

Alejandro A. Royo · Walter P. Carson

The herb community of a tropical forest in central Panamá: dynamics and impact of mammalian herbivores

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Abstract Mammals are hypothesized to either promote plant diversity by preventing competitive exclusion or limit diversity by reducing the abundance of sensitive plant species through their activities as browsers or disturbance agents. Previous studies of herbivore impacts in plant communities have focused on tree species and ignored the herbaceous community. In an experiment in mature-phase, tropical moist forest sites in central Panamá, we studied the impact of excluding ground-dwelling mammals on the richness and abundance of herbs in 16, 30×45-m plots. Within each plot, we censused the herbaceous community in 28, 2×2-m subplots (1,792 m² total area sampled). We identified over 54 species of herbs averaging 1.21 ramets m⁻² and covering approximately 4.25% of the forest floor. Excluding mammals for 5 years had no impact on overall species richness. Within exclosures, however, there was a significant two-fold increase in the density of rare species. Overall herbaceous density and percent cover did not differ between exclosures and adjacent control plots, although cover did increase over time. Mammalian exclusion significantly increased the total cover of three-dominant herb species, *Pharus latifolius*, *Calathea inocephala*, and *Adiantum lucidum*, but did not affect their density. This study represents one of the most extensive herbaceous community censuses conducted in tropical forests and is among a few that quantify herbaceous distribution and abundance in terms of both density and cover. Additionally, this work represents the first community level test of mammalian impacts on the herbaceous community in a tropical forest to date. Our

results suggest that ground dwelling mammals do not play a key role in altering the relative abundance patterns of tropical herbs in the short term. Furthermore, our results contrast sharply with prior studies on similar temporal and spatial scales that demonstrate mammals strongly alter tree seedling composition and reduce seedling density. Thus, we question the pervasiveness of top-down control on tropical plant communities and the paradigm that defaunation will inexorably lead to widespread, catastrophic shifts in plant communities.

Keywords Community structure · Diversity · Herbs · Mammals · Tropical forests

Introduction

A central goal in community ecology remains disentangling and understanding the mechanisms important to the maintenance of plant species diversity. The extraordinarily high biological diversity of tropical forests has generated numerous hypotheses, stressing both biotic and abiotic factors, as explanations for the origin and maintenance of plant diversity (reviewed by Pianka 1966 and Wright 2002 among others). Prominent among these is the hypothesis that mammals, acting as seed and seedling predators, herbivores, dispersers, or disturbance agents either promote or reduce the richness and abundance of plants in tropical forests (Janzen 1970; Connell 1971; Connell 1978; Connell et al. 1984; Dirzo and Miranda 1991; Terborgh 1992; Terborgh and Wright 1994; Wright et al. 1994; Ickes et al. 2001; Roldan and Simonetti 2001; Terborgh et al. 2001; Silman et al. 2003).

It is clear that mammals often affect plant community composition and abundance through a variety of processes; however, the net effect of mammalian activity remains controversial as experimental work has yielded two diametrically opposed outcomes. On the one hand, mammals may promote plant species diversity by preventing competitive exclusion through selective foraging

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A. A. Royo (✉) · W. P. Carson
Department of Biological Sciences, University of Pittsburgh,
A 234 Langley Hall, Pittsburgh, PA 15260, USA

A. A. Royo
USDA Northeastern Research Station, Warren, PA 16365, USA
E-mail: aroyo@fs.fed.us
Tel.: +1-814-5631040
Fax: +1-814-5631048

on seed and seedlings of dominant species, increasing resource heterogeneity via physical disturbance, and enhancing dispersal (Inouye et al. 1987; Huntly 1991; Kotanen 1995; Hulme 1996; Welander 2000; Willson and Traveset 2000). Alternatively, mammals may depress plant diversity via indiscriminate herbivory, selective browsing of rare, palatable, or uncompetitive species, and trampling and uprooting during foraging activities (Milton 1940; Pacala and Crawley 1992; Arrington et al. 1999; Ickes et al. 2001; Russell et al. 2001). These two views differ critically in the assumption of how competitively subordinate and/or rare plant species are affected by mammalian activity and ultimately, how this effect will influence overall plant community diversity. Specifically, the first view predicts a rare species advantage and the maintenance of plant species diversity; the second view posits a rare species disadvantage and consequently, a decrease in diversity.

Several studies have demonstrated that mammals can greatly alter the relative abundance of plant species in forest understories. Nonetheless, the preponderance of these data focuses on shade-tolerant trees; life forms which, in time can grow to escape the effects of ground-dwelling mammals (e.g. DeSteven and Putz 1984; Sork 1987; Terborgh and Wright 1994; Cintra 1997). This preoccupation with canopy tree species ignores the majority of the tropical forest flora and has already led to the premature rejection of the importance of over-story gaps as a force structuring tropical plant communities (see Brokaw and Busing 2000 and Schnitzer and Carson 2000). We suggest that the impact of mammals on herbaceous species diversity could contrast with their effect on tree species because herbs spend their entire life cycle in the forest understory continually subject to mammalian impacts, including both herbivory and physical disturbance during foraging. Indeed, Haukioja and Koricheva (2000) concluded that the structural, functional, and life-history characteristics inherent to many perennial herbs make them less tolerant to herbivory than woody plants. Moreover, demographic analyses suggest that herbivory may considerably depress long-term growth and reproduction of herbaceous perennials (e.g. Bierzychudek 1982; Doak 1992; Ehrlen 1995; Knight 2003). If understory species are constantly vulnerable to herbivores, they could be under strong top-down control and thus, the impact of mammals could be most pervasive and important on these life forms (but see Feeney 1976; Grime 1977; Coley et al. 1985; and Bryant et al. 1991 for alternative view). Nonetheless, despite numerous tabulations of tropical flora worldwide, efforts to elucidate mechanisms behind the distribution, abundance, and coexistence of herbaceous species are extremely limited (but see Dirzo et al. 1992 for herbs and gaps). Furthermore, only a handful of studies have examined the prevalence and importance of mammalian impacts on herbaceous community diversity (e.g. Proulx and Mazumder 1998; Rees et al. 2001; Hambäck and Beckerman 2003). To our knowledge, the rigorous experimental work needed to deter-

mine to what degree mammals alter relative abundance patterns of tropical herb species remains nonexistent. The paucity of studies on herbaceous communities is critical as herbaceous plants represent one of the most diverse plant forms in forests (e.g. Lutz 1930; Cline and Spurr 1942; Rogers 1981; Moore and Vankat 1986; Collins and Pickett 1988). This major component of the flora also manifests itself in Neotropical forests where herbs alone can comprise from 12% to 49% of the species (Croat 1978; Gentry and Dodson 1987; Gentry 1990; Poulsen and Balslev 1991; Galeano et al. 1998; Kappelle et al. 2000).

We experimentally tested the impact of mammalian activity on the herbaceous community of a tropical forest in central Panamá by testing the following two hypotheses. First, if the net effect of ground-dwelling mammals promotes plant diversity by limiting the abundance of competitively dominant herb species, we predict that (1) herbaceous species richness will ultimately be lower in exclosures when compared to controls, and (2) the density and size of the dominant herbaceous plants will be greater in experimental plots from which we exclude ground-dwelling mammals than in the unfenced control plots. Alternatively, if mammalian activity limits herbaceous diversity, we predict that (1) species richness should increase within exclosures relative to adjacent control plots, (2) this increase will consist, in part, of rare species that are able to recruit into the understory when provided with protection from mammalian activity, and (3) the total density and cover of herbaceous species will be greater within exclosures than in controls. Thus, these two hypotheses make opposing predictions with regards to rare species and overall species richness while making identical predictions with regards to herbaceous species abundance.

Methods

Research sites

We conducted our study in the Republic of Panamá at Gigante Peninsula and Barro Colorado Island (BCI). Both sites are within the 5,600 ha Barro Colorado National Monument administered by the Smithsonian Tropical Research Institute (STRI). The forests are seasonally moist, semideciduous tropical forests that receive over 2.6 m of rain per year and exhibit a marked dry season extending from January until April. The vegetation structure is typical of many other tropical forests containing a multi-tiered understory, an average canopy height of 23–30 m, and emergent trees as tall as 50 m (Foster and Brokaw 1996). Light levels at the forest floor are relatively dark ranging from 1.5% to 9.5% of full sun (Valladares et al. 2000). Further detailed descriptions of the flora, climate, and geology of the area are found in Croat (1978) and Leigh et al. (1996).

Experimental design and enclosures

In 1993, we established eight-pairs of 30×45-m plots with each pair constituting a block. Four blocks were on Gigante Peninsula and four on BCI. We randomly assigned one plot in each pair as an enclosure (fence) treatment and the other was left as an unfenced control. Within each plot, we established 28, 2×2-m (4 m²) subplots in a stratified random design. We included 5–7 m wide buffer between the perimeter of the plots and any 4-m² subplot to allow unobstructed access and minimize any potential fence effects. The enclosure construction was completed in July 1994. The fence was constructed with 12.7×12.7-cm galvanized steel fencing and extends 0.25 m below ground and approximately 2.2 m above ground. A finer 1.3×1.3-cm mesh fence stretches around the base of each enclosure to a depth of 25 cm and a height of approximately 70 cm. Continued monitoring and trapping has shown that the fences effectively excluded the most important ground-dwelling mammals in these forests such as agoutis (*Dasyprocta punctata*), pacas (*Agouti paca*), brocket deer (*Mazama americana*), white tail deer (*Odocoileus virginianus*), spiny rats (*Proechimys semispinosus*), peccaries (*Ayassu tajacu*), rabbits (*Silvilagus brasiliensis*), and tapirs (*Tapirus bairdii*). (Emmons and Feer 1997; Carson, unpublished data).

Sampling regime

Each 4 m² subplot was censused for herbaceous species composition as well as density, and percent cover for each species. Only those ramets rooted within the subplot were censused. For each individual, we visually estimated cover with the aid of templates of known percent cover. Although the flora of BCI is one of the best studied in the Neotropics, identification for several individuals was unfeasible due to sterile or juvenile forms or unfamiliarity. Therefore, we categorized these individuals as morphospecies. We completed the first census in May 1994 prior to the construction of enclosures. The plots were recensused in July 1999. We categorized all herbaceous species from rare to abundant following Croat's Flora of BCI (1978) categorizations. Additionally, for our analyses, we considered the lowest 5% of the species or morphospecies on a rank abundance curve of total number of individuals as rare.

We conducted a number of tests to examine changes in the plant community parameters of richness, density, and cover. In addition, we focused on changes in density and cover in three-dominant plants: *Adiantum lucidum*, *Calathea inocephala*, and *Pharus latifolius*. Not only these three species are designated as abundant or common in the Flora of Barro Colorado (Croat 1978), moreover these three species are accounted approximately for one-third of the total cover and number of ramets sampled at the start of the experiment and were represented in all plots. Although two other species, *Philodendron inaequilaterum*, and *Tectaria incisa*, were

also abundant, their distribution was extremely patchy. For these two species, it did not make sense to explore the effects of mammal suppression between treatments or over time as they were absent from a large number (25–44%) of plots. The inclusion of such a large number of zero values would highly skew the data and create high plot-to-plot variability, thus violating the assumptions of ANOVA (Carson and Root 1999).

Analysis

For all analyses, we used multivariate repeated-measures analysis of variance (rmMANOVA), where the response variables for each time period (1994 and 1999) were treated as different dependent variables. This procedure is the most robust test for time series data as it controls for the correlation between dates and the resulting lack of independence within replicates (von Ende 2001). The between subject factors were block and treatment (enclosure/control); within subject factors were year, year × block, and treatment × year interactions. The treatment × year interaction is the decisive test to determine whether any changes observed over time differ between control plots and enclosure plots (von Ende 2001). Statistical tests exploring the effect of the treatments on richness (number of species) used the total number of species for all 28 subplots per plot. For analyses on the community level parameters of density and percent cover, we used the average of the parameter across all 28 subplots within a plot. As our predictions for rare species density and dominant species density and cover are directional, we report the one-tailed *P*-values. We assessed normality using the Shapiro–Wilk test (Shapiro and Wilk 1965) and applied the arcsine transformation to percent cover data only when needed (Sokal and Rohlf 1995).

Results

Species richness

We censused 2,116 and 2,206 ramets in 1994 and 1999, respectively. The average density ranged from 1.17 ramets m⁻² to 1.26 ramets m⁻². We recognized 62 different herbs and were able to identify 89% of them to either species or genus level (Table 1). The results demonstrate that this flora is typical of similar diverse systems comprised of few abundant species and many rare ones. The censuses demonstrate that four species (6.5%) account for over 50% of the total number of ramets; conversely, 40 species (64.5%) comprise the lowest 5% of the total number of ramets.

Overall species richness was significantly greater within enclosures ($F=7.88$, $P=0.026$). Indeed, the data indicate an increase from a mean of 14.625 species in 1994 to 16.75 species in 1999 (a 14.5% increase) in the enclosures, whereas, the controls increased from 12.125

Table 1 Herbaceous species list and mean percent cover (percent cover per 4 m⁻²; ± 1 SE) for each treatment (controls and exclosures) at each census period along with abundance classifications (see text for explanation)

Species	Abundance	Croat	Control				Fence			
			1994	SE±	1999	SE±	1994	SE±	1999	SE±
<i>Adiantum lucidum</i>	Abundant	5	0.34	0.09	0.41	0.09	0.46	0.07	0.57	0.11
<i>Adiantum obliquum</i>	Rare	3	0.01	0.01	0.01	0.01	*	*	*	*
<i>Adiantum petiolatum</i>	Common	4	0.03	0.03	0.04	0.04	0.03	0.02	0.01	0.01
<i>Aechmea magdalenae</i>	Abundant	5	0.17	0.16	0.14	0.14	0.12	0.11	0.17	0.17
<i>Anthurium</i> spp.	Rare	—	*	*	—	—	—	—	—	—
Araceae	Rare	—	—	—	—	—	—	—	0.02	0.01
Araceae 1	Rare	—	—	—	—	—	—	—	*	—
Araceae 2	Rare	—	—	*	*	—	—	—	—	—
<i>Asplenium delitescens</i>	Rare	3	*	*	*	*	—	—	—	—
<i>Calathea inocephala</i>	Common	4	0.22	0.08	0.60	0.18	0.60	0.14	1.27	0.24
<i>Calathea insignis</i>	Rare	1	—	—	—	—	*	*	—	—
<i>Calathea latifolia</i>	Rare	2	—	—	—	—	—	—	*	*
<i>Calathea micans</i>	Rare	4	—	—	*	*	—	—	0.01	0.01
<i>Calathea</i> spp.	Rare	—	—	0.03	0.03	—	—	—	0.15	0.15
<i>Chusquea simpliciflora</i>	Rare	5	0.01	0.01	*	*	*	*	—	—
<i>Costus</i> spp.	Rare	—	0.02	0.02	0.04	0.03	0.02	0.02	0.04	0.03
<i>Dennstaedtia cicutaria</i>	Rare	1	0.08	0.08	0.05	0.05	—	—	—	—
<i>Dictyoxiphium panamense</i>	Rare	4	0.05	0.05	0.03	0.03	—	—	—	—
<i>Dieffenbachia longispatha</i>	Common	4	0.47	0.26	0.88	0.46	0.23	0.11	0.27	0.13
<i>Dieffenbachia oerstedii</i>	Rare	4	—	—	*	*	—	—	—	—
<i>Dieffenbachia pittieri</i>	Occasional	3	0.01	0.01	0.07	0.07	0.02	0.01	0.04	0.03
<i>Dieffenbachia</i> spp.	Rare	—	—	—	—	—	—	—	0.03	0.03
<i>Diplazium grandifolium</i>	Rare	5	—	—	—	—	*	*	—	—
<i>Dioscorea</i> spp.	Rare	—	*	*	*	*	0.01	0.00	0.01	0.01
<i>Geophila croatii</i>	Rare	3	—	—	—	—	*	*	0.01	0.01
<i>Geophila repens</i>	Rare	4	—	—	—	—	0.14	0.14	0.14	0.14
Unknow grass	Rare	—	—	—	—	—	*	*	—	—
<i>Heliconia</i> spp.	Rare	—	0.03	0.03	*	*	0.01	0.01	0.13	0.07
<i>Ischnosiphon pruinosis</i>	Common	4	0.04	0.04	0.06	0.06	0.13	0.10	0.07	0.07
<i>Lomariopsis vestita</i>	Rare	4	—	—	—	—	—	—	0.01	0.01
<i>Lygodium radiatum</i>	Rare	3	0.01	0.01	*	*	0.03	0.03	*	*
<i>Monstera dilacerata</i>	Infrequent	2	0.04	0.02	0.09	0.05	0.05	0.02	0.26	0.08
<i>Monstera dubia</i>	Rare	4	—	—	*	*	0.01	0.00	0.01	0.01
<i>Monstera</i> spp.	Rare	—	—	—	—	—	*	*	—	—
Maranthaceae	Rare	—	—	—	—	—	—	—	0.03	0.03
<i>Olyra latifolia</i>	Common	4	0.03	0.03	0.01	0.01	0.22	0.20	0.12	0.12
<i>Pharus latifolius</i>	Abundant	5	0.33	0.11	0.49	0.11	0.55	0.20	0.79	0.16
<i>Pharus parvifolius</i>	Rare	3	—	—	0.03	0.03	0.12	0.12	0.54	0.54
<i>Pharus</i> spp.	Rare	—	—	—	—	—	—	—	0.02	0.02
<i>Philodendron fragrantissimum</i>	Rare	4	*	*	—	—	—	—	—	—
<i>Philodendron guttiferum</i>	Abundant	5	0.22	0.07	0.32	0.15	0.10	0.04	0.19	0.09
<i>Philodendron inaequilaterum</i>	Abundant	5	0.77	0.30	0.92	0.43	0.59	0.28	0.86	0.44
<i>Philodendron</i> spp.	Rare	—	—	—	*	*	—	—	0.03	0.03
<i>Polypodium pectinatum</i>	Rare	5	—	—	—	—	0.01	0.01	—	—
<i>Scleria</i> spp.	Rare	—	—	—	—	0.03	0.02	—	—	—
<i>Selaginella arthritica</i>	Abundant	5	0.11	0.08	0.10	0.06	0.25	0.21	0.27	0.22
<i>Spathiphyllum friedrichsthalii</i>	Rare	4	0.01	0.01	—	—	0.05	0.04	0.10	0.07
<i>Spathiphyllum phrynifolium</i>	Rare	3	—	—	0.02	0.02	—	—	—	—
<i>Streptogyne americana</i>	Common	4	—	—	*	*	—	—	0.05	0.04
<i>Streptochaeta sodiroana</i>	Common	4	0.02	0.01	0.04	0.03	0.06	0.04	0.06	0.04
<i>Streptochaeta spicata</i>	Occasional	3	0.29	0.28	0.34	0.30	0.04	0.02	0.07	0.04
<i>Stromanthe jacquinii</i>	Infrequent	2	—	—	—	—	0.23	0.23	0.18	0.18
<i>Syngonium erythrophyllum</i>	Common	4	*	*	0.05	0.02	0.01	0.01	0.07	0.02
<i>Syngonium podophyllum</i>	Rare	5	*	*	—	—	*	*	—	—
<i>Syngonium</i> spp.	Rare	—	*	*	—	—	—	—	0.01	0.00
<i>Tectaria incisa</i>	Abundant	5	0.72	0.41	1.11	0.70	0.61	0.34	1.15	0.52
<i>Theiyypteris nicaraguensis</i>	Abundant	5	0.11	0.05	0.09	0.04	0.04	0.02	0.06	0.02
<i>Theiyypteris poitaena</i>	Rare	4	*	*	*	*	—	—	—	—
Unknown	Rare	—	—	0.06	0.06	—	—	—	0.03	0.03
<i>Xanthosoma pilosum</i>	Rare	5	*	*	—	—	—	—	—	—
<i>Xiphidium caeruleum</i>	Rare	4	—	—	—	—	*	*	—	—
Zingiberaceae	Rare	—	—	0.01	0.01	—	—	—	—	—
No. of Species			34		39		38		42	
No. of Ramets			1,054		1,062		1,123		1,083	

Cover estimates represent the grand mean across all eight plots within a treatment. Asterisks (*) denote cover estimates < 0.005%; endash (—) indicate absence of species

species in 1994 13.125 species in 1999 (Fig. 1). Nonetheless, species richness was highest in the exclosures even at the start of the experiment and the repeated measures analysis confirms that the slight differences between the exclosures and controls in species richness over time are not significant (treatment \times year; $F=2.97$, $P=0.129$). Thus, the data demonstrate that mammalian activity had no significant effect on overall species richness (Table 2; Fig. 1).

Abundance

We found no significant effect of excluding mammals on total cover or total plant density. Total herbaceous percent cover (but not density) increased significantly over time in both treatments (Table 2; Figs. 2a and 3a).

Excluding mammals significantly increased the cover of the dominant forest herbs (*Adiantum lucidum*, *Calathea inocephala*, and *Pharus latifolius*) by 65% (Fig. 2b). Although the cover of this group of herbs increased in both controls and exclosures over time, the significant treatment \times year interaction reveals that the increase within the exclosures was significantly greater than the increase in the control plots (Table 2; Fig. 2b). Removal of mammals for 5 years had no effect on density of dominant species as indicated by the treatment \times year term (Table 2; Fig. 3b).

Finally, excluding mammals for 5 years resulted in a significant increase in density of the rarest 40 species (treatment \times year interaction; $F=5.16$, $P=0.0285$) resulting in two-fold greater densities when compared to the adjacent control plots (Fig. 3c).

Discussion

On the diversity and abundance of herbs in tropical forests

Despite Gentry and Dodson's (1987) paper emphasizing the substantial contribution of non-tree species, to the

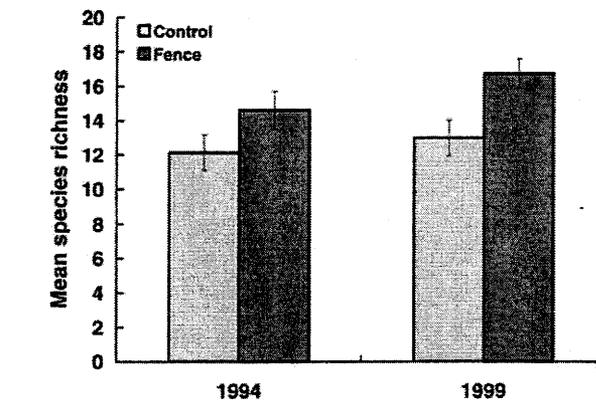


Fig. 1 Species richness (No. of species per plot) for herbaceous plants (mean \pm 1 SE) in exclosure plots and control plots in 1994 and 1999

overall plant diversity of tropical forests, there remains a paucity of studies characterizing the distribution and abundance of neotropical herbaceous communities. In fact, a literature search for work comparable to ours using the Agricola and Biological Abstracts databases as well as the literature citations of identified papers yielded only eight studies at 12 additional sites for which both herb richness and abundance (density or cover) was tallied (Table 3). Even among these studies there is considerable variation with respects to sampling effort and design, sampling location (e.g. understory vs. gap), and categorizations of herbaceous life forms. Given the suite of limitations, we find cross-site comparisons and synthesis inadequate, if not impossible, due to a lack of methodological standardization. Nevertheless, we do find that herb cover tends to increase with annual precipitation; however, this increase is predominantly due to a rise in dominance of large-leaved palms and monocots and not an increase overall stem density (Table 1 and 3; Gentry 1990; Montgomery 2004). In fact, across most forested sites, herbaceous density is generally low (1–2 ramets m^{-2}) and increases greatly only within gaps and in more open, semideciduous forests (Table 3). Despite these broad generalizations, we

Table 2 Repeated measures MANOVA results for the effects of ground-dwelling mammal exclosures on richness (No. of species), density (No. of ramets per m^2), and percent cover of the entire herbaceous community as well as the combined density and percent cover of the three dominant herbs: *Adiantum lucidum*, *Calathea inocephala*, and *Pharus latifolius*

Response	Between plot analysis over all years			Within plot analyses					
	Treatment effects			Year effects			Treatment \times year		
	df	F	P	df	F	P	df	F	P
Richness	1,7	7.88	0.026	1,7	17.08	0.0004	1,7	2.97	0.129
Total cover (%)	1,7	4.65	0.068	1,7	53.92	<0.001	1,7	3.04	0.125
Total density (no. per m^2)	1,7	0.17	0.696	1,7	0.17	0.696	1,7	0.30	0.599
Rare species density ^a	1,7	1.92	0.104	1,7	1.55	0.252	1,7	5.16	0.029
Cover of dominants ^a	1,7	18.83	0.001	1,7	85.25	<0.0001	1,7	5.63	0.025
Density of dominants ^a	1,7	8.3	0.012	1,7	3.66	0.099	1,7	2.52	0.079

^aThe predictions for these response variables are directional and justify one-tailed tests. Therefore, the P -values for treatment and treatment \times year represent one-tailed probabilities

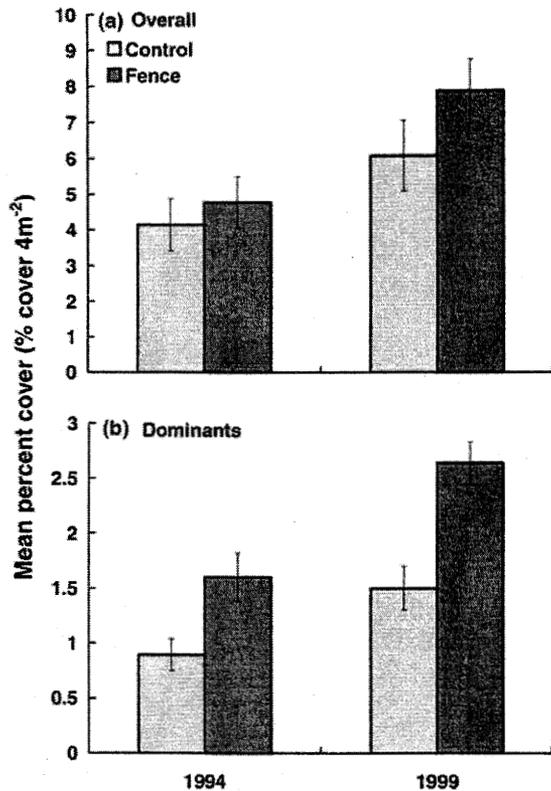


Fig. 2 a-b Mean herbaceous percent cover (percent cover 4 m⁻²; ±1 SE) in enclosure plots and control plots in 1994 and 1999 a) overall herbaceous cover, b) dominant herbaceous species as a group (*Adiantum lucidum*, *Calathea inocephala*, and *Pharus latifolius*)

suggest quantitative work on tropical herb communities is still in its infancy and true synthesis will require a concerted effort by researchers employing standardized measures across multiple sites.

Mammalian effects on herbaceous community

Several authors have recently warned that changes in the mammalian fauna could lead to 'catastrophic' or 'revolutionary' shifts in plant species composition (Dirzo and Miranda 1991; Terborgh et al. 2001; Silman et al. 2003; Wright 2003). Despite these warnings, our results do not justify these assertions. After 5 years of mammal removal, the herbaceous community did not exhibit marked increases or decrease in species richness, overall percent cover, or density. The two-fold increase in rare species density within fenced plots suggests that mammalian activity does limit the abundance of some plant species. This finding is consistent with other studies reporting an increase in rare species following release from mammals (e.g. Edwards and Crawley 1999; Cabin et al. 2000; Donlan, et al. 2002). Whether or not these species originated from the seed bank or via outside dispersal is unknown. Although dispersal may be limited within the fenced plots by the exclusion of

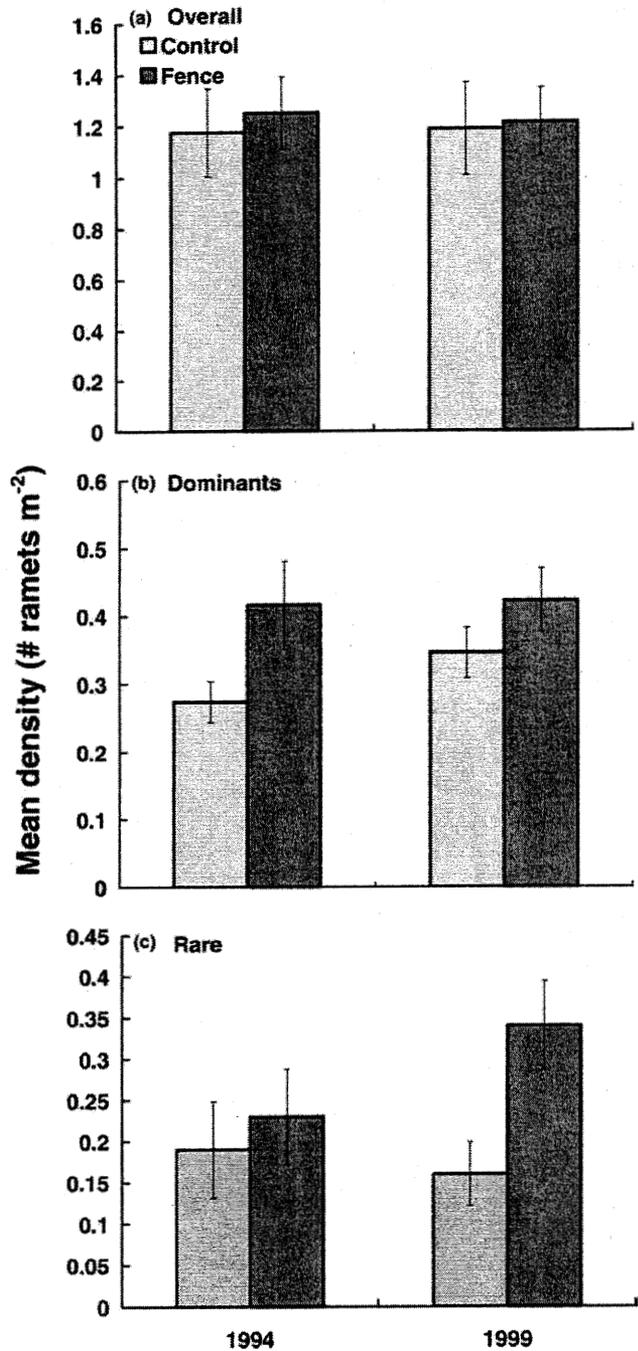


Fig. 3 a-c Mean herbaceous density (no. of ramets m⁻²; ±1 SE) in enclosure plots and control plots in 1994 and 1999 a) overall herbaceous density, b) dominant herbaceous species as a group (*Adiantum lucidum*, *Calathea inocephala*, and *Pharus latifolius*), c) rare species

the ground-dwelling mammalian fauna, several other dispersal vectors, which are not constrained by the fences remain (e.g. wind, water, arboreal mammals, birds, and insects; Beattie and Culver 1981; Lu and Mesler 1981; Howe and Smallwood 1982; Horvitz 1991; Stiles 2000; McLachlan and Bazely 2001; Pizo and Morellato 2002).

Table 3 Herbaceous species richness (No. of species), density (No. ramets per m²), and percent cover, in various Neotropical forests

Author(s)	Location	Coordinates	Mean annual rainfall (mm)	Area sampled	Terrestrial herbs	Climbers ^b	Mean density (no. per m ²)	Mean cover
Gentry and Dodson (1987)	Caperia, Ecuador	2°0'S, 79°53'W	804	1,000 m ²	50	58	2.85	—
Killeen et al. (1998)	Lornerio, Bolivia	16°13'S, 61°50'W	1,129	1,600 m ^{2a}	55	38	6.9	—
Gentry and Dodson (1987)	Jauneche, Ecuador	1°18'S, 79°35'W	1,850	1,000 m ²	18	58	~1.0	—
Fujisaka et al. (1998)	Amazonia, Brazil	9°53'S, 67°49'W	2,000	240 m ²	~24	~40	~2.0	—
Poulsen and Baslev (1991)	Cuyabeno, Ecuador	0°00'S, 76°12'W	2,479–3,244	10,000 m ²	57	26	~1.0	2.5% of total area
Royo and Carson	BCI, Panama	9°09'N, 79°51'W	2,600	1,792 m ²	47	13	~1.21	~4.25%
Gentry and Dodson (1987)	Rio Palenque Ecuador	0°32'S, 79°25'W	2,980	1,000 m ²	50	36	1.22	—
Mayfield and Daily (2004)	Las Cruces, Costa Rica	8°47'N, 82°57'W	4,000	120 m ²	26	25	6.05	—
Royo and Carson (unpublished data)	La Selva, Costa Rica	10°26'N, 83°59'W	4,000	960 m ²	25	17	2.88	13.90%
Whitmore et al. (1985)	Horquetas, Costa Rica	10°22'N, 84°05'W	4,000	100 m ²	16	21	1.12–3.52 ^c	—
Dirzo et al. (1992)	Los Tuxtlas, Mexico (Gaps)	18°34'N, 95°04'W	4,700	20 m ²	8	7	13.4	27%
Mayfield and Daily (2004)	La Palma, Costa Rica	8°40'N, 83°27'W	5,000	120 m ²	22	16	5.4	—
Mayfield and Daily (2004)	Pto. Jimenez, Costa Rica	8°31'N, 83°19'W	5,000	120 m ²	18	12	3.5	—
Galeano et al. (1998)	El Amargal, Columbia	5°29'–6°08'N, 77°10'–77°32'W	7,150	1,000 m ²	63	21	1.87	—

^aUsed Nested subplot design of various plot sizes. For forest floor flora (<2 m tall and <5-cm dbh) area sampled was 1,600 m²

^bClimbers category may include hemiepiphytes, herbaceous climbers, and woody climbers

^cLower estimate is density of free-standing herbs, higher estimate includes herbaceous climbers

The expansion in dominant herb species cover following release from ground-dwelling mammals suggests that mammalian activity may limit the abundance of these species. This result is consistent with prior studies reporting increases in abundance of a subset of plant species following mammalian exclusion or defaunation (e.g. Brown and Heske 1990; Dirzo and Miranda 1990; Bowers and Sacchi 1991; Gutierrez et al. 1997; Ritchie et al. 1998). We propose that the most likely explanation for the expansion of a few dominants is the absence of herbivory and physical disturbance by ground-dwelling mammals. In tropical forest understories, there is ample evidence that mammalian seed and seedling predation strongly reduces the abundance of many woody species (e.g. Clark and Clark 1989; Hammond and Brown 1998). Although to date analogous experiments have not been performed on non-woody plant species (Schupp et al. 1989), existing data confirms that mammalian diets include herbs (Terwilliger 1978; Robinson and Redford 1986; Brooks et al. 1997; Tobler 2002). Additionally, nontrophic interactions, including uprooting and trampling, cause considerable damage to understory vegetation and potentially alter species composition (Clark and Clark 1989; Arrington et al. 1999; Ickes et al. 2001; Gillman and Ogden 2003). Thus, either through direct consumption or nontrophic interactions, mammals could potentially limit the abundance of herbaceous species.

Long-term consequences and reconciliation of the hypotheses

Our data seemingly reveal a paradox between increasing cover of the three dominant species in conjunction with increases in rare species density. We propose that the existence of a time lag is a likely explanation that will reconcile this apparent paradox. Specifically, we suggest that competitive exclusion by dominant competitors is not instantaneous, particularly in the light-limited forest understory, and that this lag could allow a transient recruitment opportunity for rare species that will ultimately wane as the dominant plants continue to expand and overtake space though this dynamic may require decades to play itself out. Such lagged responses to herbivore removal experiments are common in herbaceous communities and their existence clearly highlights the importance of long-term research in plant communities (e.g. Carson and Root 2000; Brown et al. 2001; Rees et al. 2001). Alternatively, the increases in recruitment of rare species inside exclosures may prove robust providing solid support that mammalian activity limits plant diversity in tropical understories. However, the strongest evidence for the concept that mammals exert strong top-down control on plant diversity comes from communities with overabundant mammal populations (e.g. Donlan et al. 2002; Terborgh et al. 2001). At BCI, the existing data does not support the assumption of excessively high mammal abundances (Wright et al.

1994; Wright et al. 2000), making this alternative unlikely.

Our results are likely a conservative measure of the effects of mammals on the ground flora. Wright (2002) hypothesized that low understory plant abundances may negate the existence of competition in tropical forests. Furthermore, he predicted competition would only become important when understory plant abundance increased following, among other factors, release from herbivores. Although the BCI herbaceous layer is as speciose as other neotropical forests (Gentry 1990), the herbaceous layer is relatively sparse relative to wetter tropical forests. If Wright's prediction proves correct, release from mammalian impacts in forests containing these dense initial conditions may allow competitive exclusion to proceed at a greatly accelerated pace. Thus, although the results of this experiment demonstrate that mammals are not the major force structuring the understory herbaceous communities of semideciduous tropical forests, clearly, further experimentation is required to assess the scope and generality of their effects.

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