Seasonal and habitat differences affect the impact of food and predation on herbivores: a comparison between gaps and understory of a tropical forest

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Herbivore populations are influenced by a combination of food availability and predator pressure, the relative contribution of which is hypothesized to vary across a productivity gradient. In tropical forests, treefall gaps are pockets of high productivity in the otherwise less productive forest understory. Thus, we hypothesize that higher light availability in gaps will increase plant resources, thereby decreasing resource limitation of herbivores relative to the understory. As a result, predators should regulate herbivore populations in gaps, whereas food should limit herbivores in the understory. We quantified potential food availability and compared arthropod herbivore and predator densities in large forest light gaps and in the intact understory in Panama. Plants, young leaves, herbivores and predators were significantly more abundant per ground area in gaps than in the understory. This pattern was similar when we focused on seven gap specialist plant species and 15 shade-tolerant species growing in gaps and understory. Consistent with the hypothesis, herbivory rates were higher in gaps than the understory. Per capita predation rates on artificial caterpillars indicated higher predation pressure in gaps in both the dry and late wet seasons. These diverse lines of evidence all suggest that herbivores experience higher predator pressure in gaps and more food limitation in the understory.

Herbivore populations are controlled by a combination of available food sources (bottom-up) and by predators (top-down). The relative importance of bottom-up and top-down controls have been studied and disputed for decades. Initially the biomass in one trophic level was viewed as a simple function of the biomass in the level below it (bottom-up) (Lindeman 1942). The debate began with Hairston et. al.'s (Hairston et al. 1960) seminal paper that introduced the concept of top-down control, in which predators controlled herbivore populations allowing plant biomass to accumulate. Since then, much effort has focused on quantifying and modeling the relative roles of top-down and bottom-up forces in different communities (Price et al. 1980, Power 1992, Hunter et al. 1997, Stiling and Rossi 1997, Dyer and Letourneau 1999, Walker and Jones 2001).

Primary productivity is thought to be an important determinant of the strength of top-down and bottom-up effects on a community (Rosenweig 1971, Fretwell 1977, Oksanen et al. 1981, Polis 1999). It is hypothesized that as productivity increases there is a shift from bottom-up control to top-down control. When productivity is low, plant resources limit herbivores, which secondarily affect predators. In contrast, when plant productivity is high, herbivore populations increase to levels that can support a substantial predator population, hence their numbers become more limited by predators. In these ideal scenarios, a trophic cascade may be detected, where increases in predator populations suppress herbivore populations and enhance plant productivity (Pace et al. 1999). Support for this theory has been found in some aquatic systems and in several experimental terrestrial systems (Carpenter et al. 1985,

Wootton and Power 1993, Fraser and Grime 1997, Fraser and Grime 1998, Forkner and Hunter 2000). Generally, experimental studies of this hypothesis have come from simple food webs combined with fertilizer applications to increase productivity (Hartvigsen et al. 1995, Stiling and Rossi 1997, Fraser and Grime 1998, Sipura 1999). There are several studies that have examined the relative roles of top-down and bottom-up forces in terrestrial systems with natural variation in productivity (Fraser and Grime 1997, Letourneau and Dyer 1998, Uriarte and Schmitz 1998, Mazía et al. 2004). However, it is still undetermined how natural variation in productivity would affect a diverse forest community, such as tropical forests.

Treefall gaps are dynamic sources of heterogeneity in productivity on the forest floor. In rainforests, light is the most limiting factor for growth in the understory, which receives as little as one percent of the total sunlight (Chazdon et al. 1996). In contrast, treefall gaps have higher light and temperature, in addition to an initial influx of nitrogen and phosphorus from the fallen tree (Vitousek and Denslow 1986, Denslow et al. 1998). These changes lead to higher productivity in gaps through an increase in seedling establishment, survival and growth (summarized by Denslow 1987). For this reason treefall gaps play an important role in tropical forest species composition (Hubbell et al. 1999, Schnitzer and Carson 2001). In addition to higher productivity, gaps harbor a suite of specialist plant species that require high light (Brokaw and Scheiner 1989). The leaves of these gap species are higher in nitrogen and lower in tannins than leaves from shade-tolerant understory species (Cates and Orians 1975, Coley 1983). Thus, gap species are a high quality food resource for herbivores and suffer higher herbivory rates than shade-tolerant species (Coley 1983).

In this paper, we compare the relative influences of predator pressure and food availability on the community of herbivores in the naturally more productive treefall gaps and the neighboring understory of a lowland moist forest in Panama. Specifically, we make seasonal and habitat comparisons to determine the differences in food resources for herbivores, herbivore and predator densities and predation rates to address the question ''how does food availability and predator densities interact to control herbivores?''

Material and methods

Study site

This study took place in the lowland moist forest of Barro Colorado Island (BCI) in Panama (9.08°N, 79.50°W), a field station operated by the Smithsonian

Tropical Research Institute. On average, rainfall is 2.6 m year^{-1}, which mainly falls in the wet season from May to November. Leaves flush with the onset of the wet season and there is a mid-season flush in September. We collected data in various seasons from 2001 to 2003, years with average rainfall (2.33 m, 2.30 m and 2.89 m respectively).

Treefall gaps were selected and paired with neighboring understory sites. We selected medium to large gaps (200−500 m^2) that were one to two years old, with regrowth 1−2 m high (Brokaw 1982). Paired understory sites were established 100 m away. We did not use the same gaps every season since some grew past the requirements we established. In these cases, other gaps were subsituted.

Abiotic and biotic differences across habitats

We quantified light availability, the major limiting resource for tropical rainforest plants (Chazdon et al. 1996), by taking hemispherical photos near dusk in the middle of the gaps and understory sites. We analyzed the photos using the computer software Hemiview (Hemiview 2.1, Delta-T Devices Ltd, Burwell, Cambridge, UK), which calculates the global site factor (GSF). GSF incorporates both direct and indirect light that reaches the site. GSF is a number between 0 and 1; in which 0 is no light and 1 is 180 degrees of full sun. A large area gap may receive less light than a medium area gap if the surrounding canopy is taller. Therefore, the total light availability is a better estimate of the effective gap area (Whitmore 1996).

We quantified community level trends in densities of plants, herbivores and predators using a transect method. We recorded densities within 1 m on each side of a 10 m transect in similar orientation in gaps and their neighboring understory sites. Transects were surveyed in paired gap and understory sites between 10 and 15 o'clock and during the dry (8 pairs), early wet (9 pairs) and late wet season (10 pairs) in 2003. Along the transects, we counted all plants up to 2 m tall and all the young leaves (leaves prior to full expansion and increased toughness). In tropical forests, the vast majority of herbivory occurs on young leaves (Marquis and Braker 1994, Coley and Barone 1996). Therefore, we used young leaf density as an indicator of resource availability to herbivores. Each plant was carefully surveyed and all arthropods were counted and recorded. The arthropods were categorized into large taxonomic groups, which included Lepidoptera, Homoptera, and Orthoptera for the herbivores and ants, spiders and Hemiptera for the predators. This approach should be quite sensitive to detecting the effect of habitat heterogeneity as arthropod densities respond to both the

density and diversity of plants. The data were analyzed with ANOVA to test the effect of habitat (gap and understory) and season (dry, early wet and late wet).

Species functional groups

Since plant species composition and densities are different in gaps than in the understory, we examined a group of focal species (Table 1). These species included shade-tolerant species and gap species creating three functional groups: gap species, shade-tolerant species growing in gaps and shade-tolerant species growing in the understory. By looking at these functional groups we took into account differences in species, life histories and plant densities between gaps and the understory.

We recorded arthropod, young leaf and mature leaf abundance on five to 15 plants from each species in each functional group. Arthropods were categorized into large taxonomic and trophic groups. We used the leaf area data mentioned earlier, which included separate measurements for shade-tolerant species growing in gaps and the understory, to calculate the arthropod density per m^2 leaf area. We analyzed the data using ANOVA to test for the effect of functional group (gap vs shade-tolerant species), habitat (gap vs understory) and seasonality (dry, early wet, late wet), as well as the interaction between functional group and season and between habitat and season. These measurements allowed us to determine how functional group contributes to differences in arthropod densities. Data were collected in early wet season 2002, dry season and late wet season 2003. We did not count densities on *Annona spraguei* in the dry season because it is deciduous. *Cecropia* plants were saplings and did not have resident ant colonies.

We measured mature leaf herbivory rates during the wet season of 2003 to determine the differences between each functional group. With the onset of the wet season, we marked three to five recently matured leaves of five to 15 plants of each species in each functional group and recorded any previous herbivory.

We revisited the leaves at the end of the rainy season and recorded herbivory. Herbivory was measured by tracing total leaf area and areas of damage on a piece of paper in the field and quantifying this with a leaf area meter (LI-COR Biosciences, Lincoln, Nebraska). We used a paired t-test to compare shade-tolerant conspecifics growing in gaps and understory and used a t-test to compare gap species to shade-tolerant species growing in gaps.

Predation on artificial caterpillars

We used artificial clay caterpillars to measure potential predation rates on undefended caterpillars. Coley (unpubl. data) found that attack rates on clay caterpillars were indistinguishable from attack rates on apparently undefended real caterpillars (lacking spines, hairs or warning colors). This method has been used to compare predation between the understory and canopy (Loiselle and Farji 2002). We acknowledge that clay caterpillars do not possess many characteristics real caterpillars have, which are used in defense or by predators in detecting prey. However, this method does document a potential interaction between a predator and its prey. In addition, it documents a comparable rate in which an herbivore would interact with a possible predator. Clay caterpillars (2×20 mm) were made using a large-hole garlic press and green Sculpty II® clay. They were placed randomly on the upper side of mature leaves and attached with a small dab of rubber cement. After 24 h, we measured attack rates by recording mandible and chew marks left in the clay. Ten clay caterpillars were placed on ten random plants in paired gap and understory sites. Each pair was always measured in the same 24-h period. We collected data on potential predation rates over multiple days during four weeks in the late wet season of 2001 and 2003, early wet 2002 and dry season 2003 (see Fig. 4 for sample sizes). The data (presence or absence of predation) were tested for the main effects of habitat, season and their interaction with SAS software categorical model (Proc catmod).

Table 1. Focal species and families of functional groups.

Gap species		Shade-tolerant species			
Acalypha diversifolia	Euphorbiaceae	*Alseis blackiana*	Rubiaceae	*Psychotria marginata*	Rubiaceae
Alchornea costaricensis	Euphorbiaceae	*Coussarea curvigemmia*	Rubiaceae	*Psychotria acuminata*	Rubiaceae
Annona spraguei	Annonaceae	*Faramea occidentalis*	Rubiaceae	*Psychotria furcata*	Rubiaceae
Cecropia insignis	Moraceae	*Garcinia edulis*	Clusiaceae	*Psychotria horizontalis*	Rubiaceae
Luehea seemannii	Tiliaceae	*Hybanthus prunifolius*	Violaceae	*Rinorea sylvatica*	Violaceae
Miconia argentea	Melastomataceae	*Mouriri myrtilloides*	Melastomataceae	*Tachigali versicolor*	Fabaceae
Spondias radlkoferi	Anacardiaceae	*Pouteria stipitata*	Sapotaceae	*Tetragastris panamensis*	Burseraceae
		Protium tenuifolium	Burseraceae		

Results

Food resources available to herbivores in gaps and the understory

Gaps had twice as much light as the understory sites (GSF values 0.268 ± 0.011 compared to 0.122 ± 0.005, Mann-Whitney U, $Z = -6.210$, $p < 0.001$). There were no significant differences in GSF among seasons. There were also higher densities of plants and young leaves in gaps (Fig. 1A). Young leaf density was five times higher in gaps than in the understory and there were strong seasonal and interaction effects (habitat $F_{1,48} = 58.468$, season $F_{2,48} = 12.989$, habitat × season interaction $F_{2,48} = 5.630$, $p < 0.01$). This was because plants were twice as abundant (2.615 ± 0.263 plants

m^{-2} in gaps, 1.202 ± 0.113 plants m^{-2} in understory, $F_{1,48} = 87.587$, $p < 0.001$) and had higher leaf production per plant.

For the focal species surveys, we also found more young leaves per plant in gaps than in the understory ($F_{1,101} = 29.348$, $p < 0.001$ Fig. 1B). However, there was no significant effect of functional group on the number of young leaves per plant between gap species and shade-tolerant species ($F_{1,101} = 0.624$, $p = 0.624$). Similar to the results from the transects, there was an effect of season on young leaf densities of focal species ($F_{2,101} = 11.336$, $p < 0.001$, Fig. 1B). In addition to more young leaves, shade-tolerant species in gaps tend to have larger leaf areas than their understory counterparts (62.1 ± 12.7 cm^2 in gaps, 44.7 ± 5.6 cm^2 in understory, paired t-test, $t_{14} = 2.057$, $p = 0.059$). There was no difference in the average number of mature leaves per plant between the three functional groups ($F_{2, 101} = 2.16$, $p > 0.05$). However, there was a seasonal difference ($F_{2, 101} = 6.351$, $p < 0.01$). LSD post hoc tests indicate that the average number of leaves per plant was significantly higher in the late rainy season than in the early wet or dry season ($p < 0.01$ in both seasons).
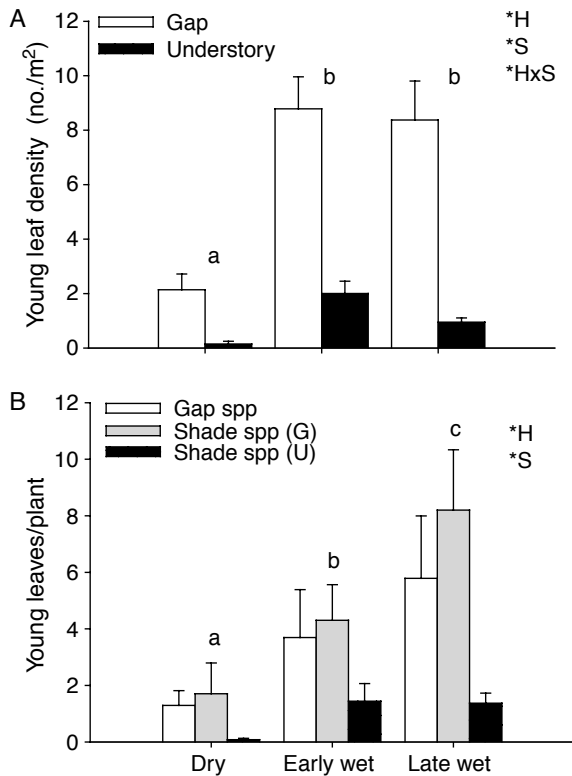

Fig. 1. (A) Young leaf densities measured along transects in gaps and the understory through out the year, there were 8, 9 and 10 paired transects in the dry, early wet and late wet respectively. (B) The number of young leaves per plant on three functional species groups in three different seasons. These data are the mean for 7 gap species and 15 shade-tolerant species in gaps (G) and understory (U) for each season. Significant effects are indicated (2-way ANOVA, $p < 0.05$). *H represents habitat effects between gap and understory. *S represents seasonal effects. *H × S represents an interaction effect. Letters indicate differences between seasons (LSD, $p < 0.05$).
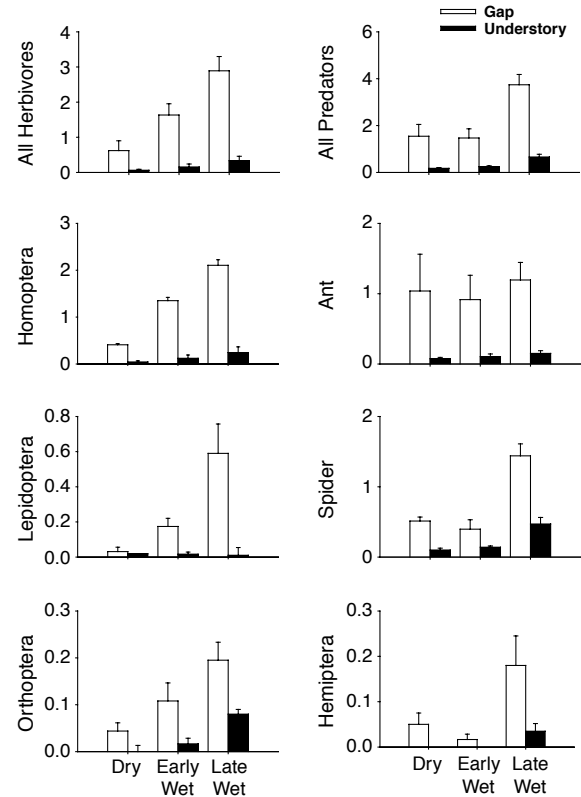

Fig. 2. Herbivore (left) and predator (right) densities in gaps and understory during the dry, early wet and late wet seasons. Densities were recorded as the number per m^2 ground.

Table 2. Analysis of variance (ANOVA) for habitat (gap, understory) and season (dry, early wet, late wet) on herbivore densities per ground area.

	DF	Homoptera			Lepidoptera			Orthoptera			Herbivores		
		MS	F	p	MS	F	p	MS	F	p	MS	F	p
Habitat	1	17.79	33.51	0.000	0.73	12.08	0.001	0.14	22.76	0.000	31.41	52.61	0.000
Season	2	3.99	7.51	0.001	0.51	8.50	0.001	0.02	3.87	0.028	7.30	12.22	0.000
Habitat × season	2	2.47	4.66	0.014	0.28	4.73	0.013	0.03	4.92	0.011	4.47	7.48	0.001
Error	48	0.531			0.060			0.006			0.597		

Herbivore densities and herbivory rates

In community transects, we found higher herbivore densities in gaps (Fig. 2). All herbivore densities showed a dramatic difference between gap and understory sites (Table 2). The habitat difference became greater through the seasons, with the greatest difference in the late wet season as indicated by a significant habitat by season interaction on herbivore densities.

Even when species identity and plant biomass were controlled, we found higher herbivore densities in gaps (Fig. 3). Herbivore densities were affected by functional group, habitat and seasonality (Table 3). Similar to findings in the community transects, there was a habitat by season interaction. There was no habitat effect on Homoptera densities, however there were significantly more on gap species (Fig. 3, Table 3).

Rates of herbivory on mature leaves were higher in gaps and mirrored herbivore densities. Within gaps, rates of damage were higher on gap species (0.38% per day) than on shade-tolerant species (0.16% per day, t-test, $t_{20} = -2.983$, $p < 0.01$). However, herbivory
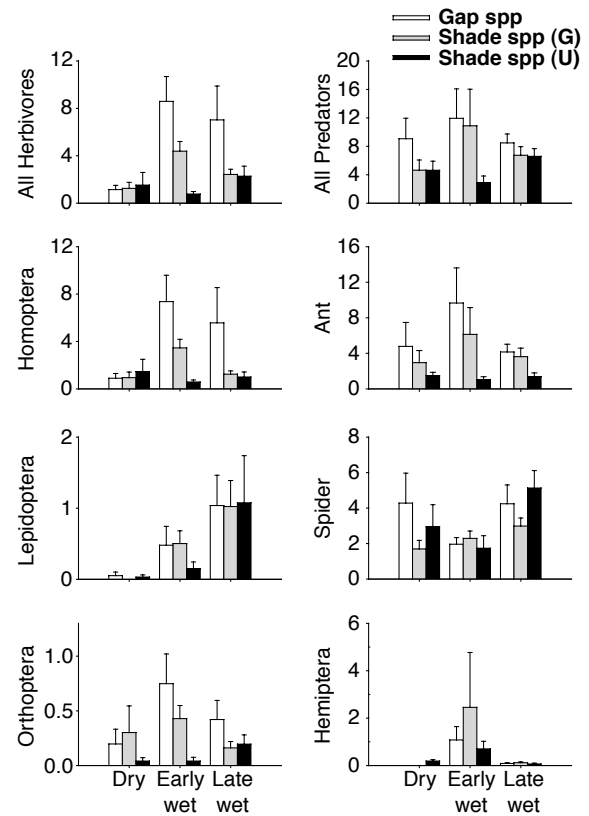

Fig. 3. Herbivore (left) and predator (right) densities on focal plant species in gaps and the understory between different seasons. Densities are the number of individuals per m^2 leaf area. These data include 7 gap species and 15 shade-tolerant species in gaps and understory.

rates did not differ greatly between shade-tolerant species in gaps (0.16% per day) and on paired understory conspecifics (0.14% per day, paired t-test, $t_{14} = 0.752$, $p > 0.05$). There were no differences in missing leaf area before the recording period between gap species and shade-tolerant species in gaps ($t_{20} = -0.358$, $p > 0.05$) and between shade-tolerant species growing in gaps and in the understory ($t_{14} = 0.799$, $p > 0.05$). Initial leaf damage was not related to subsequent herbivory rates in gap species, nor in shade-tolerant species in gaps or in the understory ($r^2 = 0.001$, 0.023, and 0.005, respectively, $p \geq 0.071$).

Predator densities and rates of predation

In all seasons, predator densities were significantly higher in gaps than in the neighboring understory (Fig. 2, Table 4). This result held when each of the predator groups was examined separately (Table 4). Spiders and Hemiptera had a seasonal effect and there was a significant habitat by season interaction for spiders.

Total predator densities on focal species of the functional groups did not differ significantly between gap and understory (Fig. 3, Table 5). Likewise, in the late wet and dry season there was no difference between shade-tolerant species in gaps and in the understory. However, there was a habitat by season interaction in predator densities on focal species. This is because there were more predators in gaps in the early wet season. This pattern differs from that found for the community survey, in which predator densities were higher in gaps in the late wet season. Predaceous hemipteran and spider densities showed seasonality (Table 5), but ants were aseasonal (Fig. 3). Ants densities were higher on plants in gaps than in the understory.

In order to be conservative, the results above do not include ants and homopterans involved in mutualistic interactions. We calculated the mean number of plants in each transect in which ant-homopteran interactions were observed and found an effect of habitat and seasonality ($F_{1,46} = 21.158$ $F_{2,46} = 5.431$ respectively $p < 0.01$). There were more interactions in gaps than in the understory (0.025 ± 0.005, and 0.001 ± 0.001 interactions plant^{-1}, respectively). There were very few interactions seen during the dry season compared to the early and late wet season (LSD, $p < 0.05$). The only focal species that had ant-homopteran interactions were *Acalypha, Alchornea, Luehea, Miconia* (gap species) and *Mouriri* (shade-tolerant species).

All the clay caterpillars placed in the field were recovered. Typical marks left by predators on the clay caterpillars were small slits from mandibles and small scrape marks. Since an immeasurable amount of clay was removed from the artificial caterpillar, it is unlikely

Table 3. Analysis of variance (ANOVA) for habitat (gap, understory), season (dry, early wet, late wet) and functional group (gap species, shade-tolerant species in gaps, shade-tolerant species in understory) on herbivore densities per leaf area.

	DF	Homoptera			Lepidoptera			Orthoptera			Herbivores		
		MS	F	p	MS	F	p	MS	F	p	MS	F	p
Habitat	1	0.07	2.29	0.133	0.46	6.00	0.016	0.07	5.22	0.024	0.87	11.37	0.001
Season	2	1.08	33.26	0.000	0.77	10.00	0.000	0.03	2.71	0.071	0.85	11.08	0.000
Functional group	1	0.15	4.66	0.033	0.16	2.04	0.157	0.04	2.88	0.093	0.55	7.14	0.009
Habitat × season	2	0.03	0.82	0.443	0.34	4.34	0.016	0.03	2.38	0.097	0.37	4.77	0.010
Functional group × season	2	0.14	4.66	0.016	0.08	0.99	0.374	0.01	0.67	0.512	0.07	0.93	0.397
Error	101	0.032			0.077			0.013			0.077		

that attack rates measured were due to arthropod use of clay. None of the attack marks were characteristic of bird beaks. Predation rates on clay caterpillars were 40% higher in gaps than in the understory during the late wet season ($\chi_1^2 = 5.20$, p $= 0.023$, Fig. 4). There was no significant effect of season ($\chi_3^2 = 3.87$, p $= 0.276$) and no interaction (habitat $\times$ season $\chi_3^2 = 2.18$, p $= 0.536$). However there was no difference in predation rates in the early wet season (Fig. 4). Predation rates in the late wet season were not significantly different between 2001 and 2003 ($\chi_1^2 = 0.44$, p $= 0.506$) and were higher in gaps.

Discussion

Herbivores appeared to be tracking the greater food availability in gaps with up to nine times higher densities in gaps than in the understory. This pattern held true even when we accounted for species and leaf area. In addition, the presence of early successional gap species contributed greatly to the higher herbivore densities in gaps, particularly in the wet season. Higher herbivory rates on mature leaves of gap species reflect higher food quality for herbivores and are consistent with previous studies (Coley 1983). Thus, there are both more young leaves and higher quality mature leaves for herbivores in gaps than in the understory.

Our results were similar to previous studies comparing sun and shade habitats, in which they found higher insect herbivore abundance in the sun (Shure and Phillips 1991, Louda and Rodman 1996, Jokimaki et al. 1998, Sipura and Tahvanainen 2000). In contrast,
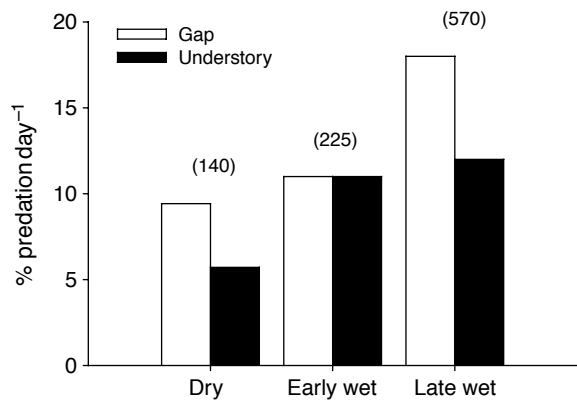

Fig. 4. "Predation" rates on artificial clay caterpillars in gaps and the understory during the dry, early wet, and late wet seasons. "Predation" rates are recorded as the average percent of the caterpillars that were attacked per day. The numbers in parentheses indicate the number of pairs. The data are pooled for the late wet season in this graph (210 pairs in 2003 and 360 pairs in 2001), however they were considered separately in the analysis.

Table 4. Analysis of variance (ANOVA) for habitat (gap, understory) and season (dry, early wet, late wet) on predator densities per ground area.

	DF	Ants			Spiders			Hemiptera			Predators		
		MS	F	p	MS	F	p	MS	F	p	MS	F	p
Habitat	1	11.81	19.04	0.000	4.02	40.39	0.000	0.06	6.76	0.012	47.86	52.21	0.000
Season	2	0.13	0.22	0.808	2.80	28.12	0.000	0.05	5.41	0.008	11.33	12.36	0.000
Habitat × season	2	0.07	0.11	0.898	0.68	6.832	0.002	0.02	2.06	0.138	5.06	5.51	0.007
Error	48	0.620			0.100			0.009			0.917		

Table 5. Analysis of variance (ANOVA) for habitat (gap, understory), season (dry, early wet, late wet) and functional group (gap species, shade-tolerant species in gaps, shade-tolerant species in understory) on predator densities per leaf area.

	DF	Ants			Spiders			Hemiptera			Predators		
		MS	F	p	MS	F	p	MS	F	p	MS	F	p
Habitat	1	1.10	10.66	0.001	0.04	0.58	0.449	0.01	0.24	0.624	0.25	2.79	0.098
Season	2	0.11	1.06	0.349	0.53	7.44	0.001	0.23	6.36	0.003	0.18	1.99	0.142
Functional group	1	0.42	4.02	0.048	0.18	2.55	0.113	0.01	0.27	0.605	0.40	4.34	0.040
Habitat × season	2	0.14	1.36	0.262	0.18	2.51	0.086	0.01	0.42	0.660	0.37	4.11	0.019
Functional group × season	2	0.04	0.351	0.705	0.07	1.04	0.357	0.01	0.39	0.677	0.01	0.16	0.854
Error	101	0.103			0.071			0.036			0.091		

Shelly (1988) found higher abundances of flying insect herbivores and predators in the understory on BCI. The differences between Shelly's findings and ours indicate that flying insects may be more susceptible and able to avoid abiotic stress of sunny and drier gaps than the less active insects we included in this study (Richards and Windsor, in press). Orthoptera are very mobile and may be preferentially feeding in gaps rather than in the understory. In comparison, lepidopteran larvae are less mobile and their locations are dictated by oviposition preference of the adults. Thus, higher lepidopteran larvae densities in gaps likely reflect differences in oviposition by adults, as demonstrated by the interaction between habitat and seasonality in lepidopteran density. In the dry season, larvae densities were low throughout the forest and there was no difference between gaps and understory. However, throughout the wet season the lepidopteran larval density increased dramatically in gaps and actually decreased in the understory.

Predator densities were higher in gaps for all seasons and for all taxonomic groups. Ants are a major invertebrate predator in the tropics and were one of the main predator groups in our study. Although Feener and Schupp (1998) found no differences in ant abundance between gaps and understory, we found significantly higher ant densities in gaps, on both gap and shade-tolerant species. Higher prey densities and extra-floral nectaries of gap species (Schupp and Feener 1991) may contribute to these higher ant densities. Three of the focal gap species had a variety of nectaries, but ant densities were no higher on these species than on species without nectaries. In addition, our ant densities were conservative as we excluded ants observed in mutualistic interactions with Homoptera. These interactions were primarily in gaps at both the community and focal plant level. The high light conditions and higher young leaf densities in gaps would allow high exudate production by homopteran herbivores (Garsed et al. 1987), which would support mutualistic interactions with ants. These ant interactions may have contributed to the higher predation rates measured on artificial caterpillars in gaps.

If the greater plant productivity in gaps caused proportional increases in both herbivores and predators, we would not expect to find the differences in per capita predation rates that we did. Predation rates were higher in gaps despite the fact that compositional and structural heterogeneity should have increased the difficulty of finding prey. However, a previous study found that habitat complexity increased the impact of spiders on planthoppers in cordgrass communities (Denno et al. 2002). These data supported our hypothesis that predator pressure would be most pronounced in the productive gap sites. In comparison, the availability of food in the understory was low. Thus,

there appears to be greater top-down control in gaps and bottom-up control in the understory.

The seasonal rhythms of young leaf production, coupled with a lag time in the response of predators to increased prey, appeared to be responsible for the seasonal shifts in the relative impacts of top-down and bottom-up effects. We observed a strong top-down effect in the late wet season and dry season, but not in the early wet season. In the dry season, there were few young leaves and herbivore populations were low in both habitats. This may be due to lower food availability as well as stressful abiotic conditions (Richards and Windsor, in press). In comparison, predator densities do not decline as much, causing higher predator to herbivore ratios and higher per capita predation rates in gaps in the dry season. However, when young leaves flushed with the onset of the wet season, herbivore densities responded quickly, especially in gaps. In contrast, predator densities lagged behind. It was not until the late wet season, when predator densities peaked, particularly in gaps, that we saw an increase in predation in gaps over the understory. Even though ants are an important predator, and are much more abundant in gaps, they show very little seasonal variation. Thus, other predators must have influenced seasonal changes in per capita predation.

Overall, our study detected a lower availability of food in the understory and a significant increase in per capita predation in gaps. This suggests significant predator influences on herbivores that were tied to pockets of increased productivity. In addition, we showed that the differences in light availability across short spatial distances could lead to dramatic changes in trophic interactions, with herbivores likely being limited by food in the understory and by predators in adjacent gaps. Thus, the fine-scale heterogeneity in productivity found in tropical forests may affect the balance between top-down and bottom-up control as hypothesized by early workers (Oksanen et al. 1981).

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