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Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem

Abstract Recent changes in the coffee agroecosystem of Costa Rica were used to study the mechanism of biodiversity loss in transforming agroecosystems, focusing on the ground-foraging ant community. Coffee farms are being transformed from vegetationally diverse shaded agroforestry systems to unshaded coffee monocultures.We tested the hypothesis that the high-light environment and lack of leaf litter cover in the unshaded system are the determinants of the differences in ground-foraging ant diversity. Four treatments were established within the light gaps of a shaded plantation: shade, leaf litter, shade plus leaf litter, and a control (no shade or leaf litter added). Ants were sampled using tuna fish baits and light and temperature were measured. Shade and leaf litter had a significant effect on the ant fauna but probably for indirect reasons having to do with species interactions. In both shade treatments, *Solenopsis geminata*, the tropical fire ant, decreased significantly while the other species increased. The possibility that the physical factor changes the nature of competitive interactions between the most abundant species is discussed.

Key words *Solenopsis geminata* · Coffee · Biodiversity · Costa Rica

Introduction

The recent focus on the preservation of biodiversity is based on the suggestion that more species are becoming extinct in the late part of the twentieth century than at any time in history (Myers 1979; Lovejoy 1980; Reid and Miller 1989). While efforts to curb these losses have intensified in recent years, emphasis has been on the preservation of a few charismatic and conspicuous organisms, or on pristine environments, mostly within national parks and reserves. In fact, such organisms comprise a very small fraction of the threatened biodiversity and such habitats represent only a small percentage of the total land area (Western and Pearl 1989; Pimentel et al. 1992). Since the combination of managed ecosystems and human settlements cover approximately 95% of the earth (Western and Pearl 1989), it might be argued that it is as important to examine biological diversity in managed ecosystems as in highly diverse unmanaged ecosystems, such as tropical rain forests. Some agroecosystems, in particular traditional systems in the tropics, have been reported to contain a very high local biodiversity.

Insects are recognized as the most diverse taxon, with over 1,115,000 described species, and estimates that range from 3 million (May 1988, 1990) to 30 million (Erwin 1988) species. Such small organisms are frequently more specialized and thus especially susceptible to extinction when vegetation and habitats are modified (Wilson 1987; Price 1988; Dourojeanni 1990). In addition, in agricultural systems, insects and other arthropods are potentially important pests and natural enemies of pests. Understanding patterns of biodiversity loss with the transformation of agriculture could shed some light on the practical problems of insect herbivores and their control by natural enemies.

The coffee agroecosystem in Central America is an ideal ecosystem to examine these patterns. This habitat, which has a forest-like structure in its traditional form and has been undergoing transformation to monoculture for the past decade, harbors a high insect diversity and displays clear patterns of biodiversity loss in vegetation and its associated insect fauna (Nestel and Dickschen 1990; Nestel et al. 1993; Perfecto 1994; Perfecto and Vandermeer 1994; Perfecto and Snelling 1995). This situation provides a useful laboratory for the study of biodiversity and its changes. As the traditional system with its diverse overstory of shade and fruit trees is transformed to a monoculture in full sun (Reynolds 1991; Babbar 1993; Boyce at al. 1994), significant changes can

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Table 1 Species list and foraging activity levels for shaded and unshaded coffee plantations. Activity levels represent the sum total of all baits in four plots for the forested and gap areas (with a maximum of 300: 25 baits×4 plots-activity level 3). Shaded plantation data were generated from total baiting in the present study. Unshaded plantation data were taken from Perfecto and Snelling 1995, and personal observations (*A* abundant, and *R* rare).

Species	Shaded (traditional) total activity		Unshaded (modern) approximate activity levels
	forested areas	light gap before experiment	on average
Solenopsis geminata		98	A
Pheidole radoszkowskii	216	130	A
Wasmannia auropunctata	164	11	
Pheidole absurda	101	6	R
Pheidole susannae	37	16	
Pheidole punctatissima	12		
Pheidole phallax	8	3	R
Linepithema humile		8	R
Myrmicinae 1	1		
Pheidole sp. 2	6		
Camponotus novogranadensis	4		
Myrmicinae 2		4	
Camponotus planatus	3		
Oligomyrmex sp. 1	1		
Brachymyrmex musculus	2		R
Pachycondyla fuscoatra	1		
Cyphomyrmex minutus	1		
Gnamptogenys regularis		1	
Eciton sp.	1	1	

be seen in biodiversity, both in terms of the planned biodiversity [i.e., the crops specifically planted by the farmer (Swift et al. in press)] and the associated biodiversity (insects and other plants and animals that are associated with the crops and the habitat they create). In particular, there is a dramatic change in the composition of terrestrially foraging ants (Nestel and Dickschen 1990; Nestel at al. 1993; Perfecto and Vandermeer 1994; Perfecto and Snelling 1995). More than 30 species of terrestrial ants have been encountered in traditional coffee agroecosystems in the Central-Valley of Costa Rica (19 species in this study alone), compared to only 6 species in the modern unshaded system (Table 1). One cause of this loss may be that microclimatic changes eliminate some species and thus enable others to dominate the area. An alternative hypothesis is that microclimatic changes favor a few species, which in turn competitively eliminate the other species.

The unshaded system is dominated by the tropical fire ant, *Solenopsis geminata*, and *Pheidole radoszkowskii* (Perfecto 1994; Perfecto and Snelling 1995). Four other species are frequently seen, but these two are by far the most common. The traditional system also seems to be dominated by a few albeit more than just two, species (Table 1). *S. geminata* is rare in the traditional systems, but can easily be found by searching for the open areas or "light gaps" in the system.

The two most obvious physical differences between the unshaded and traditional systems are the shade cast by the overstory and the leaf litter that covers the ground. Both of these are convenient features to mimic experimentally. But such an experimental setup in the unshaded system would be problematic since the ants that might colonize a shaded, leaf-littered section of a modern cof-

fee farm are not likely to be nearby. However, the species composition of the fauna in the light gaps of the traditional system bears a striking resemblance to that of the modern system (Table 1). The traditional system, with an overall high diversity of ground-foraging ants and co-dominance of *S. geminata* and *P. radoszkowskii* in its light gaps, is ideal for examining the direct and indirect effects of microhabitat changes on local species diversity. Such an examination is the purpose of the present study.

Materials and methods

Description of the system

The transformation of coffee (*Coffea arabica*) plantations involves spectacular landscape changes. The traditional system follows the common pattern of agroforestry, with a variety of shade tree species, frequently interspersed with fruit trees, and several varieties of bananas (*Musa* spp.). Due to their complex and layered structure, traditional coffee farms share many structural attributes normally associated with forests. Indeed, in much that follows we refer to the shaded areas as the "forest" for shorthand.

The new, monocultural system that is being promoted all over Central America (Rice 1990; Reynolds 1991; Babbar 1993) is dramatically different. All the shade trees are eliminated, the traditional coffee varieties are replaced by new sun-tolerant and shorter varieties which are genetically homogeneous and heavily dependent on agrochemicals, especially herbicides and fertilizers (ICA-FE-MAG, 1989). These two systems represent the two extremes in a continuum of management systems with varying degrees of complexity, and with dramatically different terrestrial ant faunas (Perfecto and Vandermeer 1994; Perfecto and Snelling 1995).

The tropical fire ant, *S. geminata*, is the most evident component of the ant community in the unshaded system. Its natural history has been studied in great detail (Risch and Carroll 1982a,b; Perfecto 1991, 1994). Its nests are very large and typically include extensive underground and covered foraging trails that extend the

foraging area of a single nest to many meters, thus allowing continued foraging activity at high temperatures. It is not uncommon for a single nest to encompass a foraging area of more than 15 m (personal observations). It appears that the brood chamber of the nest must be in a sunny location, for if an individual brood chamber is shaded, the chamber is moved within 24 h (personal observations). The species is especially efficient at foraging on large and/or defensible resources, since it is capable of rapid recruitment and is very aggressive against other ant species. Aphids in the roots of grasses appear to be an important resource for this species in the unshaded system, where grasses are abundant (Perfecto 1994). In contrast to its rapid recruitment ability, its capacity to initially find resources seems to be smaller than that of its major competitor in the modern system, *P. radoszkowskii* (Perfecto 1994).

The other major component of the ant community in the unshaded system is *P. radoszkowskii*, usually occupying about half of the area in a plantation. This species is also a very efficient recruiter and is capable of defending large resources. It seems to be competitively dominant over *S. geminata*, even though the latter frequently wins in physical conflicts over resources. In contrast to the few but large *S. geminata* colonies, *P. radoszkowskii* has many relatively small ones (Perfecto 1994).

Study site

The study was conducted on a traditional coffee farm (3.5 ha) located on the southeastern edge of Santo Domingo de Heredia, Costa Rica. The surrounding area is either cattle pasture (on the east and south borders), small-scale agriculture (on the western border), or suburban sprawl (on the northern border). The main shade trees are *Erythrina poeppigiana*, *Erythrina fusca*, and *Inga* sp., with significant numbers of plantains (*Musa* sp.). The most common of the many other tree species on the farm are citrus (*Citrus* sp.), jocote (*Splondia purpurea*), mango (*Mangifera indica*), and chirimoya (*Annona chirimoya*). The understory is naturally dominated by coffee bushes, but also includes, more or less randomly, quequisque (*Xanthosoma* sp.), malanga (*Colocassia* sp.), a curcurbit vine, and a variety of other "volunteers." While most of the farm is covered with a canopy of trees, "light gaps" exist in areas where trees have been felled or were never planted. These light gaps are usually dominated by coffee and plantain. Vegetation at ground level in the gaps is usually sparse and dominated by grasses, sedges, and *Comelina* sp., similar to what is typically found in an unshaded coffee plantation.

Experimental design

Four areas with light gaps larger than 10 × 10 m were located within the farm. A 5 × 5 m plot was established in the middle of each gap. Four treatments were randomly distributed among the

four gaps: shade only, leaf litter only, shade and leaf litter, and a control. The shade treatment consisted of dark plastic covering the 5 × 5 m plot, plus an additional 1-m border, for a total of 36 m². The plastic was placed in the form of six bands of 1 × 6 m. Irregular holes were opened in the plastic to mimic the sun flecks that reach the ground in the naturally shaded areas, and to allow rainfall to reach the ground. The leaf litter treatment consisted of adding leaf litter to the plots in quantities approximately equal to that encountered in the areas shaded by overstory trees. This was achieved by selecting an area of 36 m² in the tree-shaded areas, collecting all its leaf litter, and depositing this in the gap plot, covering an equivalent area. Additionally, four plots were established in areas shaded by trees (what we call "forest" plots), one each in the general vicinity of each of the gap plots. Although not formally part of the experimental design, these forest plots provided us with supplementary data and were used only to insure that some general change in the overall ant community did not occur in the shaded areas during the course of the experiment. Thus the experimental design was a two-way crossed design with shade versus no shade crossed with litter versus no litter. The forest plots are not part of the experimental design.

Temperature and percent shade were measured in all four of the forest plots and within each experimental plot after the treatments had been established. Five measurements of temperature at ground level were taken, 15 days after the treatments had been established, in both the light gap and the forest plots. The locations of the temperature measurements were selected at random within the 5 × 5 m area of the plot. Percent shade was measured with a LICOR-2000 canopy analyzer 20 days after treatment establishment. For this, each plot was divided into five 1-m wide strips 5 m in length. Three strips were selected at random and four light measurements, 1 m apart, were taken in each strip for a total of 12 observations per plot. These data indicated that, as intended, the experimental procedures successfully captured the microclimatic features of the naturally shaded areas (Fig. 1).

Ground-foraging ants were sampled in all plots (four experimental plots and the four naturally shaded plots) before and 24 and 31 days after the establishment of the treatments. Ants were sampled using tuna fish baits placed on the ground in a 5 × 5 m grid for a total of 25 baits per plot. Baits were checked after 30 min and ant specimens were collected for future identification. All baitings were conducted during the morning, between July 16 and August 18 1994. For all baits on which *S. geminata* was encountered during the initial baiting, a search was made for the presence of root aphids in the vicinity.

Ant activity was recorded at each bait according to the following previously used scheme: 1–3 individuals, activity level 1; 4–9 individuals, activity level 2; ≥10 individuals, activity level 3 (Perfecto 1990, 1991; Perfecto and Sediles 1992). The dependent variable for analysis was total activity level in a plot for each of the species or species group (the sum of the total activity level over the 25 baits).

Fig. 1 Temperature and shade measurements (using Licor-2000) in all plots. Note that the shade treatments (shade only, and shade and litter) are almost identical to the naturally shaded ("forest") conditions, while the nonshade treatments (litter only, and control) are almost identical to the open (gap) areas
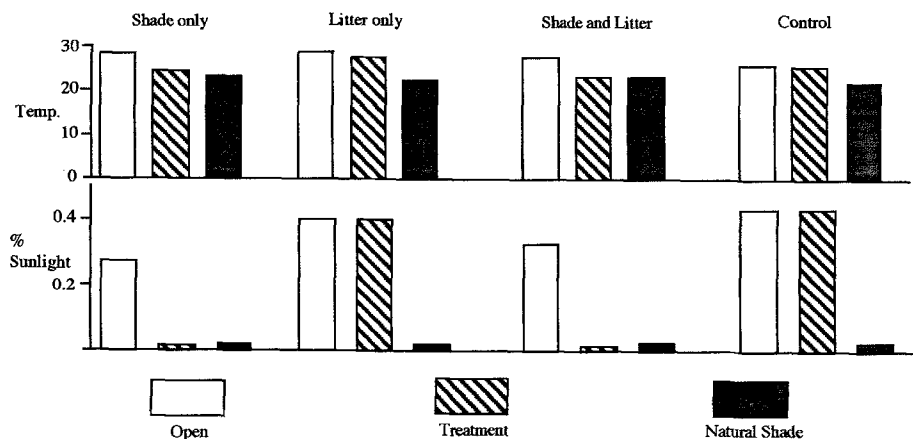
After the initial setup, the control plot (neither shade nor litter applied) was accidentally sprayed with herbicide, potentially changing the environment. Consequently, an alternative site was chosen for the control on the second sampling day (i.e., 24 days after initiation of the experiment). For this sampling date, activity data are presented as an average of the original plot and the new plot, although the change in activity level is presented as a change in the initial control plot. For the final sampling date, only the data from the alternative plot are recorded.

Results

For the analysis, we grouped all species other than *S. geminata* and *P. radoszkowskii* as "forest" species. These 17 forest species are all characteristic of the shaded habitat (Table 1). A total of 86% of the foraging activity of these other species is due to the actions of just four species, *Pheidole susannae*, *P. punctatissima*, *P. absurda*, and *Wasmannia auropunctata*.

Activity levels changed little in the forest plots over the course of the experiment (Table 2). Computing the activity of a plot as a percentage of the original activity for that plot (the activity before setting up the treatments), it is apparent that activity levels changed dramatically for the shade treatment, and subtly, if at all, for the litter treatment (Table 3). While the effect is not at all obvious after 24 days, after the experiment had run for 31 days, both *S. geminata* and the forest species showed very dramatic responses to shade.

Each of the latter two sampling days was analyzed with a two-way analysis of variance, the variable being deviation from the original activity level. So, for example, the activity of *P. radoskzowskii* in the shade plus lit-

Table 2 Baseline activity levels for the forested plots.

Species	Days after initiation of experiment		
	0	24	31
S. geminata	0	0	0
P. radoszkowskii	22.5	31.0	34.8
Forest species	40.0	47.2	37.0

Table 3 Percentage change in activity levels (percentage of initial activity in the plot) for *S. geminata*, *P. radoszkowskii*, and forest species, for the two treatments

	After 24 days		After 31 days	
	shade	no shade	shade	no shade
S. geminata				
Litter	−07	+69	−86	+06
No litter	−22	−30	−37	+13
P. radoszkowskii				
Litter	−64	−24	−25	0
No litter	0	21	+11	+14
"Forest" species				
Litter	+86	0	+500	−44
No litter	+73	−57	+273	0

Table 4 Analysis of variance (two-way, litter/no litter crossed with shade/no shade) for the three categories, *S. geminata*, *P. radoszkowskii*, and pooled forest species, 24 and 31 days after setting up the experiment. The variable is the difference between the activity level on the day of measurement and that on the same plot before the experimental treatments were set up

Source	df	Mean square	F	p
S. geminata (31 days)				
Between shade	1	676.00	676.00	0.024
Between litter	1	225.00	225.00	0.042
Error	1	1.00		
S. geminata (24 days)				
Between shade	1	110.25	17.64	0.149
Between litter	1	42.25	6.76	0.234
P. radoszkowskii (31 days)				
Between shade	1	6.25	0.069	0.836
Between litter	1	0.25	0.003	0.967
Error	1	90.25		
P. radoszkowskii (24 days)				
Between shade	1	16.00	0.444	0.627
Between litter	1	144.00	4.000	0.295
Error	1	36.00		
Forest species (31 days)				
Between shade	1	1722.25	765.44	0.023
Between litter	1	12.25	5.44	0.258
Error	1	2.25		
Forest species (24 days)				
Between shade	1	132.25	4.372	0.284
Between litter	1	12.25	0.405	0.640
Error	1	30.25		

ter plot was 28 before the experiment was set up, and 21 after 31 days, making the deviation 7 (28–21). These analyses are displayed in Table 4.

These results suggest that there was a joint response to the shade treatment, with *S. geminata* decreasing its activity and other species increasing their activity (Fig. 2). This result is consistent with the hypothesis that the absence of shade in the new unshaded system is implicated in the pattern of biodiversity loss. *P. radoszkowskii* did not show a consistent response to either of the factors, again consistent with the fact that this species is abundant in both shaded and unshaded systems. While the experimental design does not permit testing for interaction, nothing in the data would even approximately suggest such an effect. The effect of leaf litter was significant in the case of *S. geminata*.

Several qualitative observations are also worth noting. Immediately after imposing the shade treatment, new *S. geminata* nests (brood chambers) could be seen surrounding the experimental treatment. This suggests that this species avoids shady conditions for the placement of its nest, and indicates that the data reported above are actually conservative. That is, if the size of the experimental area had been larger, it is likely that the foraging activity of *S. geminata* would have been reduced even further, since the brood chambers would have has to be moved a larger distance.

Finally, in all cases in which *S. geminata* was encountered at a bait during the initial baiting, root aphids on
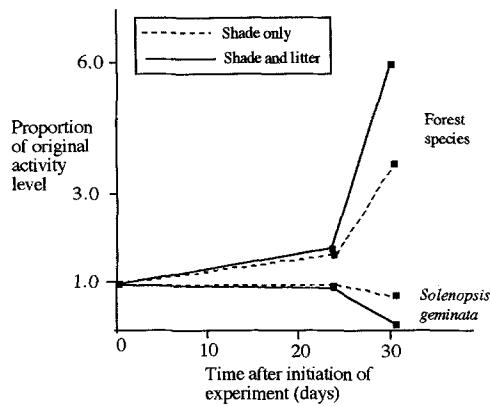
Fig. 2 Activity levels of *S. geminata* and forest species in the shaded treatments

some plant species (almost always a grass) were encountered nearby, with individual *S. geminata* in attendance.

Discussion

These results indicate that the generalist ground-foraging ant community was significantly changed by alteration of the physical conditions of shade, while leaf litter had a small but demonstrable effect. They support the idea that it is the shade of the traditional shaded coffee farms that gives rise to the difference between the ant community in shaded versus unshaded coffee systems. However, the mechanism whereby shade effects this change is not obvious.

Because of the clear aggressiveness of *S. geminata*, its removal by the application of shade might allow other species to arrive. But we feel this interpretation is not ultimately supported by these data. Rather, as encountered in previous work (Perfecto 1994), the aggressiveness of *S. geminata* is not necessarily translated into strong competitive ability under all circumstances. In particular, in those cases where resources occur in small packets, *S. geminata* is less efficient at finding them than other species, even though it is able to defend them very well once encountered. One of the key resources in the area of our study is root aphids, which occur abundantly on the roots of the many grasses that occupy the light gaps. With this abundant "defensible" resource, *S. geminata* is able to competitively dominate most of the other species in the area. Once shade is introduced, the grasses die and with them the root aphids, shifting the competitive balance in favor of the other species. No longer capable of dominating, *S. geminata* slowly disappears from the shaded situation as the forest species invade from nearby forested areas.

Circumstantial support for this interpretation is available (Fig. 2). *S. geminata* declines and the forest species increase when shade is added, although the increase is not as rapid as one might expect if *S. geminata* were simply physically prevented from foraging in shady places. Despite the fact that most *S. geminata* brood chambers

were moved within 24 h of imposing shade on the area, their foraging activity only decreased gradually over the first 21 days. This could be due to the fact that nests were moved only to the margin of the experimental plots and foragers could still forage in the shaded areas where grasses with root aphids remained. As time passed, grasses under the shade died and aphids either died or moved to areas with grasses outside the experimental plots. Furthermore, the pattern was slightly exaggerated by leaf litter, perhaps because the leaf litter accelerated the death rate of the grasses, perhaps because the leaf litter allowed a more rapid invasion of forest species (although this latter effect was not statistically significant).

These observations support the interpretation presented elsewhere regarding the shift to dominance of *S. geminata* after disturbance (Perfecto 1991, 1994). Specifically, *S. geminata* is an inefficient competitor when resources are available in small packets, since its main foraging strategy is swarming and defense of resources. More mobile species can thus easily outcompete it when an individual can quickly remove a resource that falls to the ground. On the other hand, *S. geminata* is an efficient competitor when resources occur in large or defensible packets, since this is when their aggressive swarming can make a difference. The ubiquitous root aphids that commonly attack grasses in many tropical habitats represent defensible resources. Thus, eliminating the shade in a coffee plantation allows *S. geminata* to dominate the competitive landscape more easily than other species, mainly because of its efficiency in defending large resources like groups of root aphids. Nevertheless, the rather dramatic increase in foraging activity of forest species, seemingly out of all proportion to the reduction in *S. geminata*, suggests that some of these species may be limited directly by the absence of shade or leaf litter.

We also note that this experiment suggests a case of indirect loss of biodiversity (Swift et al. in press). That is, we expect a quick and direct loss of species directly associated with ecosystem components that are eliminated through the habitat transformation (e.g., any species obligately associated with *Erythrina* spp. would automatically disappear when the shade trees are cut out of the system). But the mechanism for the loss of those species whose habitat is not directly eliminated is less clear. The general expectation is that habitat modification will alter the species-to-species interactions in such a way that some species will become locally extinct, not because of the direct effects of habitat modification, but rather because of the indirect effects that habitat modification has on species interactions – indirect biodiversity loss (Swift et al. 1994). The present study supports the notion that the observed loss of ant biodiversity as this agroecosystem is transformed is just such an indirect loss.

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