ENVIRONMENTAL FORCING AND THE COMPETITIVE DYNAMICS OF A GUILD OF CACTUS-TENDING ANT MUTUALISTS

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Abstract. In generalized, multispecies mutualisms, competition among members of one guild can influence the net benefits that each species in the other guild receives. Hence seasonal factors that affect the dynamics of competition can also affect net benefits, especially if the benefit or cost of mutualism also varies seasonally. In the Sonoran Desert, two common species of generalist ants compete for access to extrafloral nectaries on the fishhook barrel cactus *Ferocactus wislizeni*, but their relative abundances vary seasonally; one ant dominates more cacti in winter/spring, and the other in summer/autumn. Recently, a third ant species, which also varies in abundance seasonally, has appeared at our study sites and is competing with resident ants for access to cactus nectaries. This empirical system motivated us to examine a metapopulation model of competition for patches in an open system with periodic forcing. We use the model to: (1) illustrate three ways in which competing species may differ in their sensitivities to environmental conditions that are consistent with seasonally displaced patterns of abundance; (2) ask under what conditions the invasion of a third competitor into a two-species system could alter the sensitivity of the system to environmental forcing at low vs. high frequency; and (3) show how differences among competitors in the pattern of seasonal forcing alone can dramatically alter the outcome of a competitorAbstract.mayAmppcompetLppcompa2l0e.H46(sesy)-4dA7tsmuxtrac ()-319(mpavity)-8mpetLpp8m

barrel cactus nectaries. Visitation to cacti by this novel competitor also varies seasonally.

Competition between members of one mutualistic guild for the rewards or services provided by members of the other guild has commonly been observed (see reviews by Addicott 1985 and Bronstein and Barbosa 2002). In protection mutualisms, ants have often been found to be a limiting resource for which homopterans (Addicott 1978, Cushman and Addicott 1989, Cushman and Whitham 1991, Sakata 1999) or homopterans and extrafloral-nectary-bearing plants (Buckley 1983, Sakata and Hashimoto 2000) compete. On the other side of the interaction, competition among ants for reward-producing plants has almost exclusively been studied in myrmecophyte systems, in which plants are obligately dependent on the ants for protection and ants are obligately dependent on the plants for food or shelter. In obligate ant–plant mutualisms, a key question is how multiple ant species can coexist on a single, required resource despite competition (Young et al. 1997, Yu et al. 2001, Stanton et al. 2002, Palmer 2003, Palmer et al. 2003). The barrel cactus system, like most ant–plant mutualisms, is facultative; ants can utilize many resources other than barrel cactus extrafloral nectar, and their absence from nectaries does not imply that they have been excluded from the community. A full understanding of how ant competitors for barrel cacti coexist cannot be achieved by understanding the forces mediating their competition for cacti alone. Nonetheless, indirect effects of ant–ant competition are as relevant for facultative ant-plants as they are for obligate
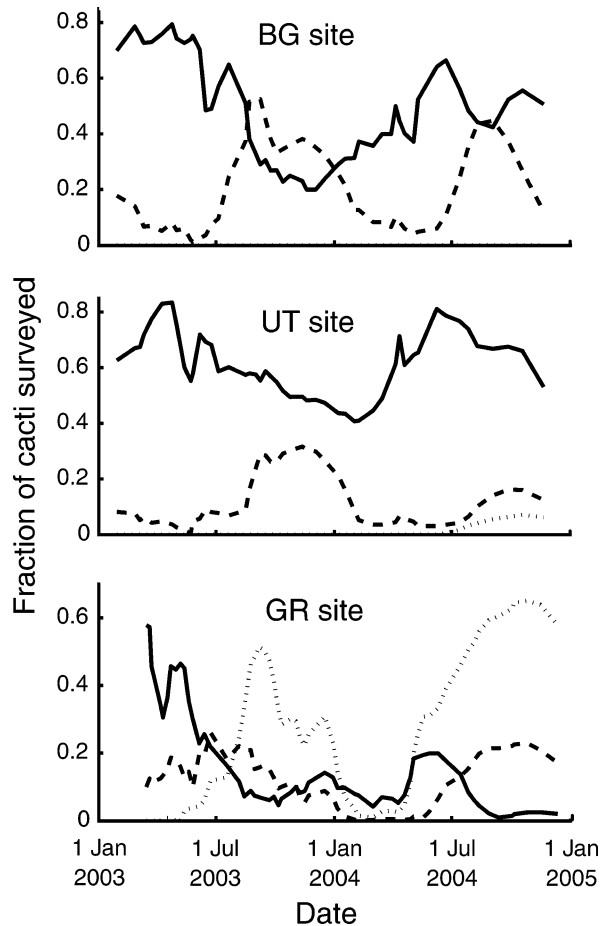
FIG. 1. Occupancies by the three most common ant species at three study sites at the Desert Laboratory, Tucson, Arizona, USA, over a two-year period. The order of sites from west to east is GR, UT, and BG. Across all sites, ; 260 plants were surveyed approximately twice monthly. Typically, at most one ant species was observed on a plant, but when more than one was found, the species with the most workers was considered the dominant species. Fractions do not add to 1 because some cacti were untended or tended by less common ants. To emphasize general trends, fractions were smoothed using a three-survey running average.

substantially during the year as individual cacti undergo transitions from being tended exclusively by one species of ant to being tended by an entirely different ant species. In particular, *C. opuntiae* is typically more frequent in winter and spring, and *S. aurea* and *S. xyloni* are more frequent in summer and autumn. B. Sullender (*unpublished manuscript*) observed the same seasonal patterns for *C. opuntiae* and *S. aurea* over two years. The fluctuation in ant occupancies is not entirely regular; although the two *Solenopsis* species have always peaked in summer or autumn, and *C. opuntiae* peaked in winter or spring in 5 of 8 site 3 year combinations (Fig. 1; B. Sullender, *unpublished manuscript*), the peak of *C. opuntiae* was delayed until summer in the year 2004 (Fig. 1), perhaps because the winter of 2003–2004 was relatively cool and wet in Tucson. Nonetheless, the princim372()-317857uctuationsum;roun341(o724; -15een)-2aetions

appeared at the next site to the east (the UT site) in the early autumn of 2004, and was still at low frequency at the time of our most recent survey. We have still never observed it at the easternmost (BG) site. Surveys of sugar and protein baits (J. H. Ness, *unpublished data*) support the hypothesis that *S. xyloni* has lately arrived at the UT site and is still absent from the BG site (and not that it is present but choosing not to forage at barrel cactus nectaries). One factor that may be contributing to the spread of *S. xyloni* is the increased suburbanization that has occurred around the Desert Laboratory as the City of Tucson has expanded. *S. xyloni* has been reported to be frequent in human-disturbed habitats (Wisdom and Whitford 1981, Hopper and Rust 1997).

The second obvious pattern in Fig. 1 is that the fraction of barrel cacti tended by each ant species changes

sive to intermediate- or high-frequency driving oscillations. Underdamped systems are characterized by equilibria having complex eigenvalues with negative real part. (In contrast, overdamped equilibria have negative, purely real eigenvalues.) Because complex eigenvalues are in general easier to obtain in three-species than in two-species competitive systems, this raises the interesting possibility that the invasion of a third competitor into a nonresonant two-competitor system could create resonance, and cause the three-species system to oscillate at a different (notably, higher) frequency than the two-species system.

However, the mere existence of complex eigenvalues is not sufficient evidence for resonance. Rather, the damped oscillations must be sufficiently persistent that they can be amplified by environmental forcing. A standard measure of the persistence of damped oscillations is the so-called ''coherence number'' n_c, which gives the number of cycles following a perturbation before their amplitude is reduced by a factor of $1/e$ (where e is the base of natural logarithms). A three-species system will have at most two complex eigenvalues (plus a third purely real eigenvalue), occurring as the complex conjugate pair $\lambda_{1,2} = a \pm bi$, where $a < 0$ if the equilibrium is stable. As b gives the angular frequency of the damped oscillations (measured in radians per unit time), their frequency (measured in cycles per unit time) is $b/2\pi$. The time required for the oscillations to reach a relative amplitude of $1/e$ is $1/|a|$. Hence the coherence number (frequency × time) is $n_c = b/2\pi|a|$. Significant resonance requires that $n_c > 1$ (Nisbet and Gurney 1982).

RESULTS

Potential mechanisms of seasonal displacement of competitors

Eq. 1 illustrates three mechanisms that can cause competitors to be seasonally differentiated. For simplicity, we consider the two-species model obtained by setting F_3 in (Eq. 1a, b). The first possibility is that only one species experiences seasonal forcing, and the second is driven to fluctuate by competitive interactions with the first (Fig. 2A). The second possibility is that both competitors have forced rates, but with seasonally opposing patterns of forcing (Fig. 2B). These two mechanism may be very difficult to distinguish from the patterns of fluctuation alone; seasonally opposed forcing results in only a slight increase in the cycle amplitudes and a slightly more rapid turnover in occupancy between seasons (Fig. 2). The third possibility is that both species experience the same seasonal pattern of forcing, but that the superior competitor displaces the other species into a ''nonpreferred'' temporal pattern (Fig. 3). The seasonal pattern that the inferior competitor would exhibit in isolation (Fig. 3A) can be
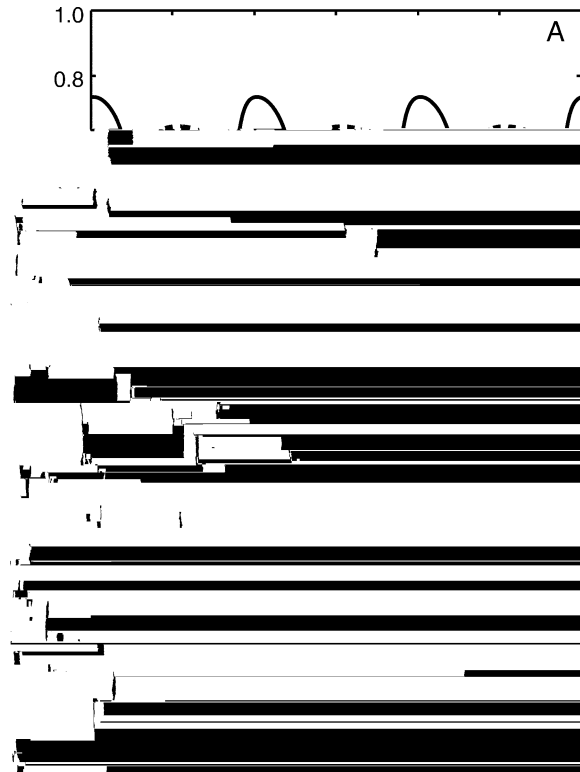

FIG. 2. Seasonal fluctuations in ant occupancies. (A) Only species 1 (solid line) experiences direct seasonal forcing of its colony expansion rate. Species 1 is the competitive dominant, but species 2 (dashed line) has a higher average colonization rate. (B) Both species' colony expansion rates are seasonally forced, species 1 with a peak on 1 February and species 2 with a peak on 1 August. Variables: s, species; a, abandonment; d, displacement; c, colonization. Parameter values for Eq. 1a, b: $s_1 = s_2 = 0.01$, $a_1 = a_2 = 0.2$, $d_{12} = 0.1$, and (A) $c_1 = 0.4 \pm 0.4$, $c_2 = 0.6$, or (B) $c_1 = 0.4 \pm 0.4$, $c_2 = 0.6 \pm 0.6$ (maximum deviation above or below the mean) ($F_3 = 0$).
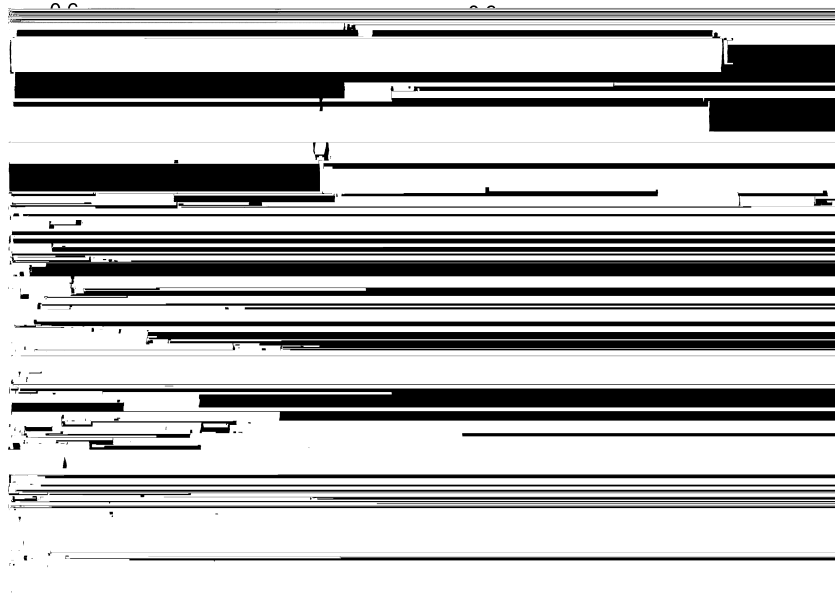
FIG. 5. Invasion dynamics of Eq. 1 with a rock–paper–scissors competitive hierarchy. The overall rate of displacement increases from (A) to (B) to (C). The colony expansion rate of species 1 (solid lines) was forced at two frequencies: one cycle per year and one cycle per week, with the weekly cycle having only 20% of the power of the annual cycle. Species 2 (dotted lines) is displaced by species 1, but has a higher average colony expansion rate. Species 3 (dashed lines), which is inferior to species 2 but dominates species 1, invades at the midpoint of each panel. Invasion-induced resonance at the higher forcing frequency occurs only in (C). (D) is a blowup of the final year of (C). Parameter values are as in Fig. 4, except: $c_1 = 0.2 \pm 0.2$ (maximum deviation above or below the mean), $d_{13} = 2d_{12}$, $d_{23} = d_{12}$, and $d_{12} = $ (A) 0.4, (B) 0.8, or (C) 2.4.

to persist as the three species displace one another sequentially).

To further illustrate the results in Fig. 4, we forced Eq. 1 at two frequencies, an annual cycle corresponding to seasonality, and a weaker, weekly cycle that might mimic the influence of small weather systems superimposed on the seasonal cycle. When an overdamped two-species system is invaded by an intransitive competitor, the three-species system does not deviate from the lower frequency driving oscillation, provided the overall rates of displacement are low (Fig. 5A, B). But when displacement is frequent overall, invasion of the third competitor diverts the system so that it now follows closely the weaker, higher frequency driving oscillation that is closer in frequency to the system's natural frequency (Fig. 5C); the preexisting seasonal cycle is almost entirely obliterated (Fig. 5D). The sequence of transfer functions corresponding to Fig. 5A–C shows that as displacement rates increase overall, the potential for amplification of environmental fluctuations becomes concentrated on an increasingly narrow range of increasingly high frequencies (Fig. 6); when the peaks of the transfer functions coincide with the frequency of a particular driving oscillation, resonance occurs and the driving oscillation is greatly amplified. Because significant resonance can only occur at high driving frequencies, the competitor invasion dampens, rather than amplifies, the annual driving oscillation (Fig. 5).

The other model parameters also influence whether resonance will occur for a given set of displacement rates. For example, the invader's colony expansion and abandonment rates must be not too different from one another (Fig. 7); otherwise, the invader's occupancy will either be always too high or always too low to allow the occupancies of all three species to resonate substantially.

Effects of interspecific differences in environmental forcing in hierarchical competitive systems

Even when competition is hierarchical rather than intransitive, interspecific differences in the pattern of environmental forcing can strongly influence the consequences of the invasion of a dominant competitor. For example, Fig. 8 illustrates three cases in which the competitive hierarchy (species 3 . species 1 . species 2) and the means of all model parameters are identical, but the patterns of forcing differ. When the invader is forced, but with a seasonal pattern that is offset from that of the dominant resident, prominent annual cycles in species 1 and 3 persist because the season in which the invader does poorly allows species 1 to recover, but species 2 is largely suppressed (Fig. 8A). In contrast, if the invader experiences no direct seasonal forcing, it cycles at intermediate occupancies with species 2, and species 1 (which is more strongly displaced by
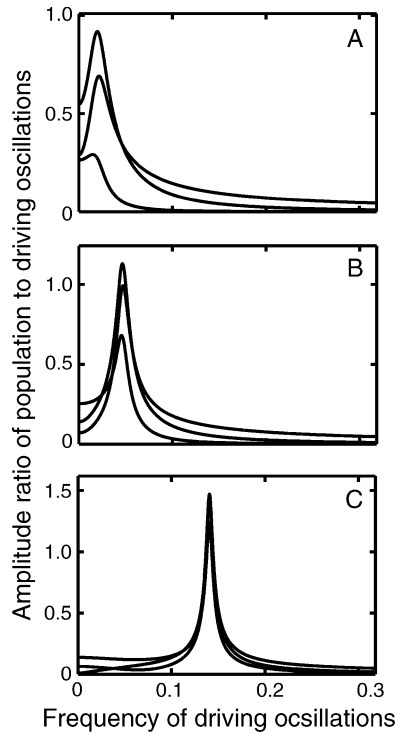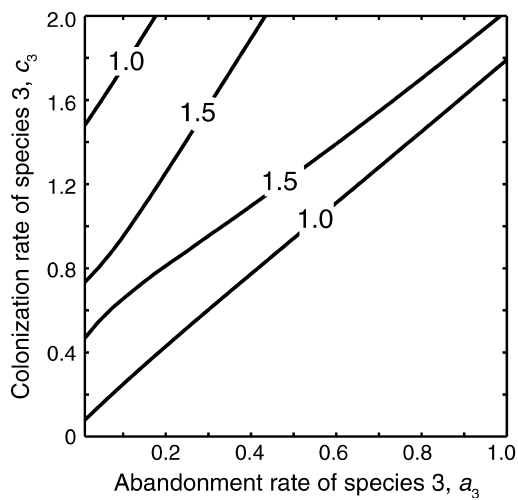
FIG. 6. Transfer functions (Eq. 2) for the corresponding panels in Fig. 5. Frequency is measured in cycles per day. Curves with highest to lowest peaks correspond to species 2, 1, and 3, respectively. The frequency of the peak in (C) corresponds to a period of 7.1 days. An annual oscillation has a frequency of 0.00274 cycles/d.
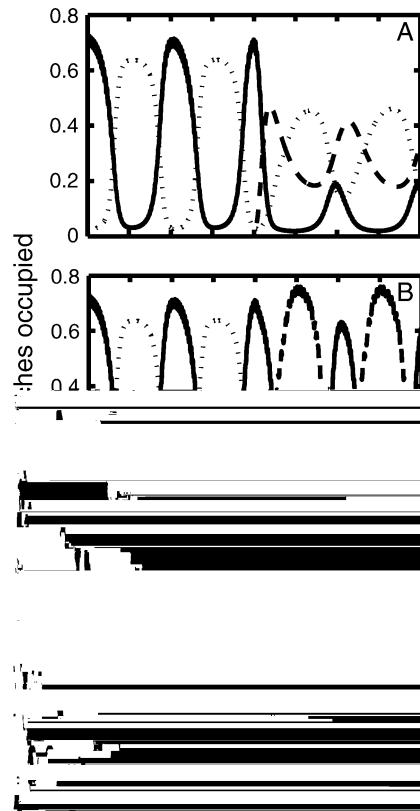

FIG. 8. Influence of environmental forcing when the invader (species 3, dashed line) is competitively superior to both resident species and species 1 (solid lines) displaces species 2 (dotted lines). (A) Species 2 is unforced, but species 1 and 3 experience strong (but seasonally displaced) forcing of their colony expansion rates: $c_1 5 0.4 6 0.4$ (maximum deviation above or below the mean), $c_3 5 0.5 6 0.5$. (B) Species 1 and 2 are as in (A), but species 3 is insensitive to seasonal forcing ($c_3 5 0.5$). (C) Weak forcing of species 1 only ($c_1 5 0.4 6 0.02$). Other parameter values: $c_2 5 0.6$, $s_1 5 s_2 5 s_3 5 0.01$, $a_1 5 a_2 5 a_3 5 0.2$, $d_{12} 5 0.1$, $d_{13} 5 20.2$, and $d_{23} 5 20.02$. Low- and high-frequency environmental forcing are present, as in Fig. 5, but no invasion-induced resonance occurs in this hierarchical competitive system.

FIG