

Drought mediates the importance of stochastic community assembly

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Historically, the biodiversity and composition of species in a locality was thought to be influenced primarily by deterministic factors. In such cases, species' niches create differential responses to environmental conditions and interspecific interactions, which combine to determine that locality's biodiversity and species composition. More recently, proponents of the neutral theory have placed a premium on how stochastic factors, such as birth, death, colonization, and extinction (termed "ecological drift") influence diversity and species composition in a locality independent of their niches. Here, I develop the hypothesis that the relative importance of stochastic ecological drift and/or priority effects depend on the harshness of the ecological filter in those habitats. I established long-term experimental ponds to explore the relative importance of community assembly history and drought on patterns of community compositional similarity among ponds that were otherwise similar in their environmental conditions. I show considerable site-to-site variation in pond community composition in the absence of drought that likely resulted from a combination of stochastic ecological drift and priority effects. However, in ponds that experienced drought, I found much higher similarity among communities that likely resulted from niche-selection filtering out species from the regional pool that could not tolerate such environmental harshness. These results implicate the critical role for understanding the processes of community assembly when examining patterns of biodiversity at different spatial scales.

disturbance | ecological drift | niche | similarity | species composition

As the human footprint continues to grow, understanding the factors that influence patterns of biodiversity across the earth is essential to understand and remedy these effects (1). However, many of the critical factors that create variation in species diversity and composition among localities remain unresolved (2). Historically, community ecologists focused on deterministic factors, including how species' niches interact with environmental conditions and interspecific interactions (e.g., competition, predation) to determine how species diversity and composition vary along environmental and/or spatiotemporal gradients (3). More recently, Hubbell's (4) "neutral" theory has challenged this view by suggesting that many natural patterns can be recreated only by considering stochastic processes of birth, death, colonization, and extinction (and speciation) (see also refs. 5 and 6). Although the biodiversity and composition of an ecological community is most likely governed by a balance between stochastic (including neutral) and deterministic (niche-related) processes (7, 8), progress will require an expanded framework that explicitly includes both processes and explores the factors that will influence the relative importance of each.

At the core of the neutral theory is the concept of "ecological drift" (analogous to genetic drift) leading to dispersal-assembled communities (4–6). The structure of such communities results from stochastic colonization and extinction processes and is not influenced by species traits. Dispersal-assembled communities are expected to have considerable site-to-site variation (unpredictability) in their community composition among otherwise similar environments (9, 10). This unpredictability can be intensified if early colonizing species are able to disproportionately

stave off invasion by subsequent colonizing species through priority effects leading to multiple stable states (11). In contrast, "niche-selection" (3) predominates if species' abilities to establish in a locality are more strongly determined by their traits, regardless of stochastic colonization and extinction dynamics. Such niche-assembled communities are expected to have more predictable community composition among sites that are similar in environmental conditions (12, 13).

Ecologists have treated niche versus dispersal assembly as a dichotomous debate (e.g., refs. 5, 6, 9, and 12–21). Here, I propose reconciliation to this debate by identifying critical features of habitats that create conditions that favor or disfavor the relative importance of these processes. In population genetics, the relative importance of genetic drift in shaping patterns of gene frequencies is determined by the balance between the strength of regional processes (dispersal), by population size, and by the strength and nature of local natural selection (22). By analogy, the relative importance of ecological drift, leading to dispersal-assembled communities, should be greater when dispersal is low, when niche-selection is weak, and/or when priority effects are strong.

One simple way to predict the relative importance of ecological drift is based on the effect of the environmental filter on the number of species that can potentially exist in a given locality combined with stochastic colonization and extinction processes. For example, in relatively benign environments, a majority of the species in the regional species pool can tolerate the physical conditions of the environment. So long as local richness is considerably less than the size of the regional pool and ecological drift is important, then the null expectation is that community composition will be quite different among localities and that communities will be highly dispersal-assembled. Alternatively, in communities with harsher environmental conditions, a large proportion of the regional species pool can be eliminated (filtered) from the "realized" pool of species. In this case, even if the process of assembly from the realized pool of species is completely random, the smaller available pool of species that can persist in the harsher conditions (due to niche-selection) leads to higher site-to-site similarity among communities, making their structure more niche-assembled.

Stochasticity in community assembly can also give rise to multiple stable states (11). Multiple stable states are not mutually exclusive from the concept of ecological drift, because variation in colonization processes leads to priority effects that are a primary mechanism creating variation in community structure. However, the multiple stable-states paradigm does not consider variation in communities through time, whereas the

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Because community similarity estimated from species' incidence (e.g., J) is biased by the number of species in the different communities (28), and because local species richness differed between the ponds that experienced drought and those that were permanent, I developed an additional null-model approach (see *Methods*). This approach allowed me to test the hypothesis of whether within-treatment similarity differed from that expected from a purely random model of dispersal assembly alone (9). Thus, I was able to quantify the relative influence of niche assembly as the deviation of the actual similarity among communities relative to the similarity expected by random chance due to dispersal assembly alone. In permanent ponds, the observed similarity among all communities averaged 0.21, whereas the null expectation was 0.19 [0.18–0.21, 95% confidence interval (CI)]. In drought ponds, the observed similarity averaged 0.50, whereas the null expectation was 0.17 (0.15–0.19, 95% CI). By comparing the effect size of the difference between the observed similarity and the null expectation [$\ln(\text{observed } J) - \ln(\text{null expected } J)$] in a randomization test, I found that the effect size of the deviation from the null expectation was considerably higher for the drought ponds (1.08; 0.97–1.17, 95% CI) than for the permanent ponds (0.07; –0.02 to 0.15, 95% CI) (randomization test: $P < 0.001$).

There are several possible interpretations of these results. First, it is possible that ecological drift (defined here to include demographic stochasticity and other intrinsic stochastic effects, such as migration; ref. 4) played a prominent role in the assembly of the permanent ponds, because the actual community similarities (J) were statistically indistinguishable from the null expectation on the basis of dispersal assembly alone. Second, priority effects leading to multiple stable states could explain this result. Among the drought ponds, compositional similarity, J , was much higher than expected for dispersal assembly alone, possibly indicating a more prominent role for niche selection in the assembly of these communities and/or a reduction in the importance of priority effects and multiple stable states. Because community structure did not vary significantly in each pond during the final 2 years of the study (*SI Text*), this finding suggests a possible role for priority effects and multiple stable states in these communities. Importantly, these two interpretations are not mutually exclusive; priority effects that lead to multiple stable states are based on the same stochastic processes that create ecological drift.

It is also important to note that variation in ecological drift and/or multiple stable states are not the only two explanations for the observed results. For example, it is possible that in the absence of drought, heterogeneities in one or more environmental factors (light levels, allochthonous inputs) could have led to more divergent community compositions. Alternatively, in the presence of drought, even the same magnitude of heterogeneity may be less important in determining the composition of the community. In addition, the magnitude of the heterogeneities themselves could have been altered by the drought. Although this experiment was established to minimize the majority of such heterogeneities and although none of the variables measured showed strong variation in the environmental conditions among the experimental ponds, I cannot rule out this alternative.

One final alternative explanation that could confound the interpretation of the results is that, after the drought, I allowed only natural resistance and/or resilience to the drought to influence community assembly, whereas during the initiation of the assembly process, I introduced species in a stochastic way. Thus, it is possible that communities in permanent ponds were less similar because of experimentally imposed initial differences, whereas ponds that received drought were only subject to species that were resistant to the drought and remained in the ponds (as diapausing life stages) or were resilient to the drought

and recolonized the ponds. My intention with this design was to maximize the potential for ecological drift and priority effects to exert a legacy in community structure if it existed. However, after the drought, I did not manipulate community recolonization to simulate the effects of such harsh conditions on already assembled communities. Thus, even though the experimentally imposed assembly process was different before and after the drought, this manipulation is relevant to understanding the effects of a harsh environmental filter on the structure and similarity among communities. In addition, natural observations of permanent pond communities (11, 25), as well as a series of simultaneously running experimental ponds that received only natural (stochastic) colonizations (J.M.C., unpublished data), showed that permanent ponds maintained a much higher degree of compositional variation than did those exposed to drought. This indicates that the results of this study are likely to be due to drought effects filtering the species pool, making communities more niche-assembled, and not due to experimental artifacts.

Drought represents an important environmental filter for species in natural ponds and wetlands (26). Species that can persist after drought do so by either resisting it through life stages that can withstand drought (e.g., diapausing eggs) and/or by being resilient to drought by being capable of rapid recolonization (26). For example, in my experiment, the producers that dominated permanent ponds included a diverse array of submerged vascular plants (e.g., *Elodea canadensis*, *Ceratophyllum demersum*, *Najas flexilis*, *Myriophyllum sibiricum*, and several *Potamogeton* species). These species have no obvious mechanisms to resist drought, and are also very poor dispersers unable to disperse readily among ponds. Alternatively, following drought, the dominant producers were much less diverse and included filamentous (e.g., *Oedogonium*, *Cladophora*, *Spirogyra*) and macrophyte-like (*Chara vulgaris*) green algae, and a single macrophyte species (*Zannichellia palustris*). All of these species can tolerate drought as cells (in the case of algae) or diapausing seeds (in the case of *Z. palustris*) and can readily disperse from nearby habitats. Similar diversity and compositional shifts were repeated across functional and taxonomic groupings. Because drought created such a harsh filter, reducing the pool of species able to persist in those habitats, deterministic niche-selective forces were more prominent in drought ponds than in permanent ponds. In permanent ponds with less of an environmental filter, niche selection was weaker, and ecological drift and priority effects left a more prominent signature on community composition.

Understanding the relative roles of dispersal versus niche assembly in the development of community structure should provide important practical information for biodiversity restoration, which heretofore has had mixed results (29). If ecological drift leading to dispersal assembly is important, as I show in permanent ponds, restoration projects aimed at particular ecological communities will need to carefully consider stochastic processes and may require intervention (e.g., seed additions, removals) to achieve a desired state. Alternatively, when dispersal assembly is less important, as I show in communities that experienced drought, restoration projects may not need to consider the vagaries of community assembly, but focus more on the restoration of desired habitat properties.

In conclusion, I have shown that the environmental harshness imposed by drought on pond communities increases the similarity, reducing β -diversity. As such, even if local species diversity is able to recover following drought, regional diversity may be compromised. As human activities alter natural disturbance rates both locally (e.g., land development, forest harvesting) and globally (altering the intensity of El Niño events; ref. 30), it is imperative that ecologists recognize the varied influences of ecological forces, such as disturbance, on patterns of biodiversity at different spatial scales.

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