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

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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).

44

45

46 **Abstract**

47 **Aim:** More than ever, ecologists seek to understand how species are distributed and have
48 assembled into communities using the ‘filtering framework’. This framework hypothesizes that
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 α -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.

68

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

71 **1. Introduction**

72 The diversity of ecological communities is increasingly compromised by ongoing global
73 changes (Pereira, Navarro & Martins, 2012). Mitigating these threats requires to understand the
74 distribution of diversity along geographic, abiotic and biotic gradients and the underlying
75 assembly processes (Lavergne, Mouquet, Thuiller & Ronce, 2010; HilleRisLambers, Adler,
76 Harpole, Levine & Mayfield, 2012). A focal question is whether abiotic constraints or rather
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
85 the evolutionary history. Combining data on distribution, traits and phylogeny in a meaningful
86 way holds promise for a revolution in community ecology by opening the door to large-scale
87 analyses of assembly processes (Webb, Ackerly, McPeck & 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).

95 In practice, this idea has mostly been implemented through the filtering framework
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. α -
119 diversity) are commonly compared to null expectations (i.e. patterns under random assembly,

120 Fig. 1c). Low trait or phylogenetic α -diversity is assumed to indicate ecological processes that
121 foster the co-occurrence of species with similar niches, such as environmental filtering (Fig. 1b,
122 community A, see also Appendix S1 in Supporting Information). Conversely, high trait or
123 phylogenetic α -diversity can reveal ecological processes that result in limiting similarity, such
124 as competition due to niche overlap (Fig. 1b, community B, see also Appendix S1, Mac Arthur
125 & 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).

139 Here, we address this question by pinpointing the major pitfalls linked to the different steps
140 of the standard filtering approach (Fig. 1). While many of the limitations of this framework
141 have already been pointed out in previous reviews with various foci and levels of detail, and
142 sometimes also in combination with possible solutions (e.g. Gerhold, Cahill, Winter, Bartish &
143 Prinzing, 2015; Lopez, Burgio, Carlucci, Palmquist, Parada et al., 2016; Pontarp, Brännström
144 & 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**

153 Applying the filtering framework requires (1) choosing the study design with focal spatial,
154 environmental and organism-level scales, (2) collecting information and (3) choosing
155 methodological approaches relevant to the research question. Finally, (4) conclusions are drawn
156 from the results while accounting for study limitations. In the following, we review 10 different
157 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

169 assume that: (P1) spatial, environmental and organism-level scale choices have no influence on
170 study results (Fig. 1).

171 (P1) Certain processes may never be detected if we chose an inappropriate scale. First,
172 ignoring large-scale factors, such as climate gradients, dispersal barriers, historical
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).

189

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 &

193 Waller, 2017). It is thus a pitfall to assume that: (P2) trait and phylogenetic diversity are always
194 good 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,
208 Westoby, Ackerly, Baruch et al., 2004; Diaz et al., 2016). However, in many aspects, trait
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.

236

237 ***2.3 Methodological approach***

238 It has been demonstrated that different methodological choices can give different answers
239 (Münkemüller, Gallien, Lavergne, Renaud, Roquet et al., 2014; Perronne, Munoz, Borgya,
240 Reboud & Gaba, 2017). Thus, pitfalls three, four and five are to assume that (P3) all supposedly
241 similar diversity indices give the same results and that the construction of (P4) adequate species

242 pools and (P5) randomization algorithms for testing deviations from expectations is obvious
243 and straightforward (Fig. 1).

244 (P3) A common pitfall is to assume that different diversity indices can be used
245 interchangeably. While some diversity indices are indeed highly redundant, others quantify
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
255 regularity (Villéger & Mouillot, 2008; Tucker et al., 2017). While classification schemes for
256 available diversity metrics can help choose an appropriate index (Pausas & Verdu, 2010;
257 Pavoine, Vela, Gachet, de Bélair & Bonsall, 2011; Tucker et al., 2017), it is not always evident
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 α -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.

290

291 ***2.4 Drawing conclusions***

292 The most basic shortcoming of the filtering approach is inherent to most observational
293 studies in ecology—it is impossible to deduce a process from an observed pattern in the strict
294 sense. However, given the complexity of nature, ecological research often uses pattern
295 observations to formulate hypotheses or to conclude that a pattern is in (dis)agreement with
296 hypothesized processes. The three major related pitfalls are to assume: (P6) that one pattern can
297 only emerge from one single process, (P7) that one major process dominates the observed
298 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,
303 symmetric niche competition is assumed to produce overdispersed diversity (i.e. co-existing
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
309 on the same species but also if different processes drive different groups of species in the
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
340 (Barabas, Michalska-Smith & Allesina, 2016; Gallien, 2017; but see Maynard, Bradford,

341 Lindner, van Diepen, Frey et al., 2017). Moreover, multi-trophic biotic interactions are so far
342 largely ignored (Grilli, Barabas, Michalska-Smith & Allesina, 2017). There are a few first
343 example studies investigating bipartite interaction networks (Van der Plas, Anderson & Olf,
344 2012; Ibanez, Arene & Lavergne, 2016). However, the great challenge lies in extrapolating
345 concepts of niche matching, associated trait and phylogenetic diversity patterns and cascading
346 feedbacks from bipartite to multi-trophic communities (Levine, Bascompte, Adler & Allesina,
347 2017).

348

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
354 (Warren, Cardillo, Rosauer & Bolnick, 2014). Common pitfalls are to assume that (P9)
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
358 pools (see also P4), diversification and historical contingencies are commonly ignored in
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

366 some cases, both evolutionary and ecological processes occur at the same local community
367 scale (Pollock, Bayly & Vesk, 2015). This problem is even more complicated by the fact that
368 some ecological and biogeographical processes can create the same taxonomic or phylogenetic
369 patterns. For example, from a community ecology standpoint, ‘phylogenetic dispersion’ in a
370 clade can be interpreted as a sign of competitive exclusion, while from a biogeographic
371 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**

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

391 theoretical advances and newly available data that could prove their utility for community
392 assembly questions.

393

394 ***3.1 Study design***

395 We have seen that the filtering approach requires a number of choices and that each of these
396 choices can affect (or even invert) the results (Münkemüller et al., 2014). It is therefore
397 especially important that, at the beginning of a study, the general research question is translated
398 into specific hypotheses and testable predictions (Fig. 2). Based on these, the study design can
399 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
415 contrasting patterns at others (P6, P8), and to identify the interplay of processes that act at

416 different scales (P7). For example, for trait diversity of plant communities there is some
417 evidence for the dominance of competitive interactions at fine spatial scales and prevalent
418 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,

441 Jorgensen et al., 2015). They can also be used to better understand the turnover of processes
442 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
446 biodiversity (e.g. P2-3), community ecologists started early on to consider complementary
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 & Machac, 2018), between
450 richness, regularity and divergence components (Ravel, 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
456 can aid the choice of trait combinations (Diaz et al., 2016). However, because different traits
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
490 example, depending on the ecological hypothesis to be tested, it can be important to account

491 explicitly for the dynamic nature of the species pool, recognizing that it is shaped by
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

516 factors) influence results of the filtering framework (Trisos, Petchey & Tobias, 2014). Thus,
517 this approach does not provide direct solutions for any pitfall, but – when using appropriate
518 simulation models – is a powerful tool to further develop or test the filtering approach and to
519 carefully interpret observed signals in diversity data (S5, Tab. 1). The limitation of this
520 approach inherently depends on the quality of the simulated data, and its conclusions are
521 restricted to cases that are comparable to these virtual data (see Zurell et al., 2010 for more
522 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:

585 (1) One strong, and certainly in most cases wrong, assumption of the filtering approach is
586 that all species interact with each other (and based on the same underlying processes). Species
587 distribution modelling techniques that allow estimating the covariation of species while
588 modelling their response to abiotic variables may help to relax this assumption (e.g. joint
589 species distribution models, Clark, Gelfand, Woodall & Zhu, 2014; Pollock, Tingley, Morris,
590 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
615 to multi-trophic community assembly (Gravel et al., 2016). Ultimately, integrating

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, Miquel 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
629 (or taxonomic units with lower resolution, depending on the reference libraries) and the
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 assignment (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.
637 data limitation for pollination networks, Pornon, Andalo, Burrus & Escaravage, 2017;
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
640 of fungi and bacteria with nematodes and plants, Anslan, Bahram & Tedersoo, 2016; Tedersoo,

641 Bahram, Cajthaml, Polme, Hiiesalu et al., 2016). Another promising new type of data comes
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
646 provide a direct assessment of physiological responses to abiotic and biotic stimuli and thus to
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**

659 Based on our critical synthesis of pitfalls and available solutions (Tab. 1), we suggest
660 considering the following steps when applying the filtering framework:

661 (1) Translate research question(s) into specific hypotheses and testable predictions. The
662 expected patterns in support of each hypothesis must be identified *a priori*, and each hypothesis
663 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 the
667 analysis at an inappropriate scale can obscure or distort any signal in the diversity patterns.

668 (3) Measure dynamic response variables in a spatially explicit context and consider
669 complementing with targeted experiments if the research question and setting allow for it (S2).
670 This seems especially important when focusing on biotic interactions or studying communities
671 that are far from equilibrium.

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

674 (5) Choose species pools and randomization techniques such that null models only break the
675 pattern to be tested and not additional patterns (S4). If this is not possible, use a combination of
676 tests that together allow an unbiased answer to the research question. Test the sensibility of this
677 methodological choice and interpret in consequence (S5).

678 (6) If possible, test for the reliability and power of the chosen approach with simulated data
679 (S5).

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).

682 (8) If your research question is complex (e.g. implies a multitude of processes or is linked to
683 evolutionary history) it may be necessary to build and parameterize a mechanistic simulation
684 model that embraces the underlying complexity and allows disentangling the different drivers
685 (S6).

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

688

689

690

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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1200 **Data Accessibility Statement**

1201 No data were used.

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1250 **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.

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

1253 [1] (Cavender-Bares et al., 2006); [2] (Conti et al., 2018); [3] (Münkemüller et al., 2014); [4] (Bryant, Lamanna, Morlon, Kerkhoff, Enquist et
 1254 al., 2008); [5] (Carboni et al., 2016); [6] (Campbell & Mandrak, 2017); [7] (Leps et al., 2006); [8] (Cadotte et al., 2013); [9] (Chalmandrier
 1255 et al., 2015); [10] (Raevel et al., 2012); [11] (Kunstler et al., 2012); [12] (Lessard et al., 2016); [13] (Pavoine, Love & Bonsall, 2009); [14]
 1256 (Hardy, 2008); [15] (Aiba, Katabuchi, Takafumi, Matsuzaki, Sasaki et al., 2013); [16] (Münkemüller et al., 2012); [17] (Molina-Venegas &
 1257 Roquet, 2014); [18] (Gallien et al., 2014); [19] (Van der Plas et al., 2015); [20] (Pigot & Etienne, 2015); [21] (Pontarp, Brännström, et al.,
 1258 2019)

1261 **Figure**

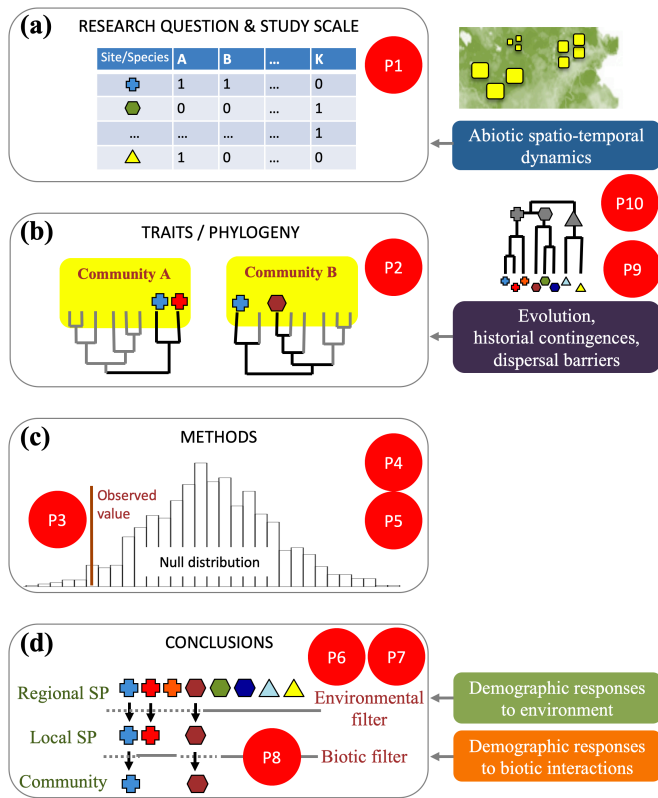
1262 **Figure 1:** Conceptual representation of the steps of the classical ecological filtering framework and related ten
1263 common pitfalls (cf. left table and red points in the figure): (a) Identifying research question(s) and study design,
1264 including focal organism level, spatial and temporal scales (potential pitfall 1); (b) sampling data, specifically
1265 choice of traits and/or phylogeny (P2); (c) choice of methodological approaches, including diversity indices, null
1266 models, species pools and statistical tests (P3-5) and, finally, (d) drawing conclusions on the potential underlying
1267 processes, an approach with inherent problems (P6-7) but specific limitations in face of complex biotic interactions
1268 (P8) and influential background factors (P9-10).

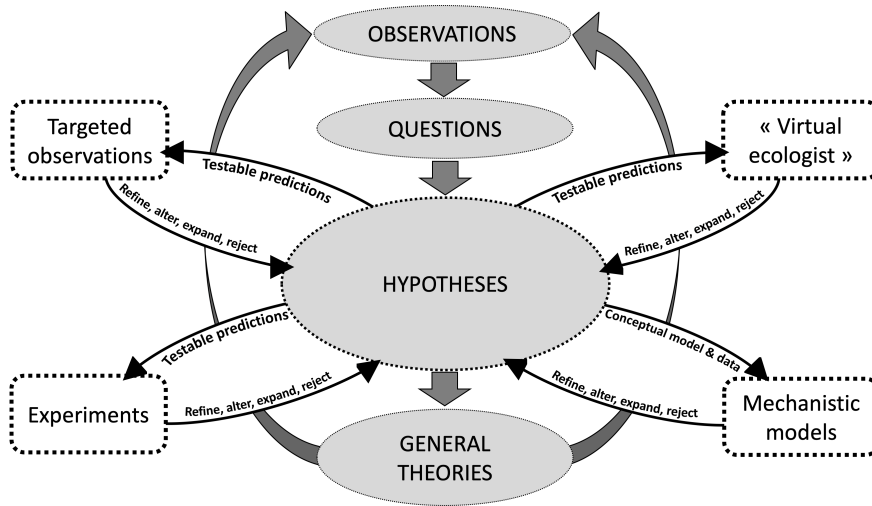
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1270 **Figure 2:** Conceptual representation of the ongoing scientific process of generating knowledge and general
1271 theories with the ecological filtering framework. The process often starts by an experience or undirected
1272 observation (e.g. “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 advance 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).

1282

Common Pitfalls:	
<i>Assuming that ...</i>	
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
P10	... communities are at equilibrium





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Figure 2

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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?*

1295