A framework for priority effects

Tadashi Fukami, Erin A. Mordecai, Annette Ostling

Fukami, T. (corresponding author, fukamit@stanford.edu)[1]
Mordecai, E. A. (emordeca@stanford.edu)[1]
Ostling, A. (aostling@umich.edu)[2]

[1]Department of Biology, Stanford University, Stanford, CA 94305, USA

[2]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA

Abstract

History of species arrival can influence plant community assembly. In this issue of the Journal of Vegetation Science, Sarneel et al. show that the strength of such historical contingency, or priority effects, varies with soil moisture in riparian plants. We discuss this study within a theoretical framework describing how and when priority effects occur via destabilizing and equalizing mechanisms.

Main text

How do plant species assemble into communities? This question has been central to vegetation science at least since Cowles (1899). Many processes affect community assembly, but one that is receiving renewed interest is priority effects, in which the impact that species exert on one other depends on the order of species arrival (Drake 1991). A fundamental goal is to predict how and when priority effects occur (Fukami 2015). This goal has been difficult to achieve because arrival order cannot be reconstructed in adequate detail in most cases. It is possible, however, to manipulate arrival order and watch what happens to community assembly (Ejrnæs et al. 2006), the approach taken by Sarneel et al. (2016) in this issue of the Journal Vegetation Science.

Three aspects of Sarneel et al.'s study are particularly worth noting. First, it involved a rare combination of greenhouse and field experiments. Greenhouse experiments afford greater experimental control, whereas field experiments yield more realistic data. The findings that were broadly consistent between the two complementary methods enhance support for the results. Second, the study made use of an environmental gradient along a river to determine if the strength of priority effects is affected by a particular environmental factor, soil moisture. Sarneel et al.'s use of the river gradient places the results in a realistic context, which few other authors have done. Third, arrival order was manipulated so as to simulate seed dispersal by flood or wind, with a clear link to understanding the effect of fluctuations in seasonal flood timing and other causes of natural variation in arrival order. These aspects of the study make the conclusion—that the strength of priority effects varies with soil moisture as well as species identity—both relevant and robust.

Experiments like Sarneel et al. (2016) are increasing in number, but papers on priority effects remain a minor part of the community assembly literature (Fukami 2015). One reason for this trend may be the lack of an intuitive conceptual framework for priority effects. Here we present one framework, building on Chesson's (2000) classification of mechanisms of species coexistence. This seminal paper is widely cited, but its potential utility for understanding priority effects is not well known.

According to Chesson (2000), there are two types of mechanisms that promote species coexistence, stabilizing and equalizing (right hand side of Fig. 1). To briefly explain these

mechanisms, let us consider coexistence of a pair of species as the simplest case. In species pair A shown in Fig. 1, the fitness difference is too large (i.e., one species is too fit compared to the other), and the niche difference is too small (i.e., the species are too similar in, e.g., resource requirements), to permit coexistence. In pair B, the niche difference—as seen in, for example, root depth—is large enough to compensate for the large fitness difference to permit coexistence. In other words, stabilizing mechanisms are strong enough to allow coexistence. In pair C, fitness difference is kept small enough—by, for example, foliar pathogens causing more harm to the competitively dominant species—to make up for the small niche difference to permit coexistence. In other words, equalizing mechanisms are strong enough to allow coexistence.

Chesson (2000) focused on species coexistence, but a similar explanation is possible for mechanisms that realize priority effects. Using Mordecai's (2011) conceptual diagram that extended Chesson (2000) and Adler et al. (2007), we can see that there are two types of mechanisms, destabilizing and equalizing (left hand side of Fig. 1). In species pair D, one species is so much more fit than the other and they are so similar in their niche requirements that coexistence is not possible. The more fit species always excludes the other regardless of arrival order, leaving little room for priority effects.

In contrast, in pair E, the fitness difference is still large, but mechanisms that make the more abundant species even more abundant operate strongly enough that whichever species gets a head start ends up excluding the other. An example of these destabilizing mechanisms is differential niche modification (*sensu* Fukami 2015), as in fire-adapted plants promoting fire through dry litter production vs. fire-sensitive plants suppressing fire by creating moist microclimate (Paritsis et al. 2015). Another example of destabilization is the reduction that each species may experience in reproduction when they are locally rare owing to mate limitation (Gerla & Mooij 2014).

In pair F, the fitness difference is small because, for example, species require a similar set of limiting factors (Levin 1970) and have similar intrinsic performance in the local environment. In this scenario, whichever species arrives early preempts the niche that the other species also needs. Mechanisms that set up such symmetric niche preemption (*sensu* Fukami 2015) act as an

equalizing force, which lowers the strength of destabilization that is needed for priority effects to occur. For example, Sarneel et al. (2016) found stronger priority effects under dry than wet soil conditions, and one potential explanation for this finding may be that dry soil makes all species, even those that are sensitive to water stress, similar in their intrinsic performance, creating an opportunity for even mildly destabilizing mechanisms to cause priority effects.

We see three reasons why a framework like this can be useful. First, it provides a way to systematically predict when priority effects will occur. As an illustrative example, wet soil that favors certain species may preclude priority effects by increasing fitness differences, but priority effects may still occur if, for example, plants alter soil microbiota greatly to their own benefits, a niche modification process contributing to destabilization. Second, knowing the strength of both destabilizing and equalizing mechanisms can inform us about the resilience of alternative community states driven by priority effects. Communities should be more resilient (i.e., harder to move between alternative states) when both mechanisms are strong, as in pair G in Fig. 1, as opposed to pairs E and F. Third, knowing which of the mechanisms is operating can help predict the extent to which alternative communities will differ not only in species composition, but also in functional properties, such as total biomass production (Körner et al. 2007) and decomposition (Dickie et al. 2012). Communities may differ greatly in function when niche modification is strong, whereas equalization and other types of destabilization that involve ecologically similar species may mostly affect the species composition, and not the functioning, of communities.

We expect that testing, refining, and expanding general concepts like the preliminary one presented here (Fig. 1) will take us in the right direction by suggesting what questions to ask and what data to collect toward more mechanistic understanding of how and when priority effects occur. Sarneel et al.'s (2016) work will serve as an exemplary case in this effort by showing how to design experiments.

Acknowledgments

References

Adler, P. B., HilleRisLambers, J. & Levine, J. M. 2007. A niche for neutrality. *Ecology Letters* 10: 95-104.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366.

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Part I. Geographical relations of the dune floras. *Botanical Gazette* 27: 95-117.

Dickie, I. A., Fukami, T., Wilkie, J. P., Allen, R. B. & Buchanan, P. K. 2012. Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. *Ecology Letters* 15: 133-141.

Drake, J. A. 1991. Community assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137: 1-26

Ejrnæs, R., Bruun, H. H. & Graae, B. J. 2006. Community assembly in experimental grasslands: suitable environment or timely arrival? *Ecology* 87: 1225-1233.

Fukami, T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46: 1-23.

Gerla, D. J. & Mooij, W. M. 2014. Alternative stable states and alternative endstates of community assembly through intra- and interspecific positive and negative interactions. *Theoretical Population Biology* 96: 8-18.

Körner, C., Stöcklin, J., Reuther-Thiébaud, L. & Pelaez-Riedl, S. 2008. Small differences in arrival time influence composition and productivity of plant communities. *New Phytologist* 177: 698-705.

Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist* 104: 413-423.

Mordecai, E. A. 2011. Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. *Ecological Monographs* 81: 429-441.

Paritsis, J., Veblen, T. T., & Holz, A. 2015. Positive fire feedbacks contribute to shifts from *Nothofagus pumilio* forests to fire-prone shrublands in Patagonia. *Journal of Vegetation Science* 26: 89-101.

Sarneel, J. M., Kardol, P. & Nilsson, C. 2016. The importance of priority effects for riparian plant community dynamics. *Journal of Vegetation Science* 27: ###-###.

Figure legends

Figure 1. Theoretical framework describing mechanisms of stable coexistence and priority effects. The x-axis quantifies the strength of stabilization or destabilization. In stabilization, a species' per-capita growth rate is negatively related to its abundance relative to the other species. In destabilization, it is positively related. The y-axis quantifies fitness difference between species. Each dot marked by a letter represents a hypothetical pair of species interacting with each other at a local site (see text for detail). Modified from Mordecai (2011).

Figure 1