

# Matchmaking and species marriage: A game-theory model of community assembly

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Theories developed to explain the processes that govern the assembly and composition of natural plant communities can be divided into two broad categories. Niche-based theories propose that coevolutionary changes among species lead to character divergence (displacement), which allows for coexistence by partitioning resources among species. In contrast, ecological-drift theories propose that species diversity results from a balance of migration, speciation, and extinction, with little microevolutionary change. We use a game-theory model to reconcile drift and niche perspectives by developing a theory of species “marriage.” Initially, ecological drift may determine which species encounter each other in a competitive arena. Once species come into contact, historical niche development as a result of prior coevolutionary molding of competitive ability determines which species may coexist. The model shows that only species that display the well-known tradeoff between seed size and competitive ability as a result of past competitive histories comply with the requisite for mutual evolutionary stability. Mutual evolutionary stability of competitive ability tends to make reproductive outputs more similar between species, increasing the chances of ecological equilibrium, i.e., the coexistence of species competing for a single resource. Moreover, mutual evolutionary stability guarantees that such an ecological equilibrium will be stable. The species-marriage model predicts that two or more plant species will coexist indefinitely (i.e., “marry”) when their difference in seed size, their densities, and the resource availability obey a specific quantitative relation. For example, when resource availability is high, married species should be characterized by a greater asymmetry in seed size than when resource availability is low. Thus, in the species-marriage model, competition can shape the detailed properties of communities without violating the postulates of ecological-drift theory.

Natural communities often contain a staggering diversity of plant species, but the processes that govern the assembly and composition of these communities are poorly understood. Plant resource requirements, namely water, nutrients, and light, are similar for all species (1, 2). Traditional niche-assembly (equilibrium) theories assert that divergence in resource requirements or temporal and spatial separation in resource acquisition is necessary to prevent the competitive exclusion of inferior competitors (3–7). In contrast, dispersal-assembly (nonequilibrium) perspectives propose that species richness and abundance are determined by a dynamic balance among speciation, extinction, and dispersal, together generating an “ecological drift” (i.e., demographic stochasticity; refs. 8–13). In niche-assembly theories, microevolutionary changes within species lead to character divergence (displacement), which maintains species coexistence; in dispersal-assembly theories, on the other hand, there is no true equilibrium, but the distribution of species can remain relatively constant, i.e., a steady state emerges despite continual turnover of species through extinction and speciation.

In a recent book, Hubbell (13) developed a neutral model of community assembly that highlights the schism between dispersal- and niche-assembly theories. Hubbell’s model assumes that *all* individuals of *all* species are ecological equivalents, i.e., they have identical probabilities of birth, death, migration, and

speciation, a patently incorrect assumption. Surprisingly, the model produces patterns of species richness and relative abundance indistinguishable from those observed in natural communities. Hubbell argues that the model succeeds in explaining observed patterns because in saturated communities that follow zero-sum dynamics, (i.e., increases in one species always imply a matching decrease in the abundance of the remaining species), different tradeoff combinations of life-history traits confer coexisting species equivalent per capita relative fitnesses (14).

We propose a game-theory model of community assembly, the species-marriage model, that predicts that microevolutionary changes can stabilize species coexistence without coevolutionary niche partitioning among the coexisting species (in contrast to predictions of niche-assembly theories). Moreover, the end result of such microevolutionary changes will be a near-equalization of the reproductive rates of competing species, as assumed (but not explained) by ecological-drift theories. Thus, our theory not only can account for cases of stable species coexistence and the long-term patterns of species distributions, but it can also quantitatively predict both the nature of the life-history tradeoffs underlying species coexistence and the magnitudes of species differences in these life-history traits. As such, it provides a rich quantitative theory of character displacement (15).

Our model assumes that traits that confer competitive ability are subject to evolutionary change. Certainly, plant species display great genetic variation in fitness under competition (15–25). Some empirical evidence has also demonstrated that plants can specialize and evolve adaptations to particular competitive environments (26–32). Phenotypic expression of such adaptations hinges on resource availability (32) and on the degree of overlap in competitors’ resource requirements (30).

## Model

Our model considers both intraspecific and heterospecific competition between plants. Two species may come into contact through a drift process (e.g., breakdown of geographical barriers accompanied by colonization, speciation event accompanied by polyploidy, etc.). Once the two species are in contact, an individual plant must choose the optimal amount of energy  $m = m^*$  to invest in its ability to compete with neighboring plants, which may be either conspecifics or heterospecifics of a second species. (Alternatively,  $m$  might refer to the amount of some limiting resource instead of energy.)

Each plant is assumed to be in an arena of competition with a total of  $n_1$  plants of species 1 and with  $n_2$  plants of species 2. The amount of energy (or limiting resource) gained by each plant in the face of competition is assumed to vary directly with the ratio of its energetic investment  $m$  in competitiveness to the appropriately weighted sum of the competitive investments of all of the plants in the same competition arena. Superior competitors may possess one or more traits such as high photosynthetic rates, early or rapid germination time, plastic interpetiolar length, high root-to-shoot allocation, and deep root system (33). In addition, we assume that species 1 produces smaller seeds,

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each of energy content  $e$ , than does species 2, which produces seeds each having energy content  $e + x$ , with  $x > 0$ . We further assume that a seed's energy content additively supplements its energy in competitive ability, as larger seeds enable faster growth of small seedlings and thus should confer a greater ability to compete for resources (34, 35). Thus, if we assume that a rare mutant plant of species 1 invests an amount  $m_1$  in competitiveness, in a population in which most plants of its species invest  $m'_1$  in competitiveness and plants of species 2 invest an amount  $m'_2$  in competitiveness, then the total (gross) amount of energy or limiting resource  $R_1$  obtained by the mutant plant of species 1 is equal to

$$R_1 = \frac{(m_1 + ae_1)v}{(m_1 + ae_1) + (m'_1 + ae_1)(n_1 - 1) + n_2[m'_2 + a(e_1 + x)]}, \quad [1]$$

where  $v$  is the total amount of energy (or limiting resource) available to the plants in the competition arena, and  $a$  is a constant that converts seed energy into competitive investment. The corresponding amount of resource  $R_2$  obtained for a rare mutant of species 2 is

$$R_2 = \frac{[m_2 + a(e_1 + x)]v}{[m_2 + a(e_1 + x)] + [m'_2 + a(e_1 + x)](n_2 - 1) + n_1(m'_1 + ae_1)}. \quad [2]$$

These components of a plant's fitness are frequency-dependent, and the associated evolutionary game is a "game against the field" (36). In this case, the "field" consists of members of both its own and the other species. That is, a plant's fitness depends not only on its own competitive decision but also on those of both its conspecific and heterospecific neighbors. Thus, the evolutionary games played by each species are inevitably coupled.

We assume that the plant's fitness is directly related to the net amount of energy (or limiting resource) that it obtains in the face of intra- and heterospecific competition. A species 1 plant's net amount of energy is equal to the amount of energy it acquires through competition minus the amount it invests in competitiveness. Thus, the mean fitness,  $w_1(m_1; m'_1, m'_2) = w_1$  of a rare species 1 mutant investing  $m_1$  in a population in which conspecifics invest  $m'_1$  in competitiveness and heterospecifics invest  $m'_2$  in competitiveness is equal to  $R_1 - m_1$  and the corresponding fitness  $w_2(m_2; m'_1, m'_2) = w_2$  for species 2 is equal to  $R_2 - m_2$ .

The evolutionary stable investments  $m_1^*$  and  $m_2^*$  are found by simultaneously solving the two equations

$$\begin{aligned} \left[ \frac{\partial w_1}{\partial m_1} \right]_{m_1=m_1^*, m'_1=m_1^*, m'_2=m_2^*} &= 0 \\ \left[ \frac{\partial w_2}{\partial m_2} \right]_{m_2=m_2^*, m'_1=m_1^*, m'_2=m_2^*} &= 0. \end{aligned} \quad [3]$$

These equations mathematically express the requirement that the evolutionary stable investments must maximize the fitness of a rare mutant in mixed populations of both species of plants exhibiting those same investments (36). Solving Eqs. 3 yields

$$\begin{aligned} m_1^* &= \frac{v(n_1 + n_2 - 1)}{(n_1 + n_2)^2} - ae_1 \\ m_2^* &= \frac{v(n_1 + n_2 - 1)}{(n_1 + n_2)^2} - a(e_1 + x). \end{aligned} \quad [4]$$

That the solutions in (Eqs. 4) refer to stable investments is verified by the conditions

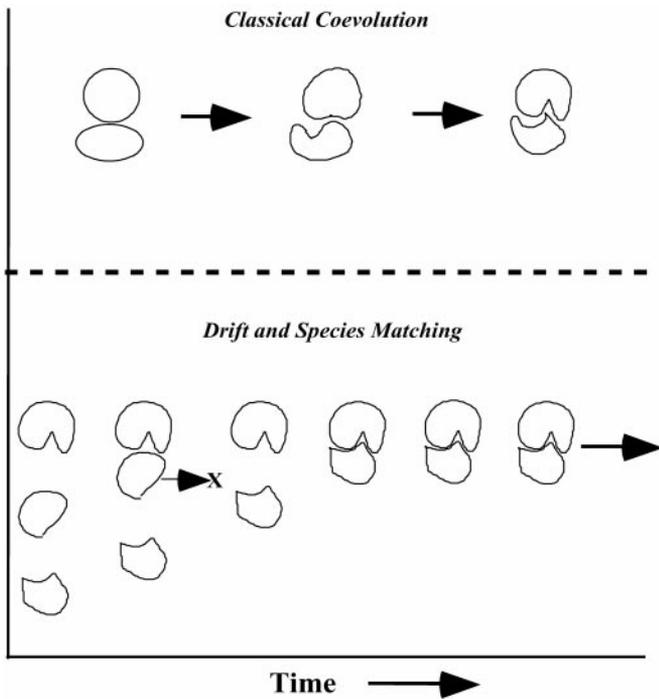
$$\begin{aligned} \left[ \frac{\partial^2 w_1}{\partial m_1^2} \right]_{m_1=m_1^*, m'_1=m_1^*, m'_2=m_2^*} &< 0, \\ \left[ \frac{\partial^2 w_2}{\partial m_2^2} \right]_{m_2=m_2^*, m'_1=m_1^*, m'_2=m_2^*} &< 0 \end{aligned} \quad [5]$$

at  $m_1 = m_1^*$  and  $m_2 = m_2^*$ . The equilibrium competitive investments,  $m_1^*$  and  $m_2^*$ , may reflect a number of traits that confer superior competitive ability (33).

Mutual evolutionary stability of the competitive investments requires that  $m_1^* > m_2^*$  because  $e_1 < (e_1 + x)$ . The solutions in Eqs. 4 immediately imply that seed size and competitive ability (e.g., rate of growth in competition for light) will be negatively correlated. A tradeoff between seed size and relative growth rate (RGR) has been reported across a broad range of species (37, 35). As detailed below, the latter tradeoff increases the possibility that two species will be able to coexist ecologically by bringing the fitness of the two competitors closer together. This conclusion generalizes to the  $N$ -species case, as the competitive investment of the  $i$ th species is equal to  $-ae_i + v[\sum(n_j - 1)]/(\sum n_j)^2$ , where the sums are over all species. It is important to note that competing species need not have originally evolved their competitive abilities in response to each other, but perhaps to other species (Fig. 1). These other species may have been encountered sequentially or simultaneously in combination, or a mix of both, as in "diffuse competition" (38, 39). When they then encounter each other in a competitive arena, selection will maintain their relative competitive abilities (because each is doing its best given the response of the other) and thus generate the potential for ecological stability.

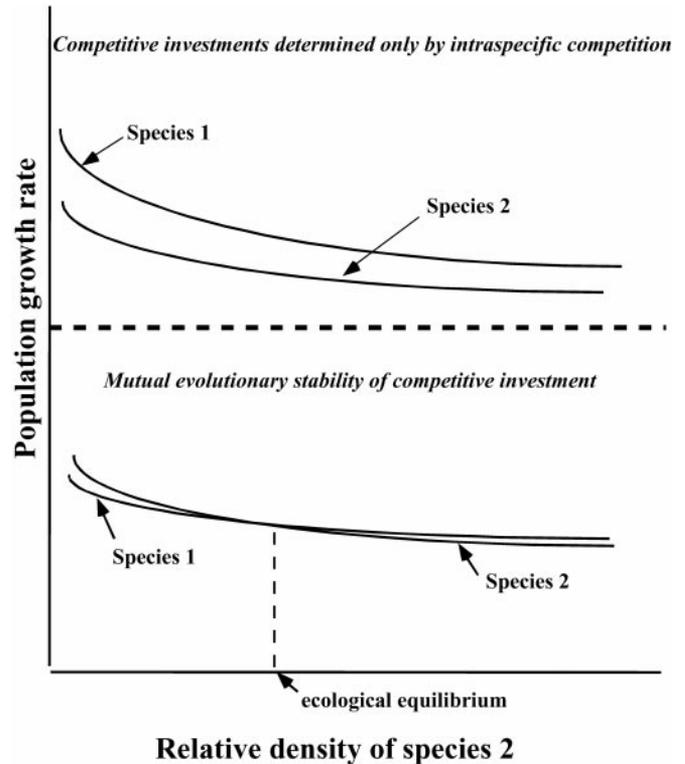
The evolutionarily stable investments described by Eqs. 4 do not necessarily imply that the two-species mixed population is ecologically stable, i.e., that the relative numbers of each species will remain the same over ecological time scales. That is, mutually evolutionarily stable investments are necessary but not sufficient for an enduring, unchanging association between the two species (they are necessary because if the two species are not matched according to Eqs. 4, their competitive characteristics will change because of subsequent coevolution, provided one does not competitively exclude the other). When competitively matched species encounter each other in a competitive arena through an ecological drift process, there are two possible outcomes: (i) some species will be inevitably lost because, although the two species are competitively matched, the population of one will grow at the expense of the other; or (ii) some species will have the potential for ecological coexistence (Fig. 1), such coexistence requiring that an additional condition be obeyed (see below). Notably, we will show that competitive matching itself generates two mechanisms that facilitate ecological stability. In other words, ecological drift will determine which species encounter each other in a competitive arena. Microevolutionary changes (niche development) resulting from the species' evolutionary prior competitive histories will influence whether species can coexist in an ecological sense.

Given that competitively matched species will not induce evolutionary changes in each other, what are the conditions for ecological coexistence? Species may coexist in ecological time *only* if small perturbations on their relative densities result in a differential spread of the species whose density has been reduced. To develop this ecological stability criterion, we must determine both the number of seeds produced by individual plants of each species and the probability that their seeds will produce successful seedlings. The "competitive-matching" conditions given by Eqs. 4 will be seen to automatically generate an ecological stabilizing force.



**Fig. 1.** The species-marriage model. In classical coevolution (*Upper*) two spatially contiguous or overlapping species coevolve until they reach a mutually evolutionarily stable state. The species' competitive characteristics are encoded in the shapes of the distinct icons representing each species. In species matching with drift (*Lower*), species come together through random drift processes and have already acquired their distinctive competitive characteristics (shapes) through prior coevolutionary interactions (for example, the top species may have acquired its characteristics through classical coevolution as shown in *Upper*). When species come together, regardless of their histories, they coexist and remain unchanged indefinitely (i.e., "marry") only if (i) their competitive investments happen to be mutually evolutionarily stable and (ii) they are ecologically stable. *x*, the exclusion of a competitively mismatched species. In either the *Upper* or the *Lower* scenario, species marriage results only if both evolutionary and ecological stability are achieved.

The number of seeds produced by an individual plant of species 1 is equal to its net acquired energy,  $w_1(m_1^*; m_1^*, m_2^*)$ , divided by the energy content per seed,  $e_1$ . Plugging the solutions from Eqs. 4 into the latter expression and dividing by  $e_1$  reveals that the number of seeds produced by an individual of species 1 is  $a + v/e_1(n_1 + n_2)^2$ . Similarly, the number of seeds produced by an individual of species 2 is  $a + v/(e_1 + x)(n_1 + n_2)^2$ . Note that species 1 produces more seeds because of its smaller seed size. However, mutual evolutionary stability entails that the two species will have more similar seed output than if they had not been competitively matched. For example, if each species had exhibited the evolutionarily stable competitive investments only for intraspecific competition, the solutions in Eqs. 4 would have predicted that the number of seeds produced by an individual of species 1 would be  $a + v/e_1(n_1)^2$  and the number of seeds produced by an individual of species 2 would be  $a + v/(e_1 + x)(n_2)^2$ , which are likely to be more unequal because the number of seeds produced by both species more closely approaches a single value,  $a$ , as the squared total number of competitors in the denominator of the second term increases. The convergence of the seed outputs of both species to the same value under the mutual evolutionary stability of competitive investments makes ecological equilibrium more likely (Fig. 2). Moreover, the smaller seed size of species 1 means that an individual of species 1 will increase its seed output more than will an individual of species 2 if there is an increase in the amount of resource  $v$ . The



**Fig. 2.** Mutual evolutionary stability of competitive ability and ecological equilibrium in married species. Mutual evolutionary stability makes stable ecological equilibrium more likely by (i) causing the population growth rates of the two species to become more similar and (ii) causing the equilibrium (where the growth rates are equal) to be stable.

latter effect is made possible by the negative relationship between seed size and the evolutionarily stable level of competitive investment, and provides another ecological stabilizing force (see *Appendix*). [This argument also applies in the general  $N$ -species case, in which the number of seeds of the  $i$ th species equals  $a + v/e_i(\sum n_j)^2$ .]

In accordance with empirical data (34), we assume that plants from larger seeds prevent nearby plants from smaller seeds from becoming established as viable plants, because of seed-stage competition. In particular, we assume that the probability of seed survival for a seed of species 1 is equal to  $1 - bxn_2$ , relative to a value of 1 for a seed of species 2, where  $b$  is a small constant. This assumption is equivalent to the idea that a species 1 seed has no chance itself of becoming established if it lands in the vicinity of a larger species 2 seed that becomes successfully established. The area of the restricted "vicinity" is incorporated into the product  $bx$ , which increases as the seed-size difference  $x$  increases. Thus, the relative probability of seed survival of a species 1 seed will be inversely related to the density of species 2 and the seed-size difference.

To develop a model of ecological stability, we need to know the population growth rates for each species, given that there are two life stages: seed and adult. In such a two-stage model, suppose that seeds survive with probability  $p$  and each adult produces  $S$  seeds. The projection matrix  $P$  appropriate for deriving the population growth rate for each species is

$$P = \begin{pmatrix} 0 & S \\ p & 0 \end{pmatrix} \quad [6]$$

The dominant eigenvalue of this matrix, i.e., the population growth rate, is  $\sqrt{pS}$  (40). For species 1,  $p = u(1 - bxn_2)$ , where

$u$  is the probability of seed survival in the absence of seed competition, and  $S = a + v/e_1(n_1 + n_2)^2$ . Thus, the finite rate of increase for species 1 is

$$z_1 = \sqrt{\left[ a + \frac{v}{e_1(n_1 + n_2)^2} \right] u(1 - bxn_2)} \quad [7]$$

and that for species 2 is

$$z_2 = \sqrt{\left[ a + \frac{v}{(e_1 + x)(n_1 + n_2)^2} \right] u}. \quad [8]$$

Interestingly, when there is no seed-stage competition, i.e.,  $b = 0$ , species 1, which has the smaller seeds, always spreads at the expense of species 2 ( $z_1 > z_2$ ). However, when there is seed-stage competition, an ecological equilibrium can be attained.

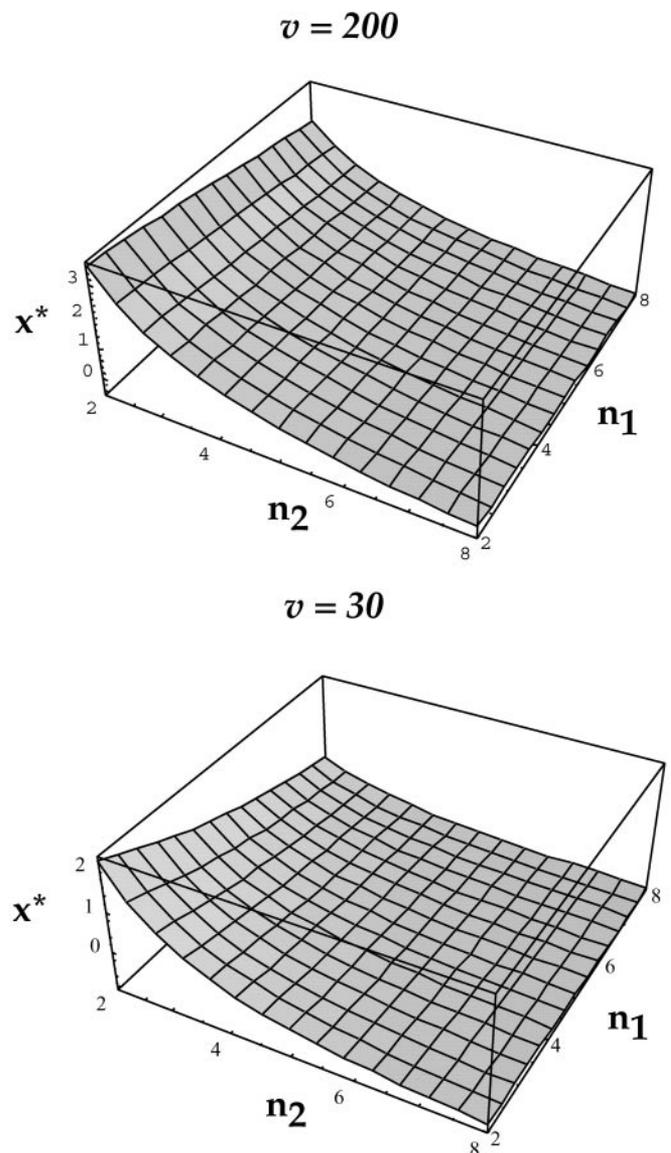
Ecological equilibrium results when  $z_1 - z_2 \cong 0$ . Using Eq. 7 and Eq. 8, we see that this occurs when the difference in seed size is equal to the critical value  $x^*$ :

$$x^* = \frac{v}{bn_2[ae_1(n_1 + n_2)^2 + v]} - e_1. \quad [9]$$

It might be thought that the equilibrium described by Eq. 9 is unstable, because a reduction in the density of species 2 would seem to increase the relative population growth rate of species 1. Remarkably, however, when the two species are at the equilibrium described by Eq. 9, this equilibrium will be always be stable (see *Appendix*). In other words, the ecological equilibrium is restored because the reduction in the density of species 1 relative to that of species 2 increases the number of established propagules produced by an individual of species 1 relative to that produced by an individual of species 2. This result occurs because reduction of the relative density of species 1 increases the available resource, and an increased resource augments the seed production of species 1 plants more than that of species 2 plants (see above). A similar argument applies for the general case of  $N$  competing species (see above general results), even though all species are competing for a single resource. Thus, evolutionary-competition games can promote ecological stability regardless of the number of competing species.

Thus, coexistence of two plant species can persist indefinitely when the difference in seed size, the species densities, and the resource availability obey the relation given by Eq. 9. When this relation is not obeyed, the species will be in a state of ecological flux. The important conclusion is that mutual evolutionary stability of the competitive investments of a group of competing species can create permissive conditions under which all species can coexist, despite the fact that they are competing for a single resource. The presence of two interlocking phases of competition, one between seedlings and one between mature plants, appears pivotal in yielding stable coexistence under these conditions.

The stable equilibrium given by Eq. 9 can be used to predict the features of evolutionarily and ecologically stable communities (henceforth referred to as *doubly stable communities*). For example,  $x^*$  increases as the resource availability  $v$  increases ( $\partial x^*/\partial v > 0$ ). Thus, when resource availability is high, a doubly stable community should be characterized by a greater asymmetry in seed size than when resource availability is low (Fig. 3). In addition,  $x^*$  decreases as the seed-stage competition intensity  $b$  increases ( $\partial x^*/\partial b < 0$ ). Thus, a doubly stable community should be characterized by a lesser asymmetry in seed size when seed-stage competition is mild. Variation in seed mass within natural plant communities covers five to six orders of magnitude (41). Yet, the factors that drive this striking variation are poorly understood. The contribution of resource availability to asymmetry in seed size can be tested by using existing data. Data on



**Fig. 3.** Seed-size difference versus species densities in doubly (evolutionarily and ecologically) stable communities (see Eq. 9), both when resources are plentiful (*Upper*) and when resources are scarce (*Lower*).  $a = 1$ ,  $b = 0.1$ , and  $e_1 = 1$ .

seed-size variation from five temperate floras compiled by Leishman *et al.* (41) would provide an excellent test of the theory on a broad geographical scale. Moreover, model predictions could be tested by using the long-term response of herbaceous communities to experimental manipulations in resource availability (37).

Previous theoretical work has shown that tradeoffs between dispersal and competitive ability (37, 42–44) or between survival and fecundity (45, 46) can allow the coexistence of several species competing for the same resource. Empirical evidence for a tradeoff between seed size and relative growth rate, a measure of competitive ability for light exists for a broad range of species (35). Our model confirms these findings and identifies selection for competitive ability as one of the potential evolutionary mechanism allowing coexistence. In addition, our model links abiotic processes (e.g., resource availability) to the evolutionary mechanism that promotes coexistence. Eq. 9 reveals that resource availability is crucial in determining the strength of the tradeoff and thus the degree of potential character displacement

(limiting similarity) in a stable community (Fig. 3). Undoubtedly, other factors such as environmental perturbations or spatial variation in resource availability will play a role in determining life-history traits of coexisting species. For instance, frequent, severe disturbance may tend to favor species with high colonizing ability and thus, numerous small seeds (35, 37). Nevertheless, disturbance typically influences resource availability and thus alters the potential range of seed asymmetry in the community at the relevant temporal scale. Similarly, spatial variation in resource availability within a community would tend to favor a particular combination of species at the relevant spatial scale. Thus, such variability enters our model and affects the outcomes through the parameters describing resource availability and seed-size differences.

Our model can be thought of as a theory of “species marriage” that has the potential to reconcile ecological drift and niche based theories. Initially, ecological drift (*sensu* Hubbell) determines which species encounter each other in a competitive arena. Once the species start competing for the same resource, historical-niche development as a result of past microevolution of competitive ability determines if species are “matched” in such a way as to prevent induction of subsequent coevolutionary changes, such matching also facilitating ecological stability by making the reproductive outputs of the species more similar. It appears that only species that display the appropriate tradeoff between competitive ability and dispersal comply with the requirements for evolutionary stability. However, these fitness tradeoffs do not guarantee that species will be in ecological equilibrium. Equilibrium will occur only when coexisting species exhibit identical rates of population growth. Thus, fitness tradeoffs *per se* do not guarantee equivalent per capita relative fitnesses, but make stable ecological equilibria more likely by reducing the difference in reproductive rates and providing a mechanism to stabilize the equilibrium (Fig. 2).

Our species-marriage model is reminiscent of the “taxon cycle” idea introduced by Wilson (39) and the “coevolution-invasion turnover” hypothesis proposed by Roughgarden (38). The idea of a coevolutionary period working in conjunction with drift (i.e., extinction) is already present in these models. Our model adds to existing theory by predicting the conditions under which “marriage” (i.e., evolutionary and ecological coexistence) will occur in natural plant communities.

### Appendix: Stability of the Ecological Equilibrium Attained by Species Exhibiting Evolutionarily Stable Competitive Investments

To determine the ecological equilibrium, we must examine how the difference between the growth rate of species 1 and that of species 2 changes as the number of species 1 plants is decreased (and number of species 2 plants correspondingly increased) by a small number  $y$ . Because the time scale of such an ecological perturbation should be much shorter than an evolutionary time scale, we assume that the species 1 and 2 plants continue to

exhibit the evolutionarily stable competitive investments given by Eqs. 4 during both the perturbation and the ecological response to it.

If the number of species 1 plants per competition arena is reduced by  $y$  (and species 2 plants increased by  $y$ ), the resource levels will be affected because individuals of the two species of plants use different amounts of resource. At an ecological equilibrium, a species 1 plant consumes a total amount  $w_1(m_1^*, m_1', m_2^*) + m_1^*$  of energy, whereas a species 2 plant consumes a total amount  $w_2(m_2^*, m_2', m_1^*) + m_2^*$ . From the solutions in Eqs. 4, it follows that a species 1 plant consumes exactly an amount  $ax$  more energy than does a species 2 plant. Thus, removing  $y$  species 1 plants and adding  $y$  species 2 plants increases the total amount of resource in the competition arena from  $v$  to  $v + yax$ .

Now we can calculate the number of established propagules ( $P$ ) produced by species 1 plants after  $y$  species 1 plants are removed as  $w_1(m_1, m_1', m_2')$ , with (i)  $n_1 - y$  substituted for  $n_1$ ; (ii)  $n_2 + y$  substituted for  $n_2$ ; (iii)  $v + yax$  substituted for  $v$ ; and (iv)  $m_1^*$  substituted for  $m_1$  and  $m_1'$ , and  $m_2^*$  substituted for  $m_2'$ . The population growth rate for species 1 then, after simplification becomes

$$z_1 = \sqrt{\left\{ \frac{v + a(n_1 + n_2)[e_1(n_1 + n_2) + xy]}{(n_1 + n_2)^2} \right\} u \left( \frac{1 - bxn_2}{e_1} \right)}. \quad [10]$$

Similarly, population growth rate for species 2 becomes

$$z_2 = \sqrt{\left\{ \frac{v + a(n_1 + n_2)[(e_1 + x)(n_1 + n_2) + xy]}{(n_1 + n_2)^2} \right\} u / (e_1 + x)}. \quad [11]$$

At the ecological equilibrium (see Eq. 9), the population growth rate of species 1 increases relative to the population growth rate of species 2 as the density of species 1 decreases if  $\partial(z_1^2 - z_2^2)/\partial y > 0$  (note: it is mathematically more convenient to take the derivative of the difference in the squares of the growth rates rather than of the raw difference in the growth rates, and this transformation does not affect the conclusions). Indeed,

$$\begin{aligned} \frac{\partial(z_1^2 - z_2^2)}{\partial y} &= \frac{a^2(n_1 + n_2)\{v - be_1n_2[ae_1(n_1 + n_2)^2 + v]\}^2}{bn_2v[ae_1(n_1 + n_2)^2 + v]} > 0 \\ &\text{at } x = x^*. \end{aligned} \quad [12]$$

Therefore, the ecological equilibrium is stable.

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