INDIRECT EFFECTS OF A TOP PREDATOR ON A RAIN FOREST UNDERSTORY PLANT COMMUNITY

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Abstract. Tropical rain forests, some of the most diverse natural communities, have been characterized either as inherently stable or as extremely fragile. Theoretically, complex food webs allow for alternative pathways and overlapping functions within and among trophic levels, such that cascading effects are buffered and perturbation is resisted. On the other hand, strong interdependence among species and trophic levels in these same systems can make them vulnerable to perturbation. To assess the ability of a tropical rain forest community to resist perturbation or to amplify perturbation through trophic cascades, we measured changes in overall vegetative cover and species richness of understory plants in response to the experimental addition of a top predator beetle.

In August 2000, 30 randomly located patches of naturally occurring Piper cenocladum shrubs were found at sites with variable soil quality and light availability, and top predator addition treatments were randomly assigned to half the patches. Using an 8-m² subplot within each P. cenocladum patch, we estimated (nondestructively) vegetative cover of understory plants for nine months and measured herbivore damage, plant longevity and plant species richness for ~1.5 years.

For all understory species in our subplots, vegetative cover and total numbers of leaves declined significantly more in predator addition patches than in control patches. Understory cover also declined significantly more on poor soils than on rich soils. Mortality of small plants was high overall, but longevity was significantly greater in control patches than in patches with top predators. Herbivore damage was lowest, plant establishment highest, and the accumulation of new plant species highest in control plots on rich soils. The cumulative effect of top predators interacting with plant resources, such that plant species richness was suppressed when beetles were present in understory communities on rich soils. Patterns of herbivore damage suggest that trophic cascades from apex predators through ant predators to herbivores altered the structure of understory vegetation. The presence of indirect effects supports the characterization of rain forests as vulnerable ecosystems whose integrity may be threatened by the slow erosion of complex tight interactions among species.

Key words: ant-plant; biodiversity; bottom-up forces; consumer vs. resource control; Costa Rica; Piper; Pheidole; soil nutrients; trophic cascade; tropical rain forest.

INTRODUCTION

By virtue of their high species diversity, rain forest communities may either exhibit relative stability (low population variances), with alternative trophic pathways buffering small disturbances, or vulnerability (high population variances), with disturbances magnified through strong links between species (McCann 2000). Vandermeer and Perfecto (1995) contrast these opposing notions of a tropical rain forest with metaphors of a stable spider web vs. a vulnerable house of cards. The presence of trophic cascades (Hairston et al. 1960, Paine 1966, Fretwell 1977, Spiller and Schoener 1990, 1994, Schmitz 1994, Brett and Goldman 1996, Schoener and Spiller 1996, Shurin et al. 2002, Preisser 2003), defined broadly as indirect effects of a change in one trophic level caused by a nonadjacent trophic level, may be an indicator of magnified effects, or vulnerability, in a rain forest community. Cascading effects should be absent in a complex community if high diversity allows for buffering and compensation among species and trophic levels (Strong 1992, Polis and Strong 1996, Polis and Winemiller 1996). In the case reported here, if the diversity of species in tropical rain forest communities promotes stability via resistance to perturbation, a change in the abundance of top predators should not affect the understory vegetation three trophic levels below. However, if species interdependence increases vulnerability in complex communities, then perturbation at the top of a food web might cause a community-wide trophic cascade (Dial and Roughgarden 1995, Terborgh et al. 2001, Schmitz 2003, Van Bail et al. 2003). The classic model of top-down trophic cascades predicts that ecological systems
with even numbers of trophic levels will have herbivore-limited plant biomass and systems with odd numbers will have resource-limited plant biomass (Hairston et al. 1960, Power 1992). Such top-down forces may also alter species diversity on nonadjacent trophic levels (Paine 1995, Kneitel and Miller 2002, Dyer and Letourneau 2003, Schmitz 2003).

In previous experiments, we have demonstrated that the pulsed addition of top predator beetles to Piper cenocladum C. DC. (Piperaceae) ant-plants cascades through its ant prey (lower ant density) and the ant’s herbivore prey (increased herbivory) to reduce the size of the ant-plants in the rain forest understory (Letourneau and Dyer 1998). The results of those experiments can be interpreted in two different ways. The first interpretation is consistent with the rain forest as diverse and stable. The effects of adding a single top predator on the size or biomass of a rain forest understory plant is evidence that indirect effects in a complex community manifest as “species-level cascades” (Polis et al. 2000) or “trophic trickles” (e.g., Halaj and Wise 2001), involving a few species, but lacking significance in the community as a whole. Additional evidence for the idea that cascading effects should be rare and confined, may reside in our findings that bottom-up factors did not have clear indirect effects in the system (Letourneau and Dyer 1998, Dyer and Letourneau 1999a). The second point of view supports the rain forest metaphor as a house of cards, which may topple if a single card is added or removed (Vandermeer and Perfecto 1995). In this interpretation, the ability of a lone species to cause cascading effects on other species on other trophic levels suggests that buffering and compensation by other species in the diverse community are not reliable processes. That is, indirect effects were neither buffered by omnivory in the system nor compensated by the existence of other species of top predators, other predators, and parasitoids of herbivores, or by the diverse array of ant-susceptible and ant-resistant herbivores in the community. The fact that neighboring P. cenocladum shrubs also experience higher herbivore damage when top predator beetles are present (Dyer and Letourneau 1999b) suggests the possibility that these effects have the capacity to extend to the entire community. The diversity of the endophytic community (>50 species of animals) residing within P. cenocladum shrubs was also affected by top predators (Dyer and Letourneau 2003).

Preliminary observations of the surrounding understory further suggested the presence of indirect, community-wide effects of our experimental perturbation (Dyer and Letourneau 1999b; L. A. Dyer and D. K. Letourneau, unpublished manuscript). Therefore, we mounted an expanded 19-month experiment in which we added the same top predator, and examined community-level parameters: relative change in understory plant cover, dynamic changes in the community, and species richness. To reinvestigate the role of bottom-up forces in determining aspects of community structure, we manipulated top predator abundance under different conditions of plant resource availability: soil quality and light. This design enabled us to consider variation in top-down forces as a function of bottom-up heterogeneity (Hunter and Price 1992). The present experiment, then, reexamines two of the conclusions from our past work. Specifically, is the “trophic trickle” from a predaceous beetle to a rain forest shrub restricted to a linear food chain, and unaffected by resource heterogeneity? Or is that conclusion an artifact of the experimental design, which emphasized a single species of shrub? Although certainly complex food webs in rain forest communities cannot be described accurately as either strictly stable or extremely fragile, if the understory in general is not affected by our manipulations, then our experiments suggest relative stability. If top predator effects cascade to the plant community, the vulnerability model is supported.

**METHODS**

**Study site**

Experiments were conducted at the La Selva Biological Station, Heredia Province, Costa Rica, located at an elevation of ~100 m on the nation’s Caribbean slope, with coordinates 10°26’N 83°59’W (Hartshorn and Hammel 1994; more information about La Selva Biological station is available online). Primary and secondary lowland rain forest comprises most of the reserve, and constitutes a complex terrestrial habitat with extremely high biodiversity (Janzen 1983, McDade et al. 1994).

**Study system**

We tested for community cascades in an understory rain forest system composed of numerous plants, herbivores, predators, and top predators interacting with P. cenocladum, an understory shrub (usually >4 m tall) that thrives in low-lying, swampy areas of La Selva Biological Station, and occurs commonly throughout the Atlantic lowlands (Burger 1971). The stems are usually hollow due to the presence of ant colonies that inhabit stems after removing the pith. Opalescent food bodies, rich in lipids and proteins, are produced on the adaxial side of sheathing leaf bases (referred to hereafter as petiole chambers). Food bodies are only abundant in petiole chambers occupied by Pheidole bicornis Forel ants or by Tarsobaenus letourneuae Barr (Coleoptera: Cleridae; formerly Phyllobaenus sp.; W. Barr, unpublished manuscript) beetle larvae (Risch and Rickson 1981, Letourneau 1990). P. cenocladum occurs only in relatively undisturbed forest; that is, the shrubs are common in primary forest at La Selva Biological Station and in areas that were selectively logged over 50 years ago, but that retain a full complement of emergent tree species. Therefore, the veg-
etation associated with *P. cenocladum* is typical of swampy understory areas at the study site, with a rich array of palms, canopy and subcanopy trees, ferns, vines, lianas, and herbs, occurring as seedlings, juvenile, and mature individuals.

Arthropods associated with *P. cenocladum* form a food web with four trophic levels, each with multiple species. The herbivores most commonly found feeding externally on *Piper* ant-plants at La Selva Biological Station are hymenopterans, orthopterans, coleopterans, and lepidopterans. Eggs and soft-bodied larvae, primarily the lepidopteran foliovores and stem-boring weevil larvae, are vulnerable to resident ants foraging on and in the plant. *Ph. bicornis* ants rapidly encounter small, soft-bodied insects on leaves and either pull them inside the hollow stem or petiole chambers (presumably as food for the colony) or drop them off the foliage to the forest floor (Letourneau 1983). Lepidoptera feeding on *P. cenocladum* foliage at La Selva include: seven specialist geometrids found feeding only on *Piper* spp., two hesperid *Piper* specialists, and a species of generalist herbivores in each of six families (Marquis 1991; L. A. Dyer, G. Gentry, and D. K. Letourneau, personal observation). Internal herbivores were not assessed in the current study (but see Dyer and Letourneau 2003).

Seven ant species have been found to inhabit *P. cenocladum* shrubs at La Selva. By far the most common species is *Pheidole bicornis*, a small, dimorphic ant (Formicidae: Myrmicinae) that occupies over 95% of *Piper* ant-plants at La Selva. This ant both stimulates the production of food bodies by the plant and harvests these protein- and lipid-rich, swollen epidermal cells for the brood. As it forages on the surface of the plant, *Ph. bicornis* removes some insects, some vines, and small phylloplane particles from the leaves (Risch et al. 1977, Letourneau 1983, 1998). In addition to the predaceous ants inhabiting the plants, we have observed numerous other predators and reared parasitoids that cause mortality to *P. cenocladum* herbivores.

Several species of ant predators occur occasionally on *P. cenocladum* shrubs. Two types consume adult ants: owly larvae (Neoptera: Ascalaphidae) resemble lichens as they flatten their bodies against the leaf blade and await foraging ant prey, and tiny spiders (Arachnida: Araneae: *Dipoena* spp.) position themselves near the entrance/exit holes used by ants. At least two species, a hover-fly larva (*Diptera: Syrphidae: Microsiphon* sp.) and a beetle larva (*Coleoptera: Cleridae: T. letourneauae*) live inside the petiole chambers and feed on ant brood. Larvae of the beetle *T. letourneauae* (*Coleoptera: Cleridae*) occur patchily, with usually one or two, but occasionally up to four individuals living in the petiole chambers of a *P. cenocladum* shrub (Letourneau 1990; D. K. Letourneau, L. A. Dyer, and G. Vega C., personal observation). Shrubs containing clerid beetles are relatively rare; locally common infestations are either the result of a single ovipositing female, many females attracted to the site, or local reproduction of resident beetles. The former is least likely because larvae in the same patch tend to be of different sizes. Adult beetles oviposit on the outside of the sheathing leaf base. We have observed both early instar larvae and pupae in partitioned off petiole chambers, separated from the ant colony by a barrier that presumably is secreted by the larva. Often, later instars are found inside petiole chambers with no barrier; sometimes there are dead ants in the chamber, and other times, ants are not found in that portion of the shrub. In all cases, the plant in the presence of the larva produces food bodies. We have reared this clerid from egg to adult on food bodies, on ant larvae (*Ph. bicornis* and other species), and on a combination of brood and food bodies. The former is particularly interesting, because to our knowledge, all clerids are carnivorous.

**Experimental design**

We conducted a 19-month experiment from August 2000 to March 2002. We used GIS to design a stratified random sample of natural stands of *P. cenocladum* throughout La Selva Biological Station. Two trail markers (~60 km of trails with markers at 50-m intervals) were randomly selected in each of 15 equal areas of ~105-ha. *P. cenocladum* patches of at least 10 shrubs with active ant colonies in a 10 × 10 m area, were located after moving 50 m off-trail into the forest from the marker (Fig. 1). A single 2 × 4 m understory plant census plot was established within each of the 30 patches. Each census plot within the patches contained a minimum of three *P. cenocladum* individuals. Half (15) of the *P. cenocladum* patches were randomly designated as treatment patches for top predator additions; six *T. letourneauae* larvae were collected from outside the experiment and manually transferred to petiole chambers of *P. cenocladum* shrubs in each treatment patch. Clerid beetle larvae were added (one per plant within or closest to the census plot) to each of the 15 10 × 10 m treatment patches every two months, for 15 months. The remaining 15 plots were used as controls for that treatment, such that any predatory *Tarsobaenus* beetles were removed from the plants, maintaining healthy colonies of *Ph. bicornis* ants.

Artificial placement of clerid beetle larvae into petiole chambers subjects early instar larvae to unnaturally high levels of ant defensive behaviors. To reduce mortality of larvae manually transferred into ant-occupied petiole chambers, we applied 0.85 mg Diazinon-50 wettable powder (0.0-diethyl-0-(2-isopropyl-6-methyl-4-pyrimidinyl) phosphorothioate; MicroFlo, Lakeland, Florida, USA) diluted with 50 mL water at 2 cm⁻² per petiole to weaken the colony 2–4 weeks before top predator beetle larvae were placed in the petiole chamber. In a previous experiment, we determined that the insecticide weakens the colony for 4–6 weeks, but does not have a lasting effect on colony size. Within two months, there was no significant difference between
ant colony size in plants with and without insecticides (Dyer and Letourneau 1999b). However, once a beetle larva was established in the plant, ant levels remained low until it pupated and emerged as an adult (2–4 months). On average, ~70% of the petiole chambers per control plant were occupied by ants compared to ~20% ant occupancy of the petiole chambers per plant in the beetle predator treatment. Occasionally, ant colony size increased sufficiently in an individual plant due to early emergence of a beetle larva, that insecticide was reapplied to successfully introduce a new beetle larvae. Although the dilute insecticide causes some ant mortality, our field trials on naturally occurring shrubs required over four orders of magnitude higher insecticide concentration applied continually (weekly or monthly) to suppress ant colonies to the level maintained by beetle larvae.

Plant resource conditions varied among the 30 patches of naturally occurring *P. cenocladum* shrubs. Using GIS coordinates, we overlaid our study plots on a soil map generated for the La Selva Biological Station (Fig. 1; Sollins et al. 1994). Although finer detail regarding both residual soils and alluvial soils is available from soil surveys based on 25 samples/1 km² throughout the forest, we used the broad designation of rich soils as inceptisols (relatively fertile, immature soils with poorly developed lower horizons) and poor soils as ultisols (highly weathered, low stock of basic cations, relatively infertile), and rechecked our designations using the most recent results available (D. A. Clark and D. B. Clark, unpublished data). Relative availability of light to each understory plot was estimated for each of three *P. cenocladum* shrubs in each plot by measuring the amount of canopy cover at four cardinal directions with a spherical densiometer (Forest Densiometers, Bartlesville, Oklahoma, USA). Forest canopy cover for understory plants at La Selva is high, ranging in our study from 89.3% to 93.3%. However, small changes in the density of the canopy have been associated with significant changes in shrub size and herbivore damage levels in past studies on this system (Letourneau and Dyer 1998, Dyer and Letourneau 1999b), and on seedling success in the understory (Montgomery and Chazdon 2002). We designated the high-light treatment to patches with a cover value less than the average cover for all plots, and regarded a patch as low light if it was greater than or equal to the mean value for percent canopy cover.

All herbs, palms, ferns, saplings, and shrubs occurring within the plot with a height $\geq$20 cm and <200 cm (referred to as plants) were tagged with a unique number, identified to genus or species, and mapped. The height, total number of leaves, herbivore damage, mortality, and species of each individual in the plot was recorded initially, and at 3, 5, 7, and 9 mo after top predator treatments were applied. The number of leaves, mortality, species identification, and herbivore damage were measured at 11, 15, and 19 mo. Similarly, every herb, fern, palm, shrub, or tree seedling with a height <20 cm (referred to as plantlets) was numbered and located on a separate map initially. For each plot the emergence, presence, or death of these
plantlets were surveyed at 3, 5, 7, 9, 11, 13, 15, 17, and 19 mo after top predator treatments were established. Herbivore damage (present or absent) was recorded on plantlets at 11, 13, 15, 17, and 19 mo. Because species identification is difficult for many understory plants, individuals were not identified until they grew to 20 cm as established recruits to the larger plant category. To measure herbivory on plants ≥20 cm, each plant was assessed one of seven categorical estimates of the proportion of total leaf tissue lost to herbivores: 0%, 10%, 15%, 25%, 50%, 75%, and 100% of leaf area lost. To test for an increase in herbivory over the course of the experiment, we compared the difference in the average estimated percentage of leaf area lost to herbivores (levels just after final predator addition at 15 mo minus initial levels before any predators were added) in top predator vs. control plots.

**Statistical analyses**

We used SAS version 8.2 for all analyses (SAS 1990). To assess the importance of top predators, soil quality, and light levels on the understory plant community, we compared differences in plant biomass accumulation (number of leaves, height, canopy width), the fate of plants over time (death, status quo, plant recruitment), and changes in herbivory levels and species richness using the General Linear Model ANOVA; data were transformed, if necessary, to meet the assumption of normality. Although periodic monitoring of each individual plant in every experimental plot was necessary logistically to track changes in each of the plant growth and survival parameters, we focused our analyses on the difference between the first (pretreatment condition) and last measurement taken, as an overall assessment of change in the understory community over the course of the experiment. Because of the small number of plots and inclusion of several independent variables, alternative statistical techniques such as ANCOVA or repeated-measures ANOVA were not possible due to lack of degrees of freedom. The association between canopy cover (light availability) in individual plots and plant mortality, growth to 20 cm, and plant species richness change was determined using Pearson’s correlation coefficient. To determine if certain results for the understory community in general were significantly different from those for the manipulated species (*P. cenocladum*), results for all plants and for all plants excluding *P. cenocladum* were compared using a MANOVA with profile analysis.

**Results**

Plant species richness in the understory, as determined only by individuals between 20 and 200 cm in height, was impressive, reflecting the high diversity expected in a complex, lowland, tropical, wet forest. The number of species of herbs, ferns, shrubs, and small trees per 8-m² plot ranged from 6 to 26. With relatively low overlap of species among plots, our sample of ~1200 plants represented 146 species in 55 plant families for the total 240-m² area. For comparison, plant species richness was 25% and 50% of this figure in much larger samples of forest understory in Alaska (alder–Sitka spruce forest had 29 species of herbs, ferns, and shrubs in plots totaling 500 m²; Deal 1997) and in coastal California redwood light gaps (72 species of ferns, herbs, grasses, shrubs, and small trees occurred in plots totaling 1024 m²; B. Blair and D. K. Letourneau, *unpublished data*), respectively.

Despite its complexity, the overall understory plant community was significantly affected by the addition of top predators to *P. cenocladum*, and resource availability influenced these effects. Although we used non-destructive measures in the 2 × 4 m subplots rather than samples of actual primary production, our results suggest that both top predator additions and poor soil conditions decreased the accumulation of plant biomass over time. The average amount of foliage per plot and average height of plants declined significantly over nine months when predaceous beetles were added to *P. cenocladum* shrubs, compared to control plots (Table 1). The average canopy width of understory plants increased, on average, in control plots and for rich-soil plots, in general, compared to predator addition plots and poor-soil plots (Table 1). The effects of light levels

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**Table 1.** Gains or losses per plot (means ± 1 se) in overall vegetative cover nine months after top predators were applied, calculated for all plants 20–200 cm at La Selva Biological Station, Costa Rica.

<table>
<thead>
<tr>
<th>Treatment or condition</th>
<th>No. leaves†</th>
<th>F</th>
<th>P</th>
<th>Plant size (summed heights; cm)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predation</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Top predator added</td>
<td>−42.8 ± 11.8</td>
<td>4.57</td>
<td>0.0440</td>
<td>−234.1 ± 100.7</td>
</tr>
<tr>
<td>No predator</td>
<td>−9.3 ± 7.8</td>
<td></td>
<td></td>
<td>−27.5 ± 73.0</td>
</tr>
<tr>
<td>Soil quality</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rich soil</td>
<td>−8.6 ± 10.2</td>
<td>3.73</td>
<td>0.0666</td>
<td>35.8 ± 45.1</td>
</tr>
<tr>
<td>Poor soil</td>
<td>−39.4 ± 10.0</td>
<td></td>
<td></td>
<td>−209.7 ± 105.0</td>
</tr>
<tr>
<td>Light level</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High light</td>
<td>−33.7 ± 8.1</td>
<td>1.30</td>
<td>0.2666</td>
<td>−76.4 ± 62.3</td>
</tr>
<tr>
<td>Low light</td>
<td>−18.4 ± 12.8</td>
<td></td>
<td></td>
<td>−130.3 ± 118.1</td>
</tr>
</tbody>
</table>

**Notes:** Gains or losses were calculated as the average difference between the total in 2 × 4 m plots in May 2001 minus initial measures in August 2000, prior to beetle additions. Significant values are shown in boldface. All df values are 1, 26.  † No significant differences in any of the interactions between predator, soil and/or light.
TROPHIC CASCADE IN RAIN FOREST

Table 1. Extended.

<table>
<thead>
<tr>
<th></th>
<th>F</th>
<th>P</th>
<th>Plant cover (summed canopy widths; cm)²</th>
<th></th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4.43</td>
<td>0.0468</td>
<td>57.1 ± 66.5</td>
<td></td>
<td>6.64</td>
<td>0.0172</td>
</tr>
<tr>
<td></td>
<td>2.74</td>
<td>0.1122</td>
<td>178.9 ± 105.5</td>
<td></td>
<td>4.50</td>
<td>0.0453</td>
</tr>
<tr>
<td></td>
<td>0.28</td>
<td>0.6024</td>
<td>143.3 ± 93.7</td>
<td></td>
<td>3.88</td>
<td>0.0616</td>
</tr>
</tbody>
</table>

were variable, and there were no significant interactions between predator treatment, soil quality, and light levels on the changes in average plant size over nine months.

Top predator additions were also associated with changes in species richness over the course of the experiment, but these effects were modified by bottom-up factors (soil quality and light; Fig. 2). Specifically, the addition of top predators depressed species richness compared to control plots, but only on rich soils (ANOVA, soil by predator interaction, $F_{1,22} = 4.68, P = 0.0417$). The average percentage of new plant species accumulated over time in rich-soil plots with no top predators was 29 ± 7%, whereas no increase in species richness occurred in rich-soil plots with top predators (2 ± 9%) (ANOVA, soil by predator interaction, $F_{1,22} = 6.61, P = 0.0174$).

Some clarification of the mechanisms underlying significant top-down and bottom-up effects on the understory community is possible using data on the fate of individual plantlets in our experimental plots. A large percentage (approximately half) of the small plants found in the understory did not survive to reach 20 cm in height, but determining the cause of death was beyond the scope of our censuses every two months (Tables 2 and 3). There was some tendency for mortality to be greater in plots in the low-light category, and lower in rich-soil plots with no top predators. These are backed up by significant correlations between canopy cover and average percentage of plantlets dying ($r = 0.74, P = <0.0001$) and the percentage of plantlets reaching 20 cm in height ($r = -0.62, P = 0.0005$). On average, new plantlets lived for 4–6 months in the various treatments, such that they were monitored and measured for two to three censuses before they disappeared from the plot. The exceptions to that rule were significantly greater, however, in the presence of top predators. Rapid mortality (the percentage of plantlets living <2 mo) was nearly three times more common in plots with top predators (18.2%) than in control plots (6.6%) (Tables 2 and 3). Plant establishment (percentage of the plantlets that were recruited to the plant category ≥20 cm in height) was significantly affected by both top-down and bottom-up factors. Plantlet success was significantly greater when top predators were absent. The effect of predators was greater on rich soils, and high-light conditions favored plantlet success (Tables 2 and 3). In contrast to the multifaceted effect on understory plants in general, the only significant factor reducing the establishment rate of $P. cenocladum$ plantlets was top predators.

The negative effect of top predators on plants in the local community suggests an herbivore-mediated response to the manipulation rather than a plant–plant competition effect. We found no evidence of beneficial effects associated with some reduction of competition from $P. cenocladum$ in top predator plots. We did, however, find that the addition of top predators to $P. cenocladum$ shrubs caused an increase in herbivore damage compared to control plots (Table 4). This increase in herbivory occurred whether or not $P. cenocladum$ itself was excluded from the analysis, so the effect was a general one, extending throughout the plant community (MANOVA treatment effect; Table 4). However, the strength of the effect on all species other than $P. cenocladum$ was significantly greater on rich soils than on poor soils, whereas the effect on $P. cenocladum$ shrubs only was not modified by soil quality (MANOVA profile analysis; Table 4).

![Fig. 2. Mean change (+1 se) in species richness of all plants (herbs, ferns, shrubs, tree saplings) 20–200 cm in height, for plots with (open bars) and without (solid bars) top predators added, on rich and poor soils.](image)
Unexpected “ripple effects” on the understory community were caused by the pulsed addition of predatory clerid beetles to their host plant *P. cenocladum*. In prior experiments, we demonstrated that the effects of top predator additions cascade through three trophic levels to finally reduce the size of *P. cenocladum* plants (Dyer and Letourneau 1999b; Letourneau and Dyer 1998). Preliminary comparisons of shrubs found in the forest with and without beetles suggested, also, that the effects of top predators may not be confined to individual plants, but may extend to other *P. cenocladum* shrubs and other plants in the understory (Dyer and Letourneau 1999b; D. K. Letourneau and L. A. Dyer, unpublished manuscript). Indeed, indirect effects on the understory plant community reached as far as changes in species richness. The inclusion of soil quality and canopy cover as factors in our experiments showed that top-down effects of clerid beetles were often complemented or modified by bottom-up factors.

The modifying influence of soil quality and light, both bottom-up factors, on the strength of top-down effects on the understory community as a whole was manifest in plant establishment rates (recruitment to ≥20 cm category), overall levels of herbivory, and the accumulation of plant diversity. Rich soils potentially give rise to higher quality food for herbivores, thus enhancing their ability to reduce the success and recruitment of new plant species in the local area (Price 1991). A significant pattern of more vegetative cover on rich soils during the course of the experiment may indicate that plant growth was slower on poor soils. The growth rate of understory plants may have determined the size and timing of indirect effects of herbivores on plants. Alternatively, species composition of the understory itself may change with soil quality such that more resistant species occur on poor soils (Coley et al. 1985). Of the 146 plant species identified in our plots, 25 species occurring in plots on rich soils did not occur in our poor-soil plots, and 45 species occurred on poor soils but not in rich-soil plots.

Two mechanisms by which top predators could affect the plant community in general were considered: relaxed plant–plant competition and herbivore release. However, the direction of the outcome was predicted to be opposite for the two mechanisms. Plant–plant competition would be relaxed by top predators, which indirectly reduce *P. cenocladum* biomass, cause *P. cen-

### TABLE 2. Comparison of plantlet (<20 cm) mortality, longevity, and success rate (recruitment to plant category) over 16 months in 2000–2001.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No. plots</th>
<th>Mortality of all plantlets (%)</th>
<th>Rapid mortality of plantlets (alive &lt;2 mo; %)</th>
<th>Plantlets established as plants (≥20 cm; %)</th>
<th>Plantlets established as <em>P. cenocladum</em> plants (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top predator added (pred.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rich soil</td>
<td>6</td>
<td>53.0 ± 5.7</td>
<td>18.8 ± 2.2</td>
<td>5.6 ± 1.4</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>Poor soil</td>
<td>9</td>
<td>52.3 ± 3.2</td>
<td>17.5 ± 1.6</td>
<td>7.1 ± 1.6</td>
<td>1.4 ± 1.4</td>
</tr>
<tr>
<td>High light</td>
<td>7</td>
<td>50.5 ± 4.9</td>
<td>16.8 ± 1.7</td>
<td>7.0 ± 1.5</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>Low light</td>
<td>8</td>
<td>54.4 ± 3.4</td>
<td>19.3 ± 2.0</td>
<td>6.0 ± 1.7</td>
<td>2.7 ± 1.4</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rich soil</td>
<td>7</td>
<td>38.6 ± 8.6</td>
<td>9.6 ± 2.2</td>
<td>26.0 ± 5.0</td>
<td>10.9 ± 3.0</td>
</tr>
<tr>
<td>Poor soil</td>
<td>8</td>
<td>56.7 ± 7.0</td>
<td>4.3 ± 1.3</td>
<td>9.8 ± 0.4</td>
<td>4.0 ± 2.8</td>
</tr>
<tr>
<td>High light</td>
<td>9</td>
<td>43.6 ± 8.8</td>
<td>2.7 ± 1.1</td>
<td>19.4 ± 4.9</td>
<td>2.4 ± 1.7</td>
</tr>
<tr>
<td>Low light</td>
<td>6</td>
<td>55.2 ± 6.1</td>
<td>10.3 ± 2.0</td>
<td>14.3 ± 4.1</td>
<td>16.0 ± 4.3</td>
</tr>
</tbody>
</table>

### TABLE 3. ANOVA values for comparison of plantlet (<20 cm) mortality, longevity, and success rate (recruitment to plant category) over 16 months in 2000–2001.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mortality of all plantlets (%)</th>
<th>Rapid mortality of plantlets (alive &lt;2 mo; %)</th>
<th>Plantlets established as plants (≥20 cm; %)</th>
<th>Plantlets established as <em>P. cenocladum</em> plants (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top predator added (pred.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil quality</td>
<td>0.76</td>
<td>0.3929</td>
<td>6.42</td>
<td>0.0189</td>
</tr>
<tr>
<td>Light</td>
<td>2.87</td>
<td>0.1043</td>
<td>0.44</td>
<td>0.5130</td>
</tr>
<tr>
<td>Pred. × soil</td>
<td>3.61</td>
<td>0.0707</td>
<td>0.85</td>
<td>0.3668</td>
</tr>
<tr>
<td>Pred. × light</td>
<td>3.32</td>
<td>0.0820</td>
<td>1.19</td>
<td>0.2872</td>
</tr>
<tr>
<td>Soil × light</td>
<td>1.28</td>
<td>0.2695</td>
<td>0.56</td>
<td>0.4610</td>
</tr>
<tr>
<td>Pred. × soil × light</td>
<td>1.87</td>
<td>0.1852</td>
<td>0.17</td>
<td>0.6854</td>
</tr>
</tbody>
</table>

Note: Significant values are shown in boldface.
† All df values are 1, 22.
‡ All df values are 1, 21.
8% of the extra plantlets recruited in control plots were also consistent with the herbivore release hypothesis rapid seedling mortality in predator addition plots, is livory compared to control patches. Only a small por-
cruitments, and, especially on rich soils, higher fo-
rapid mortality of small plants, reduction in larger plant
the experiment. Top predators were associated with
the accumulation of plant material over the course of
suppression. Both top predators and poor soils reduced
species richness in top predator plots compared to con-
direct effects of top-down and bottom-up forces on an
understory plant community in a tropical forest suggests that these communities are vulnerable to sub-
tle disturbance, at least on the temporal scale of our
experiment (Bell et al. 2003). The presence or absence
of a single species (top predator beetle) led to far-
reaching consequences in the local plant community,
from the amount of foliage and size of plants to plant
diversity. Although the system may be resilient over
longer time scales, the dramatic indirect effects shown
in our experiment do not support the notion that rain
forest communities are stable and resistant to pertur-
bance because of their complexity.

\[\begin{array}{|c|c|c|c|}
\hline
\text{Treatment} & \text{No. plots} & \text{All species} & \text{All species except} \\
\hline
\text{Predator} & 15 & 8.2 \pm 1.4 & 5.3 \pm 1.6 \\
\text{Rich soil} & 6 & 7.1 \pm 1.8 & 6.3 \pm 1.9 \\
\text{Poor soil} & 9 & 8.8 \pm 2.0 & 4.6 \pm 2.5 \\
\text{Control} & 15 & 2.9 \pm 1.6 & 1.3 \pm 1.2 \\
\text{Rich soil} & 7 & 2.9 \pm 2.7 & 0.1 \pm 1.5 \\
\text{Poor soil} & 8 & 2.9 \pm 2.1 & 2.4 \pm 1.8 \\
\hline
\end{array}\]

Note: ANOVA for all species; predator vs. control, \(F_{1,26} = 5.20, P = 0.0310\); poor soil vs. rich soil, \(F_{1,26} = 0.14, P = 0.7156\); predator by soil interaction, \(F_{1,26} = 0.15, P = 0.7015\).

\(P.\) cenocladum plants to be smaller, and thereby pose less of a competitive presence for other plants. The predicted result would be increased survivorship, longevity, recruitment, and species richness in top predator treat-
ments. Empirical studies have consistently demon-
strated that plant competition does not occur in the
understory of tropical rain forests (Wright 2002), so this outcome was not expected. In contrast, an herbi-
vore release mechanism would predict that top pred-
ators indirectly increase \(P.\) cenocladum herbivores, such that more herbivores (primarily generalist lepi-
dopterans) are available to forage on other plants. Be-
cause ants are not regulating caterpillars in the plots, a
general increase in herbivore load would result in
decreased survivorship, longevity, recruitment, and/or
species richness in top predator plots compared to con-
trol plots. This effect might be diminished if herbivores
focused on dominant plant competitors, but herbivore
release is still the only plausible mechanism to explain a
decrease in plant diversity. In all cases, indirect ef-
fects of top predators on the understory vegetation were
consistent with an herbivore release mechanism.
Because herbivory accumulated on plants to a signifi-
cantly greater extent in top predator addition plots than
in controls, and the pattern was true for \(P.\) cenocladum
and all other species combined, we suspect that both
specialist (mostly geometrids and hesperiids) and gen-
eralist lepidopterans (such as the apatelodid \(Tarchon\)
sp. and limacodid \(Euclea\)插ma) responded to ant
suppression. Both top predators and poor soils reduced the accumula-
tion of plant material over the course of the
experiment. Top predators were associated with rapid mortality of small plants, reduction in larger plant
recruitments, and, especially on rich soils, higher fo-
livory compared to control patches. Only a small por-
tion of these general results for the understory plant
community can be explained by a likely release of her-
ivores on only the \(P.\) cenocladum plantlets. Less than
8% of the extra plantlets recruited in control plots were
\(P.\) cenocladum (Tables 2 and 3). The prominence of
rapid seedling mortality in predator addition plots, is also consistent with the herbivore release hypothesis
rather than the competition reduction hypothesis.
Therefore, we suggest that top predators added to \(P.\)
cenocladum shrubs indirectly altered the structure of the
understory community by suppressing predatory plant-
ants and thereby releasing generalist herbivores,
primarily lepidopterans, which moved into the sur-
rounding vegetation. Whether or not this effect was
strong enough to manifest itself as a change in plant
diversity depended on bottom-up forces acting through
soil quality, plant quality/phenology, and/or plant spe-
cies composition.

In conclusion, the demonstration of direct and in-
direct effects of top-down and bottom-up forces on an
understory plant community in a tropical rain forest
suggests that these communities are vulnerable to sub-
tle disturbance, at least on the temporal scale of our
experiment (Bell et al. 2003). The presence or absence
of a single species (top predator beetle) led to far-
reaching consequences in the local plant community,
from the amount of foliage and size of plants to plant
diversity. Although the system may be resilient over
longer time scales, the dramatic indirect effects shown
in our experiment do not support the notion that rain
forest communities are stable and resistant to pertur-
bance because of their complexity.

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**LITERATURE CITED**

temporal scale on the outcome of trophic cascades expe-
Brett, M. T., and C. R. Goldman. 1996. A meta-analysis of
the freshwater trophic cascade. Proceedings of the National
Academy of Sciences (USA) 93:7723–7726.
Burger, W. 1971. Flora Costaricensis. Fieldiana Botany 35:
1–227.
Coley, P. D., J. P. Bryant, and F. S. Chapin, III. 1985. Re-
source availability and plant antherbivore defense. Science
Deal, R. T. 1997. Understory plant diversity in riparian alder-
conifer stands after logging in southeast Alaska. USDA
Forest Service, Pacific Northwest Research Station Re-
search Note PNW-RN-523.
of insectivores from rain forest canopy: direct and indirect
of top-down and bottom-up forces in a tropical forest com-
in a complex terrestrial community. Proceedings of the Na-
tional Academy of Sciences (USA) 96:5072–5076.
bottom-up diversity cascades in detrital vs. living food


