

Effects of Treefall Gap Disturbances on Ant Assemblages in a Tropical Montane Cloud Forest

Margaret Patrick¹, David Fowler¹, Robert R. Dunn², and Nathan J. Sanders^{1,3}

¹ Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 3996, U.S.A.

² Department of Biology, North Carolina State University, Raleigh, NC 27695, U.S.A.

ABSTRACT

The study of gap dynamics and the effects of gaps on diversity has been at the center of tropical ecology for decades. While most studies have focused on the responses of plant species and communities to gap formation, in this study, we consider the effects of treefall gap disturbances on leaf litter ant assemblages in a Neotropical montane cloud forest. We sampled leaf litter ant assemblages and estimated a suite of abiotic parameters in 12 large (>80-m²) treefall gaps across a chronosequence and in 12 paired adjacent intact forest sites in the Monteverde Cloud Forest Preserve in Costa Rica. No species were more common in gaps than in intact forests, and in fact, species that were common in gaps were also among the most common in forests. The Chao2 estimate of species richness, however, was higher in gap sites than in intact forest sites. In addition, ant assemblages in gap sites did not become more similar to those in adjacent intact sites as gaps aged. In contrast to other studies, our work demonstrates that ant assemblages in the Monteverde Cloud Forest Preserve are weakly affected by the formation of treefall gaps. Together, these results indicate that treefall gap dynamics probably play little role in promoting ant diversity at more regional scales, or coexistence among species at more local scales.

Key words: ants; chronosequence; cloud forest; Costa Rica; disturbance; Monteverde; treefall gaps.

TREEFALL GAPS ARE THE MOST FREQUENT small-scale natural disturbances in many temperate and tropical forest ecosystems (Pickett & White 1985) and have long been thought to play a role in the maintenance of diversity (Strong 1977, Brokaw 1996, Hubbell *et al.* 1999, Schnitzer & Carson 2001). Initially, treefall gaps create high light environments on the forest floor and provide opportunities for plant species with high light requirements to establish and persist in mature forest stands, thereby increasing landscape-level diversity (Schnitzer & Carson 2001). Although treefall gaps also have the potential to influence the dynamics of animal communities, the response of animal communities to treefall gap disturbances has not been as well studied as the responses of plant communities (although see Schemske & Brokaw 1981, Shelly 1988, Alvarez & Willig 1993, Feener & Schupp 1998, Beck *et al.* 2004).

Most studies that examine community-level responses to gap formation have been snapshot studies. Such studies usually compare assemblages in young (<2 yr old) treefall gaps to assemblages in intact forests and ignore whether treefall gap assemblages might change as gaps close. The only way to study the temporal dynamics of gap assemblages, other than sampling the same gap assemblages over many years, is to take advantage of a chronosequence of treefall gaps of varying ages, substituting space for time (Fukami & Wardle 2005, Palladini *et al.* 2007). Such a chronosequence approach can help to determine the extent to which age-related changes in gaps lead to changes in the abiotic conditions on the forest floor and associated changes in plant and animal assemblages (Dunn 2004, Palladini *et al.* 2007).

Our goal in this study was to examine the effects of treefall gaps on leaf litter ant assemblages. Ants make up a substantial portion of eukaryotic biomass and diversity in the leaf litter of tropical forests. Moreover, disturbance (Kaspari 1996a, Campos *et al.* 2007) and microclimate (Kaspari & Weiser 2000) can strongly affect the structure of leaf litter ant assemblages. Herein, we compared ant assemblages in gaps of different ages to ant assemblages in adjacent intact forests in a Neotropical montane cloud forest and asked a series of inter-related questions: (1) Are particular species more common in gaps than in intact forests, and do species richness and assemblage composition of leaf litter ants differ between treefall gaps and adjacent intact forests? (2) Do leaf litter ant assemblages become more similar to the assemblages in adjacent, intact forests as gaps age? (3) What abiotic and biotic factors are correlated with ant species richness, and does the relative importance of these factors differ between gap and intact forest sites. To address these questions, we sampled leaf litter ant assemblages, and measured a suite of abiotic parameters in 12 large (>80 m²) treefall gaps across a chronosequence (<1 yr to > 12 yr old) and in paired, adjacent intact forest sites at Monteverde Cloud Forest Preserve (MFCP) in Costa Rica.

METHODS

STUDY SITE.—We carried out this research in the MFCP in western central Costa Rica on the crest of the Cordillera de Tilarán. The study site is located in a 12-ha watershed on the SE side of the summit of Cerro de la Centinelas (10°12' N, 84°42' W) (Lawton & Putz 1988) at ~1500 m elevation. Annual rainfall near the MFCP averages 2450 mm/yr, although actual precipitation is

Received 9 June 2011; revision accepted 18 September 2011.

³Corresponding author; e-mail: nsanders@utk.edu

estimated to be higher (>3000 mm/yr) due to condensation that forms on the vegetation when clouds and mist are present (Clark *et al.* 1998). We limited our sampling to leeward slopes and protected ravines that comprise the majority of the 12-ha watershed to reduce the effect of environmental factors, such as wind-exposure, that are not associated with gap or forest stand age.

STUDY DESIGN.—Since 1982, treefall gaps in the 12-ha watershed have been surveyed yearly by Lawton and colleagues (Lawton & Putz 1988, Lawton 1990, Daniels & Lawton 1991). During this annual census, treefall gaps are identified according to Brokaw's (1982) definition of a gap as 'a vertical hole in the forest, which extends through the canopy to within 2 m of the forest floor'. We sampled 12 pairs of gap and adjacent intact forest sites, during the wet season, from 1 June 2007 to 31 July 2007. The gaps were between 80 m² and 100 m² and comprised a chronosequence from less than 1 yr old to more than 12 yr old (Appendix S1). The paired intact sites were located ~25 m from the gap edge in a randomly chosen direction, and were at least 25 m from any other gap.

ABIOTIC VARIABLES.—In the center of each paired gap and intact forest plot, we established a 4 × 4 grid of 16 locations 2 m apart to record a suite of abiotic variables—insolation, leaf litter temperature, and soil moisture—to examine whether any of these factors was related to ant species richness. We estimated insolation (Global Site Factor [GSF]) by taking hemispherical photographs in the middle of each gap and intact site using a Nikon 5400 camera with a fish-eye lens under uniform conditions (overcast sky between 0900–1400 h). The camera was leveled and oriented to magnetic north 1 m above the ground. We then analyzed the digital photos with HemiView 3.1 (Delta-T Devices Ltd, Burwell, Cambridge, U.K.). HemiView computes GSF by summing weighted values of total direct solar radiation (Direct Site Factor) and total diffuse solar radiation (Indirect Site Factor). GSF is expressed as a proportion (a number between 0 and 1; 0 being no light and 1 being 180° of full sun) of global radiation (direct plus diffuse) reaching the understory relative to that in an open canopy. We estimated surface leaf litter temperature to the nearest 0.1°C at 16 locations within each gap and intact forest site prior to litter extraction using a Raytek[®] ST Pro Infrared Temperature gun (Santa Cruz, CA, U.S.A.) held 1 m above the leaf litter. We calculated the mean temperature at each site from these estimates and used the mean in all subsequent analyses. We recorded soil moisture at each of the same 16 locations within each gap and intact forest site prior to litter extraction using a Decagon HydroSense TDR (Pullman, WA, U.S.A.) soil moisture probe at a depth of 12 cm. The mean volumetric water content at each site was then calculated and used in subsequent analysis. All measurements were taken during midday and early afternoon.

ANT SAMPLING.—We sampled leaf litter ants using mini-Winkler extractors (Fisher 1999). At each gap and paired intact site, we collected leaf litter from four randomly placed 1-m² quadrats

within the central 4 × 4 grid described above. The 1-m² quadrats for the mini-Winklers were randomly placed within the 36-m² 4 × 4 grid described above, such that each 1-m² quadrat was at least 2 m from the nearest sampled quadrat. We chopped the leaf litter within each 1-m² quadrat with a machete, collected it, and sifted it through a coarse mesh screen of 1-cm grid size to remove the largest fragments and concentrate the fine litter. The litter fragments, twigs, and sticks in each 1-m² quadrat that did not fit through the mesh were inspected for colonies. The concentrated fine leaf litter from each of the 1-m² quadrats was then suspended in mini-Winkler sacks for 72 h (see Fisher 1999 for a detailed description of this method). All adult worker ants from mini-Winkler samples were counted and assigned to species (or established morphospecies according to <http://academic.evergreen.edu/projects/ants/AntsofCostaRica.html>). Voucher species are stored in N. Sanders's ant collection at the University of Tennessee. As the yield from Winkler samples is generally high, many studies rely on only a few samples per site. For instance, Longino and Nadkarni (1990), working at Monteverde, collected ants from 2 to 8 L of sifted leaf litter per site; similarly, Kaspari *et al.* (2004) report on local diversity estimates based on 6 L of sifted litter. Thus, our sampling intensity is on par with that of other studies. As an additional step to correct for possible undersampling, we estimated total species richness in each gap and adjacent forest site using the Chao2 estimate of species richness. Observed species richness may mirror actual species richness. However, observed richness is also sensitive to the number of individuals collected in each sample and the total abundance of each species (Gotelli & Colwell 2001). Therefore, we used EstimateS (Colwell 2005) to calculate the unbiased Chao2 asymptotic estimate of species richness, had sampling gone to completion from mini-Winkler samples in each of the 12 paired gap and intact forest sites. Ant species were recorded as present or absent in each sample and asymptotic species richness for each site was estimated as:

$$S_{\text{Chao2}} = S_{\text{Obs}} + Q_1^2/2Q_2$$

where S_{Obs} is the observed number of species in each gap or intact forest plot, Q_1 is the number of species that occur in only one sample, Q_2 is the number of species that occur in two samples, and m is the total number of samples.

STATISTICAL ANALYSES.—We first examined whether insolation, soil moisture, and leaf litter temperature differed between treefall gaps and adjacent intact forest using paired *t*-tests. We also examined how insolation, soil moisture, and leaf litter temperature changed as gaps age by plotting each abiotic variable against gap age using linear regression analyses.

We used two separate *t*-tests to explore whether particular species tended to occur more frequently or had higher worker densities in particular habitat types. In the first, we asked whether the occurrence of species (the number of 1-m² quadrats in which a species was detected) differed between gaps and intact forests. In the second, we compared worker densities for each species (the total number of workers collected in the 1-m² quadrats)

between gaps and intact forests. As a result of the high number of statistical tests, we used a Bonferroni corrected α of 0.001. In all cases, the sample size was 12.

To address whether estimated species richness differed between ant assemblages in treefall gaps and adjacent intact forest sites, we first used paired t -tests to compare the Chao2 estimate of richness in gaps and adjacent intact forests. Then, to examine whether the Chao2 estimate of richness varied between gaps and intact forests and depended on variation in the abiotic environment, we used a Generalized Linear Model (GLM), with Poisson error distributions and log link function. In the model, the suite of predictor variables included the following: (1) treatment (whether the assemblage was in a gap or intact forest); (2) insolation; (3) leaf litter temperature; (4) soil moisture; and (5) the interactions between each abiotic variable and treatment. The Chao2 estimate of species richness was the response variable. We used standard model reduction procedures to identify significant terms in the initial models. In addition, we did not include the interactions between the abiotic variables or any three-way interaction terms because of the limited sample size (12 points).

To compare ant assemblage composition between gaps and intact forests, we constructed a matrix of pairwise comparisons among sites based on the Sørensen similarity index using PRIMER v.6 (Primer-E Ltd. Plymouth). As ants are eusocial, and workers tend to be spatially clumped, the frequency of occurrence may be a more accurate estimate of ant abundance than is the total number of workers collected (Longino *et al.* 2002). For this reason, we examined assemblage similarity using incidence-based data.

We then performed non-metric multidimensional scaling (NMDS) ordination in PRIMER v.6 with the Sørensen distance measures to examine whether ant assemblage composition varied between gaps and intact forests. NMDS is a robust ordination technique that places samples with similar assemblages, as measured by the metric, close together in ordination space, whereas samples with dissimilar assemblages are further apart (Faith *et al.* 1987). NMDS ordination treats rare and common species equally, and the resulting patterns are thus not driven by a few common species, but rather reflect assemblage-wide patterns.

We used analysis of similarity (ANOSIM) in PRIMER v.6 to test for differences in a priori-defined groups (gap vs. intact) and randomly generated groups in ordination space. ANOSIM is a non-parametric test that generates null assemblages based on a rank similarity matrix (Magurran 2004). ANOSIM generates a test statistic R_{anosim} that ranges from zero to one. Zero indicates that there is no difference between groups, whereas one indicates that groups are completely different (Clarke & Gorley 2001).

To test whether ant assemblages in gaps became more similar to the assemblages in adjacent intact forests as gaps aged, we plotted the Bray–Curtis similarity index of each paired gap and intact forest assemblage against gap age. The Bray–Curtis metric (also known as the Sørensen quantitative index) ranges from 0 to 1. The more similar the paired sites are, the higher the value of the index. The pairwise similarity between gaps and intact sites would be expected to increase as gaps age if ant assemblages

in gaps are immediately and directly affected by treefall gap disturbances and then recovery.

RESULTS

ABIOTIC FACTORS.—Abiotic conditions differed between gaps and adjacent intact forests. Insolation was 2.2 times greater ($t = 5.47$, $P < 0.01$; Fig. 1A) and soil moisture was 27 percent lower ($t = 1.79$, $P = 0.01$; Fig. 1B) in gaps than in adjacent intact forest sites. Temperature was 3 percent higher in gaps (mean = $16.9^{\circ}\text{C} \pm 0.3$) than in intact forests (mean = $16.3^{\circ}\text{C} \pm 0.2$; $t = 2.19$, $P = 0.05$; Fig. 1C). Insolation was significantly negatively correlated with gap age ($r^2 = 0.49$, $P = 0.01$; Fig. 1D). Neither volumetric water content ($r^2 = 0.23$, $P = 0.11$; Fig. 1E) nor surface temperature ($r^2 = 0.05$, $P = 0.5$; Fig. 1F) varied systematically with gap age.

ANT ASSEMBLAGES.—In total, 2426 worker ants were collected from mini-Winkler samples. From the 12 paired gap and intact sites, 37 species and morphospecies (hereafter referred to as species) from 21 genera and 7 subfamilies were collected. A total of 31 species were collected along the treefall gap chronosequence, and 28 species were collected in the intact forest sites using mini-Winkler extractors (Appendix S1). We note that Longino and Nadkarni (1990) identified 48 ground-foraging species in the general area around Monteverde.

The most common species were *Pheidole monteverdensis* (occurrence in gaps = 12, occurrence in forest plots = 12), *Solenopsis JTL-001* (occurrence in gaps = 12, occurrence in forest plots = 11), *Gnamptogenys strigata* (occurrence in gaps = 11, occurrence in forest plots = 9), *Stenamma schmidti* (occurrence in gaps = 11, occurrence in forest plots = 11), and *Pyramica myllorhapha* (occurrence in gaps = 10, occurrence in forest plots = 11).

No species occurred more or less frequently in gaps than in intact forests ($P > 0.10$ in all cases). Similarly, worker density did not differ between gaps and intact forests for any species ($P = 0.06$ for *Pyramica myllorhapha*; $P > 0.20$ for all other species). Indeed, species that were common in gaps also tended to be common in intact forests (Spearman's $\rho = 0.74$, $P = 0.0001$).

The observed species richness from mini-Winkler samples did not differ between gap and intact sites ($t = 16.5$, $P = 0.15$; Fig. 2). The Chao2 estimated species richness based on mini-Winkler samples at each paired gap and intact site, however, was 1.3 times higher in gaps than in adjacent intact forest ($t = 2.51$, $P = 0.01$; Fig. 2).

The GLM indicated that the Chao2 estimate of species richness differed between gaps and forests and was positively correlated with insolation (Table 1). Interestingly, there was a significant treatment \times temperature interaction ($P = 0.03$), indicating that the effect of temperature on estimated species richness varied between habitats.

Assemblage composition did not differ between gap and intact sites (ANOSIM, global $R = -0.014$, $P = 0.56$, Fig. 3), and ant assemblages in gaps did not become more similar to those in adjacent intact forests as gaps aged (Fig. 4).

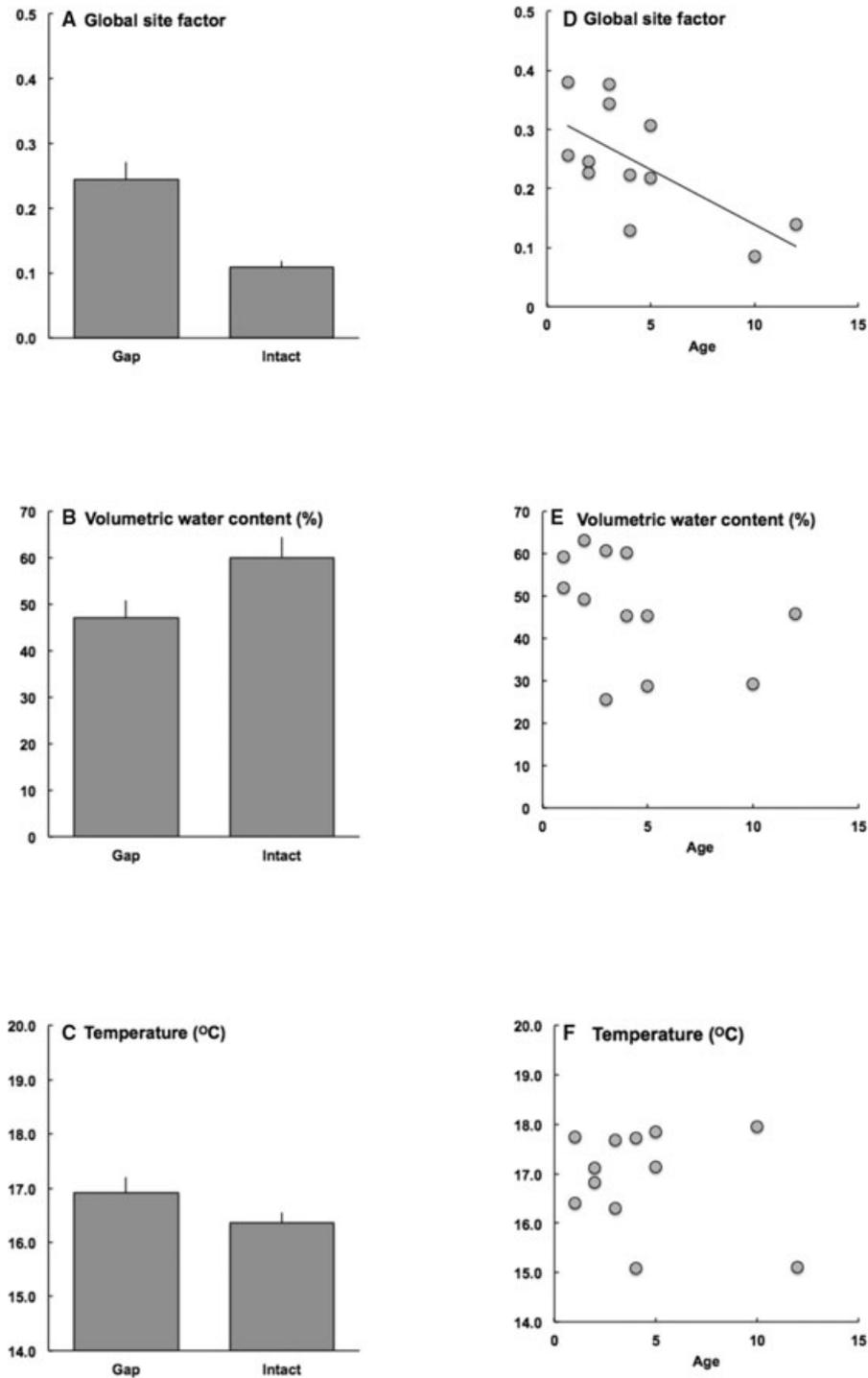


FIGURE 1. Difference in abiotic variables between habitats and along the gap chronosequence. Difference in (A) insolation, (B) soil moisture, and (C) temperature between habitats and change in (D) insolation, (E) soil moisture, (F) and temperature along treefall gap chronosequence.

DISCUSSION

Previous authors have suggested that disturbances may be a major force structuring tropical litter ant assemblages (Byrne 1994, Kaspari 1996a, b; Yanoviak & Kaspari 2000, McGlynn

2006, Campos *et al.* 2007). However, surprisingly few studies have explicitly examined the effect of treefall gaps on ant assemblages. Feener and Schupp (1998) found that the abundance, species richness, and assemblage composition of ground-foraging ants did not differ significantly between treefall gaps and adjacent

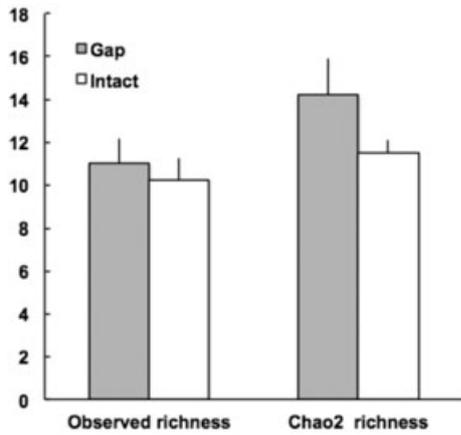


FIGURE 2. The mean (±SE) observed species richness and estimated species richness from mini-Winkler samples across all sites in each habitat.

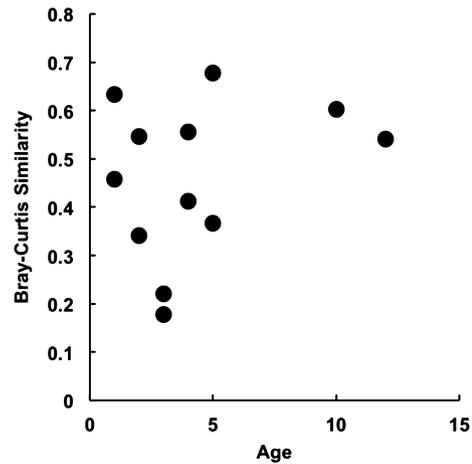


FIGURE 4. The relationship between assemblage composition in the gap and the adjacent intact forest as a function of gap age.

TABLE 1. Results from Generalized Linear Model showing the effects of habitat type, insolation, volumetric water content, temperature, and their interactions on the Chao2 estimate of richness in forest gaps and adjacent intact forests.

Source	χ^2	P
Habitat type (Gap vs. intact forest)	5.75	0.02
Insolation	4.66	0.03
Volumetric water content	0.10	0.75
Temperature	0.99	0.32
Habitat type × Insolation	1.57	0.21
Habitat type × volumetric water content	0.06	0.81
Habitat type × temperature	4.73	0.03

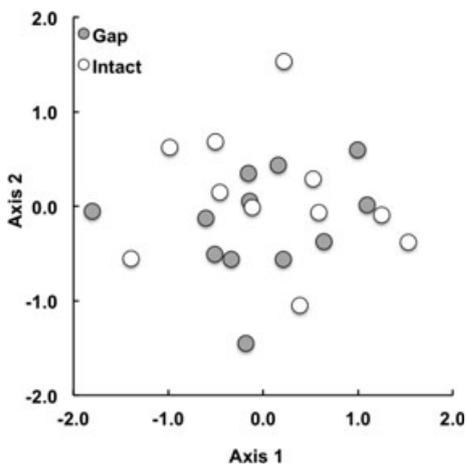


FIGURE 3. Non-metric multidimensional scaling ordination of leaf litter ant assemblage composition in gap and intact sites using presence-absence data. Ant assemblage composition does not differ significantly between gap and intact sites (ANOSIM, global $R = -0.014$, $P = 0.56$).

intact forests in the lowland tropical moist forests of Barro Colorado Island in Panama. In contrast, in the Western Ghats, in India, Basu (1997) found ant species richness was higher in intact forests than in treefall gaps. More in line with the findings of Feener and Schupp (1998), our study in the Monteverde Cloud Forest Preserve, Costa Rica, found few differences between assemblages in gaps and intact forests—namely, the Chao2 estimate of richness was higher in gaps than in intact forests, but no other measures of community structure differed between gaps and adjacent intact forests.

Feener and Schupp (1998) outlined three environmental features of gaps with the potential to influence the composition and dynamics of ant assemblages. First, treefall gaps may alter insolation, soil moisture, and temperature on the forest floor. These abiotic variables can in turn affect the foraging activity and nest site distribution of ants (Levings 1983, Kaspari & Weiser 2000). Secondly, higher plant productivity in gaps may increase food availability for ants and other taxa. Thirdly, plants with extra-floral nectaries may be more diverse and abundant in treefall gaps than in intact forest sites. Feener and Schupp (1998) thus hypothesized that, relative to the adjacent intact understory, treefall gaps should provide better conditions for ant foraging, more resources and more ant-specific resources that should in turn lead to increases in ant abundance and species richness and changes in ant species composition. We found some evidence for the abiotic predictions outlined in Feener and Schupp (1998). Both insolation and temperature were higher in gaps than in intact forests, and both abiotic factors were related to the Chao2 estimated number of ant species in gaps. It is perhaps not surprising, in this light, that warmer sites with more sunlight (*i.e.*, gaps) tended to harbor more ant species than did cooler, closed canopy sites.

Treefall gaps in the MCFP, during the wet season, represent patches of habitat on the forest floor that have higher insolation levels, slightly higher surface temperatures, and lower soil moisture levels than intact forest sites. Higher temperatures in gaps

relative to adjacent forests might lead to more suitable nest sites and higher rates of foraging activity in gaps when compared with intact forest understories, which might in turn lead to higher species richness in gaps than in intact forests (Sanders *et al.* 2007). However, the effects of gaps on ant communities, to the extent to which they occur, apparently dissipate rapidly, a point to which we now turn.

While Chao2 estimates of richness differed between gaps and intact forests, ant community composition did not. This apparent discrepancy arises because the Chao2 analysis is sensitive to the number of rare species, but the analyses of similarity we conducted largely are not. Similarly, the influence of rare species on the Chao2 estimate of diversity determines why we detect no difference in the observed species richness between gaps and intact forests, but higher Chao2 estimates were found in gaps than in intact forests—because there tend to be more rare species (singletons and doubletons) in gaps than in intact forests. Moreover, ant assemblages in gaps did not become more similar to those in adjacent intact forests as gaps aged. Treefall gap disturbances are one of many factors that increase the spatial and temporal heterogeneity of abiotic and biotic resources on the forest floor. The high dispersal ability and rapid growth rates of most colonies of most ant species (at least compared to plants) means that the direct impact of these disturbances on ant assemblages is likely to be more ephemeral than on long-lived organisms such as shade-intolerant plants (Hölldobler & Wilson 1990, Andersen 1995). That we observed no significant change in assemblage composition or increase in similarity between habitats following disturbance supports this supposition. Furthermore, because treefall gap disturbances tend to be small and low in severity, the major effects of these disturbances on ant assemblages are likely to be secondary and occur through modifications to the microclimate on the forest floor (Andersen 1995).

In sum, ant assemblages in the MCFP are weakly affected by the formation of treefall gaps through the impact of gap formation on soil moisture and temperature levels on the forest floor. These effects of gap formation on ant assemblages are short-lived and likely of little consequence in promoting ant diversity at more regional scales, contrary to what has long been hypothesized for tropical plant communities (Hubbell *et al.* 1999).

ACKNOWLEDGMENTS

We thank R.O. Lawton for access to his study area and census data, R.M. Lawton for field assistance, the Tropical Science Center for access to the Monteverde Cloud Forest Preserve, and J. Schweitzer and an anonymous reviewer for comments on a previous version of the manuscript. Funding for this research was provided by the Department of Ecology and Evolutionary Biology at the University of Tennessee and a McClure Fellowship to MP.

SUPPORTING INFORMATION

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

APPENDIX S1. List of the ant species collected at each of the 12 intact and gap sites.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

LITERATURE CITED

- ALVAREZ, J., AND M. R. WILLIG. 1993. Effects of treefall gaps on the density of land snails in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 25: 100–110.
- ANDERSEN, A. N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *J. Biogeogr.* 22: 15–29.
- BASU, P. 1997. Seasonal and spatial patterns in ground foraging ants in a rain forest in the Western Ghats, India. *Biotropica* 29: 489–500.
- BECK, H., M. S. GAINES, J. E. HINES, AND J. D. NICHOLS. 2004. Comparative dynamics of small mammal populations in treefall gaps and surrounding understory within Amazonian rainforest. *Oikos* 106: 27–38.
- BROKAW, N. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14: 158–160.
- BROKAW, N. V. L. 1996. Treefalls: frequency, timing, and consequences. *In* E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds). *The ecology of a tropical forest: seasonal rhythms and long-term changes*. pp. 101–108. Smithsonian Institution Press, Washington, D.C., USA.
- BYRNE, M. M. 1994. Ecology of twig-dwelling ants in a wet lowland tropical forest. *Biotropica* 26: 61–72.
- CAMPOS, R. B. F., J. H. SCHOEREDER, AND C. F. SPERBER. 2007. Small-scale patch dynamics after disturbance in litter ant communities. *Basic Appl. Ecol.* 8: 36–43.
- CLARK, K. L., N. M. NADKARNI, D. SCHAEFER, AND H. L. GHOLZ. 1998. Cloud water and precipitation chemistry in a tropical montane forest, Monteverde Costa Rica. *Atmos. Environ.* 32: 1595–1603.
- CLARKE, K. R., AND R. N. GORLEY. 2001. *Primer v5: user manual/tutorial*. Primer-E Ltd, Plymouth.
- COLWELL, R. K. 2005. *EstimateS: statistical estimation of species richness and shared species from samples*. Version 7.5. User's guide and application published at <http://purl.oclc.org/estimates>.
- DANIELS, J. D., AND R. O. LAWTON. 1991. Habitat and host preference of *Ficus-crassiuscula*, a Neotropical strangling fig of the lower-montane rain-forest. *J. Ecol.* 79: 129–141.
- DUNN, R. R. 2004. Recovery of faunal communities during tropical forest regeneration. *Conserv. Biol.* 18: 302–309.
- FAITH, D. P., P. R. MINCHIN, AND L. BELBIN. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57–68.
- FEENER, D. H., AND E. W. SCHUPP. 1998. Effect of treefall gaps on the patchiness and species richness of Neotropical ant assemblages. *Oecologia* 116: 191–201.
- FISHER, B. L. 1999. Improving inventory efficiency: a case study of leaf-litter ant diversity in Madagascar. *Ecol. Appl.* 9: 714–731.
- FUKAMI, T., AND D. A. WARDLE. 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proc. R. Soc. B* 272: 2105–2115.
- 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.
- HÖLDOBLER, B., AND E. O. WILSON. 1990. *The ants*. Belknap Press of Harvard University Press, Cambridge, MA, 732 pp.
- HUBBELL, S. P., R. B. FOSTER, S. T. O'BRIAN, K. E. HARMS, R. CONDIT, B. WECHSLER, S. J. WRIGHT, AND S. LOO DE LAO. 1999. Light gap

- disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554–557.
- KASPARI, M. 1996a. Litter ant patchiness at the 1-m² scale: disturbance dynamics in three Neotropical forests. *Oecologia* 107: 265–273.
- KASPARI, M. 1996b. Testing resource-based models of patchiness in four Neotropical litter ant assemblages. *Oikos* 76: 443–454.
- KASPARI, M., AND M. D. WEISER. 2000. Ant activity along moisture gradient in a Neotropical forest. *Biotropica* 32: 703–711.
- KASPARI, M., P. S. WARD, AND M. YUAN. 2004. Energy gradients and the geographic distribution of local ant diversity. *Oecologia* 140: 407–413.
- LAWTON, R. O., AND F. E. PUTZ. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69: 764–777.
- LAWTON, R. O. 1990. Canopy gaps and light penetration into a wind-exposed tropical lower montane forest. *Can. J. For.* 20: 659–667.
- LEVINGS, S. C. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecol. Monogr.* 53: 435–455.
- LONGINO, J. T., AND N. M. NADKARNI. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. *Psyche* 97: 81–93.
- LONGINO, J. T., J. CODDINGTON, AND R. K. COLWELL. 2002. The ant fauna of tropical rain forest: estimating species richness three different ways. *Ecology* 83: 689–702.
- MAGURRAN, A. E. 2004. *Measuring biological diversity*. Blackwell Publishing Ltd., U.K.
- MCGLYNN, T. P. 2006. Ants on the move: resource limitation of a litter-nesting ant community in Costa Rica. *Biotropica* 38: 419–427.
- PALLADINI, J. D., M. G. JONES, N. J. SANDERS, AND E. S. JULES. 2007. The recovery of ant communities in regenerating temperate conifer forest. *For. Ecol. Manage.* 242: 619–624.
- PICKETT, S. T., AND P. S. WHITE eds. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York.
- SANDERS, N. J., J. P. LESSARD, R. R. DUNN, AND M. C. FITZPATRICK. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Glob. Ecol. Biogeogr.* 16: 640–649.
- SCHEMSKE, D. W., AND N. BROKAW. 1981. Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62: 938–945.
- SCHNITZER, S. A., AND W. P. CARSON. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82: 913–919.
- SHELLY, T. E. 1988. Relative abundance of day-flying insects in treefall gaps vs shaded understory in a Neotropical forest. *Biotropica* 20: 114–119.
- STRONG, D. R. 1977. Epiphyte loads, tree falls, and perennial forest disruption: a mechanism for maintaining higher tree species richness in the tropics without animals. *J. Biogeogr.* 4: 215–218.
- YANOVIAK, S. P., AND M. KASPARI. 2000. Community structure and the habitat template: ant in the tropical forest canopy and litter. *Oikos* 89: 259–266.