



Herbivory in a fragmented tropical forest: patterns from islands at Lago Gatún, Panama

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Abstract. By imposing density-dependent mortality upon their hosts, specialist insect herbivores are thought to contribute to the maintenance of tree diversity in tropical forests. Forest fragmentation may alter patterns of herbivory, however, which may have important implications for tree species diversity in forest remnants. To explore effects of fragmentation on patterns of herbivory, we assessed folivory by Lepidopteran larvae on saplings of four focal tree species on eight artificial, forested islands at Lago Gatún, Panama. We explored the importance of island area, distance to larger land, exposure to dry season winds, tree species, and season in determining proportions of new leaves damaged by caterpillars, and proportions of leaf area lost to caterpillars, during two dry and wet seasons. We found that both measures of herbivory increased markedly with island area, that island isolation had no apparent effect on herbivory, and that interactions between season and exposure, and between tree species and season, were important determinants of herbivory rates. In addition, we observed species-specific differences in herbivory among host plants under various conditions imposed by fragmentation. We conclude that patterns of herbivory by Lepidopteran larvae are sensitive to fragmentation in this tropical forest. Differential herbivory among the four tree species considered here may have important implications for tree species dynamics on the islands of Lago Gatún.

Introduction

In intact tropical forests, density-dependent mortality imposed by host-specific pathogens and insect herbivores is thought to contribute to the maintenance of tree species diversity (Janzen 1970; Clark and Clark 1984; Barone 1998). Insects account for ca. 70% of herbivory in some tropical forests (Coley and Barone 1996), and Lepidopteran larvae, many of which have relatively narrow diet breadths in tropical forests (DeVries 1985; Marquis and Braker 1991; Barone 1998), are among the most damaging folivores in terms of leaf area lost (e.g., Janzen 1988; Aide and Lodoño 1989; Sagers 1992). Many authors have noted that Lepidopteran diversity and abundance tend to increase with forest fragmentation (Brown and Hutchings 1997; Cappuccino and Martin 1997; DeVries et al. 1997), suggesting that herbivory rates by caterpillars may be higher in more fragmented forests. However, species-abundance records in several sites suggest that deterministic or random loss of individual herbivore species is likely following fragmentation (e.g., Spitzer et al.

1993; Shahabuddin and Terborgh 1999). Such losses may alter patterns of herbivory in tropical forest fragments, and therefore may have important implications for maintenance of tree species diversity.

We surveyed patterns of folivory by Lepidopteran larvae on saplings of four focal tree species in a fragmented tropical forest. On eight artificial, forested islands at Lago Gatún, Panama, we assessed proportions of new leaves damaged by caterpillars, and proportions of leaf area lost to caterpillars, during two dry and wet seasons. Here, we describe the importance of island area, distance to larger land, exposure to dry season winds, tree species, and sampling season in determining herbivory rates, and explore species-specific patterns of herbivory for these focal tree species under conditions imposed by fragmentation. We then discuss possible implications of our data for tree species dynamics in Panamanian forest fragments.

Methods

Study site

Lago Gatún (~9°9' N, 79°51' W) was formed in 1914 by damming of the Río Chagres for construction of the Panama Canal (Leigh and Wright 1990). At that time, rising water isolated numerous, forested islands ranging in area from \ll 1 ha to 1500 ha; Barro Colorado Island (BCI), the largest and best-studied island in the lake [see Leigh et al. (1982) for a thorough site description]. The moist, semi-deciduous, lowland tropical forest of the region receives 2600 mm of precipitation annually, with 90% falling during the May–December wet season (Leigh and Wright 1990). The 4-month dry season is characterised by decreased humidity, negligible rainfall, higher temperatures, increased solar radiation, and strong, steady tradewinds that blow across the lake from the north and northeast (Leigh et al. 1993).

Study species

Heisteria concinna Standl. (Olacaceae) and *Ouratea lucens* (H.B.K.) Engler (Ochnaceae) are small trees found frequently in the shaded understorey of lowland, moist forest in Panama. Croat (1978) considers both to be common in the forest at BCI, where adults and saplings of each species are frequently observed in both primary and secondary forest. *Protium panamense* (Rose) I.M. Johnston and *P. tenuifolium* Engler (Burseraceae) are mid-sized trees that are frequent in secondary forest, occasional in mature forest, and common among the lakeshore of BCI (Croat 1978). Individuals of all four species co-occur on BCI, and on small and medium islands at Lago Gatún (A.E.A., personal observation). Each species has been the subject of phenological and herbivory studies in central Panama (e.g., Coley 1983; Aide 1993; Barone 1998).

Sampling procedures

We measured herbivore damage to each focal species, as available, on four small islands [<1 ha: Islands 20, 10, 7, 43; numbers correspond to island names given in Adler and Seamon (1991)], three medium islands (7–17.1 ha: Islands 3, 13, and Mona Grita), and BCI (1500 ha). Each small island was treated as a single site that was either protected from tradewinds by a larger landmass (<50 m of open water to the north and northeast; Islands 10 and 43), or exposed to tradewinds [>1 km of open water to the north and northeast, *sensu* Asquith (1999); Islands 20 and 7]. On medium islands, we chose wind-exposed sites ca. 2–10 m from the windward lakeshore using the same criteria, and wind-protected sites ca. 2–10 m from the lakeshore on the leeward side. On BCI, we used a wind-exposed edge near the laboratory cove, and a protected hillside at the start of the Fausto–Bocanegra trail. On all islands, we measured damage to new leaves on 1–15 individuals of each species, as available, at both exposed and protected sites. For consistency of scale, we assessed damage to leaflets of *P. panamense* and *P. tenuifolium*, which are similar in size to leaves of *H. concinna* and *O. lucens*. All sampled leaves were 0.5–1.5 m above the forest floor.

In the dry and wet seasons of 1996 (March, November) and 1997 (March, July), we examined 4079 leaves, including 1437 leaves of *H. concinna*, 1128 leaves of *O. lucens*, 1102 leaves (leaflets) of *P. panamense*, and 412 leaves (leaflets) of *P. tenuifolium*. We assessed proportions of leaves damaged per plant by counting the number of new leaves with caterpillar damage and dividing by the total number of new leaves produced. For damaged leaves, we then determined proportions of leaf area lost by measuring total area of each new leaf at maturity and estimating area lost to caterpillars with a clear plastic grid, as described by Sagers and Coley (1995). We reliably distinguished herbivory by caterpillars from damage by other agents by comparing leaf damage to a database containing >6 years of data on >30 understory tree species and their herbivores on BCI (Coley and Kursar, unpublished data). We noted, but did not quantify, damage by pathogens or other herbivores, and we excluded leaves that disappeared (as evidenced by petioles without associated leaves) because the damage agent was unknown.

Unit of study

Several authors have described intraspecific variation in herbivore damage (e.g., Marquis and Braker 1991; Marquis 1996; Mauricio 1998; Angulo-Sandoval and Aide 2000), implying that individual plants, rather than individual leaves, should be used as the unit of analysis in herbivory surveys. However, such an approach was impeded by several factors in the present study. At some sites and during some sampling periods, only single individuals of focal species produced new leaves, preventing comparisons among plants. Numbers of new leaves per plant also varied widely among individuals: for example, during the 1996 dry season, three saplings of *O. lucens* at the exposed site of one medium island (Island 13) produced 2, 14, and 35 new leaves (A.E.A., personal observation), decreasing the comparability of

mean values for individual plants in subsequent analyses. Finally, the focus of this study did not include assessing individual plants for genotypic variability in susceptibility or resistance to herbivory. For these reasons, we used individual leaves as the unit of study.

We assessed the validity of this approach by examining data collected in the first sampling period (dry season, 1996), for which sample sizes were sufficiently large to allow analysis using individual plants as replicate units. Using multiple regression models detailed below (Models 2 and 3), we analysed mean proportions of leaf area lost per plant, and recovered the major results generated from analyses using leaves as the study unit (see below), with the exception of interactions involving sampling season (only one season was considered in this partition of the data). We then critically evaluated the same data in order to assess the prevalence of intraspecific variation in herbivore damage. Among 18 island/exposure/species combinations containing ≥ 2 individual saplings, we found seven cases of significant variation among individuals in proportions of leaf area lost, and 11 cases in which variation among individuals was not significant (Table 1). Cases of nonsignificant variation among individuals were spread across islands of all sizes, all species, and both exposure regimes, and across a variety of sample sizes. In contrast, cases of significant variation occurred most frequently on Mona Grita, a medium island. Excluding Mona Grita from the dataset did not alter outcomes of the regression analyses presented below (Models 2 and 3). Based on these observations, our results appear to be robust, and we expect that using individual leaves as the unit of study did not introduce systematic error into the data presented here. However, because of limits imposed by our study design, we suggest that our conclusions be interpreted with appropriate caution, that our data be used as grounds for further studies in which plants serve as replicate units, and that the patterns described here be used as a basis for generating testable hypotheses regarding species interactions in fragmented tropical forests.

Data analysis

We logit-transformed ($\ln[Y/(1 - Y)]$) proportions of new leaves damaged and leaf area lost, pooled data from 1996 and 1997, and used multiple regressions to assess the relationship of these measures of herbivory to several explanatory variables (models below), including island area, distance to the nearest landmass of larger area, exposure to dry season winds, tree species, and sampling season. Island areas and distances to larger land were obtained from Adler and Seamon (1991); for two islands not described there (Mona Grita and BCI), both values were estimated using scaled maps.

We first assessed proportions of new leaves damaged by caterpillars. We logit-transformed proportions of new leaves damaged, pooled data from islands of each size class (small, medium, large) and from both sampling years, and used multiple regression to assess the relationship of proportions of leaves damaged to main effects of island size, exposure, tree species, and season, as well as interactions

Table 1. Subset of data used to assess variation in mean proportions of leaf area lost among individual plants, including those species/island/exposure combinations from the dry season of 1996 in which ≥ 2 saplings were surveyed.

Species	Island	Size	Exposure	Individuals (leaves)	P-value
<i>H. concinna</i>	43	Small	Protected	3 (56)	NS
	MG	Medium	Exposed	3 (73)	NS
	13	Medium	Exposed	11 (108)	0.0001 ^{***}
	13	Medium	Protected	8 (48)	0.0272 [*]
	BCI	Large	Exposed	6 (82)	NS
<i>O. lucens</i>	BCI	Large	Protected	9 (82)	NS
	7	Small	Exposed	2 (32)	NS
	MG	Medium	Exposed	11 (123)	0.0003 ^{***}
	MG	Medium	Protected	6 (47)	0.0021 ^{**}
	3	Medium	Protected	5 (46)	NS
<i>P. panamense</i>	BCI	Large	Protected	7 (56)	NS
	43	Small	Protected	10 (67)	NS
	MG	Medium	Exposed	8 (39)	0.0206 [*]
	MG	Medium	Protected	8 (42)	0.0001 ^{***}
	3	Medium	Exposed	6 (56)	NS
<i>P. tenuifolium</i>	13	Medium	Exposed	14 (74)	0.0022 ^{**}
	7	Small	Exposed	8 (26)	NS
	13	Medium	Exposed	6 (31)	NS

P-values were generated by ANOVA using logit-transformed data, and NS indicates nonsignificant variation among individuals; MG denotes Mona Grita. As in later tables, asterisks denote levels of significance.

between species and season, and between exposure and season. This model (Model 1) explained 64.2% of the variance observed in proportions of new leaves damaged.

We then assessed proportions of leaf area lost to caterpillars. For these analyses, we log-transformed island areas and distances to larger land, logit-transformed proportions of leaf area lost, and pooled data from both sampling years. After developing preliminary regression models, we used lack-of-fit *F*-tests, which formally assess the adequacy of fitted regression models, to assess model quality [see Ramsey and Schafer (1996) for a thorough description of the lack-of-fit *F*-test and its uses]. Based on these tests, we rejected those models for which significant *P*-values demonstrated a poor fit of the model to the data.

Our first model, in which we assessed main effects of island area, distance to larger land, exposure, tree species, and season as determinants of proportions of leaf area lost, did not adequately fit the data (lack-of-fit $F_{56, 1191} = 2.58, P < 0.0001$). Subsequent model manipulations yielded a sufficient fit only in the presence of complex interaction terms that were difficult to interpret in an ecological context; for this reason, we revised the model. Because fragment area and isolation are thought to be important, and potentially interacting, determinants of community structure in forest remnants (e.g., Bierregaard et al. 1992), we first assessed the importance of island area and distance to larger land in determining proportions of leaf area lost. Because we perceived evidence for multicollinearity (Zar 1996) resulting primarily from one small, very isolated island (Island 20: < 1 ha, and 970 m from larger land),

we excluded that island from analysis and performed a multiple regression in which main effects of island area and distance (both log-transformed), and an interaction between island area and distance, were regressed against proportions of leaf area lost (logit-transformed and pooled for both sampling years). The resulting model (Model 2) adequately fit the data (lack-of-fit $F_{3, 1230} = 1.17$, $P = 0.3214$). This approach allowed us to consider effects of island area and distance in determining herbivory rates, and in influencing exposure-related, species-specific, and seasonal patterns of herbivory.

We also wished to explore the importance of exposure, tree species, and season in determining herbivory rates without the potentially overwhelming effects of island area and distance. Therefore, from the regression of island area and distance (excluding Island 20), we generated residuals, which represented proportions of leaf area lost with variation due to island area and distance already accounted for. Against these residuals we regressed main effects of exposure, tree species, and season, and interactions between species and season, and between exposure and season. This model (Model 3) sufficiently fit the data (lack-of-fit $F_{6, 1221} = 1.43$, $P = 0.2011$).

In subsequent analyses, we included Island 20 and used simple linear regression and ANOVA to compare rates of herbivory among groups. Although transformed data were used in all analyses, we present results as raw data. All values represent means \pm one standard error (SE), and, where appropriate, are followed by sample sizes representing the number of leaves in a given sample (proportions of new leaves damaged) or the number of damaged leaves examined (proportions of leaf area lost). P -values given in the text without accompanying F -values represent probabilities obtained from the primary multiple-regression models described above.

Results

Model 1: Proportions of new leaves damaged by caterpillars

Of 1626 leaves examined in 1996, and 2453 leaves examined in 1997, 1255 leaves (30.8%) were damaged by Lepidopteran larvae. We found that island size, and interactions between tree species and season, and between exposure and season, were important determinants of proportions of new leaves damaged by caterpillars (Table 2). Island size was important as a main effect ($P = 0.0003$), with mean damage on BCI ($42.0\% \pm 5.6$; $n = 991$) exceeding that on both medium islands ($31.7\% \pm 4.1$; $n = 2165$) and small islands ($18.6\% \pm 3.3$; $n = 923$). Proportions of leaves damaged were consistent among species on BCI ($F_{3, 10} = 0.58$, $P = 0.6421$), medium islands ($F_{3, 12} = 2.77$, $P = 0.0875$), and small islands ($F_{3, 8} = 0.25$, $P = 0.8579$) (Table 3).

An interaction between tree species and season also was significant ($P = 0.0123$). During wet seasons, proportions of new leaves damaged were greater than during dry seasons for both *P. panamense* and *P. tenuifolium* ($F_{1, 20} = 9.54$, $P = 0.0058$);

Table 2. Results of regression model assessing the role of island area, exposure, tree species, and season in determining proportions of new leaves damaged by caterpillars on islands at Lago Gatún, Panama (Model 1).

Term	df	ss	F-ratio	P-value
Island area	2	10.30	10.92	0.0003 ^{***}
Exposure	1	0.37	0.79	0.3800
Tree species	3	1.98	1.40	0.2622
Season	1	0.21	0.45	0.5059
Tree species × season	3	6.08	4.29	0.0123 [*]
Exposure × season	1	1.90	4.02	0.0542 ^a

^a Value approaches significance and is described accordingly in the text.

Table 3. Mean proportions of new leaves damaged by caterpillars for each focal species on small islands, medium islands, and BCI.

Species	Island size		
	Small	Medium	Large
<i>H. concinna</i>	16.5 ± 5.6 (364)	49.4 ± 10.7 (666)	52.3 ± 11.6 (407)
<i>O. lucens</i>	13.5 ± 6.4 (249)	22.3 ± 4.6 (675)	40.9 ± 14.9 (204)
<i>P. panamense</i>	23.1 ± 2.9 (216)	25.4 ± 4.9 (635)	36.0 ± 13.9 (251)
<i>P. tenuifolium</i>	20.6 ± 11.8 (94)	29.7 ± 5.3 (189)	38.9 ± 5.1 (129)

Mean values are given as percentages followed by standard errors. Sample sizes (in parentheses) indicate total numbers of leaves surveyed. Significance values for comparisons among these data are given in the text.

in contrast, proportions of leaves damaged did not vary with season for *H. concinna* ($F_{1, 8} = 0.1093$, $P = 0.7495$), and tended to be slightly greater in dry seasons than in wet seasons for *O. lucens* ($F_{1, 8} = 4.52$, $P = 0.0663$). Notably, mean proportions of leaves damaged for *O. lucens* and *H. concinna* averaged 1.7 to 2.4 times greater than for *P. panamense* and *P. tenuifolium* during dry seasons (Figure 1).

In addition, an interaction between exposure and season approached significance ($P = 0.0542$). Proportions of leaves damaged were consistently high among exposed sites during wet seasons, protected sites during dry seasons, and protected sites during wet seasons [$F_{2, 29} = 0.29$, $P = 0.7522$; Table 4 (panel A)], and under such conditions were consistent among species [$F_{3, 28} = 1.46$, $P = 0.2469$; Table 4 (panel B)]. Although proportions of leaves damaged also were consistent among species at exposed sites during dry seasons ($F_{3, 6} = 1.18$, $P = 0.3930$), mean proportions of leaves damaged decreased by a factor of 1.4 at such sites.

Model 2: Effects of island area and distance on proportions of leaf area lost to caterpillars

Proportions of leaf area lost were influenced by island area as a main effect; however, without Island 20, this result only approached significance ($P = 0.0702$). When that small island was included in the analysis, the effect of area alone was significant ($P < 0.0001$), with mean damage on BCI (27.2% ± 1.2; $n = 473$)

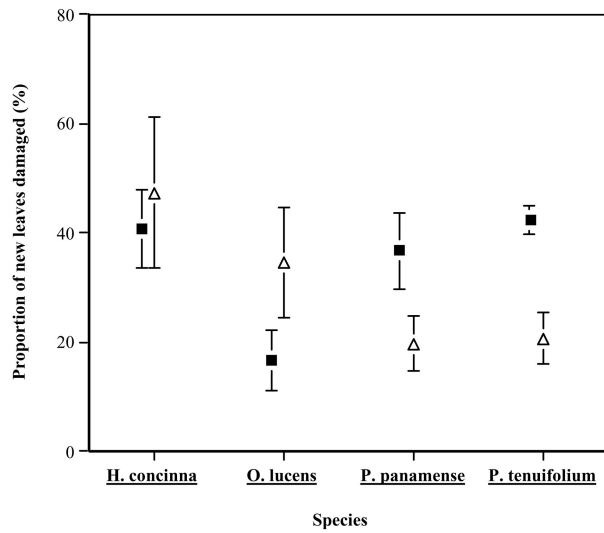


Figure 1. Mean proportions of new leaves damaged by caterpillars for each focal species during wet (■) and dry (△) seasons on islands at Lago Gatún, Panama. As in later figures, bars represent standard errors.

Table 4. Mean proportions of new leaves damaged by caterpillars under exposed and protected conditions during dry and wet seasons.

Panel A	Wet seasons		Dry seasons	
	Protected	Exposed	Protected	Exposed
Mean proportion	33.3 ± 5.1 (895)	33.5 ± 5.3 (793)	34.9 ± 7.2 (1180)	24.4 ± 5.4 (1211)

Panel B	Wet seasons (protected and exposed) and dry seasons (protected)		Dry seasons (exposed)
	Species		
	<i>H. concinna</i>	46.3 ± 8.9 (1004)	34.6 ± 11.2 (433)
	<i>O. lucens</i>	21.5 ± 6.6 (804)	37.8 ± 14.5 (324)
	<i>P. panamense</i>	33.1 ± 4.9 (813)	13.3 ± 8.5 (289)
	<i>P. tenuifolium</i>	36.3 ± 3.7 (278)	15.1 ± 7.1 (134)

Mean values are given as percentages followed by standard errors. Sample sizes (in parentheses) indicate total numbers of leaves surveyed. Significance values for comparisons among these data are given in the text.

exceeding that on both medium ($22.5\% \pm 1.1$; $n = 618$) and small islands ($11.5\% \pm 1.3$; $n = 164$). In contrast, there was no effect of distance ($P = 0.1187$), nor of an interaction between island area and distance ($P = 0.2993$). Results involving distance were qualitatively insensitive to inclusion of Island 20.

We found that seasonal patterns of damage among species were sensitive to island area. Proportions of leaf area lost were consistent among species on BCI during wet seasons ($F_{3, 204} = 0.87$, $P = 0.4562$) and dry seasons ($F_{3, 261} = 2.10$, $P = 0.1010$),

and on medium and small islands during wet seasons (respectively, $F_{3, 264} = 0.64$, $P = 0.5890$; $F_{3, 81} = 0.86$, $P = 0.4640$; data not shown). However, species-specific differences were apparent during dry seasons on medium islands ($F_{3, 345} = 10.07$, $P < 0.0001$) and small islands ($F_{3, 75} = 10.17$, $P < 0.0001$): mean proportions of leaf area lost by individuals of *H. concinna* and *O. lucens* exceeded those lost by *Protium* spp. by a factor of 2.5 on medium islands, and those lost by *P. panamense* by a factor of 4.3 on small islands (Figure 2).

Island area further influenced the effects of exposure and season in determining herbivory rates (Figure 3). Although damage on BCI was consistently high, damage on medium and small islands reflected pronounced effects of season and exposure. Proportions of leaf area lost on medium islands during wet seasons at protected and exposed sites, and during dry seasons at protected sites, were consistent ($24.6\% \pm 0.9$; $n = 998$; $F_{2, 452} = 1.23$, $P = 0.2931$), but diminished by a factor of 1.5 at exposed sites during dry seasons ($15.9\% \pm 1.3$; $n = 257$). Among small islands, mean damage on protected islands exceeded that on exposed islands by a factor of 2. On small, exposed islands, dry season damage to *O. lucens* ($9.8\% \pm 2.3$; $n = 26$) exceeded that to *Protium* spp. ($1.3\% \pm 0.6$; $n = 8$) by a factor of 7.7.

Model 3: Effects of tree species, season, and exposure on proportions of leaf area lost to caterpillars

When variation due to island area and distance was accounted for, Model 3 suggested that tree species and season interacted significantly ($P = 0.0114$) in

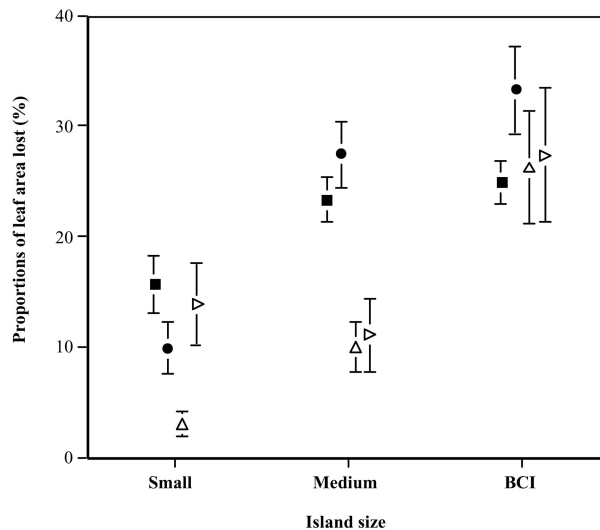


Figure 2. Mean proportions of leaf area lost by *H. concinna* (■), *O. lucens* (●), *P. panamense* (△), and *P. tenuifolium* (▷) on small and medium islands, and BCI, during dry seasons. Note that the relatively high level of damage to *P. tenuifolium* may be attributed to a very small sample size for that species: only eight leaves were available for analysis, and seven of those occurred on a single island.

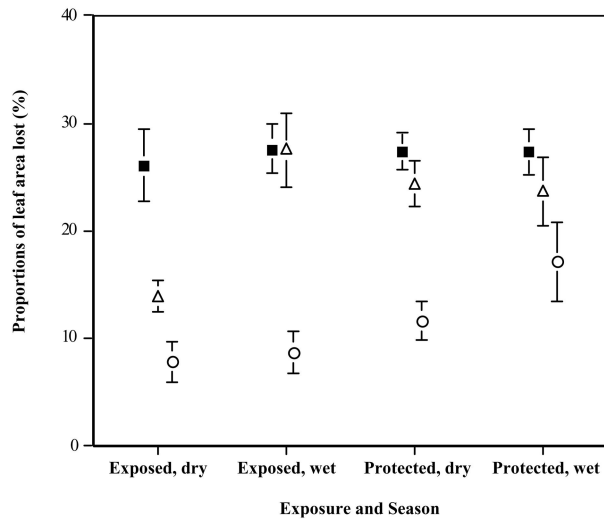


Figure 3. Mean proportions of leaf area lost due to herbivory by caterpillars for all focal species under exposed and protected conditions on small islands (○), medium islands (△), and BCI (■) during dry and wet seasons.

determining proportions of leaf area lost to caterpillars (Table 5). During wet seasons, proportions of leaf area lost from damaged leaves were high ($23.7\% \pm 1.1$; $n = 562$) and consistent among species ($F_{3, 558} = 0.63$, $P = 0.5945$). During dry seasons, overall damage remained high ($22.2\% \pm 1.0$; $n = 693$), but differences were apparent among species ($F_{3, 689} = 11.38$, $P < 0.0001$): although proportions of leaf area lost during dry seasons were comparable to wet seasons for *H. concinna*, *O. lucens*, and *P. tenuifolium*, damage to *P. panamense* decreased by a factor of 2 during dry seasons (Table 6).

Season and exposure also interacted significantly ($P = 0.0003$; Table 5) to influence proportions of leaf area lost when variation due to island area and distance was accounted for. Mean damage at protected sites during wet and dry seasons, and at exposed sites during wet seasons ($24.6\% \pm 0.9$; $n = 998$), exceeded that at

Table 5. Results of final regression model assessing the role of exposure, tree species, and season in determining proportions of leaf area lost due to herbivory by caterpillars (Model 3).

Term	df	ss	F-ratio	P-value
Exposure	1	37.75	8.56	0.0035**
Tree species	3	103.46	7.82	< 0.0001***
Season	1	24.19	5.49	0.0193*
Tree species \times season	3	48.95	3.70	0.0114*
Exposure \times season	1	59.46	13.49	0.0003***

Terms have been regressed against residuals, which were generated by multiple regression of island area, distance, and an interaction term (island area \times distance) against proportions of leaf area lost (logit-transformed; Model 2).

Table 6. Mean proportions of leaf area lost due to herbivory by caterpillars for each focal species under exposed and protected conditions during dry and wet seasons.

Species	Wet seasons			Dry seasons		
	Exposed	Protected	Mean	Exposed	Protected	Mean
<i>H. concinna</i>	24.1 ± 2.5 (109)	25.3 ± 2.4 (131)	24.8 ± 1.7	19.7 ± 2.0 (119)	25.4 ± 1.7 (198)	23.2 ± 1.3
<i>O. lucens</i>	20.5 ± 4.5 (41)	23.8 ± 3.6 (55)	22.4 ± 2.8	17.0 ± 2.5 (80)	33.7 ± 3.0 (125)	27.2 ± 2.1
<i>P. panamense</i>	20.2 ± 2.5 (92)	27.3 ± 3.4 (89)	23.7 ± 2.1	7.6 ± 2.8 (35)	14.9 ± 2.5 (77)	12.6 ± 1.9
<i>P. tenuifolium</i>	28.4 ± 7.7 (13)	17.3 ± 4.1 (32)	20.5 ± 3.7	5.4 ± 1.7 (23)	25.2 ± 4.3 (36)	17.5 ± 3.0

Mean values for each exposure type are given as percentages and are followed by standard errors. Sample sizes (in parentheses) indicate the number of damaged leaves examined. Significance values for comparisons among these data are given in the text.

exposed sites during dry seasons by a factor of 1.6. Damage did not vary among species at exposed sites during wet seasons ($F_{3, 251} = 1.10$, $P = 0.3517$), but did vary among species at exposed sites during dry seasons ($F_{3, 253} = 5.42$, $P = 0.0013$), with proportions of leaf area lost for *H. concinna* and *O. lucens* exceeding those for *P. tenuifolium* and *P. panamense*, on average, by a factor of 2.8 (Table 6).

Discussion

For four focal tree species on land-bridge islands at Lago Gatún, Panama, proportions of new leaves damaged by caterpillars, and of leaf area lost to caterpillars, appear to be strongly influenced by island area. Both measures of herbivory appear sensitive to interactions between tree species and season, and between exposure and season, and these interactive effects influence proportions of leaf area lost both within the context of, and independent of, island area. Although the importance of fragment size is widely acknowledged in studies of forest fragmentation (see below), these results suggest that exposure-related, species-specific, and seasonal differences also should be considered in the study of fragmented habitats.

Island area

Fragment area is recognised as a major determinant of species richness, abundance, and persistence in fragmented habitats (e.g., Simberloff 1976; Cunningham 2000; Maldonado-Coelho and Marini 2000; Vallan 2000). In general, larger fragments are expected to contain both higher diversities (e.g., Rosenzweig 1995) and higher abundances of species (Didham et al. 1996; see also MacArthur and Wilson 1967). Data from a calcareous grassland (Steffan-Dewenter and Tschardt 2000) and various tropical habitats (e.g., Rodrigues et al. 1993; Daily and Ehrlich 1995) suggest that butterfly species diversity and density tend to correlate positively with habitat area (but see Brown and Hutchings 1997), in part due to differential extirpation of specialist species, and/or poorly dispersing species, from small habitat fragments (Terborgh et al. 1997b; Shahabuddin and Terborgh 1999). However, whether density and richness of adult Lepidoptera adequately estimate

patterns of larval abundance, diversity, and folivory remains to be tested explicitly for tropical forest fragments.

In the present study, we observed that proportions of new leaves damaged and leaf area lost decreased markedly for all species in smaller fragments relative to larger fragments. Although the distribution of island areas in Lago Gatún prevented replication for the largest island, we interpret our results as suggesting that herbivore communities on these islands have been altered by fragmentation. Whether such alteration reflects ecological changes in herbivore abundance or diversity, a behavioural shift in oviposition or feeding patterns by adults or larval Lepidoptera, or a shift in the taxonomic composition of herbivore communities on smaller islands, remains to be explored.

We also observed that under harsh conditions imposed by dry seasons, *Protium* spp. on small, exposed islands receive very little herbivory relative to other species at the same sites, and relative to conspecifics on larger islands. Extensive surveys have shown that the vast majority of folivory by insects on BCI is caused by specialist herbivores, and feeding trials suggest that most Lepidopteran larvae in this tropical forest are monophagous or oligophagous (Barone 1998; *sensu* Steffan-Dewenter and Tschardtke 2000). Although to our knowledge, published data are not available for herbivores of *O. lucens* and *H. concinna*, Barone (1998) showed that specialist herbivores are responsible for 40–100% of damage to leaves of *Protium* spp. on BCI, suggesting that generalist herbivores play only a minor role in leaf damage to these species. Many potential mechanisms could account for the species-specific patterns of herbivory we observed on islands of different sizes, including preferential decreases in abundances of specialists attacking *Protium* spp., enhancement of leaf defenses under harsher microclimate conditions (see Givnish 1999), and others. Each of these necessitates further study.

Island isolation

Ecological theory predicts that more isolated habitat remnants will experience greater rates of extinction, and lower rates of recolonisation, relative to less isolated remnants (MacArthur and Wilson 1967; Collinge 2000), especially when fragments of terrestrial habitat become separated by water (i.e., land-bridge islands; see Terborgh et al. 1997a, b). However, we found no effect of island isolation (distance to larger land) in determining proportions of leaf area lost.

Several studies have suggested that fragment isolation *per se* is not an important determinant of Lepidopteran richness and density (e.g., Brown and Hutchings 1997; Steffan-Dewenter and Tschardtke 2000). Such conclusions are sensitive to differential dispersal and behaviour among species, and to differences in host plant distribution (Raguso and Llorente-Bousquets 1990; Shahabuddin and Terborgh 1999). Moreover, both the nature of the matrix separating fragments and the scale of fragment isolation may differentially impact different taxa, thereby influencing species diversity and abundance in fragmented habitats (Bierregaard et al. 1992; Gascon et al. 1999).

In the present study, an effect of distance may have been obscured by relatively

small distances from islands to nearest larger landmasses (mean = 152.8 ± 3.9 m). However, several authors have shown that distances < 100 m are sufficient to limit movement among tropical forest fragments by a variety of taxa, including euglossine bees (Powell and Powell 1987), dung and carrion-feeding beetles (Klein 1989), and many understorey birds (Bierregaard et al. 1992). Moreover, Shahabuddin and Terborgh (1999) showed that butterfly communities are sensitive to distances < 1 km between recently isolated, land-bridge islands and larger landmasses in the seasonal tropical forest of Lago Guri, Venezuela. Islands of both Guri and Gatún consist of land-bridge islands containing lowland forest that is subject to intense dry seasons (Terborgh et al. 1997a), such that aspects of these datasets should be comparable; however, the present study is made more complex by the inclusion of larger islands, and thus of an effect of fragment area. Comparisons between these studies may be limited further by the recent formation of the Guri islands, which were isolated only 14 years ago and are in a state of community relaxation that may contrast with the older islands of Lago Gatún (Terborgh et al. 1997b). In order to reconcile these datasets, and to explore patterns of ecological decay in isolated fragments, it would be of use to consider patterns of herbivory on the Guri islands, and conversely, to examine species richness and abundance of larval and adult Lepidoptera on the islands of Lago Gatún.

Seasonality, exposure, and tree species

On BCI, rainfall during the 4-month dry season rarely exceeds 10% of the annual total (Dietrich et al. 1982). During that time, strong, unidirectional tradewinds, increased solar radiation, and decreased humidity provide a sharp contrast to conditions typical of wet seasons. Given evidence of pronounced seasonality among many tropical insects (e.g., Wolda 1989; Lovejoy and Bierregaard 1990; Novotny and Basset 1998), and well-documented, community-wide decreases in herbivory during dry seasons in seasonal tropical forests (Coley and Barone 1996), we expected that season would affect herbivory rates. We found that the effects of season were specific to plant species, related to exposure, and influenced by island area.

Overall, patterns of herbivory among host species varied with season. In general, wet season rates of damage were consistent among species, although proportions of new leaves damaged were markedly lower for *O. lucens* than for any other species during wet seasons (Figure 1). We attribute this disparity to the large number of new leaves flushed by *O. lucens* at the onset of the rainy season; this phenological strategy may satiate herbivores such that many leaves are damaged, but some escape unscathed (Aide 1992). Among species considered here, only *O. lucens* employs this phenological strategy; a similar argument cannot explain our observation that during dry seasons, proportions of new leaves damaged for *H. concinna* and *O. lucens* exceeded those for *Protium* spp. by roughly twofold. Notably, proportions of leaf area lost reflected concomitant decreases in dry season damage to *Protium* spp. relative to other focal species, especially on small and medium islands.

In addition, we found that seasonal patterns of herbivory were shaped by

exposure. Exposure, here defined by a lack of protection by another landmass from dry season winds, is likely more important during dry seasons, when edge effects on the windward sides of islands should be more intense (Asquith 1999). In the present study, proportions of new leaves damaged decreased at exposed sites during dry seasons for all species. However, species-specific patterns were apparent in terms of leaf area lost: at exposed sites during dry seasons, damage to *H. concinna* and *O. lucens* exceeded that to *Protium* spp. by nearly threefold (Table 4). Moreover, damage on medium and small islands decreased markedly during dry seasons at exposed sites relative to protected sites, with *P. panamense* on small, exposed islands during dry seasons suffering almost no herbivory (< 2% of leaf area lost).

Lepidopteran diversity and abundance often increase at forest edges, in part due to increased vegetative growth and flower production (e.g., Brown and Hutchings 1997). However, edge effects, such as increased light penetration, higher wind speed, and lower humidity, are known to negatively affect a wide variety of forest invertebrates, especially in small fragments that cannot maintain a core of protected forest (Bierregaard et al. 1992; Didham 1997). Our data suggest that exposed edges during dry seasons may be unfavourable for sustaining herbivores at levels comparable to those found in the interior of large fragments. We postulate that exposed edges may be frequently recolonised by herbivores that persist, as evidenced by leaf damage, in protected sites on medium and large islands, and on the mainland [see Shahabuddin and Terborgh (1999) for a similar discussion]. We expect that persistence and recolonisation should be most limited on small, exposed islands, where conditions typical of edges pervade the entire forest patch (Terborgh et al. 1997b; Asquith 1999). Although potential mechanisms remain to be explored, our results suggest that Lepidopteran herbivores may be differentially sensitive to effects of exposure and season, resulting in species-specific differences in herbivory during dry seasons, at exposed sites, and especially in small, exposed fragments.

Implications for tree species dynamics

Relative to mainland forest, tree diversity on small islands in Lago Gatún has declined dramatically in 85+ years since isolation (Leigh et al. 1993). Notably, species loss has been nonrandom (*sensu* Hubbell 1979): sapling communities on small, exposed islands are dominated by only a subset of typical forest species, including *Protium* spp. Both Leigh et al. (1993) and Asquith (1999) attributed the deterministic change in species composition to altered mammal community composition and physiological stress due to exposure to dry season winds. However, neither study considered herbivory by insects, which has the potential to negatively influence plant fitness in tropical forests (e.g., Marquis 1984; Sagers and Coley 1995). Our data suggest that saplings of *Protium* spp. suffer relatively less herbivory than two other tree species under exposed conditions during dry seasons, and in particular, at small, exposed forest fragments at Lago Gatún. The observed success of *Protium* spp. on small islands may simply reflect physiological traits that allow this secondary-forest species to proliferate and survive under relatively harsh,

exposed conditions. Could lower herbivory by insects further contribute to the observed success of *Protium* spp. on these small islands?

Most recent studies have agreed that density-dependent mortality due to attack by natural enemies is prevalent in tropical forests (e.g., Wills et al. 1997). Based on these studies, we expect that tree species occurring at higher densities should suffer higher herbivory (Janzen 1970; Leigh 1996; Barone 1998; Givnish 1999; Angulo-Sandoval and Aide 2000). In extensive censuses of islands originally surveyed by Leigh et al. (1993), Asquith (1999) documented that *Protium* spp. are the most common species among saplings at all four small, exposed islands surveyed, where they represent $42.8\% \pm 6.0$ of sapling stems. In contrast, *Protium* spp. comprise the majority of sapling stems at only three of six exposed mainland sites, and at only one of six protected mainland sites, and where dominant, represent $27.0\% \pm 7.4$ of sapling stems (Asquith 1999). Despite the relatively high density of *Protium* spp. on small, exposed islands, and the low density of *O. lucens* and *H. concinna* at such sites (often < 10 stems/island; A.E.A., personal observation), *Protium* spp. suffered relatively little herbivory under such conditions. We suggest that *Protium* spp. receive less herbivory than would be expected given their density on small, exposed islands of Lago Gatún, and propose relative release from insect herbivory as another factor that may influence the success of *Protium* spp. at such sites. Further research is needed to explicitly test this hypothesis, and specifically, to relate patterns of herbivory observed among leaves to patterns of occurrence observed among tree species.

Conclusions

Habitat fragmentation is destructive to natural biotas and results in habitat loss and alteration, increased edge effects, and increased isolation of forest populations (Bierregaard et al. 1992). In general, tropical forest biotas, which contain large proportions of species with low abundances, restricted or patchy distributions, and complex interdependencies, are highly susceptible to effects of fragmentation (Laurance et al. 1997). Here, we have documented patterns of herbivory in a fragmented tropical forest. We found strong evidence that fragment area markedly influenced proportions of leaves damaged by Lepidopteran larvae, and that interactive effects of season, exposure, and tree species were important determinants of this measure of herbivory. Similarly, we found that island area was a major determinant of proportions of leaf area lost from damaged leaves, and that interactive effects of exposure, tree species, and season influenced damage rates. Further, we found strong evidence that patterns of herbivory differed among host species in forest fragments: on small, exposed islands, *Protium* spp. received less herbivory than conspecifics on larger islands, and less herbivory than two other focal taxa that co-occur at those sites. Contrary to expectations based on the Janzen–Connell hypothesis, we observed that damage to *Protium* spp. was lowest where those species occur at high densities. Based on these observations, we suggest that lower

levels of insect herbivory may contribute to the observed success of *Protium* spp. on small islands in Lago Gatún.

We conclude that herbivory by Lepidopteran larvae is influenced by several major factors associated with fragmentation, and suggest that patterns of herbivory in smaller forest remnants may differ markedly from those in larger fragments. Our data raise the possibility that fragmentation-induced changes in herbivory by insects may have an important impact on tree species diversity in tropical forest fragments.

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