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Enigmatic Biodiversity Correlations: Ant Diversity Responds to Diverse Resources

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A pattern noted in ecology is that diversity at one level begets diversity at other levels. In the case of consumers competing for similar resources, the diversity of those resources is thought to provide some degree of niche diversification in which a diverse set of consumer species can coexist. If, however, the diverse resources are not sufficiently distinct from one another, from the standpoint of the consumer species, such niche diversification will not exist. We experimentally show that a diverse array of twigs attracted 80% more species of twig-nesting ants than a monospecific collection of twigs. The specific tree species from which the twigs were derived did not explain the pattern. It appears that diversity per se at one level (twigs) creates conditions that promote diversity at another level (nesting ants).

Worldwide concern over the loss of biodiversity has risen dramatically in recent years (1, 2). However, the origin, maintenance, and significance of biodiversity remain controversial, despite many recent advances (3–7).

A common assumption is that diversity of one component in a system tends to promote diversity in other components. For example, a large number of species of plants is frequently correlated with a large number of species

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of insects (8, 9). The conventional explanation for this correlation is that one set of species constitutes a set of resources for another set, which we call consumers (10). This formulation implicitly assumes that the consumers are not equally fit on all resource types. Thus, there will be some degree of niche differentiation and consequent reduction in interspecific competition, accounting for potentially high species diversity of the consumers (11, 12). If this conventional view is not true, as would be the case when the consumers are effectively generalists, there is no particular reason to expect a correlation between diversity of resources and diversity of consumers (10).

Using ants that nest in hollow twigs in the leaf litter of a coffee agroecosystem in Co-lombia, we examined the correlation between the diversity of twigs and the diversity of twig-nesting ants in the system (13). Ant species that nest in short-lived nests (such as twigs in the leaf litter) rarely hold territories or engage in overt interference competition with neighbors, and it is highly unlikely that they exhibit strong preferences for twigs from particular species of trees, above and beyond obvious physical characteristics such as size of twig or openness of the pith (14–16). Here, we examined whether twigs derived from a diverse set of shade trees (normally associated with more traditional forms of coffee production) would harbor a greater diversity of twig-nesting ants than twigs derived from a single species of shade tree.

Our experimental design was based on twigs cut from living trees, chosen so as to minimize any species-specific difference in size (length or diameter) and artificially bored so as to make as constant as possible nesting sites among the eight source tree species (13). The twigs were placed in litter bags, after 1 month of drying in the laboratory. "Single-species" (eight twigs belonging to a single species of tree) and "mixed-species" (eight twigs belonging to eight tree species) litter bags (1-cm mesh size) were paired and placed in a grid (16 bags; eight mixed species and eight single species, alternating, in each of eight rows) in a shade coffee plantation in Colombia. The ants nesting in them were evaluated twice over a period of 5 months.

We found 228 ant colonies grouped in 22 ant species, from which 9 and 20 species were present in the single- and mixed-species treatments, respectively. Rarefaction

Fig. 1. Rarefaction curves for ants nesting in twigs. Species richness is plotted against (**A**) the number of ant colonies recorded and (**B**) the number of experimental units (litterbags), for all single-species litterbags (black triangles) and mixed-species litterbags (light squares) throughout the study.
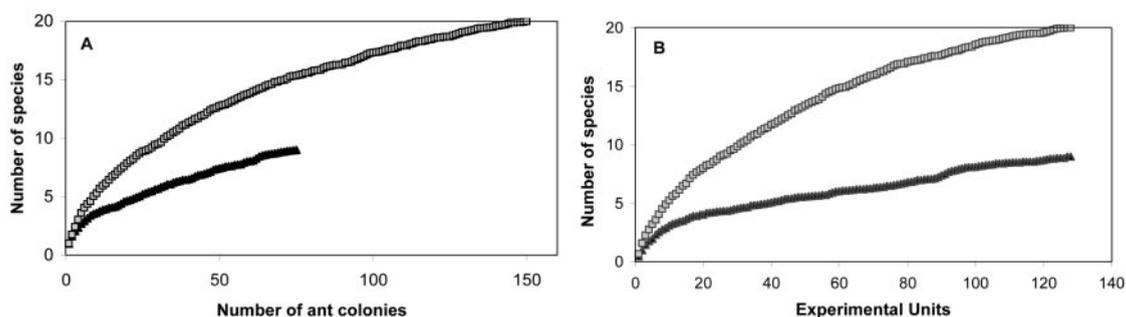
curves showed a higher species richness in the mixed-species treatment than in the single-species treatment (Fig. 1). Higher ant species diversity in bags with a diverse assemblage of twig species was not simply a result of higher colony density in those experimental units, because the difference occurs at all colony densities (Fig. 1). Rather, twig diversity, in and of itself, appears to promote ant species diversity.

Because each species of twig sampled more of the overall area when in mixed-species bags than when in single-species bags, the higher ant species diversity in the mixed-species treatment could have been due to a "spatial sampling effect" (17). To assess this possibility, we paired each single-species bag with the mixed-species bag that was closest to it in the field, and performed a paired test on species number. The result was a highly significant difference (Wilcoxon signed rank test $Z = -2.958$, $n = 64$; $P =$ 0.003). Thus, when we controlled for spatial heterogeneity by comparing only adjacent bags with one another, the elevated species diversity in mixed-species bags remained significantly higher than in single-species bags.

Ant species colonized different species of trees in different relative proportions depending on their context, i.e., single species or mixed species (Table 1). In contrast, a Chi-squared goodness-of-fit analysis revealed no differences in the proportion in which different ant species colonized the same tree between two sampling periods (single versus single species, $P > 0.1$; mixed versus mixed species, $P > 0.1$). Furthermore, colony turnover was high (almost 90% between the two periods), with only 10% and 12% of the colonies in single- and mixed-species bags, respectively, staying in the same twigs over the two sampling periods. A repeated-measures analysis of variance (ANOVA) using rows as repetitions revealed a highly significant treatment effect [higher diversity in the mixed-species treatment than in the single-species treatment; ANOVA: $F(1, 14) = 13.69$, $P = 0.0002$], but no difference between the two time periods nor in the interaction between time and treatment ($P > 0.05$). Tree species tended to be colonized at the same rate during the two time periods (with a 2-month difference between them). The species of trees that most contributed to ant richness in the mixed-species treatment were *Tabebuia rosea* and *Bauhinia purpurea*, but no relation between these two species of tree and any particular species of ant was found, nor did these tree species harbor a notably higher density or diversity of ants when in the single-species treatment (Table 1).

When we compared the presence of ants in single- versus mixed-species bags grouped per tree species (Table 1), a paired t test revealed a significant difference in the number of colonies ($t = -2.657$, df = 7, $P = 0.033$) and the number of species [Wilcoxon signed rank test $Z = -2.201$, $n = 8$; $P = 0.028$ (18)]. It is evident that *Paratrechina* cf. *steinheili* and *Solenopsis decipiens* were the most abundant in both single- and mixed-species bags (Table 2). However, these two species did not drive the general pattern. Eliminating them and repeating the analysis shows a significant difference for the remaining species ($Z = -3.408$, $n = 20$; $P = 0.001$).

The average percent relative humidity within the bags ($\pm$SD) was 81.50 ($\pm$6.47) and 84.20 ($\pm$7.33) for single- and mixed-species, respectively, a statistically significant difference (Mann-Whitney U test = 573; $N_1 = 40$, $N_2 = 39$, $P = 0.042$). Average temperature was not significantly different (23.42° $\pm$ 1.54°C for single-species and 23.19° $\pm$ 1.52°C for mixed-species bags; $P = 0.495$).

This experiment shows that the diversity of nesting resources affects the diversity of twig-nesting ants, even though these species appear to have no specialization on particular tree species. More ant colonies and more ant species colonized a diverse array of twigs than the same number of twigs of a single species. The treatments were interspersed and randomly placed in the experimental area such that it is not possible to explain the differences as a consequence of previously existing microsite effects. Also, the higher number of species in the mixed-species treatment cannot be explained as a result of the higher colonization rate. Although the number of colonies in the mixed-species treatment were more than double that found in the single-species treatment, species accumulation curves for both per experimental unit and colony number show significantly higher richness (80%) in the mixed-species than in the single-species treatment (Fig. 1).

Table 1. Number of colonies and number of species encountered in twigs of each of the tree species used in the study.

Tree species	Number of colonies		Species richness	
	Single species	Mixed species	Single species	Mixed species
Bauhinia purpurea L.	4	29	3	9
Inga densiflora Benth	12	10	3	6
Tabebuia rosea	14	31	5	10
Mangifera indica	3	12	3	6
Cordia alliodora	10	8	3	5
Quararibea cordata	7	12	3	2
Psidium guajava	17	23	6	6
Melia azederach	8	19	3	7

Table 2. Ant species that nested in twigs of eight shade tree species.

Ant species or morphospecies	Single species		Mixed species	
	Oct	Dec	Oct	Dec
Linepithema sp.	2	0	3	2
Brachymyrmex cf. *cordemoyi* Forel, 1895	0	2	0	0
Brachymyrmex sp.	0	0	1	1
Camponotus cf. *indianus* Forel, 1879	0	0	3	1
Camponotus cf. *novogranadensis* Mayr, 1870	6	5	9	10
Camponotus sp.	1	0	0	0
Paratrechina cf. *steinheili* (Forel, 1893)	16	20	21	45
Crematogaster curvispinosa Mayr, 1862	1	0	3	0
Leptothorax (*Nesomyrmex*) *pittieri* Forel, 1899	0	0	1	2
Leptothorax (*Nesomyrmex*) *tristani* Emery, 1896	1	0	3	1
Pheidole sp.	0	0	1	0
Pheidole Flavens Roger, 1863	0	1	4	1
Pheidole longiscapa Farel, 1901	0	0	2	2
Procryptocerus scabriusculus Kempf	0	0	1	1
Rogeria besucheti Kugler, 1994 cf.	0	0	0	1
Solenopsis sp.	0	0	2	0
Solenopsis decipiens Emery 1906	8	12	13	13
Wasmannia auropunctata (Roger, 1863)	0	0	0	1
Pseudomyrmex oculatus (Smith, 1855)	0	0	1	0
Pseudomyrmex boopis (Roger)	0	0	0	2
Pseudomyrmex pallens (Mayr, 1870)	0	0	0	1
Pseudomyrmex simplex F. Smith, 1877	0	0	0	1
Total	35	40	68	85

The question remains as to why ants nest significantly more in mixed-species litterbags than in single-species ones. The total number of twigs was the same (512) in both single- and mixed-species bags. The only difference was the context in which each of the twigs was placed: Twig neighbors were the same in single-species bags and different in mixed-species bags. More species nested in the mixed-species bags than in the neighboring single-species bag, either because they chose them or survived better in them, and this trend was consistent through time. Thus, ants nested (or were more successful in nesting) significantly more based on the context in which the twig was found—single species or mixed species—rather than on the species identity of the twig.

However, exactly what it is about that context that causes this different response of ant species diversity is unknown. If, for example, different twigs are structurally, biochemically, and biologically different, as might be expected in the case of tropical woods (*19, 20*), the combinations of different species of twigs could create diverse general conditions for biota around them. Perhaps such "emergent properties" could be perceived differently by chemoreceptors of founding colonies or queens. Or perhaps the mix of different species of trees could influence the pattern in which twigs retain water and decompose, favoring growth of different types of fungi and bacteria, as well as reproduction of collembolans and other kinds of invertebrates, all of which conceivably might constitute part of a food web that is conducive to a diversity of ant species (*15, 16, 21*). However, such speculations are only intended to suggest further experimentation, not to offer an explanation for our results.

We conclude that the whole (i.e., a group of diverse items) is not just the mechanical sum of its component parts, and that, in a biological context, a mix of species acquire properties that are not explained by the sum of the properties of each individual species.

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Tip20p Prohibits Back-Fusion of COPII Vesicles with the Endoplasmic Reticulum

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Directionality in intracellular trafficking is essential to ensure the correct localization of proteins along the secretory pathway. Here, we found evidence for an active mechanism that prohibited back-fusion of de novo–generated vesicles with their donor compartment. Tip20p is a peripheral membrane protein implicated in consumption of COPI vesicles at the endoplasmic reticulum. However, a specific mutant of *TIP20* did not interfere with COPII vesicle generation but allowed these vesicles to fuse back to the endoplasmic reticulum, a process that does not occur normally in the cell.

Secretion of proteins is achieved through vesicular transport between different compartments within the cell. Vesicles bud from one compartment and are targeted specifically to the next compartment (*1–3*). One layer of specificity for vectorial transport is provided by soluble NSF (*N*-ethylmaleimide–sensitive factor) attachment protein receptor (SNARE) proteins present on the vesicle and target membranes. Only upon successful interaction of cognate SNAREs is a transport vesicle consumed by the target membrane. In *Saccharomyces cerevisiae*, three different vesicle (v)-SNAREs cycle between the endoplasmic reticulum (ER) and the Golgi. They interact on the Golgi and ER membranes with different target (t)-SNAREs. However, the set of SNAREs that is included in each anterograde and retrograde vesicle in the ER-Golgi shuttle is the same. Vesicles are formed by polymerization of protein complexes on the surface of the membrane. This process is facilitated by small guanosine triphosphatases (GTPases) (*4*). Upon fission of the vesicle bud from the membrane, guanosine triphosphate (GTP) hydrolysis occurs, which leads to the depolymerization of the coat.

Why do newly formed vesicles not fuse back to the donor membrane after their formation? One possible explanation might be that the ER-derived and Golgi-derived vesicles possess different coats (COPII and

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