

Vegetation dynamics of predator-free land-bridge islands

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Summary

1 We tested the 'green world' hypothesis of Hairston, Smith and Slobodkin by monitoring vegetation change on recently created predator-free land-bridge islands in a huge hydroelectric impoundment, Lago Guri, in the State of Bolivar, Venezuela.

2 Our results affirm the green world hypothesis and expose the operation of a strong top-down trophic cascade that negatively impacted nearly every plant species present, implying that community stability is maintained through the action of predators.

3 To test the hypothesis, we monitored vegetation on nine predator-free islands and compared demographic parameters to those observed at control sites supporting complete or nearly complete suites of predators.

4 Herbivore abundance was high on 'small' (≥ 0.5 , < 2 ha) islands, moderate on 'medium' islands (> 3 , < 15 ha) and low on the 'large' landmasses that served for reference.

5 Small sapling densities on small islands were only 37% of controls in 1997 (after 11 years of isolation), and when recensused in 2002, had fallen to 25% of controls. High mortality and, especially, low recruitment contributed to the decline in sapling cohorts.

6 Sapling decline occurred earlier on small islands, although recruitment failure had become equally pronounced on medium islands by the end of the monitoring period.

7 Several mechanisms could potentially account for suppressed sapling recruitment, but the weight of evidence points to herbivory on seedlings and small saplings by leaf-cutter ants (*Atta* spp. and *Acromyrmex* sp.). Exposure to prevailing trade winds (windward vs. leeward slopes of islands) had no detectable effect on the density or diversity of seedlings or saplings.

Key-words: *Atta*, ecosystem, howler monkey, land-bridge island, Lago Guri, leaf-cutter ants, trophic cascade, tropical dry forest, vegetation dynamics, Venezuela.

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Introduction

A trophic cascade is the process by which a perturbation propagates either up or down a food web with alternating negative and positive effects at successive levels (Paine 1980). The susceptibility of nearshore, intertidal ecosystems and fresh-water lakes to trophic cascades has been well documented (Estes *et al.* 1978; Carpenter & Kitchel 1993; Menge 1995). Whether terrestrial ecosystems are capable of displaying trophic cascades

has long been debated (Oksanen 1983; Terborgh 1988; Power 1992; Polis & Strong 1996). However, accumulating evidence increasingly underscores the potential of terrestrial systems to undergo trophic cascades (Mclaren & Peterson 1994; Pace *et al.* 1999; Oksanen & Oksanen 2000; Schmitz *et al.* 2000; Ripple *et al.* 2001; Terborgh *et al.* 2001; Croll *et al.* 2005).

Nevertheless, many questions remain. Are the links between trophic levels strong or weak in terrestrial ecosystems (Halaj & Wise 2001)? Do these links follow narrow pathways through a system, affecting only a few species, or do they ramify widely and involve many species? Do the effects of predator removal lead only to minor increases in the numbers of herbivores, or do herbivores increase to densities at which they exert

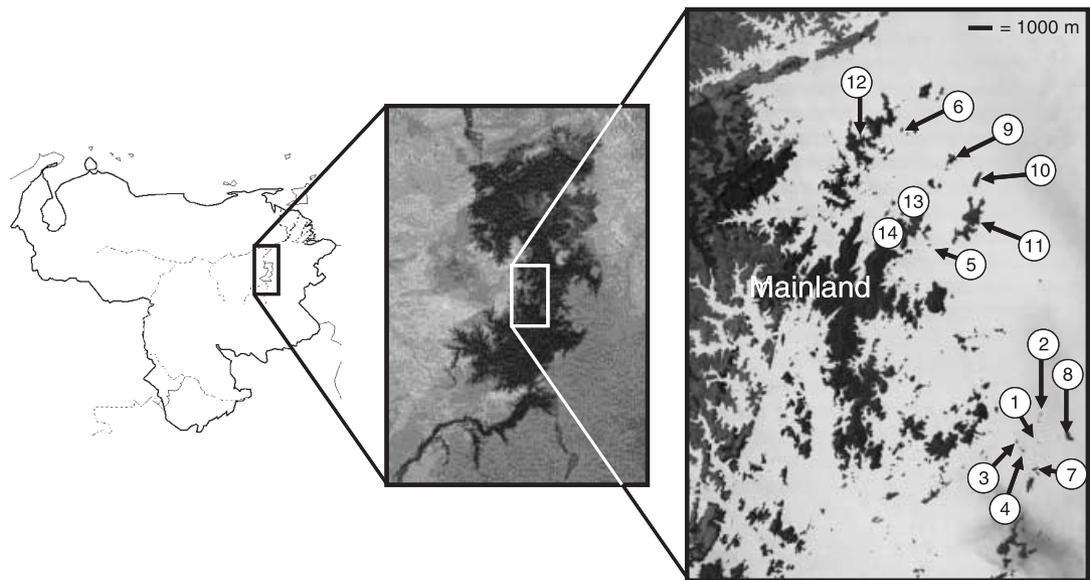


Fig. 1 Map of Venezuela indicating the location of Lago Guri (first insert) and the study islands (second insert) used to investigate long-term vegetation dynamics. Numbers are keyed in Table 1.

major impacts on the species composition and/or biomass of the vegetation (Polis *et al.* 2000)?

Here we attempt to answer these questions in the context of a particularly advantageous experiment initiated in 1986 by the formation of Lago Guri, a vast hydroelectric impoundment in the Caroni Valley of Venezuela (Morales & Gorzula 1986). Inundating an area of 4300 km², Lago Guri contains hundreds of land-bridge islands that constitute fragments of a formerly continuous landscape (Fig. 1). The smaller islands lack predators of vertebrates while retaining generalist herbivores and offer the conditions necessary to test the hypothesis of Hairston *et al.* (1960) which states that the world is green because predators prevent herbivores from becoming abundant enough to destroy vegetation.

ECOLOGICAL SETTING

Prior to the creation of Lago Guri, the Caroni Valley supported an intricate mosaic of savanna and forest that had been inhabited by Amerindians for thousands of years. Beginning in the 18th century, pioneers of European extraction began to settle in the region, but poor soils discouraged agriculture. Within forested zones, the principal impacts were cattle browsing, selective logging, hunting and fire (Morales & Gorzula 1986).

In the 1960s, EDELCA, the company that manages the Guri impoundment, assumed authority over the land to be flooded and a broad buffer zone protecting the surrounding watershed. All residents of the region were obliged to relocate. During dam construction, loggers were authorized to remove commercial timber from areas destined to be flooded and from the adjoining mainland, but not from sites destined to become islands. This policy led to one of several sources of uncontrolled variation in forest composition between

islands and the mainland. Fire has had an even more pervasive influence. During the period of our research (1990–2002), parts of the nearby mainland burned repeatedly (1990, 1993, 1996, 1998 and 2001). In contrast, islands in Lago Guri were largely spared (but see below).

Preliminary surveys of the animal communities of several Lago Guri islands revealed that most of the vertebrate species present in the regional dry forest ecosystem had disappeared from smaller (< 15 ha) islands within a few years after isolation (Terborgh *et al.* 1997b, 1997c). Species of vertebrates persisting on the smaller islands constituted a highly non-random subset of the original community. Some trophic guilds were underrepresented (frugivores, including seed dispersers and omnivores) or absent (predators of vertebrates), whereas other trophic guilds occurred at densities conspicuously higher than those observed on the mainland (seed predators, predators of invertebrates, and especially, generalist herbivores). Groups displaying ‘hyperabundance’ included birds, rodents, anurans, lizards, spiders, and generalist herbivores such as common iguanas (*Iguana iguana*), porcupines (*Coendou prehensilis*), tortoises (*Geochelone carbonaria*), howler monkeys (*Alouatta seniculus*), and leaf-cutter ants (*Atta* spp. and *Acromyrmex* sp.). On small islands, the densities of some of these herbivores were one to two orders of magnitude greater than found on the nearby mainland (Terborgh *et al.* 1997c; Asquith *et al.* 1999; Rao 2000; Terborgh *et al.* 2001; Aponte *et al.* 2003; Feeley 2003; Lambert *et al.* 2003).

RESEARCH DESIGN

The presence/absence of most species was highly correlated with island area. The faunas of different-sized islands were thus strongly nested such that islands of similar size supported similar collections of consumer

species. This fact allowed us to use sets of islands grouped by size as treatments in the experimental design.

'Small' islands (< 2.0 ha, $n = 6$) invariably harboured rodents, birds, lizards, anurans, spiders and other invertebrates, and generalist herbivores, including leaf-cutter ants, common iguana, and often howler monkey and/or porcupine (Terborgh *et al.* 1997b, 1997c). 'Medium' islands (> 3, < 15 ha, $n = 4$) harboured most or all of the species found on small islands and, in addition, armadillo (*Dasyus novemcinctus*), agouti (*Dasyprocta leporina*), tortoise and sometimes capuchin monkey (*Cebus olivaceus*), but no obligate predators of vertebrates. Large landmasses (> 75 ha, $n = 4$) supported most vertebrates present regionally, including large frugivorous and granivorous birds, a full complement of primates, paca (*Agouti paca*), deer (*Mazama americana*), peccary (*Tyassu tajacu*), coati (*Nasua nasua*), tyra (*Eira barbara*), and tamandua (*Tamandua tridactyla*). Predators of vertebrates, including large snakes, raptors and ocelot (*Felis pardalis*), were present at all large landmass sites. Top predators (harpy eagle (*Harpia harpyja*), jaguar (*Panthera onca*) and puma (*Felis concolor*) were not observed on the smallest 'large landmass', an 88 ha island, but were present on the mainland and recorded on a 190 ha island that also served as a 'large landmass' (Terborgh *et al.* 2001).

Landmass size is used as a surrogate variable to represent distinct levels of herbivore abundance. To test Hairston *et al.*'s 'green world' hypothesis, we monitored tree and sapling demography on predator-free 'small' and 'medium' landmasses in comparison to 'large' landmasses supporting complete or nearly complete guilds of vertebrate predators. We predicted increased mortality and reduced recruitment of woody plants on predator-free islands supporting elevated densities of herbivores, principally leaf-cutter ants and howler monkeys. We predicted these demographic effects to be more pronounced on small than medium islands. We also tested an alternative hypothesis that woody stems show increased mortality and/or reduced recruitment on islands due to increased edge exposure and increased wind penetration. Wind and exposure

have been proposed by Leigh *et al.* (1993) as a principle factor promoting forest change on small islands in Lake Gatun, Panama, and have been shown to have strong impacts around the margins of forest fragments near Manaus, Brazil (Kapos 1989; Laurance *et al.* 1997, 2000; D'Angelo *et al.* 2004; Laurance 2004).

Methods

PLANT DEMOGRAPHY AND COMPOSITION IN RELATION TO LANDMASS SIZE

We studied 14 sites scattered over a 200 km² area in the west-central portion of the impoundment (Table 1, Fig. 1). Small islands were characterized by high densities of leaf-cutter ants (mean of 4.5 mature colonies per ha), iguanas (at *c.* 10 times the mainland density) and howler monkeys (present on four of the islands at densities equivalent to 8–10 per ha). Medium islands consistently differed from small islands in the presence of armadillos, a known predator of leaf-cutter ants (Rao 2000). Medium islands supported lower densities of leaf-cutter ants (mean of 0.2 mature colonies per ha). Medium islands also supported lower densities of howler monkeys and iguanas relative to small islands (Terborgh *et al.* 2001). Large landmass sites served for reference. To minimize pseudoreplication of large landmasses, we used two large islands (*c.* 88 and 190 ha) and two sites on the nearby mainland. Densities of leaf-cutter ants, howler monkeys and iguanas were lowest at the large landmass sites (Terborgh *et al.* 1997c; Rao 2000; Terborgh *et al.* 2001). Transect surveys conducted elsewhere in southern Venezuela confirm the generally low density of leaf-cutter colonies (< 0.05 ha⁻¹) in mainland forests (Jaffe & Vilela 1989).

Vegetation monitoring was initiated by tagging, mapping, measuring, and identifying every live tree \geq 10 cm d.b.h. (diameter at breast height) on each of the six small islands. It soon emerged that the average number of trees on the small islands was approximately 300. We therefore decided that the standard plot to be established on medium and large landmasses would

Table 1 Characteristics of study islands used to monitor long-term vegetation dynamics

Site	Number	Landmass category	Area (ha)	Shape index (<i>SI</i>)	Distance to mainland (km)
Baya	1	Small	0.6	156.29	9.0
Colón	2	Small	0.6	228.70	9.2
Iguana	3	Small	0.7	173.64	7.6
Cola	4	Small	1.0	199.60	8.2
Palizada	5	Small	1.1	210.91	0.2
Perímetro	6	Small	1.5	149.44	3.8
Chotacabra	7	Medium	3.9	187.00	6.6
Ambar	8	Medium	8.3	68.81	7.7
Panorama	9	Medium	10.2	257.64	1.5
Lomo	10	Medium	11.4	241.35	2.0
Grande	11	Large	88.1	475.21	2.0
Danto Machado	12	Large	189.8	637.60	1.5
Mainland I	13	Large	NA	NA	NA
Mainland II	14	Large	NA	NA	NA

consist of 300 individual trees; in the dry forest at Lago Guri this corresponds to roughly 0.6 ha. A majority of the tree plots were established in 1996 ($n = 10$), the rest in 1997 ($n = 4$). Tree plots on medium and large landmasses were sited to emulate the conditions of small islands. All plots straddled the topography, so that one half had a windward exposure (NE facing) and the other a leeward exposure (SW facing). Plots began at the exposed edge of each landmass and continued upslope over the height of land and down the sheltered side.

In 1997 we also established paired 15×15 m subplots within each tree plot, one on the windward and one on the leeward slope. Within these subplots, we tagged, mapped, measured and identified all stems ≥ 1 m tall and < 10 cm d.b.h., grouping them into two categories: 'small saplings' (≥ 1 m tall and < 1 cm d.b.h.), and 'large saplings' (≥ 1 cm d.b.h. and < 10 cm d.b.h.). In addition to documenting the structure of tree populations, the sapling subplots generated population data for smaller woody species that do not attain tree status. In 2000, we sampled the smallest class of plants, those < 1 m tall (hereafter referred to as 'seedlings') in plots measuring 2×2 m each, four situated on the windward margin and four on the leeward margin of 17 additional small islands for a total of 136 plots. Overall, we marked, mapped, measured and identified 15 884 stems, including 4771 trees, 7027 saplings, and 4086 seedlings, representing > 320 woody species, not including lianas.

Provisional identifications were assigned in the field by P.N.V. or J.T. Voucher specimens were collected and deposited in herbaria in Venezuela, Perú, and the USA. Final determination of species names was based on a checklist of plants for the region (Aymard *et al.* 1997) and/or comparisons of collected specimens with previously identified herbarium material.

In 2001 and 2002, 5 years after the tree and sapling plots were established, we comprehensively resurveyed all plots. Marked stems were remeasured (height for stems < 1 cm d.b.h.; girth for all stems ≥ 1 cm d.b.h.). During the recensuses, we attempted to verify all mortality by locating the dead, tagged stems, and also searched for newly recruited stems. Special care was taken to account for trees lost to wave-induced erosion around the margins of islands (all statistical analyses were performed only on stems situated within the uneroded portions of each site). Seedlings marked in 2000 were not recensused because their numbers were decimated by a prolonged drought in 2001–02.

Fires completely destroyed one of the mainland control sites in 2001, and partially destroyed the other. The 190 ha island of Danto Machado, a large landmass control site, experienced small-scale burns in 1990, 1993, 1998, and 2001 from fires set by poachers. Fires in 2001 destroyed one of three sampling plots on the island, damaged another, and completely ravaged Perímetro, one of the small islands where vegetation dynamics were being monitored. Data from fire damaged sites were omitted from the analyses. Eleven percent of tagged adult trees were lost to fire or erosion; sapling subplots

survived intact except on Perímetro and at two large landmass sites where they were lost entirely.

To test for differences in tree dynamics between island size categories, we used a split-plot (nested) analysis of variance with square-root-transformed counts of stems alive in the 225 m^2 subplots in 1997 and 2002 as response variables. Islands were the basic experimental unit, with exposure (windward vs. leeward slope) treated as within-subject factor and landmass category (small, medium and large) as a between-subject factor. Islands within a landmass category were treated as random effects and used as error for the between-subjects test (Chambers & Hastie 1992; Neter *et al.* 1996). Due to low numbers of individuals in some size classes, the fraction of stems dying and recruiting during the 5 years was analysed by combining plots within islands and performing a one-way ANOVA with square root-transformed data. *Post hoc* analyses were performed on *t*-tests from model contrasts and Bonferroni corrected for multiple comparisons. To test for differences in the time-course of mortality, we used a MANOVA with 1997 and 2002 square-root transformed stem counts as repeated measures, landmass category as between-subject factor, and exposure and time as within-subject factors.

MORTALITY IN RELATION TO LEAF-CUTTER ANT FEEDING PREFERENCE

We investigated possible relationships between the mortality and composition of small sapling cohorts and presumed susceptibility to leaf-cutter ants. For this analysis we pooled data by landmass size class. The fraction of stems dying (square root transformed, by species) was ranked and compared with a previously determined preference ranking of leaf-cutter workers for 43 locally common woody plant species (Rao *et al.* 2001). Weighted mean preference values (by stem count, for all species for which preference values were available) were used to assess the palatability of sapling cohorts to leaf-cutter workers.

PLANT DEMOGRAPHY IN RELATION TO EDGES AND EXPOSURE

We conducted five independent tests of the alternative hypothesis that exposure to prevailing north-east trade winds was elevating mortality rates and/or suppressing sapling recruitment on Lago Guri islands: (i) we compared differences in sapling mortality and recruitment in the 225 m^2 plots located on the windward and leeward slopes of islands; (ii) we compared seedling density, diversity and composition on windward vs. leeward slopes of 17 additional small islands; (iii) we used multiple regression analysis to test the relationships between tree demographic parameters and island size after accounting for the relative degree of edge exposure; (iv) we compared the growth rates of trees ≥ 10 cm d.b.h. using a difference measure that related the rates measured on small and medium islands to 'expected' values

measured at sheltered sites on large landmasses; and (v) we analysed tree mortality on small and medium landmasses in relation to proximity to the exposed north-eastern margins of the islands.

The experimental design called for using island size as a categorical variable in ANOVA models, but this procedure ignores the negative covariation of area with degree of edge exposure. To explicitly test the effects of edge exposure on tree demography, we conducted partial regressions of the demographic parameters on area after accounting for edge exposure (test iii). The relative degree of edge exposure for each island was estimated using the non-dimensional shape index *SI* calculated as

$$SI = P/(2A^{0.5}) \quad \text{eqn 1}$$

where *P* is the length of the island's perimeter in m, and *A* is the island's area in m². *SI* is considered an index of the degree of relative edge such that islands with high *SI* (elongated polygons) have relatively more edge than islands with *SI* values approaching 1 (circular). We measured the area and perimeter of small islands (< 2 ha) using handheld compass and laser rangefinder and larger islands (> 2.5 ha) using a Landsat ETM+ image of the study area (path 001, row 055).

In order to assess the effects of island area and shape on tree growth (test iv), we calculated the mean annualized d.b.h. increment of all marked trees alive on each island at the time of the second census. This measure is potentially biased because it ignores intrinsic, size-related changes in growth (Terborgh *et al.* 1997a). To account for the confounding effect of tree size on growth measurements, we plotted the annual growth

increment vs. girth at the mid-point of the measurement interval using 5-year growth data from two large landmass sites. We then fit a loess-regression curve across the full spectrum of adult tree sizes in order to generate a predicted growth increment for trees of a given d.b.h. (Terborgh *et al.* 1997a). Tree growth rates on the small and medium islands were then calculated as the percentage deviation (ΔG) of the observed from predicted growth, and the mean ΔG was calculated for each island. The relationship between ΔG and island area and shape was then determined via multiple regression.

We determined whether tree mortality rates were elevated near windward margins of islands (after accounting for mortality due to wave erosion) by comparing the number of trees dying within roughly 15 m of the windward margin of five small islands to the number dying elsewhere on the island, using 2×2 Chi-square tests (test v).

Results

PLANT DEMOGRAPHY IN RELATION TO LANDMASS SIZE CLASS

Stem counts

Already by 1997, when the islands were 11 years old, there were profound differences between landmass categories in the number of small stems alive in the 225 m² sapling subplots (Table 2). In particular, small sapling densities on small islands were only 37% of those at the large landmass control sites. By 2002, the numbers of small saplings had further dwindled on small islands to 25% of the value for large landmasses.

Table 2 Demography of woody trees and shrubs on small, medium and large landmasses in Lago Guri, Venezuela. Small and large saplings were contained within 15 × 15 m subplots nested within the larger adult tree plots

Site category	Mean no. stems not lost to erosion	Mean no. stems died 1997–2002	Annualized mortality	Mean no. alive in 2002	Mean no. recruited up to next larger class	Mean no. recruited from smaller class	Mean no. stems in 2002
Small saplings: ≥ 1 m tall, < 1 cm d.b.h.							
Small, windward	72	37	0.10	30	5	7	38
Small, leeward	58	27	0.09	24	7	5	29
Medium, windward	120	44	0.07	73	4	6	78
Medium, leeward	165	75	0.09	80	11	15	95
Large, windward	223	70	0.06	129	24	35	164
Large, leeward	136	44	0.06	78	14	28	106
Large saplings: ≥ 1 cm d.b.h., < 10 cm d.b.h.							
Small, windward	132	48	0.07	83	1	5	87
Small, leeward	155	41	0.05	113	1	7	120
Medium, windward	173	33	0.04	140	0.5	4	144
Medium, leeward	192	53	0.06	138	0.5	11	149
Large, windward	128	21	0.03	107	0	24	131
Large, leeward	104	13	0.03	91	0.5	14	104
Adult trees: ≥ 10 cm d.b.h.							
Small islands	288	42	0.03	247		40	286
Medium islands	295	28	0.02	267		15	282
Large landmasses	345	38	0.02	307		48	355

Table 3 Results of a split-plot (nested) analysis of variance with square-root-transformed counts of stems alive in the 225 m² subplots in 1997 and 2002 as response variables. Islands were the basic experimental unit, with exposure (windward vs. leeward slope) treated as within-subject factor and landmass category (small, medium and large) as a between-subject factor. Islands within a landmass category were treated as random effects and used as error for the between-subjects test

Sapling class	Year	Effect	SS	MS	d.f.	F ratio	P > F	R ²	
Small	1997	Between	Landmass size class	140.3	70.1	2	7.3	0.01	0.86
			Residual	87.1	9.7	9			
		Within	Exposure	0.03	0.03	1	0.01	0.94	
			Size class × exposure	10.6	5.3	2	1.3	0.33	
Small	2002	Between	Landmass size class	89.1	44.5	2	9.5	0.01	0.90
			Residual	44.4	4.9	9			
		Within	Exposure	2.7	2.7	1	1.2	0.31	
			Size class × exposure	7.1	3.6	2	1.6	0.26	
Large	1997	Between	Landmass size class	22.1	11.1	2	4.4	0.05	0.64
			Residual	22.6	2.5	9			
		Within	Exposure	0.33	0.33	1	0.11	0.75	
			Size class × exposure	3.06	1.5	2	0.51	0.62	
Large	2002	Between	Landmass size class	18.2	9.1	2	3.4	0.07	0.73
			Residual	24.3	2.7	9			
		Within	Exposure	0.05	0.05	1	0.02	0.89	
			Size class × exposure	6.2	3.1	2	1.4	0.31	

Landmass category accounted for 90% of the variation in stem counts across sites (Table 3). Mean densities of small saplings on medium islands declined even more sharply from 143 in 1997 to 87 per 225 m² subplot in 2002 (Table 2). For large saplings, the effect of landmass size was marginally significant with the trend towards greater stem densities on larger landmasses in both years (Table 3).

Tree and sapling mortality

Small saplings experienced high mortality at all sites. Aggregate 5-year mortality was 46% on small landmasses, 39% on medium landmasses, and 32% at the large landmass sites (Table 2, Fig. 2). However, these differences were not significant due to high heterogeneity among islands and the availability of only two samples to represent the large landmass category. Mortality of large saplings showed greater variation across island size categories: 32% on small, 23% on medium, and 14% on large landmasses and was nearly significant ($F_{2,9} = 3.7$, $P = 0.07$).

In the repeated measures analysis of small sapling mortality there were significant effects of island size (Table 4). A significant effect of time reflected high mortality across all size classes, but there were no time by treatment interactions. For large saplings, there was no significant effect of landmass size, but significant effects of time and a significant difference in the change in stem numbers among landmass size categories.

Measurements of adult tree dynamics were complicated by ground fires that swept through part or all of

four plots. If we consider two large landmass sites and approximately two-thirds of another that escaped fire, the mean 5-year mortality of adult trees on large landmasses was 9.6% (Table 2). On small islands it was 15.2% (58% higher), whereas on medium islands, trees died at about the same rate as on large landmasses (9.4%). The differences were not significant, the test being debilitated by the small number of unburned large landmass sites (but see below).

Sapling recruitment

Recruitment of new stems into the small sapling class varied greatly between size categories, averaging six on small landmasses, 10 on medium landmasses, and 31 per 225 m² subplot on large landmasses, with similar differences when examined on a per capita basis (Table 2, Fig. 2). Landmass explained 91% of the variance ($F_{2,8} = 40.2$, $P < 0.0001$). Recruitment on small and medium islands did not differ significantly from each other but did differ significantly from that on large landmasses. Recruitment into the large sapling class from the small sapling cohort was 6 per 225 m² subplot on small, 7 on medium, and 19 on large landmasses. Landmass category explained 54% of the variance (ANOVA, $F_{2,8} = 4.7$, $P < 0.05$). Again, *post hoc* tests on absolute number of stems recruiting indicated no difference in recruitment on small and medium landmasses, but there was a significant difference with large landmasses. Recruitment of large saplings on a per stem basis showed lower recruitment on both small and medium islands in relation to large landmasses (Fig. 2).

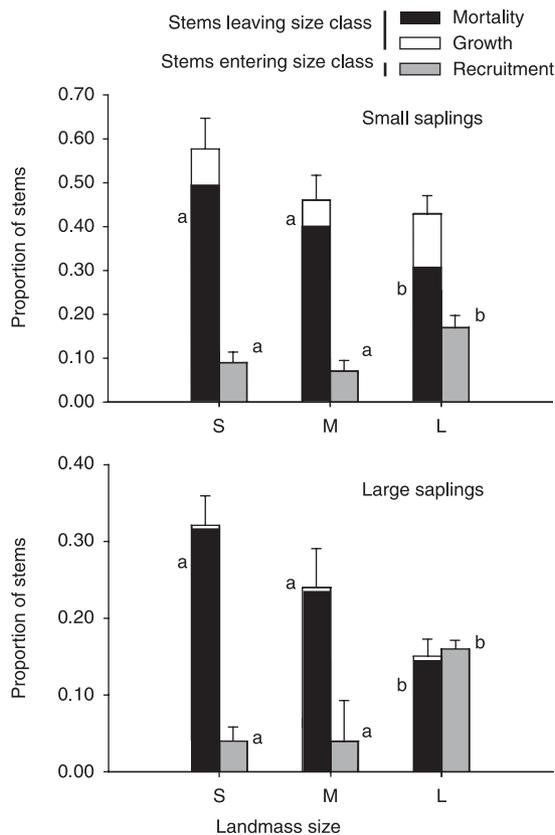


Fig. 2 Per-capita mortality plus growth out of a sapling class (left bars) vs. per-capita recruitment into the class (right bars) of small (top) and large (bottom) saplings at small, medium and large landmasses at Lago Guri, Venezuela. Values shown are the means of the proportions dying and recruiting at each site. Black portions of bars = mortality; white = growth out of the size class into the next larger; grey = recruitment into the size class from the next smaller. *Post hoc* analyses were performed on *t*-tests from model contrasts and Bonferroni corrected for multiple comparisons.

MORTALITY IN RELATION TO LEAF-CUTTER ANT FEEDING PREFERENCE

Species-specific mortality rates of small saplings on landmasses of all sizes were uncorrelated with their respective leaf-cutter preference ranks (Spearman's rho, NS). However, the weighted mean *Atta* preference indices of small saplings inventoried in 1997 on small,

medium and large landmasses were, respectively, -0.32 , -0.57 , and -0.23 (negative numbers indicating below-average preference).

PLANT DEMOGRAPHY IN RELATION TO EDGE AND EXPOSURE

1. Nested ANOVA models with exposure (windward vs. leeward slope) treated as within-subject factor and landmass category (small, medium and large) as a between-subject factor revealed no significant effects of exposure on the number, mortality or recruitment of small or large saplings. In the repeated measures analysis for small saplings there were significant effects of island size but no effect of exposure.

2. There were more seedlings on leeward than on windward margins of 17 small islands (2062 vs. 1571, respectively), but the difference was not significant (*t*-test, paired, by island, square root $n + 1$, $n = 17$, $P = 0.12$). Even in the absence of an effect of exposure on seedling numbers, there could still be effects on the diversity and/or species composition of seedling cohorts. Seedling plots on both windward and leeward margins of islands contained approximately 97 species of woody plants. Despite the similar numbers of species under both exposure conditions, there remained the possibility that exposure could influence species composition. This possibility was tested simply by combining the data from all 17 islands and correlating the number of seedlings of each species found in windward vs. leeward plots. Based on square-root-transformed data, the correlation was strongly positive (Spearman $r = 0.72$, $P < 0.0001$), indicating that most species were present in similar numbers under the two levels of exposure.

3. After accounting for the relative degree of edge exposure (*SI*), island area had a significant positive relationship with the recruitment of small saplings ($F_{7,1} = 11.75$, $P = 0.01$) and a significant negative relationship with the mortality of adult trees ($F_{8,1} = 8.09$, $P = 0.02$).

4. There was no relationship between tree growth rates (ΔG) and island area ($F_{6,1} = 0.57$, $P = 0.48$) or shape (*SI*, $F_{6,1} = 3.10$, $P = 0.13$).

5. We found no significant differences in the mortality rates of trees growing within 15 m of the windward

Table 4 Small and large saplings: change in stem counts over 5 years

Sapling class	Effect	d.f. (num, den)	Exact <i>F</i>	<i>P</i> > <i>F</i>	
Small	Between	Landmass size	2,10	16.0	0.0008
	Within	Exposure	1,10	0.11	0.75
	Repeated	Time	1,10	142.4	< 0.0001
		Time × landmass size	2,10	1.0	0.40
		Time × exposure	1,10	0.60	0.47
Large	Between	Landmass size	2,10	3.2	0.36
	Within	Exposure	1,10	0.42	0.53
	Repeated	Time	1,10	74.8	< 0.0001
		Time × landmass size	2,10	9.3	0.005
		Time × exposure	1,10	0.08	0.78

Table 5 The observed and expected mortality of adult trees growing within 15 m of exposed island edges. None of the differences are significant by Chi-square test

Island	Expected edge mortality	Observed edge mortality
Iguana	4.9	7
Baya	5.6	5
Chotacabra	6.8	6
Colón	10	12
Cola	14.4	15

margins of four small and one medium island vs. the mortality rates of trees growing elsewhere on these islands (Table 5).

Discussion

The absence of predators of leaf-cutter ants and vertebrates has unleashed a community-wide trophic cascade that is transforming the plant communities of small Lago Guri islands. Order-of-magnitude increases in densities of generalist herbivores on small islands suggest that strong trophic links stabilize the intact community. Generalist herbivores such as leaf-cutter ants and howler monkeys appear to feed less selectively at high than at low population densities, and thus are able to generate wide impacts in a plant community (Rao *et al.* 2001; Orihuela *et al.* 2005). Our data show that mortality of woody plants on herbivore impacted islands exceeds recruitment in nearly all species. These results suggest that the effectiveness of plant anti-herbivore defences is greatly diminished in the absence of top-down control.

Of the three size classes of stems we monitored over time, the small sapling class (≥ 1 m tall and < 1 cm d.b.h.) was, on average, youngest and thus most likely to have been influenced by post-inundation conditions. Accordingly, counts of small saplings in the 225 m² plots on small islands were only 37% of control values when our monitoring began in 1997 (11 years after inundation), implying that stems in this size class had in fact been experiencing high mortality for some time. By 2002, the numbers of stems in this class had dropped even further to 25% of control values. If the observed rate of decline is back extrapolated to 1986, when the islands were first isolated, the predicted small sapling density is only about 80% of the value observed on large landmasses. Either the small islands started out with a deficiency of small saplings, or the initial rates of decline in sapling densities were even higher than those observed between 1997 and 2002. In contrast, counts of large saplings (≥ 1 cm and < 10 cm d.b.h.) showed no discernible effect of landmass size in either 1997 or 2002.

High 5-year mortality of small (mean 46%) and large saplings (32%) was observed on small islands. However, contrary to expectation, mortality was high at the large landmass sites (32% for small and 14% for large saplings) resulting in non-significant differences. Inter-

mediate mortality (39% for small saplings and 23% for large) was documented on medium islands. We suspect mortality rates were above normal at all sites in response to a prolonged drought in 2001–02 that resulted in a 22-m reduction of water level in the impoundment.

Although *post hoc* tests of stem numbers and mortality rates of small and large saplings on medium islands did not differ significantly from those on large landmasses, recruitment of new stems into both these categories was severely depressed. Recruitment of new stems into the small sapling class on small islands was only 6 per 225 m² subplot over 5 years, and was only slightly higher on medium landmasses (10 per 225 m²), contrasting with a value of 31 on large landmasses. Recruitment into the large sapling class was also depressed on both small and medium landmasses (6 and 7 per 225 m² over 5 years, respectively, vs. 19 at the large landmass sites). If these results are attributable to herbivory, they imply that the impact is most severe at the earliest stages of regeneration.

Investigations of seedling establishment in other tropical forest fragments have produced mixed results. A forest remnant at Los Tuxtlas, Veracruz, México, described as 'defaunated', supported greatly elevated seedling densities compared with a site with an intact fauna in Chiapas (Dirzo & Miranda 1991). However, a more nuanced picture emerges from studies carried out near Manaus, Brazil. Recruitment of successional trees into the ≥ 10 cm d.b.h. size class was higher near edges and higher in small (1 and 10 ha) fragments than in large (100 ha) fragments and continuous forest, whereas mature forest species showed opposite tendencies (Laurance *et al.* 1998). Seedlings of mature forest tree species were present at lower densities in small fragments and near edges than in the interior of continuous forest (Benitez-Malvido 1998).

We used a series of independent tests to investigate the possibility that increased edge exposure may be responsible for the observed patterns in tree demography. In comparisons of windward vs. leeward sapling plots, we found no discernible effect of exposure on the number, mortality or recruitment of either small or large saplings. Possible effects of exposure were also examined in seedling cohorts on windward and leeward sides of 17 small islands. Here too, we failed to find significant effects, either on seedling densities or on the species richness or composition of seedling cohorts. Similarly we found no effects of exposure on either tree growth or tree mortality. After accounting for degree of edge exposure, area *per se* was found to have a significant effect on sapling recruitment and tree mortality. We conclude that exposure to dry season winds does not play a discernible role in the vegetation dynamics of Lago Guri islands. This conclusion may reflect the semi-deciduous character of the local dry forest tree community, in which many if not most species are facultatively deciduous during dry seasons and thus may be less susceptible to desiccation (Reich & Borchert 1984; Borchert 1994).

An expected pattern of higher mortality in species preferred by leaf-cutter foragers was not apparent (Vasconcelos & Cherrett 1997). This seemingly counterintuitive result may reflect either or both of two possible influences: a confounding effect of drought-associated mortality and a selective elimination of preferred species prior to the beginning of our research. The latter possibility is supported by the finding that the weighted mean preference index of saplings at all sites was strongly negative, but particularly so on small and medium landmasses (see also Rao *et al.* 2001). But this result is only suggestive because it is likely to be confounded by a tendency of preferred species to have fast growing, light-demanding saplings that are normally underrepresented in sapling cohorts (Hubbell *et al.* 1999). The fact that mortality in the small and large sapling cohorts on small islands was significantly correlated by species ($R^2 = 0.27$, $P < 0.01$) implies that similar causal mechanisms are operating on both cohorts. However, the rates at which the same species of small saplings died at the large landmass sites were uncorrelated with those observed on small islands ($R^2 = 0.001$, NS), suggesting that different mortality factors were responsible.

Systematic censuses of mature leaf-cutter ant colonies at the beginning of the census period (1996/97) documented the presence of roughly 22 times as many colonies per ha on small islands (armadillos absent) as on medium islands (armadillos present) (Rao 2000; Terborgh *et al.* 2001). In a unifactorial ANOVA, the presence vs. absence of armadillos accounted for 68% of the 2002 variation in small saplings across sites ($P < 0.002$).

Leaf-cutter colonies were not censused at the end of the study period but informal observations indicated that leaf-cutter densities increased during the period on medium islands and even the 88 ha large landmass, whereas colony numbers remained more or less stable on small islands. Rao (2000) showed with cage experiments that armadillos are effective at finding and digging out young leaf-cutter colonies, but the observed persistence of mature colonies on islands with armadillos implies that these animals may not be effective in eliminating colonies that exceed a critical size. If true, then the long-term effect of armadillos on medium islands may only be to retard the build-up of leaf-cutter ant densities.

Such indirect evidence is the best we can offer at present to support the contention that leaf-cutter ant herbivory is directly responsible for forest decline on small and medium Lago Guri islands, although more direct evidence is provided by experimental results to be presented elsewhere. Seedlings set out under leafcutter-proof exclosures survived well on small islands where unprotected seedlings suffered rapid mortality (Lopez 2003). Nevertheless, a number of alternative possibilities remain to be excluded: (i) that repeated defoliation is stressing trees and inducing them to allocate resources to vegetative growth instead of reproduction (Feeley & Terborgh 2005); (ii) that fragmentation has impeded pollination and thereby reduced the size of seed crops

(Aizen & Feinsinger 1994; Shahabuddin & Terborgh 1999); and (iii) that hyperabundant rodents on small and medium islands could potentially impact seedling recruitment, either directly via seedling herbivory, or indirectly via consumption of seeds (Lambert *et al.* 2003). Contrary to expectation, seed removal rates and seedling herbivory attributable to rodents were found to be no higher in the presence of hyperabundant rodents than on the nearby mainland or larger islands (Lopez 2003).

ANTICIPATING THE FUTURE

What will become of the vegetation on islands in Lago Guri as time passes? Mere numbers do not do justice to the bizarre condition of herbivore-impacted islets. The understorey is almost free of foliage, so that a person standing in the interior sees light streaming in from the edge around the entire perimeter. There is almost no leaf litter (Feeley 2004), and the ground is bright red from the subsoil brought to the surface by leaf-cutter workers. Dead twigs, branches and vine stems from canopy dieback litter the ground, and in places lie in heaps.

In striking contrast with this scenario of destruction, the medium islands presented a relatively normal appearance. In 1997, the numbers of stems in all size classes were essentially identical to those on large landmasses. But the number of new stems that recruited into the small sapling class between 1997 and 2002 was sharply reduced below control levels, suggesting the medium islands await a fate similar to that of small islands.

It was our good fortune to initiate the research only a few years after the islands had been isolated, for everything we documented was a transient phenomenon. Scattered around Lago Guri are occasional small islands that have passed into what we judge to be a 'post-*Atta*' (leaf-cutter) phase. As the forest canopy dies without replacement, light is appropriated by herbivore-resistant lianas that clamber up the well-lit margins of openings until they overtop the canopy, eventually smothering it and hastening tree mortality. The end point of this process is a nearly treeless island buried under an impenetrable tangle of liana stems.

Conclusion

Since the landmark paper by Hairston *et al.* (1960), ecologists have been debating whether herbivores are limited by plant defences or by predators (Murdoch 1966; Oksanen *et al.* 1981; Strong 1992). The matter is trivially simple in principle, but in practice, the challenge of experimentally creating predator-free environments in which herbivores can increase without constraint has proven almost insurmountable (Marquis & Whelan 1994; Schmitz *et al.* 2000; Sinclair *et al.* 2000).

Examples abound of herbivores running rampant on predator-free islands, but doubters dismiss such cases as

uncontrolled anecdotes (e.g. Klein 1968; Courchamp *et al.* 1999; Courchamp *et al.*, 1999, 2000). Further clouding the issue is the well-documented tendency of plants to evolve reduced chemical and physical defences on herbivore-free islands (Bowen & van Vuren 1997).

Our research controls for both these objections. The small islands we studied are free of predators that could plausibly regulate the numbers of iguanas, howler monkeys or leaf-cutter ants (Rao 2000; Terborgh *et al.* 2001). Moreover, at the time of isolation, the islands were stocked with trees and other plants possessing herbivore defences selected under mainland conditions. We are therefore confident our experiment constitutes a fair test of the 'green world' hypothesis, and that the outcome of the test is emphatically affirmative.

We suspect that our results have broad generality. Increasing numbers of studies in North America are demonstrating that wolves exert a strong top-down force that extends to the plant community (Mclaren & Peterson 1994; Ripple *et al.* 2001). In the absence of wolves, beaver, white-tailed deer and other ungulates become superabundant and begin to alter the composition of plant communities (Alverson *et al.* 1988; McShea *et al.* 1997; Pedersen & Wallis 2004). The impacts of herbivores in wolf-free North America are not as extreme as those seen on remote predator-free Lago Guri islets because humans, roads and lesser predators exert some top-down control on consumers. Nevertheless, the take-home message is clear: the presence of a viable carnivore guild is fundamental to maintaining biodiversity (Soulé & Terborgh 1999; Terborgh *et al.* 2001).

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