Opinion

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Inferring local ecological processes amid species pool influences

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Resolving contingencies in community ecology requires comparative studies of local communities along broad-scale environmental gradients and in different biogeographic regions. However, comparisons of local ecological processes among regions require a synthetic understanding of how the species pool of potential community members influences the structure of ecological communities. Here, we outline an integrative approach for quantifying local ecological processes while explicitly accounting for species pool influences. Specifically, we highlight the utility of combining geographically replicated local studies, null models of community structure, and ecologically explicit definitions of the species pool as a means to compare predominant ecological processes among regions. By uniting concepts and tools from community ecology and macroecology, this approach might facilitate synthesis and resolve many perceived ecological contingencies.

Resolving contingencies in ecology

Community ecology is often criticized for being idiosyncratic [1,2]. In a seminal paper, Lawton [1] argued that there is 'too much contingency' in community ecology to establish general laws, suggesting unpredictability in the local processes underlying patterns of community structure across ecological communities. As a result, the relative importance of ecological processes seems to differ from place to place, and findings from one study do not necessarily apply to others. As conceptual advances aiming to resolve these contingencies emerge [3–5], there is a clear need for methodological approaches that explicitly assess the potential interplay of processes across spatial and temporal scales [6].

Geographically replicated local studies based on long-term inventories have already helped place local ecological studies in a broader biogeographic context [7–9], but have not necessarily resolved contingencies. Even when local studies are replicated geographically, they often do not reveal general trends in the processes underlying community structure. For example, Adler *et al.* [10] examined the productivity–richness relation in 48 plant communities on five continents, but did not detect a consistent pattern. Part of this idiosyncrasy might arise owing to variable effects of biogeographic and evolutionary processes on the structure of local ecological communities [11]. Therefore, a central challenge for ecologists and evolutionary biologists is to not only increase the number of local studies replicated along broad-scale environmental gradients and in different biogeographic regions [4,12], but also to develop integrative approaches to help disentangle the influence of evolutionary and historical processes operating at larger spatiotemporal scales from ecological processes operating at smaller scales.

Species pool influences generate idiosyncrasies

Much of the idiosyncrasy in community ecology arises as a result of geographic variation in the evolutionary and historical processes that have shaped the structure of the species pool (i.e., the set of species that could potentially colonize a community; see Glossary). First, geographic variation in the species richness and composition of species pools influences community structure [7,11,13–15] and blurs inferences made about local ecological processes. For example, many studies invoke differences in predominant local ecological processes to explain species turnover along environmental gradients [16,17]. However, geographic variation in species turnover can emerge simply due to

Glossary

Assemblage dispersion fields: a graphic representation of the species pool obtained by overlaying on a map the geographic distribution of all species in a given assemblage.
Biological constraint: a factor that is included in a null model as a way to account for the probability that species in the species pool can co-occur in the focal community.
Dark diversity: the set of species that is absent from the local community, but could potentially colonize and establish in it.
Ecological contingencies: context dependency of ecological processes.
Natural experiments: empirical studies that take advantage of natural variation in the factor of interest.
Null model: a statistical approach that generates the pattern expected in absence of a particular process.
Regional fauna or flora: all the species known to occur in a predefined region.
Species pool: the set of species that could potentially colonize and establish within a community.
Species pool geometry: the size and shape of the species pool (e.g., dispersion field) as visualized on a geographic map.

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variation in the size of the species pool [7]. Second, geographic variation in ecological attributes of species in the pool often results in idiosyncratic responses of communities to local factors [18,19]. For example, the relation between local environmental factors, such as soil pH, and species richness often varies among regions because the response of entire communities to local factors is contingent upon environmental affinities of species (e.g., for particular levels of soil pH) in the regional pool [14,19–21]. Thus, idiosyncrasies emerge from complex interactions between local ecological processes and species pools.

Despite widespread interest in the evolutionary causes and ecological consequences of species pools [11,14,22–26], there has been relatively little progress in the development of the species pool concept over the past 20 years [27]. Conceptual advances might be limited, in part, by the difficulty of constructing species pools in a way that maximizes the accuracy and validity of local ecological inference. A second major hurdle is to consider not only how the size of the species pool influences local communities, but also how other important attributes of the species pool, such as functional diversity, enhance local inference. The multiple ways in which species pools can affect community structure and generate idiosyncrasies highlights the need to consider carefully not only how the species pool is defined, but also how multiple attributes of the species pool influence community structure.

In this paper, we outline an integrative approach for quantifying ecological determinants of community structure among biogeographic regions while accounting for species pool influences. We describe two complementary empirical approaches that have seldom been used in combination: geographically replicated local studies and null models designed to account for species pool influences. We show how the integration of these two approaches could lead to novel insights unattainable by each approach in isolation. In particular, we illustrate how considering environmental affinities of species in the pool, together with the manipulation of local factors, might eliminate much of the perceived idiosyncrasy in community structure. Finally, we provide general directions for the construction of ecologically explicit species pools, which is an essential step for quantifying and controlling for species pool influences when inferring local ecological processes.

Comparing local ecological processes among regions

Geographic replication of local studies

Geographically replicated local studies are beginning to elucidate how the importance of ecological processes might vary along broad-scale environmental gradients and in different biogeographic regions [7,13,28–30]. For example, by replicating experiments along large-scale environmental gradients, one can examine how the abiotic environment mediates local biotic interactions [31–38]. Using this approach, Callaway and colleagues [38] showed systematic variation in the relative importance of positive and negative interactions in plant communities along environmental stress gradients. Similarly, Freestone and Osman [31] studied predator effects on marine benthic communities along a latitudinal gradient and found that the importance of biotic interactions increased from temperate to tropical regions. By contrast, other replicated experiments have not revealed general trends (e.g., [10,39]). Therefore, geographic replication alone could be insufficient for uncovering general trends in local ecological processes because attributes of the species pool might blur one's perception of how local communities respond to local factors [18,19].

One way to infer whether the influence of the species pool generates idiosyncrasies is to manipulate directly the species or trait diversity of species pools, for example, through experimental introduction of species [18,40,41]. Combining this approach with geographically replicated experiments is a largely unexplored and promising approach for disentangling local ecological processes from species pool influences. However, species pool manipulation can be costly, logistically complex, or unethical, such that other approaches might be necessary in many cases.

Null models to disentangle local ecological processes from species pool influences

To complement experiments and observational studies, null models can be used test whether observed patterns of community structure differ from what would be expected after excluding specific processes of interest. Within community ecology, null models have largely been applied to local communities sharing the same species pool (e.g., [42–46]). However, when the goal of a study is to elucidate how the importance of local ecological processes varies geographically, then null models can be extended to control for the influence of multiple species pools, each of which is unique to a particular community (see 'Community-specific pool delineation' for details).

Null model approaches can be combined with geographically replicated local studies to enhance ecological inference across regional [28,29], continental [13], and global [47,48] scales. A very simple null model can be used to compare the observed pattern of community structure to what would be expected if one randomly sampled species from the species pool. Little or no deviation from the null expectation indicates that the observed pattern is largely shaped by attributes of the species pool. Geographic trends in the strength and direction of the deviation provide insight into how the relative importance of ecological process might vary among regions. However, using null models to control for species pool influences requires an ecologically informed and explicit definition of the species pool.

An integrative approach for resolving contingencies

Whereas geographically replicated studies can control for local factors, null models can be used to control for one of the most important factors that varies among biogeographic regions: differences in the structure of species pools (e.g., [7,13]). Moreover, experimental manipulations can complement null model analyses by providing insights into the mechanisms that give rise to non-random patterns, especially in cases where similar patterns can be generated by completely different mechanisms. Integrating geographically replicated studies with null models can enhance local inference by accounting for idiosyncrasies that might arise from the influence of evolutionary and biogeographic history.

As an example, suppose the goal of a study is to understand the generality of the relation between local plant species richness and water availability. Using an experiment, one could manipulate water availability and then quantify richness in both experimental and control plots (Figure 1). This experiment could then be replicated on different continents and in several climatic zones. Communities in different biogeographic regions might differ in terms of the proportion of species in their respective species pools with affinity for wet (mesic species) versus dry (xeric species) conditions. These attributes of the species pool can influence the way in which local communities respond to the experimental treatment to produce seemingly idiosyncratic patterns of local species richness (Figure 1). For example, water addition might have little influence on local richness if species in the pool are largely adapted to dry abiotic conditions. Therefore, the observed number of mesic species should be compared to the number expected, for example, by randomly sampling species from the pool. Although the increase in irrigated plot richness might be minimal, the magnitude of this increase relative to the availability of mesic species in the pool could still be high. The net effect of water addition can be estimated by quantifying the degree to which the observed response

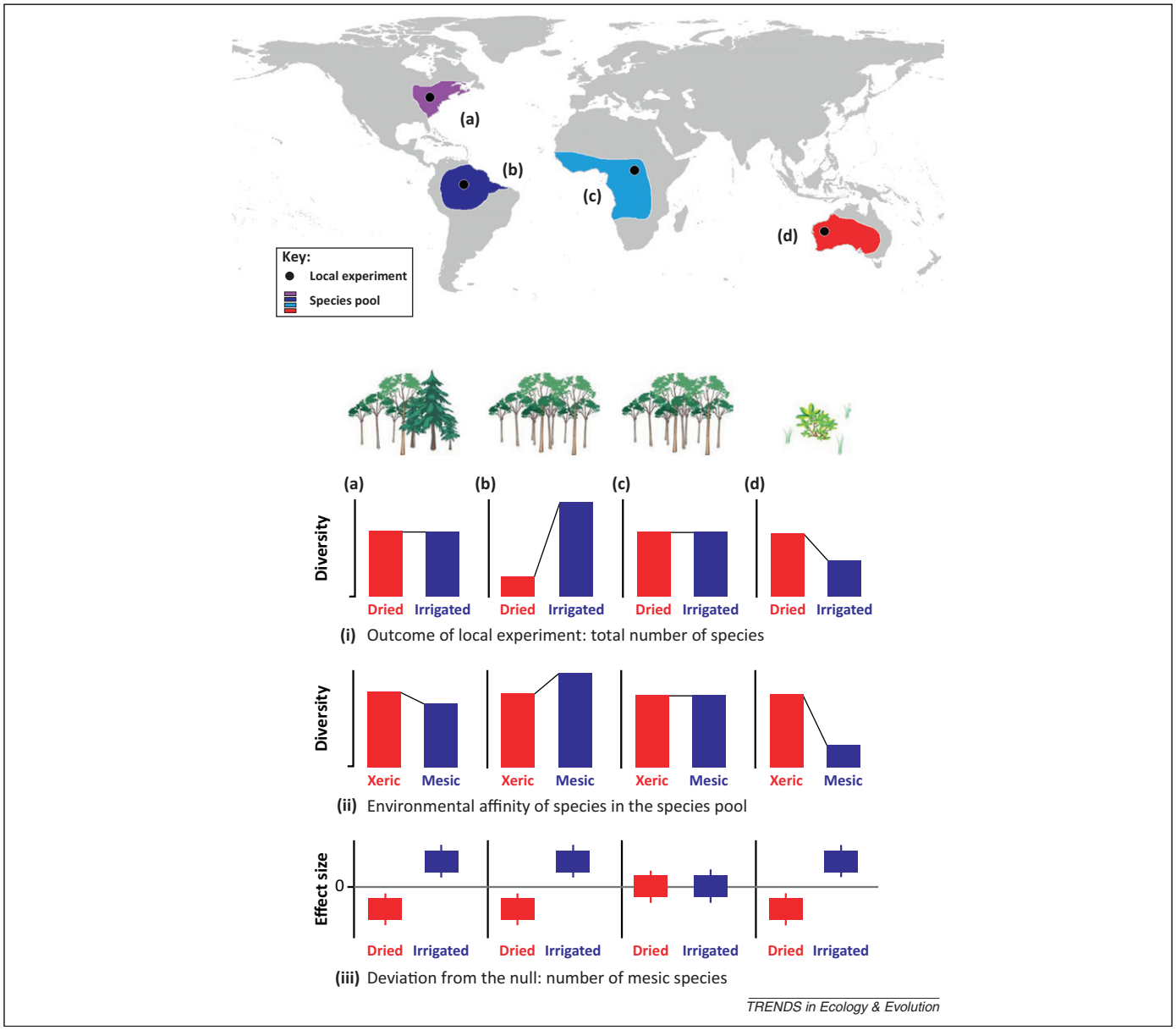

Figure 1. Local diversity patterns are jointly determined by local processes and attributes of the species pool. We illustrate this point using a hypothetical example of a geographically replicated local experiment in which plant richness is measured in experimentally dried and irrigated plots. Although the experimental design is identical in the four regions, the results of the treatments seem to be highly idiosyncratic (i), making it tempting to conclude that water has no consistent effect on plant richness. However, categorization of species in the species pool as either xeric or mesic shows that the number (i.e., diversity) of species in the species pool with affinity for xeric or mesic habitats differs substantially among regions (ii), probably reflecting geographic differences in climatic conditions and evolutionary histories. By using a null-model approach, it is possible to show that the number of mesic species in each treatment, above that expected from a random draw from the pool, is actually similar across regions a, b, and d (iii). All three regions have positive effect sizes in irrigated plots, indicating that the number of mesic species is similarly higher than that expected from their regional availability. Conversely, dried plots have negative effect sizes, indicating that the number of mesic species is lower than that expected by their regional availability. Only in region c is a truly idiosyncratic experimental outcome seen, as evident by effect sizes that do not differ from zero, indicating that the experimental manipulation influences richness in a way that is independent of species categorization as mesic or xeric. This example illustrates how explicit consideration of species pool attributes (i.e., geographic variation in the supply of available species with affinities for particular habitat types) can help reveal similarities in local ecological processes.

deviates from the random (null) expectation. In particular, a standardized effect size generated from the null model randomization procedure enables the quantification of the strength and direction of the community response after accounting for the species pool influence (e.g., [49]; Figure 1). The effect sizes can then be compared among regions to examine geographic variation in the importance of local ecological processes (e.g., water availability).

Constructing ecologically explicit species pools for null models

The definition of the species pool in null model analyses can influence, and in some cases even reverse, one's perception of the predominant ecological processes determining community structure [22,23,42,50]. In particular, inference based on null model analyses are sensitive to the delineation of the species pool and assumptions made regarding the probability that a species will disperse to, persist in, and interact with other species in the community of interest (Box 1). Here, we highlight several important attributes of the species pool that must be considered when inferring ecological processes using null model analyses.

Community-specific pool delineation

Although there might not be a single appropriate definition of the species pool, species pool delineation is unavoidable in null model analyses. Defining the species pool can be done either arbitrarily or taking into consideration fundamental ecological principles (i.e., biological constraints). Species pools have been arbitrarily delineated based on species lists (i.e., regional fauna or flora) compiled for geopolitical regions [51], biogeographic regions [52], or, more commonly, using all the species inventoried in a particular study. Using local species lists to delineate the species pool ignores the species that could potentially disperse to the focal community, but have not been detected (i.e., the dark diversity; see [53] for more information on this concept). Moreover, using species lists from predefined regions assumes that different communities within the region share the same species pool, which is unlikely. As community ecologists replicate their experiments across large-scale environmental gradients and in different regions, it is becoming important to define the species pool for each focal community individually (as in [22,54]). In addition, it is often assumed that all communities have species pools with identical size and shape, which is not necessarily the case. The spatial configuration of physical barriers and broad-scale climatic zones generates variation in the geometry of species pools [27]. Visualizing the geometry of a species pool can be achieved using assemblage dispersion fields [27]. We suggest that dispersion fields generated from data on the geographic distributions of species can be used as a starting point to delineate the species pool in its broadest sense (i.e., biogeographic species pool). Nevertheless, other attributes need to be considered to evaluate which species are likely to disperse to, and persist in, local ecological communities.

Dispersal probabilities

When defining the species pool, ecologists often assume that all species within the pool should be able to disperse to the focal community. However, this assumption might not be met if the species pool is broadly defined. Therefore, if one asks whether the structure of a community deviates from that expected by random colonization (i.e., as in a null model analysis), then dispersal probability must be considered. Dispersal probabilities depend on both site-specific and species-specific properties, and their interactions. It is possible to account for site-specific dispersal probability in null models by weighting the probability that a community draws species from other communities or regions. Site-specific dispersal probability can be assessed based on landscape connectivity [55] or estimates of geographic isolation [56]. Even more realistic null models could incorporate species-specific estimates of dispersal capabilities; however, such data are rarely available or difficult to quantify. Therefore, incidence is commonly used as a species-specific proxy for dispersal probability [13,24,43]. However, although incidence might be a suitable proxy for species-specific dispersal probability [57], it might not

Box 1. Inferring processes from patterns of phylogenetic community structure

Although the species pool definition in null model analyses has received attention in the past, new challenges are emerging with the explosion of studies focusing on the phylogenetic structure of communities. In particular, the definition of the species pool can affect inferences about the relative influence of historical and evolutionary versus ecological processes [13,42]. We illustrate this point using a recent study of hummingbird communities [28].

Along an elevational gradient in the Andes, Graham and colleagues [28] found that mean phylogenetic relatedness of species increased from low- to high-elevation communities Figure I. Based on a species pool definition that included all of the species observed in their study communities, they concluded that local environmental filtering predominates as a structuring mechanism at high elevations, whereas competition has a more important role at low elevations. Such interpretations of patterns of phylogenetic community structure are common. However, unless the definition of the species pool explicitly considers the probability that any particular species can colonize a community, inference about structuring mechanisms could be erroneous [22,23]. Systematic variation in phylogenetic community structure along the elevational gradient might arise simply because the evolutionary and historical processes shaping the size and composition of the species pool trickle down to shape the structure of local communities [13,42]. Such geographic variation in the composition of the species pool might arise from the interplay of niche conservatism and environmental filtering. For example, recent work by Zobel and colleagues [26] suggests that geographic differences in community structure result largely from differences in the contemporary availability of ancestral habitats.

If the goal is to infer local ecological processes (e.g., competition), one needs to compare the observed pattern to one generated by sampling from a species pool that accounts for the influence of evolutionary and historical processes. In this particular example, it might be appropriate to restrict the pool to species that are found within the same elevation band as the focal community. If the phylogenetic structure of hummingbird communities deviates significantly from the null expectation using this biogeographically explicit definition of the species pool, then it might be more valid to conclude that local ecological processes generate the observed pattern. As the fields of community phylogenetics and trait-based community assembly expand and evolve, it will be important to revisit some of the issues that have hindered the use of null model in the past (see [68] for a review).

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Figure I. Elevational gradient in the phylogenetic structure of hummingbird communities in the Andes. Lowland hummingbird communities comprise species from several distantly related clades, whereas highland communities comprise species from mostly two closely related clades. Differences in the morphology of the beak and plumage color mirror differences in the phylogenetic composition of hummingbird communities along this elevational gradient. Null models with an explicit species pool definition can help tease apart the role of biogeographic history from that of local ecological interactions is shaping this pattern of community structure. Painting by Jon Fjeldså.

necessarily correlate with intrinsic dispersal capabilities. Nevertheless, understanding of the processes controlling dispersal probabilities is increasing [58] and new methods for tracking dispersal routes and estimating dispersal potential are emerging [59]. Consideration of taxon-specific dispersal estimates derived from new theoretical advances and technologies will improve inferences made from null model analyses.

Environmental affinities

Dispersal probabilities say little about the probability that species will persist. Hence, species pools that consider dispersal probabilities will include species that are able to disperse to, but unable to persist in, local communities because of unsuitable environmental conditions. If one asks questions related to the role of competitive interactions in shaping community structure, for example, it is

Box 2. Hierarchical species pool definitions and hypothesis testing

Examining alternate species pool definitions provides a platform for testing hypotheses on the multiple processes involved in generating observed patterns of community structure (e.g., [13,22,57]). However, risks associated with the inadequate construction of species pools [22] and null models [68,69] have been at the center of heated debates in ecology. Controversy about the use of null models for hypothesis testing has emerged from the construction of models that inadvertently incorporate the process that is being inferred (the 'Narcissus Effect' described by [69]). Here, we outline an approach that should prevent repeating past mistakes while providing insights into the ecological and evolutionary determinants of community structure. We show that comparing null models that differ in the definition of the species pool can help evaluate the relative contribution of multiple processes.

Consider a study of body-size overlap in ant communities in southwestern deserts of North America (e.g., [70]). One might use patterns of body-size overlap to infer the processes of environmental filtering (high overlap) and competition (low overlap). Defining the species pool as all ant species in North America, one might find that body-size overlaps significantly more than expected by chance. This might be interpreted as the result of environmental filters that select for a narrow range of body sizes. However, if the species pool is restricted to desert species, one finds that body-size overlap is not different from random draws from the species pool. This apparent change in community structure under the new species pool definition would result from including broad-scale environmental filtering in the definition of the species pool. Finally, if the definition of the species pool is further restricted to ants in particular foraging guilds (e.g., granivorous), one might find significantly less body-size overlap than expected among granivorous species. This would now suggest that, within the guild of granivorous species, overdispersion of body size is a consequence of food resource partitioning facilitated by character displacement Figure I.

This hypothetical example demonstrates that the definition of the species pool is relative to the process being inferred. Consequently, it might be necessary to revise the traditional 'regional' view of the species pool to include multiple processes operating at different spatial and temporal scales. Identifying these processes and their contribution to the structure of ecological communities offers promising avenues for research.

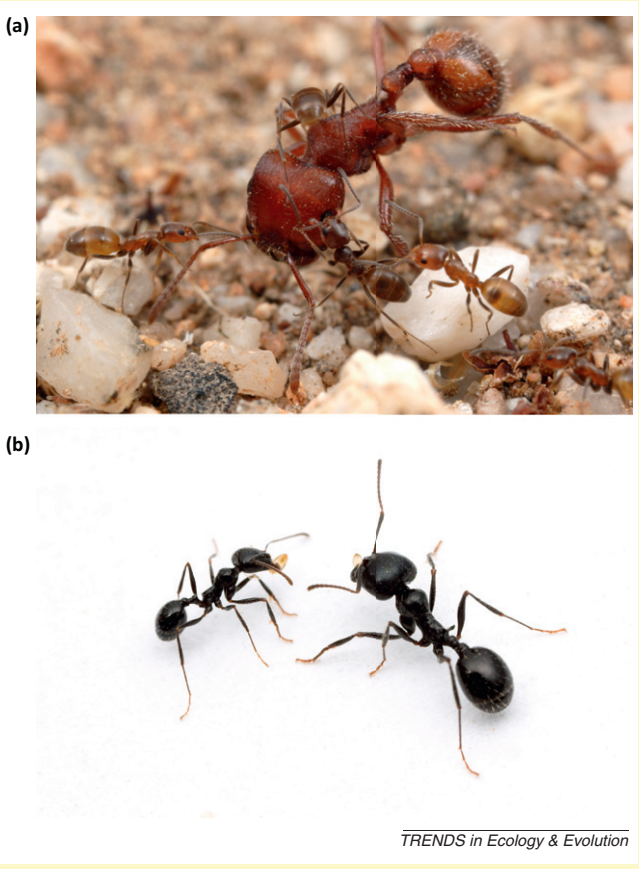

Figure I. Body-size variation among species of seed-harvesting ants correlates with the size of preferred food item. *Pogonomyrmex desertorum* **(a)** and *Messor pergandei* **(b)** are both seed-harvesting ant species found in deserts of the southwestern part of North America. Minimal overlap in body size mediates food resource partitioning and facilitates coexistence in desert ant communities. Photographs reproduced, with permission, from Alexander Wild.

important to consider whether species that can disperse to the focal community could also establish given the abiotic environment or habitat characteristics [22,54].

The environmental affinity of species in the pool can be included as constraints in a null model [25]. Two different approaches have been used: (i) species are included in the pool of a focal community based on a qualitative classification of species affinity to particular habitat types [60,61]; or (ii) the probability of inclusion in the pool is weighted using quantitative measures of environmental niche association [62]. The ideal approach for estimating species-specific environmental affinities would be to quantify directly habitat requirements and physiological limits from field observations, behavioral assays, and laboratory tests of physiological tolerance. Admittedly, comprehensive and reliable data on species autecological requirements are often difficult to obtain. As an alternative, environmental niche modeling could be used to estimate broad environmental associations [63]. However, it is important to note that it might be circular to derive environmental affinities from the same data used to delineate the 'broad-scale' species pool. Therefore, we encourage the use of independent data and experimental approaches described above. In addition to species-specific data on environmental affinities, site-specific data on habitat cover or diversity [57,64] can also be enforced as constraints in null model analyses to further increase ecological realism.

Other biological constraints

Depending on the question at hand, a multitude of other biological constraints, such as guild structure or demographic information, should be considered to increase ecological realism in the definition of the species pool. Such considerations are especially relevant to studies focusing on biotic interactions and coexistence, or 'Assembly Rules' [47]. For example, if the process being investigated (e.g., character displacement) is thought to be the result of competition for food resources, then it might be relevant to restrict the species pool to a particular guild of species that are likely to compete directly (e.g., [57]). Other relevant examples include recent studies on the role of biotic resistance in biological invasions [65] and facilitation [66].

Hypothesis testing and species pool definition

A major challenge with defining the species pool is finding the optimal tradeoff between ecological realism and adding too many constraints to the null model [54]. In addition, there is no 'proper' scale with which to delineate the species

pool, because species pools are shaped by multiple processes operating at different spatial and temporal scales, each of which can influence local patterns and processes. Nevertheless, both of these issues can be at least partially dealt with by comparing several simple null models that vary in terms of ecological processes they account for [45,57]. One can compare null models that vary in: (i) the spatial extent and geometry of the species pool; and (ii) biological constraints imposed on the selection of species from the pool to a null community [57,67]. The successive and hierarchical addition of ecological realism to null models can be used not only to avoid erroneous inference about ecological processes, but also to disentangle the relative influence of multiple processes (see example in Box 2). In sum, the definition of the species pool should be tailored to detect the signature of a particular process or suites of processes rather than arbitrarily defined.

Concluding remarks

New conceptual, analytical, and practical challenges are emerging with a rapid rise in the number of geographically replicated studies aiming to uncover general trends in the determinants of community structure. We suggest that integrating geographically replicated local studies with ecologically informed null models and species pool definitions should help with both inferring predominant processes and assessing generality. However, replicating standardized experimental studies on different continents is logistically and financially challenging. The establishment of well-coordinated international consortiums to implement such efforts will be pivotal (e.g., http://www.nutnet.umn.edu/). Another challenge, the lack of high-quality data on the distributions, phylogenetic relations, and functional traits, precludes the construction of ecologically informed species pools for many taxonomic groups and biogeographic regions. As much information on the basic life histories and functions of species is lacking, it might be too early to 'give up' on detailed autecological studies of local communities. By drawing on tools and concepts across ecological and evolutionary disciplines to resolve contingencies, it is possible to re-integrate the foundations upon which the concept of the ecological community was built [2].

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