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Maintaining Diversity in an Ant Community: Modeling, Extending, and Testing the Dominance-Discovery Trade-Off

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ABSTRACT: Ant communities often consist of many species with apparently similar niches. We present a mathematical model of the dominance-discovery trade-off, the trade-off between the abilities to find and to control resources, showing that it can in principle facilitate the coexistence of large numbers of species. Baiting studies of dominance and discovery abilities in an ant community from the Chiricahua Mountains of Arizona indicate that real communities fail to fit the assumptions of the simple model in several ways: (1) dominance depends on the size of the food resource; (2) for some ants, dominance depends on the presence or absence of specialist parasitoids; (3) pairwise dominance is not an all-or-nothing trait; and (4) a consistent negative relationship between pairwise differences in per capita discovery rates and dominance can be detected for only one bait type. Extended models incorporating these factors successfully predict the coexistence of five of the six most abundant members of this community but fail to accurately predict their relative abundances. Sensitivity analysis indicates that each complicating factor enhances the extent of coexistence.

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Many ecological studies are inspired by Hutchinson's simple question, "Why are there so many kinds of animals?" (Hutchinson 1959). The formalization of the principle of competition exclusion (Levin 1970; Armstrong and McGehee 1980) clarified the conditions under which a single species would dominate and has inspired both empirical and theoretical ecologists to search for the mechanisms maintaining biodiversity. Communities of ants, well known for being structured by competition (Hölldobler and Wilson 1990), provide an excellent testing ground for the mechanisms that can promote coexistence.

Even among ants that share the same general type of resource, careful study may find essentially no overlap in the resources used (Andersen et al. 2000). In other systems, ants coexist through different but overlapping preferences based on type of food (Morrison 2000) or size of prey (Cerdá et al. 1998a; McGlynn and Kirksey 2000). Species can differ in many other niche dimensions, such as preferred time of day for foraging (Albrecht and Gotelli 2001), thermal tolerance (Cerdá et al. 1997, 1998b; Bestelmeyer 2000; Morrison et al. 2000), or ability to cope with leaf litter (McGlynn and Kirksey 2000).

Ants exhibit both exploitation and interference competition, and the interaction between these traits can promote coexistence. In some cases, dominant ants dominate superior food sources, even when those foods are preferred by subordinate ants in their absence (Sanders and Gordon 2000, 2003; Dietrich and Wehner 2003). In other cases, the dominance-discovery trade-off (Davidson 1998) describes communities where those ants best at discovering and collecting food are defeated in direct conflict. Several studies have shown the existence of dominance hierarchies (Savolainen and Vepsalainen 1988; Savolainen 1990; Basu 1997), with a few showing a negative relationship between dominance and discovery (Fellers 1987; Holway 1999). The violation of the dominance-discovery trade-off by invasive species like the Argentine ant can lead to a nearly complete loss of ant diversity (Human and Gordon 1996; Holway 1999). Experimental removal of a dominant ant,

at least in the short term, may affect only closely related species (Gibb and Hochuli 2004) or may produce major changes in community diversity (Vepsalainen et al. 2000).

Palmer and colleagues have described a particularly compelling story of coexistence in African acacia ants (Stanton et al. 2002; Palmer 2003, 2004). Dominance depends on colony size, and colony size depends in part on resource availability. Subordinate species coexist by specializing on low-resource sites and through an advantage in colonizing new trees, as in the competition-colonization trade-off (Tilman 1994; Adler and Mosquera 2000).

Both discovery and dominance can be altered by specialized natural enemies (Feener 2000). The presence of parasitoids can vastly reduce resource collection (Morrison 1999) or the number of foragers allocated to tasks outside the nest (Mehdiabadi et al. 2004). Dominant ants can lose their position when beset by parasitoids (Feener 1981; Feener and Brown 1992; LeBrun 2005), although the effects may be small (Morrison et al. 2000) or even absent (Morrison 1999; Orr et al. 2003).

An earlier study of the system modeled in this article (LeBrun and Feener 2002) revealed two main interactions with parasitoids. First, the dominant ant *Pheidole diversipilosa* is far more likely to lose baits when parasitoids are present. Second, parasitoids are more likely to be attracted to *P. diversipilosa* during conflicts over baits.

The general framework for our model derives from verbal models of competing ants (Feener 2000; LeBrun 2005). Our model for the dominance-discovery trade-off extends models of the competition-colonization trade-off (Tilman 1994; Adler and Mosquera 2000) in several ways. First, we incorporate baits of different sizes, thereby including resource heterogeneity. Second, we include specialist natural enemies, which have been shown to enhance coexistence (Adler and Muller-Landau 2005) but have rarely been considered in models that include other trade-offs (Chave et al. 2002). Third, we include behavioral responses by the targets of these parasitoids, in the form of altered dominance. Models of such trait-mediated interactions among competing prey that share predators have tended to focus on communities with only a handful of species (Bolker et al. 2003).

Our broad goal in this article is to examine models and data describing how species interact with each other, their resources, and their parasitoids in order to understand whether such interactions are sufficient to explain patterns of persistence and abundance. Our specific goals in this article are threefold: first, to model the basic dominance-discovery trade-off in the absence of parasitoids and other complicating factors; second, to use field data to incorporate the effects of parasitoids, baits of different sizes, and nontransitive dominance hierarchies into the basic model; and third, to predict the coexistence and abundance of competing species of ants from fully parameterized models, compare with the measured abundance, and test which components of the model promote coexistence.

Modeling the Dominance-Discovery Trade-Off

Can a trade-off between dominance and discovery maintain diversity in an ant community? In this section, we present simple models to demonstrate that it can, and we investigate how the pool of available species affects the patterns of abundance in the resulting community.

Our model follows the fate of food patches (referred to as "patches") from their appearance (e.g., the death of a cricket) through discovery by one species of ant, possible usurpation by other ants, removal by other foragers, such as birds or rodents, collection, and conversion into new ants. Suppose that patches appear at rate σ. Ant species are indexed by their per capita discovery rate r, chosen from the range $r_{\min} \leq r \leq r_{\max}$, which represents the available species pool. If we denote the number of ants of the species with per capita discovery rate of r as $N(r)$, that species will discover any given patch at rate $rN(r)$. Let p_0 represent the number of undiscovered patches and $p(r)$ be the number of patches controlled by the species with per capita discovery rate r. All patches are discovered and removed at a per patch rate of b by foragers other than ants.

After discovering a food patch, an ant species harvests the resource at rate $c(r)$, producing a mean time of $1/c(r)$ for resource retrieval. During that time, the colony could lose the patch in two ways. First, the patch could be removed by other foragers at the rate b. Second, the patch could be taken over if discovered by a more dominant species of ant. In the basic models, we assume the existence of a simple form of the dominance-discovery trade-off. In particular, a species with a lower per capita discovery rate r is assumed to be completely dominant over a species with a higher r, as in simple models of the competition-colonization trade-off (Tilman 1994).

The number $N(r)$ of ants increases at a rate proportional to the resource harvest rate (the product of the harvest rate $c(r)$ and number of patches controlled by that species) and the quality of the resource ε. We assume that its increase is inversely proportional to the mass $w(r)$ of ants in order to translate biomass harvested into number of ants. It decreases because of deaths at per capita rate μ, which we assume to be the same for all species.

With these assumptions, the dynamics obey

$$\frac{dp(r)}{dt} = rN(r)p_0 - \left[\int_{r_{min}}^{r} uN(u)\,du\right]p(r)$$

$$+ rN(r)\left[\int_{r}^{r_{max}} p(u)\,du\right] - bp(r) - c(r)p(r),$$

$$\frac{dp_0}{dt} = \sigma - \left[\int_{r_{min}}^{r_{max}} uN(u)\,du\right]p_0 - bp_0, \qquad (1)$$

$$\frac{dN(r)}{dt} = \frac{\varepsilon c(r)p(r)}{w(r)} - \mu N(r).$$

The variables and parameters in this model are summarized in table 1.

The model differs from those of the competition-colonization or competition-mortality trade-off (Tilman 1994; Adler and Mosquera 2000) in several ways. First, food patches are much more ephemeral than ant colonies, unlike habitat patches, which persist longer than the individuals that inhabit them. Second, the number of patches depends on the discovery rates, collection rates and weights of the ants in the community rather than being imposed externally.

In the simplified case where $c(r)$ and $w(r)$ are constant, meaning that all species have identical collection rates and masses, we can solve for the equilibrium populations using extensions of the methods presented by Adler and Mosquera (2000). For a given r_{max}, there is a minimum per capita discovery rate r_1 that can persist (app. A in the online edition of the *American Naturalist*). If $r_{min} \leq r_1$, the community is not constrained by available species, and

$$p(r) = \frac{p_0 r_{max}}{2} r^{-3/2},$$

$$N(r) = \frac{\varepsilon c}{\mu w} p(r)$$

for $r_1 \leq r \leq r_{max}$. The value of p_0 can be found algebraically (app. A). The model thus predicts that the most dominant species present controls the most patches (fig. 1*A*), and, in this symmetric case where population size is proportional to the number of patches controlled, is also the most abundant. However, the most dominant available species (that with the per capita discover rate r_{min}) may not persist because of exploitation competition from species with high per capita discovery rates.

If $r_{min} > r_1$, the community is constrained by lack of highly dominant species. The most dominant available species excludes species with slightly higher per capita discovery rates, thus breaking the community into two separate species groups (fig. 1*B*). Removing species with high per capita discovery rates from the species pool allows species with lower per capita discovery rates to persist and leads to a community with fewer but more dominant ants and a higher crop of standing resources (fig. 1*C*).

The model can be simulated with a discrete set of species (fig. 2*A*). In this example, a slight decrease in the per capita discovery rate of the most dominant species leads to its extinction and a community with much lower overall diversity dominated by a species with a higher per capita discovery rate (fig. 2*B*). A slight increase in the per capita discovery rate of the most dominant species, however, enhances its dominance, drives the second most dominant species to extinction, and changes both the identities and the abundances of the less dominant species (fig. 2*C*).

This basic model shows that many species can, in principle, coexist solely through a dominance-discovery trade-off. When the species pool includes all possible per capita discovery rates in some range, the least dominant species (that with the higher per capita discovery rate) will always persist, while the most dominant persisting species depends on the per capita discovery rate of the least dominant species. This contrasts with the findings on the competition-colonization trade-off, where the most dom-

Table 1: Variables and parameters in the basic model

Symbol	Description	Values in simulations
$p(r)$	Number of patches controlled by species with discovery rate r	
p_0	Number of patches not yet discovered	
$N(r)$	Number of ants of species with discovery rate r	
ε	Ants produced per food patch	1 or 10[a]
b	Patch removal rate by other agents	.001/min[b]
$c(r)$	Harvest rate by ants with discovery rate r	See table 2
$w(r)$	Mass of ant with discovery rate r	See table 2
μ	Mortality rate of ants	1/yr[c]
σ	Patch renewal rate	.001/min[b]

[a] Estimated from the two sizes of cricket bait used: small crickets (second- and third-instar nymphs) and large crickets (adults).

[b] Patches are assumed to appear about once per day and last 1 day.

[c] Gordon and Hölldobler 1987; Billick 2003.
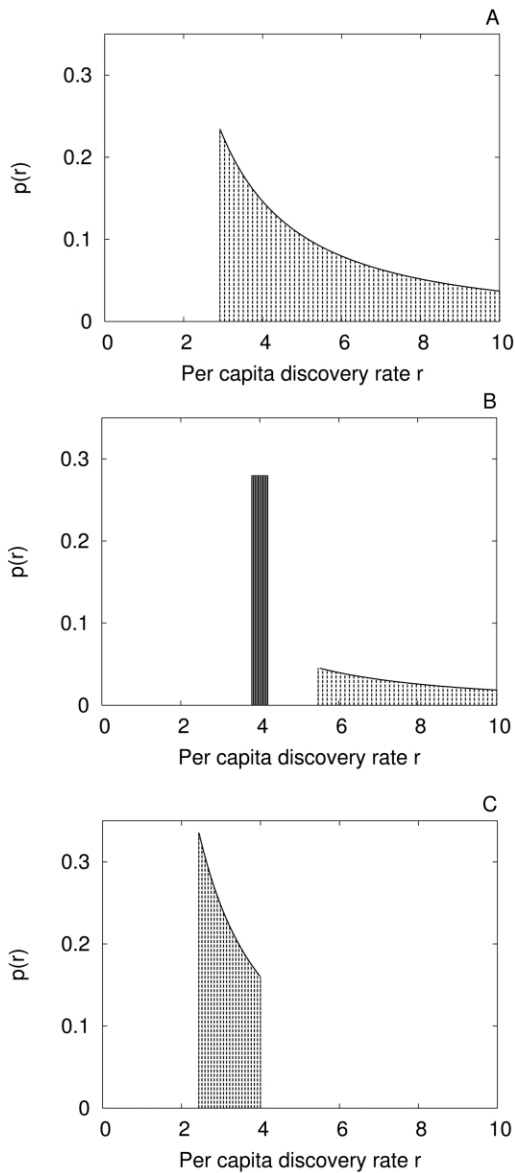
Figure 1: Equilibrium of the equation (1) with $b = c = \epsilon = \mu = \sigma = 1$. With $r_{max} = 10$, the most dominant persisting species has per capita discovery rate $r = r_1 = 2.919$. *A*, With $r_{min} = 2.0 < r_1$. In this case, $p_0 = 0.37$ at equilibrium, and the total scaled number of ants is 0.630. *B*, With $r_{min} = 4.0 > r_1$, we find $r_3 = 5.48$. In this case, $p_0 = 0.37$, $Q_{min} = 0.185$ (the scaled number of ants from the species with $r = r_{min}$), and the total scaled number of ants is 0.315. The bar centered at $r = 4.0$ represents the point mass at this most dominant species. *C*, With $r_{max} = 4.0$, $r_1 = 2.438$. In this case, $k = 1.28$, $p_0 = 0.640$ at equilibrium, and the total scaled number of ants is 0.360.

due to preemption (Calcagno et al. 2006), which allows less dominant species to persist, and to the patch dynamics such species generate. Finally, when the species represent a discrete subset of possible per capita discovery rates, the patterns of coexistence can be highly idiosyncratic.

This basic model makes many simplifying assumptions. First, finding general results when $c(r)$ and $w(r)$ are functions of r is analytically intractable except in a few special
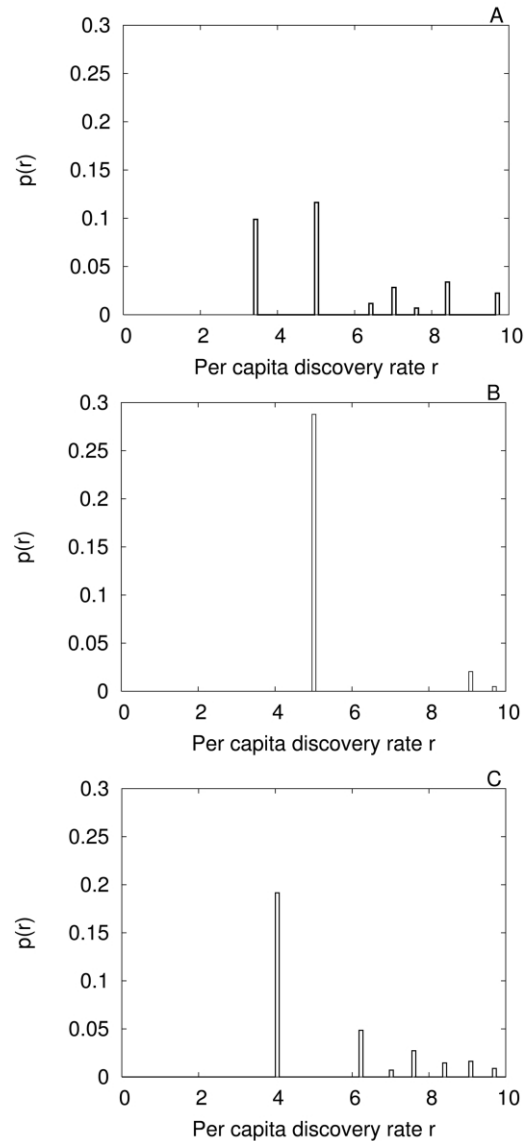
Figure 2: Equilibrium of the basic model with $b = c = \epsilon = \mu = \sigma = 1$ and a finite pool of 11 species with randomly generated per capita discovery rates 3.43, 5.01, 5.61, 6.23, 6.42, 7.02, 7.61, 7.67, 8.41, 9.09, and 9.70. *A*, The seven persisting species with the given species pool. *B*, With the lowest discovery rate, 3.43, reduced to 2.85. *C*, With the lowest discovery rate, 3.43, increased to 4.05.

inant species is unaffected by less dominant species (Tilman 1994). In this model, a species with rapid discovery can completely remove food patches before they can be found by the more dominant species. This result is thus

Table 2: Parameters for focal ants

Species[a]	Dry mass[b] (mg)	Small bait retrieval[c] (min)	Fixed bait retrieval[c] (min)	Trapped[d]	Missed[d]	$\hat{\lambda}$[e]
Formica gnava (Fg)	1.09	2	800	48	5	.00177
Monomorium emersoni (Me)	.03	240	800	21	9	.00344
Myrmica sp. (My)	.89	5	800	10	3	.00196
Pheidole bicarinata (Pb)	.05	120	400	11	4	.00111
Pheidole diversipilosa (Pd)	.12	120	400	56	4	.00148
Pheidole perpilosa (Pp)	.20	15	300	6	4	.00152

[a] Abbreviations are those used in figures 4 and 5.

[b] From LeBrun (2005).

[c] The time taken to completely harvest a bait; simplified from LeBrun (2005) or estimated from personal observation.

[d] Number of baits where discovering ant was trapped or missed in the paired pitfall trap, out of a total of 226 such pairs.

[e] Computed with equation (2) in discoveries per ant per minute.

cases (results not shown). In reality, we see no reason to expect that the resource collection rate or the mass of ants would depend on the per capita discovery rate in a simple way. Second, we assume that a slightly more dominant type always excludes a slightly less dominant type. Adding even a small amount of uncertainty to these interactions changes the predicted community structure in a model of the competition-mortality trade-off in plants and can greatly reduce the predicted degree of coexistence (Adler and Mosquera 2000), which can be infinite without such uncertainty (Tilman 1994). Even this form of uncertainty maintains the assumption that interactions are transitive. In contrast, intransitive interactions can enhance diversity (Frean and Abraham 2001). Finally, the model includes only one patch type, and foragers work under only one set of environmental conditions. As noted in the introduction to this article, different patches might be more or less difficult for different species to collect, and environmental conditions, such as temperature, humidity, and the presence of specialist parasitoids, can alter the dominance rankings and potentially increase standing diversity.

Parameter Estimation and Simulations

Study System

The study site and methods are described in detail in LeBrun (2005). Briefly, 28 grids of 12 bait stations each were established, and baits were followed for 3 h during daylight. Two types of baits were used: small crickets that could be retrieved by a single worker or a small number of workers of any species and larger, fixed crickets that were pinned to the ground to simulate immobile resources. To estimate local abundance, baits were paired with pitfall traps placed at each bait location 48 h after the baiting trial. Baits were used, as detailed below, to estimate both discovery rates and dominance.

Six of the most abundant ants in this community were chosen from the nine studied in LeBrun (2005). The excluded ants were *Camponotus sansabeanus*, *Dorymyrmex smithi*, and *Temnothorax neomexicanus*. *Camponotus sansabeanus* forages with roughly equal intensity during the day and at night and shows little aptitude for defending or collecting the baits used in this study (E. G. LeBrun, unpublished data), *Dorymyrmex smithi* occurs primarily in habitats more open than those considered in this study (Andersen 1997), and *T. neomexicanus* is an insinuator that is not directly involved in the dominance-discovery trade-off (Hölldobler and Wilson 1990; LeBrun 2005).

Key aspects of the foraging biology of the six remaining ants are presented in table 2. *Pheidole bicarinata* and *P. diversipilosa* have specialist phorid fly parasitoids. *Formica gnava* is a solitary forager, *Myrmica* is a moderate recruiter, and the others are mass recruiters (LeBrun 2005).

Estimation of Per Capita Discovery Rates

We used pitfall trap data paired with baiting trials to estimate per capita discovery rates. For each bait, the discovering species and the time of discovery were recorded. We removed all baits from further consideration if the discovering species was not found in the paired pitfall trap (table 2), and we assumed that this created no bias because the overall fraction of such baits is small, even though Fisher's Exact Test (R Development Core Team 2005) does detect a significant difference across species ($P = .004$).

For the remaining baits, indexed by i, the data for species j are summarized in three measurements: (1) n_{ij} is the number of ants trapped; (2) f_{ij} is an indicator, with $f_{ij} = 1$ meaning that species j discovered the bait and $f_{ij} = 0$ that it did not; and (3) t_{ij} gives the time to the first event, whether a discovery by species j or by some other species. When no ants found bait i in 3 h, $t_{ij} = 180$ and $f_{ij} = 0$
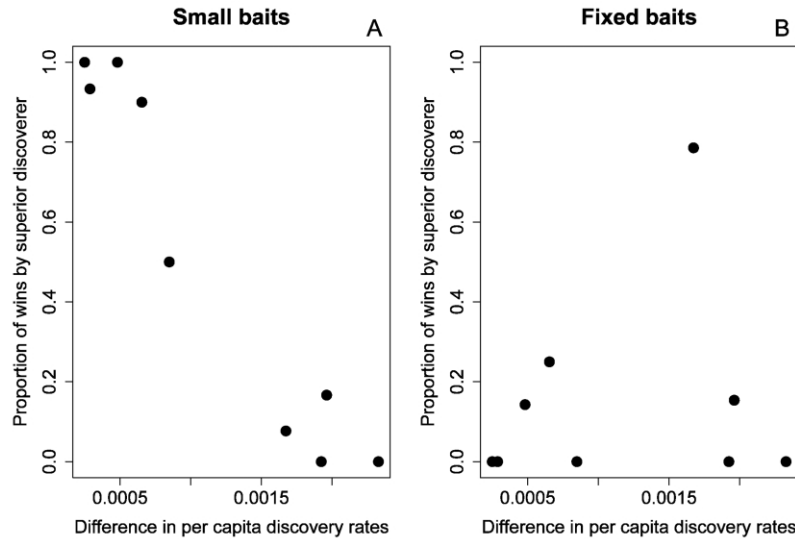
Figure 3: Relationship between the difference in estimated per capita discovery rates and the probability of a win at small baits (*A*) and fixed baits (*B*), both in the absence of parasitoids. Each symbol represents a given pair of species for which more than one dominance encounter was recorded. Pairs were used only once based on the order in table 2. In *B*, the exceptional pair is *Monomorium emersoni* and *Formica gnava*.

for all *j*. In the few cases where two species discovered the bait simultaneously, both were given $f = 1$.

For species *j*, we estimate the per capita discovery rate λ_j by maximizing the likelihood

$$L(\lambda_j) = \prod_i (\lambda_j n_{ij})^{f_i} e^{-\lambda_j n_{ij} t_{ij}},$$

under the assumptions that bait trials are independent, that ants search for baits independently, and that pitfall traps provide an unbiased estimate of the number of searching ants (Andersen 1991; Bestelmeyer 2000). The maximum occurs at

$$\hat{\lambda}_j = \frac{\sum_i f_{ij}}{\sum_i n_{ij} t_{ij}}, \qquad (2)$$

with results summarized in table 2.

Estimation of Dominance

When two species interacted at a bait, a species scored a "win" if it either expelled the other from the bait or retained a bait when challenged by another species. The other species scored a "loss" (LeBrun 2005). Matrices describing these interactions were separated by bait type (small or fixed) and by the presence or absence of parasitoids and are presented in LeBrun (2005).

Use of Parameter Values in the Simulations

The data demand two extensions of the basic model (eq. [1]). First, there are effectively four bait types, with distinct dominance hierarchies depending on bait type and on the presence or absence of parasitoids. Second, the dominance matrices may deviate from the expectation that a species with a higher per capita discovery rate will lose interference interactions with species with a lower per capita discovery rate (see table 2 in LeBrun 2005). There are nine pairs of species for which there are at least two recorded interactions. On fixed baits, the species with the higher discovery rate wins a minority of encounters in eight cases out of nine (fig. 3*B*; $P = .02$ with a one-tailed sign test), meeting the expectation. On small baits, as expected, the pattern is less clear. A dominance-discovery trade-off provides a meaningful way to partition resources only for large food items. For small items, discovery is equivalent to dominance because they are quickly retrieved intact. In the four pairs where the difference in discovery is large, the species with the higher discovery rate wins only a small minority of encounters (fig. 3*A*), but all such pairs involve the single species *Monomorium emersoni*.

To extend the model, let p_{ij} represent the number of patches of bait type *i* controlled by species *j* with number of ants N_j, and let p_{i0} represent the number of patches of type *i* not controlled by any ant species. Let a_{ijk} be the probability that ant species *k* takes over such a bait from species *j* conditional on encounter, c_{ij} be the rate of collection of bait type *i* by species *j*, w_j be the mass of species

j, and ε_i the value of bait type i. The model extensions result in the system

$$\frac{dp_{ij}}{dt} = \lambda_j N_j p_{i0} - \left(\sum_k \lambda_k a_{ijk} N_k\right) p_{ij}$$

$$+ \lambda_j N_j \sum_k a_{ikj} p_{ik} - b p_{ij} - c_{ij} p_{ij},$$

$$\frac{dp_{i0}}{dt} = \sigma - \sum_j \lambda_j N_j p_{i0} - b p_{i0}, \qquad (3)$$

$$\frac{dN_j}{dt} = \sum_i \frac{\epsilon_i c_j p_{ij}}{w_j} - \mu N_j.$$

Simulations of this system of differential equations were run in Matlab until an equilibrium was reached. Because of the very different timescales of patch dynamics and worker replacement, we assumed that the number of workers remained at a quasi-steady state (i.e., that $dN_j/dt = 0$). Although this is the reverse of the usual approach (which sets fast variables to their quasi–steady state values), we are here interested only in the equilibrium values that are approached much more quickly with this method.

The values of c (the patch collection rate) and w (the mass of a worker) are derived from table 2. We roughly estimated b and σ to be 0.001/min, meaning that new food patches appear and are collected by other foragers at a rate of about 1/day. We used $\varepsilon_i = 1$ for small crickets and $\varepsilon_i = 10$ for fixed crickets.

To take into account the uncertainty in the estimates of the per capita discovery rates and the dominance matrix, we bootstrapped the underlying data. In particular, for the per capita discovery rate, we sampled the baits with replacement and used equation (2) to compute $\hat{\lambda}_j$. For the dominance matrix $\mathbf{a}$, we resampled the events underlying the number of wins and losses and computed a_{ijk} as the fraction of wins by species k. For those elements of the matrices with no observations, we set a_{ijk} to one of the three values 0, 0.5, and 1.0 in the runs.

The simulations also require estimating the fraction of baits in each category. Using the data in LeBrun (2005), we estimated that parasitoids appeared in 40% of baiting trials. The actual fraction of patches that resemble small baits is unknown, and we used values of 0.5, 0.8, and 0.9 in the simulations. We ran 10 replicates for each parameter combination tested.

Comparison of Simulations with Data

The simulations can be used to test a range of scenarios. In our best guess of the parameters, we assumed that parasitoids would appear at 40% of food sources (independent of bait size), and we compared 10 replicates with each of three values for the fraction of small patches (0.5, 0.8, and 0.9) and three values for missing elements of the dominance matrix (0, 0.5, and 1).

Our model incorporates two forms of patch heterogeneity (food size and presence or absence of parasitoids), along with variation in dominance and discovery ability. Although these factors can support coexistence theoretically, what do they predict with the parameter values for the six focal species in this study?

We compared the prevalence and abundance of each species in the simulations and the actual data. For the data, abundance is the mean number of ants per pitfall trap and prevalence is the fraction of pitfall traps occupied. In the simulations, both abundance and prevalence are computed from the set of simulations with bootstrapped values of λ and the dominance matrix $\mathbf{a}$ pooled over the three values of the fraction of small patches.

With our best guess of the parameters, the simulations predict the coexistence of five out of the six focal species. However, the predicted and observed abundances fail to match closely (fig. 4).

We compared these results with six other cases: (1) small baits only, (2) fixed baits only and no parasitoids, (3) fixed baits only and parasitoids always present, (4) a mix of small and fixed baits but no parasitoids, (5) no dominance (setting $a_{ijk} = 0.5$ for all i, j, and k), and (6) no takeovers (setting $a_{ijk} = 0$ for all i, j, and k).

Restriction to small baits, which are collected efficiently by the solitary forager *Formica gnava*, leads to near domination by this species (fig. 5*A*). In contrast, restriction to fixed baits in the absence of parasitoids leads to coexistence of the three species of *Pheidole* that are effective mass recruiters (fig. 5*B*). With fixed baits, the presence of parasitoids reduces the abundance of the highly vulnerable *Pheidole diversipilosa* and allows coexistence of *Monomorium*, the other small mass-recruiting ant (fig. 5*C*). In the absence of parasitoids, a mixture of small and fixed baits again allows coexistence of the three *Pheidole* species, but now with the addition of the larger *F. gnava* (fig. 5*D*). In the absence of a dominance hierarchy of any sort, *Monomorium* is predicted to nearly dominate the landscape (fig. 5*E*). Finally, allowing no successful takeovers (as with strong priority effects [Yu and Wilson 2001]) predicts coexistence of the four smaller species (fig. 5*F*).

Discussion

Simplified models of a trade-off between the per capita discovery rates of ants and their ability to dominate food baits predict a high degree of coexistence in ant communities. When the species pool includes all species within a given range of per capita discovery rates, the species with
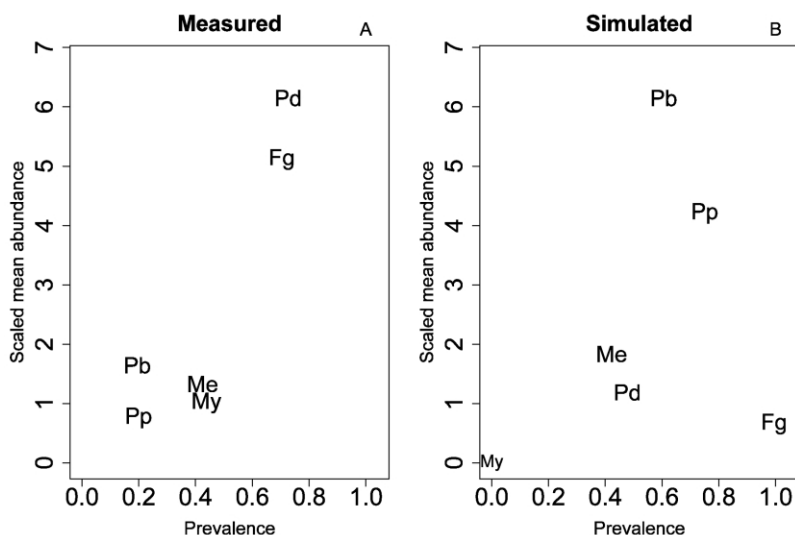
Figure 4: Comparison of measured (*A*) and simulated (*B*) patterns of abundance and prevalence. Simulations assume that 40% of baits harbor parasitoids and combine 10 replicates with each of the nine combinations of parameters describing the fraction of patches resembling small baits (0.5, 0.8, and 0.9) and the missing elements of the dominance matrices (0, 0.5, and 1). The maximum number of ants in the simulation is scaled to match the maximum measured number. See table 2 for species abbreviations.

the highest such rate always persists because it can often harvest patches before the slower, more dominant species appear. The identity of this species determines the most dominant (lowest per capita discovery rate) species that can persist, showing that the composition of the community depends on both exploitation and interference competition. This contrasts with results on models of the competition-colonization trade-off, where the persistence of the most dominant competitor is independent of the identity of the least dominant one.

When highly dominant species are absent from the species pool, the community breaks into two pieces: an abundant dominant species and a separate continuum of less dominant species. If the species pool includes only a discrete subset of the per capita discovery rates, the persistence of each individual species depends sensitively and unpredictably on the pool of available species.

On the basis of observations of the discovery and dominance characteristics of a set of six ant species, we extended this model to test whether we could predict coexistence and abundance. The model incorporates data on different sizes of baits, changes in dominance induced by the presence of specialist parasitoids on two of the species, and the complex relationship between differences in per capita discovery rate and the dominance interaction across all pairs of species.

The extended model predicts the coexistence of five out of the six species. The missing species, *Myrmica* sp., is not

an effective mass recruiter and may be governed by a trade-off missing from this model. However, the relative abundances fail to match those seen in the field. The abundances are sensitive to some of the most uncertain parameters in the model, those describing the dynamics, distribution, and relative value of resources. Reducing the diversity of resources or the variability induced by parasitoids or simplifying the structure of the dominance matrices generally reduces the predicted equilibrium diversity in the community.

Our models fail to capture two potentially important aspects of *Pheidole perpilosa*. Unlike the other five ants considered, this species forages largely during the night (E. G. LeBrun, unpublished data). This species was attacked by a parasitoid at a nearby location, although the parasitoid was not observed at the study site. This leads us to speculate that its nocturnal habit, which might restrict it from the most productive foraging times, could result from the ghost of parasitism past (Price and Pschorn-Walcher 1988) and lead to reduced abundance.

Several potentially important feedbacks are neglected in this model. Dominance can depend on population size (Morrison 2000; Palmer 2004), with success potentially enhancing success, leading to the takeover of a community by a single species (Human and Gordon 1996; Holway 1999). We also assume that parasitoids arrive independently of the size of a food resource and of whether ants are in conflict with other ants, again simplifying known
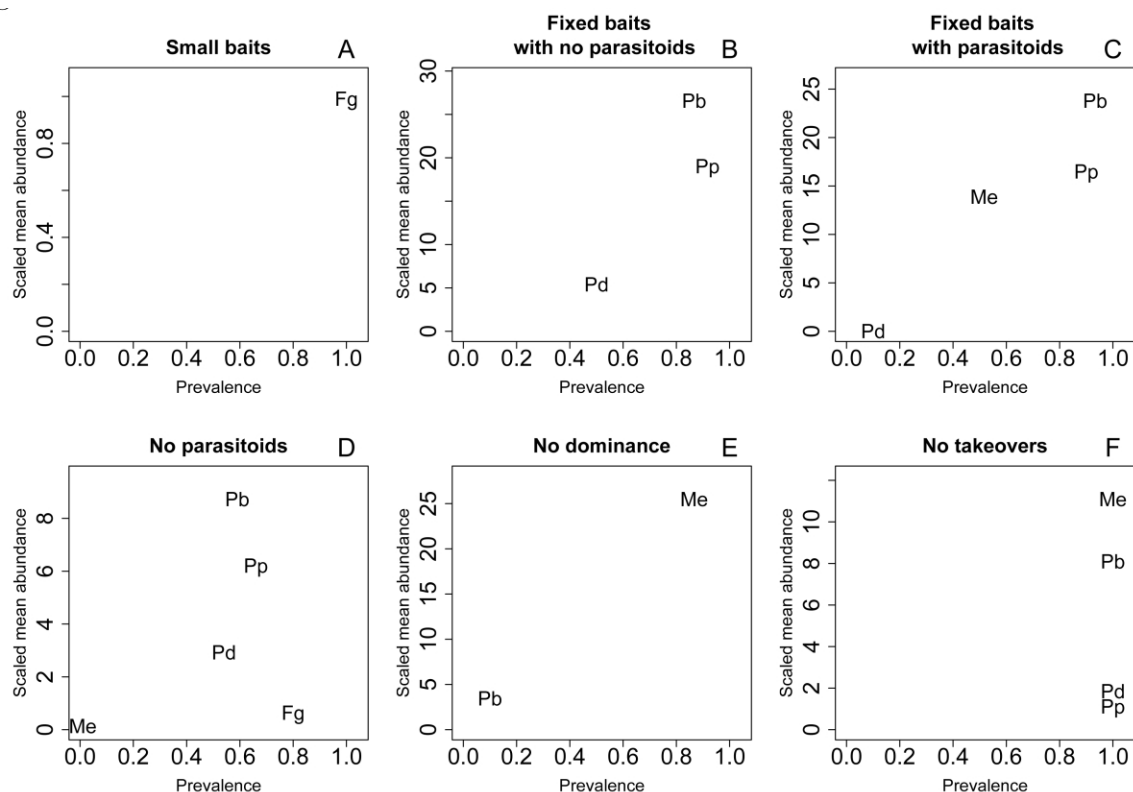
Figure 5: Results of simulation of the parameterized model equation (3) in six cases. Ant species are shown only when they have nonzero mean abundance (averaged over the 10 bootstrap replicates). Simulated ant numbers are scaled by the same factor as in figure 4. *A*, With small baits only (results are not sensitive to the presence of parasitoids). *B*, With fixed baits only and no parasitoids. *C*, With fixed baits only and parasitoids present at every bait. *D*, With a mix of small and fixed baits in the absence of parasitoids. *E*, With no dominance structure ($a_{ijk} = 0.5$ for *i*, *j*, and *k*). *F*, With no takeovers ($a_{ijk} = 0.0$ for *i*, *j*, and *k*). The position of *Pheidole perpilosa* (*Pp*) was moved down by 0.5 for visibility. See table 2 for species abbreviations.

interactions (Feener et al. 1996; Feener 2000; LeBrun and Feener 2002; Morrison and King 2003). In the long run, coexistence depends on the population dynamics of the parasitoids (Adler 1999), which feed back to the probability of parasitoid presence at food resources. Our predictions of coexistence are all made at equilibrium, and transient effects due to changes in the environment or migration from other sites cannot be included. Finally, we ignore the structuring of ants into separate nests and thus neglect the importance of nest site limitation, which has been shown to be important in other systems (Foitzik and Heinze 1998; Fonseca 1999).

Because of insufficient data, our models must neglect the many less common species in the system. We can only speculate as to whether they coexist through the dominance-discovery mechanism, but we do note that rare species with very high per capita discovery rates could persist and have a major effect on the community even though they are difficult to observe.

In addition to taking these feedbacks into account, more accurate models would explicitly model the effects of space rather than treating all ants as having an equal opportunity to reach any given resource (Adler and Gordon 2003). Our models also leave unspecified the mechanism that leads to the relationship (or lack thereof) between the dominance and discovery abilities. Explicit modeling of ant forager allocation to different tasks, particularly if done in concert with modeling of spatial foraging, could make these models more predictive (Johnson et al. 1987).

In contrast to studies designed to understand patterns of abundance and co-occurrence at large scales (Parr et al. 2005), we have tested whether the parameters of a particular local community are consistent with equilibrium coexistence of the most dominant species in that community. More thorough quantification of a small number of such communities may inform our thinking about the mechanisms underlying coexistence at larger spatial and temporal scales.

Acknowledgments

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