Research

Disentangling the importance of ecological niches from stochastic processes across scales

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Deterministic theories in community ecology suggest that local, niche-based processes, such as environmental filtering, biotic interactions and interspecific trade-offs largely determine patterns of species diversity and composition. In contrast, more stochastic theories emphasize the importance of chance colonization, random extinction and ecological drift. The schisms between deterministic and stochastic perspectives, which date back to the earliest days of ecology, continue to fuel contemporary debates (e.g. niches versus neutrality). As illustrated by the pioneering studies of Robert H. MacArthur and co-workers, resolution to these debates requires consideration of how the importance of local processes changes across scales. Here, we develop a framework for disentangling the relative importance of deterministic and stochastic processes in generating site-to-site variation in species composition (β-diversity) along ecological gradients (disturbance, productivity and biotic interactions) and among biogeographic regions that differ in the size of the regional species pool. We illustrate how to discern the importance of deterministic processes using null-model approaches that explicitly account for local and regional factors that inherently create stochastic turnover. By embracing processes across scales, we can build a more synthetic framework for understanding how niches structure patterns of biodiversity in the face of stochastic processes that emerge from local and biogeographic factors.

Keywords: β-diversity; biogeography; community assembly; ecological drift; niche selection; regional species pool

1. INTRODUCTION

A species' niche is determined by the traits that allow it to gather resources, evade enemies and any other factor that influences its relative birth and death rates [1,2]. Conditions within the *N*-dimensional hyper-volume of a species' needs [2], in which birth rates are equal to or greater than death rates, represent a species' 'requirement' (*sensu* [3,4]) or 'Grinnellian' niche (*sensu* [5]). A niche can also be described as the interactions a species has with its biotic and abiotic environment [6]. The corresponding *influence* that a species has on its environment is known as its 'impact' niche (*sensu* [3,4]) or 'Eltonian' niche (*sensu* [5]). Niche concepts were instrumental in the development of the 'local perspective' of ecological communities, which views communities as limited-membership assemblages in which interspecific biotic interactions and abiotic conditions are the primary factors influencing community composition and diversity (e.g. [7,8]). Today, niche concepts are used widely in ecology (e.g. [4]), biogeography (e.g. ecological or environmental niche models; [9]) and in the study of evolutionary processes that shape the structure of ecological assemblages (e.g. [10,11]). Armed with these distinct but related components of the niche, we can develop a wide variety of expectations for how niches influence species distributions and range limits, the distribution and co-occurrence of disparately or closely related species, and patterns of biodiversity along environmental and biogeographic gradients (e.g. [4,5,9,12–14]).

Although the niche is often heralded as one of the most important concepts in community ecology (e.g. [4,15–19]), studies of the niche are often considered tautological, owing to the seemingly insurmountable task of defining the dimensions of the niche, especially those that help maintain species diversity [16,20,21]. Furthermore, it has recently been argued that evidence for niche differences that promote stable coexistence of species is, in fact, quite sparse [22]. Empirical evidence for niche-based coexistence has been limited, in part, by the challenges associated with testing stabilizing and equalizing mechanisms that promote species coexistence in many communities [15,19]. Nonetheless, criticisms of niche theory, many quite valid, have stimulated numerous theoretical and empirical investigations that call into question the centrality of the niche concept and the role of local niche-based processes in generating patterns of biodiversity (e.g.

[8,23,24]). Consequently, there has been a major shift towards more regional perspectives on ecological communities, as well as integration of local and regional perspectives, to better understand how processes at broader scales influence biodiversity (e.g. [8,25–28]).

Here, we develop a framework for testing the importance of ecological niches in generating community structure at local and biogeographic scales. We begin by illustrating how the role of niches varies with scale using examples from pioneering studies by Robert H. MacArthur *et al.* (e.g. [29–31]). We then describe two complementary approaches that combine patterns of site-to-site variation in species composition (β-diversity) with null-model analyses to disentangle the importance of niche-based process from stochastic ecological processes at local and biogeographic scales. We contrast completely deterministic, niche-based processes with more stochastic (e.g. neutral) processes, such as chance colonization, random extinction and ecological drift (random changes in species relative abundance; [8]). Note, however, that we do not generally consider the issue of speciation (neutral or otherwise) in our conceptual framework; instead, we leave those discussions to our evolutionary biology colleagues (e.g. [14]). Throughout the paper, we use the term 'deterministic process' to refer to any ecological process that involves non-random, niche-based mechanisms, and we use the term 'stochastic process' to refer to any ecological process that gives rise to patterns of species diversity, relative abundance and composition that are indistinguishable from random chance alone. Although debate exists as to how some processes influence both stochastic and deterministic community assembly (e.g. dispersal limitation; [15,32]), it is not the goal of our paper to resolve such debates.

Our framework provides two general insights into how ecological niches influence patterns of biodiversity. First, it explicitly considers how the relative importance of stochastic processes changes with scale both within (e.g. between local habitats that vary in size) and among (e.g. between regions with large versus small species pools) biogeographic regions. Second, it offers an approach for disentangling the relative importance of deterministic and stochastic processes in generating β-diversity along ecological gradients (disturbance, productivity and biotic interactions) and among biogeographic regions that differ in the size of the regional species pool. Again, although the evolutionary processes that generate regional species pools (speciation and extinction) provide important insights into community assembly (e.g. [8,14,33]), the evolutionary causes of regional diversity are beyond the scope of this paper. Rather, our goal is to explore the ecological consequences of 'contemporary' species pools on community assembly over time scales in which regional diversity is largely uninfluenced by speciation and extinction. Within this context, we illustrate the utility of null models that explicitly account for local and regional factors that inherently create stochastic turnover. By embracing processes at multiple scales, we can begin to disentangle the relative importance of niche-based processes in the face of stochastic ecological processes that emerge from local and biogeographic factors.

(a) *The niche across scales: revisiting MacArthur's paradox*

Robert H. MacArthur's pioneering work helped to lay the foundations for several modern subfields of ecology, including evolutionary and foraging ecology [34], coexistence and biodiversity theory (e.g. [31]), island biogeography theory [29,30] and large-scale studies across biogeographic gradients (i.e. temperate versus tropical communities; [35]). Importantly, each of these fields focuses on different spatial scales, ranging from variation among individuals and populations within localities to variation among communities and regions across biogeographic provinces. The concept of the ecological niche, as developed by Grinnell [1] and Elton [6], and codified by Hutchinson (e.g. [2,36,37]), was central to MacArthur's work. However, the prominence of the niche concept—the interaction between a species' traits and its environment—varied depending on the primary spatial scale of inquiry. At one extreme, MacArthur's work on limiting similarity, competition and coexistence (e.g. [31]) viewed species trait–environment relations and interspecific trade-offs as paramount for species coexistence and diversity at local spatial scales. At the other extreme, MacArthur's work on the theory of island biogeography [29,30] ignored any differences among species in their traits (i.e. species were neutral) when predicting species diversity on islands that vary in their size and isolation from the mainland as a function of colonization and extinction rates.

'MacArthur's Paradox' [38,39] highlights the fact that his different theories placed very distinct emphasis on the relative importance of niche-based processes. His use of niche concepts in theoretical studies depended on the phenomena under investigation and the spatial scale of the study: limiting similarity and coexistence were used to understand patterns of coexisting species at local scales whereas island biogeography theory was used to understand patterns of compositional turnover and diversity at broader spatial scales. However, he was well aware of the connections between the two scales, and incorporated larger spatial processes into local community interactions using nascent metacommunity models (e.g. [40,41]), as well as aspects of species trait differences into the theory of island biogeography [30].

Interestingly, MacArthur's influence has direct historical connections to two contemporary, but seemingly diametrically opposed perspectives on how ecological communities are structured: niche and neutral theory. Modern niche theory is based on explicit consumer–resource interactions and trade-offs in the way that organisms use different resources and other factors that influence their birth and death rates (e.g. enemies, disturbance, etc.) [3,4]. Resource-based trade-offs are best epitomized by Tilman's [42,43] R* concept. Based on MacArthur's [35] consumer–resource models, in the R* concept models species coexistence is based on the minimum amount of a limiting resource that a species needs to persist in a given locality, and trade-offs

among species in their abilities to use different resources. As the antithesis to niche theory, Hubbell's [8] neutral theory challenged the dominant paradigm to suggest that pervasive dispersal limitation, ecological drift and a balance between random extinction and speciation could explain a wide variety of ecological patterns. Hubbell's 'individual-based' neutral theory was explicitly based on the ideas and formulations of the 'species-based' equilibrium theory of island biogeography [29,30], which is also a type of neutral model [44,45]. That is, species in the simple version of the equilibrium theory are inherently equivalent, in that only colonization/extinction processes influence species diversity on an island, without consideration of their traits.

The schism between deterministic and stochastic perspectives on community structure is not new, and has been present since the early days of ecology. In opposition to Clements' view of predictable community structure developing in different environments [46], Gleason considered that species–environment associations were more variable and gave rise to less predictable community structure, even under similar environmental conditions [47]. Similar concepts invoking the importance of dispersal limitation, stochasticity and priority effects can be seen in the works of Tansley (e.g. [48]) and Egler [49]. In opposition to the Hutchinson/MacArthur school of deterministic coexistence and diversity owing to competitive interactions (e.g. [50]), Simberloff and co-workers (e.g. [51]) questioned whether similar patterns could be observed owing to random chance alone. Sutherland [52] suggested that multiple states could occur on similar habitat templates, and that priority effects and stochasticity in arrival times could strongly determine community structure (see also [53,54]). By contrast, Connell & Sousa [55,56] argued that these patterns were more probably owing to deterministic variation in the underlying environmental templates. Likewise, Sale [57,58] suggested that lottery processes could maintain high diversity in coral reef communities, and Hubbell [59] suggested similar processes in high-diversity rainforests, but these were countered by a more deterministic perspective on the maintenance of diversity (e.g. [60,61]). Most recently, there has been a resurrection of the stochastic perspective by Hubbell's [8] elegant and powerful neutral theory, which has spawned a cottage industry of tests in support, and refutation, of its main tenets [23,45].

Given the frequency (and sometimes fervent intensity) by which debates about stochastic versus deterministic processes have arisen, it seems rather apparent that both processes must be operating in ecological communities. Indeed, as with most diametrically opposed concepts in science (e.g. selection versus genetic drift; [62]), the divide between niche and neutral theories has begun to close in recent years. Not only are the niche and neutral perspectives related by intellectual descent (e.g. from MacArthur and co-workers), they represent two complementary parts of a more complete picture that examines how determinism and stochasticity (among other factors) interact to create community structure [15,18, 63–66]. Nonetheless, the division between proponents of deterministic

versus stochastic processes remains prominent (e.g. [67–69]).

(b) *Towards a more comprehensive framework for niche-based community ecology*

The key to resolving MacArthur's paradox and contemporary debates in community ecology (e.g. niches versus neutrality) lies in our ability to understand how deterministic and stochastic processes interact in space and time to structure biodiversity. To achieve this synthesis, we need to understand the extent to which species traits, species interactions and environmental conditions contribute to deterministic community structure relative to stochastic forces. In approaching this topic, we emphasize that it is not our intent to develop an elegant mathematical or statistical model to advocate one approach over another. Our goal is simply to reinforce how stochastic ecological processes that emerge within and among regions can influence the importance of deterministic processes in generating community structure, sometimes quite strongly.

At least three fundamental sets of observations demonstrate how basic niche theory, based solely on local processes (e.g. [4]), cannot always explain patterns of diversity in natural communities. First, within a given regional pool of species, there are often many species that are rare or absent from sites in which they could otherwise persist (e.g. [70]), often reflecting barriers to dispersal [71]. Even when there are no physical barriers to dispersal, populations of many species in the regional pool, and especially those with low relative abundance (rare species), will be recruitment limited owing to limited fecundity or dispersal (e.g. [72–74]). When propagules arrive to sites, recruitment and local population sizes can be further constrained by establishment limitation owing to demographic stochasticity, Allee effects (e.g. [13]) and local habitat conditions (e.g. [75]).

Second, the size of the regional species pool can strongly influence the numbers and types of species that co-occur locally (e.g. [26,71]). For example, it is often the case that more species co-occur locally when there are more species in the regional pool, a pattern that suggests that local assemblages are unsaturated with species (e.g. see discussions and debates in [28,76–78]). In addition, the number of species that do not co-occur locally is also strongly influenced by the number of species in the regional species pool. When the size of the species pool is large relative to the number of species that can co-occur in any given locality, a smaller fraction of the species pool can potentially attain membership in any given local community, resulting in higher β-diversity [79,80].

Third, local and regional processes often interactively structure local communities. At the community level, the influence of propagule arrival (i.e. regional dispersal or immigration) on patterns of species diversity and composition may depend on niche-based environmental filters (e.g. [81,82]), as well as habitat size and isolation (e.g. [29,30]). In both plant and animal communities, there is widespread evidence

that arrival of propagules from the species pool strongly limits local species richness, further suggesting that many communities are not saturated with species [7,82–84]. Likewise, local diversity is typically higher in metacommunities where dispersal rates among localities are more frequent relative to those with less-frequent dispersal [83]. Moreover, the extent to which propagule arrival influences species richness and composition will depend on the nature of biotic and abiotic filters through space and time (e.g. [79,82]). Priority effects, for example, which result from the interaction of stochastic colonization and deterministic interactions between early colonizing and later colonizing species, increase β-diversity among sites that are otherwise similar in environmental conditions, resulting in multiple stable equilibria [79]. The propensity for communities to achieve multiple stable equilibria can also vary with environmental conditions, local community size and the size of the regional species pool [79]. Finally, there can be unseen deterministic causes of the seemingly stochastic variation in community structure either owing to high dimensionality in the environmental factors by which individuals respond (e.g. [21,85]) or cryptic species interactions (e.g. host–pathogen interactions) that create a variable mosaic of species relative abundances (e.g. [33]).

The processes described above fit nicely within Vellend's [66] recent synthesis of the four general processes that influence community structure: selection, drift, dispersal and speciation. Selection in Vellend's vernacular is analogous to our 'niche selection,' a deterministic process in which environmental factors interact with species traits to determine which species (and how many) occur in different areas; within the metacommunity framework, this process is referred to as 'species sorting' (e.g. [25]). Moreover, ecological drift, dispersal (e.g. chance colonization) and speciation can all be envisioned as components of more stochastic processes that create deviations from expectations based solely on niche theory. Ecological drift can act alone through probabilistic factors, particularly in small communities [86,87] or when the regional pool is very large relative to the size of local communities [79].

Although these four processes act in concert, we emphasize that they can also interact directly or indirectly with each other. Selection and drift can be envisioned as two sides of the same coin. If selection is strong, drift will be necessarily weaker, and vice versa. Further, drift can interact with selection to create multiple stable equilibria [88]. Dispersal alters the nature by which both selection and drift can act by altering colonization and extinction dynamics. Finally, speciation influences the size of the regional species pool, and areas with higher rates of speciation (or lower rates of extinction) have larger species pools, and thus a greater propensity to exert strong regional influences on the relative importance of drift versus selection. In regions with larger species pools, drift will necessarily play a stronger role in creating variation among local communities, although this does not necessarily imply that selection is any weaker relative to regions with smaller species pools. In §2 we describe how the relative importance of niche selection, ecological drift and dispersal can be disentangled along ecological

gradients and among biogeographic regions that differ in the size of contemporary species pools. For a more dynamic and long-term perspective on species pools, see e.g. [14].

2. USING PATTERNS OF β-DIVERSITY TO DISENTANGLE DETERMINISTIC AND STOCHASTIC PROCESSES

Beta-diversity can provide considerable insights into the importance of deterministic and stochastic processes in generating community structure along ecological gradients (e.g. [65,69,79,88–94]). For example, consider how β-diversity would change under extreme cases in which only stochastic or deterministic processes give rise to community assembly (reviewed in [95]). In Hubbell's [8] neutral theory, β-diversity is predicted to increase along spatial (distance) gradients (figure 1a) owing solely to dispersal limitation (i.e. the failure of propagules to reach local communities). Because the neutral model assumes that all individuals are ecologically equivalent (i.e. that niches do not exist), the model also predicts that β-diversity will not change systematically along environmental gradients (figure 1c). Niche theory, in contrast, predicts that β-diversity varies deterministically along environmental gradients, but not along spatial gradients among communities that share the same regional species pool (figure 1b,d). Under strict niche assembly, species membership in local communities is determined solely by their niche requirements and local habitat conditions. Although these simple examples illustrate how patterns of β-diversity may reflect underlying ecological processes, they undoubtedly represent extreme cases in natural communities. Below, we present additional approaches that allow one to discern how the relative importance of deterministic and stochastic processes changes through space or time.

Ecologists have attempted to disentangle the relative influence of deterministic and stochastic processes using observational and experimental approaches. A common approach is to use variance-partitioning methods to decompose variation in community composition explained by spatial, environmental and spatially structured environmental processes (e.g. [90,92,93]). With the growing recognition that both deterministic and stochastic processes operate simultaneously (e.g. [15,96,97]), several studies have also sought to identify ecological factors that might shift the relative importance of the two processes within a single regional species pool, such as disturbance (e.g. [65,98]), productivity [88], predation [99], competition [100] and local community size [87]. At larger scales, studies have also compared deterministic and stochastic processes among regions that vary in the size of the species pool (e.g. [101,102]).

Because deterministic and stochastic processes are fundamentally intertwined, disentangling their relative importance with varying local or regional factors requires careful consideration of the processes that influence β-diversity. At first glance, it might seem relatively straightforward to simply compare differences in β-diversity among ecosystems or regions and to attribute those differences to variation in the
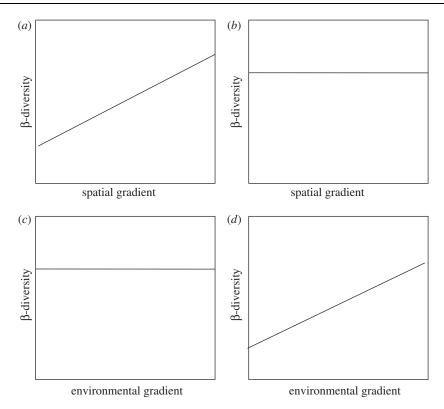
Figure 1. Predicted change in β-diversity along (*a*,*b*) spatial and (*c*,*d*) environmental gradients for a completely (*a*,*c*) stochastic (neutral) and (*b*,*d*) deterministic (niche-based) models of community assembly. Here, β-diversity represents the dissimilarity in species composition between pairs of communities. Figure modified from [95].

strength of environmental and spatial processes (e.g. figure 1; [92]). However, because β-diversity represents the scalar that links local (α-diversity) and regional (γ-diversity), it is often necessary to account for how β-diversity is expected to change owing simply to changes to α-diversity (e.g. within a regional species pool) or γ-diversity (e.g. among regional species pools). Although the interdependence of β-diversity and α-diversity has been well established [e.g. [94,103–105]], studies examining interdependence between β-diversity and γ-diversity and how it influences the strength of deterministic processes along biogeographic gradients have only just begun ([101,102,106]; N. B. Kraft *et al.* 2011, unpublished data; J. A. Myers *et al.* 2011, unpublished data). Importantly, because $\beta = \gamma/\alpha$, even the calculation of 'true β-diversity' [104,107,108] can vary when the size of the regional species pool varies [106]. Because of this interdependence, 'raw' metrics of β-diversity cannot be used to disentangle the relative contributions of deterministic and stochastic processes [105].

Here, we espouse an empirical null-model approach that allows us to disentangle the relative importance of deterministic processes in the face of stochastic processes that emerge at local and biogeographic scales. The approach allows one to detect the signature of deterministic processes even when the specific details that influence niches and coexistence within and among large and taxonomically diverse groups of species might be very difficult, if not impossible, to discern (e.g. [15,69,88,109]). We can then use the magnitude by which communities deviate from a stochastic null expectation, which assumes niches are irrelevant to patterns of community structure, to

compare the relative importance of deterministic processes among ecosystems that vary in local and regional factors that inherently create stochasticity. Large deviations from the null expectation indicate a strong role for deterministic processes, whereas smaller deviations indicate that stochastic processes prevail (e.g. [105]).

Because of the nature by which diversity is partitioned (e.g. $\gamma = \alpha \times \beta$), if some ecological filter such as disturbance or productivity reduces α-diversity by eliminating coexistence mechanisms (e.g. [4]), this will automatically influence β-diversity among localities that all experience that filter (so long as the size of the regional species pool remains the same). This will also be true simply if the scale at which α-diversity is sampled is reduced (e.g. [110]). That is, so long as γ-diversity is sampled over a reasonably large area, any factor that decreases α-diversity in a locality will increase β-diversity, and this is also true for the many pairwise metrics that are often used to estimate β-diversity (e.g. Jaccard's, Sorenson's index) [103]. However, even though the relative influence of stochastic processes can increase because of decreased α-diversity, a null model that takes into account the expected increase in stochasticity is needed to discern how the relative importance of determinism has changed.

Likewise, at regional and biogeographic scales, when the size of the regional species pool (γ-diversity) increases, β-diversity will also increase so long as α-diversity does not increase at the same rate as γ-diversity. Here, the signal of deterministic processes can be masked or reduced owing to the large amount of stochasticity expected simply with an increase in

the size of the regional species pool. To discern whether the strength of deterministic processes varies with the size of the regional species pool, related but distinct null-model approaches are necessary to discern how patterns of β-diversity deviate from expected patterns as γ-diversity increases (e.g. [101,102,111]; N. B. Kraft *et al.* 2011, unpublished data; J. A. Myers *et al.* 2011, unpublished data).

To disentangle the underlying importance of deterministic processes that may or may not lead to β-diversity, we need to explicitly recognize and account for the fact that β-diversity will vary systematically as the ratio of γ : α changes, but that this does not, in-and-of-itself, imply differences in the relative importance of different community assembly processes (e.g. deterministic versus stochastic). Instead, a series of null-model approaches are needed to begin to disentangle these processes (e.g. [105,111]). In the following two subsections, we explore how to disentangle deterministic and stochastic processes using two different but related approaches. In §2a we discuss how to discern the relative importance of deterministic processes when α-diversity varies among localities (e.g. owing to local processes that influence the number of co-occurring species), but the size of the regional species pool is relatively constant (i.e. where the area sampled is sufficiently large so that any local variation in α-diversity owing to ecological filters has little overall influence on γ-diversity). In §2b we explore how to compare the relative importance of deterministic ecological processes relative to stochastic ones among regions where evolutionary and biogeographic processes have generated highly divergent regional species pools (γ-diversity).

(a) *Disentangling the strength of deterministic processes when local processes vary*

Within regions, heterogeneity in both ecological and spatial factors influences the number of species that co-occur locally (α-diversity). Ecological factors include biotic interactions (e.g. dominant predators and competitors), environmental conditions (e.g. productivity) and disturbance, whereas spatial factors include habitat size, isolation and dispersal limitation. In turn, many of these factors can either increase or decrease β-diversity, depending on whether the factor acts in a stochastic or deterministic way [99]. A local factor can alter patterns of α-diversity, even while acting in a completely stochastic way (e.g. generalist predators; [99]), by altering the probability of colonization or extinction without respect to species identity. In this case, if the factor decreases α-diversity, this will lead to a concomitant increase in β-diversity. Alternatively, if a local environmental filter selectively eliminates particular species from persisting in any locality, the 'realized' species pool will be smaller (but not the actual species pool, i.e. γ-diversity), and β-diversity among the localities experiencing this filter will be lower. The strength of the filter, in turn, will be influenced by both the size of the local community and the size of the regional species pool.

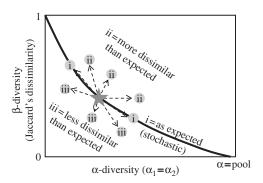Two environmental factors that have a well-known influence on β-diversity are disturbance and

Figure 2. Hypothetical depiction of how β-diversity (Jaccard's dissimilarity) should vary as α-diversity changes within a given species pool. When α-diversity is very low relative to the pool, dissimilarity is expected by random chance to be very high, and when α-diversity is high relative to the size of the pool, dissimilarity is expected to be very low. This relationship is depicted by the solid line (modified from [104]). The star represents the expected dissimilarity at one value of α-diversity, and the arrows pointing in different directions indicate hypothetical cases where some environmental factor either decreases (pointing to the left) or increases (pointing to the right) α-diversity. In each case, measured values of dissimilarity that are not significantly different from the null expectation (points labelled with i) would indicate that community assembly is completely stochastic. This contrasts with measured values of dissimilarity that are higher than expected (points labelled with ii) and lower than expected (points labelled with iii), each indicating some degree of determinism in community structure. The magnitude of the deviations from the null expectation can provide insights into whether the relative importance of deterministic processes varies along ecological gradients that might influence α-diversity.

productivity. Several studies have shown reduced levels of both α- and β-diversity among localities that experience relatively 'harsh' environmental conditions, such as higher disturbance [65,112,113] or lower productivity [88,114–116]. From these observations, we could infer that harsh conditions impose a deterministic filter on community assembly. However, because disturbance and productivity often reduce α-diversity, which we would expect *a priori* to increase β-diversity simply for probabilistic reasons, these processes could have no influence on the relative importance of deterministic and stochastic processes. Furthermore, because some disturbances (e.g. fire) could simultaneously increase niche selection by causing deterministic local extinction of resident species, and decrease niche selection by increasing stochastic recruitment from the species pool in post-disturbance environments [98], the net effect of an environmental factor at the community level could appear relatively stochastic, even when it has a deterministic influence on community assembly.

Mechanisms underlying shifts in β-diversity can result from complex interactions among species and a wide range of environmental factors (e.g. [4,80,86,87,117–119]). The fundamental signature of deterministic processes, however, can be described in very simple but phenomenological way. Figure 2 illustrates how using a null model of expected β-diversity (e.g. Jaccard's dissimilarity) (e.g. [105]) can help us to understand how different local factors influence

both α- and β-diversity. For a given regional pool, there is an expected pairwise dissimilarity among localities if community assembly is completely stochastic (solid line in figure 2). If an environmental factor decreases or increases the number of species locally, there is a concomitant change in the expected dissimilarity (figure 2). Values of dissimilarity greater than the null expectation indicate communities that are more different than expected by random chance owing to deterministic factors; this could happen, for example, if the environments among those sites differ considerably, or if species interactions create 'checkerboards' (*sensu* [120]) in the environment. Values of dissimilarity less than the null expectation indicate communities that are more similar than expected by random chance, which would occur if communities occur in similar environments and those environments select for a similar composition of species. Importantly, there are many other types of null models that one could use to address these sorts of questions (e.g. species-level versus assemblage-level models), and the nature of the conclusions can vary accordingly.

We might expect that a majority of the species in the regional species pool can persist in at least some of the localities that are more benign, whereas only a subset can persist in those that are harsher (e.g. [65]). In such cases, the *realized* species pool is nested, where most species are found at least somewhere among the more benign localities, while fewer are found at least somewhere among the harshest localities. Here, we might expect to find a decrease in α-diversity, but an increase in the relative importance of deterministic processes with increasing environmental stress (e.g. moving to the lower-left in figure 2 towards the point labelled iii). Alternatively, if harsh environmental conditions filter species randomly from the species pool, we would expect a decrease in α-diversity leading to an increase in the observed importance of stochasticity (e.g. moving left along the line in figure 2 towards the point labelled ii). It is important to note that an increase in the importance of stochasticity does not necessarily imply a concomitant decrease in the importance of deterministic processes; the deviation from the null expectation (i.e. deterministic processes) could be the same even though the absolute amount of stochasticity is higher.

Space can also influence our ability to detect the signal of deterministic processes through its effects on α-diversity. Stochasticity is expected to have a stronger influence in smaller or more isolated habitats owing to lower α-diversity, and correspondingly, a higher γ:α ratio, in those habitats [4]. Mechanistically, this can manifest through changes in the interactions among species as they assemble into local communities [80,118]. Just as with genetic drift in populations, ecological drift in communities can sometimes over-ride deterministic processes in smaller and more isolated localities [86,87]. The signature of this process could be detected and differentiated from the above scenario using a null-model approach (e.g. see [105] for details).

We illustrate this approach using observational and experimental studies from pond communities

[65,79,88,99,115]. Small freshwater ponds provide a model ecosystem for studying patterns of β-diversity. Some β-diversity can be explained by environmental factors: different species tend to live in high- versus low-productivity ponds (e.g. [121,122]), high- versus low-disturbance ponds [123], and fish versus fishless ponds (e.g. [124]). However, even within environments that are relatively homogeneous, there is often a great deal of variation in species composition that cannot be explained by environmental factors alone [79,125]. Instead, dispersal limitation, priority effects and ecological drift can sometimes play an important, if not predominant, role in the assembly of some pond communities. Results from experiments in mesocosms show that when conditions are relatively benign (e.g. high productivity, low disturbance and no predators), a large proportion of the regional species pool can persist in at least some localities, and community composition tends to be structured by stochastic factors (e.g. colonization history). Alternatively, under harsher environmental conditions (e.g. low productivity, drought and predators), niche selection prevents a subset of the regional pool from persisting in some localities, resulting in more deterministic communities [65,88,99]. Further, spatial factors such as habitat isolation interact with these local processes; more isolated communities experience a greater degree of ecological drift, and thus higher β-diversity, than more connected communities [126,127]. However, it is worth noting that these studies and experiments are only performed in a limited part of the range of the component species. Conducting these sorts of experiments (or comparisons) at different spatial scales might lead to a more complete understanding of the processes leading to β-diversity across scales.

(b) *Disentangling the strength of deterministic, stochastic and spatial processes among biogeographic regions*

Among biogeographic regions that differ in the size of the regional species pool, a related, but distinct approach must be considered in order to disentangle the relative importance of deterministic and stochastic processes. For example, consider the fact that β-diversity tends to decrease with latitude [128–131]. One explanation for this pattern is that the processes involved in community assembly might also vary along latitudinal gradients (e.g. [132,133]). Indeed, many local processes have been suggested to maintain high β-diversity or species richness in the tropics, including stochastic assembly (e.g. ecological drift), pervasive recruitment limitation, environmental determinism and density dependence mediated by natural enemies (e.g. [73,89,134,135]). Before invoking possible differences in processes that influence β-diversity in temperate and tropical regions, however, it is necessary to recognize that turnover is a function of the size of the regional species pool ([101,102]; N. B. Kraft *et al.* 2011, unpublished data). While we make no attempt to explain the latitudinal gradient of species diversity, which is undoubtedly structured by evolutionary processes such as speciation (e.g. [136]), we can use the variation in the size of the regional pool
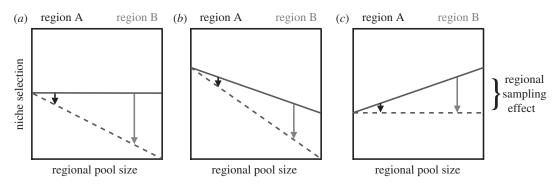
Figure 3. The influence of regional species pools on the signature of deterministic processes (niche selection) in different biogeographic regions. The figure shows three hypothetical examples in which regional sampling effects influence the relationship between niche selection and the size of the regional species pool. In (*a*), niche selection does not vary with increasing regional pool size in nature (solid line, actual), but stronger regional sampling effects in high-diversity regions (i.e. region B relative to region A) result in an observed pattern (dashed line, observed) where niche selection decreases with regional pool size. In (*b*), niche selection decreases with increasing regional pool size in nature (e.g. via stronger ecological drift in regions with more rare species), but stronger regional sampling effects in high-diversity regions result in an observed pattern where the negative correlation is steeper. By contrast, in (*c*), niche selection increases with increasing regional pool size (e.g. via more species sorting in high-diversity regions), but stronger sampling effects in high-diversity regions result in no observed correlation. In all cases, it is necessary to account for differences in the regional sampling effect (e.g. using a null-model approach) before comparing the relative importance of niche selection among biogeographic regions. For simplicity, we have only plotted linear relationships between niche selection and regional pool size, while recognizing that nonlinear relationships may exist in empirical datasets.

to help disentangle the relative importance of deterministic processes in generating patterns of β-diversity. To that end, as we discuss above, the same fundamental concept applies *within* regions. Just as it is necessary to control for variation in α-diversity before comparing the relative importance of processes *within* a given regional species pool [105], it is also necessary to control for differences in the size of the regional species pool (γ-diversity) before comparing processes influencing community assembly among biogeographic regions.

To begin to compare processes among biogeographic regions, it is necessary to account for the fact that the influence of stochastic processes should be higher in regions with larger species pools owing simply to regional sampling effects. Higher β-diversity is expected in regions with large species pools because a smaller fraction of the individuals and/or species in the species pool can potentially attain membership in any given local community [79]. Using simulations, for example, N. B. Kraft *et al.* (2011, unpublished data) showed that β-diversity will increase as γ-diversity increases simply owing to a regional sampling effect based on random sampling from the species pool [111], without the need to invoke differences in the strength of local ecological processes along latitudinal gradients.

Although regional sampling effects are generally expected to have a stronger influence on patterns of β-diversity in high-diversity relative to low-diversity regions, this does not necessarily imply that deterministic processes are weaker in high-diversity regions. In fact, deterministic processes may have similar or greater influences in high-diversity relative to low-diversity regions, but the signature of these processes on observed patterns of β-diversity could be 'masked,' to some degree, by regional sampling effects (figure 3). For example, consider a hypothetical case in which the relative importance of niche selection does not change along a biogeographic gradient spanning

small to large regional species pools (figure 3*a*, solid line). This pattern could emerge, for example, if density-dependent processes were a primary determinant of niche selection, and acted in a similar way, in both temperate and tropical regions (e.g. [137]). If β-diversity at the low (region A) and high (region B) ends of this gradient were measured, and observed β-diversity was found to be higher in region B relative to region A, it might suggest that the strength of niche selection decreases along this gradient (figure 3*a*, dashed line). However, because observed patterns of β-diversity will be more strongly influenced by regional sampling effects when the species pool is large (figure 3*a*, grey arrow), we would need to control for differences in the size of the regional pool before invoking differences in the strength of niche selection. By contrast, the strength of niche selection could decrease in more diverse regions (figure 3*b*) if recruitment limitation was more pervasive (e.g. [73,138]) or pairwise species interactions were more diffuse (e.g. [139,140]). Finally, the strength of niche selection could increase in more diverse regions (figure 3*c*) if strong environmental gradients (e.g. [89]) contribute to species sorting. In each case, however, it would be necessary to first account for differences in the size of the regional species pool before comparing the relative importance of deterministic or spatial processes between biogeographic regions.

Null-model approaches can be used to explicitly compare the importance of deterministic, stochastic and spatial processes among biogeographic regions that differ in regional diversity. If deviations from null expectations are similar among regions, this could indicate that similar processes have similar effects on community structure across regions, or alternatively, that different processes have similar effects across regions. By contrast if deviations from the null expectation differ, this would imply different processes occur along the regional pool gradient. One approach to disentangling these

alternative hypotheses is to compare the extent to which spatial and environmental processes (i.e. dispersal and selection; [66]) explain deviations from null-model expectations between high-diversity (e.g. tropical) and low-diversity (e.g. temperate) regions. Finally, as a complement to observational studies and null-model analyses, mechanistic experiments can be replicated across gradients (e.g. [141]) to further uncover the identity and importance of local processes in community assembly.

3. CONCLUSIONS

The goal of our paper has been to highlight how and when niches should be important in generating patterns of biodiversity. Although deterministic processes associated with species niches and their responses to environmental conditions can be critical in community assembly, especially under conditions imposed by strong abiotic and biotic filters, we recognize that stochastic processes such as colonization and extinction dynamics can be just as important, if not more important in some cases, in structuring natural communities. Just as it is difficult to hear a specific sound when there is a lot of white noise in the environment, it is sometimes difficult to detect the signal of niches when there are a lot of stochastic processes that emerge from local and biogeographic factors. Specifically, when the regional species pool is large relative to the number of species that can co-occur locally, stochasticity has a greater propensity to manifest, so long as the environmental heterogeneity among localities remains similar. It is therefore important to recognize that both deterministic and stochastic processes, which occupy the two extreme ends of a continuum [15,63], are occurring simultaneously. We extend this conceptual framework by showing how an increase in the relative importance of stochasticity observed either locally (among local communities that differ in the size) or regionally (among local communities with different biogeographic species pools) does not necessarily imply a concomitant decrease in the relative importance of deterministic processes. Moreover, we illustrate how null-model approaches can be used to disentangle the importance of deterministic processes after controlling for local and regional factors that increase stochasticity in the absence of any potential change in the relative importance of niche selection.

Wiens' [14] companion paper complements and extends our framework by exploring how abiotic and biotic components of species' niches influence large-scale biogeographic patterns. His focus on the niche concept from a broader, biogeographic perspective, illustrates how many of the processes studied by ecologists occur at spatio-temporal scales that are much smaller than those typically of interest for understanding large-scale, biogeographic patterns. As Wiens points out, however, progress will be made by integrating ecological and biogeographic perspectives using a variety of approaches, such as the use of local interspecific interactions to help understand species range limits. At the same time, progress is being made towards examining local ecological processes at broader scales. Historically, ecology has been a study of place, in which researchers study species interactions and co-occurrence at single (or a few) locations. Over time, the scope of studies has expanded to include comparisons of ecological process and pattern at global scales. These include observational (e.g. coral reefs [101,102] and tropical forests [142]) and experimental (e.g. invertebrate [141] and herbaceous plant [143] communities) studies replicated across biogeographic regions, as well as meta-analyses examining how regional processes influence and interact with local processes to structure patterns of diversity (e.g. [82,83,92]).

Observational and experimental studies, when combined with null-model approaches, will help us to discern how the importance of niche-based processes varies among biogeographic regions. Hutchinson [144] famously discussed the 'ecological theater and the evolutionary play' to depict how microevolutionary processes (e.g. selection, drift and migration) occur within the context of ecological constraints (e.g. energy, isolation and interspecific interactions). While useful, it is clear that this analogy is not comprehensive enough to fully capture the interplay between local niche-based and broader biogeographic and macroevolutionary processes. Larger-scale processes strongly influence the types, numbers, phylogenetic diversity and functional diversity of species that can co-occur in a given area, and thus the way that niches influence species distributions, composition and co-occurrence (e.g. [12,26,28,71]). Our challenge, then, is to develop a more general theory that has ecological niches at its core, but also considers the litany of countervailing processes that can emerge both regionally and globally.

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