Density Patterns of Piper Ant-Plants and Associated Arthropods: Top-Predator Trophic Cascades in a Terrestrial System?

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\textbf{ABSTRACT}

Top-predator (fourth-trophic-level) controlled trophic cascades are thought to be uncommon in terrestrial systems, but actual quantitative tests and comparisons of bottom-up and top-down forces in systems with more than three linear trophic levels are rare. Here, we describe the density patterns of the arthropod community associated with Piper ant-plants in Costa Rican wet forests. Consumers in this community comprise a complex, interacting web of herbivores, predaceous ants, and predators of ants. Although the hollow stems and petioles of the Piper plants provide some protection to resident ants from predation, specialized Dipoena spiders and Phyllobaenus beetles exploit Pheidole ants inhabiting Piper plants. We report abundance patterns of plants, ants and predators in four forests. These patterns of abundance are consistent with predictions of top-down cascades across four trophic levels when the top predators are effective (beetles). We discuss how top-down and bottom-up forces may interact in systems with less effective top predators (spiders).

\textbf{RESUMEN}

Se ha pensado que las cascadas tróficas controladas por alta predadores (cuarto nivel trófico) son poco comunes en los sistemas terrestres, pero son raras las pruebas y comparaciones cuantitativas de las fuerzas que se mueven de la base hacia arriba y de la cima hacia abajo en sistemas con más de tres niveles tróficos lineales. En este trabajo describimos los patrones de densidad de la comunidad de artrópodos asociados con las plantas-hormiga del género Piper en los bosques húmedos de Costa Rica. Los consumidores en esta comunidad comprenden una compleja e interactuante red de herbívoros, hormigas predadoras, y predadores de hormigas. Aunque los tallos y los pecíolos huecos de las plantas Piper proporcionan alguna protección contra la predación a las hormigas residentes, las arañas especializadas Dipoena y los escarabajos Phyllobaenus explotan a las hormigas Pheidole que habitan las plantas Piper. Reportamos evidencia de diferentes sitios que sugiere que los sistemas de cuatro niveles tróficos con un alto predador efectivo pueden ser regulados por fuerzas que actúan de la cima hacia abajo, y, discutimos como estas fuerzas y las que actúan de la base hacia arriba pueden interactuar en sistemas con un alto predador inefectivo.

\textit{Key words}: ant-plants; Costa Rica; multi-trophic interactions; Piper; trophic cascades; tropical wet forest.

Traditionally, studies on ant-plant associations have focused on tests of mutualistic interactions, but recent studies of these multi-trophic level systems are revealing patterns and complexities that contribute to understanding ecological systems in general (McKey 1988, Davidson & Fisher 1991). In this study, we examined the relative abundance of plants, ants, and top predators in an ant-plant system to determine if the patterns were consistent with predictions from trophic cascades theory.

In multi-trophic level communities, bottom-up effects manifest when organisms on each trophic level are limited by the resources available from the level below (e.g., Roininen et al. 1996, Wallace et al. 1997). Of course, plants have primacy in biotic systems because the absence of primary producers would preclude resources for consumers to comprise a trophic structure (Hunter & Price 1992). However, given that resources are sufficiently available to support a biotic community, its structure may depend on the relative effects of resources and consumers.

Top-down forces, first elaborated in the classic work of Hairston et al. (1960) and clarified by Slobodkin et al. (1967), can drive community structure as successive trophic levels alternate between consumer limitation and resource limitation. Smith (1969) and Frentell (1977) extended these ideas to predict that primary producers will be resource-limited in chains that contain odd numbers of trophic levels (i.e., predators reduce herbivores (and herbivory) in a three-trophic-level system) and pri-
TABLE 1. Predicted relative densities of individuals in each of four trophic levels as a result of top-down or bottom-up forces. Each hypothesis begins with high or low densities of top predators (for top-down) and high or low plant densities (for bottom-up) and the arrows indicate the direction of the subsequent trophic cascade.

<table>
<thead>
<tr>
<th>Trophic level</th>
<th>Densities</th>
<th>Top-down</th>
<th>Bottom-up</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top predators</td>
<td>High</td>
<td>Low</td>
<td>Zero</td>
</tr>
<tr>
<td>Ants</td>
<td>Low</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Herbivores</td>
<td>High</td>
<td>Low</td>
<td>Low</td>
</tr>
<tr>
<td>Plants</td>
<td>Low</td>
<td>High</td>
<td>High</td>
</tr>
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</table>

Primary producers will be consumer-limited in communities with an even number of trophic levels (Schoener 1989, Power 1990).

The prominence of trophic cascades has been established in aquatic systems (Carpenter & Kitchell 1993, Brett & Goldman 1996), but their role is still debated in terrestrial communities (Strong 1992). Furthermore, whereas manipulative studies suggest that trophic cascades operate in some three-trophic-level terrestrial ecosystems (e.g., Cooke 1987, Atlegrim 1989, Marquis & Whelan 1994, McLaren & Peterson 1994, Carter & Rypstra 1995, Stiling & Rossi 1997), experimental or correlational evidence of trophic cascades in four-trophic-level terrestrial ecosystems is rare (Spiller & Schoener 1990, Moran et al. 1996).

One approach to advancing theory about the role of top-down trophic cascades in four-trophic-level terrestrial systems is to compare natural communities that differ in their relative abundance of the fourth trophic level. If terrestrial systems are sufficiently complex that different species act as functional substitutes or compensate for each other, then cascading effects would be buffered, and these communities would lack the predicted patterns (e.g., Bronmark & Weisner 1996). However, if trophic cascades occur, strong asymmetries in the strength of top-down versus bottom-up forces would lead to different outcomes in the relative prominence of the lower trophic levels. For example, if the abundance of predators drives a trophic cascade, then communities that have relatively fewer predators should have some evidence of prey release, and consequent depression of the next lower trophic level; a system with a high abundance of predators would have the opposite pattern (Table 1). Conversely, if bottom-up forces are relatively more important in terrestrial communities, then high numbers of predators would occur when primary productivity and consumer biomass are high, and a scarcity of predators would mean that resources on all levels are limited. Thus, if top-down forces commonly structure terrestrial communities, then accumulations of comparative data showing the alternating pattern (Table 1) would lend plausibility to this hypotheses; if the data and the prediction conflict, then alternative hypotheses may be supported (Oksanen et al. 1981).

Although manipulative experiments were not feasible in this study, we compared relative abundance indicators of interacting species on four trophic levels among four species-rich, relatively undisturbed, terrestrial forests that varied naturally with respect to the density of top predators (fourth trophic level) associated with several species of understory Piper plants. Piper ant-plants occur throughout Costa Rica in wet forests, and are associated with an array of arthropod herbivores, primarily a single species of ant and several arthropod ant predators. Correlative data on the relative abundance of successive trophic levels were used to assess the general top-down, trophic cascade hypothesis: that forests with high densities of top predators will have low densities of ants, high densities of herbivores, and low densities of plants, and that forests with low densities of top predators will have relatively high densities of ants, low densities of herbivores, and high densities of plants (Table 1).

Our general bottom-up hypothesis is that forests with high densities of plants will have high densities of all the other trophic levels (or will have more trophic levels), while forests with low densities of plants will have relatively low densities of all the other trophic levels (Table 1). This hypothesis assumes that there are no top-down forces acting on a plant-dominated framework which would affect densities of other trophic levels.

STUDY SITES AND METHODS

Censuses were taken in Costa Rica of Piper ant-plants in three lowland, tropical wet forests (La Selva, Carara, and Corcovado) and a tropical premontane wet forest (Loma Linda) in March and April, 1991. The La Selva study sites at the Organization for Tropical Studies' La Selva Biological Station, at ca 100 m elevation on the Caribbean side of Costa Rica, receive an average of 3962 mm annual rainfall. Study sites in Corcovado National Park, Osa Peninsula, between the Pacific Ocean and the Golfo Dulce, at <100 m elevation, receive ca 3500
mm annual precipitation. The Carara Biological Reserve sites, on the Pacific Coast near Jaco (elevation <100 m) receive ca 2000 mm precipitation annually. Our sites at Hacienda Loma Linda were located on the Pacific side near Agua Buena, Coto Brus at 1185 m and receive 3265 mm annual precipitation. Study sites in each of these forests were within 1 km of the forest edge, with the size of the forest preserve decreasing in size from Corcovado (ca 43,000 ha), to La Selva (ca 1,500 ha), to Carara (ca 900 ha), to Loma Linda (ca 75 ha).

Plants.—*Piper* ant-plants are understory shrubs (treelets) that begin to produce flowers when they are between 1 and 15 m in height and reproduce vegetatively through layering (fallen treelets root adventitiously) or fragmentation (petioles and twigs break off and root) (Greig 1993). The leaves are large (approximately 20 to 40 cm long when fully expanded) and long-lived (at least 2 yrs). The stems are usually hollow due to the presence of ant colonies that remove the pith. Single-celled, opalescent food bodies rich in lipids and proteins are produced on the adaxial side of the hollow petioles when occupied by *Pheidole bicornis* Forel ants (Risch *et al.* 1977, Risch & Rickson 1981). *Piper sagittifolium* C.D.C., *P. obliquum* Ruiz & Pavon, and *P. fimbriatum* C.D.C. occur on the Pacific slopes of Costa Rica, and the range of *P. cenocladium* C.D.C. extends throughout the Atlantic lowlands. The latter three species are closely related as part of the *P. obliquum* complex (Burger 1971).

Herbivores.—The herbivores most commonly found feeding on *Piper* ant-plants at our study sites are lepidopterans and coleopterans. These are probably specialist feeders on *Piper* species. However, feeding damage from generalist herbivores, including leafcutter ants (Hymenoptera: Formicidae: *Atta* spp.) and orthopterans (primarily Orthoptera: Tettigoniidae) is also common. The main herbivores that eat leaf tissue (at least 10 spp.) are geometrid moth larvae (Lepidoptera: Geometridae), skippers (Lepidoptera: Hesperiidae), weevils (Coleoptera: Curculionidae: *Anabates* spp.), and flea beetles (Coleoptera: Chrysomelidae: *Physimera* spp.; Marquis 1991, Letourneau, pers. obs.).

Herbivore abundance was not surveyed in this study because accurate estimates of herbivore loads would have required extensive sampling and host plant testing of hundreds of potential consumers in various guilds whose abundance patterns vary throughout the year. However, the average amount of herbivory on *Piper* ant-plants has been sampled over several years at these forest sites (Letourneau, pers. obs.) using visual estimates of the proportion of leaf area eaten on every leaf per tree (Letourneau 1998). As a cumulative measure, we would expect relatively larger amounts of folivory to provide an adequate estimate of the prominence of the second trophic level. That is, herbivory should be greater if: (1) herbivores are more abundant in the system, (2) herbivores are larger, or (3) mortality rates of herbivores are lower. However, if higher levels of herbivory were a result of plants being easier to locate in the forest, individuals exhibiting a longer tenure on the plant, or foliage persisting longer and accruing more feeding, then herbivory levels would be less relevant to decisions about trophic cascades.

Ants.—*Pheidole bicornis* is a small, dimorphic species (Formicidae: Myrmicinae) that occupies all the *Piper* ant-plants in the study. The ants feed primarily on food bodies produced by the plant, and eat soft-bodied insects, insect eggs, and spores found on the leaves and flowers (Risch *et al.* 1977, Letourneau 1983; Letourneau 1998). Ants also remove or kill herbivores by tossing them off the plant (Letourneau 1983). Thus, although ants have a primary and direct effect as predators on herbivores, more energy flows from the bottom-up via plant production of food bodies for ants than from plants to herbivores to ants (Fig. 1).

Top predators.—*Dipoena* spp. spiders (Arachnida: Araneae), including *D. banksii*, specialize on ants, and occur almost everywhere *Piper* ant-plants are found. They capture ants at the entrance/exit hole on the hollow petiole. *Phyllobaenus* spp. (Coleoptera: Cleridae) occur as larvae inside the sheathing leaf bases where they kill adult ants and feed on both ant brood and food bodies (Letourneau 1990). Different species of *Phyllobaenus* occur on the Caribbean and Pacific sides of the Central Cordillera, and several other species of predatory larvae occur on *Piper* ant-plants, including ascalaphids (Neuroptera: Ascalaphidae), and sypphids (Diptera: Syrphidae: *Microdon* spp.).

Comparative census and spider observations.—To determine the relative density of *Piper* ant-plants, ants, and top predators at the four sites, we conducted a comparative census. In 1991 we located the largest patches of *Piper* ant-plants within 1 km of the station (La Selva, Carara), within 100 m of the major trail (Corcovado), or within the forest fragment (Loma Linda), and counted the individuals within a 1 ha area measured around each
of three distinct patches of plants in each forest. For each plant, all leaves were counted (2–65 per plant) and every accessible petiole (2–25 per plant) was searched for *Dipoea* spp. spiders before it was gently pried open to record the presence or absence of *P. bicorin*s, other ants, *Phyllobaenus* spp. larvae, scale insects or other inhabitants.

In addition, in April 1986, at Loma Linda, we took daily observations of eight marked individual spiders to record their movement patterns on trees with and without resident ants for up to two weeks. These observations included the number of petioles with ants, the number of other *Dipoea* spiders on a plant, the number of ants captured in silk, and the location of the spider (number of petioles from the top of the plant).

**Statistical Analyses.**—We used nonhierarchical loglinear models to test for associations between predators (two levels—presence or absence of *Dipoea* spp. spiders or *Phyllobaenus* spp. beetles), *P. bicorin*s ants (three levels—numbers of petioles containing ants), densities of *Piper* plants (four levels—one for each forest). The two models therefore included 3 variables and 24 cells. Loglinear models were appropriate because all the variables were at least functionally categorical. Many plants were not occupied by spiders or beetles, and plants with resident predators usually had only one individual; the predator variables were therefore dichotomous—no predator, or some predators (usually meaning only one spider or beetle). Ant densities were expressed as: plants without ants, plants with some ants (at least one petiole with ants), and plants with all petioles containing ants. Field observations (Ltourneau, pers. obs.) and preliminary data from experiments with *Piper cenocladum* suggest that the extent of petiole occupancy is mainly due to a combination of host quality, predation of ants, and the time since colonization by ant queens. We dissected plants of this species and counted all of the individuals (adults and brood in petioles and stem) to assess the accuracy with which non-destructive counts of the number of occupied petioles on a plant predicts colony size (Pearson's correlation).

Since beetles never occurred on the same plant as a spider, different models were run for beetles and spiders. Nonhierarchical models were appropriate because we were testing specific hypotheses. All cells containing zero counts were treated as sampling zeroes (*sensu* Bishop et al. 1975) and were assigned values of $1 \times 10^{-20}$ (SAS 1985). We used the maximum likelihood method for parameter estimation of linear models and chi-square statistics for hypothesis testing (SAS 1985).

**RESULTS**

Since associations between the plant species and densities of beetles ($X^2 = 1.09$, $df = 2$, $P = 0.580$), spiders ($X^2 = 2.59$, $df = 2$, $P = 0.274$), and ants ($X^2 = 0.67$, $df = 2$, $P = 0.716$) were never significant, data for the different species of *Piper* were pooled. Most *Piper* ant-plants had resident ant colonies (822 of 919 unmanipulated trees in this study) and 67 percent of the 822 plants that housed ants had ants in every petiole. In the entire sample of *Piper* ant-plants, colony size (% of petioles occupied) averaged 78.7 percent ($\pm 0.01$ SE, $N = 919$) per plant. For *Piper cenocladum* (and we suspect for the other species) the percent occupancy of petioles on the plant was a good indicator of colony size (Pearson's correlation coefficient $= 0.80$, $P < 0.0001$). Individual *Piper* ant-plants that lacked ant colonies fell into two categories: those that had been occupied at some time in the past, and those small fragments or saplings that had not yet been colonized by a *Pheidole* queen.

Relative densities of top predators, ants, herbivory, and ant-plants per ha patch differed among the four forests (Table 2); however, we observed very different patterns for *Phyllobaenus* beetles than...
for Dipoea spiders, both of which are members of the fourth trophic level. Overall, the top-down hypothesis of alternating densities of top predators, ants, herbivores and plants was supported only when Phylobaenus beetles (as opposed to Dipoea spiders) were the top predators. A significant three-way association between beetle, ant, and ant-plant densities ($X^2 = 39.30, df = 6, P < 0.0001$) indicated that beetles were common when Piper plants were sparse and ants were uncommon; and beetles were rare in forests with high Piper density and high levels of ant occupancy (Table 2). In contrast to the beetles, a significant three-way association between the densities of spiders, ants, and ant-plants ($X^2 = 28.56, df = 6, P = 0.0001$) supported a functionally three-level top-down trophic cascade (Table 2). Spider density patterns differed among forests, but there were usually high numbers of ants in plants with spiders.

Observations of the eight individually marked Dipoea spp. spiders indicated that they were not particularly voracious predators. The mean number of dead ants found/spider/d was 0.18 ± 0.12, and the mean number of other Dipoea spp. spiders on a plant was 1.73 ± 0.8; this provides a conservative estimate that the average predation rate of ants by spiders on an individual plant was only one ant every few days. Even if the predation rates were much higher, which may be the case if not all ants killed by the spiders were found in silk, the spiders did not appear to substantially reduce ant populations. During the observation period of individual spiders on Piper ant-plants (up to two wk), the numbers of petioles with ants always remained the same for each of the plants containing the spiders. None of the marked spiders moved from one plant to another and movements between different petioles was rare during the observation period.

**DISCUSSION**

Our general top-down hypothesis, that forests with high densities of top predators will have low densities of ants, high densities of herbivores, and low densities of plants, was supported in part by forest census data of the four-trophic-level community associated with the Piper ant-plant system. The density of beetles was highest in the Carara forest, which had the lowest ant and ant-plant densities, whereas beetle density was the lowest at Loma Linda which had high densities of ants and ant-plants (Table 2). Furthermore, herbivory levels were greatest at Carara and lowest at Loma Linda (Letourneau, pers. obs.; Table 2). Forests with intermediate plant densities (Corcovado & La Selva) had relatively intermediate herbivory levels, low levels of beetles and relatively high, somewhat more variable, levels of ants. One plausible hypothesis to explain these correlations is that at Carara, the fourth trophic level (beetles) had diminished populations of the third trophic level (ants) which released herbivores (second trophic level) from their density dependent controls; the subsequent increase in herbivory had a serious impact on plant vigor and/or reproductive capacity and led to much sparser ant-plant populations.

However, what happens if the fourth trophic level does not really influence the third level? Oksanen (1990) argues that predators must control the biomass of their prey in order to be considered a functional trophic level in a top-down cascade. Our observations indicate that Dipoea spiders did not have a significant impact on the ants, and as a result, there are functionally only three trophic levels in communities consisting of spiders, ants, herbivores, and ant-plants; herbivory should be controlled by the third trophic level (ants), and these communities should have higher Piper ant-plant densities (depending on plant resources and competition). And in fact, the forests where spiders were more common were forests that had relatively low herbivory and relatively high Piper ant-plant densities. These patterns fit top-down predictions for three functional trophic levels. Also, in the case of either Pheidole or Phylobaenus as predators in this system, but not spiders, donor-controlled resources (sensu Polis & Strong 1996) were available in the form of food bodies. That is, if ants were limiting, which could happen if ants avoid leaves that have resident spiders (Gastreich, pers. comm.), plant resources may have allowed increased numbers of ants or beetles and enabled the cascading effect of these predators.

Some elements of the bottom-up hypothesis may also explain spider density patterns. The fact that spiders were common in the forests with high ant-plant density could support the assumption that the productivity of the first trophic level establishes the number of trophic levels (Fretwell 1987, Oksanen 1991). Dipoea spider density was lowest in the forest with sparse Piper ant-plant density (Carara). Although levels of herbivory seem to be inconsistent with the bottom-up hypothesis (Table 3), energy flows primarily from plants to ants via food bodies (Letourneau 1983) and secondarily through herbivores (Fig. 1). Thus, top-down forces of predation (or killing) in this system show a weak link between spiders and ants, and a strong link
between ants and herbivores. Bottom-up, resource-dominated forces were weak between herbivory and ants. Also, since the spiders did not seem to function as a control of lower trophic levels, they constitute a better test for cascading up effects than do Phyllophaenus beetles, which initially may be more common in more productive forests, but would eventually cause higher mortality and lower reproductive success for the plants.

We also considered several alternative hypotheses (unrelated to cascading trophic interactions) that may explain the quantitative patterns observed among and within the four forests. First, the quantitative data on plants, ants, and top predators reflect a single temporal sample in each forest, and major differences could be explained by short-term, stochastic events that cause large population fluctuations (Andrewartha & Birch 1954, Wolda 1992). However, the patterns derived from these “snapshots” of each forest, reflected general observations from five years of work at Carara and over ten years of work at the La Selva, Corcovado, and Loma Linda sites (Letourneau, pers. obs.). More likely alternative explanations for the relative density patterns of ants, ant-plants and herbivory in these four forests would rely on fundamental, or at least long-term, differences between the forests themselves. Although these forests are all classified as wet forests (Holdridge 1967), by virtue of their locations in different regions of the country they represent a range in total precipitation, elevation, and size. These factors, alone or in combination, could influence the relative densities of ant-plants and their associated arthropods. The patterns of herbivory among forests, for example, could be explained if a somewhat longer dry season encouraged plant stress, which encouraged herbivory (at Carara) and that herbivores are limited in higher elevations (at Loma Linda), resulting in herbivory levels lower than in the two lowland forests with short dry seasons (La Selva and Corcovado). However, ants would be unlikely to respond to climate/elevation in an opposite pattern to herbivores, and their abundance in the plants would have to be explained by independent processes. None of the abundance patterns discovered for plant density, ant density, herbivory, or predator density correlates with changes in elevation, rainfall, or size of the forest, and we are not aware of theoretical predictions for the relative prominence of different trophic levels based on abiotic factors or “island” size.

Speculation about events that created the initial differences in beetle densities among the four forests is beyond the scope of our correlational data. Geographic differences could, however, affect beetle density and subsequent cascading effects could be responsible for the density patterns of the other trophic levels. The patterns in our data are more consistent with this hypothesis than with the notion that geographic patterns explain the densities of all trophic levels. Indeed, indirect trophic effects are often ignored when explaining geographical patterns of species abundance.

In conclusion, density patterns of organisms associated with an ant-plant system in different forests were consistent with predictions of trophic cascades theory. Our quantitative data showed that the presence of one top predator (Phyllophaenus) was associated with sparser densities of intermediate predators (Pheidole), higher levels of herbivory, and lower densities of plants (Piper ant-plants). We have now shown, with experimental manipulations, that Phyllophaenus beetles cause trophic cascades in the P. cecnocladum system at La Selva (Letourneau & Dyer, in press). On the other hand, in areas where the top predator may be ineffective (Didopaena), a three-level trophic cascade

### TABLE 3. Relative densities of individuals in all the trophic levels in the Piper plant systems for Carara and Loma Linda, contrasting beetles with spiders. Densities are categorized as high and low to compare results with predictions from Table 1.

<table>
<thead>
<tr>
<th>Trophic level</th>
<th>Carara</th>
<th>Loma Linda</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beetles/Spiders</td>
<td>High/Zero</td>
<td>Low/High</td>
</tr>
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<td>Ants</td>
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<td>Herbivory</td>
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<td>Low</td>
</tr>
<tr>
<td>Plants</td>
<td>Low</td>
<td>High</td>
</tr>
</tbody>
</table>

### FIGURE 1. Asymmetry of bottom-up forces (energy flow depicted by upward, solid arrows) and top-down forces (impact of consumers/killers depicted by downward, dashed arrows) on *Piper* ant-plant systems with beetles and spiders. Thickness of arrows indicates strength of energy flow or predation.
may prevail. Additionally, for spiders, bottom-up cascades may occur; the presence of the *Dipoena* spiders is associated with high plant densities and large ant colonies.

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**LITERATURE CITED**


