PROCEEDINGS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The devil to pay: a cost of mutualism with *Myrmelachista schumanni* ants in 'devil's gardens' is increased herbivory on *Duroia hirsuta* trees

Megan E Frederickson and Deborah M Gordon

Proc. R. Soc. B 2007 **274**, 1117-1123
doi: 10.1098/rspb.2006.0415

PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2007) **274**, 1117–1123
doi:10.1098/rspb.2006.0415

The devil to pay: a cost of mutualism with *Myrmelachista schumanni* ants in 'devil's gardens' is increased herbivory on *Duroia hirsuta* trees

Megan E. Frederickson* **and Deborah M. Gordon**

Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, USA

'Devil's gardens' are nearly pure stands of the myrmecophyte, *Duroia hirsuta*, that occur in Amazonian rainforests. Devil's gardens are created by *Myrmelachista schumanni* ants, which nest in *D. hirsuta* trees and kill other plants using formic acid as an herbicide. Here, we show that this ant–plant mutualism has an associated cost; by making devil's gardens, *M. schumanni* increases herbivory on *D. hirsuta.* We measured standing leaf herbivory on *D. hirsuta* trees and found that they sustain higher herbivory inside than outside devil's gardens. We also measured the rate of herbivory on nursery-grown *D. hirsuta* saplings planted inside and outside devil's gardens in ant-exclusion and control treatments. We found that when we excluded ants, herbivory on *D. hirsuta* was higher inside than outside devil's gardens. These results suggest that devil's gardens are a concentrated resource for herbivores. *Myrmelachista schumanni* workers defend *D. hirsuta* against herbivores, but do not fully counterbalance the high herbivore pressure in devil's gardens. We suggest that high herbivory may limit the spread of devil's gardens, possibly explaining why devil's gardens do not overrun Amazonian rainforests.

Keywords: ant–plant interactions; density dependence; diminishing returns; Janzen–Connell hypothesis; pure stands; resource concentration hypothesis

1. INTRODUCTION

What limits the growth of populations engaged in mutualism? Some factor must keep the growth of mutualistic populations under control else they would grow to be infinitely large (Heithaus *et al.* 1980; May 1981; Boucher *et al.* 1982). Current models of mutualism emphasize that mutualisms can be stabilized by diminishing returns to the mutualism as populations grow (Holland *et al.* 2002; Bronstein *et al.* 2003). These models propose that the costs and benefits of mutualism are density dependent, as has been demonstrated by a few empirical studies (Breton & Addicott 1992; Morales 2000; Bronstein 2001).

Recently, we examined the cost due to herbivory in the mutualism between the ant species, *Myrmelachista schumanni* Emery (Formicinae), and the plant species, *Duroia hirsuta* (Poeppig and Endl.) K. Schum (Rubiaceae). In the rainforests of the western Amazon, *M. schumanni* ants nest in the swollen, hollow stems (domatia) on *D. hirsuta. M. schumanni* creates large, nearly monospecific stands of *D. hirsuta* by killing other plants using formic acid, thereby promoting the growth and establishment of *D. hirsuta* trees (Frederickson *et al.* 2005). These stands are called *supaychacras* or 'devil's gardens' because an Amazonian legend tells that the stands are cultivated by an evil forest spirit. Here, we define a 'devil's garden' as three or more *M. schumanni*-occupied trees clustered together in an area that is largely devoid of other plants.

The mutualism between *M. schumanni* and *D. hirsuta* begins when a *M. schumanni* queen colonizes a single isolated *D. hirsuta* tree. The ants kill plants around the *D. hirsuta* tree and over time other *D. hirsuta* trees establish in the vegetation-free zone created by the ants. The ant colony expands to occupy these new *D. hirsuta* trees and clears the vegetation around them. Devil's gardens grow in this manner, sometimes reaching sizes of 600 trees or more. The density of *D. hirsuta* trees is 40 times higher inside than outside devil's gardens, and a single devil's garden can cover more than a thousand square meters (M. E. Frederickson 2004, unpublished work). Nonetheless, each devil's garden is tended by one polygynous colony of *M. schumanni* (M. E. Frederickson & D. M. Gordon 2007, unpublished manuscript). Since *M. schumanni* colonies have multiple queens, they are potentially immortal and can live for hundreds of years (Frederickson *et al.* 2005). These results raise the question: what limits the spread of devil's gardens?

Here, we investigate whether herbivory could create costs to the mutualism between *M. schumanni* and *D. hirsuta,* and thus potentially limit the growth of devil's gardens. In addition to killing encroaching vegetation around their host plants, *M. schumanni* workers also protect their host plants against herbivores, significantly reducing leaf herbivory in an ant-exclusion experiment (Frederickson 2005). In this way, *M. schumanni* behaves similarly to many other ant species that act as mutualists by reducing herbivory on plants in return for food or shelter (Bronstein 1998; Heil & McKey 2003). However, *D. hirsuta* trees occupied by *M. schumanni* often sustain high herbivore damage, despite the protection against herbivores provided by *M. schumanni* workers.

Outside devil's gardens, *D. hirsuta* trees are sometimes occupied by young *M. schumanni* colonies that spread over just one or two *D. hirsuta* trees. Alternatively, outside

---

*Author and address for correspondence: Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA (megan@post.harvard.edu).

Received 17 December 2006
Accepted 18 January 2007

devil's gardens, *D. hirsuta* trees can be occupied by another ant species, *Azteca depilis*, or they can be unoccupied. Like *M. schumanni*, *A. depilis* protects *D. hirsuta* against herbivores, but unlike *M. schumanni*, *A. depilis* does not kill encroaching vegetation to make devil's gardens (Frederickson 2005). As a result, one colony of *A. depilis* ants usually occupies only one *D. hirsuta* tree, while one colony of *M. schumanni* ants can occupy from one to several hundred *D. hirsuta* trees.

Previous work showed that herbivory is higher on *M. schumanni*-occupied *D. hirsuta* than on *A. depilis*-occupied *D. hirsuta* (Frederickson 2005). However, this study measured herbivory on *M. schumanni*-occupied *D. hirsuta* trees only in devil's gardens and thus could not separate the effect of having *M. schumanni* from the effect of growing in a devil's garden. Hence, two factors could explain the results of this study. Either *A. depilis* protects *D. hirsuta* against herbivores better than *M. schumanni*, or herbivores are more abundant inside than outside devil's gardens. Here, we test the latter hypothesis.

Owing to the activities of *M. schumanni*, devil's gardens are patches of very low plant diversity within an otherwise hyper-diverse Amazonian rainforest. Devil's gardens provide a rare opportunity to compare naturally occurring pure and mixed stands of plants in the Amazonian rainforest. Herbivore abundances are often higher in pure stands than in mixed stands; the evidence for this comes mostly from agricultural settings (Root 1973; Andow 1991). In tropical forests, a few studies have shown that herbivore pressure changes with conspecific plant density (Denslow 1980; Clark & Clark 1985; Blundell & Peart 1998; Sullivan 2003). A positive correlation between herbivore (or pathogen) pressure and conspecific plant density is thought to explain the spacing of tropical trees and even the extraordinary diversity of tropical forests (Janzen 1970; Connell 1971; Clark & Clark 1984; Peters 2003; Adler & Muller-Landau 2005). Here, we ask whether herbivore pressure on *D. hirsuta* is higher in large, monospecific stands of *D. hirsuta* than in the diverse rainforest understory. We also consider whether herbivory on *D. hirsuta* imposes a density-dependent cost to mutualism with *M. schumanni*. If so, this may explain why devil's gardens do not take over Amazonian rainforests.

2. MATERIAL AND METHODS

(a) *Study system and site*

This study was carried out at Madre Selva Biological Station ('MSBS', 3°37′14.3″ S, 72°14′48.4″ W, 90 m) on the Rio Orosa in Loreto, Peru. At MSBS, *D. hirsuta* accounts for 93% of the trees in devil's gardens; the other 7% of trees are almost all *Cordia nodosa* (Boraginaceae), another ant-plant in which *M. schumanni* sometimes nests (Frederickson 2005). The biological station manages 592 ha of land within a much larger area (hundreds of thousands of hectares) of mostly primary tropical rainforest. The forest at MSBS is a mixture of seasonally flooded and *terra firme* forest, dissected by small creeks. At MSBS, devil's gardens are common in the clay-soil *terra firme* forest. Elsewhere in the region, *M. schumanni* also makes devil's gardens comprised almost entirely *D. hirsuta* on nutrient-poor white sand soils (M. E. Frederickson 2004, personal observation).

Myrmelachista cultivates nearly pure stands of myrmecophytes (ant-plants) throughout the western Amazon. It is not clear whether the ants are all *M. schumanni* or several species of *Myrmelachista*. In different regions of the western Amazon, *Myrmelachista* cultivates different species of ant-plants. In the Sira Mountains of Peru, *Myrmelachista* makes nearly pure stands of *Tococa guianensis* (Melastomataceae; Morawetz *et al.* 1992). At Jatun Sacha Biological Station in Ecuador, *Myrmelachista* makes stands consisting of a mixture of *T. guianensis* and *Clidemia heterophylla* (Melastomataceae; Renner & Ricklefs 1998). In Madre de Dios, Peru, *Myrmelachista* makes nearly pure stands of *C. nodosa* (M. E. Frederickson 1999, personal observation). It is not known how *Myrmelachista* recognizes its host plants (Frederickson *et al.* 2005), nor why *Myrmelachista* cultivates only one or two species of myrmecophytes when many species of myrmecophytes co-occur locally.

At MSBS, annual rainfall averages 2400–2800 mm, and daily maximum and minimum temperatures average 31 and 23°C, respectively (Sombroek 2001; M. E. Frederickson 2003, personal observation). The climate of the region is often considered aseasonal, because no month of the year receives less than 100 mm of rain (Sombroek 2001; Vieira *et al.* 2004). However, rainfall is greater from November to April than from May to October in most, but not all years (Madigosky & Vatnick 2000; Frederickson 2006). In tropical forests with strongly seasonal climates, herbivore abundances are usually lowest in the dry season (Wolda 1978; Coley & Barone 1996). However, because the seasonality of climate at MSBS is so weak, there may be little seasonal change in herbivore abundances at this site.

(b) *Standing leaf herbivory*

We investigated the hypothesis that herbivory is higher in pure than in mixed stands of *D. hirsuta*. We measured standing leaf herbivory on: (i) *A. depilis*-occupied *D. hirsuta* trees, (ii) *M. schumanni*-occupied *D. hirsuta* trees growing singly or at most in pairs, and (iii) *M. schumanni*-occupied *D. hirsuta* trees growing in devil's gardens comprising at least three, but usually many more, *D. hirsuta* trees. The *D. hirsuta* trees in groups 1 and 2 were growing in mixed stands because they were surrounded by trees of many other species. In contrast, the *D. hirsuta* trees in group 3 were surrounded mostly by other *D. hirsuta* trees, and hence were growing in nearly pure stands.

Devil's gardens differ from the surrounding rainforest in more ways than just tree species richness. There is also less canopy cover, and therefore more light, inside than outside devil's gardens (Frederickson 2005). The light environment in devil's gardens might affect herbivory in devil's gardens, much as it does in tree fall gaps. Herbivory is usually higher in gaps than in the shady rainforest understory, largely because the light environment makes plants more productive in gaps (Coley 1983). We investigated whether *D. hirsuta* trees in devil's gardens, like trees in gaps, are more productive than trees in the rainforest understory by measuring the fraction of *D. hirsuta* producing young leaves inside and outside devil's gardens.

In 2002, we established a 4 ha plot at MSBS. The 4 ha plot was oriented along cardinal directions and divided into sixteen 50×50 m squares. In July 2002 and again in July 2003, each square was exhaustively searched for all domatia-bearing individuals of *D. hirsuta* by walking each square back and forth in a series of 2.5 m transects. We numbered and tagged each *D. hirsuta* plant we found. For each plant, we recorded: (i) which species of ant occupied the tree, if any, (ii) which devil's garden the tree was growing in, if any, and (iii) whether or not there were any young leaves on the plant.

In July 2003, we measured the standing level of leaf herbivory on 80 *D. hirsuta* trees in the 4 ha plot. We measured herbivory on all 17 *M. schumanni*-occupied *D. hirsuta* that were growing outside devil's gardens. Thirteen of these trees were growing singly; four were growing in pairs, in which case one *M. schumanni* colony occupied both the trees. We also measured herbivory on 42 *M. schumanni*-occupied *D. hirsuta* trees selected at random from among the 9, 11, 14, 15, 96 and 282 *D. hirsuta* growing in the six devil's gardens in the plot. In addition, we measured herbivory on 21 trees that we selected at random from among the 72 *A. depilis*-occupied *D. hirsuta* trees in the plot.

To measure standing leaf herbivory, we photographed five leaves on each tree using a digital camera. The lowermost five leaves for plants with mature leaves only, or the lowermost three mature leaves and two young leaves for plants bearing young leaves, were photographed against a white background attached to the camera at a fixed distance. The percentage of herbivory was measured by comparing the actual leaf area in an image to the area encompassed by a digital trace of the inferred leaf margin in the absence of herbivory (IMAGEJ v. 1.34s). We calculated the average standing leaf herbivory on each plant. Since per cent data form a binomial rather than a normal distribution, the average standing leaf herbivory was transformed using an arcsine square root transformation (Zar 1999). We used an ANOVA followed by Tukey–Kramer *post hoc* tests to compare standing leaf herbivory among *D. hirsuta* with *A. depilis*, *D. hirsuta* with *M. schumanni* outside devil's gardens and *D. hirsuta* with *M. schumanni* inside devil's gardens.

(c) *Ant-exclusion experiment*

In 2004–2005, we conducted an ant-exclusion experiment in 10 devil's gardens at MSBS. Since naturally occurring saplings growing inside and outside devil's gardens could differ systematically in nutritional quality or palatability to herbivores, nursery-grown saplings were used in this experiment. Forty *D. hirsuta* saplings were grown from seed to heights of 40–100 cm in a common nursery environment. The saplings were grown in a Lumite screen tent (Bioquip) to keep them free of ants. At the start of the experiment, all the *D. hirsuta* saplings had at least two domatia. Owing to the short duration of the experiment (two weeks), it is unlikely that plants acquired differences in nutritional quality or palatability during the experiment.

The experiment was conducted in August 2004 in seven devil's gardens and in July 2005 in three devil's gardens at MSBS, outside the 4 ha plot described previously. The size distribution and plant composition of these devil's gardens were similar in both years. The devil's gardens ranged in size from 4 to 119 *D. hirsuta* trees; both the largest and the smallest devil's gardens were used in 2005. Herbivory on *D. hirsuta* was evaluated in both the presence and the absence of ants. Two *D. hirsuta* saplings were planted at haphazardly chosen spots inside each devil's garden. To exclude ants from one of the *D. hirsuta* saplings, Tanglefoot insect barrier was applied over flagging tape wrapped around the base of the stem. Flagging tape was also wrapped around the other *D. hirsuta*, but no Tanglefoot was applied. At the same time, two *D. hirsuta* saplings, one treated with Tanglefoot and the other not treated, were planted 50 m outside each devil's garden, within primary rainforest. *Duroia hirsuta* saplings were randomly assigned to treatments.

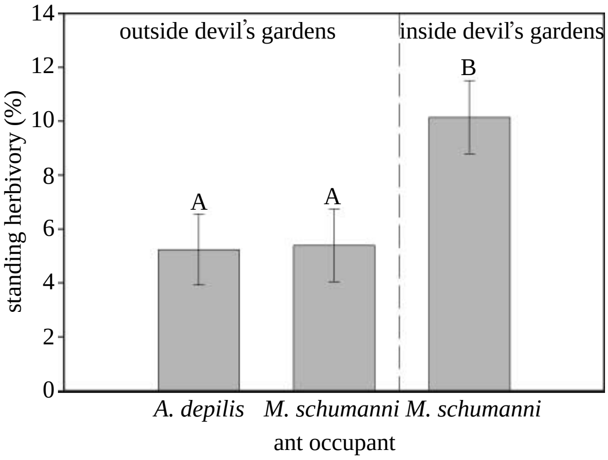

Figure 1. Standing level of leaf herbivory (±s.e.) on *D. hirsuta* with *A. depilis*, *D. hirsuta* with *M. schumanni* outside devil's gardens and *D. hirsuta* with *M. schumanni* inside devil's gardens. Different letters show statistically significant differences among treatments according to Tukey–Kramer *post hoc* tests ($p<0.05$).

Before planting, all of the leaves on each *D. hirsuta* sapling were inspected for herbivory. Damaged leaves were individually marked and photographed, again using a digital camera attached to a white background at a fixed distance. Two weeks after planting, saplings were inspected for the presence of ants and all of the leaves on each sapling were photographed. The percentage of herbivory was measured on all leaves as in §2*b*. The herbivory rate over the two weeks of the experiment was calculated by subtracting, for each leaf, the initial percentage of herbivory (zero for leaves that were whole at the time of planting) from the final percentage of herbivory. We did not count leaves that were entirely consumed over the course of the experiment; therefore, herbivory rates may be underestimates.

We calculated the average herbivory rate on each plant and transformed the average herbivory rate using an arcsine square root transformation. Data from three plants were excluded from the analysis because leaves on two plants were torn by spines during transportation, and the Tanglefoot barrier on one plant was breached by ants. Treatments were compared using an ANOVA followed by Tukey–Kramer *post hoc* tests. All statistical analyses were conducted in STATVIEW v. 5.0.1 (SAS Institute).

3. RESULTS

(a) *Standing leaf herbivory*

Standing leaf herbivory on *D. hirsuta* trees was significantly higher inside than outside devil's gardens (figure 1; ANOVA, $F_{2,77}=5.47$, $p=0.006$). Outside devil's gardens, there was no significant difference in standing leaf herbivory between *M. schumanni*-occupied and *A. depilis*-occupied *D. hirsuta* trees (figure 1). Hence, when a *M. schumanni* colony occupied only one or two *D. hirsuta* trees, these trees sustained no higher herbivory than *D. hirsuta* trees occupied by *A. depilis*. However, as the number of *D. hirsuta* trees occupied by a *M. schumanni* colony increased, so did herbivory on *D. hirsuta* trees (figure 2; $r^2=0.49$, $p=0.05$), such that *D. hirsuta* trees in the largest devil's garden (282 trees) sustained the most herbivory (figure 2; mean±s.e.: 13.2±2.8%).

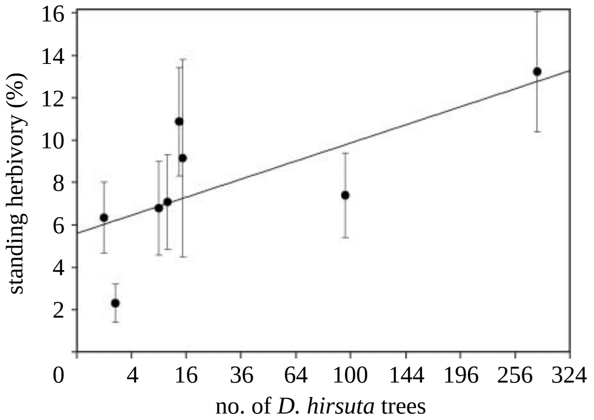

Figure 2. Standing level of leaf herbivory (±s.e.) on *M. schumanni*-occupied *D. hirsuta* plotted against the number of *D. hirsuta* trees occupied by the *M. schumanni* colony. The solid line is the regression relationship ($r^2=0.49$, $p=0.05$).

Table 1. Standing leaf herbivory (% ±s.e.) on young and mature leaves of *D. hirsuta*.

	outside devil's gardens	outside devil's gardens	inside devil's gardens
	A. depilis	*M. schumanni*	*M. schumanni*
mature leaves	5.1±1.3 ($n=21$)	6.2±1.4 ($n=17$)	9.7±1.4 ($n=42$)
young leaves	4.6±3.3 ($n=7$)	0.3±0.2 ($n=7$)	10.7±3.9 ($n=19$)
all leaves	5.2±1.3 ($n=21$)	5.4±1.4 ($n=17$)	10.1±1.4 ($n=42$)

Table 2. Percentage of *D. hirsuta* trees with young leaves.

	outside devil's gardens	inside devil's gardens
A. depilis	35% ($n=72$)	—
M. schumanni	53% ($n=17$)	38% ($n=412$)
no ants	42% ($n=76$)	44% ($n=50$)
overall	39% ($n=165$)	39% ($n=462$)

Levels of standing leaf herbivory were similar on young and mature leaves (table 1). There was one exception: herbivory was less on young than on mature leaves for *M. schumanni*-occupied *D. hirsuta* outside devil's gardens (table 1), although this was probably an artefact of small sample size. Young leaves on *D. hirsuta* trees were as frequent inside as outside devil's gardens. At the time when we measured standing herbivory, 7 out of 21 *A. depilis*-occupied *D. hirsuta* had young leaves, 7 out of 17 *M. schumanni*-occupied *D. hirsuta* outside devil's gardens had young leaves and 19 out of 42 *M. schumanni*-occupied *D. hirsuta* inside devil's gardens had young leaves ($\chi^2_2=0.819$, $p=0.664$). For all the *D. hirsuta* trees in the MSBS plot, the fraction of trees bearing young leaves was the same inside and outside devil's gardens (table 2).

(b) *Ant-exclusion experiment*

In the absence of ants, herbivory was significantly higher inside than outside devil's gardens (figure 3). The initial and final percentage of herbivory was measured on a total of 877 leaves on 37 plants. The rate of herbivory on *D. hirsuta* saplings varied according to treatment (figure 3; ANOVA, $F_{3,33}=4.04$, $p=0.015$). Ant-excluded *D. hirsuta* saplings planted inside devil's gardens sustained significantly higher herbivory (mean±s.e.: 0.119±0.048% per day) than *D. hirsuta* saplings planted outside devil's gardens in control (0.014±0.007% per day) and ant-exclusion (0.016±0.011% per day) treatments. *Duroia hirsuta* saplings planted inside devil's gardens and not subjected to an ant-exclusion treatment experienced intermediate rates of herbivory (0.044±0.016% per day) that were not significantly different from herbivory rates on saplings in the other treatments. There were no significant differences in the initial percentage of herbivory among treatments.

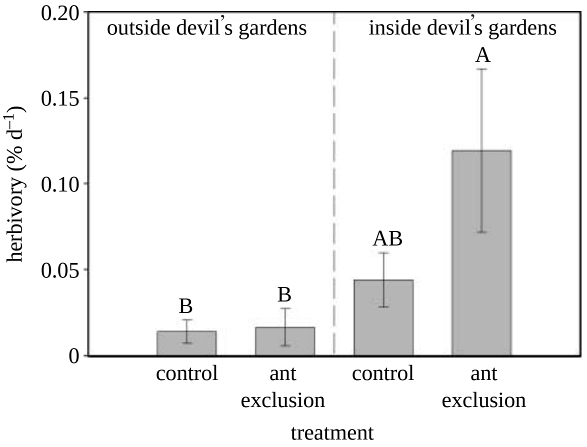

Figure 3. Herbivory rate per day (±s.e.) on *D. hirsuta* saplings planted outside devil's gardens, outside devil's gardens with ants excluded, inside devil's gardens and inside devil's gardens with ants excluded. Different letters show statistically significant differences among treatments according to Tukey–Kramer *post hoc* tests ($p<0.05$).

Tanglefoot was an effective barrier against ants during the experiment. Two weeks after planting, there were no ants present on *D. hirsuta* saplings treated with Tanglefoot, with one exception. On one plant, *M. schumanni* workers breached the Tanglefoot barrier; this plant was excluded in the data analysis. Two weeks after planting, *M. schumanni* workers were present in the domatia of all *D. hirsuta* saplings planted inside devil's gardens and not treated with Tanglefoot. Outside devil's gardens, none of the *D. hirsuta* saplings we planted were colonized by ants during the experiment.

4. DISCUSSION

By creating devil's gardens, *M. schumanni* increases herbivore pressure on its host plants. *Myrmelachista schumanni* benefits *D. hirsuta* by killing other plants, a behaviour which results in large, nearly pure stands of *D. hirsuta* (Frederickson *et al.* 2005). However, the same behaviour that benefits *D. hirsuta* trees also imposes a cost. There is higher herbivore pressure in these stands than elsewhere in the rainforest. High herbivory on *D. hirsuta* trees in devil's gardens occurs in spite of the protection against herbivory provided by *M. schumanni* ants, and is more probably a result of *D. hirsuta* density *per se* than of the light environment in devil's gardens.

Frederickson (2005) showed that *D. hirsuta* in devil's gardens with *M. schumanni* ants sustains three times higher herbivory than *D. hirsuta* outside devil's gardens with *A. depilis* ants, even though both ant species defend their host plants against herbivores. In that study, herbivory on *M. schumanni*-occupied *D. hirsuta* was measured only on plants growing in devil's gardens. Here, we found that outside devil's gardens, herbivory on *M. schumanni*-occupied *D. hirsuta* was similar to herbivory on *A. depilis*-occupied *D. hirsuta*, while herbivory on *M. schumanni*-occupied *D. hirsuta* in devil's gardens was much higher. We also found that herbivory increased with the number of *D. hirsuta* trees occupied by a *M. schumanni* colony. Hence, the size of the devil's garden where a *D. hirsuta* tree is located, and not the identity of the ant species occupying the *D. hirsuta* tree, appears to be the key to understanding high herbivory in devil's gardens.

The herbivore damage to *D. hirsuta* leaves in devil's gardens was substantial. Outside devil's gardens, herbivory on the *D. hirsuta* saplings we planted averaged 0.015% per day, somewhat less than the average herbivory rate for shade-tolerant plants in tropical forests (0.03% per day; Coley & Barone 1996). Inside devil's gardens, however, herbivory on *D. hirsuta* was 0.044% per day with *M. schumanni* ants and 0.119% per day without ants. Using these rates, we estimate that annual leaf area loss to herbivores in devil's gardens is 16% on *D. hirsuta* with *M. schumanni* ants and 43% on *D. hirsuta* without ants, compared with only 5.5% on *D. hirsuta* outside devil's gardens. The higher herbivory in devil's gardens is likely to be biologically significant. Smaller reductions in leaf area of 8–10% have been shown to reduce plant fitness, sometimes severely (Clark & Clark 1985; Marquis 1992; Coley & Barone 1996).

In the ant-exclusion experiment, the herbivory rate on plants with *M. schumanni* was not significantly different from the herbivory rate on plants in other treatments; in figure 3, there was no statistically significant difference between the control treatment inside devil's gardens and any of the other treatments. However, previous work showed that *M. schumanni* ants do protect plants against herbivores (Frederickson 2005). There are several possible reasons why there was no statistically significant difference in herbivory rate between plants with and without ants in devil's gardens, even though *M. schumanni* defends *D. hirsuta* against herbivores. After planting the *D. hirsuta* saplings in devil's gardens, it might have taken some time for *M. schumanni* ants to colonize the plants and begin defending them. Similarly, the time it took for ants to colonize plants might have varied from one devil's garden to another. Finally, the short duration of the experiment probably hindered our ability to detect an effect of *M. schumanni* ants on herbivory. These factors might have decreased the mean difference in herbivory rate between plants with and without ants in devil's gardens, and increased the variance in herbivory rate on plants with *M. schumanni* ants.

In other studies of ant–plant mutualisms, differences in herbivory on plants with different ant species have been linked to differences in protective efficacy among ant species (Bruna *et al.* 2004). Patrolling behaviour, level of aggression towards herbivores and recruitment to cues associated with herbivory can all differ among plant–ant species (Suarez *et al.* 1998; Gaume & McKey 1999; Lapola *et al.* 2003; Bruna *et al.* 2004; Tillberg 2004). However, the present study shows that higher herbivory on *M. schumanni*-occupied plants is the result of a greater herbivore load on these plants, rather than poorer protective efficacy of *M. schumanni* ants relative to *A. depilis*.

Ant-excluded *D. hirsuta* saplings planted inside devil's gardens sustained eight times the herbivory of ant-excluded *D. hirsuta* saplings planted outside devil's gardens. These saplings had no contact with ants during the course of the experiment, hence the difference in herbivory is a result of the environment surrounding the plants. It is possible that differences in abiotic factors inside and outside devil's gardens explain differences in herbivore loads. Frederickson (2005) showed that there is less canopy cover, and hence more light, inside than outside devil's gardens. In this way, devil's gardens are much like tree fall gaps. Gap specialists tend to sustain higher herbivory than shade-tolerant plants, in large part because there is more light and hence greater productivity in gaps (Coley 1983; Coley & Barone 1996). A similar reason could explain the high herbivory in devil's gardens, if *D. hirsuta* trees in devil's gardens are more productive because there is more light in devil's gardens than in the rainforest understory. However, our data suggest that *D. hirsuta* is no more productive inside than outside devil's gardens; *D. hirsuta* trees do not flush more young leaves inside than outside devil's gardens (table 2). Hence, it is unlikely that herbivores are attracted to devil's gardens because the trees in devil's gardens offer better forage (in the form of more young leaves), as a result of the increased light availability there. Nonetheless, it is possible that herbivores prefer the warmer, sunnier conditions in devil's gardens, even though the trees are not more productive there. However, studies of herbivore abundances in tropical forests have found the opposite, that herbivores often prefer the shade (Coley & Barone 1996; de la Fuente & Marquis 1999; Kersh & Fonseca 2005). Thus, it is unlikely that the light environment of devil's gardens is responsible for the higher herbivory there.

Alternatively, low plant diversity could explain high herbivory in devil's gardens. *Duroia hirsuta* saplings planted inside devil's gardens were surrounded by a nearly pure stand of *D. hirsuta*, while *D. hirsuta* saplings planted outside devil's gardens were surrounded by a diverse rainforest understory. Root (1973) gives two reasons to expect that herbivores will be more abundant on plants growing in pure stands than on plants growing in mixed stands. The 'resource concentration hypothesis' states that herbivores, especially specialist herbivores, will be more likely to find and remain in patches where their food plants are concentrated. The 'enemies hypothesis' states that mixed stands support a greater abundance of predators and parasites of herbivores than pure stands, keeping herbivore outbreaks in check in mixed stands. In a review of over 200 studies, mostly done in agricultural settings, Andow (1991) found ample empirical support for 'associational resistance', or reduced herbivore abundances in mixed stands relative to pure stands as a result of the resource concentration hypothesis, the enemies hypothesis or both. Thus, the low plant diversity of devil's gardens may explain high herbivore loads on plants in devil's gardens. Further research is needed to determine the identities of the herbivores in devil's gardens, and whether they specialize on *D. hirsuta*.

In tropical forests, support for 'associational resistance' comes from studies investigating the Janzen–Connell hypothesis, which seeks to explain the extraordinary biodiversity of the tropics (Janzen 1970; Connell 1971). The Janzen–Connell hypothesis proposes that the density-dependent actions of species-specific natural enemies (herbivores, pathogens or seed predators) can maintain high diversity in tropical forests by generating an advantage to being rare. The Janzen–Connell hypothesis has been hotly debated and has generated an enormous literature, but most empirical studies have supported the two main assumptions of the model. First, attacks by natural enemies are often density dependent (Denslow 1980; Clark & Clark 1985; Gilbert *et al.* 1994; Blundell & Peart 1998; Sullivan 2003). Second, density-dependent mortality is common in tropical forests (Harms *et al.* 2000; Peters 2003). Here, we provide a further example in which local plant dominance may be kept in check by herbivore pressure.

Herbivore pressure increases as devil's gardens grow. When a *M. schumanni* queen first colonizes a single *D. hirsuta* tree and begins to produce workers, that tree sustains no higher herbivory than a *D. hirsuta* tree with an *A. depilis* colony. As the *M. schumanni* colony grows, however, the workers clear an ever-expanding area of vegetation, gradually reducing canopy cover. This facilitates the growth and establishment of other *D. hirsuta* trees by reducing interspecific competition for resources, increasing the local density of *D. hirsuta*. However, the changing environment in devil's gardens also attracts more herbivores. Here, we found that herbivory increases as the number of *D. hirsuta* trees in a devil's garden increases (figure 2), although the scarcity of medium and large devil's gardens in our sample made it difficult to determine the exact form of this relationship, be it linear, or a threshold, etc. If as a devil's garden grows, the cost of increased herbivore pressure eventually outweighs the benefit to *D. hirsuta* of reduced competition, the growth of the devil's garden may stagnate. If this hypothesis is correct, density-dependent herbivory could be the mechanism by which devil's gardens are prevented from taking over the Amazon. An in-depth test of this hypothesis is in progress.

We thank B. Bohannan, R. Dirzo, E. A. Herre and one anonymous reviewer for their helpful comments on this manuscript. A. Coral, N. Sinojara, R. Arauco, C. Davis, A. Sunshine and E. Gillum provided invaluable assistance in the field. We also thank D. Graham and the Project Amazonas staff at Madre Selva Biological Station. The Instituto Nacional de Recursos Naturales (INRENA) provided permits to carry out this research in Peru. The Natural Science and Engineering Research Council of Canada (NSERC) and both the Center for Evolutionary Studies and the Field Studies Program in Biological Sciences at Stanford University provided financial support.

REFERENCES

Adler, F. R. & Muller-Landau, H. C. 2005 When do localized natural enemies increase species richness? *Ecol. Lett.* **8**, 438–447. (doi:10.1111/j.1461-0248.2005.00741.x)

Andow, D. A. 1991 Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* **36**, 561–586. (doi:10.1146/annurev.en.36.010191.003021)

Blundell, A. G. & Peart, D. R. 1998 Distance-dependence in herbivory and foliar condition for juvenile *Shorea* trees in Bornean dipterocarp rain forest. *Oecologia* **117**, 151–160. (doi:10.1007/s004420050643)

Boucher, D. H., James, S. & Keeler, K. H. 1982 The ecology of mutualism. *Annu. Rev. Ecol. Syst.* **13**, 315–347. (doi:10.1146/annurev.es.13.110182.001531)

Breton, L. M. & Addicott, J. F. 1992 Density-dependent mutualism in an ant–aphid interaction. *Ecology* **73**, 2175–2180. (doi:10.2307/1941465)

Bronstein, J. L. 1998 The contribution of ant–plant protection studies to our understanding of mutualism. *Biotropica* **30**, 150–161. (doi:10.1111/j.1744-7429.1998.tb00050.x)

Bronstein, J. L. 2001 The costs of mutualism. *Am. Zool.* **41**, 825–839. (doi:10.1668/0003-1569(2001)041[0825:TCOM]2.0.CO;2)

Bronstein, J. L., Wilson, W. G. & Morris, W. F. 2003 Ecological dynamics of mutualist/antagonist communities. *Am. Nat.* **162**, S24–S39. (doi:10.1086/378645)

Bruna, E. M., Lapola, D. M. & Vasconcelos, H. L. 2004 Interspecific variation in the defensive responses of obligate plant-ants: experimental tests and consequences for herbivory. *Oecologia* **138**, 558–565. (doi:10.1007/s00442-003-1455-5)

Clark, D. A. & Clark, D. B. 1984 Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen–Connell model. *Am. Nat.* **124**, 769–788. (doi:10.1086/284316)

Clark, D. B. & Clark, D. A. 1985 Seedling dynamics of a tropical tree: implications of herbivory and meristem damage. *Ecology* **66**, 1884–1892. (doi:10.2307/2937384)

Coley, P. D. 1983 Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* **53**, 209–234. (doi:10.2307/1942495)

Coley, P. D. & Barone, J. A. 1996 Herbivory and plant defences in tropical forests. *Annu. Rev. Ecol. Syst.* **27**, 305–335. (doi:10.1146/annurev.ecolsys.27.1.305)

Connell, J. H. 1971 On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of populations* (eds P. J. den Boer & G. R. Gradwell), pp. 298–312. Wageningen, The Netherlands: Centre for Agricultural Publishing and Documentation.

de la Fuente, M. A. S. & Marquis, R. J. 1999 The role of ant-tended extrafloral nectaries in the protection and benefit of a Neotropical rainforest tree. *Oecologia* **118**, 192–202. (doi:10.1007/s004420050718)

Denslow, J. S. 1980 Notes on the seedling ecology of a large-seeded species of Bombacaceae. *Biotropica* **12**, 220–222. (doi:10.2307/2387975)

Frederickson, M. E. 2005 Ant species confer different partner benefits on two neotropical myrmecophytes. *Oecologia* **143**, 387–395. (doi:10.1007/s00442-004-1817-7)

Frederickson, M. E. 2006 The reproductive phenology of an Amazonian ant species reflects the seasonal availability of its nest sites. *Oecologia* **149**, 418–427. (doi:10.1007/s00442-006-0460-x)

Frederickson, M. E., Greene, M. J. & Gordon, D. M. 2005 'Devil's gardens' bedevilled by ants. *Nature* **437**, 495–496. (doi:10.1038/437495a)

Gaume, L. & McKey, D. 1999 An ant–plant mutualism and its host-specific parasite: activity rhythms, young leaf patrolling, and effects on herbivores of two specialist plant-ants inhabiting the same myrmecophyte. *Oikos* **84**, 130–144.

Gilbert, G. S., Hubbell, S. P. & Foster, R. B. 1994 Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. *Oecologia* **98**, 100–108. (doi:10.1007/BF00326095)

Harms, K. E., Wright, S. J., Calderón, O., Hernández, A. & Herre, E. A. 2000 Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**, 493–496. (doi:10.1038/35006630)

Heil, M. & McKey, D. 2003 Protective ant–plant interactions as model systems in ecological and evolutionary research. *Annu. Rev. Ecol. Evol. Syst.* **34**, 425–453. (doi:10.1146/annurev.ecolsys.34.011802.132410)

Heithaus, E. R., Culver, D. C. & Beattie, A. J. 1980 Models of some ant–plant mutualisms. *Am. Nat.* **116**, 347–361. (doi:10.1086/283632)

Holland, J. N., DeAngelis, D. L. & Bronstein, J. L. 2002 Population dynamics and mutualism: functional responses of benefits and costs. *Am. Nat.* **159**, 231–244. (doi:10.1086/338510)

Janzen, D. H. 1970 Herbivores and the number of trees species in tropical forests. *Am. Nat.* **104**, 501–528. (doi:10.1086/282687)

Kersh, M. F. & Fonseca, C. R. 2005 Abiotic factors and the conditional outcome of an ant–plant mutualism. *Ecology* **86**, 2117–2126.

Lapola, D. M., Bruna, E. M. & Vasconcelos, H. L. 2003 Contrasting responses to induction cues by ants inhabiting *Maieta guianensis* (Melastomataceae). *Biotropica* **35**, 295–300.

Madigosky, S. R. & Vatnick, I. 2000 Microclimatic characteristics of a primary tropical Amazonian rain forest, ACEER, Iquitos, Peru. *Selbyana* **21**, 165–172.

Marquis, R. J. 1992 A bite is a bite is a bite? Constraints on response to folivory in *Piper arieianum* (Piperaceae). *Ecology* **73**, 143–152. (doi:10.2307/1938727)

May, R. M. 1981 Models for two interacting populations. In *Theoretical ecology: principles and applications* (ed. R. M. May), pp. 78–104, 2nd edn. Sunderland, MA: Sinauer Associates, Inc.

Morales, M. A. 2000 Mechanisms and density dependence of benefit in an ant-membracid mutualism. *Ecology* **81**, 482–489. (doi:10.2307/177441)

Morawetz, W., Henzl, M. & Wallnöfer, B. 1992 Tree killing by herbicide producing ants for the establishment of pure *Tococa occidentalis* populations in the Peruvian Amazon. *Biodivers. Conserv.* **1**, 19–33. (doi:10.1007/BF00700248)

Peters, H. A. 2003 Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecol. Lett.* **6**, 757–765. (doi:10.1046/j.1461-0248.2003.00492.x)

Renner, S. S. & Ricklefs, R. E. 1998 Herbicidal activity of domatia-inhabiting ants in patches of *Tococa guianensis* and *Clidemia heterophylla*. *Biotropica* **30**, 324–327. (doi:10.1111/j.1744-7429.1998.tb00067.x)

Root, R. B. 1973 Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* **43**, 95–124. (doi:10.2307/1942161)

Sombroek, W. 2001 Spatial and temporal patterns of Amazon rainfall: consequences for the planning of agricultural occupation and the protection of primary forests. *Ambio* **30**, 388–396. (doi:10.1639/0044-7447(2001)030[0388:SATPOA]2.0.CO;2)

Suarez, A. V., Do Moraes, C. & Ippolito, A. 1998 Defense of *Acacia collinsii* by an obligate and nonobligate ant species: the significance of encroaching vegetation. *Biotropica* **30**, 480–482. (doi:10.1111/j.1744-7429.1998.tb00083.x)

Sullivan, J. J. 2003 Density-dependent shoot-borer herbivory increases the age of first reproduction and mortality of neotropical tree saplings. *Oecologia* **136**, 96–106. (doi:10.1007/s00442-003-1233-4)

Tillberg, C. V. 2004 Friend or foe? A behavioral and stable isotopic investigation of an ant–plant symbiosis. *Oecologia* **140**, 506–515. (doi:10.1007/s00442-004-1601-8)

Vieira, S. *et al.* 2004 Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* **140**, 468–479. (doi:10.1007/s00442-004-1598-z)

Wolda, H. 1978 Seasonal fluctuations in rainfall, food and abundance of tropical insects. *J. Anim. Ecol.* **47**, 369–381. (doi:10.2307/3789)

Zar, J. H. 1999 *Biostatistical analysis*, 4th edn. Upper Saddle River, NJ: Prentice-Hall, Inc.