

COMMUNITY PHYLOGENETICS AND ECOSYSTEM FUNCTIONING

Community assembly, coexistence and the environmental filtering metaphor

Nathan J. B. Kraft^{*,1}, Peter B. Adler², Oscar Godoy³, Emily C. James², Steve Fuller² and Jonathan M. Levine⁴

¹Department of Biology, University of Maryland, College Park, Maryland, 20742, USA; ²Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah, 84322, USA; ³Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, PO Box 1052, Sevilla E-41080, Spain; and ⁴Institute of Integrative Biology, ETH Zurich, Universitätstrasse 16, 8092 Zurich, Switzerland

Summary

1. One of the most pervasive concepts in the study of community assembly is the metaphor of the environmental filter, which refers to abiotic factors that prevent the establishment or persistence of species in a particular location. The metaphor has its origins in the study of community change during succession and in plant community dynamics, although it has gained considerable attention recently as part of a surge of interest in functional trait and phylogenetic-based approaches to the study of communities.

2. While the filtering metaphor has clear utility in some circumstances, it has been challenging to reconcile the environmental filtering concept with recent developments in ecological theory related to species coexistence. These advances suggest that the evidence used in many studies to assess environmental filtering is insufficient to distinguish filtering from the outcome of biotic interactions.

3. We re-examine the environmental filtering metaphor from the perspective of coexistence theory. In an effort to move the discussion forward, we present a simple framework for considering the role of the environment in shaping community membership, review the literature to document the evidence typically used in environmental filtering studies and highlight research challenges to address in coming years.

4. The current usage of the environmental filtering term in empirical studies likely overstates the role abiotic tolerances play in shaping community structure. We recommend that the term ‘environmental filtering’ only be used to refer to cases where the abiotic environment prevents establishment or persistence in the absence of biotic interactions, although only 15% of the studies in our review presented such evidence. Finally, we urge community ecologists to consider additional mechanisms aside from environmental filtering by which the abiotic environment can shape community pattern.

Key-words: competition, functional traits, habitat filtering, niche differences, phylogenetic relatedness, species pool

Introduction

One of the most enduring concepts in the study of community assembly and dynamics is that of the environmental or habitat filter. While the understanding that the abiotic environment shapes the distribution of species across the landscape predates much of the modern study of ecology

(e.g. Humbolt & Bonpland 1805; Schimper 1898), the current use of the environmental filtering concept has its roots in the study of plant community assembly and dynamics in the late 1970's and early 1980's (Nobel & Slatyer 1977; van der Valk 1981; Bazzaz 1991; Woodward & Diament 1991). These foundational studies described the environment as a metaphorical ‘sieve’ or ‘filter’ that only permits species with particular traits or phenotypes to establish and persist, excluding all others. The concept has grown in usage

*Correspondence author. E-mail: nkraft@umd.edu

considerably since this time, playing an important role in many studies of community assembly, succession, invasion biology and biogeography (e.g. Weiher, Clarke & Keddy 1998; Richardson *et al.* 2000; Webb 2000; Cornwell, Schwillk & Ackerly 2006; Swenson *et al.* 2012; Whitfeld *et al.* 2012).

Despite the widespread use of the term, the environmental filtering metaphor is still used in a form today that is largely unchanged from its original meaning. As with any metaphor, there are circumstances where the environmental filtering concept is potentially useful, and other circumstances where the usage of the metaphor is misleading and may in fact obscure the ecological forces at work. The goal of this review is to critically explore the environmental filtering concept by (i) revisiting the filtering metaphor in the light of recent developments in coexistence theory, (ii) proposing more stringent criteria for empirical evidence of environmental filtering in ecological studies, (iii) reviewing the ecological literature on environmental filtering in relation to these criteria and (iv) highlighting key issues to consider going forward in the study of the relationship between the abiotic environment and community assembly.

It is worth noting that most authors use the terms 'environmental filtering', 'abiotic filtering' and 'habitat filtering' interchangeably to refer to the role of the abiotic environment. However, recently some authors have made a distinction between these terms, using 'habitat filtering' as a more general term to refer to the combination of both biotic and abiotic factors (e.g. Maire *et al.* 2012). Here, we use 'environmental filtering' throughout to reduce ambiguity and to emphasize our focus on abiotic factors, which is closer to the original meaning of the concept.

Environmental filtering and coexistence theory

At its core, the environmental filtering concept focuses on the relationship between an organism and the environment, recognizing that not all organisms will be able to successfully establish and persist in all abiotic conditions. From this perspective, the environment is seen as a selective force, culling species unable to tolerate conditions at a particular location. If species that are able to survive at a location share common phenotypic traits conferring abiotic tolerance, certain phenotypic similarities reflecting this tolerance may be seen among community members. This logic leads to some of the most widely tested predictions in environmental filtering studies – specifically that species at a site exhibit phenotypic convergence in key ecological dimensions, relative to a null expectation based on random sampling from the species pool (e.g. Weiher, Clarke & Keddy 1998; Cornwell, Schwillk & Ackerly 2006; Kraft, Valencia & Ackerly 2008; Swenson & Enquist 2009). If these phenotypic traits show phylogenetic signal (*sensu* Blomberg, Garland & Ives 2003), then by the same logic, those same species may also be more related (phylogenetically clustered) than expected (e.g. Webb *et al.* 2002). This

differential success of species can also lead to shifts in the abundance (e.g. Whittaker 1960) and functional identity (e.g. Cornwell & Ackerly 2009; Shipley 2009; Swenson *et al.* 2012) of species across environmental gradients, another set of patterns that are often interpreted as evidence for environmental filtering.

While this conceptual framework has been widely used in investigations of environmental filtering (see review below), recent critiques emphasize that patterns of functional and phylogenetic clustering are often insufficient to clearly establish the role of abiotic tolerances in determining community membership. For example, shifts in species abundances across the landscape often reflect changes in both biotic and abiotic factors (e.g. the realized niche of a species) rather than purely abiotic factors (the fundamental niche) (Malanson, Westman & Yan 1992; McGill *et al.* 2006). Likewise, phenotypic (and phylogenetic) convergence can result from a number of processes aside from environmental filtering, including plant–pollinator interactions and facilitation (reviewed in Cavender-Bares *et al.* 2009). Finally, it is now clear from both theory (e.g. Chesson 2000; Mayfield & Levine 2010; HilleRisLambers *et al.* 2012) and experiments (e.g. Narwani *et al.* 2013; Godoy, Kraft & Levine 2014) that competition, which the community assembly literature originally hypothesized to drive phenotypic (and/or phylogenetic) divergence, may also result in phenotypic or phylogenetic convergence among community members if the phenotypes in question are associated with competitive dominance.

In an emerging framework developed for understanding coexistence, the outcome of competition depends on both the niche differences that stabilize coexistence and the average fitness differences that determine competitive dominance (Chesson 2000). Stabilizing niche differences are those species differences that cause intraspecific effects to exceed interspecific effects, and they are expected to arise from species differences in resource use, their responses to a heterogeneous environment or interactions with specialist consumers, among other potential factors (HilleRisLambers *et al.* 2012; Adler *et al.* 2013). If one considers the traits that underlie these stabilizing differences, the niche differences should be strong for species with large trait differences, but weak for species with very similar traits. As a result, competitive exclusion should be common among pairs of similar species, leading to overdispersion in the traits or phylogenetic relatedness of coexisting species, in contrast to the clustering that is predicted to occur by environmental filtering (Weiher, Clarke & Keddy 1998; Webb *et al.* 2002; Stubbs & Wilson 2004; Cornwell, Schwillk & Ackerly 2006).

However, the potential for a pair of species to coexist also depends on their average fitness differences. Fitness differences drive competitive dominance and might arise from species differences in their ability to draw down a common limiting resource or tolerate a shared generalist natural enemy. If high average fitness is associated with particular traits (or a particular region of the phylogenetic

tree), competitive exclusion can result in trait or phylogenetic clustering within the community (Mayfield & Levine 2010; Godoy, Kraft & Levine 2014). As a result, trait or phylogenetic clustering in a community can result from both environmental filtering (abiotic factors) as well as competitive processes. These and other findings suggest that it is important to revisit the criteria that are used in empirical studies to establish environmental filtering.

Reconciling perspectives

While there is a clear need to update our approach to studying environmental filtering in the light of these advances in coexistence theory, there are several challenges in reconciling the two perspectives. The first is the issue of the species pool. Environmental filtering is often quantified by comparing community members to a broader species pool representing potential colonists, some of which have presumably arrived at the site but failed to establish or persist. The concept of a pool of potential community members that cannot persist in a community is rarely considered explicitly in coexistence theory, which typically focuses on the dynamics of species that are able to tolerate the abiotic conditions within the community. Therefore, one could view environmental filtering, as originally defined, as a step occurring before many of the processes that coexistence theory addresses. Thus, the abiotic factors that prevent species from establishing or surviving when alone can reasonably be ascribed to environmental filtering from both a conceptual and empirical standpoint, as we discuss below.

Another challenge in finding common ground between coexistence theory and the environmental filtering concept is that many existing discussions of environmental filtering assume that abiotic and biotic drivers of community pattern can be separated into independent effects (but see Maire *et al.* 2012). For example, many community assembly studies represent environmental filtering and biotic interactions as sequential steps in the assembly process. In reality, both factors interact dynamically to drive the community pattern, as the strength and direction of biotic interactions can be strongly influenced by the abiotic context (e.g. Callaway *et al.* 2002) and abiotic events throughout the life span of an organism can have strong influences on community membership (e.g. Engelbrecht *et al.* 2007). Truly detecting environmental filtering may require studies of tolerance in the absence of other interacting species (such as potential competitors or natural enemies), although these studies are rarely performed in this context. Many community assembly analyses that report environmental filtering may in fact be describing the combined effect of both biotic and abiotic processes.

A final challenge in any discussion of environmental filtering is the issue of strong scale dependence. The environmental filtering concept is intimately linked to the spatial scale of analysis, as often it requires identifying species that could be present at a site (via dispersal) but are not.

At broad geographic scopes of analysis across large environmental gradients, environmental filtering is likely to be so common as to be trivial (e.g. palm trees cannot grow in the arctic or underwater), but even at more modest spatial scales, the designation of the species pool can have critical implications in the strength of filtering that is reported (Cavender-Bares, Keen & Miles 2006; Swenson *et al.* 2006; Kraft & Ackerly 2010). These considerations mean that care needs to be taken in matching spatial scales (and associated temporal scales that may be implied in defining the pool of potential colonists) when making any comparisons between studies or approaches. Despite differences in the treatment of the species pool, as we explain in the next section, recent developments in coexistence theory can be reconciled with the environmental filtering concept if care is taken in defining the scales of interest. With these issues in mind, the next step is to consider a more robust framework for investigating the role of the abiotic environment in shaping community pattern.

A framework for quantifying the role of the environment in shaping community assembly

From our perspective, the original meaning of the environmental filtering concept captures an important process in community assembly, where species arrive at a site but fail to establish or persist due to an inability to tolerate the abiotic conditions. The problem is that many studies fail to separate environmental filtering from biotic processes and that the term 'environmental filtering' is often used as a generic term to describe any perceived abiotic influence on community structure, which is imprecise and potentially misleading. With this in mind, we advocate that the term environmental filtering, *sensu stricto*, be used only in cases where an inability to tolerate abiotic conditions leads to the failure of a species to establish and persist at a site. Of course, biotic factors like the absence of pollinators or presence of certain consumers can also 'filter' out taxa by preventing their establishment. However, lumping these interactions with abiotic interactions into 'environmental filtering' because they both generate the same phenotypic or phylogenetic patterns leads to circular reasoning if these patterns are used to infer community assembly processes. Here, we present a framework to guide empirical studies when considering environmental filtering (Fig. 1). Our goal in this framework is not necessarily to cover every possible outcome or process, but instead to highlight the data that are needed to better support claims of environmental filtering and to distinguish it from closely related phenomena. For researchers simply interested in documenting environmental filtering, only steps 1–3 below are needed.

DEFINE THE SCALE

Studies of environmental filtering are most easily interpreted by clearly defining the spatial extent of the community or assemblage for which environmental filtering is of

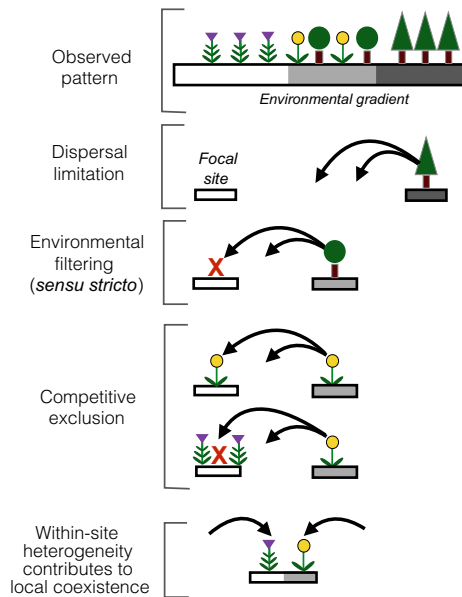


Fig. 1. Environmental filtering in relation to other community assembly processes in the context of species abundance changes across an environmental gradient. Firstly, a species may be absent from a focal site on the gradient because of dispersal limitation. Next, environmental filtering (*sensu stricto*) occurs when a species arrives at a focal site but fails to establish or persist with neighbours removed. Competitive exclusion occurs when a species arrives and can persist in the absence of neighbours but not in their presence. Finally, at a different focal site, within-site abiotic heterogeneity (not typically defined as environmental filtering) can contribute to the ability of community members to persist locally. Note that in this hypothetical example, the observed pattern of species abundance shifts across the gradient emerges from the combined action of all four processes.

interest. Defining this scale is important for properly accounting for the role of spatial environmental heterogeneity in the filtering process. Geographically smaller species pools typically contain fewer potential colonizing species that are drawn from a smaller range of environmental conditions and a smaller diversity of clades, likely decreasing the role of environmental filtering in shaping community membership. Similarly, broadening the spatial definition of a local community to include heterogeneous abiotic patches will decrease the role of environmental filtering in shaping community membership (Kraft & Ackerly in press), but may increase the potential for local abiotic heterogeneity to contribute to coexistence within the community (step 5, below). We expect that environmental filtering, *sensu stricto*, will be most prevalent when the species pool is drawn from a broad area containing high abiotic heterogeneity, but the local community is defined to be restricted and abiotically homogeneous. For example, in studying a desert plant community, one would expect to find stronger evidence of filtering if a geographically broad species pool is used that includes a number of nearby non-desert plant communities, relative to a geographically restricted species pool containing just desert-adapted species.

DOCUMENT THE POTENTIAL FOR SPECIES ARRIVAL

Environmental filtering occurs when a species arrives at a site but fails to establish or persist (Fig. 1). Therefore, a necessary step in any discussion of the environmental filtering of a specific species is to first establish that it has the potential to arrive at the site (as a propagule or as an immigrant, for example) within the time-scale of interest. The strongest evidence comes from direct quantification of arrival (e.g. measuring seed inputs, Wright *et al.* 2005), or through inferences based on geographic proximity of source populations and estimates of dispersal distances. Without this information, it is difficult to distinguish putative environmental filtering from dispersal limitation (Fig. 1).

QUANTIFY SURVIVAL IN THE ABSENCE OF NEIGHBOURS

Once the potential for the arrival of species at a site has been established, the next step is to assess the ability of the species to tolerate the conditions present at the site in the absence of interactions with other species. This evidence (when collected) typically comes from removing or excluding other strongly interacting species in an experimental context, or in some cases, from laboratory-based measures of physiological tolerance. We suggest that environmental filtering, *sensu stricto*, should be defined as species that arrive at a site but are unable to tolerate the environmental conditions at the site in the absence of other species. Much of the community assembly and coexistence literature in this area is focused on the role of potential competitors at a site that can exclude colonists, but there is no reason that other processes (such as facilitation, see below) cannot be treated in the same way. Any interaction not removed at this step (for example- soil microbes) will inadvertently be lumped into the effect of the 'abiotic environment', so care should be taken when drawing inferences in field conditions.

QUANTIFY PERSISTENCE IN THE BIOTIC MILIEU

If species are able to arrive at a site and survive in the absence of neighbours, the next logical step is to quantify the ability of species to persist in the presence of other interacting species at the site. In the context of competitive interactions, we suggest that the most direct approach quantifies the establishment of species in the presence of the competitive community through experimental invasions (e.g. Going, HillerisLambers & Levine 2009). If an investigator was specifically interested in understanding the contributions of low average fitness and insufficient stabilizing niche difference to competitive exclusion, these quantities could be quantified with far more labour-intensive approaches (e.g. Levine & HilleRisLambers 2009; Godoy & Levine 2014). Depending on the community in question, it may also be important at this stage to quantify positive interactions with other species, which may increase

the performance of focal species, or even permit persistence of species that are unable to tolerate conditions in step 3 above.

CONSIDER ADDITIONAL ABIOTIC INFLUENCES ON COMMUNITY STRUCTURE

Environmental filtering, *sensu stricto*, is but one of many ways in which the abiotic environment can influence community structure. For example, local abiotic heterogeneity can contribute to species coexistence if species differ in their response to abiotic conditions within the community (Chesson 2000; Snyder & Chesson 2004; Adler *et al.* 2013), and the outcome of biotic interactions are often strongly influenced by the abiotic context (Callaway *et al.* 2002). A full consideration of the role of the abiotic environment in driving community pattern should include an examination of additional abiotic influences aside from environmental filtering.

This framework offers a way for researchers to gather the evidence needed to document environmental filtering, as well as to distinguish filtering from other closely related processes. The data needed to establish environmental filtering are straightforward in theory- all that is needed is evidence that species can arrive at the site (step 2) but cannot survive in the absence of neighbours (step 3), although practically speaking for many organisms this step can be logistically challenging. For species that are able to persist at a site (step 3), the assessment of the ability of the species to persist at the site in the presence of neighbours (step 4) offers a way to distinguish environmental filtering from competitive exclusion and other biotically mediated community outcomes. Step 5 emphasizes that environmental filtering is but one way in which the abiotic environment contributes to community structure and pattern. The first step in the framework- defining the scale- emphasizes the inherently scale-dependent nature of environmental filtering concept.

Reviewing the environmental filtering literature

With this framework in mind, we searched the ecological literature for articles that reported 'environment* filter*' or 'habitat filter*' in the title or topic fields in Web of Science for all years. We then reviewed the resulting papers to assess the organisms of study, the spatial scales of analysis, the abiotic factors that were implicated in driving the filtering, and the type of empirical data that were used to test for environmental filtering. Full details on the search and the resulting papers are given in (Appendix S1, Supporting information).

We reviewed 258 articles published between 1992 and October 1, 2013 that were returned in our search (Fig. 2). Of these, the majority (62%) focused on plants, although all major taxonomic groups were represented. Over 79% of the studies reported some sort of evidence or criteria for establishing environmental filtering in the study. The most

common criterion was shifts in the realized abundance of species across environmental gradients (44%), followed by shifts in trait means across gradients (29%) and tests of trait and phylogenetic dispersion (19% and 30%, respectively). Only 15% of studies considered evidence that species could tolerate conditions at the site in the absence of neighbours, one of our primary criteria for establishing environmental filtering *sensu stricto*. Next, we qualitatively divided studies into those that focused on filtering across microsites within a major habitat type, across habitat types within a region, across regions or across continents. The vast majority of studies focused on the smallest two scales, with fewer than 10% of the studies addressing regional or continental-scale patterns. Finally, we recorded any discussion by the authors of the specific abiotic drivers of filtering. Over 50% of studies either did not mention specific drivers or were ambiguous in the discussion of them. Of those that did consider explicit abiotic drivers, soils and climate were the most widely discussed.

Overall, our review suggests that greater care is needed in the literature in assessing environmental filtering, as 85% of the papers we reviewed did not include evidence that species could tolerate conditions at the site in the absence of neighbours or other potentially interacting species, focusing instead on patterns of abundance or trait and phylogenetic patterns in intact communities. While there is valuable information contained in these patterns (see discussion below), as we highlight above, it is difficult to fully ascribe the drivers of these patterns to environmental filtering.

As a final note on the literature survey, empirical research on physiological tolerances of many organisms can be used directly to inform discussions of habitat filtering and community assembly. We have not attempted to incorporate this information into our review, but future studies focusing on environmental filtering for specific organisms may do well to draw on prior research beyond the confines of the community ecology field to guide studies and interpretations.

The future of the environmental filtering concept

A CALL FOR GREATER PRECISION

Environmental filtering is a pervasive concept in community ecology. In theory, the data required to demonstrate environmental filtering are clear: one needs to show that a species can arrive at a site but cannot tolerate the abiotic conditions present there, independent of other biotic effects. In practice, however, these data can be difficult to obtain, particularly given the logistical challenges of the manipulations that are typically required to assess tolerance in the absence of biotic interactions. These obstacles are reflected in the fact that most environmental filtering studies rely on alternative lines of evidence, such as shifts in abundance or trait values along abiotic gradients or

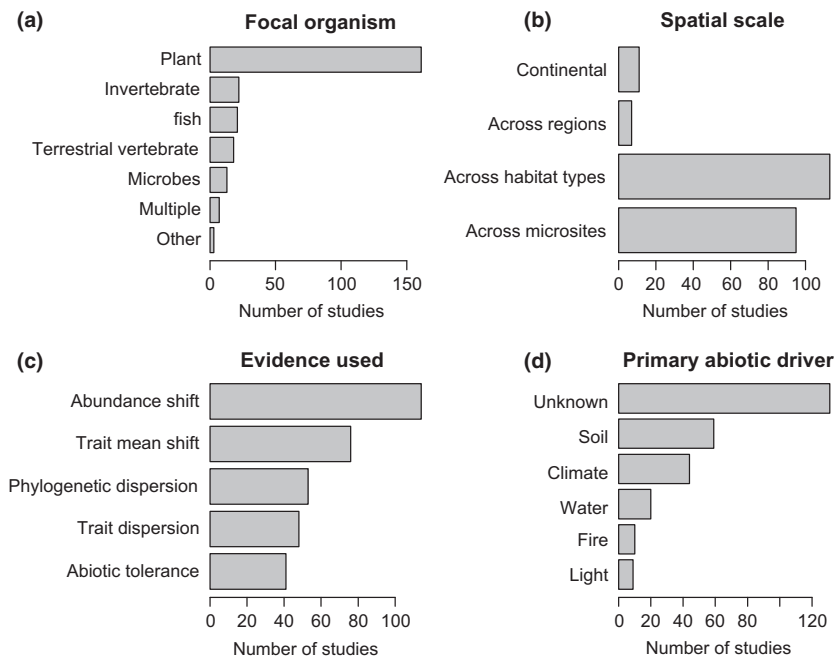


Fig. 2. Summary of literature review of papers using the environmental filtering concept. Panel a shows the focal organism of the study (if indicated). The 'other' category includes algae, fungi and lichens. Panel b shows a qualitative assessment of the spatial scale of the study, including across continents, across regions, across major habitat types within a region, or across microsites within a single habitat type. Panel c shows the categories of evidence used to assess environmental filtering in the study – some studies used multiple tests. Evidence includes species abundance shifts along environmental gradients, community average trait shifts along gradients, tests of phylogenetic and functional trait dispersion, and direct assessments of the ability of organisms to tolerate the conditions at a site in the absence of neighbours. Panel d shows the primary abiotic drivers of environmental filtering hypothesized by the authors of the studies to be responsible for the filtering, if they could be identified. Multiple drivers were reported for some studies. Additional details of the criteria used to select and classify studies are given in the supplementary material.

reduced phenotypic or phylogenetic dispersion at a site relative to the species pool. However, for the reasons outlined above, these patterns cannot provide strong evidence of environmental filtering in the absence of other information.

Going forward, we suggest first that the term 'environmental filtering' be restricted to circumstances where abiotic conditions alone are the primary reason for the absence of species from a site, therefore reflecting the original meaning of the concept. Secondly, we suggest that more caution is needed in interpreting shifts in abundance or trait values along gradients, as well as patterns of functional and phylogenetic dispersion in communities, as strong evidence for environmental filtering. Recent work has illustrated the range of ecological phenomena, many of them biotically driven, that can produce patterns in nature that have been interpreted in the past as evidence for filtering (Cavender-Bares *et al.* 2009; Mayfield & Levine 2010; Adler *et al.* 2013). Ascribing these patterns entirely to the abiotic environment overestimates the role of the environment in shaping communities, while simultaneously downplaying the influence of biotic interactions. This issue is particularly important if results are to be used to project species or community responses to future climates, as is often a stated goal of a number of studies in this area. For example, in communities undergoing directional climate

change, species may disappear from a site either because they are unable to tolerate the new abiotic conditions (step 3 in the framework) or simply because the changing conditions result in altered biotic interactions (e.g. resulting in increased fitness differences with competitors – step 4 in the framework). These two possibilities have very different implications for the potential for management to mitigate the impacts of climate change.

SEPARATING ABIOTIC TOLERANCE FROM FITNESS DIFFERENCES

A key issue in many trait and phylogeny-based studies of environmental filtering is a failure to distinguish between species absences due to abiotic tolerance (step 3 in the above framework) and species absences due to competitive fitness differences with other residents (step 4, Fig. 1). This distinction echoes decades of discussion of the differences between the fundamental and realized niche of the species (Malanson, Westman & Yan 1992; McGill *et al.* 2006). From a phenotypic perspective, both of these processes can result in greater phenotypic similarity among species within a community (Mayfield & Levine 2010). As the phenotypic traits are associated with fitness, differences between species are generally unknown for most communities (but see Gaudet & Keddy 1988; Goldberg & Landa

1991; Godoy & Levine 2014); this raises the possibility that there may be phenotypic traits associated with tolerance that are distinct from the traits associated with fitness differences. If this is the case, then patterns in particular traits could be used to distinguish between environmental filtering vs. competitive exclusion in observational data, for example, although much work is needed to establish these links in most communities. One potential difficulty here is that there may be positive or negative correlations among traits linked with tolerance and competitive outcomes, which would complicate inferences drawn from observed phenotypic patterns alone. For example, many traits associated with abiotic tolerance are predicted to result in trade-offs in reduced allocation to growth and reproduction and therefore reduced competitive ability (e.g. Grime 1977; Grime *et al.* 1997).

THE VALUE OF OBSERVATIONAL DATA SETS

We have emphasized refocusing the environmental filtering concept on the abiotic tolerance of species and highlighted the value of experimental data in assessing the tolerance of organisms. Many of the challenges that we discuss here are not specific to just the study of environmental filtering – they are challenges for observational studies of community assembly in general. However, we do not want to discount the value of observational data sets that document species abundance or trait shifts across the landscape or that document changes in functional trait or phylogenetic dispersion patterns of community members. Experimental manipulations may be impractical, if not impossible, in many ecological communities of interest, and these observational lines of evidence still indicate an important role of abiotic variation in shaping communities. However, as we have highlighted, it is difficult to ascribe these patterns to environmental filtering without additional lines of evidence and/or a careful consideration of the context of the study. In the absence of physiological or experimental information about the species, the magnitude of environmental dissimilarity between a study site and the surrounding areas could be used to further assess the potential for environmental filtering. Shifts in abundance across a strong environmental gradient may well be driven by environmental filtering where species may be unable to tolerate some of the abiotic conditions found at various points along the gradient. In contrast, shifts in abundance across a modest gradient at a small spatial scale likely are driven by a combination of both abiotic and biotic effects, reflecting the fact that species average fitness varies across the abiotic gradient. We urge researchers working with observational data sets to carefully evaluate the abiotic context of their study before making strong claims of environmental filtering.

Conclusions

The abiotic environment undoubtedly plays a central role in shaping the distribution and abundance of organisms

across the planet. Despite this widespread understanding, our review here has highlighted several of the key challenges that have faced community ecology studies in accurately capturing the mechanisms through which environmental variation shapes community assembly. Our review of the environmental filtering literature suggests that the data used to test for environmental filtering are often too broad and therefore unable to confidently distinguish between biotic and abiotic influences. We suggest that, for greater clarity going forward, the application of the environmental filtering concept should be narrowed and reserved for cases where failure to tolerate the abiotic environment is the reason for the absence of a species within a community. At the same time, greater attention in community assembly studies needs to be paid to the role of within-community abiotic heterogeneity in promoting diversity, as well as greater emphasis on the strong interplay between environmental conditions and biotic interactions. By addressing these issues, ecologists can come to a clearer understanding of the multitude of ways in which environmental variation shapes patterns of diversity across communities.

Acknowledgements

We thank Anita Narwani for the opportunity to participate in this special issue, and Claire Fortunel, Jeremy Fox, Rong Li, Ian McFadden and Kristin Powell for helpful comments and discussion.

Data accessibility

The list of all papers reviewed here is included in the supplementary material.

References

- Adler, P.B., Fajardo, A., Kleinhesselink, A. & Kraft, N.J.B. (2013) Trait-based tests of coexistence mechanisms. *Ecology Letters*, **16**, 1294–1306.
- Bazzaz, F.A. (1991) Habitat selection in plants. *American Naturalist*, **137**, S116–S130.
- Blomberg, S.P., Garland, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Cavender-Bares, J., Keen, A. & Miles, B. (2006) Phylogenetic structure of Floridian plant communities depends on spatial and taxonomic scale. *Ecology*, **87**, S109–S122.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.
- Cornwell, W.K. & Ackerly, D. (2009) Community assembly and shifts in the distribution of functional trait values across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.
- Cornwell, W.K., Schilck, D.W. & Ackerly, D.D. (2006) A trait-based test for habitat filtering: convex hull volume. *Ecology*, **87**, 1465–1471.
- Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. *et al.* (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–82.
- Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature*, **334**, 242–243.

- Godoy, O., Kraft, N.J.B. & Levine, J.M. (2014) Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters*, **17**, 836–844.
- Godoy, O. & Levine, J.M. (2014) Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology*, **95**, 726–763.
- Going, B., Hillerislambers, J. & Levine, J. (2009) Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia*, **159**, 839–847.
- Goldberg, D.E. & Landa, K. (1991) Competitive effect and response – hierarchies and correlated traits in the early stages of competition. *Journal of Ecology*, **79**, 1013–1030.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H. *et al.* (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259–281.
- HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* (ed. D. J. Futuyma), pp. 227–248. Annual Reviews, Palo Alto, California, USA.
- Humboldt, A.V. & Bonpland, A. (1805) *Essai sur la géographie des plantes*. Chez Levrault, Schoell, Paris.
- Kraft, N.J.B. & Ackerly, D.D. (2010) Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs*, **80**, 401–422.
- Kraft, N.J.B. & Ackerly, D.D. (in press) The assembly of plant communities. *The Plant Sciences: Ecology and the Environment* (ed. R. Monson). Springer-Verlag, Berlin.
- Kraft, N.J.B., Valencia, R. & Ackerly, D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, **322**, 580–582.
- Levine, J.M. & HilleRisLambers, J. (2009) The importance of niches for the maintenance of species diversity. *Nature*, **461**, 254–257.
- Maire, V., Gross, N., Borger, L., Proulx, R., Wirth, C., Pontes, L.D. *et al.* (2012) Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist*, **196**, 497–509.
- Malanson, G.P., Westman, W.E. & Yan, Y.L. (1992) Realized versus fundamental niche functions in a model of chaparral response to climatic change. *Ecological Modelling*, **64**, 261–277.
- Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.
- Narwani, A., Alexandrou, M.A., Oakley, T.H., Carroll, I.T. & Cardinale, B.J. (2013) Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters*, **16**, 1373–1381.
- Nobel, I.R. & Slatyer, R.O. (1977) Post-fire succession of plants in Mediterranean ecosystems. Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems (eds H. A. Mooney & C. E. Conrad), pp. 27–36. United States Forest Service, Palo Alto, California, USA.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.
- Schimper, A.F.W. (1898) *Pflanzen-geographie auf physiologischer grundlage*. G. Fischer, Jena.
- Shipley, B. (2009) *From Plant Traits to Vegetation Structure: Chance and Selection in the Assembly of Ecological Communities*. Cambridge University Press, Cambridge.
- Snyder, R.E. & Chesson, P. (2004) How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. *American Naturalist*, **164**, 633–650.
- Stubbs, W.J. & Wilson, J.B. (2004) Evidence for limiting similarity in a sand dune community. *Journal of Ecology*, **92**, 557–567.
- Swenson, N.G. & Enquist, B.J. (2009) Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, **90**, 2161–2170.
- Swenson, N.G., Enquist, B.J., Pither, J., Thompson, J. & Zimmerman, J.K. (2006) The problem and promise of scale dependency in community phylogenetics. *Ecology*, **87**, 2418–2424.
- Swenson, N.G., Enquist, B.J., Pither, J., Kerkhoff, A.J., Boyle, B., Weiser, M.D. *et al.* (2012) The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography*, **21**, 798–808.
- van der Valk, A.G. (1981) Succession in wetlands – a Gleasonian approach. *Ecology*, **62**, 688–696.
- Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist*, **156**, 145–155.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Weiher, E., Clarke, G.D.P. & Keddy, P.A. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, **81**, 309–322.
- Whitfield, T.J.S., Kress, W.J., Erickson, D.L. & Weiblen, G.D. (2012) Change in community phylogenetic structure during tropical forest succession: evidence from New Guinea. *Ecography*, **35**, 821–830.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.
- Woodward, F.I. & Diment, A.D. (1991) Functional approaches to predicting the ecological effects of global change. *Functional Ecology*, **5**, 202–212.
- Wright, S.J., Muller-Landau, H.C., Calderón, O. & Hernández, A. (2005) Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology*, **86**, 848–860.

Received 28 March 2014; accepted 30 July 2014

Handling Editor: Jeremy Fox

Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Literature review details.