PRIMARY PRODUCTIVITY AND MACRO-INVERTEBRATE DIVERSITY IN FOUR TROPICAL FORESTS

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Abstract: The current high rate of ecosystem degradation necessitates an effort to understand ecosystem functioning. Biodiversity may influence ecosystem function, and productivity has been suggested as a driving factor of biodiversity. We studied the relationship between biodiversity and productivity in tropical forests. Biodiversity is a complex concept, and multiple metrics are required to define it. We used a standard sampling method to compare diversity of the macro-invertebrate communities in four different tropical forests. Depending on the spatial scale that was considered, both evenness and diversity, but not richness, increased with increasing productivity. However, results varied at different scales, indicating that patterns of biodiversity are scale-dependent.

Key words: alpha diversity, evenness, gamma diversity, heterogeneity, invertebrates, productivity-diversity curves, richness, scale

INTRODUCTION

In recent years, biodiversity has gained the attention of ecologists and the public as an important factor in ecosystem functioning. Because ecosystems around the world are being degraded and as a result species are disappearing, it is important to understand spatial and temporal patterns of biodiversity and the mechanisms that drive these patterns. While biodiversity is difficult to quantify, it has several measurable aspects. Species richness is a straightforward count of the number of species that occur in a given area; species evenness is a measure of the relative abundance of species; heterogeneity indices measure both richness and evenness (Magurran 1988). Taking all three measures into account provides a complete picture of ecosystem diversity.

Waide et al. (1999) suggests that productivity is a determinant of biodiversity. As productivity increases, the resource base increases and can support higher biodiversity. Several empirical curves have been constructed, though the shape of these curves is far from universal. Some studies have found both unimodal and linear patterns, while others have found no relationship (Mittelbach et al. 2001).

One drawback of the empirical patterns is that sampling methods often vary across multiple sites, so it is difficult to make comparisons among available diversity data. We used identical sampling methods at four different sites in Costa Rica to characterize the productivity-diversity relationship for macro invertebrates.

METHODS

We sampled invertebrate populations at four sites in Costa Rica: Palo Verde National Park on 13 January 2004, Monteverde National Park on 21 January 2004, Corcovado National Park on 3 February 2004, and La Selva on 13 February 2004. All samples were collected between 0830 and 0930. At each site, ten sweep net samples were collected along forest edges, defined as areas where vegetation changes from grass and shrubs to trees. Each invertebrate sample was taken with 16 continuous sweeps of a net, covering an area of approximately 2 m^2.

Macro-invertebrates in each sample were identified to order and grouped by morphospe-

cies. Morphospecies identities were consistent across all samples at each site, but not between sites.

We calculated three diversity measures to evaluate the relationship between biodiversity and productivity. Species richness was calculated as the total number of unique morphospecies in each sample. The heterogeneity index used to calculate diversity was the Shannon-Weiner index (H', hereafter referred to as diversity)

$$H' = -\sum (p_i)\ln(p_i)$$

where p_i is the proportion of individuals found in the ith species. Evenness was calculated using the formula

$$J = H' / H'_{max}$$

where H'_{max} = ln(number of unique species).

Data were analyzed at scales of both individual sample (10 per site) and site. Estimates of above-ground net primary productivity (ANPP) for Palo Verde and Corcovado National Parks were obtained from Oak Ridge National Laboratory Active Archive Center's Net Primary Productivity database <http://www.daac.ornl./gov/NPP>, and estimates for Monteverde and La Selva biological stations were obtained from M. Kaspari (pers. comm.).

RESULTS

We found no relationship between species richness of invertebrates and ANPP at the level of individual samples within a site (r = 0.03, df = 39, P = 0.83; Fig. 1A) or total cumulative richness from all samples within a site (r = 0.50, df = 3, P = 0.50; Fig. 1B). Species evenness increased significantly with productivity at the individual sample level (r = 0.35, df = 39, P = 0.03; Fig. 2A), but not at the site level (r = 0.66, df = 3, P = 0.35; Fig. 2B). Diversity was not related to productivity at the individual sample level (r = 0.14, df = 39, P = 0.38; Fig. 3A), but increased significantly with productivity in sites overall (r = 0.98, df = 3, P = 0.02; Fig. 3B).

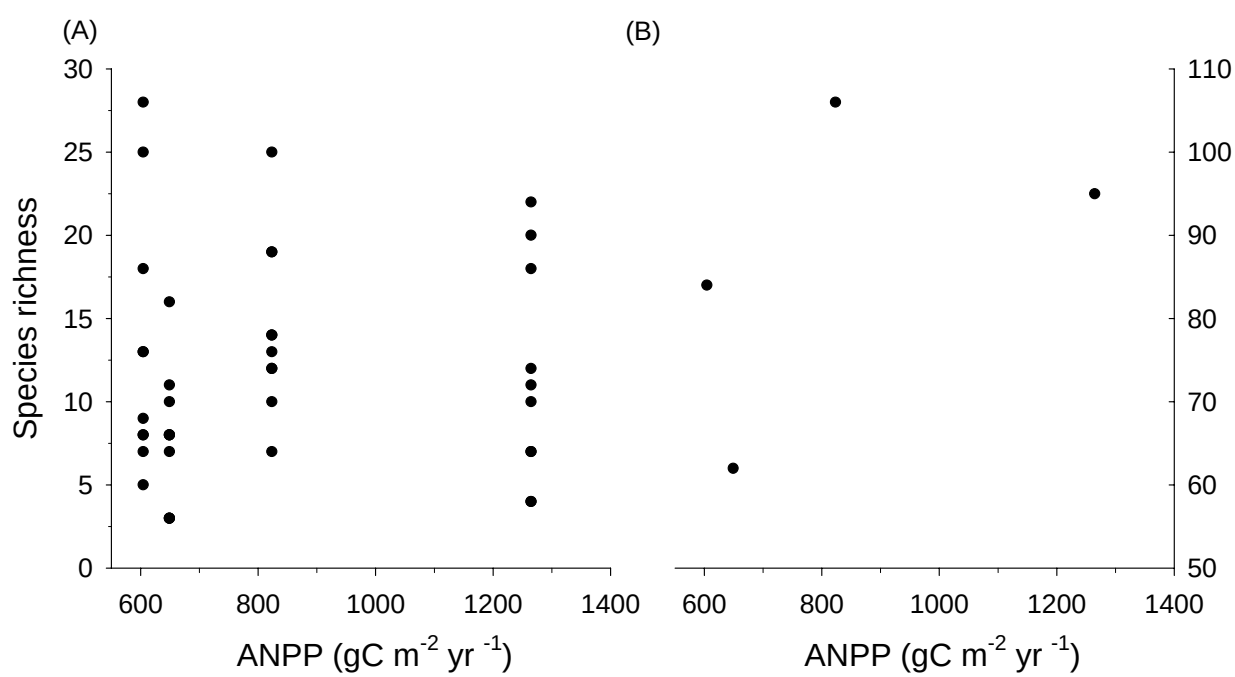

Figure 1. Species richness of invertebrates vs. productivity (above-ground net primary productivity) at each of four sites in Costa Rica: Palo Verde, Monteverde, Corcovado, and La Selva (in order of increasing productivity). Richness was calculated as (A) the total number of species in each of 10 sweep net samples at each site, and (B) the total number of species per site. Some data points are overlapping.

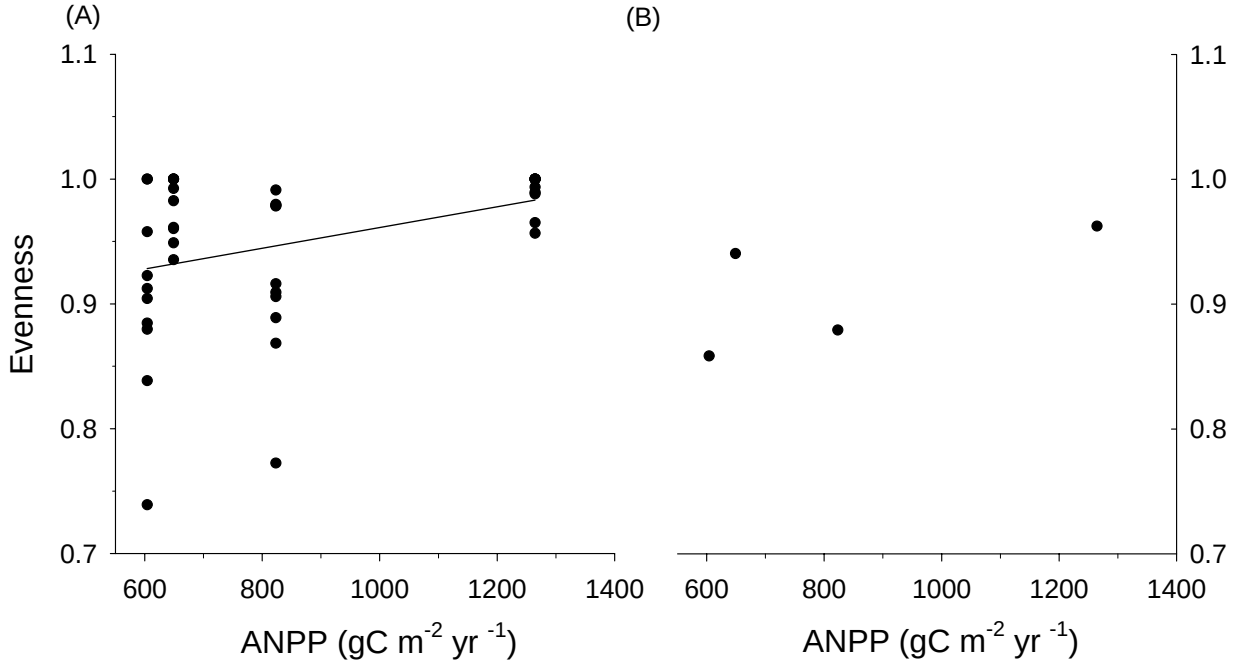

Figure 2. Evenness of invertebrates vs. productivity (above-ground net primary productivity) at each of four sites in Costa Rica: Palo Verde, Monteverde, Corcovado, and La Selva (in order of increasing productivity). Evenness was calculated for (A) each of 10 sweep net samples at each site, and (B) each site overall. A regression line indicating a significant relationship is shown in (A) for evenness of individual samples vs. productivity. Some data points are overlapping.

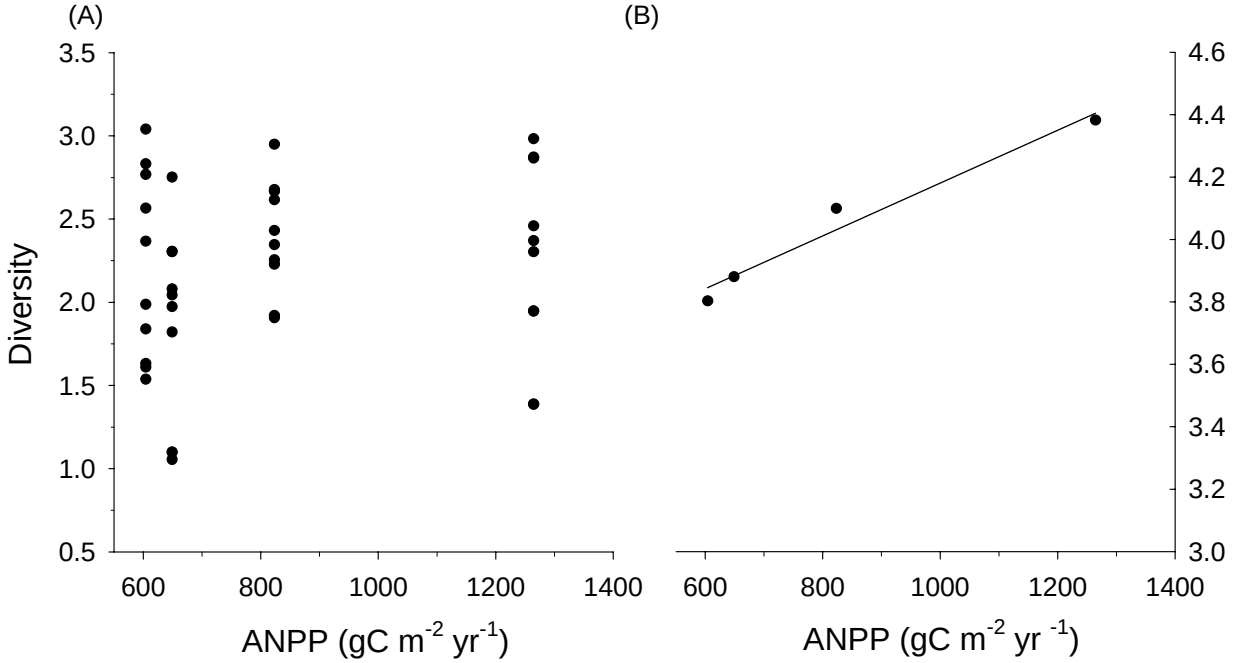

Figure 3. *H'* (Shannon-Wiener index of diversity) of invertebrates vs. productivity (above-ground net primary productivity) at each of four sites in Costa Rica: Palo Verde, Monteverde, Corcovado, and La Selva (in order of increasing productivity). Diversity was calculated for (A) each of 10 sweep net samples at each site, and (B) each site overall. A regression line showing a significant relationship is shown in (B) for diversity at each site vs. productivity. Some data points are overlapping.

DISCUSSION

We calculated three measures of biodiversity (diversity, richness, and evenness) from this data set at two spatial scales, by sample and by site. When analyzed using the individual samples (n = 10 at each site; alpha diversity), neither diversity nor richness changed with in-

creased productivity. Evenness, however, increased with increasing productivity. If increased productivity does not lead to an increase in range of niche-limiting resources, but rather, an increase in the amount of similar resources, it is possible that no new species would be added even though individual species may increase in abundance (Begon et al. 1990). More comprehensive measurements of resource availability and resource variety, and how species use the resources within each environment could clarify the causes of patterns in richness, diversity, and evenness.

When analyzed at the site level (gamma diversity), diversity increased with productivity. This was a mathematical result of increases in both richness and evenness (although neither was significantly correlated with productivity by itself). Increased productivity may lead to an increase in resources that can support both a greater number of species and of individuals. This is consistent with the global trend of high biodiversity in areas of high primary productivity.

Our results indicate the difficulty in identifying a single biodiversity index and that the relationship between productivity and biodiversity is affected by scale. Since our study sites represent only a fraction of the global productivity range, future studies should compare a broader range of sites to better determine the shape of the productivity-biodiversity curve. This study contributes to our understanding of patterns in biodiversity, an area which should be a priority for further study because humans are changing biodiversity at a high rate and changes in biodiversity can produce feedbacks that further influence ecosystem structure and function.

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AVIAN GUILD STRUCTURES IN EDGE VS. FOREST HABITATS IN FOUR COSTA RICAN FORESTS

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Abstract: One hypothesis for increased bird diversity at tropical latitudes is that the tropical forests are more spatially heterogeneous than temperate forests. It has also been shown that edge habitats have higher bird diversity than forest habitats. To test whether habitat heterogeneity has an effect on avian diversity, we compared avian guild structures between forest and edge habitats in four Costa Rican forests. Specifically, we compared the distribution of relative bird abundance across guilds. We predicted that if resources differ between forest interiors and edges, birds should be more evenly distributed between guilds in edge than forest. In three of four locations, we found distribution of abundance across guilds to be no more even in edge than in forest habitats. Edge habitat may not provide the heterogeneity of resources to birds that has been reported previously. Alternatively, perhaps the two habitats do differ in the heterogeneity of available resources, but this difference only appears in niche partitioning at the species level, not in generalized guild structure.

Key words: birds, comparative, Corcovado, diversity, heterogeneity, Kemp effect, La Selva, Monteverde, Palo Verde

INTRODUCTION

Bird species diversity is much greater at tropical latitudes than at temperate latitudes. For instance, Stiles and Skutch (1993) report that 840 species of birds have been recorded in Costa Rica, while the total number of breeders in the state of New Hampshire is less than 200 (Holmes, pers. comm.). Because birds often have very specific habitat requirements, diversity may arise from the variety and abundance of food resources, the availability of suitable nesting sites and the structure of vegetation (which affects foraging behavior). It has been hypothesized that tropical bird diversity occurs because tropical habitats are more spatially heterogeneous, offering more foraging opportunities and resources for birds that in turn can support more species.

In tropical forests, increased spatial heterogeneity of habitats could also lead to an increase in avian species diversity. As edges contain higher spatial heterogeneity, they could serve as a proxy for tropical settings. Goodwin et al (1997) reported more bird taxa and higher abundances at forest edges than in forest interiors within four tropical forest sites. We hypothesize that a broader range of resources in edge than in forest habitats may provide more foraging opportunities for birds, leading to more individuals and higher diversity. If resources do differ in this way, then we also predict that birds will be more evenly distributed among guilds (spatial feeding groups) in edge habitats than in forest habitats.

METHODS

At four field sites, Palo Verde, Monteverde, Corcovado and La Selva three pairs of recorders walked transects through forest and edge habitats and recorded any birds that were seen. Transects on trails within primary forest were considered forest habitat, while transects of forest along open fields or roads were considered edge habitat. Sampling was conducted from 0700 to 1030, and equal amounts of time were spent sampling in forest and edge habitats. To minimize effects that time of day has on bird activity, pairs switched between forest and edge habitats repeatedly throughout the morning. At Palo Verde, groups sampled from the main road

and trails El Cactus, Cerros Calizos and La Venada. At Monteverde, groups sampled from the main road and trails Sendero Rasbolon, Ermitaño, Yos, Gongolona, Quituri, Targua and El Potrero. At Corcovado, groups sampled along both sides of the airstrip, around the station and from trails Sendero Ollas, Rio Claro, Naranjos and Rio Sirena. At La Selva, groups sampled from around the cleared areas at the station and from trails SHO, SOR, CCL, CCC, STR, SOC, SLV and CEN.

We excluded non-foraging birds that flew over transects. Each species was assigned to a foraging guild based on observed behaviors or referenced from Stiles and Skutch (1989). Conspecifics were recorded together if they were foraging as a group. Guilds observed in extremely small numbers or with an expected abundance of less than four were excluded from analyses. To analyze guild structure, we compared the distributions of abundance versus guild rank for forest and edge for each site using a chi-squared test.

Results

We observed 12 guilds, 154 species, and 537 total birds (Appendix 1). Most guilds tended to contain more individuals in edge habitat than forest interior, but there was much variation in this pattern (Fig. 1). Exceptions to this trend were the bark-gleaning and foliage-gleaning insectivores, which had higher abundances in the forest. The abundance of birds appeared to be more even across guilds in edge habitat than in forest interior (Fig. 2). However, this trend had only weak statistical support: guild structure differed between forest and edge habitats (in the predicted direction) at La Selva ($X^2 = 19.10$, df = 4, P = 0.0008) but not at Palo Verde ($X^2 = 3.40$, df = 2, P = 0.18), Monteverde ($X^2 = 0.09$, df = 2, P = 0.96), or Corcovado ($X^2 = 1.01$, df = 2, P = 0.60).

Discussion

Avian guild structure did not differ between the forest and edge habitats at three out of the four sites. One possible explanation is that edge and forest habitats at these three sites are similar in terms of the types of resources and the foraging space available to different birds. Another potential explanation is that our definition of guilds did not accurately capture the biological variation in resource use within these habitats. It could be that the two habitats differ in heterogeneity of available resources but that this is apparent only in niche partitioning at the species level, not in generalized guild structure. Future studies could investigate these hypotheses by quantifying structural heterogeneity and variation in the types of resources available to birds in edge versus forest habitats.

One possible explanation for the differing guild structures between edge and forest habitats at La Selva is the difference in the nature of edge habitats at each site. Edge habitat exists as an interface between primary forest and disturbed areas, and the type of disturbed areas may have differed between the sites (e.g. regularly mowed air strip at Corcovado vs. secondary forest at Monteverde).

One caveat to our study is that there is a potential for sampling bias in the forest versus edge habitats. Birds are easier to see in edge habitats where the trees tend to be less dense, and more intensive sampling may be necessary to adequately describe forest bird communities. Nevertheless, our results suggest that increased habitat heterogeneity may not be sufficient to explain the high diversity of birds in the tropics although it may be a contributing factor.

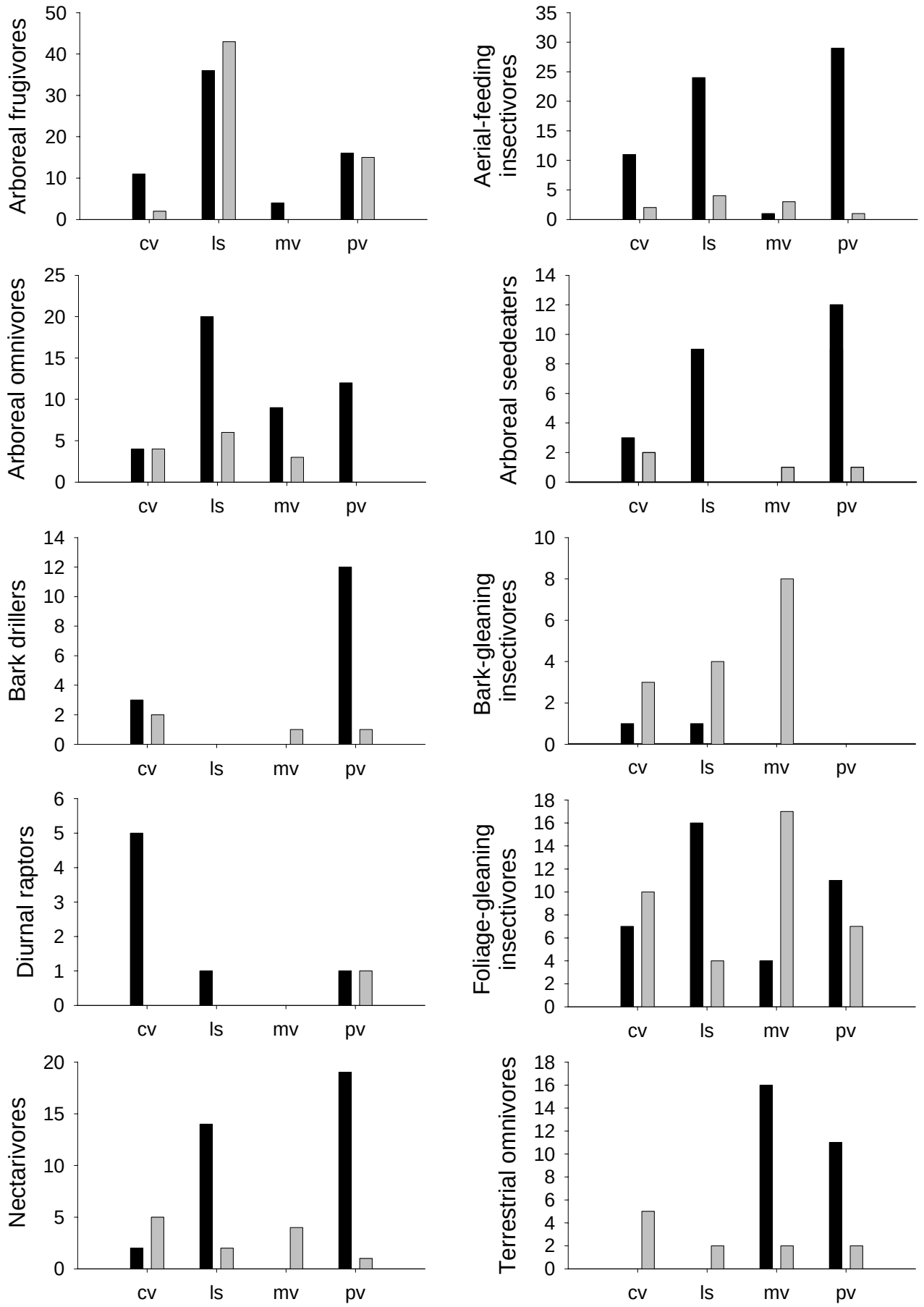

Figure 1. Abundance of individual birds recorded within the ten most common guilds in edge (black bars) and forest habitat (gray bars) at four sites (cv = Corcovado; ls = La Selva; mv = Monteverde; pv = Palo Verde). Scales vary among histograms.

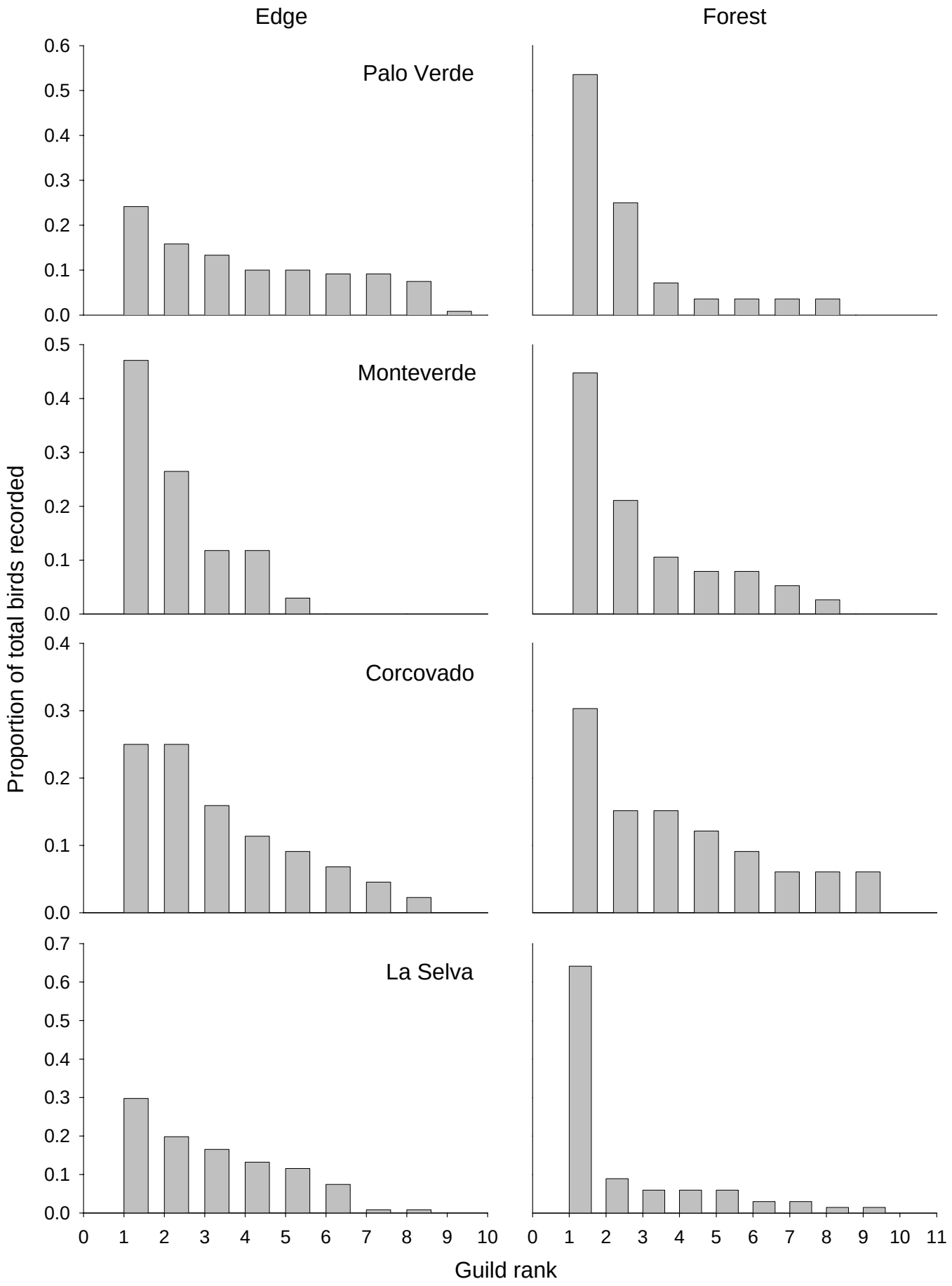

Fig. 2. Relative abundance versus guild rank. Only La Selva displayed a significant difference between edge and forest.

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Appendix 1. Bird species (or type), their guild assignment, and the number of individuals recorded in edge and forest habitat (E vs. F) at four sites in Costa Rica.

		Corcovado		La Selva		Monteverde		Palo Verde	
Species	Guild	E	F	E	F	E	F	E	F
Baird's trogon	aerial-feeding insectivore		1						
Barn swallow	aerial-feeding insectivore							11	
Bright-rumped attila	aerial-feeding insectivore			1	1				
Brown-crested flycatcher	aerial-feeding insectivore							3	
Cinnamon becard	aerial-feeding insectivore			1					
Collared redstart	aerial-feeding insectivore						1		
Flycatcher sp.	aerial-feeding insectivore	3		2	2			1	
Gray-capped flycatcher	aerial-feeding insectivore			3					
Great kiskadee	aerial-feeding insectivore	2		5				5	
Great-crested flycatcher	aerial-feeding insectivore							1	3
Long-tailed tyrant	aerial-feeding insectivore			1					
Nutting's flycatcher	aerial-feeding insectivore							2	
Ochre-bellied flycatcher	aerial-feeding insectivore				1				
Olive-striped flycatcher	aerial-feeding insectivore					1			
Piratic flycatcher	aerial-feeding insectivore			1					
Rose-throated becard	aerial-feeding insectivore							1	
Slate-throated redstart	aerial-feeding insectivore					1	1		
Social flycatcher	aerial-feeding insectivore			5					
Swallow sp.	aerial-feeding insectivore	4							
Swift sp.	aerial-feeding insectivore			1					
Tawny-faced gnatwren	aerial-feeding insectivore				1				
Tropical kingbird	aerial-feeding insectivore	1		1	1			8	1
Unidentified sp.	aerial-feeding insectivore						1		
Violaceous trogon	aerial-feeding insectivore	1							
White-ringed flycatcher	aerial-feeding insectivore			1					
Yellow-bellied flycatcher	aerial-feeding insectivore			3					
Yellow-olive flycatcher	aerial-feeding insectivore								1
Spotted antbird	ant-follower				1				

Appendix 1. Continued from previous page.

		Corcovado		La Selva		Monteverde		Palo Verde	
Species	Guild	E	F	E	F	E	F	E	F
Baltimore oriole	arboreal frugivore			2				2	
Bananaquit	arboreal frugivore					1			
Black-faced grosbeak	arboreal frugivore			5					
Black-headed saltator	arboreal frugivore			2					
Buff-throated saltator	arboreal frugivore			3					
Chestnut-mandibled toucan	arboreal frugivore	1		2	14				
Collared aracari	arboreal frugivore				3				
Crested guan	arboreal frugivore		2		1				
Golden-hooded tanager	arboreal frugivore			2					
Keel-billed toucan	arboreal frugivore				4				
Long-tailed manakin	arboreal frugivore								1
Masked tityra	arboreal frugivore	2		2					
Montezuma oropendola	arboreal frugivore			1	12				
Olived-backed euphonia	arboreal frugivore				2				
Orange-chinned parakeet	arboreal frugivore			6					
Orange-fronted parakeet	arboreal frugivore							10	
Palm tanager	arboreal frugivore			3					
Parakeet sp.	arboreal frugivore							2	6
Parrot sp.	arboreal frugivore	2			4			2	3
Prong-biled barbet	arboreal frugivore					3			
Red-lored parrot	arboreal frugivore				2				
Scarlet macaw	arboreal frugivore	5							
Scarlet-thighed dacnis	arboreal frugivore			1					
Short-billed pidgeon	arboreal frugivore	1			3				
Summer tanager	arboreal frugivore			1					
Tanager sp.	arboreal frugivore				1				
White-collared manakin	arboreal frugivore			1					
White-crowned parrot	arboreal frugivore			1	1				
Yellow-crowned euphonia	arboreal frugivore			2					
Yellow-naped parrot	arboreal frugivore								1
Azure-hooded jay	arboreal omnivore						2		
Black-headed trogon	arboreal omnivore		1					1	
Black-throated trogon	arboreal omnivore			1	2				

Appendix 1. Continued from previous page.

		Corcovado		La Selva		Monteverde		Palo Verde	
Species	Guild	E	F	E	F	E	F	E	F
Blue-grey tanager	arboreal omnivore	1		2					
Broad-billed motmot	arboreal omnivore				4				
Brown jay	arboreal omnivore					9			
Groove-billed ani	arboreal omnivore							8	
Mangrove cuckoo	arboreal omnivore							2	
Passerini's tanager	arboreal omnivore			16					
Rufous motmot	arboreal omnivore				2				
Rufous piha	arboreal omnivore		3		1				
Scarlet-rumped tanager	arboreal omnivore	3							
Slaty-tailed trogon	arboreal omnivore				2				
Squirrel cuckoo	arboreal omnivore			2				2	
Trogon sp.	arboreal omnivore		1				1		
Turquoise-browed motmot	arboreal omnivore							2	
White-throated magpie-jay	arboreal omnivore							1	
Yellow-billed cacique	arboreal omnivore	1		1					
Blue-black grassquit	arboreal seedeater			1					
Thick-billed seed-finch	arboreal seedeater			8					
White-collared seedeater	arboreal seedeater							9	
Golden-naped woodpecker	bark driller	2							
Hoffman's woodpecker	bark driller							12	1
Pale-billed woodpecker	bark driller	1	1						
Woodpecker sp.	bark driller		1				1		
Buff-throated woodcreeper	bark-gleaning insectivores						1		
Plain-brown woodcreeper	bark-gleaning insectivores				1				
Spinetail sp.	bark-gleaning insectivores						2		
Streak-headed woodcreeper	bark-gleaning insectivores			1					
Tawny-winged woodcreeper	bark-gleaning insectivores	1							
Woodcreeper sp.	bark-gleaning insectivores		3		3		5		

Appendix 1. Continued from previous page.

		Corcovado		La Selva		Monteverde		Palo Verde	
Species	Guild	E	F	E	F	E	F	E	F
Double-toothed kite	diurnal raptor	2							
Hawk sp.	diurnal raptor	1						1	1
Laughing falcon	diurnal raptor							2	
Roadside hawk	diurnal raptor	1							
Swallow-tailed kite	diurnal raptor	1							
Antwren sp.	foliage-gleaning insectivore						1		
Bay wren	foliage-gleaning insectivore			1					
Bird sp.	foliage-gleaning insectivore		1						
Black-throated green warbler	foliage-gleaning insectivore					1			
Buff-rumped warbler	foliage-gleaning insectivore			3	1				
Chestnut-backed antbird	foliage-gleaning insectivore	2	3		3				
Chestnut-sided warbler	foliage-gleaning insectivore			3					
Common tody-flycatcher	foliage-gleaning insectivore			3					
Golden-winged warbler	foliage-gleaning insectivore			1					
Gray-headed tanager	foliage-gleaning insectivore		1						
Great antshrike	foliage-gleaning insectivore			1					
Rufous-naped wren	foliage-gleaning insectivore							11	2
Scarlet-rumped cacique	foliage-gleaning insectivore		3						
Slaty antshrike	foliage-gleaning insectivore				1				
Streaked-breasted treehunter	foliage-gleaning insectivore						1		
Striped-breasted wren	foliage-gleaning insectivore				2				
Tanager sp.	foliage-gleaning insectivore						7		

Appendix 1. Continued from previous page.

		Corcovado		La Selva		Monteverde		Palo Verde	
Species	Guild	E	F	E	F	E	F	E	F
Tennessee warbler	foliage-gleaning insectivore							2	
Three-striped warbler	foliage-gleaning insectivore						3		
Vireo sp.	foliage-gleaning insectivore								2
Warbler sp.	foliage-gleaning insectivore			1		1	5		
White-breasted wood-wren	foliage-gleaning insectivore				1				
White-flanked antwren	foliage-gleaning insectivore			1					
White-lored gnatcatcher	foliage-gleaning insectivore							1	4
Wilson's warbler	foliage-gleaning insectivore					1			
Wood thrush	foliage-gleaning insectivore			2					
Wren sp.	foliage-gleaning insectivore		1		3				
Yellow warbler	foliage-gleaning insectivore							2	
Yellow-throated vireo	foliage-gleaning insectivore	1							1
Black-cowled oriole	nectarivores			2					
Blue-throated goldentail	nectarivores							1	
Cinnamon hummingbird	nectarivores							1	
Fork-tailed emerald	nectarivores							1	
Green hermit	nectarivores		1						
Green honeycreeper	nectarivores			1					
Green violet-ear	nectarivores						1		
Hummingbird sp.	nectarivores	2	3	5	2		3	11	1
Long-tailed hermit	nectarivores		2	2					
Plain-capped starthroat	nectarivores							1	
Ruby-throated hummingbird	nectarivores							2	

Appendix 1. Continued from previous page.

		Corcovado		La Selva		Monteverde		Palo Verde	
Species	Guild	E	F	E	F	E	F	E	F
Rufous-tailed hummingbird	nectarivores			3					
Steely-vented hummingbird	nectarivores							1	
White-necked jacobin	nectarivores			1					
Great potoo	nocturnal raptor				1				
Black vulture	scavenging carrion	1		1					
Turkey vulture	scavenging carrion	8							
Fasciated tiger-heron	stream hunter	1							
Common ground-dove	terrestrial frugivores							2	
Dove sp.	terrestrial frugivores							1	1
Great currasow	terrestrial frugivores		2						2
Great tinamou	terrestrial frugivores				1				
Inca dove	terrestrial frugivores							7	
Tinamou sp.	terrestrial frugivores				1				
White-fronted parrot	terrestrial frugivores								4
White-tipped dove	terrestrial frugivores							2	1
Cattle egret	terrestrial omnivore	3						1	
Marbled wood-quail	terrestrial omnivore		3						
Nightingale-thrush sp.	terrestrial omnivore						1		
Quail sp.	terrestrial omnivore					9	1		
Robin sp.	terrestrial omnivore					7			

Forest structure and the effects of tree-falls on heterogeneity in four types of tropical forest in Costa Rica

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Abstract: Forests are dynamic systems in a perpetual state of regeneration from disturbance events. Disturbances in the form of tree-falls create texture and heterogeneity in forest structure by creating gaps. To study the relationship between forest structure and disturbance events, we sampled four types of primary forest in Costa Rica: dry deciduous forest, pre-montane cloud forest, seasonally wet forest, and tropical wet forest. Forests were generally distinguishable based on structural features, and plots within forests differed in some predictable ways depending on the presence or absence of recent tree-falls. While structural changes in forests are generally attributed to the presence of tree-fall gaps, our results suggest a reciprocal interaction between forest structure and gap formation.

Key words: charismatic megaflora, Corcovado, disturbance regime, La Selva, Monteverde, Palo Verde, principle components analysis

Introduction

Within Costa Rica there are many different described forest types including dry deciduous forest, pre-montane cloud forest, seasonally wet forest, and tropical wet forest (Hartshorn 1983). While these forests are geographically proximate, they represent very different forest types. These forests are demonstrably different in water and nutrient availability, seasonality of precipitation, elevation, temperature, species composition, herbivore communities, and soil type (Osterling et al. 1995). The forests could also differ in their disturbance regimes (Lieberman et al. 1989). We studied these four forest types to test if these differences correspond to variation in physical structure of the forests.

The tempo and scale of disturbance events may change forests in numerous ways, including species composition. Intermediate levels of disturbance are hypothesized to maximize species diversity (Connell 1978). Disturbance events such as tree-falls also add heterogeneity or texture to forest structure. We examined whether disturbance caused by tree-falls created increased forest heterogeneity via the processes of regeneration and succession. To determine the effects of tree-falls in these four forests types, we compared structural characteristics of the forests in areas with and without tree-falls. Our sampling was designed to determine what structural characteristics differ between the forests and if some variation within forests can be understood as a product of tree-fall disturbances.

Methods

We measured forest characteristics at four sites across Costa Rica: Palo Verde National Park (9 January 2004), Guanacaste; Monteverde Biological Reserve, Monteverde (15 January 2005); Corcovado National Park, Osa Peninsula (3 February 2004); and La Selva Biological Station, La Selva (13 February 2004). At each site, we walked a transect of primary forest, stopping every 50 m to measure forest characteristics in plots with 10 m radius. We noted all tree-falls along the transect and the presence of any tree-fall in plots. We examined six to ten plots at each forest site. All plots were centered at least

15 m away from existing paths and unnatural disturbances. We measured six variables: (1) From the center of each plot, we measured basal area using an English 4X forestry prism for forests with low stem density (Palo Verde and Corcovado) and 10X forestry prism for forests with high stem density (Monteverde and La Selva). (2) Using a laser hypsometer, we measured the height of the tallest tree within the 10 m radius of each plot. (3) We measured percent open canopy using a spherical densitometer, taking readings at the center of each plot, as well as one reading in each of four quadrants of the plot. (4) We estimated percent ground cover as all plant growth below chest height by visually assessing how much ground would appear covered if viewed from directly above. (5) To measure sapling density, we walked four 10 m transects in each plot, counting the number of sapling within reach of our standardized outstretched arms (~ 1 m height and 2 m width). (6) We measured the diameter at breast height (DBH) of all trees > 6 cm in diameter within the radius of the plot.

Height of tallest tree, basal area, percent ground cover, variance in sapling density, variance in percent open canopy, and variance in DBH, which were estimated from a single measurement per plot, were analyzed with an ANOVA model that included forest and tree-fall presence. Percent of open canopy, sapling density and DBH, which were estimated from variables composed of multiple measurements within each plot, were analyzed with a nested ANOVA that included forest, tree-fall presence, and plot within forest and tree-fall presence (plot was considered a random effect). We constructed a correlation matrix (based on 32 plot means) of all nine of the above variables. This correlation matrix was the basis for a principle component analysis (PCA).

RESULTS

Many variables differed among the four forests (Fig. 1), and some patterns within forests were related to tree-falls (Table 1). The incidence of tree-falls was 0.4 tree-falls / 10 m transect in Palo Verde and Monteverde, and 0.8 tree-falls / 10 m transect in Corcovado and La Selva.

Height of tallest tree

The height of the tallest tree varied among forests, with the tallest trees located in Corcovado and La Selva ($F_{3,24}$ = 15.72, P < 0.0001). Trees were taller in plots that had tree-falls ($F_{1,24}$ = 6.02, P = 0.0013). The interaction of forest and tree-fall presence was not significant ($F_{3,24}$ = 0.80, P = 0.51).

Basal area

The basal area at Monteverde was higher than all the other forests ($F_{3,24}$ = 27.66, P < 0.0001). In all forests, basal area was higher in the plots that had tree-falls ($F_{1,24}$ = 6.46, P = 0.02). The interaction of forest and tree-fall presence was not significant ($F_{3,24}$ = 2.05, P = 0.14).

Percent ground cover

The percent ground cover was highest in Monteverde and lowest in Palo Verde ($F_{3,24}$ = 31.65, P = 0.001) and did not differ among plots with and without tree-falls ($F_{1,24}$ = 0.02, P = 0.89). The interaction of forest and tree-fall presence was not significant ($F_{3,24}$ = 1.78, P = 0.18).

Sapling density

Sapling density was lowest in Palo Verde, highest in Monteverde, and intermediate in both Corcovado and La Selva ($F_{3,64}$ = 17.39, P < 0.0001). While plots within a forest differed ($F_{24,64}$ = 2.99, P = 0.0001), there was no pattern with respect to tree-falls ($F_{1,64}$ = 0.17, P = 0.68). There was also no interaction between forest and tree-fall presence ($F_{3,64}$ = 0.37, P = 0.77). The

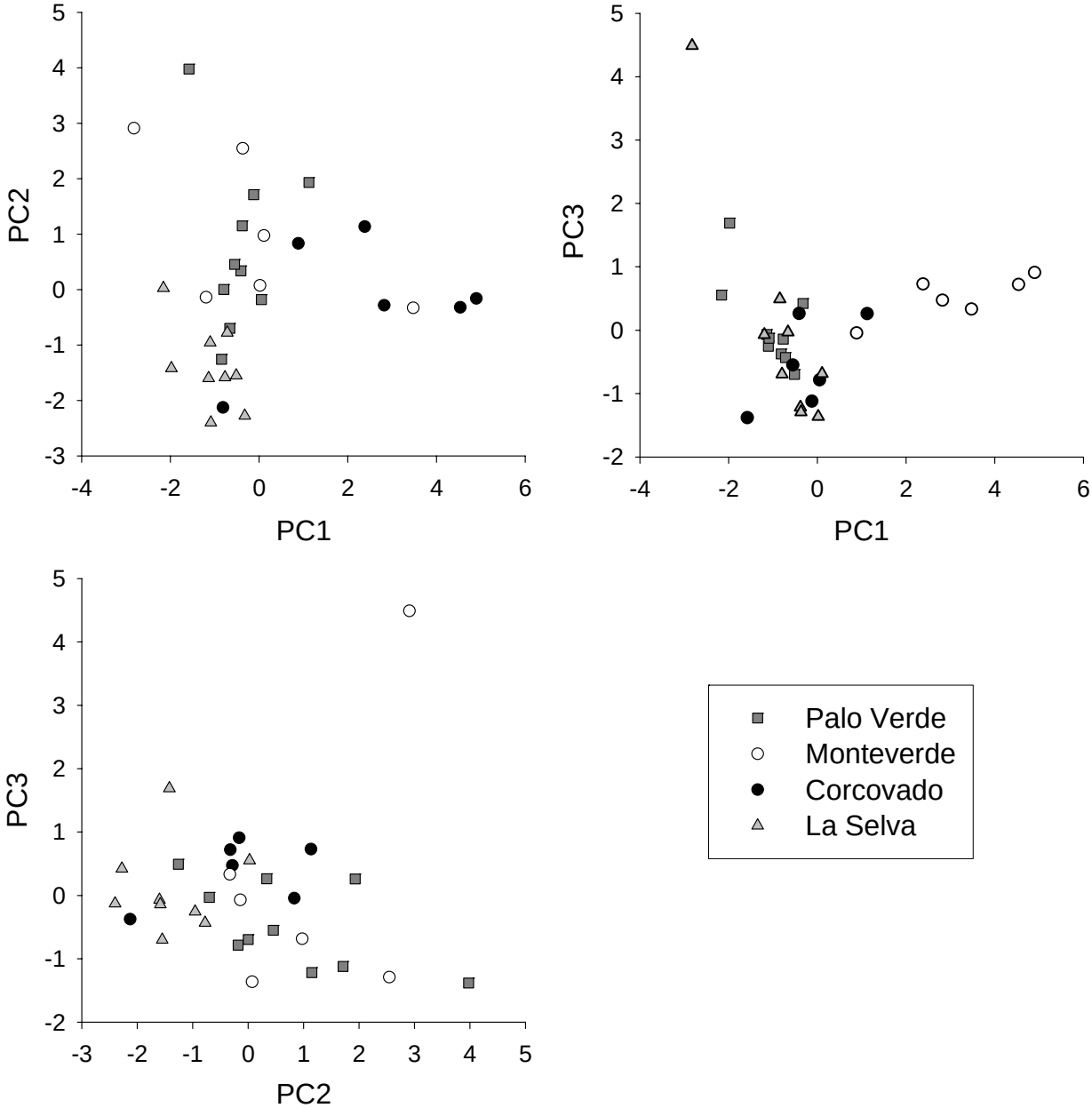

Figure 1. Replicate samples from each of four forests plotted with respect to first three axes of a principle components analysis Spatial separation of points from the same forest indicates differences in forest structure.

variance in sapling density followed the same pattern between forests ($F_{3,24}$ = 6.50, P = 0.002), with respect to tree-fall presence ($F_{1,24}$ = 0.31, P = 0.58), and with respect to the interaction of forest and tree-fall presence ($F_{3,24}$ = 0.11, P = 0.95).

DBH

The mean tree diameter did not differ among the forests ($F_{3,64}$ = 2.06, P = 0.12) or with respect to tree-fall presence ($F_{1,64}$ = 1.59, P = 0.21). However, in all of the forests except for Corcovado, the tree diameters were smaller in plots with tree-falls. There was a significant interaction of forest and tree-fall presence ($F_{3,64}$ = 1.09, P = 0.0003). The variance in tree diameter did not significantly differ among forests ($F_{3,24}$ = 1.82, P = 0.17), between plots with and without tree-falls ($F_{1,24}$ = 0.08, P = 0.78), or with the interaction of forest and tree-fall presence ($F_{3,24}$ = 1.27, P = 0.31).

Table 1. Measures of forest structure at four biogeographically distinct sites in Costa Rica. Means ± SE were calculated separately for plots with and without a still recognizable tree-fall. Final three columns are the factor loadings from a principle components analysis (see Fig. 1).

	Tree-fall	Palo Verde	Monteverde	Corcovado	La Selva	PC1 37.4%	PC2 63.7%	PC3 77.4%
Tallest tree (m)	yes	14.7	15.7 ± 0.3	28.3 ± 0.9	26.4 ± 3.3	-0.09	0.52	0.00
	no	9.5 ± 0.9	12.5 ± 1.8	22.9 ± 0.5	17.4 ± 1.7			
Basal area (ft^2 / acre)	yes	82	255.0 ± 45.0	51.3 ± 9.2	105.0 ± 10.4	0.40	0.11	0.17
	no	53.5 ± 3.6	165.0 ± 31.7	43.1 ± 10.3	92.0 ± 12.4			
% ground cover	yes	12	70 ± 20	52.5 ± 5.9	37.5 ± 7.8	0.38	0.29	0.21
	no	9.9 ± 1.4	85.0 ± 3.5	50.0 ± 15	24.4 ± 2.6			
Ave. sapling density	yes	3.8	27.3 ± 6.8	12.6 ± 2.8	8.3 ± 0.9	0.51	0.05	0.13
	no	9.1 ± 1.2	26.1 ± 4.8	11.4 ± 0.9	8.9 ± 0.8			
Var. sapling density	yes	4.9	121.8 ± 26.8	43.3 ± 32.1	14.2 ± 5.8	0.46	0.07	0.19
	no	12.1 ± 4.7	97.8 ± 48.1	24.9 ± 14.0	6.7 ± 2.4			
Ave. DBH	yes	22.2	16.6 ± 2.7	16.7 ± 1.5	21.3 ± 0.7	-0.17	0.53	-0.13
	no	14.8 ± 0.8	15.2 ± 0.5	25.1 ± 4.9	17.9 ± 1.1			
Var. DBH	yes	27.05	142.0 ± 110.1	265.1 ± 74.9	313.9 ± 78.6	-0.18	0.55	-0.09
	no	127.9 ± 30.7	140.7 ± 62.2	452.7 ± 354.6	192.5 ± 42.4			
Ave. % open canopy	yes	20.0	7.9 ± 2.7	7.1 ± 1.2	20.2 ± 9.1	-0.33	-0.16	0.55
	no	13.1 ± 1.2	6.4 ± 0.9	11.9 ± 3.1	8.9 ± 2.3			
Var. % open canopy	yes	56.1	4.7 ± 3.6	13.7 ± 5.5	242 ± 143.7	-0.22	0.14	0.74
	no	40.9 ± 14.7	10.8 ± 3.1	9.5 ± 0	22.9 ± 9.6			

Percent open canopy

The average percent open canopy did not vary among forests ($F_{3,64}$ = 1.09, P = 0.37) or between plots with and without tree ($F_{1,64}$ = 0.53, P = 0.47). The interaction of forest and tree-fall presence was not significant ($F_{3,64}$ = 1.04, P = 0.39). The variance in percent open canopy followed the same pattern between forests ($F_{3,24}$ = 0.91, P = 0.45), with respect to tree-fall presence ($F_{1,24}$ = 0.60, P = 0.45), and with respect to the interaction of forest and tree-fall presence ($F_{3,24}$ = 0.64, P = 0.60).

PCA

Using a 3-axis PCA, we explained 77.4 % of the variation in the four forests. Sapling density and variance in sapling density were strongly positively weighted into PC1. Tree diameter and variance in tree diameter were the largest components of PC2. Characteristics of open canopy measures accounted for the most variance in PC3 (Table 1). Using those three axes, the forests of Monteverde and Palo Verde were quite distinct from each other and from the other forests. La Selva and Corcovado are broadly overlapping (Fig 1).

DISCUSSION

Height of tallest tree

The smaller heights of the tallest trees in Monteverde and Palo Verde may be attributed to constraints imposed by altitude and moisture. The greater height of the tallest tree associated with the presence of tree falls is likely a product of older stands with taller trees being more susceptible to agents of gap formation, such as wind and epiphyte loads.

Basal area

The higher basal area at Monteverde was due to high stem density, not high tree diameter, (see DBH below). Higher basal area in plots with tree-falls was likely the result of high densities of younger trees filling in gaps.

Percent ground cover

The percent ground cover, highest in Monteverde and lowest in Palo Verde, is likely affected by seasonality and nutrient availability. Surprisingly, the lack of difference between plots with and without tree falls suggests that gap formation does not facilitate the growth of understory species.

Sapling density

Sapling density and variance in density, highest in Monteverde and lowest in Palo Verde, may be indicative of recruitment, and is likely the product of abiotic conditions combined with effects of herbivore communities, which differ among the four forests. Interestingly, sapling density did not differ in plots with tree falls, suggesting that recruitment does not necessarily increase in response to a gap. The lack of higher variance in plots with tree falls contradicts the hypothesis that gap formation increases heterogeneity.

DBH

Mean tree diameter was not a characteristic that differed across sites. While DBH may differ among forests of different ages, the four forests we sampled were primary growth. The average DBH may have been lower in plots with tree falls as a result of greater relative abundance of younger trees, though the number of larger trees might not necessarily be different. The reverse pattern in Corcovado remains to be explained. The lack of higher variance in plots with tree falls contradicts the hypothesis that gap formation increases heterogeneity.

Percent open canopy

The lack of difference between plots with and without tree falls suggests that gaps are

quickly filled, though the height to canopy cover may be lower where a gap was recently filled. The lack of higher variance in plots with tree falls again contradicts the hypothesis that gap formation increases heterogeneity.

PCA

Multivariate analyses seemed to reflect the separation of Monteverde and Palo Verde from La Selva and Corcovado with respect to water and nutrient availability, seasonality of precipitation, elevation, temperature, species compositions, herbivore communities, soil type, and other factors. Rates of tree-fall were also similar in La Selva and Corcovado, perhaps as a consequence or as a partial cause of similarities in forest structure.

We identified important structural differences and similarities between the four forests. The vegetation and ecosystem differences between these forests were understood prior to this study, but a systematic comparison of the forest structures was lacking. Within forests, gap formation does not appear to affect heterogeneity in forest structure as we predicted. However, tree-fall gaps have other effects on forest structure. Presumably, there is a feedback in that forest structure also affects susceptibility to gap formation.

Global climate change may affect disturbance regimes, which in turn influence tree-fall dynamics of forests. It is possible that global climate change will influence forest structure and the rate of disturbance events. It is difficult to predict how forest dynamics will be influenced, but this is an area of considerable ecological and social concern. Dealing with the effects of climate change requires deeper understanding of the nature and mechanisms by which it may alter forest structure.

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