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Coexistence and Relative Abundance in Annual Plant Assemblages: The Roles of Competition and Colonization

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ABSTRACT: Although an interspecific trade-off between competitive and colonizing ability can permit multispecies coexistence, whether this mechanism controls the structure of natural systems remains unresolved. We used models to evaluate the hypothesized importance of this trade-off for explaining coexistence and relative abundance patterns in annual plant assemblages. In a nonspatial model, empirically derived competition-colonization trade-offs related to seed mass were insufficient to generate coexistence. This was unchanged by spatial structure or interspecific variation in the fraction of seeds dispersing globally. These results differ from those of the more generalized competition-colonization models because the latter assume completely asymmetric competition, an assumption that appears unrealistic considering existing data for annual systems. When, for heuristic purposes, completely asymmetric competition was incorporated into our models, unlimited coexistence was possible. However, in the resulting abundance patterns, the best competitors/poorest colonizers were the most abundant, the opposite of that observed in natural systems. By contrast, these natural patterns were produced by competition-colonization models where environmental heterogeneity permitted species coexistence. Thus, despite the failure of the simple competition-colonization trade-off to explain coexistence in annual plant systems, this trade-off may be essential to explaining relative abundance patterns when other processes permit coexistence.

Keywords: annual plants, colonization, competition, coexistence, niche.

Environmental heterogeneity underlies most classic explanations for the diversity of coexisting competitors in nat-

ural communities. Because species differ in their performance under various physical or biotic conditions, those with different “niches” coexist by dominating different locations across heterogeneous landscapes (Cody and Diamond 1975; Whittaker 1975). Although this general mechanism continues to motivate considerable research, recent work on diversity maintained by an interspecific trade-off between competitive and colonizing ability (Nee and May 1992; Tilman 1994) has shifted attention toward coexistence achieved in physically homogeneous systems. That a superior competitor and a superior colonizer can coexist without traditional niche differences has long been recognized (Skellam 1951; Levins and Culver 1971; Horn and MacArthur 1972; Levin 1974; Armstrong 1976; Hastings 1980), but the recent demonstration that this mechanism extends to any number of species (Tilman 1994), coupled with growing attention to the ecological consequences of spatial structure (Hanski and Gilpin 1997; Tilman and Kareiva 1997), has led to a surge of interest in diversity maintained by a competition-colonization trade-off. Coexistence is achieved because competitively superior species are so limited by colonization that they can only occupy a fraction of available habitats, leaving space for more poorly competing, but better colonizing, species. The conditions for coexistence under this mechanism (Holmes and Wilson 1998; Geritz et al. 1999; Kinzig et al. 1999; Adler and Mosquera 2000; Yu and Wilson 2001) and its implications for species sensitivity to habitat destruction (Tilman et al. 1994; Kareiva and Wennergren 1995; Banks 1997; Klausmeier 1998) have been the focus of numerous studies.

Despite the attractiveness of the competition-colonization trade-off as an explanation for the maintenance of diversity, its ability to explain coexistence or relative abundance patterns in real communities remains unresolved. Working with the model of Levins (1969) and Tilman (1994), several theoretical studies have suggested that whether or not this mechanism applies to natural systems will depend on the functional form of the trade-off and the mechanics of com-

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petition (Adler and Mosquera 2000; Yu and Wilson 2001) and dispersal (Holmes and Wilson 1998). Thus, the critical next step for evaluating the relevance of this mechanism for natural communities is to evaluate these models with quantitative trade-offs empirically derived from real assemblages. Unfortunately, for most systems, competition-colonization trade-offs are difficult to quantify, and building reasonable models also requires information about interspecific differences in longevity and age structure. Annual plant assemblages, in contrast, are relatively free of these limitations. They contain species with short and simple life cycles, well-supported competition-colonization trade-offs, and consistent patterns of relative abundance previously hypothesized to suggest recruitment limitation (Rees 1995).

In this article, we use models to determine whether the coexistence and relative abundance patterns characteristic of annual plant assemblages can be explained by empirically documented competition-colonization trade-offs or, alternatively, by such trade-offs operating in conjunction with environmental heterogeneity. We first describe the interspecific variation in seed size observed in annual systems and its quantifiable relationships with competitive ability, colonization ability, and tolerance of environmental factors. We then use models that relate these empirically derived trade-offs to the observed patterns of coexistence and relative abundance in these systems.

Species Traits and Abundance Patterns in Annual Plant Systems

In annual plant communities, seed size commonly varies over two orders of magnitude among species. The distribution is typically lognormal, with many small-seeded species and fewer larger ones (Salisbury 1942; Westoby et al. 1992). In addition, because annual plants have a limited amount of resources to allocate toward reproduction and because this allocation is roughly consistent across species within a community, species can produce many small seeds or fewer larger ones (Harper 1977). A clear example is shown in figure 1A. This well-supported seed size/seed number trade-off (Shipley and Dion 1992; Greene and Johnson 1994; Rees 1995; Turnbull et al. 1999; Jakobsson and Eriksson 2000; Leishman 2001) gives rise to a competition-colonization trade-off for annual plants.

Species producing smaller seeds produce more of them and thus have a colonization advantage relative to larger-seeded species. Small-seeded species may also disperse better in time because they live longer in soil seed banks and suffer less seed predation (Harper et al. 1970; Rees 1993; Guo et al. 2000), although results are highly variable. Another potential advantage of small seededness, better-dispersed propagules, is only poorly supported by empir-

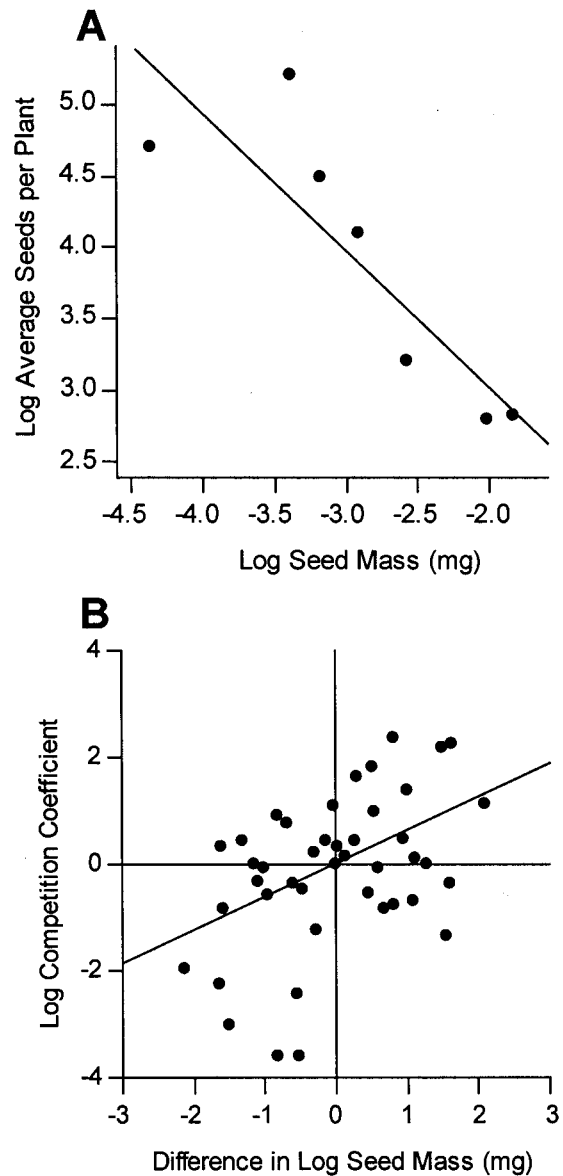


Figure 1: A, Relationship between seed mass and seed number for annual plants occurring in a limestone grassland ($R^2 = 0.74$), redrawn from Turnbull et al. (1999). Turnbull et al. (1999) report a slope that was not significantly different than -1 , which is consistent with equation (2). B, Relationship between the difference in seed mass between two species and their competitive equivalence coefficients (α). Data are from Freckleton's and Watkinson's (2001) reanalysis of Goldberg's and Landa's (1991) competition experiments ($R^2 = 0.21$; $P < .001$).

ical evidence (Leishman 2001). Nonetheless, greater numbers alone are sufficient to give small-seeded species a colonization advantage. This advantage, however, is counterbalanced by reduced competitive ability of the germinating seedlings. That larger-seeded species are better

competitors has long been hypothesized and has received consistent empirical support for both perennial and annual systems (Black 1958; Gross and Werner 1982; Gross 1984; McConnaughay and Bazzaz 1987; Rees 1995; Eriksson 1997; Turnbull et al. 1999; Freckleton and Watkinson 2001; Leishman 2001; see Leishman 2001 for review). This relationship has been quantified in recent analyses of Goldberg's and Landa's (1991) experiments, where species with different seed sizes were grown in competition with one another (fig. 1B; Freckleton and Watkinson 2001). Specifically, these studies have shown that the difference of the logs of the seed masses of two species is linearly related to their pairwise competition coefficients. Although these data come from perennial plants, the experiments were short term (5 wk), and the advantage of seed mass for competitive ability is known for both perennial and annual species (Black 1958; Gross and Werner 1982; Gross 1984; McConnaughay and Bazzaz 1987; Rees 1995; Eriksson 1997; Turnbull et al. 1999). These quantitative relationships between seed size, competitive ability, and seed number allow us to include empirically derived competition coefficients in our models of annual plant dynamics.

Annual plant systems also display characteristic patterns of community structure. At the most basic level, coexistence is a feature of these systems; they commonly contain around five to 10 species (Rees 1995). A second community pattern, which is more specific to these systems, is the negative correlation between seed size and abundance (fig. 2; Grubb et al. 1982; Maranon and Grubb 1993; Rees 1995; Pake and Venable 1996; Rees et al. 1996; Guo et al. 2000; Coomes et al. 2002). The smallest-seeded, best-colonizing species tend to be the most common, while the largest-seeded, competitive species are the least abundant. This relationship is more accurately described by a constraint line, where small-seeded species can be either common or sparse, while large-seeded species are consistently rare (Guo et al. 2000). Leishman and Murray (2001) have recently shown that seed size abundance relationships are not nearly so consistent for perennial systems or for annuals in competition with perennials. Similarly, we do not expect all annual systems necessarily to show the relative abundance patterns in figure 2. Rather, we examine these patterns here because they emerge in nearly all annual studies we know of and have previously been hypothesized to result from a competition-colonization trade-off (Rees 1995; Guo et al. 2000). Specifically, Rees (1995) argued that the rarity of the large-seeded species might be attributed to their poor colonization, while their competitive superiority enabled their persistence. Meanwhile, the greater abundance of the small-seeded species may be attributed to their superior ability to colonize vacant sites (Rees et al. 2001).

Large-seeded competitive species may also be limited

by their tolerance of environmental factors. Although larger seededness was classically hypothesized by Salisbury (1942) and Baker (1972) to enable plants to establish under a range of conditions, recent reviews by Westoby et al. (1992, 1996) find that consistent support for this hypothesis only comes from environments and experiments where shade is the major stress. Moreover, in contrast to the classic hypothesis, recent evidence suggests that, in some systems where shading is not the major establishment problem, small-seeded species may be found in the more stressful habitats. Maranon and Grubb (1993) found this result for a range of Mediterranean annual systems and cite comparable evidence from other systems. Similarly, in the coastal dunes of southern Britain, the small-seeded species are found on the thinnest soils (M. Rees, unpublished data). Seed addition experiments by Turnbull et al. (1999) also support this observation for annuals in a limestone grassland. Because of this seed size–stress tolerance relationship, we explore the importance of the competition-colonization trade-off in both physically homogeneous and heterogeneous model systems. In heterogeneous systems, we explore two contrasting models. In the first, smaller-seeded species better tolerate a range of environmental conditions (as in Maranon and Grubb 1993), while in the second, seed size is unrelated to the tolerance of physical factors.

Models

Among the simplest models for annual plant community dynamics is that of Rees and Westoby (1997), modified from Hassell (1975) and Watkinson (1980):

$$N_{t+1,i} = \frac{N_{t,i}\lambda(sw_i)}{1 + \sum_j \alpha(sw_i, sw_j)N_{t,j}}. \quad (1)$$

The number or density of individuals of the i th species at time t is $N_{t,i}$. Its per capita rate of increase or colonization rate in the absence of competition as a function of its seed mass (sw_i) is $\lambda(sw_i)$. The competitive effect of an individual of the j th species on an individual of the i th species as a function of their seed mass is $\alpha(sw_i, sw_j)$. Overall, this model states that the number of individuals of the i th species in the next year is the number of individuals in the current year multiplied by its fecundity and divided by the total competition experienced. Thus, competition reduces numbers not by killing individuals but by reducing their seed output (see Hassell 1975 and Watkinson 1980 for a more detailed discussion of the scramble/contest competition in this model).

This simple model can incorporate the empirically derived competition-colonization trade-offs on the basis of

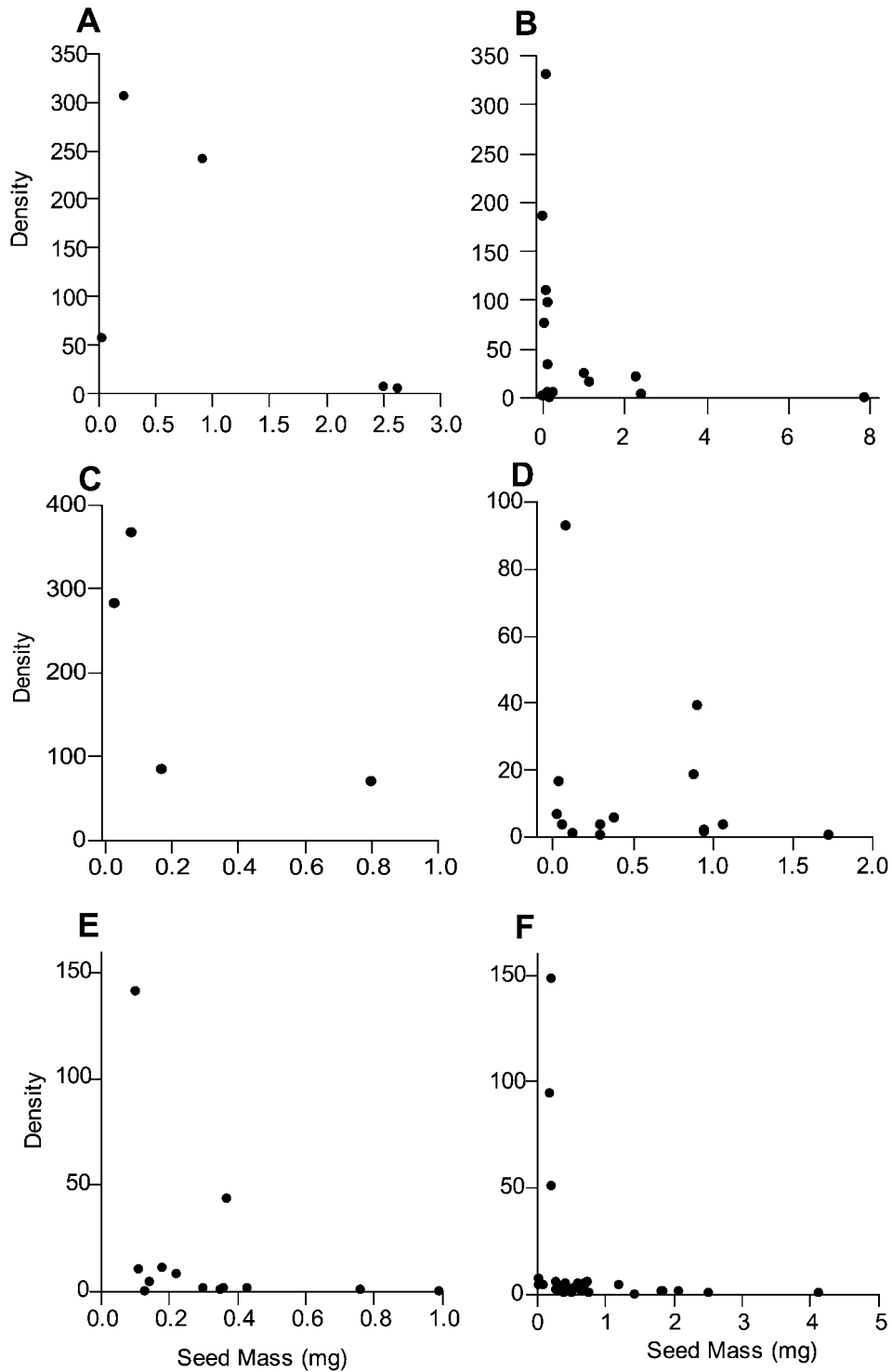


Figure 2: Seed mass–abundance relationships for a range of annual plant communities. *A*, Density (number in 10 dm²) of Mediterranean annuals of dehesa grassland in Spain (Maranon and Grubb 1993). *B*, Density (number/m²) of annuals across eight British dune systems (Rees 1995). *C*, Density (number/m² averaged over 10 yr and two sites) of annuals in the Holkham dune system studied by Grubb et al. (1982) and Rees et al. (1996). *D*, Density (number/m² averaged over 3 yr) of winter annuals in an Arizona desert community (Pake and Venable 1996). *E*, Summer and *F*) winter annual plant density (average number of individuals/m² over 18 yr) in the Arizona desert (Guo et al. 2000; different sites than Pake and Venable 1996).

seed mass shown in figure 1. The per capita rate of increase or colonization rate (λ) in the absence of competition is given by

$$\lambda(sw_i) = \frac{c}{sw_i}. \quad (2)$$

The parameter c corresponds to the energy allocated to reproduction across species. Equation (2) is consistent with the linear relationship between log seed mass and log seed number shown in figure 1A and numerous other studies (Shipley and Dion 1992; Greene and Johnson 1994; Rees 1995; Turnbull et al. 1999; Jakobsson and Eriksson 2000; Leishman 2001). The number of germinating seeds produced per individual in the absence of competition is λ ; thus, it and the value of c incorporate seed viability and the fraction lost due to predation. By plotting log seed number against log seed mass (mg), we can estimate c as the exponential of the y -intercept. To cover the range of values reported in our subsample of the literature, we present model simulations with high (100) and low (5) values of c . With $c = 5$, species with seed mass > 5 mg have $\lambda < 1$.

Functional relationships between seed mass and competitive ability can also be derived from empirical data. Here, we use the following function:

$$\alpha(sw_i, sw_j) = \left(\frac{sw_i}{sw_j}\right)^s. \quad (3)$$

The parameter s dictates the relative competitive advantage of larger-seeded species. Note that this equation describes the seed weight–competition coefficient relationships shown in figure 1B, where s is the slope. The value of s in figure 1B is 0.62. This value cannot be applied too precisely because the competition coefficients in figure 1B describe competitive effects on biomass, while the coefficients in equation (3) influence seed production. However, because seed production is often proportional to biomass (Rees and Crawley 1989), this is unlikely to change the slope of the relationship, s . To cover the range of competition we might find in natural annual systems, we explored model simulations with $s = 0.5$ and 1.5 , corresponding to weak and strong competition, respectively.

We simulated this model with n species, with seed masses sw_1, sw_2, \dots, sw_n . Specifically, we drew the n seed masses from a lognormal distribution with an untransformed mean of 1 mg and a variance of 1 (similar to fig. 2A and 2B).

Spatial Structure and Asymmetric Competition

Our model thus far examines the importance of a competition-colonization trade-off in a nonspatial system. However, the finding that such a trade-off permits the coexistence of numerous competitors emerged from a spatially structured system (Tilman 1994). We explored how spatial structure influenced coexistence in our annual plant model by simulating the model (eqq. [1]–[3]) over a series of patches connected by dispersal. These patch models do not incorporate the distance between patches or local dispersal as in Holmes and Wilson (1998) or Bolker and Pacala (1999) and are thus spatially implicit.

Specifically, we simulated a system of 10,000 patches, where within-patch dynamics were described by equation (1). We assumed that dispersal is random, and thus the number of arriving seeds for the i th species follows Poisson distribution with parameter μ_i , the mean number of seeds produced by the i th species per patch in the previous generation (the right side of eq. [1]). The initial distribution of seeds among patches has $\mu_i = 0.1$ for all species. We also ran simulations with clumped and regular initial distributions of seeds, and this did not affect the final results.

In order to compare our results from a spatially structured system to the more general model of Tilman (1994), we also ran simulations with qualitatively different competition. In equation (3), inferior competitors exert some negative effect on the superiors (although a smaller effect than the reverse). In contrast, in Tilman (1994), competition is completely asymmetric, meaning that for annual systems, even a species with a small seed size advantage over another immediately displaces it and suffers no competition. The nature of competition in our model is potentially important since Adler and Mosquera (2000) have argued that the nature of competition and not spatial structure generates coexistence in Tilman's model.

To incorporate completely asymmetric competition into our model simulations, we determined our competition coefficients with the following rules (and not eq. [3]):

$$\begin{aligned} \text{if } sw_i > sw_j, & \text{ then } \alpha(sw_i, sw_j) = 0; \\ \text{if } sw_i < sw_j, & \text{ then } \alpha(sw_i, sw_j) = \infty; \\ \text{if } sw_i = sw_j, & \text{ then } \alpha(sw_i, sw_j) = 1. \end{aligned} \quad (4)$$

We also assumed that patches are sized to hold one individual of the i th species, producing $\lambda(sw_i)$ seeds, so the dynamics can be approximated by the following annual plant analogy to Tilman's (1994) spatially implicit model:

$$P_{t+1,i} = \{1 - \exp[-\lambda(sw_i)P_{t,i}]\} \prod_{n=1}^{i-1} \exp[-\lambda(sw_n)P_{t,n}]. \quad (5)$$

The proportion of patches occupied by species i at time t is $P_{t,i}$. Species are ranked in competitive ability according to their seed size. The term before the product is the probability that a patch receives one or more seeds of the i th species, or one minus the probability of zero-arriving seeds, assuming Poisson dispersal. The product describes the probability of zero-arriving seeds for all better competitors than i (those ranked 1 to $i-1$).

Environmental Heterogeneity

An alternative mechanism of coexistence for annual plants involves species specialization on different environments within a heterogeneous habitat (Coomes et al. 2002). As described above, a number of studies suggest that, in some systems, large-seeded species can be more specific in their requirements of the physical environment (but not competitive environment) than smaller-seeded species. We incorporated this into our model by assigning patches a “favorability” integer from 1 to N , with patch 1 being the most favorable for growth and patch N the least favorable. The number of patch types (N) matches the number of species in the system. On the basis of a British dune system (M. Rees, unpublished data), we explored simulations with niche structure as in figure 3A. In such a system, all species can tolerate a large fraction of the patches (one-half), while the remaining patches are equally divided into progressively more stressful habitats. The stress might be soil thickness, metals content, salinity, or a biotic factor such as seed predation. We simulate the system by assuming that seeds of species whose seed size rank (the largest is assigned a “1”) is less than the favorability rank for the patch die with germination (or are eaten before). So the largest-seeded species (rank 1) can only tolerate patches assigned a “1” (the least severe), while the smallest-seeded species (rank N) can tolerate all patches. This is analogous to the included niche models (reviewed by Colwell and Fuentes 1975) typically used to explain plant zonation across environmental gradients (see citations in Levine et al. 1998) and is also hypothesized to contribute to coexistence by Turnbull et al. (1999).

These simulations with habitat heterogeneity assume a very specific type of niche use, one where the small-seeded inferior competitors tolerate a wider range of environmental conditions, and environmental factors affect plants in a threshold manner. This clearly does not describe all systems; thus, we also explored a completely different type of niche model, one where species can tolerate all habitats in the system but seed size confers a competitive advantage

at different points along the niche axis (fig. 3B). We base this model on Pacala and Tilman (1994) and Hurtt and Pacala (1995).

In the model, patches are assigned an integer p from 1 to N and species are assigned an integer n in order of decreasing seed size. For each patch assigned p , the species with n closest to p is the superior competitor. The greater the distance between n and p , the poorer the competitor in that patch. Specifically, for species i and j in a patch assigned quality p ,

$$\alpha_{ij} = \exp[S(|n_i - p| - |n_j - p|)]. \quad (6)$$

If n_i is closer than n_j to p , then the expression in the outer parentheses is negative and the effect of j on i (α_{ij}) is less than 1. If n_j is closer, then $\alpha_{ij} > 1$. For intraspecific competition, and for species equally distant from the optimal rank, $\alpha_{ij} = 1$. As with s in equation (3), S is a parameter dictating relative competitive advantage. However, since S relates ranks and not seed masses to competitive ability, s and S are not directly comparable. We conducted simulations with strong ($S = 2$) and weak ($S = 0.1$) competition. These values were not derived from a particular system but, rather, were selected to cover the broad range

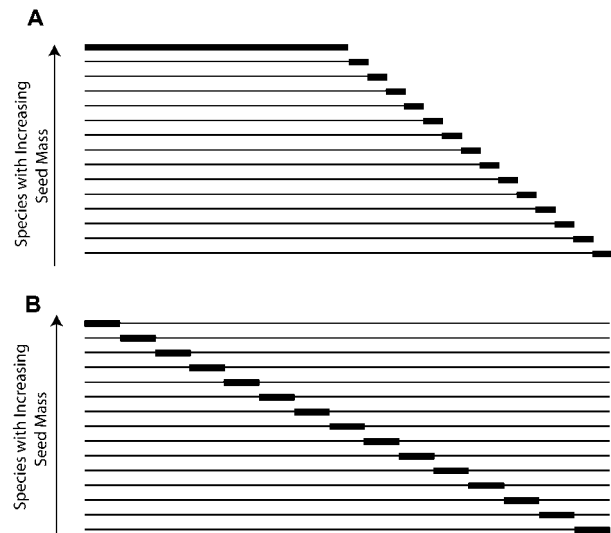


Figure 3: Niche structures for model simulations including environmental heterogeneity. Thin lines represent the range of tolerable habitats by a species. Thick lines show those habitats where a species is the superior competitor. A, Included niche model where half the habitat is tolerable by all species (and the largest-seeded species is the competitive dominant) and of the remaining, each species has some habitat not tolerated by superior competitors. B, Niche model based on Pacala and Tilman (1994) and Hurtt and Pacala (1995), where species tolerate the full range of habitats but differ in the regions over which they are the superior competitor.

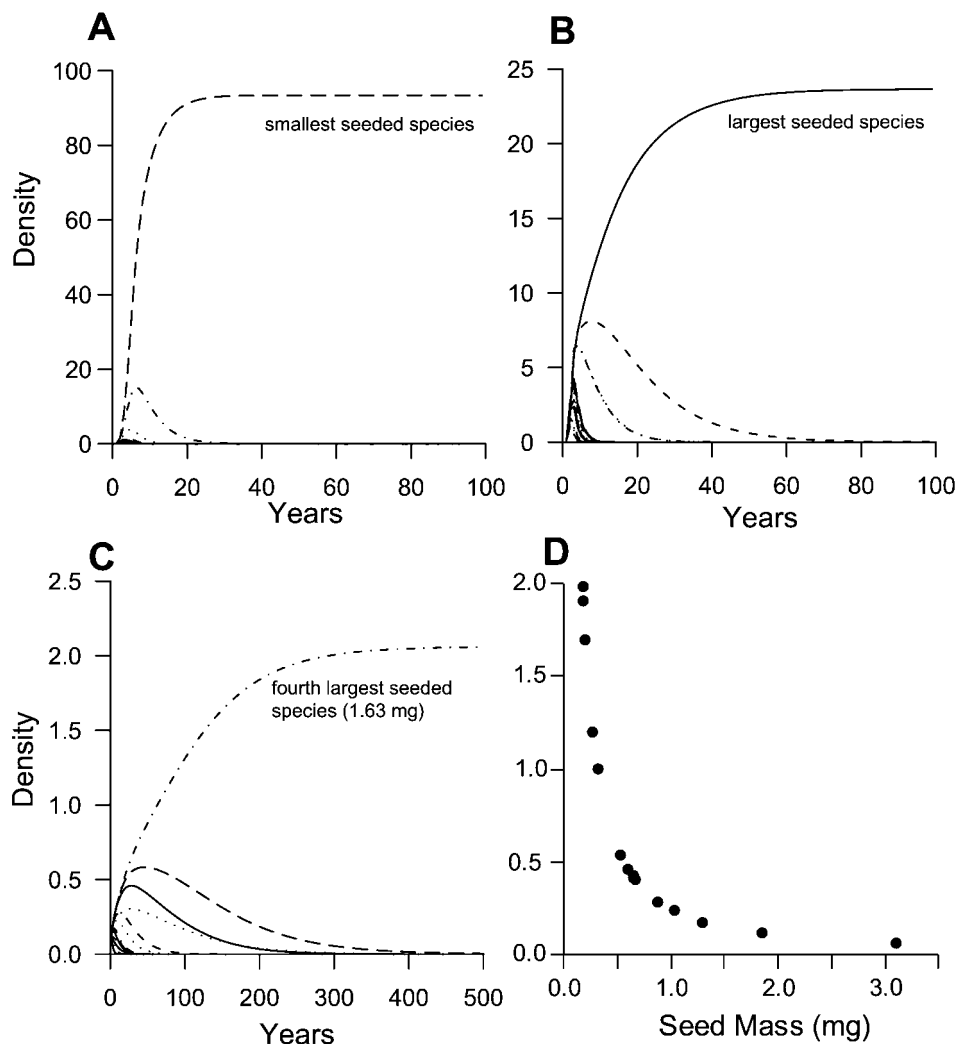


Figure 4: Simulations produced by the nonspatial model (eqq. [1]–[3]) with (A) low fecundity ($c = 5$) and weak competition ($s = 0.5$), (B) high fecundity ($c = 100$) and strong competition ($s = 1.5$), and (C) low fecundity ($c = 5$) and strong competition ($s = 1.5$). D, Relationship between density and seed mass after 3 yr, with parameters as in A.

of competition in annual systems. We also examined a system where the location of the optimal habitat along the niche axis was independent of seed size, and these results were highly similar. Although we do not model systems where large-seeded species better tolerate physical stress, our results can be extended to these systems (see “Discussion”).

All models were simulated in *R* version 1.2, and the code is available by request. One thousand simulations were used to test for coexistence and estimate all means and confidence intervals. Variation in the distribution of seed sizes drawn for simulation, random dispersal in the patch models, and random assignment of patch quality introduce stochasticity.

Results

Nonspatial and Patch Models

The simplest nonspatial model incorporating a competition-colonization trade-off (eqq. [1]–[3]) never yielded the stable coexistence of two or more species. For all combinations of high and low fecundity and competition, the species with the optimal combination of competitive and colonization traits dominated the system, driving its competitors to extinction (fig. 4A, 4B). With low fecundity and weak competition, this was the smallest-seeded species (fig. 4A). This occurs because the total competitive effect of a species is the product of its total numbers (N_i) and its per capita competition coefficients (α_i). Thus, a competitively

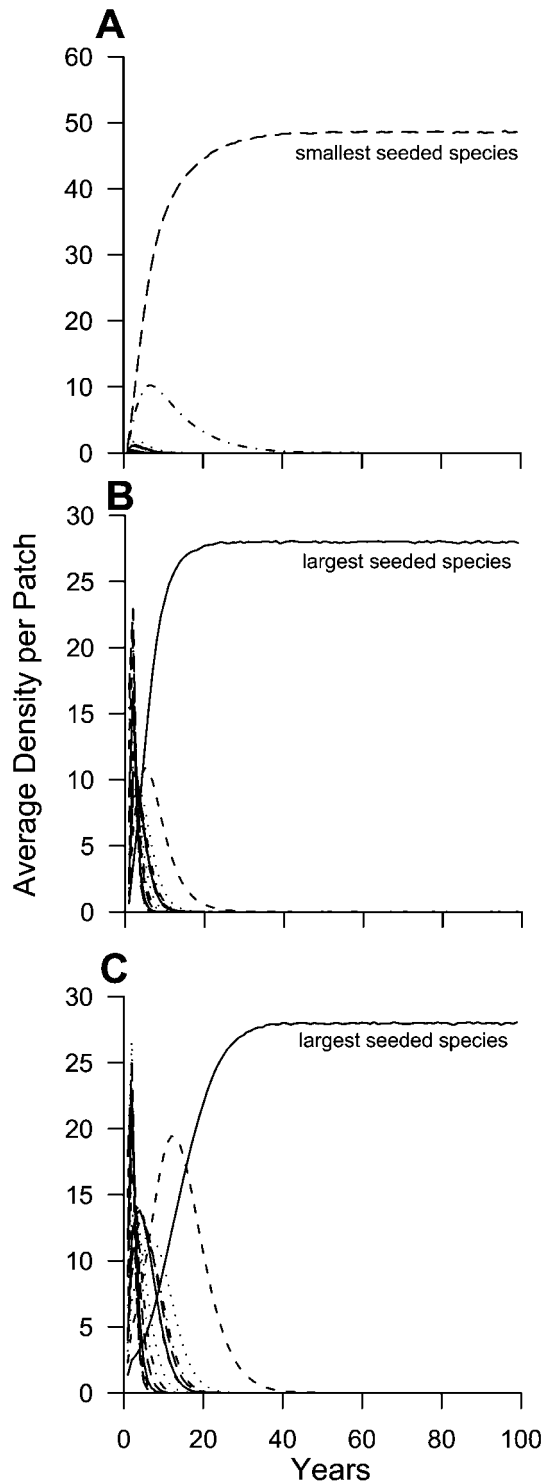


Figure 5: Simulations produced by the patch model with (A) low fecundity ($c = 5$) and weak competition ($s = 0.5$) and (B) high fecundity ($c = 100$) and strong competition ($s = 1.5$). C, Parameters as in B, but greater local (within-patch) dispersal of the larger-seeded species. Spe-

cially, seeds of the largest-seeded species had a probability 0.05 of dispersing outside the source patch, while the probability for the smallest-seeded species was 1. Species in between had probabilities assigned from regular sequence between 0.05 and 1.

inferior species with a greater colonization rate (λ) can displace superiors by producing more individuals. With high fecundity and strong competition, the largest-seeded species displaced all others (fig. 4B). With other parameter combinations ($c = 5$, $s = 1.5$), intermediate seed sizes prevailed (fig. 4C).

Examination of the invasibility criteria for our model (see Rees and Westoby 1997; Adler and Mosquera 2000) demonstrates that with competition coefficients derived as in equation (3) and figure 1, the coexistence of two species is impossible. Moreover, in 1,000 simulations with each of the parameter combinations in figure 4A–4C (and other combinations), coexistence was never observed. When competition coefficients are a saturating function of the difference in seed size, coexistence is possible (Rees and Westoby 1997), but such relationships are inconsistent with empirical data (fig. 1). Furthermore, using the evolutionarily stable strategy (ESS) approach of Rees and Westoby (1997), the ESS seed mass, $s\tilde{w}$, for our nonspatial model can be derived:

$$s\tilde{w} = c \left(1 - \frac{1}{s} \right). \quad (7)$$

Thus, when $s > 1$, an ESS seed size exists. When $s < 1$, Rees and Westoby (1997) show runaway selection for small seed size, and thus the smallest-seeded species possesses the dominant strategy. For simulations in figure 4B, where $c = 100$ and $s = 1.5$, the ESS seed mass is 33.33 mg and, as predicted, the largest-seeded species at 4.1 mg dominates. When $c = 5$, and $s = 0.5$, the smallest-seeded species is the predicted and simulated (fig. 4A) dominant. With $c = 5$, and $s = 1.5$, an intermediate seed size (1.67 mg) is the expected dominant, and this correctly predicts the simulation result (fig. 4C). Although this model predicts dominance by a single species, if we stopped the simulations after 3 yr, species had yet to be competitively displaced and small-seeded species were consistently more abundant than large-seeded ones (fig. 4D; a negative rank correlation between seed mass and density, $r_s = -1$, was observed in each simulation).

Adding spatial structure to the model did not markedly change the results (fig. 5A, 5B). It was possible for two species to coexist if fecundity was very low and competitive differences much larger than observed in figure 1 ($s = 4$). However, coexistence of three or more species was

rarely obtained, and with more realistic competition coefficients ($s = 1.5$), it was never observed in our simulations (fig. 5A, 5B). Similarly, incorporating the fact that larger seeds are less likely to disperse out of a patch did not change these results (fig. 5C). We determined this by simulating the system where each seed produced had a species-specific probability ρ of remaining in the patch and $(1 - \rho)$ of entering the globally dispersed seed rain.

With completely asymmetric competition (eq. [4]), we obtained multispecies coexistence (fig. 6A) in the patch model. The approximation of this model in equation (5) produced the same results (fig. 6C), with an average of 6.4 coexisting species (two and 10 species define the 95% confidence interval [CI]). Furthermore, like the Tilman (1994) model, this model could generate unlimited coexistence (fig. 6E). Completely asymmetric competition, however, is unrealistic and inconsistent with our existing data (fig. 2B; Mack and Harper 1977; Law and Watkinson 1987; Turnbull 1998). In addition, coexistence was only possible when the superior competitor could barely maintain positive growth, producing an average of only 1.1 germinating seeds per individual with no competition. Although these results cannot be interpreted too literally, coexistence achieved with this model is highly dependent on very severe dispersal limitation of the dominant ($c = 5$).

For the systems for which we have data, competition between annual plants does not appear completely asymmetric. Nonetheless, this type of competition may be a reasonable approximation for some other systems (Geritz et al. 1999). However, when we simulated the annual plant community analogue to the generalized Tilman (1994) model (eq. [5]), we found a positive correlation between seed mass and abundance (fig. 6D; mean $r_s = 0.58$; 0.07 and 0.91 define the 95% CI), the opposite of the relationships in natural systems (fig. 2).

Heterogeneous Systems

Both our models incorporating niche-based mechanisms of coexistence support the hypothesis that the competition-colonization trade-off may be essential for explaining relative abundance patterns when other processes drive coexistence. When each competitively inferior, smaller-seeded species was more tolerant of environmental conditions (fig. 3A) and $s = 1.5$ and $c = 100$, an average of 6.89 species coexisted with four and 10 species defining the 95% CI (fig. 7A). Furthermore, the negative relationships between abundance and seed mass produced by the model (fig. 7B; mean $r_s = -0.74$; -1 and -0.42 define the 95% CI) were consistent with those in real annual systems (fig. 2). These correlations emerged despite the fact that the largest-seeded species could tolerate half the patches, while all other species

had an equal fraction of patches in which they were the superior competitor. Furthermore, even when the largest-seeded species tolerated 90% of patches, similar patterns emerged (J. Levine and M. Rees, unpublished data).

These patterns also hold when different species were the competitive dominant at different points along the stress gradient (fig. 3B; eq. [6]). In the simulations with parameters as in figure 7C and 7D, an average of 14.11 species coexisted (13 and 15 define the 95% CI), and the smaller-seeded species were consistently the most abundant (fig. 7C, 7D; mean $r_s = -0.83$; -0.96 and -0.55 define the 95% CI). These results depend on strong enough competition and high enough fecundity for the largest-seeded species to win suitable sites. In both niche models, if competition was weak and fecundity low, the smallest-seeded species always dominated the system (fig. 7E, 7F).

Discussion

Our models incorporating empirically derived competition-colonization trade-offs suggest that because of the reciprocal nature of competition in annual plant assemblages, the competition-colonization mechanism of coexistence is unlikely to maintain diversity in these systems. Nonetheless, when niche-based mechanisms generate coexistence, the competition-colonization trade-off may be an essential determinant of relative abundance patterns.

Coexistence in Nonspatial and Spatial Models

Our nonspatial annual plant community model (eq. [1]–[3]) never yielded coexistence (fig. 4A–4C). The species with the optimal seed size had a sufficient colonization advantage to displace all superior competitors and a sufficient competitive advantage to displace all superior colonizers. Without completely asymmetric competition, smaller-seeded species can have greater total competitive effects (per capita effect \times density) than larger-seeded ones owing to their high colonization rate. When the system was simulated over a series of patches, the multispecies results were unchanged (fig. 5A, 5B). Although patch structure favors more poorly competing/better-colonizing species by introducing sites that remain uncolonized by recruitment limited competitors, it does not prevent the better colonizers from displacing their competitors through higher fecundity. For this reason, results were unchanged by allowing smaller-seeded species to disperse a greater fraction of their seeds globally versus within the patch (fig. 5C). Similarly, giving the smaller-seeded species the advantage of greater dispersal in time (increased longevity in the seed bank) would not change the results unless we also introduced temporal variability (Rees and Long 1992). This does not conflict with Holmes's and

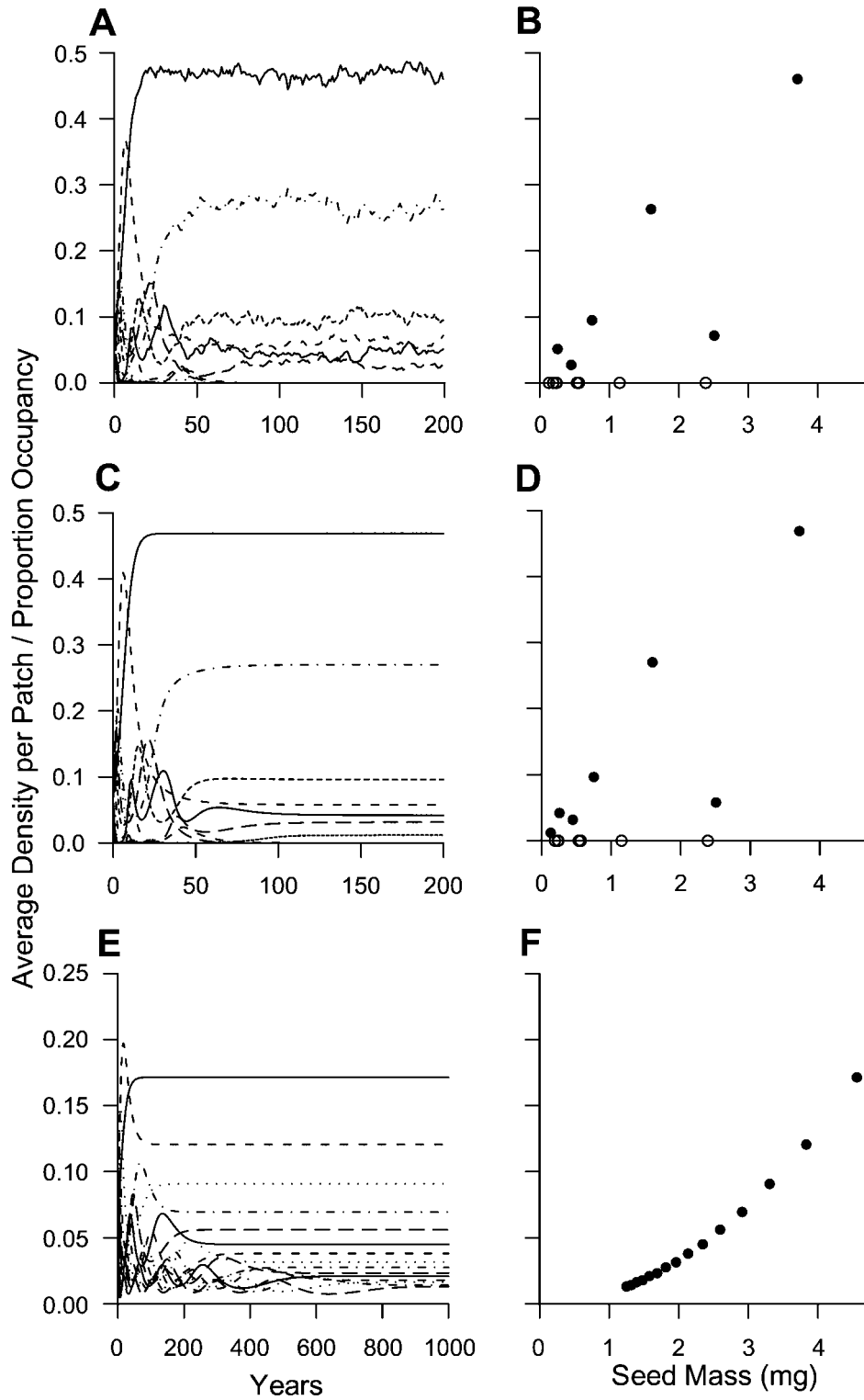


Figure 6: *A*, Simulations and *(B)* relative abundance patterns produced by the patch model, with asymmetric competition and low fecundity ($c = 5$). *C*, Simulations and *(D)* relative abundance patterns produced by the completely asymmetric competition patch model approximated by equation (5), an annual plant analogue to Tilman's (1994) general model ($c = 5$). *E*, Simulations and *(F)* relative abundance patterns produced (eq. [5]; $c = 5$), when seed masses are selected for coexistence. Open circles in *B* and *D* show seed mass of species that did not persist.

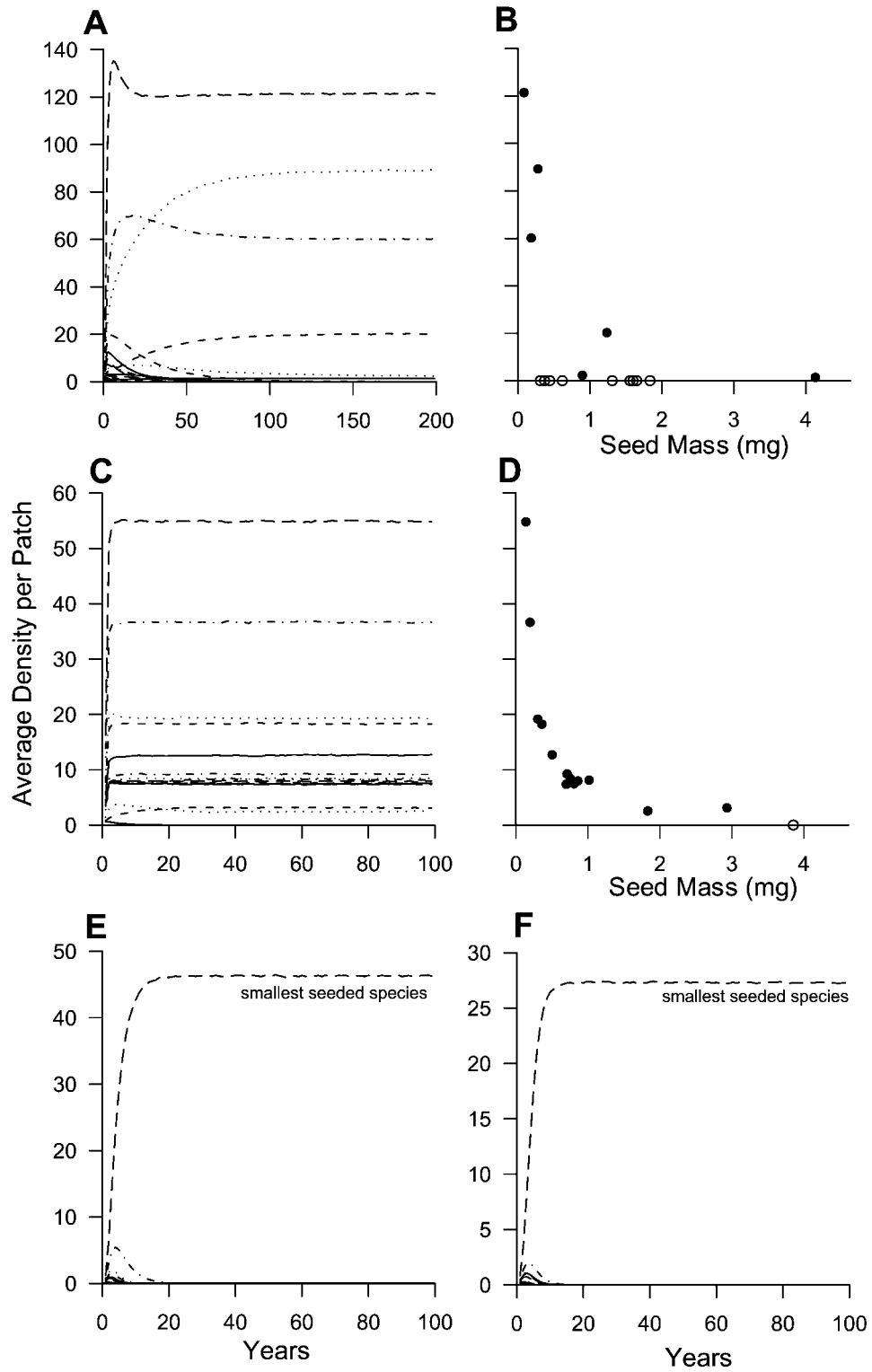


Figure 7: *A*, Simulations and *(B)* relative abundance patterns produced by the included niche patch model (fig. 3A), with strong competition ($s = 1.5$) and high fecundity ($c = 100$). *C*, Simulations and *(D)* relative abundance patterns produced by the patch model, with niche structure as in figure 3B, strong competition ($S = 2$), and high fecundity ($c = 100$). *E*, *F*, Simulations of the model with patch structure as in figure 3A and 3B, respectively, low fecundity ($c = 5$), and weak competition ($s = 0.5$; $S = 0.1$).

Wilson's (1998) results that greater long-distance dispersal by an inferior competitor may favor coexistence because their model is spatially explicit and also includes true local dispersal and completely asymmetric competition.

Despite our finding that empirically derived competition-colonization trade-offs in annual plant systems do not generate coexistence, the trade-off may be essential for explaining the relative abundance patterns in transient annual systems (Leishman 2001). If we stopped our simulations well before competitive displacement (fig. 4D), the largest-seeded species were the least abundant, and this matches relative abundance patterns in natural systems (fig. 2). Annual plant assemblages are often characterized by a high degree of disturbance (Rees 1995; Turnbull et al. 1999; Coomes et al. 2002), and in some of these systems, the observed relative abundance patterns may be transient effects of fecundity differences as in figure 4D. However, where these patterns persist from year to year (e.g., Grubb et al. 1982; Rees et al. 1996), transient dynamics cannot explain community structure.

Asymmetric Competition

The primary difference between our annual community results and the more general competition-colonization results of Tilman (1994) and others relates to the reciprocal nature of competition in annual plant systems. When, for heuristic purposes, we included the unsupported assumption of completely asymmetric competition, coexistence resulted (fig. 6). The competitively superior species were recruitment limited because of low fecundity ($c = 5$), while asymmetric competition precluded inferior species, regardless of their abundance, from displacing superiors. More general models by Geritz et al. (1999) and Adler and Mosquera (2000) demonstrate the overriding importance of asymmetric competition for the unlimited coexistence that can result from a competition-colonization trade-off.

Completely asymmetric competition might be expected in annual plant systems because larger seed size is thought to confer an early size advantage (Westoby et al. 1992, 1996). If competition is for light, taller individuals shade shorter competitors, while the reverse effect is negligible. However, the existing data for these systems do not support this type of competition. In figure 1B, smaller-seeded species exert significant negative effects on their larger-seeded competitors. Mack and Harper (1977), Law and Watkinson (1987), and Turnbull (1998) found similar interactions. Although this leads us to believe that completely asymmetric competition is an inappropriate description for annual plant interactions, we have only a limited number of studies on which to base conclusions. However, even without additional data, it seems highly improbable

that individuals with small seed size advantages can completely displace their competitors or prevent reproduction and suffer no competition.

As a secondary point, even if we accept the completely asymmetric competition assumption, the competition-colonization model then predicts positive relationships between seed size and abundance (fig. 6B, 6D, 6F), the opposite of the negative relationships documented for annual plant communities (fig. 2). Kinzig et al. (1999) and Adler and Mosquera (2000) have demonstrated more generally that for species coexisting via a simple competition-colonization trade-off with completely asymmetric competition, the most competitive/largest-seeded species will be the most abundant. Still, this type of result must be cautiously related to natural patterns. Part of the reason for the positive correlation between seed mass and abundance in figure 7B, 7D, and 7E relates to the occupied-unoccupied nature of space and the completely asymmetric nature of competition in Tilman-type models (1994). Even if asymmetric competition were strong enough to completely prevent inferior competitors from flowering, field censuses would still record these individuals unless competition completely eliminates them. With respect to the patch model in figure 7A and 7B, this is analogous to measuring density in the period before competition but after dispersal and germination, when patches can contain multiple individuals and species. We found that over this period, seed mass could be negatively related to density in our models, even if at the end of the growing season the relationship was always positive as in figure 7B, 7D, and 7E (unpublished). Thus, our ability to relate model predictions to natural patterns depends on how asymmetric competition operates in the field.

Dispersal Limitation

Coexistence via a competition-colonization trade-off also requires severe recruitment limitation of superior competitors. In fact, in our annual plant community models, the best competitor cannot have a per capita rate of increase much greater than one. Our finding of severe constraints on the dispersal of the superior competitor agrees with other studies. In Holmes's and Wilson's (1998) models, the advantage of global dispersal by inferior competitors only manifests itself when the superior competitor has a per capita growth rate near one. Similarly, in Bolker and Pacala (1999), poor reproduction of locally dispersing dominant species is required for the invasion of alternative colonization strategies.

Dispersal limitation so severe that the superior competitor barely persists, as is suggested by our model, might seem inconsistent with evidence from real annual plant systems. However, the realized fecundity of annual plants

is difficult to estimate, and the requirement that large-seeded species are barely viable may be consistent with some unproductive systems (Mack 1976; Watkinson and Harper 1978). Thus, the failure of the simple competition-colonization model to generate annual plant coexistence with empirical trade-offs stems more from the nature of the competition than colonization.

Environmental Heterogeneity

We found that several forms of environmental heterogeneity coupled with interspecific niche differences could generate annual plant coexistence (fig. 7). This was found in an included niche model, where poorer competitors were more tolerant of environmental conditions (based on results of Maranon and Grubb [1993], Rees [1995], and Turnbull et al. [1999]), and in a model where seed size conferred competitive advantages at different points along an environmental gradient. If parameters were such that the largest-seeded species was the predicted dominant in a homogeneous system, niche structure as in figure 3A favors coexistence by providing smaller-seeded species with a refuge from competition (fig. 7A). In our alternative niche model, based on Pacala and Tilman (1994) and Hurtt and Pacala (1995), coexistence occurs because competitive dominance changes with habitat type. In contrast to these results, if the inferior competitor was the predicted dominant in a homogeneous environment, as occurs with weak competition and colonization limitation, niche structure as in figure 3A and 3B does not allow coexistence (fig. 7E, 7F). In this case, a niche structure where larger-seeded species were more tolerant of environmental conditions (e.g., Baker 1972; the reverse of fig. 3A) would favor coexistence. Similar to these niche model results, Yu and Wilson (2001) showed that in a physically homogeneous habitat, spatial heterogeneity in patch density can give more poorly competing, better-colonizing species a refuge from competition and thereby favor coexistence.

When niche differences generate coexistence in these systems, the relative abundance patterns that emerge are consistent with what we observe in real annual assemblages (fig. 2). We regard this result as more general than the specific environmental heterogeneity models presented here. For example, if we incorporate variation in seed size into a simple lottery model (Chesson and Warner 1981; Venable et al. 1993) where species-specific germination responses permit coexistence, similar relative abundance patterns can arise (J. Levine and M. Rees, unpublished data). In our niche models, smaller-seeded species with tremendous seed output land many seeds in patches outside their preferred habitat. Even though these individuals could not initiate a self-sustaining population, a "spatial mass effect" (Shmida and Ellner 1984) arises, where seeds

from high-quality patches subsidize otherwise unsustainable populations in other patches (also see Comins and Noble 1985; Loreau and Mouquet 1999; Yu and Wilson 2001). In contrast, superior competing, large-seeded species disperse relatively little seed and are restricted to their most favorable habitats. In addition, even if all species are restricted to an equal fraction of patches, smaller-seeded species are likely to have landed more individuals within their patches and thus maintain higher densities in the system.

These effects are strong enough to overwhelm the underlying niche structure. Part of the robustness relates to the functional relationship between seed size and seed number (eq. [2]). For example, with $c = 5$, species producing 0.1-mg seeds can produce 50 of them, while a species with 0.01-mg seeds can produce 500. Thus, small decreases in seed size yield huge fecundity advantages that overwhelm variation in niche structure. This strong dependence of fecundity/colonization on seed weight also means that our results are robust to between-species variation in c , the overall reproductive output of the species. Following from equation (2),

$$-\frac{\partial \lambda}{\partial sw} = \frac{\partial \lambda}{\partial c} \lambda. \quad (8)$$

When $\lambda \gg 1$, λ is much more sensitive to variation in seed mass than c .

Conclusion

We found that, contrary to the suggestion of several previous studies, a simple competition-colonization trade-off is unlikely to explain coexistence in annual plant systems. This conclusion is consistent with experiments by Turnbull et al. (1999) showing that even when colonization limitation was eliminated from a system, small-seeded species persisted. It is also consistent with empirical results by Coomes et al. (2002) for dune annuals and Leishman (2001) for perennial and mixed annual-perennial systems. Given that annual systems were such a likely candidate for coexistence to occur via a competition-colonization trade-off (Yu and Wilson 2001), we find it unlikely that such trade-offs explain coexistence in other systems with more complex life histories, competitive interactions, and competition-colonization trade-offs. Despite this, we do see a central role for the trade-off in community ecology. When other processes permit coexistence, such as environmental heterogeneity, the competition-colonization trade-off may be an essential determinant of observed relative abundance patterns. Incorporating competition-colonization trade-offs into other models of community

structure may further our understanding of relative abundance.

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