

# Seeds of understanding of plant diversity

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**F**orests, grasslands, and other plant communities often contain large numbers of plant species; in the extreme, over a thousand tree species may be present in a single square kilometer of tropical forest (1). Ecologists have long sought to understand what factors govern the array of plant species present in any particular area, and indeed, how so many species can coexist at all given that all plants require essentially the same resources: light, water, and nutrients (2, 3). The classical explanation is that species can coexist if they are sufficiently different in their “niches,” the particular habitats or conditions in which they thrive or in the resources they exploit, and have corresponding weaknesses in other areas, so that no one species is able to out-compete the others (4). In this view, species composition of a community essentially reflects which niches are available. Alternatively, some ecologists have argued that chance events of immigration, local extinction, and speciation play a dominant role in determining which species are present in a community, so that species composition essentially “drifts” (5, 6). Empirical studies have demonstrated the importance of both sets of processes: there are meaningful differences among plant species in competitive ability under varying conditions, and yet historical factors are also involved in determining whether a species that could thrive in an area is actually present.

A full understanding of plant communities thus requires consideration of both niche- and drift-related factors, as well as of both evolutionary and ecological forces (7). Such an integrated approach is attempted by Uriarte and Reeve (8) in this issue of PNAS, in their theoretical study of the conditions for long-term ecological and evolutionary stability of coexisting plant species. Previous studies often focused exclusively on ecological stability, that is, on the conditions under which species can coexist indefinitely provided that each species is unchanging (does not evolve). As Uriarte and Reeve point out, however, traits important to competitive ability and thereby to coexistence are variable and subject to evolutionary change; thus, evolutionary as well as ecological stability is required for long-term stable species coexistence, what Uriarte and Reeve term species “marriage” (8). The set of trait values of a species is said to

be evolutionarily stable if in a population where most individuals have this set of traits, a mutant individual having any other set of traits is disadvantaged; thus, the traits of the species do not change over time (9).

In their article, Uriarte and Reeve address a classic problem: the diversity of seed sizes among coexisting plant species (10, 11). Natural plant communities exhibit tremendous variation in seed sizes among species, with variation often spanning more than five orders of magnitude (12) (Fig. 1). Differences in seed size among species are related to differences in seed production (13) and seedling establishment and growth (14), with seed size underlying a tradeoff between these traits. Plants can either produce many small seeds or few large seeds, with large seed size typically conferring an advantage in seedling competition. It has long been proposed that plant species of different seed sizes can coexist ecologically if the increased seed production of the small-seeded species allows it to persist as a “fugitive,” arriving and succeeding at sites that are not reached by the competitively superior larger-seeded species (15). Many models have documented conditions under which coexistence of two or more such

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species is ecologically stable (16–18); however, these models assume species trait values to be fixed and thus do not consider whether the seed sizes of the species are evolutionarily stable (in the most common model, they aren't). More recently, the problem of seed size variation has also inspired studies employing novel techniques of adaptive dynamics, which incorporate both ecological and evolutionary dynamics. Most notably, pioneering work by Geritz and collaborators (19–22) examines how the seed size of one species evolves over time, and under what conditions a single species could diverge into two or more coexisting species varying in seed size.

Uriarte and Reeve (8) investigate conditions permitting long-term coexistence

of two species with different seed sizes after the species come into contact through drift (e.g., immigration of one species into the range of the other). In their model, a species is characterized by its seed size and its additional investment in competitive ability. The amount of resources captured by an individual plant depends on its total “competitiveness”: its competitive investment plus the competitive value of its seed size. Specifically, each plant captures a fraction of available resources equal to its competitiveness divided by the sum of competitiveness values for all individuals in the community. Seed production is assumed to be proportional to net resource gain (resource capture minus the competitive investment) divided by seed size. Seed survival is assumed to vary among species, with the smaller-seeded species having lower seed survival that declines linearly with increasing abundance of the larger-seeded species.

Uriarte and Reeve first ask how values of competitive investment will evolve in two-species communities when seed sizes are fixed (nonevolving) and species abundances are unchanging. Because the benefits of a particular competitive investment depend on the investments of other individuals in the same community, a game theoretic approach is necessary. Thus, Uriarte and Reeve solve for the evolutionarily stable strategy for competitive investment for both species simultaneously. They find that the resulting competitive investments for the two species are “matched”; indeed, the total competitiveness values (competitive investment plus the competitive value of seed size) are equal, and depend only on the total number of individuals in the community and total resource availability. These results generalize to communities with greater numbers of species.

Uriarte and Reeve then separately examine the potential for ecological coexistence among species that have evolutionarily matched competitive investments. This involves calculation of the population growth rate of each species, which is a function of seed production times seed survival. Because stable ecological coexistence requires that the potential population growth rates of the two species be equal, Uriarte and Reeve

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**Fig. 1.** Seeds of 17 tree species, all from the family Fabaceae, that cooccur in the Peruvian Amazon. The largest seed pictured is 5.8 cm across. The seeds photographed here are a small sample of the 1,200 species of Peruvian Amazonian rainforest seeds in the collection of Susan J. Mazer (Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara) and represent a tiny fraction of the diversity of seed sizes and types represented among the thousands of Amazonian tree species.

solve for the difference in seed size at which this condition is met. They find that this ecological equilibrium is stable to perturbations in species abundances if such perturbations are assumed to affect the total resources available in the community; that is, if a decrease in the species with a higher competitive investment results in lower total resource uptake and higher resource availability.

Uriarte and Reeve argue that their results show that prior evolutionary matching of species competitive investments increases the potential for ecological coexistence. Indeed, if the total number of plants in the two-species community is greater than the total numbers of plants in communities of each species in isolation, then the competitive investments that are evolutionarily stable in the two-species community will be more similar than the competitive investments that would evolve in each one-species community in isolation. Under these circumstances, seed production levels will also be more similar. If seedling establishment probabilities are not too different, this will

result in more similar population growth rates as well, thus enhancing prospects for coexistence. However, under some parameter values, the opposite outcome (decreased potential for coexistence) is also possible.

The approach taken by Uriarte and Reeve is nonstandard in a number of ways, leaving several unanswered questions. Ecological stability analyses typically search first for equilibrium abundances (abundances at which both species have population growth rates of zero) as a function of species' trait values. Similarly, evolutionarily stable strategy analyses usually assume that ecological dynamics are so much faster than evolutionary dynamics that species abundances are always at their ecological equilibria for the current trait values (thus implicitly incorporating ecological stability). In contrast, Uriarte and Reeve assume the abundances of both species are fixed and independent of trait values, and thus presumably not generally at ecological equilibrium. Indeed, it is not clear how one could solve for non-trivial equilibrium abundances in the

model they present; it appears that additional assumptions are needed. Another departure in the methods of Uriarte and Reeve is the different treatment of resources in the evolutionary and ecological models. In the evolutionary model, total resource availability is independent of species trait values and competitive abilities (and all resources are taken up by plants). In the stability analyses of the ecological model, however, total resource availability is made a function of species abundances and competitive investments. As Uriarte and Reeve themselves note, if total resource availability is held constant as in the evolutionary model, then the ecological "equilibrium" of equivalent population growth rates is unstable to perturbations in abundances.

Like prior studies employing adaptive dynamics, the analyses of Uriarte and Reeve combine considerations of ecological and evolutionary dynamics to investigate trait evolution and community assembly, with particular focus on the problem of explaining variation in seed size within communities. The major innovation over this previous evolu-

tionary work (19–23) is the consideration of cases in which new species do not evolve *in situ* from species already in the community, but instead arrive via immigration (drift), and thus may start with trait values substantially different from those of any species previously present in the community. The introduction of such novel types is analogous to the approach taken in many studies of ecological coexistence (18). Understanding the potential of such distant types to invade requires examination of fitness not just of individuals with trait values similar to the main type, but of individuals from the entire range of trait values (as in ref. 24).

Theoretical studies have now convincingly demonstrated that tradeoffs such as those mediated by seed size can in principle promote ecologically and evolutionarily stable coexistence of plant species. In addition to the much-studied tradeoff between fecundity and seedling competitive ability, there are potential tradeoffs between fecundity and dispersal (25), age at reproduction and reproductive output (26), and many others (27). Many of these tradeoffs are capable of producing similar ecological and evolutionary dynamics; the implications

for coexistence differ among functional forms and parameter values more than among tradeoffs *per se* (28). At the same time, neutral model studies have shown that many, but not all (29), community-level patterns can be reproduced by models lacking such tradeoffs and the stability that they provide (6).

Given the many models that can produce qualitatively realistic community patterns (30), the major challenge now is to assess the actual relative contributions of tradeoffs underlying niche-based mechanisms and of drift due to stochastic events in determining these patterns. Such an effort requires comparisons of the predictions of different models to assess which patterns are useful in discriminating among models (30), investigation of the sampling distributions of these patterns (of how much scatter is to be expected; ref. 31), and quantitative comparisons between observed patterns in a particular community and models parameterized for that community (29). Several studies have already tested whether observed distributions of seed size and other traits within communities are more regular than a random assemblage (32, 33), under the assumption that coexistence via tradeoffs involving

particular traits should be reflected in overly regular trait distributions among species. Unfortunately, we have no good way to quantitatively evaluate such results because the regularity of the trait distribution produced by models will depend on model details, and will vary stochastically to an unknown degree. Closer integration of theoretical and empirical studies promises to make possible more rigorous tests of models such as the one presented by Uriarte and Reeve (8) using the abundant empirical data on seed size variation in different plant communities (34). Ultimately, it is this marriage of theory and data that will bring us a better understanding of plant diversity.

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