Seasonal variation of arthropod abundance in gaps and the understorey of a lowland moist forest in Panama

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Abstract: Treefalls gaps contribute to the habitat heterogeneity of tropical forest floors. Previous studies have shown that these gaps play an important role in plant and bird communities, however less is known about their role in arthropod communities. Using eight Malaise traps we investigated the difference in arthropod abundance of 19 taxonomic groups between gaps and understorey for 21 wk during the rainy season and 8 wk in the dry season on Barro Colorado Island, Panama. More (33.8%) arthropods were collected in gaps during the rainy season and 32.2% more in the understorey during the dry season. To assess the possible factors contributing to these differences we measured light, plant densities and young leaf densities, as indicators of abiotic factors and food resources for insect herbivores. Arthropod abundance was negatively correlated with light in the dry season. Thus, abiotic stress may explain the pattern of abundance in the dry season. While there was no correlation with light in the rainy season, predator abundance was positively correlated with herbivore abundance. The plant and young leaf density data suggest that there is significantly higher food availability for herbivores in gaps. Thus, less stressful abiotic conditions and more food resources may contribute to more herbivores followed by more predators in gaps during the rainy season.

Key Words: Coleoptera, communities, Hymenoptera, Malaise traps, Panama, seasonality, treefall gaps, tropical forest

INTRODUCTION

Tropical forests are a patchwork of closed canopy and treefall gaps at different stages of regeneration. These gaps play an important role in the species composition and diversity of plant and bird communities (Brokaw & Scheiner 1989, Hubbell *et al.* 1999, Levey 1988, Ricklefs 1977, Schemske & Brokaw 1981, Schnitzer & Carson 2001). However, surprisingly, the role of gaps on insect communities has received little attention (Feener & Schupp 1998, Hill *et al.* 2001, Shelly 1988). In this study, we explored differences in the arthropod communities between treefall gaps and the understorey. We compared Malaise trap samples from paired gap and understorey sites during the dry season and rainy season in a lowland moist forest in central Panama. We also examined the possible differences in biotic and abiotic conditions in gaps and the understorey that could affect insect activity.

Treefall gaps contribute substantially to resource heterogeneity of the forest floor. The understorey of mature forest generally receives only 1% of full sunlight (Chazdon & Fetcher 1984). However, gaps have significantly more light, soil moisture and higher temperatures (Denslow *et al.* 1998). Additionally, litter from fallen trees contributes an initial influx of nitrogen and phosphorus (Vitousek & Denslow 1986). These changes lead to higher productivity in gaps, which increases seedling establishment, survival and growth (summarized in Denslow 1987). Schowalter (1994, 1995) has found evidence that canopy invertebrate communities change in response to disturbances, such as treefall gaps. Thus, we suggest that changes in biotic and abiotic conditions associated with gaps should have large effects on insect communities.

Forest insects could respond to the higher quantity and quality of food resources in gaps. Gaps increase plant growth resulting in more young leaves, which are less defended, more nutritious and preferred by herbivores (Coley 1983, Coley & Barone 1996). In addition, gaps have light-demanding plant species that take advantage

of the ideal conditions in gaps by growing quickly (Brokaw & Scheiner 1989) and investing less in defences (Coley *et al.* 1985). In comparison, shade-tolerant species invest more in plant defences, such as toughness and tannins, relative to gap species (Coley *et al.* 1985). Accordingly, gaps have higher plant densities, higher quality plant species and more young leaves contributing to higher overall availability of quality resources for insect herbivores.

Insects are also affected by the abiotic conditions in gaps, which can act as a filter that excludes many species. The combination of high temperature and low relative humidity can have a negative impact on insects, thus they may seek refuge in the understorey when gap conditions become stressful. Warmer temperatures of gaps may increase metabolism and insect activity (Shelly 1982, 1984). In addition, Chase (1996) found that alterations in light and temperature conditions affect feeding behaviour in grasshoppers, thus affecting their ability to compensate for population losses to predation.

In this paper, the abundances of 19 different arthropod groups are compared between gaps and the understorey during the rainy and dry seasons. We were interested in determining the relative abundance of these arthropods in gaps and in the intact understorey and seasonal change in habitat use (Smythe 1996, Wolda 1978). We were also interested in determining if the differences could be explained by differences in biotic and abiotic factors. In contrast to many Malaise trap studies which focus on exhaustively collecting a focal taxonomic group (Brown & Feener 1995, Longino *et al.* 2002), this study addresses ecological patterns in seasonal habitat use by a suite of major taxonomic groups.

METHODS AND MATERIAL

Study site

This study was conducted on Barro Colorado Island (BCI), a field station located in the middle of Gatun Lake in the Panama Canal and operated by the Smithsonian Tropical Research Institute (9.08 °N, 79.50 °W). The island is covered by lowland tropical moist forest. Average rainfall on BCI is 2.6 m y^{-1}, 90% of which falls in the rainy season from mid-May to November (Windsor 1990). Young leaves generally flush at the onset of the rainy season with a smaller flush occurring in the late rainy season (Aide 1993). The frequency of treefall gap formation peaks in the middle of the rainy season (Brokaw 1982).

We selected large gaps (estimated at >250 m^2) of 1–2 y in age, with saplings 1–2 m tall. Gaps contain both shade-tolerant and light-demanding species. We paired each of four gap sites with understorey sites separated by approximately 100 m. Two of the paired sites were located in old growth forest (>400 y old), two in young tall forest (∼125 y since human disturbance) (Foster & Brokaw 1982). Two gap and understorey paired sites, one in each of the forest types were used in both rainy and dry seasons. However, in the two other gap sites, many of the light-demanding plants had become too tall and were shading other plants. To maintain consistent successional stages between all sites and seasons, we established two new paired sites in young and old growth forest with saplings 1–2 m tall in the dry season.

Because the study spanned 12 mo, we expect that these results would vary from year to year, depending on the intensity of rainfall and the length of the dry season. This study took place during a year with average rainfall (2.3 m in 2002 and 2.8 m in 2003; average is 2.6 m) and a slightly drier than average dry season (dry season 2003 received 0.2 m of rain; average is 0.3 m).

Arthropod sampling

We set up a total of eight 'Townes Style' Malaise traps (www.santetraps.com, Townes 1962) in the middle of the four gap sites and four paired understorey sites. These are non-attractive traps that intercept and funnel flying insects up and into a bottle of 70% ethanol. This method has been useful in identifying insect communities in different forest stands (Hutcheson 1990, Hutcheson & Kimberley 1999). We set up the traps in the rainy season of 2002 from 21 May to 30 October and at the end of the dry season of 2003 from 26 March to 21 May. In the rainy season, the traps were collected weekly until the end of July and then were collected approximately every 2 wk until October. In the dry season, the traps were collected weekly. The collections were then sorted into 19 different arthropod groups. We estimated the mean number of individuals collected per day to normalize the data for different collecting intervals. Data from gap and understorey traps are referred to as G traps and U traps, respectively. Insect groups that were collected, but not counted, were excluded from the analysis. All specimens from this study are stored in a voucher collection at the Smithsonian Tropical Research Institute, Panama.

We compared data from our experimental traps to data from ten long-term traps which simultaneously collected insects in the understorey of the closed-canopy old forest (>400 y) along the west boundary of the 50-ha plot on BCI (D. Windsor and J. Pickering, unpubl.). The traps are maintained as part of a long-term study of insect populations. Samples were sorted into six families of Coleoptera (Chrysomelidae, Cerambycidae, Languriidae, Curculionidae, Cicindelidae and Buprestidae) and two families and one suborder of Hymenoptera (Ichneumonoidae, Mutillidae and Symphyta). We compared data of the same taxa from the

G/U traps to the long-term traps. From this, we determined whether the smaller sample sizes of the G/U traps were consistent with insect activity for BCI.

Habitat conditions

We quantified light availability, the major limiting resource for tropical rain-forest plants (Chazdon *et al.* 1996), by taking hemispherical photographs near dusk in the middle of the gaps and understorey sites. We analysed the photographs 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 represented as a number between 0 and 1, in which 0 is no light and 1 is 180 degrees of full sun. Measuring total light availability also estimates effective gap area. Gap area alone may not provide a good estimate of total light availability in that a large gap in a taller canopy forest can receive less light than smaller gaps in shorter canopy forest. Light availability may also indicate differences in temperature and humidity.

Meteorological and hydrological data collected on BCI (Environmental Science Program URL http://striweb.si.edu/esp/index.php) were used to indicate how relative humidity and temperature might differ between gaps and understorey. These data are available through the Smithsonian Tropical Research Institute's Terrestrial-Environmental Sciences Program. Temperature and relative humidity were collected in the understorey of old-growth forest 1 m above the ground and in the laboratory clearing, an area with grass and low vegetation.

We also measured plant and young leaf densities as an indicator of productivity and resource availability to herbivores. We counted all the plants and young leaves within a 10 × 2-m transect in the middle of the gaps and the paired understorey site.

Statistical analysis

All data were tested for normality and equality of variance (Kolmogorov–Smirnov test and Levene's Test, respectively) and non-parametric tests were used when these assumptions were not met (SPSS 10.0, SPSS Inc., Chicago USA). Light availability and plant density were analysed with a two-way ANOVA to test for differences between the main effects of habitat (gap and understorey), season (rainy and dry) and their interaction, followed by a LSD post-hoc analysis. Young leaf densities failed the test for equality of variance, therefore were analysed with the Kruskal–Wallis test followed by pairwise Mann–Whitney analysis to identify the statistically different values.

The number of arthropods collected per day was analysed using a Friedman's test with repeated measures. This non-parametric test was used instead of repeated-measures ANOVA because some collection dates were missing. Freidman's test with repeated measures was used to analyse total collections, herbivores, predators and each arthropod group to test for differences between gaps and the understorey and between old-growth and young-growth forest. Rainy and dry seasons were analysed separately. We analysed the relationship between predator and herbivore activity in the rainy and dry seasons using a regression. Taxa considered herbivores included the orders Homoptera, Lepidoptera, Orthoptera and Coleoptera (families Buprestidae, Languriidae, Chrysomelidae and subfamilies Cerambycidae, Curculionidae) and the Hymenoptera suborder Symphyta. Taxa considered predators and parasitoids included the orders Odonata, Hymenoptera (superfamilies Ichneumonoidea and Vespoidea, and families Formicidae and Mutillidae), Coleoptera (families Cicindelidae, Lycidae and Staphylinidae), Hemiptera (family Reduviidae) and Araneae. In addition, we used a regression analysis to compare the relationships between light availability and total collections.

RESULTS

Biotic and abiotic differences

Gaps received more light than the understorey in both the rainy and dry seasons ($F_{1,12} = 85.9$, $P < 0.001$, Table 1). There was slightly more light in both gaps and understorey in the dry season than in the rainy season ($F_{1,12} = 4.49$, $P = 0.056$), but there was no significant interaction between season and habitat ($F_{1,12} = 0.171$, $P > 0.05$). Plant and young leaf densities were statistically higher in gaps ($F_{1,12} = 7.55$, $P < 0.05$ and $\chi_1^2 = 5.33$, $P < 0.05$ respectively). Additionally, young leaf densities

Table 1. The mean differences between gap and understorey sites in the rainy and dry season for light availability and plant and young leaf density. Light availability is represented by the mean global site factor (GSF) ($\pm$SE). Plant and leaf densities are the number m^{-2} of ground along the transects. Superscripts denote differences between values within a column at $P < 0.05$ (LSD).

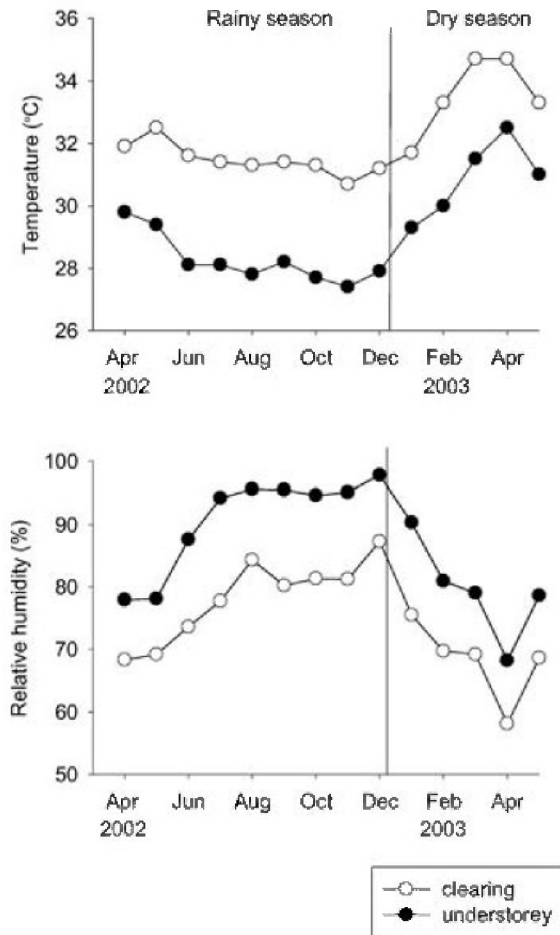|		Light availability (GSF)	Plant density (plants m^{-2})	Young leaf density (young leaves m^{-2})
Rainy season	Gap	0.25 ± 0.02^a	2.40 ± 0.18^a	5.23 ± 0.26^a
	Understorey	0.10 ± 0.01^b	1.79 ± 0.41^{ab}	0.88 ± 0.29^{bc}
Dry season	Gap	0.27 ± 0.02^a	1.87 ± 0.13^{ab}	1.85 ± 0.57^c
	Understorey	0.14 ± 0.01^b	1.12 ± 0.18^b	0.08 ± 0.05^b

Figure 1. Average monthly temperature and relative humidity on BCI in the laboratory clearing and a nearby understorey site. These data are summarized from data collected by the Smithsonian Tropical Research Institute's Meteorological and Hydrological Monitoring Program. The rainy season and dry seasons are indicated at the top.
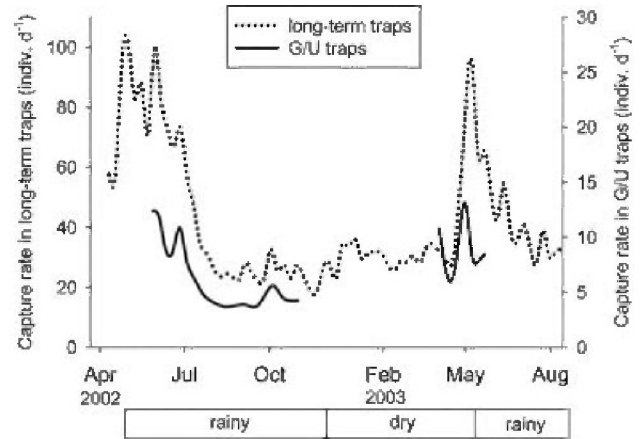

Figure 2. Weekly mean of Coleoptera and Hymenoptera collected in long-term traps (D. Windsor and J. Pickering unpubl.) and G/U traps of this study period. Rainy season and dry season are indicated on the x-axis. The y-axis for plateau traps is on the left and G/U traps is on the right.

were significantly higher in the rainy season ($\chi_1{}^2 = 11.3$, P < 0.001).

The differences in temperature and relative humidity between the laboratory clearing and the forest understorey were the greatest during the rainy season (Figure 1). The conditions in the clearing during the rainy season were similar to those in the understorey in the dry season. Both sites were hotter by 2–3 °C and had 13–17% lower humidity in the dry season. The highest temperatures and lowest humidity were recorded in the clearing during the dry.

Arthropod captures

A total of 47 526 insects were collected and sorted into major taxa. A total of 48 trap samples were collected in the dry season and 120 in the rainy season, with half of those coming from gaps and the other half from the understorey.

There were 24 250 insects collected from gap traps (31.8 ± 3.53 individuals d^{-1}), 23 273 from understorey traps (33.4 ± 3.60 individuals d^{-1}); 18 417 in the dry season (36.8 ± 4.49 individuals d^{-1}) and 29 106 in the rainy season (27.2 ± 2.02 individuals d^{-1}). The relative abundance of Coleoptera and Hymenoptera in the G/U traps was 83.9 % lower than that of the long-term traps (Figure 2). However, the overall pattern in insect activity in the G/U traps matched seasonal trends from the plateau traps. The average number of insects collected per trap per week was not significantly different between seasons when gap and understorey traps were combined (Mann–Whitney, Z = −1.68, P > 0.05).

The total number of individuals collected in gaps and understorey differed seasonally (Figure 3). There were significantly more individuals collected per day in gaps in the rainy season (Figure 3, $\chi_1{}^2 = 8.07$, P < 0.01) and more individuals were collected per day in the understorey during the dry season ($\chi_1{}^2 = 4.5$, P < 0.05). Mean daily collections and light availability were negatively correlated in the dry season ($r^2 = 0.638$, P < 0.05), but were not correlated in the rainy season. In addition, more individuals were collected from traps in young-growth forest than in old growth (in dry season 40.2 ± 1.9 individual d^{-1} in young forest and 33.5 ± 1.7 in old forest, $\chi_1{}^2 = 4.5$, P < 0.05 and in the rainy season 33.4 ± 5.9 individuals d^{-1} in young forest and 20.8 ± 3.2 in old, $\chi_1{}^2 = 11.3$, P < 0.01). Arthropod groups that had significantly higher capture rates in young forests were Homoptera, Orthoptera, Lycidae (Coleoptera), Languriidae (Coleoptera), Curculionidae (Coleoptera) and Reduviidae (Hemiptera) (Friedman's test, P < 0.05).

This seasonal pattern in gap and understorey capture rates was found in both herbivores and predators. In
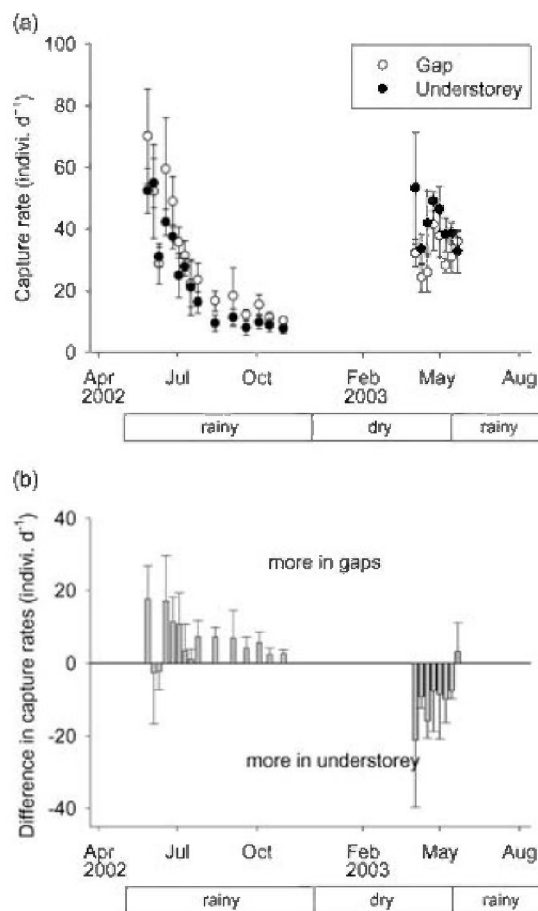
Figure 3. Mean total arthropods collected per day in gap and understorey traps (a) and the differences between paired gap and understorey traps (G-U) for each sampling interval (b). Values above zero indicate more insects collected in gaps and below zero indicate more arthropods collected in the understorey. Seasons are indicated and based on rainfall data.
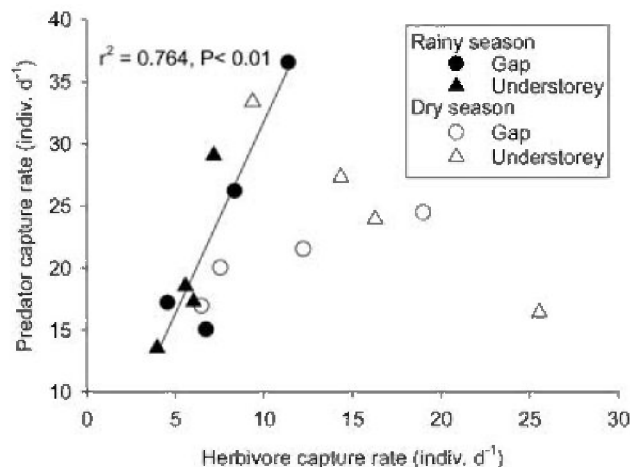

Figure 4. The relationship between predator abundance and herbivore abundance for the rainy (solid line, $y = 1.07 + 3.06x$) and dry season (dashed line, $y = 25.2 - 0.16x$). Each data point represents the daily mean throughout the season for a trap. There was a significantly positive correlation in the rainy season and not in the dry season. The r^2 value is the adjusted estimate.

the rainy season, more herbivores and predators were collected in gaps ($\chi_1^2 = 11.3$, $P < 0.001$ and $\chi_1^2 = 5.4$, $P < 0.05$) and during the dry season more herbivores and predators were collected in the understorey ($\chi_1^2 = 4.5$, $P < 0.05$ for both herbivores and predators). Predator abundance correlated with herbivore abundance in the rainy season but not in the dry season (Figure 4).

The pattern of arthropod activity varied among groups between seasons and habitat. Some, but not all of the 19 arthropod groups, displayed higher capture rates in gaps throughout the year, others groups during a single season, and still others showed no differences between habitats (Table 2). Phytophagous beetles were more active in gaps, whereas other phytophagous insects, such as Orthoptera and Homoptera, were more active in the understorey (Table 2). Major predaceous taxa, in general, were more active in gaps, with the exception of Ichneumonoid parasitoids, which were more active in the understorey throughout the year.

DISCUSSION

Overall, we found higher insect abundance of both herbivores and predators in gaps during the rainy season and higher activity in the understorey during the dry season. We suggest this pattern can be explained by seasonal changes in abiotic conditions and resource availability. In the rainy season, insect abundance was higher in gaps when more resources were available for herbivores and temperatures and humidity were moderate. However, in the dry season, insect abundance was lower in gaps when food resources for herbivores were lower and there were higher temperatures and lower relative humidity in the forest.

Gaps have more food resources for herbivores due to higher plant densities and young leaves. This pattern is particularly true in the rainy season when abundant water and light allow plants to flush young leaves. On BCI, young leaf production peaks in May with the onset of the rainy season and is the lowest during the dry season from October to February (Aide 1988, Leigh & Windsor 1982). The peaks in total insect abundance coincide with seasonal flushes of young leaves in the understorey. In the rainy season, gaps have five times more young leaves and higher herbivore activity. Thus not only do gaps have more food resources for herbivores there are also higher resources for predators. This is reflected in the positive correlation between herbivore and predator abundance in the rainy season. This correlation suggests that insect abundance in the rainy season is resource driven. In contrast, in the dry season there was no correlation between herbivores and predators suggesting that abiotic conditions were determining predator location. It is also

Table 2. Average capture rate (individuals d^{-1}) over the rainy season and dry season for the arthropod groups sorted from malaise traps (N = 4). Bold values indicate a significantly higher capture rate in gaps or the understorey in that season (Friedman's test with repeated measures, P < 0.05).

	Rainy season		Dry season	
	Gap	Understorey	Gap	Understorey
Araneae	0.21 ± 0.02	0.39 ± 0.14	0.36 ± 0.12	0.51 ± 0.05
Coleoptera				
Buprestidae	**0.05 ± 0.01**	0.004 ± 0.004	0.07 ± 0.03	0.004 ± 0.004
Cerambycidae	0.04 ± 0.01	0.03 ± 0.01	0.22 ± 0.16	0.08 ± 0.03
Chrysomelidae	**1.16 ± 0.33**	0.89 ± 0.29	0.65 ± 0.24	0.43 ± 0.12
Cicindelidae	0.06 ± 0.01	0.05 ± 0.03	0.03 ± 0.01	0.03 ± 0.01
Curculionidae	**2.27 ± 1.04**	0.87 ± 0.20	**4.45 ± 2.23**	1.29 ± 0.34
Languriidae	**0.08 ± 0.04**	0.02 ± 0.01	0.12 ± 0.6	0.06 ± 0.04
Lycidae	**0.36 ± 0.10**	0.16 ± 0.03	**0.23 ± 0.13**	0.07 ± 0.02
Staphylinidae	0.67 ± 0.18	0.47 ± 0.12	0.62 ± 0.18	**0.80 ± 0.33**
Hemiptera				
Reduviidae	0.02 ± 0.005	0.01 ± 0.004	0.13 ± 0.07	0.05 ± 0.02
Homoptera	1.54 ± 0.20	1.59 ± 0.37	1.89 ± 0.17	8.94 ± 2.64
Hymenoptera				
Formicidae	**19.2 ± 4.58**	13.2 ± 2.75	15.0 ± 1.49	17.4 ± 3.13
Ichneumonoidea	3.12 ± 0.33	**5.09 ± 0.89**	3.48 ± 0.57	**5.08 ± 0.36**
Mutilidae	**0.26 ± 0.04**	0.13 ± 0.04	0.78 ± 0.21	1.01 ± 0.07
Symphyta	0.05 ± 0.03	0.05 ± 0.01	0.05 ± 0.19	0.02 ± 0.004
Vespoidea	0.12 ± 0.02	**0.19 ± 0.07**	0.17 ± 0.04	0.34 ± 0.06
Lepidoptera	1.88 ± 0.08	1.66 ± 0.16	3.20 ± 0.39	4.52 ± 1.21
Odonata	**0.05 ± 0.01**	0.01 ± 0.01	**0.10 ± 0.03**	0
Orthoptera	0.34 ± 0.08	0.41 ± 0.10	0.43 ± 0.11	**0.97 ± 0.26**

intriguing that we found a switch in insect activity from the understorey to gaps in the last sampling period at the end of the dry season. The last two data points were from the onset of the rainy season.

In addition to strong seasonal biotic patterns, abiotic patterns may also explain the distinct patterns we found in insect activity between gaps and the understorey. Greater quantities of direct radiation in gaps can raise temperature and lower humidity. Although this pattern is consistent throughout the year, the hottest and driest conditions are reached in the dry season. In fact, the understorey during the dry season was hotter and drier than the lab clearing in the rainy season. A negative correlation between arthropod abundance and light in the dry season indicates that the lower activity in gaps could be a result of stressful abiotic factors. In comparison, we found no correlation in the rainy season, indicating that the higher activity in gaps is not a result of abiotic factors. Therefore, in the rainy season, abiotic conditions in gaps may have had negligible or positive effects on insect activity. In comparison, exposure to high temperatures and low humidity of gaps in the dry season negatively affected insects, resulting in lower activity.

Weekly fluctuations in arthropod captures in the G/U traps were similar to fluctuations in captures from the long-term traps. Thus, although the sample size was small for the G/U traps, we were able to detect patterns in arthropod activity that were characteristic of patterns found in the old-growth forest of the plateau.

There are several biases inherent in insect collections from Malaise traps. First, the visibility of the trap may vary under different light conditions and may depend on how clean the trap is. This may account for the differences in capture rates between the long-term traps and G/U traps. Second, the insects captured in the trap represent activity levels and not true abundances. For example, insects captured in gap traps can be inhabitants of gaps and visitors from the neighbouring understorey or the canopy. It is hard to distinguish between insects captured dispersing to or from the site, foraging in the site or passing through. Overall those captured in the trap were active in the site. Third, different taxonomic groups have different capture rates. For example, it would be expected that a predator would be more active searching for prey than a herbivore. In addition, we included taxa in which Malaise traps are not the most effective sampling method (Casson & Hodkinson 1991). Despite these caveats, malaise traps are a useful tool for comparing relative insect activity between two habitats (Hutcheson 1990). A previous study found that insect assemblages captured by Malaise traps were the least variable between sites than other sampling methods (Kitching *et al.* 2001). Thus, the differences found between these two habitats are especially significant.

The capture rates of the arthropod groups varied between seasons, habitat and forest age. For example, Ichneumonoidae were collected more in the understorey throughout the year, but there was no difference between

old and young forest. This is inconsistent with a study by Shapiro & Pickering (2000), which found a higher abundance in old-growth forests than in second-growth forests. They found the differences were especially pronounced in the dry season and concluded that Ichneumonoidae are particularly sensitive to changes in relative humidity. This explains the low capture rates of Ichneumonoidae in gaps. Another example is that phytophagous Coleoptera activity was higher in gaps than in the understorey. This may be a response to higher food resources in gaps. Higher capture rates of wood-boring Buprestidae in gaps may be due to adult dispersal from the dead wood of a fallen tree. Odonata were also found in gaps all year and rarely found in the understorey. This may be because the open space of the gap clearing and light are advantageous for visually detecting prey. Shelly (1982) found that the damselfly *Argia difficilis* preferred gaps and was more active all year than the shade-seeking counterpart *Heteragrion erythrogastrum*, which preferred the understorey and were not active during the dry season. The greater activity of the gap specialists could also explain the higher capture rates of Odonata in gaps.

In conclusion, although arthropod groups displayed differences in the relative abundance between habitats, season and forest type, there was an underlying pattern of higher activity in gaps during the rainy season and higher activity in the understorey during the dry season. This underlying pattern can be explained by the combination of food availability and abiotic conditions. Thus, the habitat heterogeneity may not only enhance diversity of arthropods, as has been seen for plants and birds (Schemske & Brokaw 1981, Schnitzer & Carson 2001), but may also allow seasonal shifts to accommodate pulses in food resources and periods of abiotic stress.

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