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Summary

1. The subdiscipline of 'community phylogenetics' is rapidly growing and influencing thinking regarding community assembly. In particular, phylogenetic dispersion of co-occurring species within a community is commonly used as proxy to identify which community assembly processes may have structured a particular community: phylogenetic clustering as a proxy for abiotic assembly, *i.e.* habitat filtering, phylogenetic over-dispersion as a proxy for biotic assembly, notably competition.

2. We challenge this approach by highlighting (typically) implicit assumptions that are, in reality, only weakly supported, including: (1) phylogenetic dispersion reflects trait dispersion; (2) a given ecological function can be performed only by a single trait state or combination of trait states; (3) trait similarity causes enhanced competition; (4) competition causes species exclusion; (5) communities are at equilibrium with processes of assembly having been completed; (6) assembly through habitat filtering decreases in importance if assembly through competition increases, such that the relative balance of the two can be thus quantified by a single parameter; and (7) observed phylogenetic dispersion is driven predominantly by local and present-day processes.

3. Moreover, technical sophistication of the phylogenetic-patterns-as-proxy approach trades-off against sophistication in alternative, potentially more pertinent approaches to directly observe or manipulate assembly processes.

4. Despite concerns about using phylogenetic dispersion as a proxy for community assembly processes, we suggest there are underappreciated benefits of quantifying the phylogenetic structure of communities, including (1) understanding how coexistence leads to the macroevolutionary diversification of habitat lineage-pools (*i.e.* phylogenetic-patterns-as-result approach); (2) understanding the macroevolutionary contingency of habitat lineage-pools and how it affects present-day species coexistence in local communities (*i.e.* phylogenetic-patterns-as-cause approach).

5. We conclude that phylogenetic patterns may be little useful as proxy of community assembly. However, such patterns can prove useful to identify and test novel hypotheses on (i) how local coexistence may control macroevolution of the habitat lineage-pool e.g. through competition among close relatives triggering displacement and diversification of characters (ii) how macroevolution within the habitat lineage-pool may control local coexistence of related species, e.g. through origin of close relatives that can potentially enter in competition.

6.

I. Introduction

Community ecologists have a long tradition of inferring mechanisms of community assembly from observed patterns of species occurrences. Though this inductive approach can lead to insights (e.g. Watt 1947, recent summary in Mittelbach 2012), ecologists also have a long tradition of pointing out when story telling appears to go too far. Among the best known examples is Connell (1980) paper in which he brought the 'ghost of competition past' to the attention of ecologists, arguing that the

commonly-held notion of co-evolutionary shaping of competitors´ niches had surprisingly little direct support. A core lesson taken from this episode in ecology's history is that many stories can be told from the same ecological pattern, and without studying actual processes, pattern description can be of limited value for understanding mechanisms. Here, we suggest ecologists are presently heading down a similar path – this time in conjunction with new phylogenetic tools and more sophisticated statistical methodology.

Many ecologists use phylogenetic dispersion of co-occurring species *per se* to infer mechanisms of community assembly. Some of the recent examples of this approach are Diaz *et al.* (1999), Webb (2000), Webb *et al.* (2002, see also Kembel 2009), though the underlying idea continues back to the application of taxonomic ratios (e.g. species/genus ratio) to infer ecological processes (Elton 1946). Combined, the studies suggest that observed patterns of phylogenetic dispersion found among co-occurring species within a community could be a suitable means by which one can understand the processes of community assembly, even if one is unable to specifically identify the traits, filters or species interactions operating in a particular location. Most notable is the idea that (A) abiotic assembly, *i.e.* habitat filtering (*sensu* Diaz *et al.* 1999) results in phylogenetic clustering, as closely related species are more likely to possess the traits 'needed' to survive under a given set of environmental conditions, and (B) biotic assembly, such as competition and other negative density-dependent interactions, result in phylogenetic over-dispersion, because relatedness is assumed to increase trait similarity and the likelihood of competitive exclusion. The number of such studies using phylogenetic dispersion of communities as a proxy for community assembly processes has increased exponentially (from 1 publication in 1997 to 5 publications in 2007 and 41 publications in 2014; see Fig. S1 in Supporting Information). We note that although many biotic assembly mechanisms other than competition, such as mutualism, facilitation, etc., can structure natural communities, this ecological reality has not been fully integrated into the

community phylogenetics approach (but see Elias *et al.* 2009; Sargent *et al.* 2011, Venail *et al.* 2014). Thus, here we focus on competition as the main biotic assembly mechanism.

Though the use of phylogenetic patterns as proxies of the processes of community assembly is rapidly increasing, there has also been an increase in critiques (e.g. Mayfield & Levine 2010; Pavoine *et al.* 2013; HilleRisLambers *et al.* 2012 challenging the use of assembly proxies in general). The concerns include spatial and temporal scale-dependency of phylogenetic patterns (Emerson & Gillespie 2008; Cavender-Bares *et al.* 2009) and lack of correlation between measures of phylogenetic dispersion and trait dispersion (Pavoine & Bonsall 2011; Pavoine *et al*. 2013; Srivastava *et al.* 2012; Swenson 2013), questioning the interpretation of assembly mechanisms using phylogenetic data. Overall, there may be a number of often unspoken and ignored assumptions underlying the phylogenetic-patterns-as-proxy approach (Prinzing *et al.* 2008; Cavender-Bares *et al.* 2009; Mayfield & Levine 2010; Srivastava *et al.* 2012), but so far there is no review that focuses on a systematic identification and evaluation of all these assumptions. We are also lacking a broad perspective for identifying the situations in which phylogenetic patterns within communities might be useful to identify hypotheses on (i) ecological factors driving lineage diversification and (ii) the effect of lineage diversification on coexistence (see Emerson & Gillespie 2008; Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012 for possible scenarios of evolutionary community assembly or examples of ecological consequences of coexistence among related species).

Our goal in this paper is to identify several hidden assumptions underlying the "phylogenetic patterns-as-proxy" approach (Fig. 1) and review their empirical support. We will show that these assumptions are typically weakly supported by existing data and in some cases they are also not consistent with modern coexistence theory (Section II). We also suggest that continued reliance on

phylogenetic proxies for community assembly without incorporation of more mechanistic studies to "ground-truth" the statistical pattern may lead to collateral damage to our understanding of processes (see Appendix S2). We will finally refer to future directions by exploring two alternative approaches on how processes of local assembly accumulate into diversification of entire phylogenetic lineages, and how phylogenetic diversification of lineages causes the observed patterns of local community assembly. In doing so we will profit from prior approaches developed by evolutionary biologists and paleo-ecologists (e.g. Boucot 1996; Brooks & McLennan 2002). While feedbacks of community processes on evolution have been described before (e.g. Cavender-Bares *et al.* 2009; HilleRisLambers *et al.* 2012) we will show that phylogenetic community structure can play an important role in testing these evolutionary hypotheses (Section III). For consistency, most of our examples come from plants, but the concepts and mechanisms we are talking about apply equally well outside the plant kingdom.

II. Assumptions (Fig. 1)

Assumption 1: Phylogenetic dispersion reflects dispersion of phylogenetically conserved functional traits.

Community assembly is assumed to be mediated via functional traits and trait dispersion of a community is hence indicative of particular assembly processes. Phylogenetic dispersion is then used as a proxy for trait dispersion and the underlying assembly processes. However, we will outline below that closely related species co-occurring in a local community may not necessarily share similar functional traits, even if across an entire region they mostly do (Fig. 1, caveat of assumption 1).

Studies using phylogenetic relatedness as a proxy for trait dispersion often justify this by referring to phylogenetic niche conservatism, *i.e.* species ecological niches and niche-related traits tend to be maintained between ancestors and descendants (e.g. Prinzing *et al.* 2001). We leave aside here the potential problem of mixing notions of similar traits (in ecology) with synapomorphic traits (in phylogeny Ridley 2003). We also note that the assumption does not require niche evolution to be constrained (Blomberg & Garland 2002; Münkemüller *et al.* 2012; Pan *et al.* 2014) or niche evolution to be slower than any theoretical evolutionary model like Brownian motion (which may often not be the case possibly because selective environments themselves changed much faster than Brownian motion; e.g. Prinzing *et al.* 2014). It suffices that niches are more similar among closely related species than among distantly related species (*i.e.* "phylogenetic signal" according to Losos 2008 or Münkemüller *et al.* 2014). Support of niche conservatism seems dominant (Peterson 2011) but numerous counter examples exist (Losos 2008; Mouquet *et al.* 2012). Niche evolution can be more labile or more conservative due to convergence of niches between lineages or due to character displacement within lineages, and these can result from interactions among coexisting species, a link that we will further discuss in section III.

However, what applies to a regional species pool does not necessarily apply to local communities, as the latter are typically small and possibly non-representative samples of a large pool (see Weiher *et al.* 2011 for the importance of such scaling). Tests for niche conservatism have usually occurred at regional scale only (but see Silvertown *et al.* 2006). Results at local scale may be different from those at regional scale: a single patch community containing a smaller range of niche conditions, trait values and lineages than an entire region (Willis *et al.* 2010). Across such limited ranges of niches, trait values and phylogenetic lineages, the relationship between phylogenetic distance and trait dissimilarity might disappear (Srivastava *et al.* 2012). In fact all examples of studies failing to detect niche conservatism listed by Losos (2008) are within-genus comparisons, *i.e.* each

covering a limited range of phylogenetic lineages. Additionally, in most lineages there is still a

minority of species pairs that are dissimilar in traits and it might be specifically these dissimilar pairs

that are selected into local communities (Prinzing *et al.* 2008). Finally, character displacement

between coexisting, often congeneric species (known at least since Lack 1942) can result in the local

loss of the regional correlation between phylogenetic distance and trait dissimilarity. Overall, even if

across a region related species may tend to share similar traits and niches, dissimilar related species

or similar non-related species might be filtered into a local community (Fig. 1).

The existing tests do not seem to support a blanket acceptance of the assumption "*Increased

local phylogenetic dispersion corresponds to increased local trait dispersion*". Silvertown *et al.* (2006)

found no relationship between relatedness of species within communities and their local ("alpha")

niches, while Prinzing *et al.* (2008) found even a negative relationship for most niche-axes and traits

tested (see also Gerhold *et al.* 2011). Kluge & Kessler (2011) found no significant pattern of

phylogenetic diversity along the elevation gradient, whereas functional-trait diversity did vary along

the gradient. Spasojevic & Suding (2012) found also no correlation between phylogenetic and

functional diversity along a stress-resource gradient (see also Purschke *et al*. 2013). In fact, Kraft *et

al.* (2007) have shown that local phylogenetic over-dispersion is indicative of a local trait over-

dispersion only if traits are very strongly conserved across the regional pool.

Overall, traits that are phylogenetically conserved across an entire major lineage or region

can be phylogenetically convergent or divergent within a local community (Tofts & Silvertown 2000;

Silvertown, Dodd & Gowing 2001; Prinzing *et al.* 2008). As a result, within a community trait

dispersion does not necessarily increase, but may even decrease with phylogenetic dispersion (Fig.

1). This triggers many interesting questions such as which traits show positive and which show

negative relationships (Silvertown *et al.* 2006). But it precludes simple application of phylogenetic distance as a proxy for trait distance, and thereby for negative interactions or filtering.

Assumption 2: A single ecological function can only be performed by a single trait state or combination of trait states.

It is assumed that a given assembly process (i.e. habitat filtering) selects for one specific state of a trait (e.g. tall plants when light is limiting), or combination of correlated trait states (e.g. large plants and fast growth) realized in one particular lineage. Phylogenetic dispersion of a community is then assumed to indicate the corresponding assembly processes structuring the community. However, we will outline below that multiple (combinations of) traits may be equally appropriate to ´solve an ecological problem´ (Fig. 1, caveat of assumption 2).

For example, a diversity of traits can be associated with increased ability to competitively suppress neighbours. Competitive ability can be enhanced through increased dispersal distance among ramets (Semchenko *et al.* 2013), increased plant height (Gaudet & Keddy 1988), altered root growth (Wang *et al.* 2010), and potentially shifts in growth *vs* architectural traits (Herben & Goldberg 2014). Thus, though it may be possible to suggest that a given trait of a plant species will influence competitive dynamics, we find little reason to believe that focusing on a single trait within a community is sufficient to understand the role competition has played in the assembly of that community – as other critical traits may be overlooked.

Complexities such as those described above for trait-competition relationships are commonplace among trait-function relationships. For example, some plant species in arid environments can deal with prolonged drought through drought tolerance, involving traits such as slow growth rates and high water use efficiency, while others use drought avoidance strategies,

involving traits such as prolonged seed dormancy and rapid growth during rain events (Kozlowski & Pallardy 2002). Plants can respond to herbivory by avoidance, tolerance, resistance or by profiting from herbivores as mutualists (e.g. for dispersal), each related to a different set of traits (Tiffin 2000; Nunez-Farfan, Fornoni & Valverde 2007).

We acknowledge that there may be environmental conditions for which there is only a single appropriate trait, or to which each species may develop multiple trait responses, including one that is shared among species. Light limitation, for instance, will trigger height growth in most species, in addition to one of multiple other solutions such as early phenology or thin leaves (Larcher 2003). In such hypothetical cases a single trait or a single phylogenetic lineage might dominate. However, in the bulk of the examples above, a single ecological problem can be resolved by fundamentally different traits or trait combinations, all potentially effective and evolutionarily stable. If these different trait solutions are represented by different phylogenetic lineages, we would not necessarily expect a given assembly process to cause any particular phylogenetic signal (Fig. 1, caveat of assumption 2).

Assumption 3: Trait similarity causes enhanced competition.

Drawing from both The Origin of Species *(Darwin 1859) and limiting similarity theory (MacArthur & Levins 1967), a common assumption in community phylogenetics is that differences in competition-related traits reduces the strength of competition among species. Consequently, it is commonly assumed that phylogenetic over-dispersion occurred because coexisting closely related species have more similar trait states (assumption 1), compete most intensely (this assumption), and exclude each other (below assumption 4; Webb et al. 2002). Below we will outline how trait similarity does not necessarily cause competition but it may even facilitate co-existence (Fig. 1, caveat of assumption 3).*

Surprisingly, though there exist mountains of opinion, theory, and conceptual papers discussing issues of trait similarity and competitive interactions (Webb 2000; Weiher & Keddy 2001; de Bello *et al.* 2012), empirical studies have until recently been rare. The most comprehensive study addressing functional similarity and competition found that the strength of 275 interaction coefficients among potentially coexisting tree species was not related to functional similarity (Kunstler *et al.* 2012). Additional studies have tested the hypothesis that more closely related species should compete more strongly than more distantly related species (e.g. Burns & Strauss 2011). The current empirical focus on this question began with Cahill *et al.* (2008), in which they report little support for the competition-relatedness hypothesis. Venail *et al.* (2014) list 15 independent empirical studies since 2008 testing this hypothesis, finding full support in only four studies, mixed results in two, and a lack of empirical support in nine of fifteen studies. We hence question the generality of this hypothesis, and recognize the potential impacts on the validity of the phylogenetic pattern-as-proxy approach.

Alternatives to the limiting similarity model predict that trait dissimilarity within a community may have different consequences on competition. Grime (2006) suggests that competition may be the strongest among species dissimilar in fitness-related traits such body size as there will be one stronger and one weaker competitor (see also Adler, HilleRisLambers & Levine 2007; Mayfield & Levine 2010; Narwani *et al.* 2013) (Fig. 1, assumption 2). Scheffer & van Nes (2006) suggest that among species similar in niche-related traits such as rooting depth, competition is symmetric and no species will win over another, enhancing again coexistence among similar competitor species (see also Yan *et al.* 2012). The alternative models are endpoints of a continuous gradient of assembly scenarios (Adler, HilleRisLambers & Levine 2007). Moreover, trait similarity may increase processes alternative to competition such as predation pressure (Yguel *et al.* 2011) or facilitation or shared mutualisms (Elias *et al.* 2009; Sargent *et al.* 2011). Finally, Venail *et al.* (2014)

suggest that not trait similarity or phylogenetic relatedness but species identity most strongly

impacts competitive and facilitative interactions. Combined, we suggest the data supporting the

limiting similarity model of plant competition is substantially more limited than one would imagine,

given how widely this concept is used in modern community ecology. This should be a high priority

for empirical studies.

Assumption 4: Competition necessarily causes species exclusion.

It is commonly assumed that competition leads to exclusion of species, and that the remaining

species are then phylogenetically over-dispersed. However, we will outline below how competition

may not always cause exclusion, but it may be without losers or winners (Fig. 1, caveat of assumption

4).

Gause's competitive exclusion principle serves as the foundation for much of the current

thinking on how competition may influence community assembly (Gause 1934). Despite substantial

numbers of examples of how coexistence can be maintained even when competition occurs (e.g.

temperature dependent competitive abilities; Park 1954, etc.) community phylogeneticists appear to

have adopted the assumption that competition leads to exclusion. Further, it is assumed such

exclusion will be non-random based upon evolutionary similarity (see assumption 3), resulting in

phylogenetic over-dispersion (*i.e.* limiting similarity *sensu* MacArthur & Levins 1967) or clustering

(*i.e.* weaker competitor exclusion *sensu* Mayfield & Levine 2010).

Different observations have been used to argue in favor of competitive exclusion among

closely related species. First, in forests, the adult trees in the canopy tend to be phylogenetically

over-dispersed in comparison to the young trees (Enquist, Haskell & Tiffney 2002; but see Gonzalez

et al. 2010), possibly because as competitive effects compound over the trees´ life time, exclusion

occurs. However, phylogenetic dispersion of the canopy might also reflect the large range of microclimates or the small effect of individual masting years on species composition. Second, laboratory experiments suggest competitive exclusion of phylogenetic proximate species (e.g. Violle *et al.* 2011). However, laboratory communities inevitably are sampled from very small species pools (10 species in Violle *et al.* 2011), and hence better reflect any pattern of niche conservatism in the pool (assumption 1). Moreover, petri-dishes in the laboratory may render coexistence particularly difficult as spatial or temporal segregation of microhabitat niches is rarely possible (Silvertown *et al.* 2006). In addition, even in the laboratory phylogenetic distance may be unrelated to coexistence (Best, Caulk & Stachowicz 2013; Narwani *et al.* 2013). The two existing studies that, in the field, compare competition to exclusion do not find any increase of phylogenetic dispersion with competition (Brunbjerg *et al.* 2012; Bennett *et al.* 2013). One possible explanation is that competition among closely related species is symmetric (e.g. among roots; Lamb & Cahill 2008), and hence causes no exclusion. Also, the outcome of competition among closely related species depends on the relative strength of the two types of species differences: while differences in competitive ability drive some species to dominance and others to elimination, niche differences stabilize species coexistence as individual fitness increases when species' density decreases (Adler, HilleRisLambers & Levine 2007).

Overall, it appears that though competition can cause exclusion, exclusion is not a necessary consequence of competition (Fig. 1, caveat of assumption 4).

Assumption 5: The system is at "rest" such that the process of assembly has played out.

When community structure, such as phylogenetic dispersion, is interpreted as the result of community assembly processes this implies that such processes operated both constantly and for a sufficiently long time (i.e. multiple years or generations) for community structure to respond.

However, we will outline below that species communities are often at non-equilibrium and

community structure only incompletely reflects assembly processes (Fig. 1, caveat of assumption 5).

Species losses or gains due to assembly processes typically happen only after shifts in species abundances, and are hence slow (e.g. Booth & Grime 2003; Fig. 1). We often observe non-equilibrium communities, particularly if organisms are long-lived or if disturbances are frequent. Many systems are maintained in permanent non-equilibrium, for instance grasslands maintained by grazing (Fig. 1, caveats of assumption 5). As a result, despite strong competition among species in grasslands (Cahill *et al.* 2008) this competition may not leave a signature in species composition if grazing is sufficiently frequent (e.g. Zobel 1992). Moreover, Paine *et al.* (2012) found that different processes during different stages of succession may result in the same phylogenetic pattern within a community, reflecting different degrees to which the system is at rest. Gerhold *et al.* (2013) found assembly processes that are generally seen as mutually exclusive operating at different stages of assembly of the community. While dynamic, successional sequences have been studied using community phylogenies, the underlying assumption remained implicitly static: that strong interactions operate for sufficiently long time to lead to species exclusion and hence influence the patterns of phylogenetic diversity (e.g. Letcher 2010; Graham *et al.* 2012; Purschke *et al.* 2013).

Overall, studies on phylogenetic (and other) community structure are typically temporal "snapshots", and we do not know whether they portray endpoints or transient dynamics, in particular in the presence of disturbances or long-lived species. Moreover, interpreting such snapshots of co-occurrence as co-existence is notoriously difficult due to spatial and temporal variability in population demography of the co-occurring species (Siepielski & McPeek 2010). Consequently, assumptions 1-4 can all be true but there will be still no consistent, predictable

changes in phylogenetic (or in any other) community structure due to a non-equilibrium state of the community.

Assumption 6: Habitat filtering and competition are alternative processes, not operating together nor interacting.

Inferring the role of habitat filtering and competition from a single parameter (i.e. phylogenetic dispersion) only makes sense if the two processes are truly alternative – strong filtering implies little competition and weak filtering corresponds to strong competition. However, we will show below that habitat filtering and competition may also be independent or mutually imply each other (Fig. 1, caveat of assumption 6).

We acknowledge that studies using phylogenetic patterns as proxy of assembly tend to ask what is the *relative* importance of filtering and competition. The interpretation, however, tends to be *absolute*. To our knowledge no study insists that the factor ranked as relatively less important might in fact still have a major absolute importance or that the factor ranked as relatively more important might still only have a minor absolute importance. These absolute magnitudes of filtering and competition effects on assembly may change independently; the situation of "no filtering, no competition" might then result in a similar phylogenetic pattern of "strong filtering, strong competition" (Fig. 1, caveat of assumption 6). Alternatively filtering and competition may operate in parallel at larger and finer spatial scales, respectively (Helmus *et al.* 2007, Harmon-Threatt & Ackerly 2013; Parmentier *et al.* 2014) and may interact, too (Kraft *et al.* 2007). Habitat filtering can increase competition among the species suitable for the habitat (Kunstler *et al.* 2012). Also, increased habitat filtering of unadapted species may be confused with increased competitive exclusion (Grime 2006), when relying on trait or lineage dispersion (Mayfield & Levine 2010; Kunstler *et al.* 2012). Finally,

differences in ecological niches (e.g. soil texture requirement) may permit coexistence between competitors, whereas differences in traits determining competitiveness and fitness (e.g. plant height in light competition) may lead to exclusion of either of the competitors (Chesson 2000, Adler, HilleRisLambers & Levine 2007). Hence, habitat filtering of niches might reinforce competitive exclusion, whereas habitat filtering of traits determining competitiveness may increase coexistence of competitors. No single trait or phylogenetic proxy can sort out this complexity.

Assumption 7: Community phylogenetic dispersion depends on local and present-day processes only; without such local processes phylogenetic dispersion is random.

The structure of local communities, such as their phylogenetic dispersion, has been traditionally used to infer local processes of assembly. This implies that this structure only depends on local processes. However, we will show below that phylogenetic structure of a local community may reflect phylogenetic structure of the habitat type of this particular community rather than local assembly processes (Fig. 1, caveat of assumption 7).

Assembly of a community in a local habitat patch is influenced by dispersal, either short-distance dispersal from adjacent patches of other habitats or from refuges ("mass effects" in Leibold *et al.* 2004, post-glacial recolonisations in Leibold, Economo & Peres-Neto 2010) or by long-distance dispersal between patches of the same habitat type ("species sorting", and "patch dynamics" at equilibrium in Leibold *et al.* 2004). Within-habitat type dispersal results in the formation of different species pools in different habitat types. Multiple studies have shown that such large-scale species pools of different habitats are characterized by different phylogenetic structures (e.g. Cavender-Bares, Keen & Miles 2006; Swenson *et al.* 2007; Cavender-Bares *et al.* 2009) - habitat species pools are in fact habitat lineage-pools (Pärtel 2002). Moreover, recent evidence suggests that the lineage-

pool of a habitat type (e.g. grasslands) can influence the phylogenetic structure of local communities (Lessard *et al.* 2012). For example, in a habitat type occupied by lineages that have only relatively recently diversified, the lineage-pool is composed of more closely related species than expected by chance (Bartish *et al.* 2010). Past abundance of habitat types may drive present patterns of species diversity (Zobel *et al.* 2011) and possibly of phylogenetic diversity of habitat lineage-pools. Local communities within habitat patches are sampled from these habitat lineage-pools and can consequently reflect their macroevolutionary diversification (*i.e.* evolution at or above the level of species). This might result in phylogenetic over-dispersion in communities of evolutionary old habitat types and clustering in communities of evolutionary young habitats (Fig. 1, caveat of assumption 7). To our knowledge it has not been studied to which degree clustering of the habitat lineage-pool explains clustering of the communities in local habitat patches. We further develop this point in section III.

There are multiple methodological approaches that may help identifying the effect of lineage-pools of habitats (Hardy 2008) and there are others permitting to filter them out (Hardy & Senterre 2007, Baraloto *et al.* 2012). However in the next section we will show that the very differences between the phylogenetic structures of habitat lineage-pools are interesting in themselves as they connect local coexistence within habitat patches to the macroevolution of lineages. These differences deserve to be the focus of a research program in itself instead of being used as co-variables.

III. Where to go: put evolution into community phylogenetics

Despite an increasing number of pictures of Charles Darwin in conference presentations of community ecologists, the questions asked in many of these studies do not concern any evolutionary processes. Phylogeny is often used only as a proxy for aspects of ecology, though as stressed by

Losos (2011), using phylogenetic approaches helps in finding patterns rather than identifying evolutionary (let alone ecological) processes. The obvious solution would be to use community phylogenetic dispersion not as a proxy for ecological processes, but to develop hypotheses on how phylogenetic diversification of lineages results from, or causes, community assembly. The phylogenetic patterns-as-result approach asks: Do particular assembly processes control the coexistence and adaptation of closely related species, and how do coexistence and adaptation of closely related species control patterns of phylogenetic diversification? The phylogenetic-patterns-as-cause approach asks: How do patterns of diversification of lineages control the phylogenetic structure of communities, and how does phylogenetic structure control assembly? We will develop both approaches.

If phylogenetic diversification and local coexistence interact, the widely-held view of a distinction between macroevolutionary and ecological scale would no longer hold. For too long macroevolution has been thought to operate at a "regional scale" and ecological assembly at the scale of local patches within communities (Cornell & Lawton 1992; Lawton 1999), ignoring that these patches form networks of a given habitat often stretching across multiple regions. We are certainly not the first to think about these relationships between coexistence and diversification (e.g. Johnson & Stinchcombe 2007; Cavender-Bares *et al.* 2009; 2012), but most of the existing studies are restricted in their coverage of concept or in their generality. Many studies are restricted to only one step in the chain connecting phylogenetic diversification and local coexistence (for instance to the relationship between openness of local communities to aliens and the phylogenetic dispersion of the communities, without further explaining the historical causes of phylogenetic dispersion; Gerhold et al. 2011). Other studies are restricted to cases of a single, minor lineage such as a genus (e.g. lizards in Glor *et al.* 2003), or to one particular environment (e.g. one extreme environment compared to others; Anacker *et al.* 2011). We believe that the existing methods to describe the phylogenetic

structure of a large number of communities across a large taxon (such as fishes or angiosperms) and a large range of environments (such as all lakes in a region or an entire vegetation survey) provide a tool permitting to overcome these restrictions of case studies. Applied within the below approaches (and not as a proxy) these tools would permit ecoevolutionary analyses to cover the full range of lineages that species are facing within a community and the full range of environments that lineages are encountering throughout their evolution. In short, tools from community phylogenetics may help to identify interactions between diversification and coexistence. The fact that such studies are currently rare is unfortunately a collateral damage caused by current extensive focus on the phylogenetic-patterns-as-proxy, as we explain in Appendix S2.

1. Phylogenetic-patterns-as-result: How ecological co-existence can affect macroevolutionary processes.

Interactions influence macroevolutionary diversification.

Species interactions are known to affect diversification: competition may trigger speciation, lineage diversification or the origin of dissimilar swarms of similar species (Scheffer & van Nes 2006; Moen & Wiens 2009; Rabosky *et al.* 2011); arms races with natural enemies may trigger speciation (e.g. Smith & Benkman 2007; Benkman, Parchman & Mezquida 2010), and lineage diversification (Vermeij 2011); and the same is true for mutualist interactions (Janson *et al.* 2008; but see Smith *et al.* 2008; Herrera & Pellmyr 2002); notably between natives and "invading" non-native species, Vellend *et al.* 2007). In plants, such interactions with locally coexisting species may in part explain the abundance of local speciations (Givnish 2010). Moreover, some key innovations that characterize entire lineages are likely the outcome of such interactions (such as defensive silicas in grasses; e.g. Massey, Ennos & Hartley 2006). There is however, to our knowledge, no consistent theory spanning the entire range from local co-existence to macroevolutionary diversification (but see Bruun & Ejrnaes 2006).

Community structure influences interactions and hence macroevolutionary diversification.

The presence of many species in a community can induce many interactions and possibly trigger the origin of even more species (Emerson & Kolm 2005; but see Cadena *et al.* 2005). Specifically, coexistence among closely related species can trigger character displacement to reduce competition intensity (Dayan & Simberloff 2005), or character convergence to reduce competition asymmetry (Scheffer & van Nes 2006). The former can accelerate character diversification within lineages, which in turn can, potentially, contribute to a reduction in niche conservatism (Ackerly 2009). The latter can do the opposite. Predation on coexisting closely related butterflies of repellent taste leads to convergence of warning signals (Elias *et al.* 2009) or escaping behaviors (Stoks & McPeek 2006). Enemy release of hosts growing in a phylogenetically distant neighborhood (above references) might facilitate the host's colonization of such neighbourhoods and promote niche diversification (Yguel *et al*. 2014). Finally, closely related species often interact by hybridization. Hybridization in turn is one of the major evolutionary forces of diversification, creating species of increased genetic diversity (with strong potential ecological consequences, e.g. McArt, Cook-Patton & Thaler 2012), and hybridization of plant hosts may trigger the speciation of phytophages (Evans *et al.* 2008).

Habitat type controls community structure, interactions, and hence diversification.

The importance of the various above mentioned species interactions can vary strongly between communities of different habitat types and taxa. For example, the intensity of competition or the number of trophic levels might increase in communities in habitats of high soil fertility (Oksanen *et al.* 1981). The long-term implications of such habitat-specific interactions within communities for lineage diversification have so far rarely been searched, probably due to supposed ephemeral nature of local communities. However, local communities are connected into persistent networks (e.g. all calcareous, temperate prairies of the planet) maintaining persistent habitat lineage-pools. Within-

community ecological processes affecting natural selection and drift can ultimately scale up to macroevolutionary diversifications of entire lineage-pools of habitats (see e.g. Zobel *et al.* 2011). This evolutionary diversification of the habitat lineage-pools will then be reflected in local communities sampled from these pools. In some fields of evolutionary ecology, such as plant-pollinator interactions, this reflection is trivial. In other fields of ecology this reflection remains unrecognized. If habitats differ in local assembly processes, and local assembly processes can scale up to the evolutionary diversification of the lineage-pool of that habitat, this creates differences in diversification of lineage-pools among habitat types. We will outline in the next section some examples how these differences can be studied.

Turning assumptions and caveats of the phylogenetic-patterns-as-proxy approach into hypotheses of the phylogenetic-patterns-as-result approach.

As an example of a testable set of hypotheses on how co-existence can affect macroevolution we come back to the above set of assumptions made by the phylogenetic-patterns-as-proxy approach. Instead of making assumptions about assembly processes we can ask how these processes explain phylogenetic patterns of evolutionary interest. For example, should one find (instead of assume) that strong habitat filtering indeed decreases phylogenetic dispersion in specific habitats, then we can hypothesize occurrence of sympatry and niche convergence among closely related species in these habitats (Fig. 1, right part; see Tab. S3 for details). Also, should one find (instead of assume) that in specific habitats strong competition results in increased phylogenetic dispersion, then we can hypothesize occurrence of sympatry and habitat-niche convergence among distant relatives and allopatry and niche divergence of closely related species in these habitats (Fig. 1, right part). We also suggest a phylogenetic-pattern-as-result hypothesis for each of the seven assumptions listed in chapter II (Fig. 1). We stress that each of these hypotheses describes what theory predicts as a consequence of a given assembly process. This assembly process would have to be demonstrated

(and not inferred) a priori using the approaches outlined in Tab. S3. The hypothesis then makes objective, testable predictions. Overall, the phylogenetic-patterns-as-result approach can contribute to explaining patterns of prime interest to evolutionary biologists, such as the major variation in sympatry or in habitat niche between related species, ranging from virtually total overlap to total mutual exclusiveness (Barraclough & Nee 2001).

The interaction between macroevolutionary diversification and co-existence, however, is not one-way. In the next section we will treat the opposite direction, how phylogenetic patterns can be a cause of ecological co-existence. Obviously, these two directions of the interaction are mutually non-exclusive and may actually mutually reinforce each other.

2. Phylogenetic-patterns-as-cause: How macroevolutionary processes can affect interactions among co-existing species.

Macroevolution within habitat lineage-pools constrains phylogenetic dispersion of local communities.

The phylogenetic structure of a local community is often understood as being constrained by the phylogenetic structure of the regional lineage-pool (Ricklefs & Schluter 1993), which is hence used as a null model to study community phylogenetic structure. However, the habitat lineage-pool may be no less important than the regional lineage-pool (Pärtel 2002). Usually, habitats have been considered as being nested within regions, which implies that they are younger than the regions. However, there is no reason for such a nested hierarchy of habitats within regions. In fact, the ´global´ lineage-pool of a habitat type may be more important than the regional lineage-pool across all habitat types in determining community phylogenetic structure (Fig. 2). For instance, the phylogenetic relatedness of plant species in two grassland communities on two distinct continents can be higher than the phylogenetic relatedness of a grassland and a forest patch on the same continent, even though macroecological studies often pool such distinct habitat types across grid

cells (Winter *et al.* 2009). In fact, Ortega *et al.* (1997) found that across the Canary archipelago in the Atlantic Ocean lineages seem to be more capable of jumping between islands than between habitat types, *i.e.* vegetation zones (note that smaller organisms might perceive habitats at a scale much finer than vegetation zones, e.g. litter, tree trunks, tree canopies, e.g. Prinzing & Woas 2003). Similarities among communities of the same habitat type on different continents are further increased by the unprecedented introduction of non-native species in all places of the world (Winter *et al.* 2009), combined with the tendency of species to maintain their habitat niche after introduction (e.g. Petitpierre *et al.* 2012).

While local communities are ephemeral, habitat types and their lineage-pools can persist for geological time periods. Hence, species compositions in contemporary communities of a given habitat type might correspond to lineage-pools of that habitat type even for millions of years. Indeed, relationships between biota and environments have been found to persist across millions of years despite temporary disintegration of these relationships for thousands or few million years (Boucot 1996). Paleo-ecologists have even suggested that lineage-pools will re-assemble after temporal disappearance and reappearance of the habitat type (DiMichele *et al.* 2004). Many of the present habitats may appear at first sight unique and recent, given the strong and dynamic impact of recent quaternary climate changes and human transformation. However, many of the dynamic, present environmental impacts on habitats may trigger environmental constraints that have existed in other forms already in earlier geological epochs. Artificial ponds or live-stocking, for example, can trigger submerged and grazed conditions colonized by lineages adapted to these conditions since many million years (Antonelli *et al.* 2011). Ultimately this may explain why we tend to find particular past phylogenetic lineages in particular present-day habitats (e.g. Prinzing *et al.* 2001).

Often being formed during millions of years, lineage-pools of distinct habitat types possess distinct evolutionary histories which are inevitably reflected in the phylogenetic structure of

contemporary communities sampled from these lineage-pools. The maximum age of many lineages has been found to be linked to the age of habitat types, which is particularly straightforward if the lineages themselves physically construct these habitat types such as trees constructing forest habitats (Wang *et al.* 2009). Hence, lineage-pools of ancient habitat types may have diversified for a long period. Moist or aquatic habitats, for instance, are more ancient than Angiosperms (Wing & Boucher 1998), contrary to, for instance, habitats dominated by grazing of large mammals (Sues *et al.* 1992). As a possible result, aquatic habitats today show a phylogenetic over-dispersion of incumbent Angiosperm species pools (Bartish *et al.* 2010). Evolutionary young habitat types, in contrast, have undergone rapid recent diversification and are phylogenetically clustered. For instance, dry open habitats can be relatively recent in the history of Angiosperms and may have acted as arena of the recent radiation, e.g. of the Mediterranean flora with only very limited immigration of lineages from more ancient habitats (Ackerly 2003; Bartish *et al.* 2010), or fynbos compared to subtropical thicket in South-African vegetation (Procheş *et al.* 2006). As a result, contemporary communities of the evolutionary old habitat types can draw their constituent species from a wider range of major, old lineages than the communities of the young habitat types (see also Gerhold *et al.* 2008). Consequently, phylogenetic dispersion may be much higher in local communities of evolutionary older than in younger habitat types. Similar ideas have been discussed by Wiens and Donoghue (2004) for tropical vs. temperate habitats and have recently been expanded to different altitudinal levels at square kilometers resolution (Hutter, Guayasamin & Wiens 2013). To our knowledge these ideas have not yet been applied to at the scale of habitats differentiated in local patches of only hundreds of square meters, the scale most community ecologists study.

Phylogenetic dispersion of a local community might hence be the result of macroevolutionary diversification in lineage-pools of habitat types, instead of or in addition to ongoing assembly processes (Hubert *et al.* 2011). There is however, still an alternative scenario of

evolutionary community assembly not involving conserved lineage-pools: on remote oceanic islands

closely related species might overcome niche conservatism and adapt to new habitats in order to

colonize empty niches (Emerson & Gillespie 2008, for similar phenomena in urban „island" of

artificial habitats see for instance Donihue & Lambert 2014). We can hypothesize that such a

scenario is more likely when niche conservatism is low and dispersal is a limiting factor in

determining community phylogenetic structure.

Phylogenetic dispersion of a local community being the result of macroevolutionary

diversification of the corresponding habitat lineage-pool contradicts above assumption 7 of the

proxy approach. However, it also triggers a number of interesting new questions. First we can ask

whether age and rate of diversification within a given habitat type influence present structure of the

lineage-pool of the habitat and of the local communities within the habitat. Such a relationship

implies that the lineage-pool of a present habitat results to a large degree from diversification within

this or similar habitats, and indeed this appears likely, for instance, in elevational habitat zonations

(Hutter, Guayasamin & Wiens 2013). Early diversification will be represented by high mean

phylogenetic distances among species, whereas a high rate of diversification will be represented by

low distances among closely related species. These two distances are standard parameters used in

community phylogeny (Webb et al. 2002), but without possible macroevolutionary interpretation so

far. Second, we can ask how patterns of macroevolutionary diversification may affect the

microecological coexistence mechanisms in local communities. Below we will give some examples of

possible effects of phylogenetic pattern on local coexistence. Our goal is not to provide a compact

body of theory but to demonstrate that searching for effects of phylogenetic pattern on local

coexistence can be pertinent in many fields in ecology. We stress that in none of the examples we

use community phylogenies as a proxy, and hence they do not suffer from the problems of the proxy

approach outlined in section 2.

Example 1: Does phylogenetic clustering of local communities increase character displacement? Character displacement represents the divergence of trait-states of competing species too similar to one another could not coexist without diverging (Dayan & Simberloff 2005). Ecologists have long searched for, and found, character displacement among some closely related species (Lack 1942), albeit in general the phenomenon may be only moderately frequent (Stuart & Losos 2013). We should thus find character displacement in phylogenetically clustered communities rather than in over-dispersed communities. This was found recently for plant communities (Prinzing *et al.* 2008) but evidence had accumulated for a long time. For instance, Becerra (2007) observed that species in the plant genus *Bursera* possess more dissimilar defense chemicals if they locally coexist than if they do not. We admit that it can be methodologically challenging to confirm character displacement in one trait among other traits which possibly serve the same ecological function (see assumption 2 in Section II).

Example 2: Does phylogenetic clustering of local communities increase or decrease invasibility (Fig. 3b)? Successful establishment of aliens may be more likely for aliens with no close relatives in the recipient native community, due to lack of competitive exclusion ('Darwin's naturalization hypothesis'; Strauss, Webb & Salamin 2006; Parker *et al.* 2012), but the opposite has also been found (reviewed in Thuiller *et al.* 2010 and Maitner *et al.* 2012). Everything else being equal, an alien is more likely to face related natives in a recipient community representing many phylogenetic lineages than in a phylogenetically clustered community representing only few lineages. The latter should thus be more open to aliens than the former. This is what Gerhold *et al.* (2011) observed, albeit paleo-ecological scenarios indicate the opposite (e.g. DiMichele & Bateman 1996). Gerhold *et al.* suggest that phylogenetically clustered communities are sampled from "naïve" habitat lineage-pools that have been closed to immigration from distant lineages during the

evolutionary past (environmental islands; Ackerly 2003) rendering these communities open to aliens today (Fig. 3b).

Example 3: Does phylogenetic clustering of local communities increase enemy pressure? Natural enemies such as phytophages or parasitoids tend to be neither specialized on a single host species nor completely generalist, but specialized on a set of closely related hosts ("oligophages"; Strong, Lawton & Southwood 1984). In a phylogenetically clustered community coexisting species are closely related and are hence likely to exchange more natural enemies than in a phylogenetically over-dispersed community (Jactel & Brockerhoff 2007; Yguel *et al.* 2011). Consequently, higher evolutionary proximity instead of contemporary spatial proximity of neighboring plants may drastically increase phytophagy (Yguel *et al.* 2011; Parker *et al.* 2012) and constrain phytophage community assembly (Vialatte *et al.* 2010). Inversely, hosts in phylogenetically over-dispersed communities tend to be surrounded by phylogenetically distant neighbors and hence might profit from reduced pressure by natural enemies.

Example 4: Does phylogenetic clustering of local communities increase or decrease mutualism and facilitation? Mutualistic or facilitative interactions between species are often the result of complementary capacities of the involved species, reflecting complementary traits, which are often expressed in distantly related species. Coexisting distantly related species are hence considered more likely to be complementary and to engage in mutualism than coexisting closely related species (Verdu *et al.* 2009; Valiente-Banuet & Verdu 2013, but see Venail *et al.* 2014 who found no effect). In that case, species profit from growing in communities composed of distantly related species. However, mutualism/facilitation may also result from similarity, in particular when mediated via a third species. Elias *et al.* (2009) and Sargent *et al.* (2011) show that closely related

neighbors can benefit from each other by mutually repulsing of shared predators or attracting shared pollinators (chapter II). These species hence profit from growing in communities composed of closely related species.

We acknowledge that both approaches, phylogenetic-patterns-as-result and phylogenetic-patterns-as-cause, are methodologically challenging. The biggest challenge is probably to sort out cause and effect. We see four promising approaches that have been suggested in the literature to infer causal relationships, but stress that none of them is a perfect cure. First, we increasingly need in situ, local observational and experimental studies of the processes inferred from phylogenetic patters (Losos 2011; Weber & Agrawal 2012). The performance of species needs to be studied in the presence of closely or distantly related species (e.g.Venail *et al.* 2014). „Performance" include reproductive output and abundance but also characters permitting to avoid competitors (e.g. self thinning), lack of resources (high C/N), or pathologies (grazing, necrosis). Such direct tests will only cover subsets of the phylogeny and short time periods, and may hence be non-representative for patterns of coexistence and phylogenetic diversification in the geological past when macorevolution happened. However, these tests are the only way to really manipulate processes, even if most manipulations will affect multiple processes at a time (HilleRisLambers *et al.* 2012). Second, when studying whether patterns of co-existence are consistent with the predictions of hypotheses we should increasingly follow co-existence through time over many years. This would truly permit identifying causes and consequences for community assembly. Under-exploited tools to do so are permanent-plot data-bases as available from forestry, for instance (e.g. Joyce & Rehfeldt 2013). Third, when studying patterns of co-existence across phylogenetic trees, reconstructing the temporal order at which patterns of diversification and of coexistence occur is important to identify what is cause, *i.e.* comes early, and what might be effect, *i.e.* comes late (e.g. Brooks & McLennan 2002; Moen, Smith & Wiens 2009). Finally, we suggest profiting from the experiments that nature has already replicated,

such as the impact of environments on the replicated diversification of multiple lineages (e.g. Kiessling, Simpson & Foote 2010). Consistent evolutionary trajectories across multiple lineages strongly increase the confidence in the conclusions. Such studies searching for patterns „consistent with" a hypothesis can cover larger ground than the in situ tests described before, but are often less safe in the interpretation.

IV. Conclusions

Phylogenetic dispersion of communities is of limited value for understanding ecological assembly processes, but of high value to address other questions in eco-evolutionary research. The links between ecological assembly processes and trait patterns, and between trait patterns and phylogenetic dispersion of communities, might be too complex and weak. Instead, information on phylogenetic community structure is a potentially valuable tool to answer evolutionary questions, where community ecology can be seen as macroevolution in action. Phylogenetic community structure may permit to identify macroevolutionary idiosyncrasies of habitats, of their associated lineage-pools and hence of the communities sampled from these pools. The phylogenetic structure may also help to clarify how local interactions between closely or distantly related species help to maintain macroevolutionary diversity of species and traits.

Acknowledgements

Data Accessibility

This paper does not use data, but additional supporting information may be found in the online
version of this article.

Figure legends

Figure 1. Phylogenetic-patterns-as-proxy approach: The concept of using community phylogenetic

dispersion as a proxy for ecological assembly processes (*i.e.* habitat filtering and competition),

assumptions underlying the concept and the respective caveats. The arrows indicate the species that

reach the communities (solid boxes) from their phylogenetic position or with their specific trait

values. "Traits" is short for "traits state". Trait state ranges from small (small dots) to big values (big

dots). ☺ = viable co-existing species; ☹ = co-existing species with reduced fitness due to

competition. **Phylogenetic-patterns-as-result approach:** Macro-evolutionary patterns resulting from

the assembly processes presented in the left part of the figure (see Tab. S3 for details).

Figure 2. Conceptual figure of phylogenetic structures of communities in different habitats (squares:

grasslands, triangle: forest, star: swamp) and on different continents. Lineage-pools of habitats (solid

circle) may encompass similar sets of phylogenetic lineages while the lineage-pool of a region

(dashed circle) encompasses different sets of lineages. This indicates that evolution of lineages has

been more strongly constrained by habitat type across regions than by region across habitat types.

Figure 3. (a) Phylogenetic-patterns-as-result approach: An example of ecological co-existence affecting macroevolutionary diversification – e.g. interaction between preys and predators may result in selection, extinction and speciation (e.g. Smith & Benkman 2007) and finally macroevolutionary diversification of some lineages and disappearance of others (Vermeij 2011). Communities with less predators (e.g. due to lower prey abundances or due to higher numbers of top predators) would not lead to these patterns of predator-induced prey diversification. These processes are classical at the level of predator-prey interactions, but might also operate at the level of competitive or other interactions. **(b)** Phylogenetic-patterns-as-cause approach: An example of macroevolutionary diversification affecting ecological co-existence in local communities – e.g. receptiveness to invasions. These diversifications and assembly processes are classical at the level regional lineage-pools of spatially isolated islands but might also operate at the level of distinct lineage pools (environmental islands *sensu* Ackerly 2003; see e.g. Gerhold *et al.* 2011).
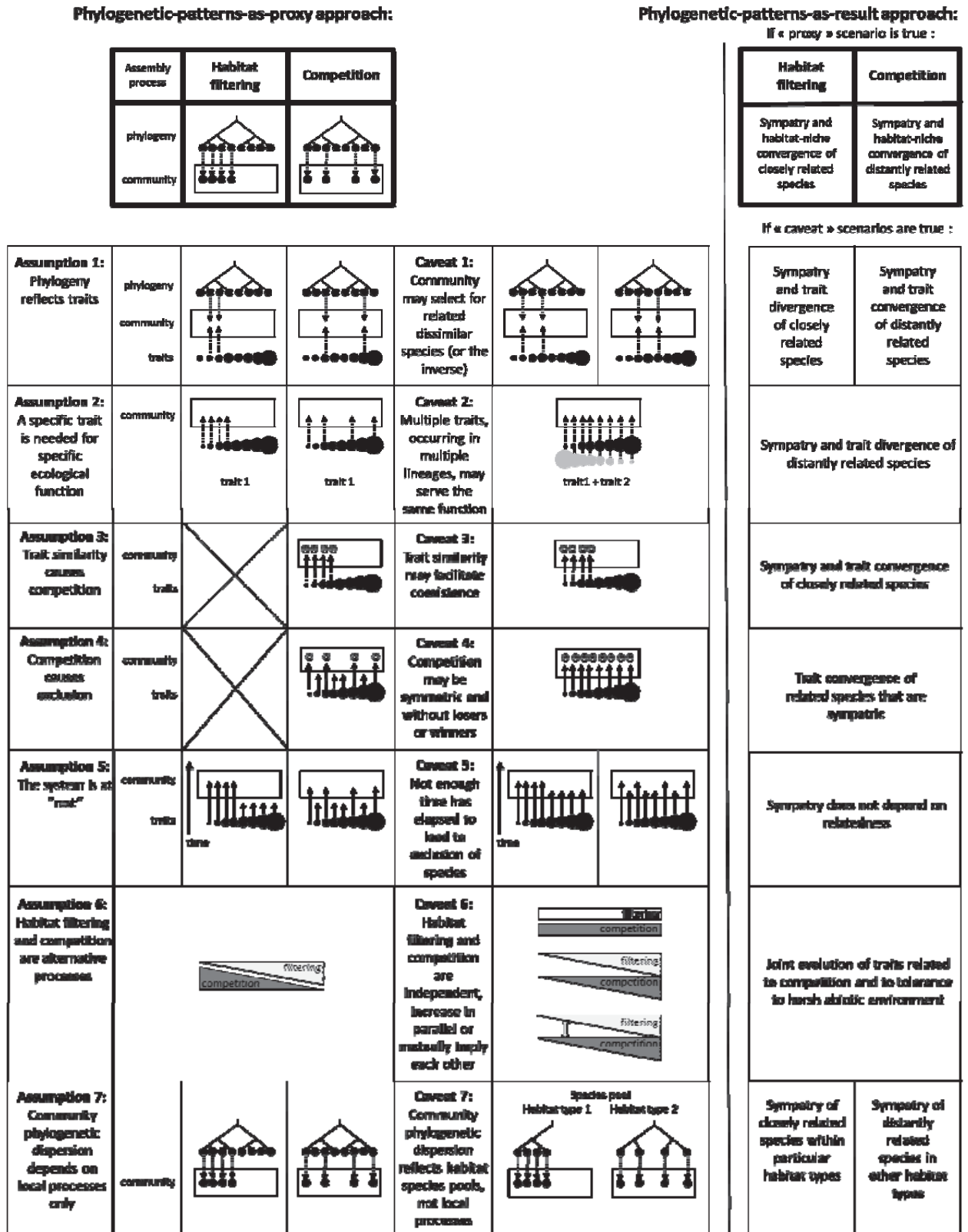
Figure1

Figure 2

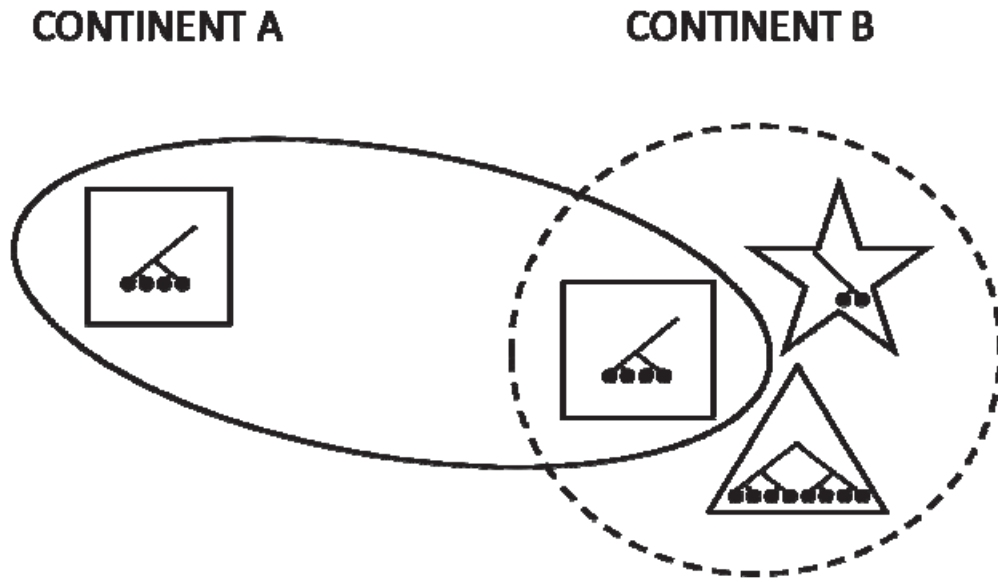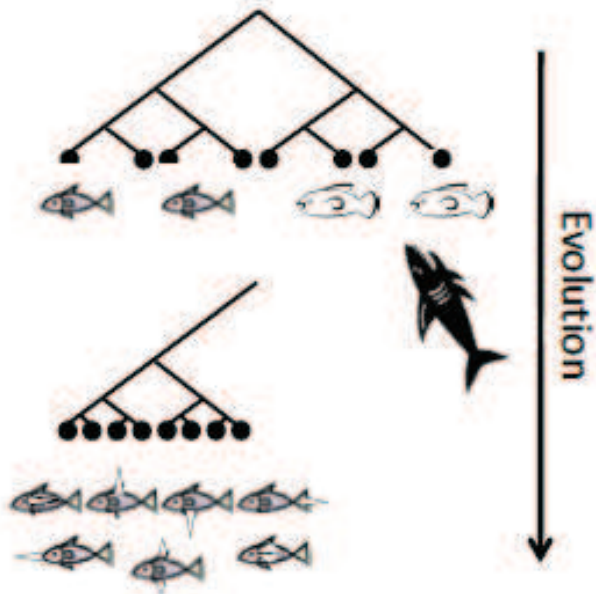CONTINENT A   CONTINENT B

Figure 3

(a) Negative interactions in present-day local communities may result in selection...

... potentially leading to disappearance of some lineages and in other lineages to macroevolutionary diversification through arms races (arms of prey indicated as spines).

(b) Diversification of a single lineage and resulting phylogenetic clustering in isolated regional species pools.

Present-day local communities sampled from these isolated habitat species pools are more receptive to aliens as many of them belong to lineages not represented within the local community.

Evolution

Assembly
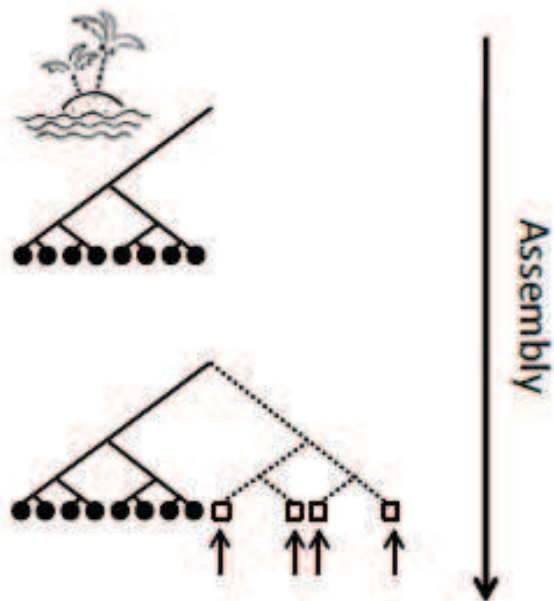
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SUPPORTING INFORMATION

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

Figure S1 Number of publications using the phylogenetic-patterns-as-proxy approach.

Appendix S2 Possible detriments of the phylogenetic-patterns-as-proxy approach to other approaches in community ecology.

Table S3 Hypotheses of phylogenetic-patterns-as-result approach.

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