

Opinion

Should Environmental Filtering be Abandoned?

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Environmental filtering, where the environment selects against certain species, is thought to be a major mechanism structuring communities. However, recent criticisms cast doubt on our ability to accurately infer filtering because competition can give rise to patterns identical to those caused by environmental filtering. While experiments can distinguish mechanisms, observational patterns are especially problematic. The environment determines community composition not only directly via survival, but also by influencing competition. If species population growth rates covary with environmental gradients, then outcomes of competitive exclusion will also vary with the environment. Here, we argue that observational studies remain valuable, but inferences about the importance of the environment cannot rely on compositional data alone, and that species abundances, population growth, or traits must be correlated with the environment.

Paradigms Lost: Mounting Critiques of Filtering Metaphors

To explain local community composition and structure, ecologists frequently use a heuristic describing a set of discrete, sequential mechanisms (Figure 1A) that filter a larger **species pool** (see Glossary) of potential residents to the subset that occurs within a community [1]. Three types of ecological process ('filters') dominate this perspective (dispersal, the abiotic environment, and biotic interactions) and they are understood to shape patterns of ecological diversity across multiple spatial scales and different ecosystems [2–4]. In practice, all three filters are difficult to quantify [5,6], but notably the environmental filter has recently been criticized for being ill defined and inappropriately applied [7].

The classic environmental filter has been broadly defined as the effect of environmental conditions selecting those species capable of survival and persistence at a given locale [2,7]. Unfortunately, as skillfully argued by Kraft and colleagues [7], this heuristic is theoretically flawed and difficult to confirm with observational data on the occurrences of species. Filters are abstractions of ecological processes and ignore the reality that such processes regularly interact in complex ways. For example, it is well known that species occurrence patterns are determined by both biotic and abiotic factors simultaneously [8–10]. Species absences from a community can reflect exclusion due to not only an environmental filter, but also other mechanisms (e.g., dispersal limitation or local competition), and observational studies often cannot distinguish among these mechanisms. Still, the simplicity of the environmental filter concept underlies its popularity: the presence of species at a particular site should reflect its tolerance of particular environmental conditions. The issue here is one of interpreting false negatives. We believe that a species can survive in an environment when they are observed there, but we cannot conclude that their absence from an abiotic environment means they cannot survive there. Note that false positives are also a concern, because species that otherwise fail to successfully reproduce in a particular environment might maintain a presence due to immigration. For these types of reason, Kraft *et al.* argue for a strict definition of an

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The role of the environment for shaping community composition has been criticized recently.

Other mechanisms, such as competition, could produce similar patterns to environmental filtering.

We recognize that competition and the environment do not have separable effects on species and their interactions.

Researchers should use additional information to determine whether fitness–environment covariances influence composition.

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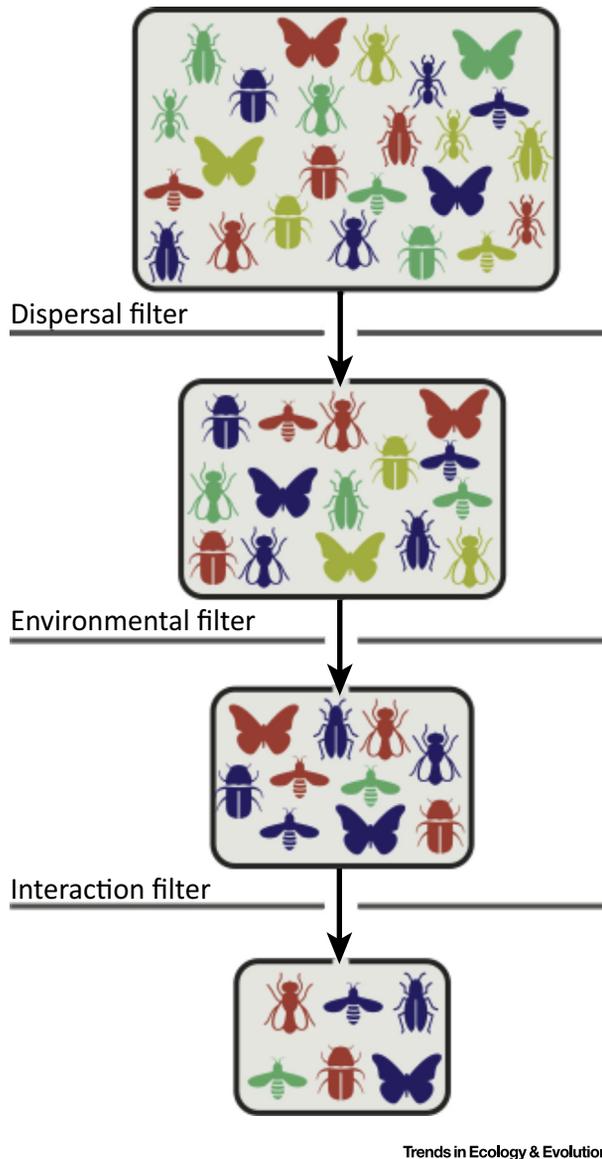
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Figure 1. The Traditional View of the Series of Hierarchical Filters that Reduce a Pool of Potential Local Residents into Those that Occur There.

environmental filter, where the term ‘environmental filtering’ should only be used to refer to cases where the abiotic environment prevents establishment or persistence in the absence of biotic interactions’ ([7] p. 592).

A natural interpretation of the original environmental filtering paradigm is that, if phenotype reflects tolerance to particular abiotic conditions, then phenotypic similarities (often referred to as ‘convergence’ or ‘**clustering**’; **Box 1**) among co-occurring species will be observed when environmental filtering structures local assemblages. This logic motivated a body of research looking at the role of environmental filtering in patterns of functional and phylogenetic **community dispersion** [11–15]. However, such patterns can arise from processes other than environmental filtering, including competition [6]. A set of species that share phenotypic attributes and exhibit small niche differences might still co-occur at a site, producing patterns of clustering if those species have higher local intrinsic growth rates than other species, thus

Glossary

Clustered: also referred to as ‘underdispersion’; refers to communities comprising species that are more similar to one another (measured as functional or phylogenetic distances) than expected by chance.

Community dispersion: the mean, range, or variance of functional or phylogenetic distances within communities; usually relative to a null distribution.

Functional diversity: the extent of trait differences in a community or assemblage; measures may include the mean, total, or distribution of these trait differences.

Overdispersed: refers to communities comprising species that are more dissimilar to one another (measured as functional or phylogenetic diversity) than expected by chance.

Phylogenetic diversity: the extent of differences in evolutionary history in a community or assemblage; measures may include the mean, total, or distribution of phylogenetic distances.

Species pool: the set of species at a larger geographic scale that includes the community of interest; often believed to represent the pool of potential colonists that could reach a specific habitat.

Box 1. Statistical Methods to Test for Environmental Filtering

Environmental filtering is most often inferred from the presence of nonrandom community patterns. One such approach is to test whether assemblages contain species that are similar to one another in terms of phylogenetic or trait-based distances. Accordingly, researchers measure a suite of traits on their target species or obtain trait information, sequences, or full phylogenies from online repositories. With these data, researchers calculate trait-based indices, such as the community-weighted mean trait value(s) or a multivariate measure of functional diversity (e.g., [15,27,61]), or a phylogenetic distance based measure, frequently mean pairwise distances among species (e.g., [62]). To assess whether these measures reflect nonrandom community patterns, specifically whether functional and phylogenetic diversities are lower than expected (e.g., clustered), they are compared with null distributions generated from randomization procedures that subsample the **species pool**. Typically, species names are swapped among communities, trait values, or phylogenetic tip labels and an index is calculated for these random assemblages. Observed index values can be directly compared with a null distribution and *P* values estimated directly from the position of the observed value relative to the null expectation. Furthermore, standardized effect sizes, or *z*-values, are computed using Equation 1:

$$z = \frac{X_{\text{obs}} - \mu_{\text{null}}}{\sigma_{\text{null}}} \quad [1]$$

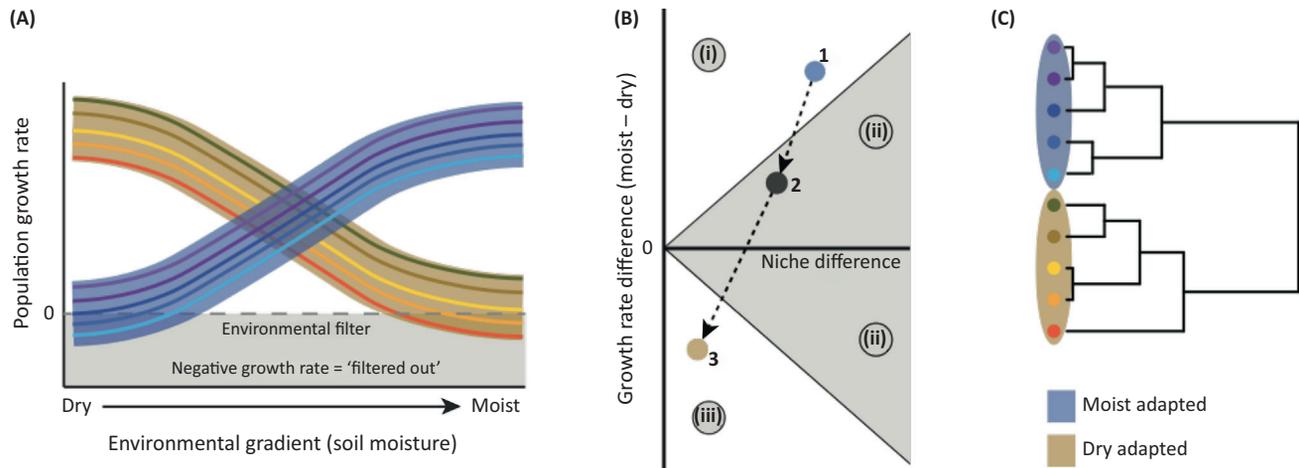
An alternative approach that is not based on traits or phylogeny is to determine whether compositional similarity is correlated with environmental variables. In this case, community dissimilarity or beta diversity is correlated with environmental distances among communities, often after accounting for the influences of space [63,64].

ultimately excluding them [6] [note here and in the remaining text we refer to intrinsic growth rates, but recognize that this concept of density-independent growth rates has also been called ‘fitness’ (*k*) under the Chessonian framework]. This low niche difference but high-performing assemblage could coexist if species perform equivalently, requiring only minimal niche differences to stabilize coexistence [16]. As a result, Kraft *et al.* argue that experimental tests of survival in the absence of neighbors must be used to truly measure whether a species passes through an environmental filter: patterns of functional and phylogenetic clustering would be insufficient to support the conclusion that strict environmental filtering structures community composition, calling into question the utility of observational data for such queries.

We argue that observational data are still informative so long as researchers do not adhere to a strict definition of environmental filtering dependent only on abiotic limits, and that additional data about underlying environmental conditions and growth rate– or trait–environment correlations validate compositional changes. Strong relationships between organisms and their environments, and apparent clustering of phenotypically similar species, are common ([17], see ‘Generalities’ section below). Furthermore, the concern that the relationship between the spatial distributions of species and the environment is not independent of biotic interactions and dispersal has long been expressed: clarifications of the niche concept to differentiate between the fundamental niche and realized niche have sought to address this issue [18]. It is likely that most observational data reported as evidence for environmental filtering in fact reflect the combined effects of the environment and local competition. However, this should not invalidate its value for inferring the role of the environment in community structure.

Focusing on Growth Rate–Environment Covariance

Modern coexistence theory estimates separate and discrete terms for differences in average growth rate and niche overlap [19]. However, in practice, it is difficult to tease apart differences between species in terms of their ecological niches and their intrinsic growth rates versus trait and phylogenetic measurements (e.g., [20]). Furthermore, differences in both intrinsic growth rates and niche breadth and overlap (and, therefore, coexistence) likely depend on the local environment. As a result, species survival and persistence and the outcome of competitive interactions will vary along environmental gradients. Even if we assume that niche overlap is independent of local environments, and only the intrinsic growth rates of species change across environmental gradients, competitive exclusion or coexistence can still be influenced by changes in environment (Figure 2). We should move away from simply inferring that



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Figure 2. Coexistence and Phylogenetic Community Patterns Depend on the Response of Growth Rates to an Environmental Gradient. (A) Species responses to an environmental gradient or the growth rate–environment covariance, illustrated with a group of dry-adapted and a group of moist-adapted species. Some species have growth rates <0 in their suboptimal habitat, but most do not and could persist in the absence of competitors. (B) The interaction between a typical moist and dry species from (A) depends on the environment. There are three regions describing competitive outcomes: (i) competitive exclusion of a dry specialist by a moist specialist in the moist environment (Scenario 1); (ii) coexistence of both types of species in intermediate environments (Scenario 2); and (iii) competitive exclusion of a moist specialist by a dry specialist in the dry environment (Scenario 3). (C) The underlying phylogenetic relationship between these specialists, and how the growth rate–environment covariance would lead to an observation of phylogenetically clustered communities even though competition is also important for determining species presence/absence patterns.

environmental filters are present or absent and instead assume that communities are influenced by covariance between the environment and species growth rates. Such correlations can produce patterns typical of strict environmental filtering regardless of whether species are excluded by the environment, or whether competitive differences change with the environment, resulting in the exclusion of species that could coexist elsewhere.

As a hypothetical example, consider two clades of plants that are adapted to different soil moisture regimens, one dry adapted and one moist adapted (Figure 2). Some of the species in these clades conform to expectations for a strict environmental filter (i.e., intrinsic growth rates <0), but as the growth rate changes continuously along the environmental gradient, some species simply have low local growth rates (just above zero) in suboptimal environments. Such species suffer from being in suboptimal environmental conditions and, in the face of competition from better-adapted species (higher local growth rates), resulting presence–absence patterns will be the same as those expected from a strict environmental filter. Thus, clustering on its own is not evidence for the presence of a strict environmental filter, but can instead be indicative of how environmentally correlated demographic rates influence persistence in a particular biotic milieu. Note that, although this scenario is put in terms of local growth rates, dispersal can increase the realized growth rate in a site if immigrants establish and populations are maintained despite failing to reproduce.

The fact that the environment affects both growth rates and niche breadth is not novel, and researchers working on coexistence research have recognized this fact [21]. However, under the framework of Chessonian coexistence, growth rate and niche breadth are represented as separate mathematical quantities. Moreover, observational research often takes a binary approach to inferring community structure without considering that growth rate–environment covariance can affect both environmental constraints on reproduction and survival as well as competitive exclusion. We would argue that, at the spatial scales at which community

ecologists typically work, a strict environmental filter is unlikely to be the dominant structuring mechanism. We say this because any reduction in a species growth rate due to suboptimal environmental conditions will likely lead to competitive exclusion well before environmentally induced mortality leads to exclusion.

Mechanisms other than Competition Can Also Give Rise to Patterns Consistent with Environmental Filtering

The environment and competition are the dominant explanations for phylogenetic and functional diversity patterns in analyses of community structure, despite the fact that evidence supporting these inferences is often lacking [6,22]. Other ecological processes also influence community composition and, undoubtedly, multiple mechanisms simultaneously influence community patterns and are themselves affected by environmental conditions. A number of these could dominate community composition, creating nonrandom community patterns, such as clustering. For example, any exploitative trophic relationship, such as predation or herbivory, can remove species from communities by increasing mortality. Predators and herbivores might prefer certain groups of species or, conversely, avoid some species groups that, say, contain unpalatable chemical compounds. Local outbreaks of leaf beetle species in the genus *Trirhabda* can defoliate multiple goldenrod species (*Solidago* and *Euthamia* spp.) (e.g., [23]), potentially giving other groups of plant species a local advantage. Similarly, pathogen outbreaks can affect groups of closely related species, shaping local diversity patterns [24]. Finally, mutualistic interactions can potentially reverse community patterns expected under environmental filtering by providing refuge for diverse groups of species that would otherwise be excluded under stressful environmental conditions [25,26].

What Generalities Can We Take from Past Environmental Filtering Research?

Given that covariance between the environment and the intrinsic growth rates of species will produce competitive shifts across a gradient (Figure 2), we recognize that a strict environmental filter might be dominant at the spatial scales work at by community ecologists. However, this does not mean that most nonrandom functional and phylogenetic diversity patterns have inferred a role for environment in influencing diversity patterns incorrectly. Such phenotypic clustering in communities could also result from covariance between species traits and growth rates across environmental gradients [6,27], such that species with particular traits or from certain evolutionary clades tend to have maximal growth rates in similar environments.

Indeed, strong relationships between organisms and their environments, and apparent clustering of phenotypically similar species, are frequently found (e.g., [28,29]). Such trait or phylogenetic patterns have been reported in diverse taxa and ecosystems, including tropical hummingbirds [30], bees [31], zooplankton [32], tropical trees [12], and human microbial communities [33], even though this research has been dominated by work on plants [7]. Of course, the observation of phylogenetic or trait clustering requires an appropriate null model (Box 1). Despite this diversity of organisms and systems, patterns of underdispersion in association with environmental conditions share several general ecological contexts.

First, phylogenetic and functional clustering have frequently been associated with specific environmental conditions or along measured environmental gradients, where certain environmental conditions are thought to select for groups of species with shared traits, or because competition is greatly reduced. In particular, clustered communities are commonly observed in locations with relatively colder temperatures or otherwise stressful climates [34–36]. For example, elevation, which, at least in temperate systems, is used as a proxy for **environmental stress** or harshness, is frequently correlated with clustering in communities [37]. Furthermore, clustering has been associated with anthropogenic stressors, such as disturbance [31,38] and

urban habitats [39–41]. This is most common at larger spatial scales that span multiple habitat types, with the general trend that communities within a particular environment are more likely to be clustered; furthermore, these communities tend to be phylogenetically or functionally similar to communities in similar environmental conditions elsewhere [32].

Second, plant communities tend to be phylogenetically and functionally **overdispersed** at smaller spatial scales, but show clustering when plots are examined across larger spatial scales [42], where environmental gradients are more pronounced. This appears especially true in temperate regions, but less certain for tropical moist forests, in which several studies have observed phylogenetic and functional clustering [4,14,43–47]. Although covariance between the environment and dispersion is commonly observed, the mechanisms are less clearly associated with purely environmental effects. It might be that small-scale environmental heterogeneity is important for species that have evolved in relatively stable tropical environments. However, it could also be a consequence of the fact that tropical forests are more likely to have distantly related species present in regional species pools (e.g., palms, gymnosperms, magnolias, dicots, etc.) and so estimates of standardized effect sizes (Box 1) will be sensitive to the local absence of a distantly related species [43,48–51].

Third, early-successional plant communities tend to be functionally and phylogenetically clustered, while later stages appear random or overdispersed [12,52–55]. Many studies attribute this pattern to greater environmental stress in early successional communities (e.g., high light, dry soils, etc.), but detailed environmental data confirming this are often lacking. An alternative explanation is that early successional species have a temporal advantage and share key traits or are closely related [29]; specifically, they have rapid growth and reproduction, and high dispersal capacity. Ecologists now need to determine how species performance correlates with the environmental changes associated with succession, and how these changes alter community-level measures of dispersion.

Guidelines for Assessing the Role of the Environmental Filter Using Observational Data

Given the difficulty in separating a strict environmental filter, where mortality is greater than recruitment, from a scenario with growth rate–environment covariance with unequal responses among species, a strict definition of the environmental filter may not be useful for observational data. A more nuanced definition would view the environment as a filter that acts on the components of direct survival and reproduction and on intrinsic growth rate simultaneously and, as a result, leads to shifts in the abundance and/or presence/absence of a species. It is important to ask: 'What evidence is required to conclude that there is meaningful covariance between the environment and species intrinsic growth? And: Can this produce the patterns observed in functional and/or phylogenetic diversity?' We argue that concision among three lines of evidence is required. First, there must be evidence of clustering of phenotypes or evolutionary relationships in communities, such as those described in the 'Generalities' section above. This means that communities with standardized effect sizes of trait or phylogenetic distances (Box 1) significantly less than zero must be identified in relation to an appropriate null expectation. Second, there must be a demonstrable environmental gradient, which is associated with the degree of clustering within communities [49,51,56–59], and, with this, we can determine how community structure correlates with an environmental gradient, supplying a plausible mechanism driving changes in population growth. Thus, environmental qualities, including temperature, soil moisture, mineral elements, light, and others, must be measured, followed by statistical analyses determining whether these are associated with observed standardized effect sizes. Finally, the environmental conditions where species are found, or where they attain maximal abundance, must show a phylogenetic signal or be nonrandomly related to species traits [51,60]. This last point ensures that we correctly infer that species

abundance or occupancy in certain lineages or with particular traits are explained by the environment, thus drawing a direct link between community structure and the likely environmental drivers.

These criteria ensure that independent lines of evidence are used to support an inference that the environment explains community patterns in observational data. Observational data remain one of the cornerstones of ecological research, having the power to evaluate competing hypotheses, but only if proper evidence is utilized. Studies that simply test dispersion patterns within plots (first line of evidence above) are not sufficient to infer that environmental conditions have produced clustering. Thus, the other lines of evidence are necessary to conclude that underlying environmental conditions likely influence community assembly.

Concluding Remarks

Despite critiques, there is still good reason to explore how patterns of trait or phylogenetic dispersion change in response to the environment. While the environment as a filter of community structure remains a useful concept, it rarely follows the strictest definitions. Observational data, the focus of most such analyses, are important for driving restoration and conservation decisions (e.g., [31,32]). Local environmental conditions are key variables for determining the appropriate species lists for restoration activities, while large-scale relationships between species and climate motivate plans for the protection of species against changing climate. Furthermore, species conservation can involve the protection or restoration of specific habitats that involve identifying and preserving environmental elements (such as fire or flooding regimens). The strong relationships often observed between community dispersion and environmental conditions provide useful information for these activities, regardless of whether a pure environmental filter or a mix of community structuring mechanisms is at play. Furthermore, the knowledge that such relationships reflect growth rate–environment covariance should guide research into predicting expected ecological changes with changing climatic conditions. Thus, while the nature of the precise mechanisms influencing species in communities is often unknown, that the environment is an important component is not in doubt.

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Outstanding Questions

How commonly are species excluded from communities solely due to the environment?

At what spatial scale is environmental filtering more important than competition?

Are fitness–environment covariances driven by single or multiple environmental axes?

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