

Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments

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Net primary productivity is a principal driver of biodiversity; large-scale regions with higher productivity generally have more species. This pattern emerges because β -diversity (compositional variation across local sites) increases with productivity, but the mechanisms underlying this phenomenon are unknown. Using data from a long-term experiment in replicate ponds, I show that higher β -diversity at higher productivity resulted from a stronger role for stochastic relative to deterministic assembly processes with increasing productivity. This shift in the relative importance of stochasticity was most consistent with the hypothesis of more intense priority effects leading to multiple stable equilibria at higher productivity. Thus, shifts in community assembly mechanisms across a productivity gradient may underlie one of the most prominent biodiversity gradients on the planet.

Variation in the net primary productivity of a given ecosystem (e.g., the rate of carbon fixation through photosynthesis per unit area) plays a fundamental role in driving variation in biodiversity of both plants and animals across regions; more productive regions typically have higher levels of biodiversity (1–4). This positive productivity-biodiversity relationship typically manifests when biodiversity is measured at relatively large spatial scales; when biodiversity is measured at smaller spatial scales, the pattern is weaker and more variable (4, 5). The discrepancy between productivity's effect on biodiversity at smaller and larger spatial scales can be resolved by recognizing that site-to-site variability in species composition, known as β -diversity, often increases with increasing productivity (6–12). However, the mechanisms leading to the increase in β -diversity with increasing productivity remain largely unknown; most studies to date have been correlational. The factors that cause variation in β -diversity represent one of the most important, but poorly understood, influences on global variation in biodiversity (13–15).

β -diversity can arise from community assembly mechanisms involving (i) purely deterministic processes when habitat heterogeneity creates different niches across localities to which different groups of species are favored; (ii)

purely stochastic processes including ecological drift, dispersal limitation, and differential colonization/extinction dynamics across localities; or (iii) the interaction between stochastic and deterministic processes when stochastic variation in the history of colonization leads to more deterministic priority effects that vary across localities (16). To account for the generally observed pattern of increasing β -diversity with increasing productivity (6–12), one or more of these mechanisms must increase in its relative importance with increasing productivity. Deterministic processes could lead to increased β -diversity with productivity if the magnitude of variation in productivity among localities generally increases as the mean productivity of a region increases. However, studies that have specifically examined correlations between the magnitude of among-site heterogeneity and average productivity in a given region, and how that might influence β -diversity, have found no such relationships (6, 8, 17). As a result, it is often more likely that variation in the importance of stochastic processes, or in the interaction between stochastic and deterministic processes, leads to the observed increase of β -diversity with productivity.

There are two distinct mechanisms by which the relative importance of stochasticity in community assembly, leading to high β -diversity, can increase with productivity. First, stochastic variation in colonization or extinction among localities can result in ecological drift and dispersal limitation (18), or temporally variable metacommunities with locally unstable dynamics (19), both of which can create high β -diversity among localities. This spatiotemporal variability in community structure (β -diversity) may increase in frequency with increasing productivity if rates of colonizations or extinctions increase, or if interspecific interactions leading to unstable dynamics increase, with productivity (20). Second, stochasticity in colonization history can lead to priority effects, which can then deterministically create multiple stable equilibria of community structure in different localities, leading to high β -diversity [e.g., (16)]. There are at least two related theoretical reasons as to why priority effects leading to multiple stable equilibria might be more frequent in higher-productivity regions: (i) If a smaller proportion of the species in the species pool can persist in lower productivity, and if

that smaller proportion is relatively nested within the group of species that can persist in higher productivity, at least in the absence of interspecific interactions, priority effects leading to multiple stable equilibria can be more frequent at higher productivity from simple probability (21). (ii) In a food web where multiple species share common resources and common predators, increasing the level of productivity can create a saddle between dominance by species that are more effective competitors for shared resources and dominance by species that are more effective apparent competitors mediated through shared predators. This can lead to a higher propensity for multiple stable equilibria at high productivity, depending on which species with which traits (resource or apparent competition specialists) colonize a given community first (22). Similar effects should emerge under different combinations of traits and species interactions, as long as the balance of a species' interspecific effects on other species in the community becomes more likely to exceed its intraspecific effects as the level of primary productivity increases.

Here, I present the results from a 7-year experiment in 45 experimental freshwater ponds arrayed in an old-field at Washington University's Tyson Research Center, near Saint Louis, Missouri (21). This experiment was used to explicitly address (i) the relative contribution of stochastic processes (mediated through differential colonization history, ecological drift, or colonization/extinction dynamics) to within-treatment β -diversity, and the resulting effect of productivity on species diversity at local and regional spatial scales; and (ii) the potential mechanisms by which variation in the importance of these stochastic processes across productivity treatments manifests—through asynchronous temporal variation, or through priority effects leading to possible multiple stable equilibria. I treated ponds with three levels of nutrients to stimulate productivity and replicated each treatment with 15 ponds to observe any differences in within-treatment β -diversity. To create stochasticity in colonization, allowing for possible priority effects, I randomly varied the order of introduction of several species of producers and animals among each replicate pond over the first 2 years of the experiment; many other species colonized on their own accord, albeit somewhat stochastically (see table S1 for a list of species and whether they were introduced or colonized on their own). After these initial colonizations, stochastic processes (colonization and extinction dynamics, ecological drift, dispersal limitation) and deterministic processes (species sorting, priority effects) occurred naturally to influence patterns of β -diversity over the final 5 years of the experiment.

At the local (within-pond) scale, there were no significant effects of the productivity treatments on the richness of producers or animals within a given pond (α -diversity)

[Producer analysis of variance (ANOVA): $F_{2,44} = 1.21$, $P > 0.31$; Animal ANOVA: $F_{2,44} = 1.48$, $P > 0.25$]. However, using pairwise dissimilarity metrics [1-Jaccard's (incidence-based), 1-Bray-Curtis (abundance-based)] as a proxy for β -diversity, I found considerably and consistently high β -diversity among replicate high-productivity ponds, intermediate levels of β -diversity among replicate intermediate-productivity ponds, and low β -diversity among replicate low-productivity ponds (Fig. 1 and table S2). Although similar results have been seen in correlational studies (6–12), the few experimental studies that have been examined in this context (17, 23) have not been able to quantify whether higher β -diversity among replicates in higher-productivity habitats was a stable phenomenon, nor could they discern the mechanisms underlying this effect.

I found that only a subset of the total species pool could persist in the lowest-productivity treatment, imprinting a strong environmental filter on community assembly. Alternatively, the majority of species in the species pool could persist, at least on occasion, in the highest-productivity treatment, suggesting a much smaller role for environmental filtering in this treatment; ponds in the intermediate-productivity treatment were intermediate in the strength of the environmental filter. Specifically, 21 species of macroscopic producers (vascular plants and filamentous algae and cyanobacteria) were recorded from at least one experimental pond (no attempts were made to identify unicellular algae) (table S1). Of those species, 90% (19 of 21) were observed at least once in the highest-productivity treatments, whereas only 33% (7 of 21) were observed in the lowest-productivity treatments. Although too numerous to list, producer species that were able to persist in the lowest-productivity ponds included the vascular macrophyte *Elodea canadensis* and the macrophyte-like algae *Chara vulgaris*, both of which are known to be common in nutrient-poor waters. Likewise, of the 77 species of animals observed in at least one experimental pond (table S1), 88% (68 of 77) were observed at least once in the highest-productivity ponds, whereas only 39% (30 of 77) were observed at least once in the lowest-productivity ponds. Species able to persist in low-productivity ponds included small snails (e.g., *Gyraulus parvus*, *Physella gyrina*) and mayflies (*Callibaetis* spp.), which are species that appear to experience a trade-off between resource acquisition and risk of predation from larger predatory species (e.g., dragonfly larvae, hemipteran water bugs) (24) that were more likely to occur in the higher-productivity treatments.

Because the group of species that persisted in at least one pond of the low-productivity treatment was almost entirely a nested subset of the group of species that persisted in at least one pond of the high-productivity treatment, there was scale dependence in the relationship between productivity and species richness [as has been observed in surveys of natural

ponds (6)]. That is, although neither producer nor animal richness was influenced by productivity treatment at the scale of the local pond (see above), at the scale of the entire treatment (γ -diversity) ($N = 15$ replicates), producer richness increased by nearly a factor of 3 (7 to 19 species) and animal richness increased by more than a factor of 2 (30 to 68 species) from low to high productivity.

If higher-productivity ponds had more individuals than lower-productivity ponds, one possible explanation for the increased species richness observed in the high-productivity ponds could be that rare species were simply easier to detect because of a sampling effect. However, this was not likely to be the case for several reasons. First, as part of my sampling methods, I specifically targeted rare species to ensure adequate sampling (21). Second, rarefying local species richness did not change the lack of a significant relationship between productivity and local species richness (Producer ANOVA, $F_{2,44} = 2.27$, $P > 0.12$; Animal ANOVA, $F_{2,44} = 2.30$, $P > 0.13$). Finally, because the relative abundance of species was highly variable among replicates within a treatment, rarefying richness across the entire treatment to account for differences in abundance had no influence on the richness observed at the scale of the entire treatment, nor on β -diversity among replicates within a treatment. That said, because there was no effect of productivity on local richness but a large effect of productivity on the number of species observed in the entire treatment, the species in the higher-productivity treatments had lower occupancy rates on average, and thus were regionally rarer, than those in the lower-productivity treatments.

Because I observed consistently higher β -diversity among otherwise identically treated ponds in the high-productivity treatments relative to the low-productivity treatments, this suggests that stochastic processes were likely to play a stronger role in the assembly of higher-productivity communities. However, most measures of β -diversity are influenced by changes in the ratios of the numbers of species that live locally and regionally (e.g., $\alpha:\gamma$). Thus, to tease apart the relative importance of stochastic versus deterministic mechanisms underlying community assembly along this experimental productivity gradient, I performed a null model analysis (21) on the community-level data from the final year of the experiment. I found that the observed β -diversity (measured as Jaccard's dissimilarity) among high-productivity communities was indistinguishable from the null expectation that included only stochastic community assembly processes [permutational analysis of multivariate dispersions (PERMDISP) comparing the observed dissimilarity relative to the average dissimilarity produced by the null model: Producers, $F_{1,28} = 1.35$, $P > 0.4$; Animals, $F_{1,28} = 0.59$, $P > 0.8$]. Alternatively, the degree of dissimilarity observed in both intermediate-productivity

communities (PERMDISP: Producers, $F_{1,28} = 3.18$, $P < 0.04$; Animals, $F_{1,28} = 5.59$, $P < 0.03$) and low-productivity communities (PERMDISP: Producers, $F_{1,28} = 11.35$, $P < 0.01$; Animals, $F_{1,28} = 15.54$, $P < 0.01$) was significantly lower than the null expectation, indicating that some degree of determinism likely structured these communities. To more directly test the deviations from the null expectation among productivity treatments, I calculated a probability distribution of deviations from the null-expected number of shared species among pairwise community comparisons (21). I found that the values of this metric were larger, and thus less deviant from the null expectation, among replicates of higher-productivity ponds relative to replicates of lower-productivity ponds; replicates of intermediate-productivity ponds were intermediate in their deviation from the null expectation (PERMDISP: Producers, $F_{2,42} = 43.50$, $P < 0.001$; Animals, $F_{2,42} = 132.59$, $P < 0.001$; all pairwise comparisons $P < 0.02$) (Fig. 2). This confirms an increasing role for stochastic assembly processes leading to higher β -diversity with increasing productivity.

Above, I showed that the magnitude of β -diversity within treatments was consistent over the last 4 years of the experiment. However, this does not indicate whether the observed variation in β -diversity emerged because of higher asynchronous temporal variability in community structure (18–20) or because of more intense priority effects potentially leading to more frequent multiple stable equilibria (16). By measuring the rates of change in community composition within each experimental pond over the final 4 years of the experiment (21), I was able to test whether asynchronous temporal variability could be implicated or eliminated as a possible underlying mechanism behind the observed patterns of β -diversity. Perhaps surprisingly, given the large amount of spatial variability in community composition (i.e., β -diversity) seen across the array of experimental ponds, and particularly in the high-productivity treatment, there was little temporal change in the structure of the communities within a given pond from year to year, and there were no systematic differences in the rates of temporal change within ponds among the productivity treatments (Table 1). These results are inconsistent with hypotheses of purely stochastic community assembly (e.g., ecological drift and dispersal limitation) or unstable local community dynamics (18–20), and are more consistent with the hypothesis that stochastic colonizations in higher-productivity ponds lead to more frequent priority effects and multiple stable equilibria (16). The relative temporal uniformity of community structure within the ponds across 4 years encompassed tens to hundreds of generations of a majority of organisms in these ponds, and thus provides some indication of stability among different community states. However, these data alone cannot be used to definitively test stability, and experimental

perturbations of species densities would be required to unequivocally discern multiple stable equilibria (25).

The results from this long-term experiment show that the deterministic processes inherent in niche-based theories of community assembly predominate in lower-productivity systems, whereas stochastic processes due to differential colonization history and priority effects predominate in higher-productivity systems. The key mechanism underlying this relationship was that the realized pool of species that could potentially live in lower-productivity sites was more or less nested within the pool of species that could potentially live in higher-productivity sites. Although the generality of this specific mechanism in other ecosystems remains to be elucidated, I would argue that it is likely to be a rather general phenomenon. Species that are tolerant of harsh conditions such as low productivity can often be found on occasion in adjacent, more benign habitat types, and indeed can flourish in those habitats in the absence of interspecific interactions (26). For example, a large number of experiments have manipulated productivity in grassland ecosystems, and these experiments often show that lower-productivity treatments have a smaller, nested, pool of plant species that can potentially exist in those treatments relative to higher-productivity treatments that have a larger species pool (17). Similar patterns of nestedness along a productivity gradient seem to be evident in large-scale surveys of freshwater fish in lakes (10).

Some of the best evidence for stochastic processes underlying community assembly comes from relatively productive environments such as tropical rainforests and coral reefs (13, 18, 27, 28), whereas deterministic processes may play a stronger role in less productive temperate forests (29, 30), grasslands (31, 32), and marine intertidal habitats (33). As such, the results from this experimental study are likely to be general, suggesting that the relative importance of stochasticity increases with increasing productivity, and providing a likely mechanism for the positive relationship between increasing productivity (and lower latitude) and increasing biodiversity at large spatial scales, even in the absence of systematic variation in habitat heterogeneity or biogeographic constraints.

References and Notes

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34. I thank T. Knight, E. Marnocha, and C. Goss for help setting up the experiment; R. Shulman, B. Biro, J. Mihjalevic, P. Hanley, A. Strauss, and dozens of Tyson researchers for help sampling organisms; Tyson staff for logistical support; and T. Knight, K. Smith, R. Ricklefs, J. Losos, the reviewers, and my lab group for discussions and comments. Supported by Washington University and by NSF grants DEB-0241080 and 0816113.

Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1187820/DC1

Materials and Methods

SOM Text

Tables S1 and S2

References

2 February 2010; accepted 26 April 2010

Published online 27 May 2010; 10.1126/science.1187820

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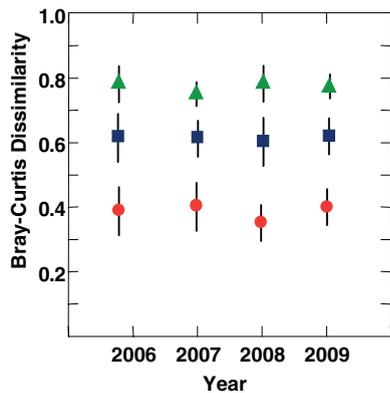
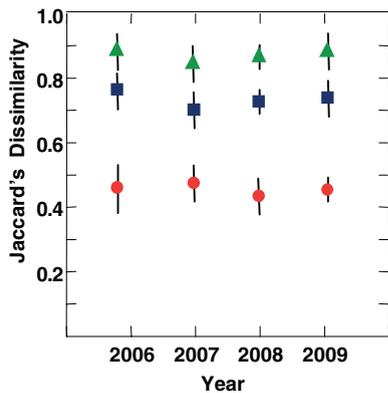
Fig. 1. Average dissimilarity among ponds within each treatment over the final 4 years of the experiment. **(A)** Data for producers, measured as Jaccard's (left) and Bray-Curtis (right) dissimilarity. **(B)** Data for animals, measured as Jaccard's (left) and Bray-Curtis (right) dissimilarity. Green triangles, blue squares, and red circles indicate the average dissimilarity among replicates within high-, intermediate-, and low-productivity treatments, respectively. Error bars represent 1 SE. Because these data are nonindependent, significance tests for treatment and time effects require a randomization procedure (21), results of which are presented in table S2.

Fig. 2. Nonmetric multidimensional scaling ordination plots of community composition in two-dimensional space: **(A)** data for producers, **(B)** data for animals. Each point represents the composition of a community in multidimensional space, and the distance between any two points represents the difference between those two communities according to a modified Raup-Crick dissimilarity metric, which indicates the degree to which the null-expected number of shared species between any two communities deviates from the observed number of shared species (21). Communities that are closer together are more deviant from the null expectation, whereas communities that are farther apart are less deviant from the null expectation. Symbol shapes and colors are as in Fig. 1. Lines represent the minimum convex hulls around the data.

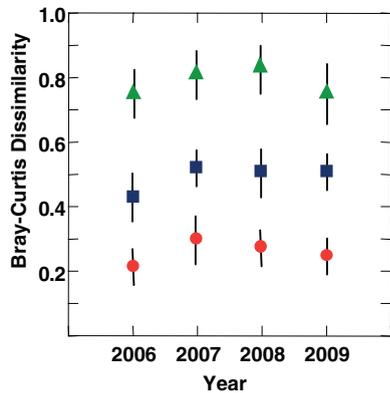
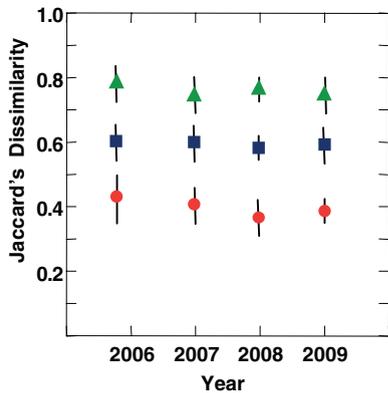
Table 1. Comparison of the average within-pond dissimilarity among years (2006 to 2009) in each treatment.

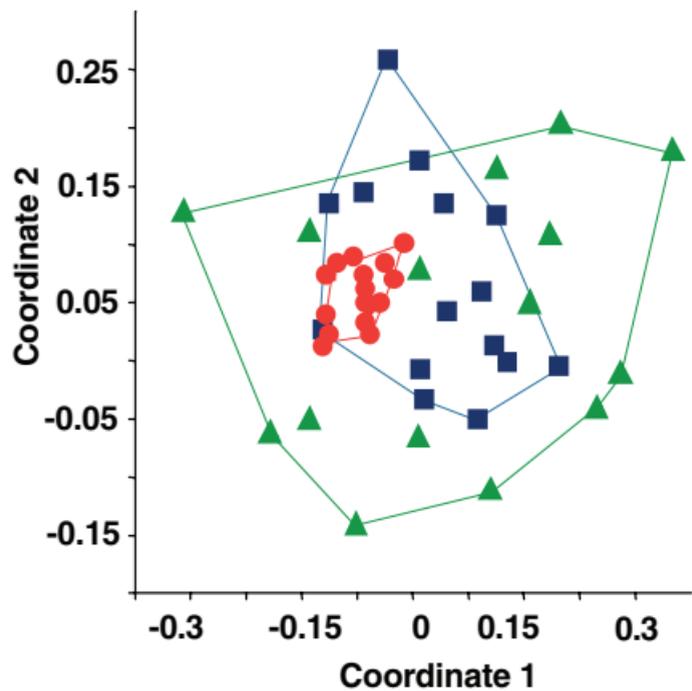
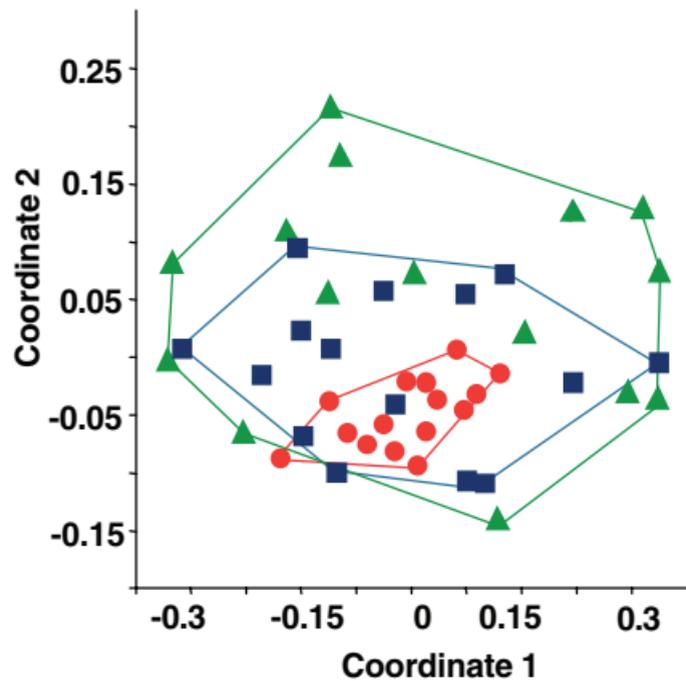
Productivity treatment	Jaccard's dissimilarity		Bray-Curtis dissimilarity	
	Producer	Animal	Producer	Animal
Low	0.03 ± 0.03	0.19 ± 0.13	0.18 ± 0.05	0.24 ± 0.13
Medium	0.02 ± 0.02	0.13 ± 0.12	0.15 ± 0.07	0.27 ± 0.17
High	0.02 ± 0.03	0.16 ± 0.14	0.15 ± 0.04	0.29 ± 0.17
ANOVA (df 2, 42)				
<i>F</i> ratio	1.28	1.03	1.16	0.33
<i>P</i> value	0.29	0.36	0.33	0.72

A Producers



B Animals



A Producers**B** Animals**Productivity Treatment**

High



Medium



Low