Review

Advances, challenges and a developing synthesis of ecological community assembly theory

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Ecological approaches to community assembly have emphasized the interplay between neutral processes, niche-based environmental filtering and niche-based species sorting in an interactive milieu. Recently, progress has been made in terms of aligning our vocabulary with conceptual advances, assessing how trait-based community functional parameters differ from neutral expectation and assessing how traits vary along environmental gradients. Experiments have confirmed the influence of these processes on assembly and have addressed the role of dispersal in shaping local assemblages. Community phylogenetics has forged common ground between ecologists and biogeographers, but it is not a proxy for trait-based approaches. Community assembly theory is in need of a comparative synthesis that addresses how the relative importance of niche and neutral processes varies among taxa, along environmental gradients, and across scales. Towards that goal, we suggest a set of traits that probably confer increasing community neutrality and regionality and review the influences of stress, disturbance and scale on the importance of niche assembly. We advocate increasing the complexity of experiments in order to assess the relative importance of multiple processes. As an example, we provide evidence that dispersal, niche processes and trait interdependencies have about equal influence on trait-based assembly in an experimental grassland.

Keywords: community assembly; niche; neutral; dispersal; trait

1. INTRODUCTION

Recently, our understanding of the development and maintenance of ecological communities has been enhanced by integrating approaches from evolution [1–4], genetics ('community genetics') [5,6] and ecosystem ecology [7–9].

This paper is part of a collection that is intended to build a bridge and synthesis between ecology and biogeography [10,11], and here we address the issue of community assembly from the perspective of community ecology. A biogeographical approach to community assembly is addressed by Emerson *et al.* [12] in which they contrast phylogeography and community assembly and provide useful guidance on the study of difficult taxa, including cryptozoans such as Collembola. The concept of niche is addressed by Chase & Myers [13] and Wiens [14] who also address key questions in community assembly. Chase & Myers [13] outline some useful ways in which beta diversity can be used to assess the degree to which communities deviate from neutral assembly. Wiens [14] reviews

phylogeography and niche concepts and presents evidence supporting Ricklefs' [15] model of regional community assembly in which niche-based processes play a complementary role to evolutionary history, habitat choice and diversification of largely equivalent species with neutral assembly.

A synthesis can start with some simple observations. Biogeographers are focused on phylogeny, geographical range, climatic limits to range, history, dispersal and individual clades. Community ecologists are focused on species functional traits (i.e. traits that are associated with species ability to gain resources, disperse, reproduce, respond to loss and generally persist), gradients of stress and disturbance, interspecific interactions and local assemblages. The vocabulary might be common [10], but the differences in spatial, temporal and phylogenetic scale have kept the two fields largely isolated.

Community ecologists often invoke a niche-based, pool–filter–subset concept of community assembly, in which local assemblages are viewed as subsets of a regional species pool delimited by a set of filters [16–19]. The filters are characterized as abiotic/fundamental niche filters that determine whether a species has the requisite traits to colonize, establish and persist in a given habitat, and a set of biotic/realized niche filters that are imposed by the interactive

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milieu of competitors, mutualists and consumers. The first set of filters tends to cause overall similarity in the trait values of coexisting species because of common, requisite adaptations to physical conditions, while the second tends to cause trait overdispersion associated with limits to similarity and resource partitioning. Communities can be simultaneously constrained by both types of filters, so that traits associated with environmental filtering may be clustered, while traits associated with interactions may be overdispersed [20,21]. In addition, individual traits within assemblages can be constrained in their range and overdispersed within that range [22,23]. A neoclassic model of niche assembly argues that both abiotic-environmental and biotic-interaction filters should cause convergence in traits, but traits associated with regeneration and establishment should be overdispersed [24].

A general model of how community assembly might vary with scale and along gradients made the following predictions [25]: (i) community assembly should be neutral where both competitive adversity and environmental adversity are weak, (ii) trait overdispersion should be limited to small spatial scales over which species actually interact, and (iii) as scale increases, patterns of trait overdispersion should first become increasingly neutral and then should shift to trait underdispersion/convergence. This can be thought of as a pattern of trait overdispersion within a certain community type (e.g. vertical stratification in forests) giving way to trait convergence when comparing among community types (such as among biomes). The model has received some clear, although limited, support [26–30]. As originally stated, scale was left undifferentiated between grain size (the size of the sample unit) and extent (the total area of the study), but it seems clear that spatial grain size is critical for ascertaining and understanding patterns of species co-occurrence [31]. The effects of scale are critically important, because our ability to understand local versus regional effects on community composition depends on both the spatial scale at which we define local and regional communities and the scale at which actual processes operate.

These views of niche-based community assembly make several simplifying assumptions. (i) Functional traits are the currency of assembly, just as phenotype is the currency of selection [18,32,33]. (ii) Species traits are essentially fixed because trait evolution proceeds more slowly than community assembly [34,35] and speciation usually takes several orders of magnitude longer than competitive exclusion [36]. (iii) There is greater trait variation among species than within species, while also recognizing that many species have similar traits. This is largely a simplification for numerical analysis, in that the mean trait values of each species are often used, but trait values can also be measured as they are expressed in each assemblage [23]. (iv) Dispersal limits are small relative to the effects of the abiotic and biotic filters in determining functional community composition. That is, species composition may be largely dispersal limited [37,38], but functional composition is much less so [39]. In addition, traits associated with dispersal ability can be incorporated to assess the degree of dispersal limitation [37,40].

Degree of determinism, equilibrium and absence of neutral processes are not highly specified by niche-based models of assembly. Niche-assembly does not require that species composition is highly predictable or deterministic, especially in terms of species composition. For example, communities can converge in terms of their functional parameters while failing to do so in terms of their species composition [39]. This is because different subsets of the regional pool can be selected by their traits while historical dispersal and drift determine the actual species composition. This is one reason why it is not surprising that species composition is usually not particularly predictable [37], and why ecologists are sceptical when it is predictable [41–43]. There is no real assumption of equilibrium, but rather on-going, iterative filtering and sorting processes constrain community assembly and make some assemblages less likely to persist than others [44–46]. Similarly, neutral processes occur alongside niche processes, and therefore it is more insightful to investigate the degree to which niche processes and neutral processes are occurring [47–50]. It is probably more appropriate to think of niche-based processes as affecting the likelihood of particular mixtures as opposed to determining them.

2. RECENT ADVANCES
(a) *Changes in vocabulary*
Recent conceptual advances and refinements have led to some conspicuous changes in vocabulary. In the past, ecologists were interested in community assembly rules, and some were narrowly focused on patterns caused by competition because that was Jared Diamond's intent when he first sought assembly rules [51]. Some ecologists took a broader view that community assembly is a more general phenomenon [17,25,52,53], and today this broader concept of community assembly appears to be well accepted. We note a change in vocabulary in which assembly 'rules' are now rarely mentioned.

The formal development of neutral theory [54] means that we no longer look at communities as 'random assemblages', but rather we say that they are neutrally or stochastically assembled by dispersal, ecological drift and historical inertia. Neutral theory not only provides a clear alternative to the niche-based approach outlined above but it has also broadened the field to make it more inclusive of other processes [55]. Neutral theory counters the idea that coexistence is primarily the result of stabilizing mechanisms, such as resource partitioning, and privileges equalizing mechanisms which reduce overall fitness differences to allow coexistence over ecological time-scales [56]. However, neutral theory requires that we distinguish stochastic assembly that may be deterministic and niche-based from actual neutral assembly. The former relates to cases where stochastic events such as climate variability strongly affect community assembly due to deterministic, niche-based processes that may be unpredictable and thus assembly may appear to be random [57]. Neutral assembly is also stochastic, but it is generally restricted to cases where species equivalence makes the importance of stochastic processes

paramount. Under niche assembly, the same stochastic processes occur, but are considered to be of considerably less importance because species are not equivalent.

In addition, we now refer to collections of communities as metacommunities. Metacommunity theory explicitly includes dispersal among communities, thereby forming a theoretical framework that is both ecological and biogeographic [58–60].

(b) *Niche-based constraints on trait dispersion*
Evidence continues to grow that supports niche-based community assembly because of non-random trait dispersion [3,25,53,61]. In addition, community phylogenetics has added an important tool for assessing niche-based community assembly in a way that precludes a strict reliance on traits. Community phylogenetics provides for greater understanding of how trait evolution affects community assembly, especially in cases where traits are obscure and identification challenging [1,3,62–64]. Even so, phylogenetic community analysis supplies only a partial view of community assembly, because phylogenetically overdispersed communities can have either overdispersed traits that are conserved within lineages or clustered traits that converged across lineages. A similar line of reasoning can be made for phylogenetically clustered communities. Therefore, phylogenetic community analysis in the absence of trait data provides limited insights [65]. While there are certainly good reasons to substitute phylogenetic relatedness for trait similarity [12,64], more often than not, some functional traits can almost certainly be measured (e.g. body size). Phylogenetic assembly is not a proxy for traits, but rather it is a complementary approach that provides insight on evolution and biogeography [66,67].

Examples supporting a significant role for niche-based community assembly continue to increase in number [25]. New World and Malaysian bat assemblages are overdispersed in body size and other ecomorphological traits [68,69]. Oaks in Florida tend to be phenotypically clustered and phylogenetically overdispersed [21]. Hawaiian spider assemblages are phenotypically overdispersed [70]. Niche-based processes are highly important in the assembly of mutualistic butterfly assemblages [71]. North American warblers that are closely related tend not to co-occur [72]. Plethodon salamander assemblages show size overdispersion in the eastern USA [73]. Range overlap in North American mammals is positively related to the degree of difference in dentition [74]. Wood density tends to be convergent across broad gradients in the Americas [27]. South American tropical forest trees show functional trait convergence across a moisture gradient and some traits simultaneously show even spacing among co-occurring species [22]. Similar patterns of assembly were observed in shrublands in California [23]. New World monkey assemblages and North American ground squirrel assemblages are phylogenetically overdispersed, but Australasian possums are not [75]. Ungulate, primate and fruit bat (megachiropteran) assemblages on islands tend to be phylogenetically overdispersed although patterns

were influenced by the island type (land bridge versus oceanic), richness, maximum elevation and habitat diversity [76]. Dutch plant communities show trait convergence for persistence-related traits and a mixture of trait convergence and overdispersion for dispersal traits [40]. Larval mosquito assemblages in bromeliads partition space and habitat size [77]. Pacific rockfish assemblages are simultaneously overdispersed in traits associated with resource acquisition and convergent in a trait associated with habitat tolerance [78]. This progress is largely due to the ability to use phylogeny as a substitute for traits (given the assumption of widespread trait conservatism), better statistical control for indentifying significant structure and an increasing interest in measuring functional traits.

(c) *Trait–environment relationships*
There has also been growth in assessing how both the mean and variance of traits in a community change along environmental gradients. For example, fish assemblages in Europe and North America have consistent trait-based responses to hydrologic variability, supporting a significant degree of convergent evolution of the species pools and consistent niche assembly [79]. Trait diversity in bat assemblages decreases with latitude and is highly dependent on regional diversity [80]. In Mediterranean shrublands, mean plant traits change with successional age [41]. Among-species variation in wood density decreases with latitude and elevation, and increases with annual precipitation and temperature [27]. The cessation of human land-use across Europe has consistent effects on the functional traits of the vegetation, even though floristic composition is highly variable [81]. Plant trait variation (diversity) decreases with fire history and drought [29]. In Californian shublands, the richness of plant species was independent of soil water availability, but there were significant shifts in the mean and variance of specific traits suggesting strong niche-based constraints [23]. These examples represent a growing appreciation of the connections between niche assembly, in terms of trait dispersion, and gradient analysis, which focuses on diversity (including functional diversity, i.e. trait dispersion [67,82]) and trait-based community functional parameters [81,83], which vary along stress, disturbance and temporal gradients. Indeed, examples of consistent trait-based responses [79,81] suggest that there may indeed be some general niche-based assembly rules, and these rules exist at the level of functional traits.

There have also been significant conceptual and methodological advances. For example, Garnier *et al.* [81] suggested standard protocols for assessing the functional responses of communities to change. Pavoine & Bonsall [67] reviewed trait and phylogenetic diversity metrics and suggested ways they can be used to explore community assembly. Webb *et al.* [19] described a framework for incorporating functional traits into Bayesian and dynamical models of community assembly.

The formal description and quantification of trait–environment relationships remains surprisingly rare. Perhaps, the lack of progress in this area has arisen

from (i) the broadest patterns (e.g. Bergmann's rule and other ecogeographic rules) are old and well known [84], (ii) gaps among ecophysiologists, community ecologists and biogeographers, and (iii) a perception that quantification of such patterns is perceived as a technical description that does not lead to theoretical advances.

(d) *Experimental assembly*

Recent experiments have increased our understanding of the factors that influence the degree of niche assembly. In a series of experiments and complementary field studies, pond communities show increasing constraints on species composition with increased disturbance [85], predation [50] and resource stress [86]. The reduction in niche dimensionality leads to reduced coexistence in grasslands [87,88], again supporting an increased role of niche filtering under resource stress or eutrophication. In oligotrophic pine savannas, the removal of dominant bunchgrass caused no response in species composition [89,90], but the removal of dominant shrubs did alter composition as did enhanced dispersal via seed addition [90]. Therefore, the importance of biotic interactions and niche assembly may not only be reduced in oligotrophic systems, but also dependent on the presence of competitor species with sufficient size differences to overcome species equivalence [90]. In model microbial systems, disturbance can act as a filter and increase the constraints on assembly [91] and the role of historical assembly is reduced with increasing productivity [92]. Greater connectivity can lead to increased coexistence [93], which lends support to the idea that increased connectivity and dispersal suppress niche processes.

Experimental manipulation of dispersal suggests that priority effects may be common and can have considerable effects on community composition and diversity. Experiments that manipulated the order of species arrival (i.e. dispersal history) have repeatedly shown effects on subsequent colonization [91,94,95] and support earlier work on priority effects [96–98]. The history of assembly can also lead to alternative dynamical states in which predators and prey can either cycle or not cycle [92]. A history of closed assembly in which a simple community is allowed to mature in the absence of colonization can reduce subsequent colonization when barriers to colonization are removed [99]. This suggests the possibility of historical inertia in the degree of community openness to colonization. These examples suggest that historical priority effects can lead to differential community composition that is largely stochastic (but note that it could also be partly deterministic owing to species differential dispersal abilities). Such historically assembled communities may appear to be unstructured by niche-based assembly processes, but they are probably far from neutral.

3. WAYS FORWARD: TOWARDS CONCEPTUAL SYNTHESIS

The neutral versus niche debate is unproductive, and a synthesis of the two views is more helpful [46–49, 100,101]. Vellend [4] provided a conceptual synthesis of community ecology in which he aligned community theory with population genetics and evolution to cogently argue that diversity (the outcome of assembly) is affected by four classes of processes: drift (neutral and stochastic processes), selection (niche processes), dispersal (a combination of stochastic and trait-dependent processes) and speciation (which shapes the species pool and could be expanded to include the functional evolution of the species pool). Indeed, there is a growing interest in determining how these processes combine to affect community assembly [90,102]. Even though drift and dispersal were originally both central to neutral theory (indeed, 'dispersal assembly' was the alternative to 'niche assembly' [54]), Vellend's synthesis distinguishes them in order to more clearly define them as distinct processes. Vellend also puts equal emphasis on speciation in the species pool itself, because local assemblages are influenced by the regional processes that have shaped the regional species pool [15,103].

(a) *Trait evolution and assembly*

Trait evolution and the degree of niche conservatism [62,104–106] may make community assembly of some taxa inherently more or less neutral. Some mechanisms of evolution may be more likely to produce ecologically equivalent taxa. Examples might include drift in barriers to reproduction, sexual selection for traits unrelated to resource acquisition or defence, polyploidy and perhaps hybridization. Trait convergence across lineages should not lead to overall ecological equivalence because of other traits which are likely to be conserved [21]. Ackerly [62] suggested three broad cases in which one might expect reduced trait conservatism: (i) evolution on insular habitats, including true islands (which may promote divergence) [70,107] or ecological islands with distinctive stresses (which may promote convergence in terms of habitat-related traits but with a legacy of otherwise conserved traits [21]), (ii) evolution at the 'trailing edge' of a shifting biota (e.g. due to climate change) where there are few species that are preadapted to the new conditions, and (iii) evolution in species with broad niche breadths along only some niche dimensions in a changing climate. The three cases also require a lack of dispersal, because of either barriers or abilities. Even under selection, clusters of similar species may co-evolve, because species may coexist through either equalizing or stabilizing processes [108].

There may also be a small set of functional traits and life history attributes that confer increased neutrality and regionality (table 1). Ricklefs [15] suggested that communities should be thought of as regional entities that are largely open, and patterns among small-scale local assemblages cannot be used to scale up to understand the more important regional processes. Local assemblages may therefore exist at a scale that is largely trivial because the collections of individuals that make up a local assemblage are each members of a regional metapopulation and metapopulations are regional entities. Indeed, when scale is sufficiently reduced, assembly is more neutral [109]. Although a regional model is compelling for birds and other animals that have a high degree of habitat choice, it is not as

Table 1. Species traits and attributes that may contribute to increasing appearance of neutrality of community assembly and regionality, in terms of dependence on regional processes and conceptualization of the community as a regional construct.

trait/attribute	neutrality	regionality
motility, vagility	+	+
low density	+	+
large body size	+	+
large foraging area	+	+
long lifespan	+	+
wide or absent regeneration niche	+	
omnivory/intraguild predation	+	
ontogenic niche shift	+	
insensitivity to predators	+	

compelling for sessile organisms, such as plants, because sessile organisms are forced to interact intimately with their neighbours. The question here is whether we think of communities as points in space where populations of multiple species happen to overlap [15], or if communities are collections of individuals of different species in a particular place that potentially interact and give rise to ecosystem processes [32]. Both views have merit and utility, and it is unlikely that community assembly can fully be understood without incorporating both. We suggest that just as the niche versus neutral debate is distracting and unproductive, so would privileging regional processes over local processes (or vice versa) hinder progress towards understanding community assembly. Instead, it may be useful to consider how the importance of regional and local processes may differ among organisms. Allen [110] suggested that plant and animal assemblages are in many ways fundamentally different because of the lack of mobility and high density of plants (consider the density of plants versus birds). These traits mean competitive and other interactions tend to be tied to a specific location and the interactions are often persistent over time as a result of the lack of mobility. This also makes the concept of 'local' inherently less important for motile organisms with high vagility and those that maintain comparatively low density. In addition, the scale at which an organism forages for resources is dependent on body size and traits associated with motility and vagility. Therefore, the relative importance of regional versus local processes may differ among taxa in a somewhat predictable way [111].

The same set of traits that reduce the importance of 'local' should also reduce the importance of niche processes in community assembly. This is partially because high rates of dispersal can theoretically suppress niche-based assembly [47], there may simply be no 'local assemblage' for some kinds of organisms [15], and because niche processes, especially involving interactions, occur at the local scale. Indeed, in stream invertebrates, the degree of neutral assembly was found to be more important among taxa with high dispersal ability [102]. In addition, traits associated with vagility should increase the role of neutral processes, because they increase the degree to which species integrate or average heterogeneity across the landscape. When heterogeneity is integrated, home ranges and

foraging areas become less distinctive, thus acting as an equalizing process for landscape patches. Lifespan should accomplish the same integration, but in time.

Some organisms have a distinct regeneration niche [112] that differs from adult requirements (e.g. light and temperature requirements for germinating and establishing plants, nest sites for fish, *Asclepias* plants for monarch caterpillars, parasites with alternating hosts). The relative importance and degree of specificity of the regeneration niche should increase the role of niche assembly. Indeed, groups of species with a wide niche breadth (generalists) should have more neutral assembly.

Guild or trophic fidelity and completeness may also influence our perception of niche and neutral processes. This is closely related to the issue of phylogenetic scale. Some groups of organisms clearly form a single guild or trophic level (e.g. nearly all plants share the same set of required resources). However, some animals exhibit ontogenic niche shifts (e.g. fish change their diet as they mature) or intraguild predation. Species that are sensitive to predators, either behaviourally or because of a lack of strong defences may exhibit greater niche assembly, because increased predation leads to increased constraints on assembly [50]. Trophic guilds other than primary producers are rarely, if ever, monophyletic (e.g. fish and invertebrate predators share prey, granivorous birds, mammals and insects share diet, and insectivorous crepuscular birds and bats also share diet). Competition between unrelated species is well documented (e.g. ants and rodents [113], birds and bats [114], fish and urchins [115], invertebrates and tadpoles [116]). Therefore, many studies are trophically incomplete, in that potential competitors are not considered. Whether or not this is an important issue rests on the assumption that closely related species are the most important competitors affecting community assembly. While niche conservatism is common and closely related species may often compete intensely, more distantly related species often compete more asymmetrically [117,118] producing more clear winners and losers. Therefore, we need to investigate how our perception of community assembly is affected by phylogenetic scale [119] and the degree of trophic completeness.

(b) Environmental gradients and assembly

There are two somewhat conflicting ways of viewing assembly in terms of environmental gradients. One approach focuses on mechanisms promoting coexistence and considers community openness to invasion as a proxy for neutrality, based on the logic that if species are easily added to communities then composition is dependent on dispersal history [90]. Communities with low alpha diversity are seen as relatively closed because of niche-based filtering (e.g. severe resource stress, eutrophication or severe dominance). This means that communities with high alpha diversity became diverse because they had a history of relative openness and constraints on assembly were weak [44]. Moreover, most species are rare in diverse communities, and this increases the importance of demographic stochasticity over niche processes [120]. Therefore, we might expect neutral assembly where alpha diversity is high. A second approach focuses on mechanisms

promoting alternative community states and considers an increasing dissimilarity among communities as a proxy for neutrality based on the logic that different communities assembled under similar conditions reflect different dispersal histories [13,97,98,100]. This means that metacommunities with high beta diversity became diverse because niche-based constraints on assembly are relatively weak. Therefore, we might expect neutral assembly where beta diversity is high [50,85,86]. High beta diversity could also be due to strong priority effects leading to stochastic, but not necessarily neutral assembly. There is no fundamental relationship between alpha and beta diversity (the relationship is a matter of scale [121]), but even so, we expect that environmental gradients may have different effects on the two. For example, connectance and dispersal between patches should increase alpha diversity and decrease beta diversity [100]. Productivity and disturbance should produce unimodal effects on alpha diversity, but have monotonic effects on beta diversity (either increasing or decreasing, respectively [100]). Regional pool size should increase both [100].

We suggest that part of the problem may be a reliance on diversity indices and species composition as a way of understanding community assembly. If a trait-based approach were applied, we may find different patterns [39]. While alpha diversity is usually strongly related to trait diversity, we know very little about trait-based beta diversity [82]. It is possible that alternative species states are nonetheless congruent trait states [44] and we can have deterministic niche assembly by traits, but historical assembly by species.

(c) *Scale and assembly*

Scale, in terms of grain size, spatial extent and phylogeny, can have strong effects on our perceptions of niche assembly. Biogeographers and community ecologists tend to focus on different scales for all three terms and this has limited synthesis. Swenson *et al.* [122] suggested that scale dependency is actually an opportunity to develop scaling concepts that help merge community ecology and biogeography.

Some generalities are emerging. When grain size is reduced, patterns of phylogenetic and trait dispersion can be enhanced [28]. This is because interactions occur over small grain sizes and because larger grain sizes integrate heterogeneity. Methods for estimating an ideal grain size have been suggested [123], but have not been sufficiently tested. When spatial extent is reduced as much as possible, communities may appear increasingly neutral [124], because of a combination of low heterogeneity [109], low species pool size [121] and possibly an increased ubiquity of some taxa. Narrowing the phylogenetic scale of a study can often lead to clearer evidence of niche processes and can provide insights regarding which taxa are strongly influenced by niche processes [118,125]. The scaling of assembly is clearly an area that deserves increased attention.

4. WAYS FORWARD: THEORY, MECHANISM AND PREDICTION

We need to support and encourage the development of mechanistic theory, theoretical explorations and predictive modelling to support or challenge conceptual theory. For example, stochastic niche assembly suggests that plant species density is limited by the degree of size difference between seeds and adults and that communities are open, but the rate of successful invasion slows logarithmically, making them effectively closed over ecological temporal scales [46]. Other theoretical models suggest that increasing immigration overwhelms niche processes [47], and ecological drift is greater in small local communities [126]. Scale transition theory has been applied to metacommunities in order to begin to understand how local scale processes translate to larger scales [127]. Community ecologists and biogeographers need to test such ideas on real landscapes [128].

Predictive modelling remains an important goal. Recent advances include an approximation procedure that reduces the number of parameters in individual-based models, thereby making them more useful [129]. Statistical mechanics have been used to predict the relative abundance of species from trait–environment relationships [41,130]. Mechanistic models are ideally the most powerful way forward, for example, global patterns of tree form can be predicted and explained by hydraulics and thermodynamics [131], forest stand structure and dynamics can be predicted with metabolic scaling theory [132], and resource competition theory explains the (ecologically) long-term dynamics of experimental grass mixtures [133]. However, mechanistic models do not yet predict community composition in terms of species or traits. Webb *et al.* [19] describe a promising framework for trait-based modelling in which they compare modelling approaches.

5. WAYS FORWARD: MULTIVARIATE COMPARATIVE EXPERIMENTS

Experiments in community assembly have largely focused on altering environmental factors and/or altering dispersal history and assessing their influence on components of diversity or their role in assembly. Here, we present another approach to experimental assembly in which our goal was to assess the relative influence of niche-based processes, dispersal history/regional species pool, and the influence of trait interdependencies on functional community assembly. In other words, we were mimicking assembly at the regional scale in which habitat patches vary in quality and have different dispersal histories. This is essentially a systems approach that integrates the relative influence of processes across a long gradient of environmental variation. This approach is presented as a way to move beyond demonstrating that ecological processes occur and to develop a multivariate comparative mode focused on assessing relative influences.

Dispersal history was altered by planting 45 unique mixtures (six or seven graminoids, zero, eight or 16 forbs, and zero, four or eight legumes from a pool of 41 species) in 0.1 ha plots. Because the plots are large relative to the size of the plants and the size of the sample quadrats (1 m^2), the altered dispersal history may also be thought of as different regional species pools. Resource availability was altered by applying fungicide (to suppress mycorrhizal fungi) and nitrogen
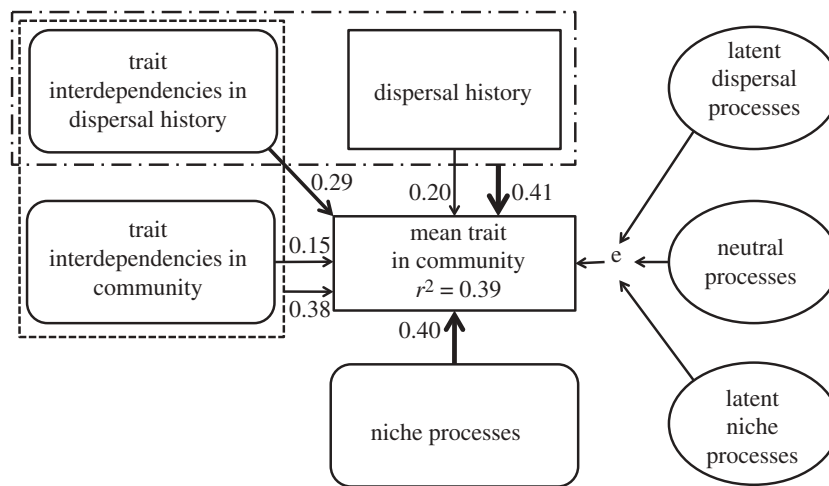
Figure 1. Summary diagram of a structural equation model describing the relative influence of dispersal history, trait interdependencies and niche processes on community mean values of four functional traits in an experimental grassland. The average standardized path coefficients are shown. The total effect of dispersal history when combined into a conceptual construct is shown with a dot-dashed line, while the total effect of trait interdependencies is shown with a dashed line. Measured variables are in rectangles, composite variables are in rounded boxes and latent variables are in ellipses.

in a random factorial combination. Prior to planting, herbicide was applied three times over two years. The plots were not weeded; core volunteer species were present in all plots, but satellite (low frequency and abundance) volunteer species were stochastically distributed. Data are reported as the average of three 1 m^2 quadrat samples from each plot ($n = 540/3 = 180$) from year 4. Functional trait data were collected on well-grown individuals in control plots ($n > 10$ for nearly all species; for species that were not present in any plot, plants from nearby sites were used, and one planted species was not located because of rarity and was excluded). The treatments produced a significant variation across the experiment. Biomass ranged from 240 to 1130 g m^{-2} (a 4.7-fold range) and species density ranged from 2 to 15 species m^{-1} (a 7.5-fold range). Based on these ranges, we suggest that the experiment captured much of the regional range of grassland production and diversity [134].

We used structural equation modelling to assess the relative influence of history, environmental filtering and trait interdependencies on community mean functional traits. Four mean trait values of the planting mixtures were used as manifest variables of historical processes (specific leaf area, leaf dry matter content, height and seed mass). Three manifest environmental variables (fungicide treatment, nitrogen treatment and plot slope) were grouped as a composite variable [135,136] to estimate the overall effect of niche processes. Because traits are not independent in terms of both their evolution and their influence on species performance [137], we included the composite effects of trait interdependencies in the species pool (e.g. the effect of leaf and seed traits in the pool on height in the assemblages) and the composite effects of traits in the extant assemblages where necessary (e.g. the effect of leaf traits in the assemblage on height in the assemblage). We modelled these effects as causal, but we recognize that, for some relationships, causation is ambiguous or not well understood. We simplified and generalized the resultant model by averaging the standardized path coefficients across the four

functional traits. Overall, model fit was very good, with $\chi^2 = 7.53$, df = 18, $p = 0.985$ (i.e. there is little evidence to suggest that the covariance structure of the data significantly differs from the model), goodness-of-fit index = 0.992 (values above 0.95 indicate good model fit), root mean square error of approximation (RMSEA) < 0.001, $p = 0.999$ (values below 0.05 indicate the good model fit).

Our model suggests that niche processes had the overall largest single effect on functional composition (figure 1). However, when dispersal history and trait interdependencies in the dispersal history are combined into a single composite variable, the effect was about the same as niche processes. Similarly, if trait interdependencies are combined into a single composite that includes both historical and extant community, then it also had an effect equivalent to niche processes. Therefore, we suggest that dispersal, niche and trait interdependence had relatively equal effects on functional assembly. The model explained an average of 40 per cent of the variation in mean traits, but we cannot conclude that the assembly was 60 per cent neutral. In all likelihood, there were also latent (unmeasured) niche and dispersal processes at work, as well as true error, and therefore we can say that between 0 and 60 per cent of variation was because of neutral processes. We suggest that this type of multivariate experiment and analysis may be an important way to build comparative understanding of community assembly.

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