

REPORT

## Top-down and bottom-up diversity cascades in detrital vs. living food webs

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### Abstract

Apex predators and plant resources are both critical for maintaining diversity in biotic communities, but the indirect ('cascading') effects of top-down and bottom-up forces on diversity at different trophic levels are not well resolved in terrestrial systems. Manipulations of predators or resources can cause direct changes of diversity at one trophic level, which in turn can affect diversity at other trophic levels. The indirect diversity effects of resource and consumer variation should be strongest in aquatic systems, moderate in terrestrial systems, and weakest in decomposer food webs. We measured effects of top predators and plant resources on the diversity of endophytic animals in an understory shrub *Piper cenocladum* (Piperaceae). Predators and resource availability had significant direct and indirect effects on the diversity of the endophytic animal community, but the effects were not interactive, nor were they consistent between living vs. detrital food webs. The addition of fourth trophic level beetle predators increased diversity of consumers supported by living plant tissue, whereas balanced plant resources (light and nutrients) increased the diversity of primary through tertiary consumers in the detrital resources food web. These results support the hypotheses that top-down and bottom-up diversity cascades occur in terrestrial systems, and that diversity is affected by different factors in living vs. detrital food webs.

### Keywords

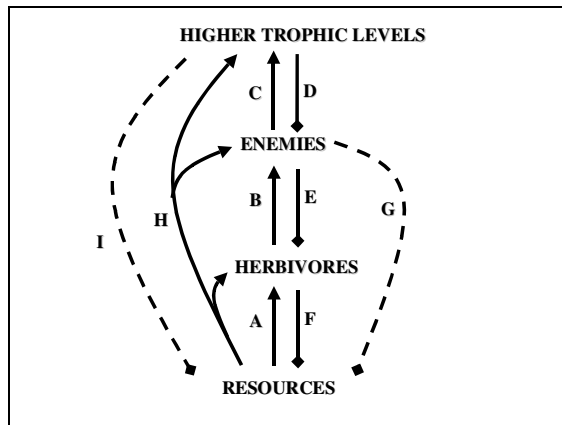
Diversity, food webs, indirect effects, *Piper*, tropics, trophic cascades.

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### INTRODUCTION

For decades, ecologists have investigated the roles of top-down and bottom-up forces in structuring biological communities, with early debates polarized between hypotheses on predator-based regulation of lower trophic levels and resource-based regulation of upper trophic levels (Lindeman 1942; Slobodkin 1960; Ehrlich & Raven 1964), with respect to productivity ( Hairston *et al.* 1960) or biotic diversity (Paine 1966). A dramatic increase in terrestrial studies (Persson 1999) has shifted the debate from the primacy of top-down vs. bottom-up forces to development of a series of hypotheses about how these forces may work in concert to structure communities (Oksanen 1991; Schmitz 1992; Leibold 1996); vary over space, time, and taxa (Power 2000; Schmitz & Sokol-Hessner 2002); act on components of complex food webs (Polis & Strong 1996; Persson 1999); and maintain heterogeneity and biodiversity (Hunter & Price 1992; Terborgh 1992; Dunne *et al.* 2002) in complex ecosystems.

A closely related and overlapping body of work has examined the role of indirect effects in communities (Wootton 1994; Abrams *et al.* 1995), and one of the most celebrated indirect effects studied in ecology is the top-down trophic cascade, where primary productivity is increased by the presence of a third trophic level that regulates herbivores (Hairston *et al.* 1960; Polis 1994; Pace *et al.* 1999; Persson 1999; Fig. 1). Some authors have argued that cascades are more likely to occur in less diverse systems (Strong 1992; Polis & Strong 1996; Persson 1999; Shurin *et al.* 2002) and predict that indirect effects (up or down) are less likely to be found as one moves from aquatic to terrestrial to decomposer food webs, but empirical studies have still not resolved this issue. The focus of trophic cascade studies, as well as top-down vs. bottom-up comparisons, has typically been on the causes and consequences of variation in biomass at different trophic levels, but some experimental studies have also examined variables such as behaviour (Trussell *et al.* 2002) or diversity. It is clear that consumers and resources affect diversity in aquatic



**Figure 1** Path diagram summarizing hypotheses of direct and indirect effects in trophic interactions (direct effects with solid lines, indirect effects with dashed lines). “Resources” refers to primary producers in a living food web or detritus in a detrital food web. Arrows indicate a positive effect of one trophic level on another, whereas squares indicate that the effect could be positive or negative, depending on the parameter (diversity vs. abundance) or food web (living vs. detrital). Letters next to arrows represent values that are unique to particular food webs and to the type of independent or response variable measured at each trophic level. For example, pathways A, B, C represent effects of resources on diversity; D, E, F represent effects of consumers on diversity; H represents direct effects of primary producers on diversity; H combined with D, E, F represent interactive effects of primary producers and pressure from consumers; G and I represent top-down trophic cascades.

(Carpenter & Kitchell 1993; Hillebrand *et al.* 2000; Nielsen 2001; Kneitel & Miller 2002), terrestrial (Hunter & Price 1992; Terborgh 1992; Terborgh *et al.* 1999), and detrital (Scheu & Setälä 2002) food webs (Fig. 1). Multivariate models predict that primary productivity and pressure from consumers have interactive effects on species diversity (Huston 1994; Fig. 1), and some empirical studies support this prediction (Worm *et al.* 2002). Two issues that are not clear are if diversity cascades exist (Hunter & Price 1992; Terborgh 1992) and how these effects vary in fundamentally different communities, such as aquatic vs. terrestrial vs. detrital food webs. Because of problems with consistency in definitions (Hunter 2001), here we define a diversity cascade as an indirect effect that causes or is a consequence of changes in diversity on nonadjacent trophic levels. Diversity cascades can go up or down (Hunter & Price 1992).

To test the direct and indirect effects of top predators and plant resources on animal biodiversity, we manipulated biotic and abiotic factors associated with a living and a detrital endophytic community found within a tropical, myrmecophytic shrub, *Piper cenocladum* C. DC. (Piperaceae). Previous studies on this system documented the following features.

- 1 Top-down cascades (Fig. 1), in which top-predators (fourth trophic level) negatively affected plant biomass in small-scale experiments (for fragments, Letourneau & Dyer 1998a; for shrubs, Dyer & Letourneau 1999a; Gastreich 1999) and in large-scale correlational studies (Letourneau & Dyer 1998b).
- 2 Strong bottom-up effects of light and nutrients on plant biomass that did not cascade up to arthropod abundance and did not alter the top-down effects of ants (Dyer & Letourneau 1999b).
- 3 Considerable investment in chemical defence (Dodson *et al.* 2000) that augments the biotic defence provided by the ants (Dyer *et al.* 2001).

These results corroborated results from many other studies with myrmecophytes (e.g. Janzen 1966; Beattie 1985; Jolivet 1996; Vasconcelos & Casimiro 1997).

The hypotheses tested in this study are similar to the bottom-up and top-down cascades examined in previous studies, but we examine diversity rather than biomass at each consumer trophic level and treat the model system as a mesocosm that contains two unique, interacting communities – the living and detrital food webs. The first hypothesis tested was one that has been tested in many other systems – that key consumers and moderately enhanced resource availability can increase overall animal diversity. In this case the consumers were the predatory clerid beetle and the resources were light and soil nutrients, both of which were shown to affect herbivory, plant biomass, and phytochemistry in previous studies (Letourneau & Dyer 1998a; Dyer & Letourneau 1999b). The second hypothesis was that top-down and bottom-up forces are interactive in their effects on diversity. In particular, top-down effects on diversity are likely to be strong and positive only when high (or balanced) resources are available (Huston 1994). The third hypothesis was that that top-down cascades are less likely to occur in the detrital vs. living food web (as proposed by Scheu & Setälä 2002). Finally, we tested the hypothesis that diversity cascades exist in this system. There are two components to this hypothesis: (1) addition of a top predator will directly increase predator diversity and indirectly (via predator diversity) affect herbivore diversity and plant quality, and (2) enhancement of nutrients or light available to plants will indirectly increase diversity of upper trophic levels.

## MATERIALS AND METHODS

### Study area and organisms

Field experiments were conducted from April 1996 to August 1997 in Costa Rica at the Organization for Tropical Studies, La Selva Biological Station, Heredia Province at

10°25' N, 84°5' W, *c.* 100 m elevation. This lowland rain forest reserve receives a mean annual precipitation of *c.* 4000 mm and has a mean temperature of 26 °C. The tropical shrub, *Piper cenocladum* is nearly always inhabited by a *Pheidole bicornis* Forel ant colony (Hymenoptera: Formicidae: Myrmicinae), which forages in or on the plant, and harvests lipid- and protein-enriched epidermal cells (food bodies) produced by the plant in the hollow petiole chambers. As predators of both internal and external herbivores, *Pb. bicornis* kills stem boring weevils and foliage feeding lepidopterans. This dominant ant species has many different predators (Letourneau & Dyer 1998a), but we manipulated densities of a single species: *Tarsobaenus letourneaue* Barr (= *Phyllobaenus* sp.) (Coleoptera: Cleridae). This relatively rare, but patchily occurring predatory beetle inhabits the plant in its larval stages, and can disrupt whole colonies of *Pb. bicornis*. Shrubs produce small numbers of food bodies when unoccupied by the dominant ant and beetle species, but food body production is facultatively increased by at least an order of magnitude in the presence of *Pb. bicornis* and increased somewhat less when a petiole chamber contains the clerid beetle (Letourneau 1990). *Tarsobaenus letourneaue* feeds on food bodies in its early larval instars, and preys on the ant brood as it matures.

### Experimental design

Eighty *Pi. cenocladum* shrubs ( $\geq 50$  cm tall,  $\geq 12$  leaves) occurring from 1 to 10 m apart in a 0.25-ha site on ultisol soil (Dyer & Letourneau 1999a) were exposed to three treatments in a factorial design: high vs. low light environment, fertilizer additions vs. no fertilizer, and introduction of top predators vs. no top predator. Hollow stems and petiole chambers of all shrubs were checked initially for the presence of *Pb. bicornis* ant colonies, and were also presumably occupied by other endophytic invertebrates. Later stage beetle larvae were added four times to top-predator-treatment shrubs (Dyer & Letourneau 1999a). Light availability was determined for all shrubs in the study area as the mean of four spherical densitometer readings, converted to estimate percentage canopy cover. We located 40 shrubs in high-light (95–96% cover) and 40 shrubs in low-light (97–98% cover) conditions, then randomly assigned the shrubs in these two light levels to the fertilizer and predator treatments in the factorial design. Initial measure of shrubs in high light showed no significant differences in height or herbivory levels from those placed in the low-light category (Dyer & Letourneau 1999a). We fertilized half of the shrubs (randomly selected in each light treatment) with 15 g of Once® brand slow release fertilizer (NPK 13 : 13 : 13 with trace levels of Ca, Mg, S, B, Cu, Fe, Mn, Mo, and Zn). Top-predator treatments were applied to half of the plants (randomly selected in each light treatment) by collecting

early instars of the predatory clerid beetle (*T. letourneaue*) outside the experiment and manually transferring one beetle larva to a petiole chamber of each treatment plant (Dyer & Letourneau 1999a). To increase the success rate of the beetles, which can be vulnerable to ant defensive behaviours when the small larvae are transferred manually, we weakened the ant colony in those shrubs with 0.2 mL of very dilute insecticide (1–2 drops of 0.85 mg Diazinon® wettable powder per litre of distilled water) introduced into each petiole 2 weeks before beetle larvae were introduced in June 1996. Although a single application of dilute Diazinon is not sufficient to suppress ant colonies over the long-term (Dyer & Letourneau 1999a), the presence of a clerid beetle larva maintained ant numbers sufficiently low that subsequent beetle introductions did not require application of insecticides. Since beetles are likely to oviposit eggs in petioles with few or no ants, this treatment reflected natural colonization by beetles.

Surviving shrubs were removed after 15 months and dissected to quantify all components of the community. The entire endophytic fauna (Arthropoda, Annelida, Crustacea and Nematoda) was collected from each shrub to determine the total number of invertebrate species and their relative abundance, and the density of food bodies available to consumers in each petiole was estimated by counting all food bodies within a 0.5-cm diameter circle. We described and counted each consumer in every shrub, with the exception of *Pb. bicornis* ants. The number of individual ants per *Pb. bicornis* colony was estimated from the dry weight of each colony based on a regression of colony dry weight on number of ants in the colony ( $r^2 = 0.99$ ,  $P = 0.0048$ ). All taxa were then assigned to one or more trophic levels, based on current knowledge of their feeding biology. Abundance ( $A$ ), species richness ( $S$ ), and biodiversity (Shannon's diversity index,  $H'$ ) were measured for each shrub. We also assigned each taxon to one of two food webs: living or detrital. Trophic groups were defined as: (a) herbivores (2nd trophic level) and predators (3rd and 4th trophic levels) supported by living plant tissues (1st trophic level) and (b) detritivores (2nd trophic level), their predators (3rd trophic level) and top predators (4th trophic level) supported by frass, dead plant and animal tissue (1st trophic level), and their associated bacteria and fungi (2nd trophic level). A second calculation of  $H'$  for each trophic group (Persson 1999), defined as the 2nd, 3rd, or 4th trophic level within the living compartment or detrital compartment of the food web, allowed for an examination of bottom-up vs. top-down forces for food webs within the community.

### Hypothesis tests

We assessed the effects of plant resource and top predator manipulation on the diversity ( $H'$ ) of the endophytic fauna

of *Pi. cenocladum*, using analysis of variance (ANOVA; SAS 1990). This ANOVA explicitly tested our first two hypotheses: (1) top-down and bottom-up forces affect animal diversity, and (2) these effects are interactive. We then utilized multivariate ANOVA, followed by profile analysis (Scheiner 2001) to examine the diversity ( $H'$ ) of organisms in different trophic groups: all predators and herbivores in the living resources food web; and top predators, predators, and herbivores in the detrital resources food web. The detrital and living food webs were analysed separately to test our third hypothesis, that top-down cascades are less likely to occur in detrital food webs. All  $F$ -values reported are Wilks' lambda for the profile analyses. Profile shapes analysis tested the hypothesis that diversity values at different trophic levels differed in their response to treatment effects, which was important for testing the hypothesis that diversity cascades exist. All assumptions of ANOVA were tested and were met in most cases; when normality assumptions were not met, log transformations were used.

Path coefficients (SAS Institute, CALIS procedure) were combined with  $\eta^2$ -values from ANOVAs to construct a path diagram. For this analysis, plant quality was a composite variable of stem height, number of petiole chambers, and food body density per chamber (each equally weighted). The path analysis was used primarily as a heuristic tool to illustrate direct and indirect effects (Mitchell 2001), but was also used to test the specific hypothesis that diversity cascades exist in the living and detrital food webs. The direction of the cascade pathways (top-down or bottom-up) was determined by results from the ANOVAs. We used  $P > 0.05$  as the criterion indicating a statistical fit between the data and an indirect pathway (Mitchell 2001). Path coefficients and  $\eta^2$ -values measure relative strengths of top-down and bottom-up effects in the endophytic community, and these analyses test for indirect effects that imply diversity cascades.

## RESULTS

The entire endophytic fauna living within the petiole chambers and stems of 77 shrubs (three shrubs died) after

15 months comprised approximately 43 188 invertebrates, representing more than 50 species. Although *Pb. bicornis* ants no longer inhabited 20% of the shrubs, this was, overall, the most abundant species with up to 2842 individuals per occupied shrub. Six other ant species were distributed among the shrubs, totalling 1260 individuals. The remaining 969 individuals were minute annelids, nematodes, crustaceans, and other arthropods, including collembolans, dip-terans, coleopterans, and at least 17 mite species.

The mean species richness within an individual shrub was 5.1, and ranged from 1 to 14 species of invertebrates per shrub. The endophytic invertebrate biodiversity, as described by Shannon's Index ( $H'$ ) (Krebs 1999) was 0.31 on average, and ranged from 0 to 2.0 for individual shrubs. Animal diversity ( $H'$ ) was significantly affected by top predator addition but not by bottom-up treatments of fertilizer and light (Table 1). Shrubs with top predator additions had twice the animal diversity, on average, of shrubs without additions of the predatory clerid beetle. The primary mechanism for this increase in diversity was the action of top predators, which lowered the abundance of the dominant species, *Pb. bicornis* ants, four-fold on average per shrub. There was no significant effect of resources nor were there interactive effects of resources and predators on diversity (Table 1).

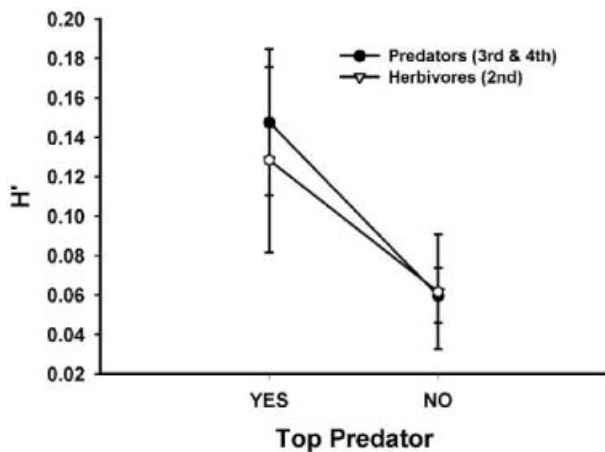
The living food web included an average of two species and 551 individuals per shrub feeding on stem and petiole chamber tissues such as vascular tissue, pith and food bodies. The detrital food web within *Pi. cenocladum* comprised an average of three species and approximately 13 individuals per shrub. Primary detrital resources within the plant (e.g. frass from ants and stem borers, discarded plant tissue from the stem, pith, and food bodies) supported from 0 to 82 individuals per shrub. Top predator addition significantly increased the diversity of predators and herbivores in the living tissue food web (Table 2, Fig. 2), and the strength and direction of the effects were consistent on both trophic levels (profile analysis, Table 2). Top predator addition increased ant species richness per shrub ( $X_{\text{without predators}} = 0.28 \pm 0.08$  SE;  $X_{\text{with predators}}$

**Table 1** Diversity of endophytic community. Analysis of variance for effects of predator, fertilizer, and light on diversity ( $H'$ ) of the endophytic invertebrates inhabiting *Piper cenocladum*

| Effect                                    | Level | Mean (+ SE) $H'$ | $F$ -value, $P$ -value |
|---|-------|------------------|------------------------|
| Fertilizer                                | Yes   | 0.40 (0.7)       | 0.42, 0.5              |
|   | No    | 0.38 (0.06)      |                        |
| Predator                                  | Yes   | 0.55 (0.05)      | 14.9, 0.0003           |
|   | No    | 0.25 (0.07)      |                        |
| Light                                     | High  | 0.38 (0.07)      | 0.04, 0.9              |
|   | Low   | 0.41 (0.07)      |                        |
| Fertilizer $\times$ Light                 |       |                  | 1.4, 0.2               |
| Fertilizer $\times$ Predator              |       |                  | 0.8, 0.4               |
| Predator $\times$ Light                   |       |                  | 0.01, 0.9              |
| Fertilizer $\times$ Beetle $\times$ Light |       |                  | 2.0, 0.2               |

**Table 2** Living food web. Multivariate analysis of variance of overall effect of treatment (prd = top predator, lgt = light, frt = fertilizer) on the diversity, as measured by Shannon's  $H'$  index, within trophic levels (herbivores – 2nd trophic level, and predators – 3rd and 4th trophic levels) of the living tissue food web in the endophytic community of *Piper cenocladum*

| Factor          | MANOVA profile levels |                      |         | Effects on predators vs. herbivores (profile shapes) |                      |         |
|-----------------|-----------------------|----------------------|---------|--|----------------------|---------|
|                 | Wilks' lambda         | F-value, d.f. = 1,69 | P-value | Type III SS  | F-value, d.f. = 1,69 | P-value |
| Frt             | 0.99                  | 0.00                 | 0.9902  | 0.0034   | 0.39                 | 0.5355  |
| Prd             | 0.94                  | 4.76                 | 0.0325  | 0.0170   | 1.91                 | 0.1713  |
| Frt × Prd       | 0.99                  | 0.05                 | 0.8288  |  |                      |         |
| Lgt             | 0.99                  | 0.35                 | 0.5565  | 0.0013   | 0.14                 | 0.7053  |
| Frt × Lgt       | 0.99                  | 0.08                 | 0.7773  | 0.0000   | 0.00                 | 0.9648  |
| Prd × Lgt       | 0.99                  | 0.33                 | 0.5672  |  |                      |         |
| Prd × Frt × Lgt | 0.99                  | 0.04                 | 0.8384  |  |                      |         |



**Figure 2** Diversity ( $H'$ ) of endophytic animals in the living tissue food web significantly increased in the presence of top predators, with a similar effect on both the second and third trophic levels.

=  $0.57 \pm 0.11$  SE) and also increased stem borer species richness per shrub ( $X_{\text{without predators}} = 0.08 \pm 0.04$  SE;  $X_{\text{with predators}} = 0.22 \pm 0.07$  SE). No significant effect of fertilizer, light, or their interaction was detected, even when the food web was re-analysed placing all consumers of food bodies, including omnivorous predators, on the second trophic level (ANOVA,  $F_{7,69} = 1.55$ ,  $P = 0.1643$ ). This was done to include a more liberal test of a bottom-up hypothesis.

In contrast to the top-down effects on the living food resource web, an interaction between light availability and fertilizer significantly affected the diversity of organisms on three trophic levels of the detrital community (Table 3). Diversity ( $H'$ ) was higher under conditions of balanced plant resources compared to unbalanced light and fertilizer conditions, and this response was consistent for all trophic levels (profile analysis, Table 3). The mean augmentation of

animal diversity for shrubs with balanced resources (high light and high nutrients or low light and low nutrients) was, for the second, third, and fourth trophic levels, respectively, 4.3, 1.7, and 1.9 times that in shrubs with unbalanced resources (low light, high fertilizer or high light and no fertilizer).

We used path analysis to test the relative strengths of top-down and bottom-up forces within and between the two food webs in *Pi. cenocladum* shrubs (Fig. 3). For the living tissue food web, the top-down pathway statistically fits the data ( $\chi^2 = 1.63$ , d.f. = 1,  $P = 0.20$ ), yielding significant standardized path coefficients for negative effects of predator diversity ( $H'$ ) on herbivore diversity and positive effects of herbivore diversity on plant quality (Fig. 3). For the detrital food web, the pathway fits the data ( $\chi^2 = 6.5$ , d.f. = 3,  $P = 0.09$ ), with positive path coefficients for effects of 3rd trophic level predator diversity ( $H'$ ) on 4th trophic level predator diversity (path coefficient = 0.44), detritivore diversity on 3rd trophic level predator diversity (0.049), and plant quality on detritivore diversity (0.048).

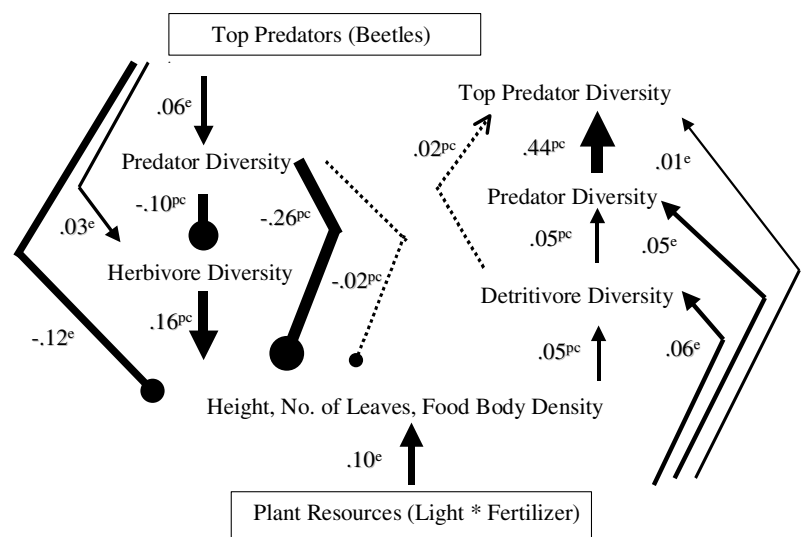
## DISCUSSION

In this experimental system, an overall increase in diversity and an increase in species richness of some taxa was associated with top predator introduction; thus, as has been demonstrated in other studies, the strength of predation was sufficiently strong and directed toward the dominant species, such that it increased diversity (Macguire 1971; Addicott 1974). The unique aspect of this result is that a top-down diversity cascade existed for the living food web. Path analysis showed correlative evidence of indirect effects of predator diversity on plant quality (quantity of resources available) and of detritivore diversity on secondary predator diversity, suggesting that diversity effects can cascade both up and down, a result predicted by some researchers

**Table 3** Detrital food web. Multivariate analysis of variance of overall effect of treatment on the diversity, as measured by Shannon's  $H'$  index, within three trophic levels (detritivores – 2nd trophic level, primary predators – 3rd trophic level, and secondary predators – 4th trophic level) of the detrital food web in the endophytic community of *Piper cenocladum*

| Factor          | MANOVA profile levels |                 |            | Top pred vs. pred |            | Pred vs. herb   |            | Top pred vs. Herb |            |
|-----------------|-----------------------|-----------------|------------|-------------------|------------|-----------------|------------|-------------------|------------|
|                 | Wilks' lambda         | $F$ , d.f. 1,69 | $P$ -value | $F$ , d.f. 2,68   | $P$ -value | $F$ , d.f. 2,68 | $P$ -value | $F$ , d.f. 2,68   | $P$ -value |
| Frt             | 0.99                  | 0.31            | 0.5802     | 0.45              | 0.5045     | 0.37            | 0.5477     | 0.01              | 0.9265     |
| Prd             | 0.99                  | 0.13            | 0.7171     | 0.33              | 0.5670     | 0.17            | 0.6776     | 2.30              | 0.1338     |
| Frt × Prd       | 0.99                  | 0.11            | 0.7406     |                   |            |                 |            |                   |            |
| Lgt             | 0.99                  | 0.17            | 0.6852     | 2.26              | 0.1376     | 1.95            | 0.1672     | 0.08              | 0.7798     |
| Frt × Lgt       | 0.92                  | 5.82            | 0.0185     | 2.97              | 0.0894     | 0.73            | 0.3974     | 0.92              | 0.3420     |
| Prd × Lgt       | 0.99                  | 0.24            | 0.6240     |                   |            |                 |            |                   |            |
| Prd × Frt × Lgt | 0.99                  | 0.15            | 0.7001     |                   |            |                 |            |                   |            |

**Figure 3** Path diagram shows relative strengths of effects (direct effects with solid lines, indirect effects with dashed lines) of top-down and bottom-up treatments on food webs and relative strengths of association among diversity values for different trophic levels within food webs. Arrows signify positive effects, balls signify negative effects, pc-values were derived as path coefficients (CALIS) and e-values are  $\eta^2$  values from MANOVA analyses.



(Hunter & Price 1992), but one which has not been demonstrated experimentally. The overall positive effects of beetle additions on predator and herbivore diversities in the living food web could be a consequence of some of the seven species of ants being less conducive to maintaining herbivore diversity than others. In particular, the negative effect of top predator additions on the dominant ant species, *Ph. bicornis*, allowed other species of ants to colonize the plants. These other ant species may maintain higher herbivore diversity than when *Ph. bicornis* is dominant through different or variable prey preferences or rapid depletion of the food body resources. The strong negative effect of predator diversity on herbivore diversity (Fig. 3) may be due to the reduction of food bodies, which are produced by the plant in large quantities only in the presence of *Ph. bicornis*.

More tests of diversity cascades in terrestrial ecosystems are needed to determine the generality of these results. One criticism of empirical studies that have attempted to

demonstrate any type of cascade in terrestrial systems is that the cascades are not community-wide (Persson 1999) because the effects are localized on one or a few species. It is difficult to manipulate entire trophic levels, thus many studies have manipulated a focal predator, which has cascading effects that may not be community-wide (reviewed by Polis 1994; Pace *et al.* 1999; Persson 1999; Schmitz *et al.* 2000). Mesocosm communities, such as those found in phytotelmata (e.g. Kneitel & Miller 2002) and the endophytic community examined in the current study, are ideal for testing trophic cascades and top-down, bottom-up effects on diversity (Deutschman 2001; Downing & Leibold 2002). Terrestrial studies should also focus on how top-down cascading effects on a focal plant species might lead to changes in plant community diversity, but such an approach was beyond the scope of this study.

For both the living and detrital food webs, there were no interactive effects of resources and predators on animal diversity. All previous trophic studies with this system

suggest that the bottom-up and top-down effects on biomass are not interactive either, even with extreme manipulations of resources (Dyer & Letourneau 1999b), long-term manipulations (Letourneau & Dyer 1998a), and studies at much larger scales (Letourneau & Dyer 1998b). Other studies have suggested that it is not informative to manipulate consumers and resources in isolation because their effects on diversity are strongly interactive (Worm *et al.* 2002). The lack of an interactive effect in our system could be an artifact of the small size of our endophytic community compared to the large aquatic and terrestrial communities for which these diversity hypotheses have been developed, and represents a potential weakness of this approach. For the detrital food web, it is possible that a study that is designed to manipulate predators in that web would uncover an interactive effect of consumers and resources. The very strong correlation between detrital web predator diversity and detrital web top predator diversity (Fig. 3) suggests that an additional trophic level in this system is more likely to be supported with enhanced plant resources, as predicted by Oksanen *et al.* (1981). Given time, the addition of this trophic level could cascade downward, causing depleted detrital resources (Oksanen *et al.* 1981).

As predicted, a top-down cascade did not occur in the detrital food web. However, resources affected the diversity of organisms on three trophic levels. Because the effects decreased in relative strength as they moved up the trophic web, and are not likely to be simple, direct effects of light or soil quality, these results suggest an attenuated series of indirect effects of light and fertilizer plant resources over four trophic levels in the detrital food web. These indirect effects should be less likely in complex detrital webs because of the same factors that may prevent top-down cascades, such as dense species packing and the prevalence of omnivory and generalist diets (Scheu & Setälä 2002). An alternative explanation for the absence of a top-down cascade in the detrital community is that the prey range of the manipulated predator (*T. letourneauae*) does not generalize to the detrital compartment of the endophytic community (Paine 1992). Thus, although top-down effects were not demonstrated for the detrital web in this study, we cannot conclude that they are not functioning in that system.

The absence of bottom-up effects on diversity in the living resources food web and presence of those effects in the detrital food web is likely to reflect a true dichotomy, and there are two potential mechanisms that are not mutually exclusive. First, the decreased quality of consumer resources (in the living web) due to secondary compounds produced in plant tissue (Dyer *et al.* 2001) was partially responsible for halting bottom-up effects through external herbivores on *Pi. cenocladum* (Dyer & Letourneau 1999b).

This same response is unlikely in the detrital food web because effects of secondary compounds or food quality are likely to be stronger in living tissues than in dead plant tissues and frass. The second mechanism may involve leaf turnover rates and the fact that the detrital food web is relatively more sessile. It is possible that high  $H'$  in the detrital food web depends on habitat stability, and retention of petiole chambers (leaves) is enhanced under balanced nutrient conditions.

In conclusion, our manipulative experiments of consumers and resources in a complex endophytic community show that both top-down and bottom-up forces determined animal diversity, but their relative importance depended on the food web that was examined. The strength of top-down and bottom-up forces on a community-level parameter (Shannon's diversity index) varied in intensity and relative importance among trophic levels and between detrital vs. living food webs. Patterns of biodiversity in the endophytic community of *Piper cenocladum* in a tropical wet forest support the hypotheses that top-down and bottom-up diversity cascades occur in terrestrial systems and that the effects cascade down from top predators in living food webs and up from primary resources in the detrital food webs.

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