ABSTRACT

The diversity of mutualistic interactions influences many ecological components of community structure, including biodiversity and ecosystem stability. However, mutualistic interactions are not well resolved because of a historical bias toward examining antagonistic interactions. Here we examine both antagonistic and facilitative interactions between tropical plants and arthropods by characterizing the biotic interactions between a common myrmecophytic shrub, *Piper immutatum* Trel. (Piperaceae), the ants hosted by this plant, *Pheidole* sp. (Formicidae: Myrmicinae), and their associated communities of herbivorous and predatory arthropods. To determine if ant mutualists affect the altitudinal distribution of Neotropical myrmecophytes, *P. immutatum* interactions with arthropods were quantified across a tropical elevational gradient. *P. immutatum* was most abundant in lower montane forests (1000–1600 m asl) and disappeared above 1600 m asl, and colonies of *Pheidole* sp. inhabited 90 percent of the sampled plants. The myrmecophyte was then transplanted within and beyond its altitudinal range, excluding ants from half of the transplanted plants. Plant survival was affected primarily by elevation, with only 20 percent surviving above 1600 m asl. Ant exclusion did not significantly affect plant mortality. Nevertheless, ant colony size did affect both herbivory and nutrient availability for surviving *P. immutatum*, with nutrient availability having a stronger effect than ant herbivore defense on growth and biomass. This approach of studying the contributions of ant mutualisms across the myrmecophyte’s habitat range yields an improved picture of the role of mutualistic interactions in determining community structure.

Key words: elevation; mutualistic ants; myrmecophytes; nutrient procurement; plant defense.

ANT-PLANT INTERACTIONS ARE GEOGRAPHICALLY WIDESPREAD, common in many ecological communities and important in plant defense against herbivores. As such, spatial variation in plant–ant interactions can depend on the environmental and ecological context in which they occur (Holland et al. 2005). Obligate ant–plant mutualisms, which are uniquely tropical, comprise an important part of the diversity of resource–consumer interactions, especially in lowland wet forests. Facultative ant–plant mutualisms are even more widespread and also contribute significantly to interaction diversity. More than 40 angiosperm orders contain species producing ant attractants (Rico-Gray & Oliveira 2007). In a meta-analysis of terrestrial trophic cascades, ants were the main predator in 62 percent of studies, and exclusion of these predators significantly increased plant damage (Schmitz et al. 2000). Mutualisms are as important to community stability and diversity as any other multispecies interactions (Christian 2001, Hay et al. 2004, Savage & Peterson 2007, Bulleri et al. 2008), but greater attention to the mechanisms by which these mutualisms evolve and are maintained is necessary to understand the community role of mutualistic interaction diversity. For ant–plant mutualisms in particular, it is important to understand how specific interactions are linked to other species, such as herbivores or potential competitors (Holland et al. 2005). One way by which mutualistic interactions can affect populations and communities is via altering the acceptable habitat range of the mutualistic populations. Here we consider how ant mutualists might affect the altitudinal range of their host plants and examine the mechanisms by which ants enhance conditions for these plants.

Myrmecophytes are broadly defined as plants that host ant colonies in modified plant tissues that provide domatia or nesting sites (e.g., Janzen 1966; Letourneau 1983, 1998; Folgarait & Davidson 1994, 1995; Fiala et al. 1999). In most well-characterized plant–ant mutualistic interactions, ants act as predators of insect herbivores in exchange for extradermal nectar, food bodies, and shelter (Janzen 1966; Risch & Rickson 1981; Letourneau 1983, 1998; Fischer et al. 2002; Rico-Gray & Oliveira 2007). Myrmecotrophy, the potential ability of plants to absorb nutrients from debris piles of ant nests, is another benefit of housing ants (Benzing 1991, Sagers et al. 2000, Fischer et al. 2003, Rico-Gray & Oliveira 2007). Despite much variation in the nature of myrmecotrophic mutualisms, they usually occur under suboptimal survival conditions such as sites that are poor in nutrients (Rico-Gray & Oliveira 2007). Myrmecophytes that are also myrmecotrophs can receive...
both protective and nutritive benefits from their resident ants. As part of understanding the roles of mutualisms in affecting communities, we also explore the relative roles of these benefits.

The strength of plant–ant interactions is expected to depend on changes in the ant species, herbivores, environmental conditions, and array of ant/herbivore defenses used by the host plant (Agren & Schemske 1993, Gaume et al. 2005, Kersch & Fonseca 2005). For example, ant colony size, a measure of effectiveness of defense, and colony relocation are correlated with soil nutrient availability (Heil et al. 2001, 2002; McGlynn et al. 2003). As a result, plants in nutrient-rich soils, such as those of tropical montane soils, could harbor larger ant colonies that are more effective at protection than plants on poor soils, such as tropical lowland ultisols. On the other hand, the lower temperatures in the montane protection may favor nutrients procure-ments: (1) What are the indirect effects of elevation on interactions between P. immutatum and its ant, Pheidole, and associated herbivores? (2) Are ants benefiting P. immutatum by providing nutrients or by reducing herbivory (Fig. 1)? (3) Which environmental conditions, within and outside the plants’ elevational range, favor nutrient procurement vs. ant/ herbivore defense?

METHODS

STUDY SYSTEM.—Study sites were located in the northeastern Andes of Ecuador in the provinces of Napo and Sucumbios along an elevational gradient from the Amazonian lowland rain forest to the Andean paramo (200–3200 m asl). Temperature along this gradient drops linearly with elevation at a rate of approximately –0.5°C/200 m in elevation. Precipitation ranges from 3900 to 4500 mm/yr. The sampled area includes three mountain ranges: the Huacamayos ridge (0°40’ S, 77°44’ W; 1400–2000 m asl), the Sumaco ridge (0°37’ S, 77°50’ W; 400–2600 m asl) and

Sumaco, Huacamayos, and Reventador regions, as well as continuous lowland and mountainous rain forests, which are part of the Cayambe-Coca and Antisana Gran Sumaco natural reserves.

Piper immutatum is an understory shrub that ranges in height from 30 cm to 2 m and occurs in the eastern Andes from Bolivia to Colombia. Its altitudinal distribution in these mountains ranges from 325 to 1500 m asl (Tropicos, MOBOT, 2008). This tropical shrub hosts colonies of a single species of ant throughout its range: Pheidole sp. nov. (J. Longino, reference number JTL 174, 2008). This study exclusively includes observations and experiments involving this species of ant from P. immutatum. The stems are hollowed out by the ants, and the plants produce food bodies early in plant development (Tepe et al. 2009). This adaptation is known from other myrmecophytic Piper species that produce food bodies when ant colonies are present (Risch et al. 1977, Risch & Rickson 1981). Pheidole workers have been observed patrolling new leaves of P. immutatum and removing small eggs and early instar Eois herbivores from leaves. Based on observations of other Pheidole–Piper mutualism, we assumed that the number of queens inside the stem is correlated with ant colony size (Risch et al. 1977).

OBSERVATIONAL METHODS.—We pooled data from surveys of P. immutatum in 10 m diam vegetation plots (98 surveys in total). We sampled 7 ± 0.81 plots per 200-m interval along a gradient that ranged from 280 to 3200 m. The plots included three main altitudinal transects within the Cayambe-Coca and Antisana natural reserves: the Sumaco region (0°40’ S, 77°44’ W; 1400–2000 m asl), the Huacamayos ridge (0°37’ S, 77°50’ W; 400–2600 m asl) and

FIGURE 1. Hypothesized causal relationships between Piper immutatum biomass, Pheidole ant colony size, herbivory, and elevation. Solid lines indicate direct effects and dashed lines denote indirect effects; arrow heads indicate positive effects and bulleted heads denote negative effects; the width of the line is proportional to the hypothesized magnitude of the interaction.
areas surrounding Volcán Reventador and Cayambe-Coca (0°06′ S, 77°34′ W; 1000–3200 m asl). Inside each plot we tagged the base of all Piper plants present, and then harvested all of the leaves and stems of each individual plant leaving the root systems intact. We excavated the roots of all Piper plants and kept each individual in a separate bag, identified by plot number and plant number, and transported them to laboratories and rearing centers at Yanayacu Biological Station (2200 m asl) and Jatun Sacha (400 m asl). At the laboratory, each Piper plant was weighed and identified to morphospecies. We counted all leaves, measured the leaf area of three leaves per plant, estimated percent herbivory per leaf and carefully surveyed plants for interactions (i.e., herbivorous and predatory arthropods). When the plants were occupied by ants, we placed the ants into labeled vials with 75 percent ethanol. Each caterpillar found was assigned a unique number and reared to adult. Plant specimens were pressed, dried, and sent to the Herbario Nacional del Ecuador, where E. J. Tepe identified the Piper spp.; J. Miller at the American Museum of Natural History identified the adult moths; and the ants were sent to J. Longino for identification.

To estimate leaf quality, we collected three fully expanded young leaves of each plant inside each 10 m diam plot for a total of 12 plots for every 200 m in elevation within the Tena-Huacamayos mountain range. Leaves were oven-dried and ground, and nitrogen:carbon ratios were analyzed using combustion analysis at the Tulane University Coordinated Instrumentation Facility.

**TRANSPLANT EXPERIMENT.—** In order to understand the effect that foraging ants had on *P. immutatum* and to evaluate how elevation and ants influence plant growth, we performed a transplant experiment. We collected 120 *P. immutatum* cuttings (> 50 cm tall, 5 ± 0.11 leaves, each) from a border population located near 1400 m asl (0°40′96″ S, 77°48′27″ W) and transplanted in pots ten cuttings each to locations at 200 m elevational intervals from lowland Amazon forest (400 m asl) to high montane forest (2600 m asl, Table S1). Transplants at 1400 m asl, where all cuttings were obtained, were treated as control plants for elevation and transplant treatments. When the plants were occupied by ants, we placed the ants into labeled vials with 75 percent ethanol. Each caterpillar found was assigned a unique number and reared to adult. Plant specimens were pressed, dried, and sent to the Herbario Nacional del Ecuador, where E. J. Tepe identified the Piper spp.; J. Miller at the American Museum of Natural History identified the adult moths; and the ants were sent to J. Longino for identification.

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To evaluate the effects ants had on the surviving transplants; we grouped plants into three different categories depending on final ant colony size: No ants, < 50 ants, and > 50 ants. We did so to evaluate ant effects on plants because ant exclusions were followed by some ant colonization and some plants without exclusion treatment had no ant colonies. We used MANOVA analysis to evaluate the effects elevation and ant exclusion on net weight as well as the net production of new leaves and percent herbivory by specialists and generalists. The net biomass and new leaf production were measured as the difference between initial and final measurements (i.e., after 18 mo of being transplanted). We then used path analysis to test causal hypotheses about the effects of ants on: (1) final plant biomass (measured as wet plant weight); (2) plant growth (measured from new leaf production); and (3) herbivory (measured as the sum of generalist and specialist herbivory). All statistical analyses were conducted using SAS 9.1.

**STATISTICAL ANALYSIS.—** We calculated plant abundance, herbivory, and ant colony size across the elevational distribution of *P. immutatum* to determine the natural distribution of the ant–plant association. Mean plant abundance across the elevational gradient was calculated for each 200 m interval of elevational rise (corresponding to a −0.5 °C temperature change) as well as the correlation between elevation and the proportion of plants with ant colonies at 200 m intervals across the altitudinal gradient. We also utilized a logit model with plant mortality as a response variable and elevation and treatment as predictor variables. The gradient was divided into three strata: lowland rain forests (0–1000 m asl), low montane forest (1000–1600 m asl), and a third stratum where *P. immutatum* was transplanted outside its natural range (1600–2600 m; Table 1). Using these three elevation zones, we determined whether treatment or elevation predicted plant survival by the logit model, followed by two-dimensional contingency tables.

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**TABLE 1.** Elevational strata with the elevations and number of transplanted plants included at each stratum of the experiment.

<table>
<thead>
<tr>
<th>Elevation zones (m asl)</th>
<th>Specific elevations included (m asl)</th>
<th>Transplanted plants (n)</th>
<th>Transplanted plants surviving after 1.5 yr (final n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>400–1000</td>
<td>400, 600, 800, 1000</td>
<td>40</td>
<td>25</td>
</tr>
<tr>
<td>1100–1600</td>
<td>1200, 1400, 1600</td>
<td>30</td>
<td>15</td>
</tr>
<tr>
<td>1700–2600</td>
<td>1800, 2000, 2100, 2200, 2400, 2600</td>
<td>60</td>
<td>18</td>
</tr>
</tbody>
</table>
RESULTS

We surveyed Piper species in 98 plots and found that the genus Piper occurs up to 3200 m asl along our gradients, but P. immutatum is restricted to 400–1600 m asl, with the highest mean abundance at 1400 m asl. This species was absent from elevations above 1600 m asl (Fig. 2). We found a total of 300 individual P. immutatum plants. It was the most abundant Piper species in plots at riparian sites in lower montane forests (1000–1400 m). Ant colonies in this myrmecophytic plant ranged from 1–15 queens per plant, and Pheidole sp. nov. ants occurred on 90 ± 4 percent of the P. immutatum individuals collected. Piper immutatum plants from lowland forests had 47 percent more queens than the plants found in montane forests (t-test = 2.53, P < 0.01). In addition to Pheidole, we found ants in the subfamilies Ponerinae and Myrmecinae foraging on 5 percent of the lowland plants. Other natural enemies of P. immutatum herbivores were spiders (present on 17% of the sampled plants) and predatory beetles.

Mean leaf damage on P. immutatum across all elevations was consistent at 13.1 ± 0.6 percent, and there was no significant difference between the leaf damage inflicted by specialist (Eois spp.: Geometridae and beetles) vs. generalist herbivores (mainly Phasmatidae, and leafcutter ants 5.4 ± 1.2 and 6.9 ± 1.1, respectively; Wilks’ λ = 0.98, F = 0.05, P > 0.95). Fifty-seven percent of the myrmecophytes sampled hosted internally feeding herbivores (i.e., leaf miners and gall midges), while exposed feeders (arctiid, geometrid, and pyralid caterpillars, spittlebugs, tettigoniids, gryllids, and phasmatids) were found only on 14 percent of the sampled plants. The remaining plants had no herbivores or herbivore damage. We found three species of specialist caterpillars in the genus Eois (Larentiinae: Geometridae) feeding on P. immutatum: Eois nigricosta Prout., Eois fusicosta Dognin, and Eois sp. nov. 12.

Path analysis of observational data across the altitudinal range supported the causal hypothesis that increases in elevation cause decreases in: the abundance of P. immutatum plants, the mean leaf area per plant, and the colony size of resident ants; leaf nitrogen content increased with elevation (Fig. 3; model fit to the data: χ² = 0.073, df = 2, P = 0.96). In addition, ant colony size had a positive effect on leaf nitrogen, while leaf nitrogen had a negative effect on herbivory; thus, ant colony size had an indirect negative effect on herbivory, through increasing leaf nitrogen (Fig. 3).

Although half of the transplants died, the logit model showed no effect of treatment on plant mortality (χ² = 0.01, df = 2, P > 0.93). However, the transplanted plants had higher chances of dying at elevations outside of their natural range (greater than 1600 m; χ² = 6.49, df = 2, P < 0.01; Fig. 4). Survival at elevations ≥2200 m was 20 ± 14 percent. After 18 mo, the surviving plants that hosted large colonies of ants had higher leaf production and

FIGURE 2. Piper immutatum dominance (Mean ± SE). Percent of all Piper species that were P. immutatum in 10 m diam plots along the plant’s altitudinal range of distribution.

FIGURE 3. Path analysis examining relationships between variation of Piper immutatum biomass, herbivory, and ant colony size across a continuous elevational gradient. Solid lines indicate direct effects and dashed lines denote indirect effects. Arrow heads indicate positive effects and bulleted heads denote negative effects; the width of the line is proportional to the magnitude of the path coefficient. Only path coefficients greater or equal to 0.1 are included. P < 0.05 for all path coefficients.

FIGURE 4. Proportion of Piper immutatum transplants that died and survived at three elevation zones. **The elevations at which death/survival probabilities were significantly different based on a χ² contingency table (P < 0.01).
biomass. The initial biomass of surviving transplants did not differ among location or ant exclusion treatment ($F = 0.97$, $df = 43$, $P > 0.47$; Fig. 5A); after 18 mo, we found a significant effect of resident ants on plant biomass, especially at montane elevations outside the species’ natural range ($F = 4.11$, $df = 45$, $P < 0.001$; Fig. 5B).

After the first 3 mo, elevation had a significant effect on plant growth (measured as number of new leaves per plant) and there was a significant interaction with ant colony size ($F = 3.40$, $df = 46$, $P < 0.004$; Fig. 6A). The effect of ant colony size on plant growth, especially at elevations outside of the species’ natural range, was stronger after 18 mo ($F = 2.36$, $df = 45$, $P < 0.03$; Fig. 6B). We did not find effects of ant colony size or elevation on specialist herbivory after 3 and 18 mo ($F = 0.50$, $df = 41$, $P > 0.85$, and $F = 0.52$, $df = 46$, $P > 0.84$, respectively). In addition we did not find effects of ant colony size on generalist herbivory after 3 and 18 mo ($F = 0.43$, $df = 39$, $P > 0.9$, and $F = 1.30$, $df = 46$, $P > 0.26$, respectively).

For the surviving plants, after 18 mo the path model of ants protecting and facilitating nutrients to plants across the elevational gradient was a good fit to the data ($\chi^2 = 0.25$, $P = 0.96$; Fig. 7). Based on this model and path coefficients, elevation did not have a significant effect on ant colony size (path coefficient = $-0.02$), plant biomass ($-0.03$), plant growth (0.004), or herbivory (0.08). We found evidence indicating that ants’ facilitation of nutrients explained a large proportion of the variation in plant biomass (0.53) and growth (0.4). Notably, we found the ants also protect the plant from herbivores (0.19) and herbivores had a negative effect on plant biomass (0.11). However it does not cascade to an increase in plant biomass or growth (0.02).

**DISCUSSION**

Our study documented a robust ant–plant interaction, with ant colonies living inside 90 percent of *P. immutatum* individuals collected throughout the plant’s altitudinal range. Furthermore, our transplant experiment supports the hypothesis that the primary benefit of resident ants to *P. immutatum* was the nutrients that the ants provided to the host plant. This effect was more evident at sites outside the plants’ range where overall transplant survival rates were the lowest. Plant defense was a secondary benefit, mainly due to low herbivory rates suffered by plants with or without ants. It is clear that such mutualistic interactions are an important component of determining the range of multiple interacting species, because these myrmecophytes also supported specialist herbivores.
Path analysis of the observed *P. immutatum–Pheidole* interaction in the northeastern Andes suggests that ants may only have a weak positive indirect effect on plant biomass via reduction in herbivory (Fig. 3). When we eliminated the effect of elevation on ant colony size by transplanting cuttings with and without ants across the gradient, we found evidence that ants protect plants from herbivores. However, the strength of this interaction was weak because leaf herbivory was low for all the *P. immutatum* plants we transplanted. *Pheidole* ants are probably too small to be effective against large generalist predators but can be very effective at cleaning lepidopteran eggs and early instar caterpillars from leaf surfaces (Letourneau 2004). In the lowland forests in Costa Rica, this passive defense can result in trophic cascades when herbivory is high (e.g., Dyer & Letourneau 2003), but a meta analysis on trophic cascades revealed that biotic interactions that cause lower plant productivity are milder in cloud forests (Rodríguez-Castañeda 2009).

Several *Piper* species occur above 3200 m asl, yet the range of *P. immutatum* is limited to below 1600 m asl. In fact, both ants and plants disappeared at higher elevations, which are associated with sharp decreases in temperature that are known to reduce ant abundance (Novotny et al. 1999, O’Donnell & Kumar 2006, Sanders et al. 2007). Other studies have demonstrated that lower temperatures at high elevations are associated with smaller colony size in social insects (Purcell & Aviles 2007) and lower ant activity (Kaspari et al. 2000, O’Donnell et al. 2007). Such effects on ant populations are likely to be associated with lower interaction diversity, given the importance of ants in a variety of antagonistic and mutualistic interactions. Plant–ant interactions disappear from habitats with low temperatures and high precipitation (e.g., Koptur 1985, Rico-Gray et al. 1998). Nevertheless, the transplanted *P. immutatum* in our experiments showed increased performance at high elevations when ant colonies are present. We suggest the contribution of nutrients by *Pheidole* sp. nov. to *P. immutatum* have important effects on the plant’s survival and this effect may become more important when the plant is in a marginal habitat or acclimating to a new habitat where additional nutrient availability in the form of ant middens may be crucial. In combination with other studies demonstrating important roles of antagonistic interactions in determining plant distribution (e.g., Fine et al. 2006), our results indicate that characterizing and quantifying antagonistic and beneficial interactions will provide insight into community assemblages.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. Latitude, longitude and elevation of sampling. Plots were situated within the elevation range denoted for each site.

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