the era of the 374 Anthropocene, many observed communities are already exposed to changing environmental 375 conditions and/or the invasion of alien species and thus represent a transient phase. In a transient 376 phase, rapid changes in abiotic and biotic conditions can lead species to not completely fill their 377 potential range, or to occur in unsuitable habitats (Ackerly, 2003). Thus, in these transient 378 communities current diversity patterns may not well reflect ongoing assembly processes but 379 rather responses to past conditions (Mittelbach & Schemske, 2015; Chang & HilleRisLambers, 380 2016). For example, a recent study shows that climatic legacies can explain a relevant part of 381 the variation in current community assembly (Delgado-Baquerizo, Eldridge David, Travers 382 Samantha, Val, Oliver et al., 2018).

383

#### 384 **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 in Appendix S3 on the importance of competition at large spatial scales as a showcase). 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 (Tab. 1). Next, we highlight novel methods, theoretical advances and newly available data that could prove their utility for communityassembly questions.

393

## 394 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 (Fig. 2). Based on these, the study design can be developed.

400 The scale dependence of assembly processes was recognized early on, with most studies 401 focusing on the effects of spatial scales (Kraft & Ackerly, 2010; Carboni, Münkemüller, 402 Gallien, Lavergne, Acosta et al., 2013), less on the level of description of organisms (e.g. 403 functional group vs. species vs. individual level) or different life-stages (Conti, Block, Parepa, 404 Münkemüller, Thuiller et al., 2018), and very few on temporal scales (Chang & 405 HilleRisLambers, 2016). To deal with scale dependence, studies have compared diversity 406 patterns across different scales to separately test for signals of small- vs. large-scale processes 407 (solution S1, Tab. 1). A straightforward approach is a sampling design across different spatial 408 grains and extents, levels of description of organisms and temporal scales (Cavender-Bares et 409 al., 2006; Weithoff, Rocha & Gaedke, 2015), including space-for-time substitutions (Bhaskar, 410 Dawson & Balvanera, 2014). Sampling and studying diversity patterns across several scales 411 (either using a multi-scale sampling design or *a posteriori* data aggregation approaches) is an 412 obvious solution when scale choices are important but not easy to make (pitfall P1), for example 413 when influential background factors are scale-dependent as well (e.g. dispersal, P9). This 414 approach can also help to disentangle processes that create similar patterns at one scale but contrasting patterns at others (P6, P8), and to identify the interplay of processes that act at 415

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 (Cavender-Bares et al., 2006; Carboni et al., 2013).

419 Applying the filtering approach to dynamic response variables (S2, Tab. 1), such as 420 demographic rates, is a well-known solution for several pitfalls but mostly hampered by data 421 availability. Instead of asking 'do species occur more often with similar or different species?' 422 we ask 'do species perform better with similar or different species in the neighbourhood?', 423 thereby relating the measured performance of focal individuals to their trait and phylogenetic 424 (dis)similarity with their neighbours. At larger spatial scales this has been tested in systems 425 where time-series of species performance are available, like in long-term forest plots (Kunstler, 426 Lavergne, Courbaud, Thuiller, Vieilledent et al., 2012), or in systems that provide natural 427 experiments, such as invaded communities (Carboni, Münkemüller, Lavergne, Choler, Borgy 428 et al., 2016). More recently, researchers set up experiments to test for the link between 429 community assembly and trait or phylogenetic diversity patterns (Fayle, Eggleton, Manica, 430 Yusah & Foster, 2015; Conti et al., 2018). Experimentally manipulating the environmental and 431 biotic factors that drive assembly filters allows controlling a number of influential background 432 factors (P9-10) and scale dependencies (P1). In such experiments, individual success is not 433 approximated by a single presence or abundance measure, but is captured via demographic rates 434 at different stages (Li, Guo, Cadotte, Chen, Kuang et al., 2015; Conti et al., 2018). Performance 435 is often more responsive to ecological drivers than survival and may thus be more suited to 436 measure responses in non-equilibrium situations. Moreover, long time-series can reveal insights 437 into community assembly and provide solutions for non-equilibrium situations (P9-10). For 438 example, time series can be used to estimate the relative importance of environmental filtering, 439 historical legacies and new biotic interactions in the species composition of a community in the 440 face of past, current, and future climates (Blonder, Nogues-Bravo, Borregaard, Donoghue, Jorgensen et al., 2015). They can also be used to better understand the turnover of processes
during succession (Letten, Keith & Tozer, 2014).

443

## 444 3.2 Collecting information

445 Because numerous pitfalls can bias results when focusing solely on one partial aspect of biodiversity (e.g. P2-3), community ecologists started early on to consider complementary 446 447 facets of diversity (S3, Tab. 1), by comparing diversity indices between phylogenetic scales and 448 at different levels of trait similarity, e.g. close to the root vs. tips in a trait-based tree (Swenson, 449 Erickson, Mi, Bourg, Forero-Montana et al., 2012; Graham, Storch & Machae, 2018), between 450 richness, regularity and divergence components (Raevel, Violle & Munoz, 2012), as well as by 451 varying the importance of species abundances (Chalmandrier et al., 2015; Götzenberger, Botta-452 Dukát, Lepš, Pärtel, Zobel et al., 2016) and intraspecific variability (Pavoine & Izsak, 2014; 453 Chalmandrier, Münkemüller, Colace, Renaud, Aubert et al., 2017). Guidelines for choosing the 454 right trait and phylogenetic information come from studies from related fields. For example, 455 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 456 457 drive different processes, there is now reasonable consensus that analysing multiple traits 458 separately can uncover important signals in the data that would have remained undetected if all 459 traits had been analysed together (Saito et al., 2016). Moreover, complementing trait diversity 460 indices with community-weighted mean (CWM) traits can inform about differences in 461 functional strategies between communities and thus can allow teasing apart drivers that leave 462 the same signal in trait diversity. For example, while both environmental filtering for infertile 463 soils and hierarchical competition for light should result in clustering (Appendix S1), the former 464 should select for slow-growing, small species while the latter should select for fast-growing, 465 taller species (Kunstler et al., 2012).

466 For phylogeny-based analyses, approaches that account for the uncertainty of the phylogeny 467 (Rangel, Colwell, Graves, Fucikova, Rahbek et al., 2015) and the uncertainty concerning the 468 underlying trait evolution process (Gerhold et al., 2015) can aid in more correctly interpreting 469 phylogenetic pattern analyses. Ultimately, because trait and phylogenetic information might not 470 give equivalent information on species niches (P2), considering them jointly probably 471 represents the most sensible course of action. For example, one may complement phylogenetic 472 measures with trait information (Pavoine & Bonsall, 2011; Lopez et al., 2016; de Bello, 473 Smilauer, Diniz, Carmona, Lososova et al., 2017; Gianuca, Declerck, Cadotte, Souffreau, De 474 Bie et al., 2017), or integrate trait and phylogenetic information in a single measure in order to 475 converge as close as possible to the multidimensional niche (Cadotte et al., 2013). In sum, 476 moving forward from traditional single-metric analyses, a combination of different trait and 477 phylogenetic metrics can help to disentangle processes and to detect multiple interacting 478 processes, including different modes of competition (P6-8) and ecological vs. evolutionary 479 processes (P9, Weinstein, Tinoco, Luis Parra, Brown, McGuire et al., 2014).

480

## 481 3.3 Methodological approach

482 In our description of pitfalls P4 and P5, we highlighted that the choice of species pools and 483 randomization schemes can decisively influence the outcomes of an analysis (Ulrich & Gotelli, 484 2013). Often different choices are (more or less) implicitly linked to different ecological 485 hypotheses (Gotelli & Ulrich, 2012). Thus, by explicitly linking each ecological hypothesis 486 with the correct combination of species pool and randomization we can develop a set of tests 487 for disentangling different ecological scenarios (S4, Tab. 1). This approach offers a direct 488 solution to the methodological pitfalls (P3-5) and can help circumvent the challenge of 489 disentangling patterns and processes by providing multiple-pattern comparisons (P6-7). For example, depending on the ecological hypothesis to be tested, it can be important to account 490

explicitly for the dynamic nature of the species pool, recognizing that it is shaped by 491 492 metacommunity dynamics as well as speciation, extinction, and dispersal (Mittelbach & 493 Schemske, 2015). Indeed, Lessard et al. (2016) have demonstrated that the implementation of 494 several process-based species pools, i.e. species pools that already account for selected 495 processes and thus can be used to test for the remaining candidates, allows the identification of 496 otherwise hidden filters of biotic interactions. Manipulations of the species pools can also be 497 used to simulate cross-scale sampling instead of investing the time and money to actually 498 sample across different scales (Chalmandrier et al., 2013). For example, aggregating 499 communities or cutting out smaller study areas can create ranges of spatial scales, whereas 500 aggregating species or transforming phylogenies can create ranges of different levels of 501 description of organisms (Münkemüller et al., 2014). Following a similar logic, it is also 502 possible to build reduced functional species pools already accounting for environmental and 503 dispersal limitation filters at broader scales that can then be used to test simultaneously acting 504 processes at community-scale (de Bello, Price, Münkemüller, Liira, Zobel et al., 2012). In 505 addition, manipulations of the randomization algorithm can be used to account for dispersal 506 limitations by down-weighting species that do not occur in the larger surroundings (P9), and 507 improve the detection of biotic interactions by down-weighting species for which the local 508 environment is not suitable (Peres-Neto, Olden & Jackson, 2001; Chalmandrier et al., 2013). 509 More recently, community ecologists started to validate their methods and models with the 510 "virtual ecologist" approach, where simulated data are used to mimic real species and how they 511 are "virtually" observed and analysed (Zurell, Berger, Cabral, Jeltsch, Meynard et al., 2010). 512 This validation allows testing the reliability and power of metrics, species pool and 513 randomization choices (Münkemüller et al., 2012; Botta-Dukat & Czucz, 2016; Miller et al.,

514 2017). Additionally, it allows investigating how interacting processes and constraints 515 (including biotic interactions, scale-dependency, 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 – is a powerful tool to further develop or test the filtering approach and to carefully interpret observed signals in diversity data (S5, Tab. 1). The limitation of this approach inherently depends on the quality of the simulated data, and its conclusions are restricted to cases that are comparable to these virtual data (see Zurell et al., 2010 for more detail).

523 To avoid P7 (assuming that one process dominates the patterns), more and more approaches 524 are being developed to jointly model multiple processes instead of testing for a single, dominant 525 process (S6, Tab. 1). The range of approaches is large. Some are simple extensions of the 526 original filtering framework. For instance, it is possible to account simultaneously for 527 environmental filtering and symmetric competition by relying on the (strong) assumption that 528 this should lead to a pattern where species are not too similar (i.e. due to competitive exclusion) 529 and not too dissimilar (due to environmental filtering) to each other at the same time and by 530 testing for this pattern (e.g. with a quadratic term in a regression model, Gallien et al., 2014). 531 Another possibility is to build elaborate null models that allow the inclusion of multiple 532 ecological and evolutionary processes (see also S3). Van der Plas et al. (2015) introduced static, 533 stepwise algorithms of community assembly that simulate processes such as dispersal, 534 environmental filtering or competition and allow estimating their relative importance. Pigot and 535 Etienne (2015) developed a dynamic null model of assembly that allows estimating the effect 536 of allopatric speciation, colonization and local extinction. Ultimately, the idea is to build more 537 mechanistic, dynamic models of community assembly (Connolly, Keith, Colwell & Rahbek, 538 2017; Pontarp, Brännström, et al., 2019) that are general enough to include and contrast 539 different ecological theories and processes and can be parameterized inversely with a selection 540 of complementary diversity patterns (Cabral, Valente & Hartig, 2017). The logic of this inverse

541 parameterization, in simple terms, is to run the model across the relevant parameter space, to 542 compare simulated patterns with observed patterns using appropriate summary statistics, and 543 to choose the parameter combinations that lead to the best match between simulated and 544 observed patterns (Grimm, Revilla, Berger, Jeltsch, Mooij et al., 2005; Hartig, Calabrese, 545 Reineking, Wiegand & Huth, 2011). A coherent and efficient statistical method for this inverse 546 parameterization of complex ecological and evolutionary models is approximate Bayesian 547 computation (Csilléry, Blum, Gaggiotti & François, 2010). Interpretation of the identified best 548 parameter values allows quantifying the relative influence of the different ecological, 549 biogeographic and evolutionary processes (Pontarp, Bunnefeld, Cabral, Etienne, Fritz et al., 550 2019). Very importantly, the parameterized model could also be used to account for transient 551 dynamics (P10) and to make predictions, so far largely unattained aims in large-scale 552 community ecology. Examples of such mechanistic models exist already (Kalyuzhny, Kadmon 553 & Shnerb, 2015; Cazelles, Mouquet, Mouillot & Gravel, 2016; Lohier, Jabot, Weigelt, Schmid 554 & Deffuant, 2016) but many processes and process combinations are still understudied in this 555 young research field (Cabral et al., 2017). Interestingly, developing and applying such 556 mechanistic models in community ecology will strongly benefit from the solutions outlined 557 here (S1-4) as these provide a range of partly independent diversity patterns (e.g. trait vs. 558 phylogenetic patterns, abundance weighted patterns, small vs. large-scale patterns), an 559 indispensable requisite for inverse parameterization (Grimm, Frank, Jeltsch, Brandl, 560 Uchmanski et al., 1996). Even though this approach of jointly modelling different processes of 561 assembly is very promising, substantial challenges remain (Cabral et al., 2017). For example, 562 calibration and validation are data hungry, computationally demanding, and requires strong 563 expert knowledge.

564

#### 565 3.4 Drawing conclusions

566 Observational approaches, including the filtering framework, were never meant to provide 567 final answers to questions about ecological mechanisms and processes, but to feed an ongoing 568 scientific process of generating knowledge and general theories (Garland, 2015). Observational 569 studies are supposed to help refine, alter, expand and test hypotheses and to inform further 570 observations, experiments and mechanistic models (see Fig. 2). In a single observational study, 571 it is typically not possible to sample all the necessary data or to apply all the above outlined 572 solutions. For very complex filters (e.g. complex biotic interactions that differ for different 573 species pairs) there may not exist solutions at all. This is not a problem *per se* as long as these 574 limitations are considered in the conclusions drawn from results. Ultimately, a combination of 575 studies using observations, experiments and mechanistic models with different strengths and 576 limitations will advance our understanding of ecological processes and their importance in 577 realistic vs. laboratory environments.

578

#### 579 *3.5 Future developments and challenges*

580 Novel methods, theoretical advances and newly available data offer opportunities, but also pose 581 challenges to the study of community assembly. Their application for inferring assembly rules 582 from diversity patterns has just started. While broad-scale testing remains to be undertaken, we 583 highlight here general ideas and the potential benefits to community assembly research in each 584 of these areas:

(1) 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 estimating the covariation of species while modelling their response to abiotic variables may help to relax this assumption (e.g. joint species distribution models, Clark, Gelfand, Woodall & Zhu, 2014; Pollock, Tingley, Morris, Golding, O'Hara et al., 2014). The estimated residual covariance matrices in JSDMs can result

591 from model misspecification, influential but hidden abiotic variables, but could potentially also 592 result from biotic interactions and thus be a signal of assembly rules (Ovaskainen, Tikhonov, 593 Norberg, Blanchet, Duan et al., 2017; Tikhonov, Abrego, Dunson & Ovaskainen, 2017; Zurell, 594 Pollock Laura & Thuiller, 2018). To better understand the ecological meaning of these residual 595 covariance matrices, one could test them using simulated data (Zurell et al., 2018), or one could 596 link empirically estimated covariance matrices to trait and/or phylogenetic diversity patterns 597 assuming that a strong correlation would indicate ecological meaning. However, since they rely 598 on correlation matrices, these approaches can only focus on testing for symmetric interactions, 599 which strongly limit their application for inferring interactions.

600 (2) Recent advances in multi-trophic network theory have highlighted the links of trait 601 (Albouy, Guilhaumon, Villeger, Mouchet, Mercier et al., 2011; Crea, Ali & Rader, 2016) and 602 phylogenetic relationships (Aizen, Gleiser, Sabatino, Gilarranz, Bascompte et al., 2016; Peralta, 603 2016) with biotic interactions in the networks. Specific interactions are linked to specific trait 604 combinations and thus to trait and phylogenetic diversity patterns. For example, it has been 605 shown for plant-insect interaction networks that certain traits define sets of potentially 606 interacting species and define clear patterns of clustering on the phylogenies of plants and 607 insects (Ibanez et al., 2016). For food webs, Morlon et al. (2014) have suggested and applied a 608 novel framework to estimate the strength of filters of "trophic environment" vs. food-mediated 609 interspecific competition in community assembly. The framework uses trophic similarities, 610 measured via shared predators or prey, and null models. In a similar approach, for multi-trophic 611 tropical fish communities, it was recently highlighted that traits linked to feeding strategies or 612 trophic level (measured based on stable isotope ratios) played an important role in community 613 assembly and accordingly left significant signals in trait diversity (Fitzgerald, Winemiller, 614 Sabaj & Sousa, 2017). Advances in this direction open the door for moving from single-trophic to multi-trophic community assembly (Gravel et al., 2016). Ultimately, integrating 615

616 complementary information on species differences from traits, phylogenies and interaction
617 networks promises a better understanding of community assembly in space and time (Morlon
618 et al., 2014).

619 (3) Finally, new types of data are becoming rapidly available. One example is amplicon-620 based DNA analysis of environmental samples (i.e. metabarcoding data, eDNA, Taberlet, 621 Prud'homme, Campione, Roy, Miguel et al., 2012; Creer, Deiner, Frey, Porazinska, Taberlet et 622 al., 2016). These data provide new information on the potential presence of organisms for 623 calculating diversity patterns (Martinez-Almoyna, Thuiller, Chalmandrier, Ohlmann, Foulquier 624 et al., 2019; Calderón-Sanou, Münkemüller, Boyer, Zinger & Thuiller, 2020). Combined with 625 databases or expert knowledge on functional traits, phylogenies or trophic meta-webs 626 (containing information on all predator-prey interactions in a regional pool of present taxa) 627 these diversity patterns allow to better approximate niche overlap in communities. The great 628 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 629 630 integration over time (for example species are not missed only because they were not visible at 631 the sampling time). While promising, eDNA data also bring new uncertainty with respect to 632 traditional surveys, such as amplification errors, DNA degradation and contamination and 633 barcode assignation (Taberlet et al., 2012), because reference databanks of DNA sequences that 634 can be used to identify taxonomic units are still incomplete and impede the traditional use of 635 diversity indices based on species concepts (Coissac, Taberlet, Roquet, Boleda, Gielly et al., 636 2015). However, methodological advances in this area will help address earlier limitations (e.g. data limitation for pollination networks, Pornon, Andalo, Burrus & Escaravage, 2017; 637 638 Calderón-Sanou et al., 2020), and allow studying entirely new types of ecosystems (e.g. by 639 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, 640

Bahram, Cajthaml, Polme, Hiiesalu et al., 2016). Another promising new type of data comes 641 642 from transcriptomic and meta-transcriptomic approaches (Gotelli, Ellison & Ballif, 2012; 643 Wang, Kong, Li & Xie, 2016). These high-throughput methods allow identifying the proteins 644 or genes being produced by individuals or entire communities at the time of sampling (e.g. 645 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 646 647 the niche use of individuals or communities. The diversity of expressed functions could help 648 give insights into assembly processes that are much more tightly linked to the actual 649 physiological responses than the standard trait diversity measures that are often based on "soft" 650 traits (i.e. few easily measurable features). For example, a recent community-wide 651 transcriptomic analysis has supported the Janzen-Connell hypothesis by demonstrating that 652 growth rates and survival of individual trees were higher when the neighbourhood consisted of 653 trees with dissimilar (rather than similar) defense genes (Zambrano, Iida, Howe, Lin, Umana 654 Maria et al., 2017). However, even more than with metabarcoding, this approach adds 655 uncertainty with respect to traditional surveys that are linked to sampling, laboratory work and 656 interpretation of results (Wang et al., 2016).

657

#### 658 4. Guidelines

Based on our critical synthesis of pitfalls and available solutions (Tab. 1), we suggest considering 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 (Fig. 2 and solution S4).

664 (2) Assemble all data necessary to answer the research question (across scales and diversity 665 facets) but not more (S1, S3). Importantly, use existing naturalist knowledge to decide on 666 ecologically relevant traits. Including extraneous species or irrelevant traits, or conducting the667 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 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.

672 (4) Select the diversity metrics most appropriate to the question of interest based on the673 conceptual framework and existing naturalist knowledge (S3).

(5) Choose species pools and randomization techniques such that null models only break 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 sensibility of this
methodological choice and interpret in consequence (S5).

(6) If possible, test for the reliability and power of the chosen approach with simulated data(85).

680 (7) Test whether signals identified as significant are congruent across the *a priori* identified
681 relevant patterns for each research hypothesis and always interpret them together (Fig. 2, S6).

(8) 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 disentangling the different drivers
(S6).

686 (9) Remember that studying causal processes in the strict sense always requires an experiment687 and accordingly report results of pattern analyses with the necessary care (Fig. 2).

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689

#### 691 *Conclusion*

692 If we are to fully exploit the filtering framework for a better understanding of community 693 assembly, we need to: (i) ensure we rely on the solutions provided for most of the known pitfalls 694 (Tab. 1) and follow the guidelines suggested here for good scientific practice, (ii) improve 695 current solutions that begin to accommodate multiple confounding processes, more complex 696 biotic interaction types, and different spatial scales, and (iii) integrate the rapidly accumulating 697 types of new data (e.g. environmental metabarcoding) that represent more diverse and so far 698 largely unknown communities (e.g. soil microbes) across an ever-increasing spatial scope. 699 Adapting the filtering approach to circumvent traditional pitfalls, account for uncertainty, and 700 accommodate new data -all while retaining core fundamental ideas- holds promise to 701 significantly improve our understanding of the ever-widening definition of the ecological 702 community.

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- 1198 **635**.
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1200	Data	Accessibility	Statement
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## **Table**

- **Table 1.** Six solutions to pitfalls with examples from the literature: In green the pitfall they
- 1251 directly address, in blue the pitfalls that they can indirectly help to solve; Check marks
- 1252 indicate how well developed the solutions are.

	Pi	tfall	ls:							
Solutions:	(P1) scale choices not important	(P2) funct./phylo $\approx$ 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 & history	(P10) equilibrium assumption
(S1) Consider alternative scales of analysis VV										
sample at different spatial and taxonomic scales [1]										
account for temporal (e.g. seasonal) dynamics in sampling design [2]										
• simulate a variation of spatial and taxonomic scales with adapted null models [3]										
• across environmental gradients and variation [4]										
(S2) Measure more dynamic responses 🗸										
demographic rates as response variable [2]										
• set up experiments [2]										
<ul> <li>invasive species as "natural experiments" [5]</li> </ul>										
• sample time-series [6]										
(S3) Consider different biodiversity aspects and indices $\checkmark\checkmark$										
• traits need to be adequately chosen and grouped [7]						-				
integrate trait and phylogenetic diversity [8]										
• weight species by their abundances [9]						-				
incorporate intra-specific variability [9]						-			-	
compare richness, regularity and divergence [10]										
different indices for testing symmetric vs. hierarchical competition [11]										
(S4) Consider alternative species pools and randomizations $\checkmark\checkmark$										
use more ecological based species pools [12]										
partition diversity across evolutionary periods [13]										
choose appropriate randomization algorithms [14]										
(S5) Validate and test the approaches applied $\checkmark$										
undertake robustness analyses to identify mismatches between tests [15]										
apply virtual ecologist approach, with tests of analyses using simulated data [16]										
account for uncertainty in phylogenies [17]										
(S6) Model multiple processes jointly 🗸										
indirectly with regressions by accounting for non-linear responses [18]										
estimating relative importance of env. filtering, competition and dispersal [19]										
explicitly account for allopatric speciation, colonization and local extinction [20]										
<ul> <li>mechanistic models with inverse parameterization based on diversity patterns [21]</li> </ul>										

[1] (Cavender-Bares et al., 2006); [2] (Conti et al., 2018); [3] (Münkemüller et al., 2014); [4] (Bryant, Lamanna, Morlon, Kerkhoff, Enquist et al., 2008); [5] (Carboni et al., 2016); [6] (Campbell & Mandrak, 2017); [7] (Leps *et al.*, 2006); [8] (Cadotte et al., 2013); [9] (Chalmandrier *et al.*, 2015); [10] (Raevel et al., 2012); [11] (Kunstler et al., 2012); [12] (Lessard *et al.*, 2016); [13] (Pavoine, Love & Bonsall, 2009); [14] (Hardy, 2008); [15] (Aiba, Katabuchi, Takafumi, Matsuzaki, Sasaki et al., 2013); [16] (Münkemüller et al., 2012); [17] (Molina-Venegas & Roquet, 2014); [18] (Gallien et al., 2014); [19] (Van der Plas et al., 2015); [20] (Pigot & Etienne, 2015); [21] (Pontarp, Brännström, et al., 2019)

#### 1261 Figure

Figure 1: Conceptual representation of the steps of the classical ecological filtering framework and related ten common pitfalls (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 pitfall 1); (b) sampling data, specifically choice of traits and/or phylogeny (P2); (c) choice of methodological approaches, including diversity indices, null models, species pools and statistical tests (P3-5) and, finally, (d) drawing conclusions on the potential underlying processes, an approach with inherent problems (P6-7) but specific limitations in face of complex biotic interactions (P8) and influential background factors (P9-10).

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1270 Figure 2: Conceptual representation of the ongoing scientific process of generating knowledge and general 1271 theories with the ecological filtering framework. The process often starts by an experience or undirected 1272 observation (e.g. "plants in alpine meadows are often smaller than in sub-alpine meadows") that leads to further 1273 reflection about ecologically interesting questions (e.g. "why are plants smaller?"), related hypotheses (e.g. "plants 1274 may be smaller due to environmental constraints") and testable predictions (e.g. "plant height of alpine species is 1275 a non-random selection from the mountain plant species pool"). To test these hypotheses, we suggest an interplay 1276 of studies using observations, experiments, virtual ecologist approaches (to test the logic of process-pattern-1277 predictions and methodological approaches) and/or parameterized mechanistic models to refine, alter, expand and 1278 reject the hypotheses on ecological assembly processes. Each of the cycles can repeat many times until a hypothesis 1279 becomes so well supported that it can advances community ecology as a corner stone of a more general theory 1280 (inspired by the figure "The scientific method as an ongoing process" developed by Theodore Garland, University 1281 of California, 2015).

Common Pitfalls:
Assuming that
P1 spatial, environmental and
organism-level scale choices
have no influence
P2 trait and phylogenetic diversity
are good proxies for niche
overlap
P3 all diversity indices give the
same answer
P4 construction of adequate
species pools is obvious
P5 adequate randomization is
obvious
P6 one pattern can only emerge
from one process and
P7 one major process dominates
the observed pattern
P8 biotic interactions are simple
P9 dispersal and historical
contingencies can be ignored



1286 Figure 1





- 1292 Appendix S1 Assembly processes and hypothesized diversity patterns
- 1293 Appendix S2 Interest in the filtering framework over the last decade
- 1294 Appendix S3 Showcase: No signal of biotic interactions?