BOTTOM-UP AND TOP-DOWN EFFECTS ON ARTHROPOD COMMUNITIES ACROSS A SUCCESSIONAL GRADIENT

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Abstract: Understanding mechanisms of community change during succession is important for understanding biotic regeneration following disturbance. Both top-down and bottom-up effects may drive changes in herbivorous arthropod community structure across a successional gradient. Bottom-up effects may include increasing plant species richness, which may drive increasing herbivore richness, or decreasing leaf quality, which may drive decreasing herbivore richness. Arthropod predators may act as a top-down effect; in the extreme case predator biomass would be inversely proportional to herbivore biomass over a successional gradient. We sampled arthropod communities in three plots (cleared 1 year, 3 years, and 5 years ago) in a lowland tropical rainforest to examine patterns in plant, arthropod herbivore and predator communities. Plant species richness increased with time since disturbance, while herbivore richness decreased. Herbivore biomass was not inversely related to predator biomass. Thus, bottom-up effects based on leaf quality may drive changes in arthropod herbivore communities.

Key Words: succession, arthropods, herbivores, predators

INTRODUCTION

Understanding the mechanisms by which community characteristics change during succession is important for understanding community regeneration following disturbance. Tropical systems experience extremely rapid early succession, and therefore are excellent systems to study the effects of succession on community structure. The herbivore-based trophic system can be abstracted into three levels: plants (primary producers), arthropod herbivores and predators (here we ignore vertebrate herbivores. Herbivore communities may be influenced by plant communities ("bottom-up") and by predatory arthropods ("top-down").

Increases in plant species richness with succession may exert bottom-up effects on herbivore communities (Connell 1978). Increased plant species richness may lead to a greater variety of plant resources available to herbivores and thus a greater richness of herbivores with plot age. Alternatively, changes in plant tissue quality across a successional gradient may exert bottom-up effects on herbivore communities. According to the resource availability hypothesis of plant defense theory, fast growing, gap specialists (early colonizers) will have fewer chemical and structural defenses and are therefore more palatable to herbivores than slow growing, late successional plant species (Coley et al. 2003). Thus, leaf quality may decrease across a successional gradient, decreasing herbivore species richness by eliminating many generalist species.

In contrast to bottom-up effects, top-down effects may influence herbivore communities by reducing herbivore biomass. In extreme cases, total predator biomass would be inversely related to total

herbivore biomass. We tested these broad predictions for how bottom-up versus top-down effects influence arthropod communities across a successional gradient in a lowland tropical rainforest at La Selva, Biological Station.

METHODS

We examined 3 successional plots on the morning of 12 February 2006, along Holdrige trail in La Selva National Park, Costa Rica. The plots were 100 x 100 m areas cleared 1, 3 and 5 years ago. We sampled six 3-m radius subplots within each plot, three at 10 m and three at 20 m from the edge. We collected arthropods using sweep netting, with 20 aggressive passes in a circular pattern off the ground within each subplot. We also collected arthropods from ≈40 g of randomly selected dead leaves suspended within reach. We sorted all arthropods to family and feeding guild (herbivore, predator, or detritivore), and measured volume as a proxy for biomass (mm^3).

To determine how time since disturbance influences the species richness and biomass of plants, herbivores, predators, and detritivores, we ran a one-way ANOVA, followed by a linear contrast when appropriate to test the directionality of the relationship. We used JMP 5.0.1 for all analyses.

RESULTS

In total, we collected 205 arthropods in 13 orders and 60 families. Plant species richness increased with plot age (Fig. 1; $F_{2,15} = 29.61$, $P < 0.001$) while herbivore species richness decreased with plot age (Fig. 2; $F_{2,15} = 2.50$, $P = 0.12$). Predator species richness did not change with increasing plot age

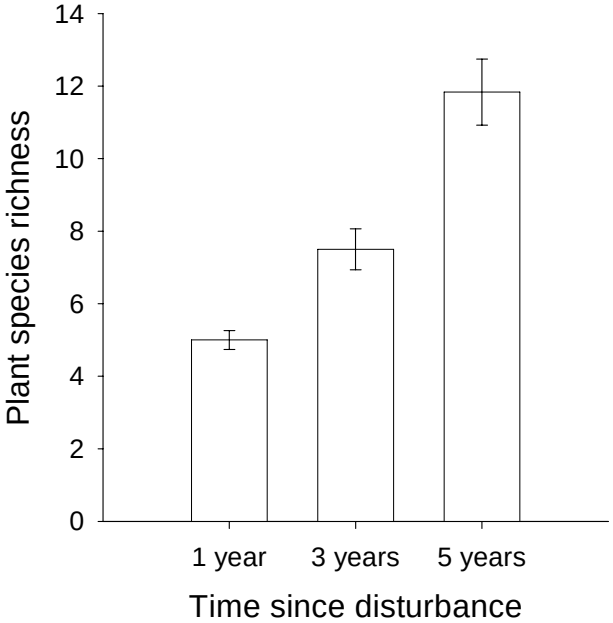

Figure 1. Plant species richness (mean ± SE) across 3 successional plots (cleared 1, 3, and 5 years ago) at La Selva Biological Station, Costa Rica ($F_{2,15} = 29.61$, $P < 0.0001$; $P < 0.0001$ for linear trend).

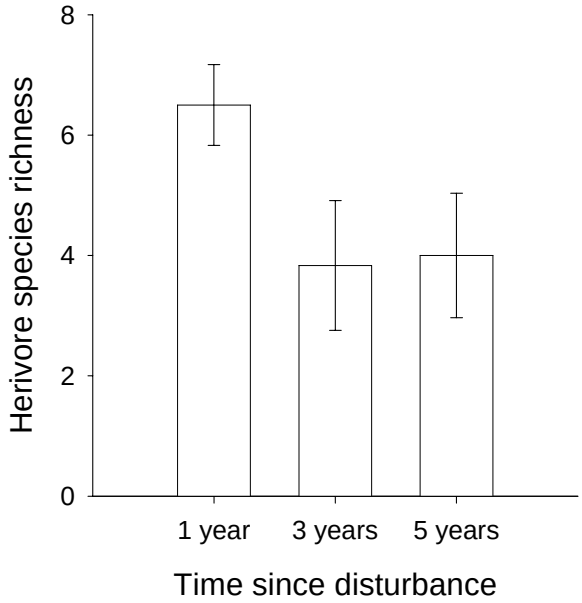

Figure 2. Arthropod herbivore species richness (mean ± SE) across 3 successional plots (cleared 1, 3, and 5 years ago) at La Selva Biological Station, Costa Rica ($F_{2,15} = 2.50$, $P = 0.12$; $P = 0.081$ for linear trend).

Table 1. Comparison of alpha taxa richness (mean ± SE, n = 6) plots to total taxa richness in three successional plots at La Selva Biological Station, Costa Rica. Total taxa richness was based on the pooled samples for a plot.

Plot age (years)	Alpha Herbivore Richness	Total Herbivore Richness	Alpha Predator Richness	Total Predator Richness
1	6.50 ± 0.95	29	3.83 ± 0.95	4
3	1.67 ± 0.32	16	1.67 ± 0.32	5
5	0.67 ± 0.25	13	0.50 ± 0.25	3

($F_{2,15}$ = 0.09, P = 0.91). All three successional plots showed evidence of β diversity as species richness increased with additional subplots (Table 1). Herbivore biomass did not change with plot age ($F_{2,15}$ = 1.22, P = 0.32). Predator biomass did not change with plot age ($F_{2,15}$ = 0.88, P = 0.44). As our sampling techniques were designed to sample arthropod herbivores and predators we did not analyze the incidental captures of detritivores.

Discussion

Results indicated the importance of bottom-up effects on herbivore richness. Plant species richness increased with time since disturbance as predicted for areas during early succession (Connell, 1978). However, herbivore species richness decreased with time since disturbance. One possibility is that decreased plant nutritional quality drives decreased herbivore species richness. We found no relationship between herbivore and predator biomass. Thus, as is generally found in terrestrial communities (Shurin et al. 2002), bottom-up effects on herbivore communities appear more important than top-down for early successional tropical forest at La Selva.

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