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Arboreal Ant Species Richness in Primary Forest, Secondary Forest, and Pasture Habitats of a Tropical Montane Landscape[1]

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ABSTRACT

Canopy invertebrates may reflect changes in tree structure and microhabitat that are brought about by human activities. We used the canopy fogging method to collect ants from tree crowns in primary forest, secondary forest, and pasture in a Neotropical cloud forest landscape. The total number of species collected was similar in primary forest (21) and pasture (20) habitats, but lower in secondary forest (9). Lower diversity in secondary forest was caused by lower species density (no. of species per sample). Rarefaction curves based on number of species occurrences suggest similar community species richness among the three habitats. This study has implications for conservation of tropical montane habitats in two ways. First, arboreal ant species density is reduced if secondary forest replaces primary forest, which increases the chance of extinction among rare species. Second, pasture trees may serve as repositories of primary forest ant communities due to similar tree structure.

RESUMEN

Los disturbios antropogénicos sobre la estructura de los árboles y microhabitat afectan la diversidad de invertebrados del dosel. Se usó la técnica de fumigación para colectar hormigas de las copas de los árboles en tres ambientes en un bosque nuboso Neotropical; bosque primario, bosque secundario, y pastizal. La cantidad total de especies colectadas fue similar entre el bosque primario (21) y el pastizal (20), pero menor en el bosque secundario (9). La baja riqueza en el bosque secundario fue consequencia de menor densidad de especies (cantidad de especies por muestra). Las curvas de rarefacción basada en presencia/ausencia de especies sugieren que la riqueza a nivel de la comunidad es similar entre los tres tipos de hábitat. Estos resultados puede aportar a la conservación de los hábitat tropicales nubosos de dos maneras. Primero, sugieren que la densidad de especies de hormigas es baja cuando un bosque primario es reemplazado por un bosque secundario. Segundo, los árboles grandes de pastizales pueden servir como refugios para las comunidades de hormigas, debido a que presentan similitud con la estructura de un bosque primario.

Key words: *ants; biodiversity; canopy; canopy fogging; cloud forest; Costa Rica; disturbed habitat; Formicidae; Monteverde; species richness.*

As concern mounts over the effects of climate change on global biodiversity (Parmesan & Yohe 2003), cloud forests have emerged as habitats of special concern due to high levels of endemism, insularity, and documented sensitivity to climate change (Pounds 1994, Pounds *et al.* 1999, Wheelwright 2000, Lawton *et al.* 2001, Nadkarni & Solano 2002). The assessment of differences in species richness and species composition in disturbed habitats may help predict ecosystem response to habitat fragmentation, biomass removal, or climate change (Torres 1984, Perfecto 1991, Alonso & Agosti 2000, Wheelwright 2000). Many studies of responses to disturbance have been carried out in the temperate zone or in lowland tropical habitats, but tropical cloud forests have been understudied in this regard (Estrada & Fernández 1999, Fisher & Robertson 2002).

Many invertebrate taxa respond rapidly to environmental change (Kremen 1992, Kremen *et al.* 1993). Large-scale disturbances in forests tend to have dramatic effects on arthropod diversity and abundance (Lawton *et al.* 1998, Floren & Linsenmair 1999, Wagner 2000). Arthropod communities vary across disturbance gradients in lowland

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forests and agricultural settings (Lawton *et al.* 1998, Goehring *et al.* 2002), but few studies (Estrada & Fernández 1999, Fisher & Robertson 2002) have documented arthropod response to disturbance in cloud forests. Recent work by Nadkarni and colleagues in a Neotropical cloud forest suggests that disturbance reduces arthropod diversity in epiphyte mats (Yanoviak & Nadkarni 2001), but has limited effects on spider assemblages (Yanoviak, Kragh *et al.* 2003). In this paper, we examine the arboreal ant community in a primary Neotropical cloud forest and compare it to nearby secondary forest and to relict trees that have been left in cleared pastures. This is the first study to contrast cloud forest arboreal ant communities in primary versus secondary forest and the first study to examine the ant fauna of relict pasture trees.

Ants are a useful group to study in regard to disturbance effects in tropical forests (Alonso 2000, Alonso & Agosti 2000). They dominate the biomass of arthropods (Fittkau & Klinge 1973, Erwin 1983, Tobin 1995) and are taxonomically diverse in these systems. Moreover, ants occupy various trophic levels and make substantial contributions to ecosystem processes (Hölldobler & Wilson 1990). Ant taxonomy has received more attention than the taxonomy of most other tropical insects (Bolton 1994), and species lists are available for some sites.

Ant abundance declines precipitously with elevation in tropical forests (Brown 1973). Cloud forest canopies appear devoid of ants because workers are rarely seen foraging on foliage surfaces; however, ants are abundant in and under the canopy soil and epiphyte mats of mid-elevation cloud forests (Longino & Nadkarni 1990, Yanoviak *et al.* 2004). Given their high abundance and frequent tending of coccoid Hemiptera, ants may have major ecosystem-level effects on nutrient cycling through the movement of plant nutrients from trees (Longino 2000, Davidson *et al.* 2003). Thus, ants have the potential for ecosystem-level importance in cloud forests even though their abundance is low relative to lowland forests.

Ant abundance and species richness vary across gradients of habitat disturbance (Perfecto & Vandermeer 1996, Vasconcelos 1999). There is a tendency for greater ant abundance in habitats more heavily affected by human activity or in the process of regeneration (Vasconcelos 1999). Decreased species richness among ground-foraging ants has been documented in more heavily disturbed habitats (Roth & Perfecto 1994, Lawton *et al.* 1998, Vasconcelos 1999). Other studies, however, have reported increased species richness of canopy ants (Lawton *et al.* 1998) and ground-foraging ants (Torres 1984, Fisher & Robertson 2002) in more disturbed habitats. Kalif (2001) found little variation in species richness but significant differences in community composition.

In Costa Rica, humans have deforested much of the once interconnected highland forests, leaving behind isolated patches of forest. The forests of the Monteverde area in the Cordillera de Tilarán are one of Costa Rica's largest relatively intact areas of highland forest. The landscape is characterized by a patchwork of primary and secondary forests, pastures containing relict primary forest trees, and developed areas (Harvey & Haber 1999, Wheelwright 2000). The objective of this study was to contrast canopy ant species richness and species composition among trees in primary forest, secondary forest, and pasture.

MATERIALS AND METHODS

This study was conducted in the research forest at the Monteverde Cloud Forest Preserve (MCFP) and adjacent pastures, Cordillera de Tilarán, Costa Rica (10°20′N, 84°45′W). These sites are located at 1400 to 1500 m elevation and fall within the lower montane wet forest life zone (Haber 2000). The region receives an average of 2500 mm of seasonal rainfall annually and substantial (>1000 mm) precipitation in the form of cloud moisture and wind-driven mist (Nadkarni & Wheelwright 2000). This study was conducted from 17 to 23 May 2001 during the wet season at Monteverde.

We collected ants from the crowns of five trees in primary forest, four trees in secondary forest, and five trees in a maintained pasture. In primary forest, we sampled one individual each of *Meliosma vernicosa, Pouteria fossicola,* and *Dussia macroprophyllata*, and two trees of *Ocotea tonduzii*. These trees have crowns ranging from 20 to 30 m above the ground and trunk diameters at breast height (DBH) of 60 to 90 cm. They are among the most common species in the MCFP (Nadkarni *et al.* 1995). In secondary forest, we sampled three *Conostegia oerstediana* and one *Hampea appendiculata*, both of which dominate large forest gaps and regenerating secondary forests (Haber 2000, Nadkarni & Wheelwright 2000). The secondary forest and the pasture were cleared 50–100 years ago. The sampled trees in secondary forest were smaller (35–45 cm DBH) and shorter (10–15 m crown height) than the primary forest trees. In the pasture setting, we collected ants from the crowns of five relict *O.*

tonduzii, which except for their more spreading crowns, were physically similar to the trees we sampled in primary forest. This species is common in both mature forest and pastures of the region (Nadkarni *et al.* 1995). Within each habitat type, focal trees were spaced 20–200 m apart, with greater clumping in the secondary forest and pasture due to the smaller area of the habitat. Trees in primary and secondary forest were at least 300 m from forest edges, although some were near small natural gaps. All three habitats (primary, secondary, and pasture) were within 3 km of each other.

We collected ants from the focal trees in each of the three habitats using the pyrethrin fogging technique as part of a larger project (Yanoviak, Nadkarni, *et al.* 2003). For each of 14 fogging events, we used a portable fogger to disperse a 1 percent pyrethrin formulation for three minutes. Nine ($N = 2$) or ten ($N = 12$) knockdown samples were collected from each tree in collection funnels placed beneath the crown. The funnels were inverted cones with a catchment area of 1 m^2. Fogging was conducted between 0700 and 1000 h, followed by a two-hour drop time. Additional details of the fogging method are described elsewhere (Stork & Hammond 1997, Gering & Crist 2000, Yanoviak, Nadkarni, *et al.* 2003).

Specimens from each funnel were stored separately in vials of alcohol until they were separated in the lab. Ants were extracted from samples and examined under a dissecting microscope; the species of worker ants were recorded. Voucher specimens were deposited in the collection of J. T. Longino (Evergreen State College).

Each fogged tree was treated as one replicate ($N = 5$ trees for primary forest and pasture, $N = 4$ for secondary forest). Two within-tree variables were examined: total species richness (no. of species) and total number of species occurrences (no. of funnels in which a species occurred summed across all species). The latter was used as an index of colony abundance and is considered superior to abundances of individuals for ecological studies of social insects (Longino *et al.* 2002) because individuals occur in colonies and thus exhibit extremely clumped distributions. Differences in mean values across the three habitats were evaluated with one-way ANOVAs and *posthoc* Tukey tests (SAS 2002).

Overall species richness in the habitats was compared by visual inspection of species accumulation curves calculated using EstimateS Version 5 (http://viceroy.eeb.uconn.edu/EstimateS). Species accumulation curves were derived from the means of 50 randomizations of sample order. Species accumulation curves were examined both as a function of number of fogged trees and as a function of number of species occurrences. The latter approach better depicts whole community diversity by reducing the effect of variation in species density (Gotelli & Colwell 2001, Longino *et al.* 2002).

RESULTS

We collected a total of 27 species in 13 genera (Table 1). Three subfamilies (Formicinae, Ponerinae, and Myrmecinae) were represented. The Dolichoderinae, a subfamily with many arboreal representatives in the lowlands, was conspicuously absent from the samples. This taxon was also absent from another canopy ant study in the MCFP (Longino & Nadkarni 1990).

Twenty-one species were collected from primary forest samples; 20 from pasture samples; and 9 from secondary forest samples (Table 1). Fogged trees in primary forest had a mean (SE) of 10.0 (2.6) species per tree; secondary forest trees had 3.8 (3.8) species; and pasture trees had 9.4 (3.7) species. Twelve species (44%) occurred in only one habitat type; 7 (26%) were found in two habitats; and 8 (30%) were found in all three habitats. Fourteen species were shared by primary forest and relict pasture trees; 9 by primary and secondary forest trees; and 8 by relict pasture and secondary forest trees. Of the 12 species found in only one habitat type, 6 were in primary forest and 6 were in pasture. No species was found exclusively in secondary forest (Table 1).

The three habitats showed significant differences in both species per tree ($F_{2, 11} = 8.02$, $P = 0.007$) and total species occurrences per tree ($F_{2, 11} = 13.74$, $P = 0.001$). A Tukey test applied to both analyses showed that these measures were significantly lower in secondary forest than in both primary forest and pasture, which did not differ from each other. Visual inspection of species accumulation curves revealed that between-tree patterns were the same as those within trees. Species accumulation rate was distinctly lower in secondary forest compared to primary forest and pasture when measured as a function of number of trees fogged (Fig. 1A); however, species accumulation rates were similar when measured as a function of species occurrences (Fig. 1B). Thus, the differences among habitats were due to differences in species density and not necessarily to differences in whole community species richness.

TABLE 1. *Ant species occurring in canopy fogging samples (this study) and Winkler samples of canopy leaf litter (Longino & Nadkarni 1990). Table entries are number of trees in which each species occurred. Columns are fogged primary forest trees (5 total), fogged secondary forest trees (4), fogged relict pasture trees (5), all fogged trees (14), and primary forest trees from which Winkler samples were taken (12). The table is sorted by descending frequency in total fogged trees.*

Species	Primary	Secondary	Pasture	Total	Winkler
Solenopsis JTL-002	5	4	5	14	7
Camponotus JTL-017	5	1	5	11	0
Camponotus JTL-010	4	0	5	9	0
Stenamma JTL-006	5	2	1	8	11
Pheidole diana	3	1	4	8	0
Brachymyrmex JTL-004	3	2	2	7	0
Myrmelachista JTL-011	2	1	3	6	2
Leptothorax JTL-007	2	0	4	6	0
Solenopsis JTL-001	3	1	1	5	10
Pheidole innupta	3	1	1	5	7
Procryptocerus batesi	2	0	3	5	0
Myrmelachista zeledoni	3	0	1	4	0
Pheidole exarata	0	0	4	4	0
Brachymyrmex JTL-003	1	2	0	3	4
Hypoponera JTL-003	1	0	1	2	6
Brachymyrmex JTL-005	0	0	2	2	0
Myrmelachista JTL-013	1	0	1	2	0
Procryptocerus mayri	2	0	0	2	0
Brachymyrmex JTL-002	1	0	0	1	5
Pheidole monteverdensis	1	0	0	1	2
Paratrechina JTL-004	0	0	1	1	1
Wasmannia auropunctata	0	0	1	1	1
Adelomyrmex silvestrii	0	0	1	1	0
Hypoponera opacior	1	0	0	1	0
Pachycondyla aenescens	1	0	0	1	0
Pheidole hizemops	1	0	0	1	0
Pheidole specularis	0	0	1	1	0
Adelomyrmex tristani	0	0	0	0	2
Eurhopalothrix JTL-001	0	0	0	0	2
Pheidole verricula	0	0	0	0	2
Pyramica microthrix	0	0	0	0	2
Pyramica myllorhapha	0	0	0	0	2
Solenopsis JTL-005	0	0	0	0	2
Hypoponera JTL-001	0	0	0	0	1
Pheidole bilimeki	0	0	0	0	1
Pheidole biolleyi	0	0	0	0	1
Pyramica brevicornis	0	0	0	0	1
Simopelta JTL-002	0	0	0	0	1
Stenamma schmidti	0	0	0	0	1

DISCUSSION

We provide the first fogging-based assessment of canopy ant diversity in habitats that are common in a tropical montane landscape. Our results showed that secondary forest canopies had dramatically lower species density compared to nearby primary forest trees and relict trees left in pastures. Species composition was similar across the three habitats.

Gotelli and Colwell (2001) made the important distinction between species richness and species density. Species richness is a whole-community parameter that is very difficult to measure and usually requires exhaustive inventory effort (Longino *et al.* 2002). Species density, in contrast, is the number of species per sampling unit, and is relatively easy to assess and compare among communities. The variation in species density that we observed may be explained by a number of factors. In general, ants are affected by habitat disturbance through changes in temperature (Kaspari *et al.* 2000), moisture (Kaspari & Weiser 2000), nest site availability (Young 1982, Wilson 1987), food supply, and microhabitat structure (Yanoviak *et al.* 2004). These variables act in synergy with com-

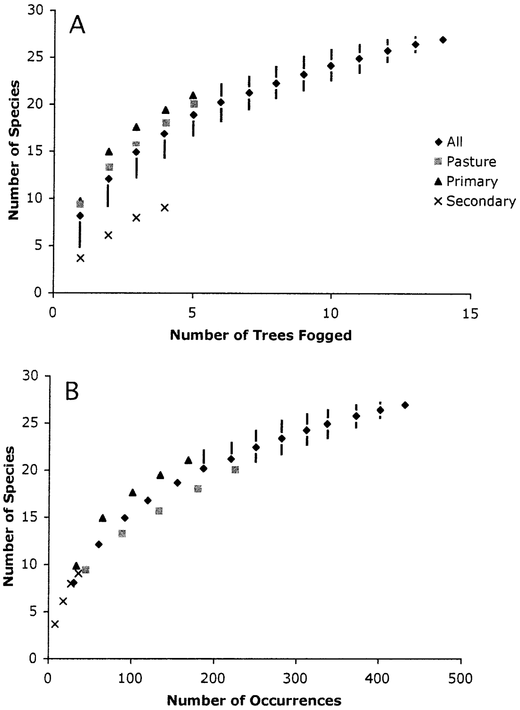

FIGURE 1. Species accumulation curves as a function of (a) number of trees fogged and (b) number of species occurrences in primary forest, secondary forest, relict pasture trees, and all three habitats combined. Curves are plotted from the means of 50 randomizations of sample accumulation order. Error bars on the combined curve are ± 1 SD (omitted from parts of the curve to avoid clutter).

petition and behavioral dominance (Andersen 2000). In our Monteverde study site, nest site availability was probably the most important factor. Tree and epiphyte diversity is lower in secondary forest than in primary forest (Ingram 2000, Merwin *et al.* 2003). Epiphyte mats, an important microhabitat for canopy ants, are far less developed in secondary forest (Yanoviak, Nadkarni *et al.* 2003, Yanoviak *et al.* 2004). In contrast, relict trees in pastures retain a dense, rich epiphyte community similar to that found in primary forest. Lack of thick epiphyte mats in secondary forest undoubtedly decreases nest site availability for many ant species.

Depressed species density may be caused by an overall lower abundance of ants or by the selective decrease in abundance of particular species. The latter appears to be the case in our study. Ants in general were not rare in second-growth forest. A species of small *Solenopsis* was very abundant in all habitats. This species has colonies scattered under thin patches of epiphytes and in small pieces of dead wood (Longino 2000). In contrast, other species of ants, in particular larger ants in the genera *Camponotus* and *Procryptocerus*, did appear to have much lower density in second-growth forest. These larger ants require thicker clumps of epiphytes or larger pieces of dead wood.

Primary forest and pasture habitats also overlapped in tree species, with two of the five primary forest trees and all of the pasture trees being *O. tonduzii*. Thus, similarities in ant communities could also have been caused by tree species effects. This is unlikely because (1) species accumulation curves comparing *O. tonduzii* to other tree species in primary forest were largely overlapping and (2) other studies of rain forest arboreal ant communities have not shown strong tree species effects (Longino & Colwell 1997).

The use of different sampling methods in the same forest revealed biases inherent to each method. Longino and Nadkarni (1990) sampled canopy ants in the same MCFP site as this study. They extracted arthropods from single Winkler samples of sifted canopy epiphytes and humus in each of 12 primary forest trees. When compared with the fogging results reported here, 16 species were obtained only by fogging, 12 species only by Winkler samples, and 11 species were obtained by both methods (Table 1). Some of the lack of overlap is due to rarity. But among the more abundant species, some predictable biases occur. Fogging is much better at capturing stem and twig nesting groups such as *Camponotus*, *Procryptocerus*, *Leptothorax*, and *Brachymyrmex* that are likely to be found foraging on foliage. Fogging obtains taxa that inhabit canopy humus less efficiently than Winkler sifting. Winkler sifting captured small, slow-moving ants in the genera *Pyramica* and *Eurhopalothrix*, and these were completely lacking from the fogging samples. *Pheidole*, a hyperdiverse genus that contains both stem-nesting and soil-nesting species, had some species preferentially sampled by fogging and some preferentially sampled by litter sifting. Because the volume of canopy humus is much higher in primary forest trees and relict pasture trees than in secondary forest trees, it is likely that species density differences observed in this fogging study would have been even greater if arthropod extraction from canopy humus were carried out.

Our results have implications for conservation of cloud forest biodiversity. The lower species density in second-growth forest may cause higher rates of extinction given equal habitat area. A much larger area of second-growth forest would be needed to provide the same species richness as a small patch of primary forest.

Farmers and other land managers should be encouraged to leave and maintain individual relict trees in pasture to preserve these repositories of primary forest canopy ant biodiversity. Many forest-dwelling ants appear to have low tolerance to high temperature (Torres 1984), allowing species better adapted to open areas to become dominant after logging (Perfecto & Vandermeer 1996, Kalif 2001). The relative similarity between primary forest and pasture relict tree canopy ant communities indicates that individual tree crowns may maintain microhabitat and structural characteristics needed for primary forest ants, despite the greater exposure to sunlight. This effect of serving as a repository for canopy ant (and perhaps other invertebrate) biodiversity will last only as long as the individual trees remain standing. These "living dead" trees (*sensu* Janzen 1986) that are relicts from primary forest could serve as a colonization source if forest were to grow up around them. Relict trees in secondary forest may play a similar role.

Given the proximity of habitats in our study, it is not clear if populations of species, especially those with low densities, are self-sustaining in second-growth forest and relict pasture trees. They may be the result of continual or periodic immigration from nearby primary forest. Longer-term data are needed to resolve this problem, and would be a useful extension of the work reported here.

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LITERATURE CITED

Alonso, L. E. 2000. Ants as indicators of diversity. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 80–88. Smithsonian Institution Press, Washington, DC.

———, and D. Agosti. 2000. Biodiversity studies, monitoring, and ants: An overview. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 1–8. Smithsonian Institution Press, Washington, DC.

Andersen, A. N. 2000. A global ecology of rainforest ants: Functional groups in relation to environmental stress and disturbance. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 25–24. Smithsonian Institution Press, Washington, DC.

Bolton, B. 1994. Identification guide to the ant genera of the world. Harvard University Press, Cambridge, Massachusetts.

Brown, W. L., Jr. 1973. A comparison of the Hylean and Congo–West African rainforest ant faunas. *In* B. J. Meggers, E. S. Ayensu, and W. D. Duckworth (Eds.). Tropical forest ecosystems in Africa and South America: A comparative review, pp. 161–185. Smithsonian Institution Press, Washington, DC.

Davidson, D. W., S. C. Cook, R. R. Snelling, and T. H. Chua. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. Science 300: 969–972.

Erwin, T. L. 1983. Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. *In* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (Eds.). Tropical rain forest: Ecology and management, pp. 59–75. Blackwell, Oxford, England.

Estrada, M. C., and F. Fernández C. 1999. Diversidad de hormigas (Hymenoptera: Formicidae) en un gradiente sucesional del bosque nublado (Nariño, Colombia). Rev. Biol. Trop. 47: 189–201.

Fisher, B. L., and H. Robertson. 2002. Comparison and origin of forest and grassland ant assemblages in the high plateau of Madagascar. Biotropica 34: 155–167.

Fittkau, E. J., and H. Klinge. 1973. On biomass and trophic structure of the Central Amazonian rain forest ecosystem. Biotropica 5: 2–14.

Floren, A., and K. E. Linsenmair. 1999. Changes in arboreal arthropod communities along a disturbance gradient. Selbyana 20: 284–289.

Gering, J. C., and T. O. Crist. 2000. Patterns of beetle (Coleoptera) diversity in crowns of representative tree species in an old-growth temperate deciduous forest. Selbyana 21: 38–47.

Goehring, D. M., G. C. Daily, and C. H. Sekercioglu. 2002. Distribution of ground-dwelling arthropods in tropical countryside habitats. J. Insect Conserv. 6: 83–91.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4: 379–391.

Haber, W. A. 2000. Plants and vegetation. *In* N. M. Nadkarni and N. T. Wheelwright (Eds.). Monteverde: Ecology and conservation of a tropical cloud forest, pp. 39–70. Oxford University Press, New York, New York.

Harvey, C. A., and W. A. Haber. 1999. Remnant trees and the conservation of biodiversity in Costa Rican pastures. Agrof. Syst. 44: 37–68.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, Massachusetts.

Ingram, S. W. 2000. Epiphytes. *In* N. M. Nadkarni and N. T. Wheelwright (Eds.). Monteverde: Ecology and conservation of a tropical montane forest, pp. 72–73. Oxford University Press, New York, New York.

Janzen, D. H. 1986. The future of tropical ecology. Ann. Rev. Ecol. Syst. 17: 305–324.

Kalif, K. A. B. 2001. The effect of logging on the ground-foraging ant community in Eastern Amazonia. Stud. Neotrop. Fauna Environ. 36: 215–219.

Kaspari, M., L. Alonso and S. O'Donnell. 2000. Three energy variables predict ant abundance at a geographical scale. Proc. R. Soc. Lond. B 267: 485–489.

Kaspari, M., and M. Weiser. 2000. Ant activity along moisture gradients in a Neotropical forest. Biotropica 32: 703–711.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. Ecol. Appl. 2: 203–217.

———, R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: Their use in conservation planning. Conserv. Biol. 7: 796–808.

Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391: 72–76.

Lawton, R. O., U. S. Nair, R. A. Pielke Sr., and R. M. Welch. 2001. Climatic impact of lowland deforestation on nearby montane cloud forests. Science 294: 584–587.

Longino, J. T. 2000. The ants of Monteverde. *In* N. M. Nadkarni and N. T. Wheelwright (Eds.). Monteverde: Ecology and conservation of a tropical cloud forest, pp. 132–136. Oxford University Press, New York, New York.

———, J. Coddington, and R. K. Colwell. 2002. The ant fauna of a tropical rain forest: Estimating species richness three different ways. Ecology 83: 689–702.

———, and R. K. Colwell. 1997. Biodiversity assessment using structured inventory: Capturing the ant fauna of a tropical rain forest. Ecol. Appl. 7: 1263–1277.

———, and M. Nadkarni. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a Neotropical montane forest. Psyche 97: 81–93.

Merwin, M., S. Rentmeester, and N. M. Nadkarni. 2003. The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. Biotropica 35: 37–47.

Nadkarni, N. M., T. Matelson, and W. Haber. 1995. Structural characteristics and floristic composition of a Neotropical cloud forest, Monteverde, Costa Rica. J. Trop. Ecol. 11: 481–495.

———, and R. Solano. 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: An experimental approach. Oecologia 131: 580–584.

———, and N. T. Wheelwright (Eds.). 2000. Monteverde: Ecology and conservation of a tropical cloud forest. Oxford University Press, New York, New York.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.

Perfecto, I. 1991. Dynamics of *Solenopsis geminata* in a tropical fallow field after ploughing. Oikos 62: 139–144.

———, and R. Vandermeer. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. Oecologia 108: 577–582.

Pounds, J. A. 1994. Amphibian declines and climate disturbance: The case of the golden toad and the harlequin frog. Conserv. Biol. 8: 72–85.

———, M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature 398: 611–615.

Roth, D. S., and I. Perfecto. 1994. The effects of management systems on ground-foraging ant diversity in Costa Rica. Ecol. Appl. 4: 423–436.

SAS. 2002. SAS/STAT user's guide, version 9. SAS Institute Inc., Cary, North Carolina.

Stork, N. E., and P. M. Hammond. 1997. Sampling arthropods from tree-crowns by fogging with knockdown insecticides: Lessons from studies of oak tree beetle assemblages in Richmond Park (UK). *In* N. E. Stork, J. Adis, and R. K. Didham (Eds.). Canopy arthropods, pp. 3–26. Chapman and Hall, London, England.

Tobin, J. E. 1995. Ecology and diversity of tropical forest canopy ants. *In* M. D. Lowman and N. M. Nadkarni (Eds.). Forest canopies, pp. 129–143. Academic Press, San Diego, California.

Torres, J. A. 1984. Diversity and distribution of ant communities in Puerto Rico. Biotropica 16: 296–303.

Vasconcelos, H. L. 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in Central Amazonia. Biodiv. Conserv. 8: 409–420.

Wagner, T. 2000. Influence of forest type and tree species on canopy-dwelling beetles in Budongo Forest, Uganda. Biotropica 32: 502–514.

Wheelwright, N. T. 2000. Conservation biology. *In* N. M. Nadkarni and N. T. Wheelwright (Eds.). Monteverde: Ecology and conservation of a tropical cloud forest, pp. 419–453. Oxford University Press, New York, New York.

Wilson, E. O. 1987. The arboreal ant fauna of Peruvian Amazon forests: A first assessment. Biotropica 19: 245–251.

Yanoviak, S. P., G. Kragh, and N. M. Nadkarni. 2003. Spider assemblages in Costa Rican cloud forests: Effects of forest level and forest age. Stud. Neotrop. Fauna Environ. 38: 145–154.

———, and N. M. Nadkarni. 2001. Arthropod diversity in epiphytic bryophytes of a Neotropical cloud forest. *In* K. N. Ganeshaiah, R. U. Shaanker, and K. S. Bawa (Eds.). Tropical ecosystems: Structure, diversity, and human welfare. Proceedings of the International Conference on Tropical Ecosystems—Structure, Diversity, and Human Welfare: 15–18 July 2001, Bangalore, pp. 416–419. Science Publishers, Enfield, New Hampshire.

———, N. M. Nadkarni, and J. C. Gering. 2003. Arthropods in epiphytes: A diversity component that is not effectively sampled by canopy fogging. Biodiv. Conserv. 12: 731–741.

———, H. Smith, and N. M. Nadkarni. 2004. Arthropod diversity in vegetative vs. humic portions of epiphyte mats in a Neotropical cloud forest. Pedobiologia 48: 51–58.

Young, A. M. 1982. Population biology of tropical insects. Plenum Press, New York.