To the Graduate Council:

I am submitting herewith a thesis written by Margaret Patrick entitled “The Effects of Treefall Gap Disturbances on Litter Ant Assemblages in a Tropical Montane Cloud Forest.” I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Masters of Science, with a major in Ecology and Evolutionary Biology.

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We have read this thesis
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The Effects of Treefall Gap Disturbances on Litter Ant Assemblages in a Tropical Montane Cloud Forest.

A Thesis Presented for
the Master of Science Degree
The University of Tennessee, Knoxville

Margaret Patrick
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ABSTRACT[1]

In this study, we considered the effects of treefall gap disturbances on leaf litter ant assemblages in a Neotropical montane cloud forest. We asked a series of questions: (1) Do species richness, number of workers, 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 forest 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 estimated a suite of abiotic parameters in 12 large (> 80-m^2) treefall gaps across a chronosequence and in 12 paired adjacent intact forest sites in the Monteverde Cloud Forest Preserve in Costa Rica. Estimated species richness was higher in gap sites than in intact forest sites, but worker abundance and assemblage composition did not differ significantly between habitats. Ant assemblages in gap sites did not become more similar to those in adjacent intact sites as gaps aged. Our study demonstrates that ant assemblages in the Monteverde Cloud Forest Preserve are weakly affected by the formation of treefall gaps. However, variation in local assemblage structure appears to be influenced by landscape-level processes, which operate at larger spatial scales than those occurring between treefall gaps and intact forest sites.

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[1]My use of "we" in this thesis refers to my co-authors and myself. My primary contributions to this thesis include: 1) development of ideas and hypotheses; 2) collection and preparation of data; 3) data analysis; 4) and writing. A slightly modified version of this thesis was recently submitted for publication.

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INTRODUCTION

TREEFALL gaps are the most frequent small-scale natural disturbances in many temperate and tropical forest ecosystems (Pickett & White 1985). 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 2000). Though treefall gaps also have the potential to play an important role in animal community dynamics, the response of animal communities to treefall gap disturbances has not been well studied relative to the responses of plant communities (although see Schemske & Brokaw 1981, Shelly 1988, Alvarez & Willig 1993, Feener & Schupp 1998, Beck et al. 2004, Richards & Coley 2007).

Most studies which 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 changes in gaps as they age 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. In particular, we compared ant assemblages in gaps of different ages to ant assemblages in intact forests. Ants are abundant in tropical forests (Hölldobler & Wilson 1990, Longino et al. 2002) where they are important predators, scavengers, herbivores, soil aerators, and seed dispersers (reviewed in Folgarait 1998). Because ant colonies, like plants, are largely sedentary and modular, ant responses to treefall gaps might be expected to be similar to those of plants (Andersen 1995). However, a key difference between ants and plants is that there is no equivalent in ant assemblages to the seed bank, such that ants must colonize gaps either by moving their colonies or via mating flights of new queens.

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). Yet, few studies have explicitly examined the effect of treefall gaps on ant assemblages, and the two that have provide somewhat conflicting results (Feener & Schupp 1998, Richards & Coley 2007). Feener & Schupp (1998) found that the abundance, species richness, and assemblage composition of ground-foraging ants did not differ significantly between treefall gaps and adjacent intact forest understories in the lowland tropical moist forests of Barro Colorado Island (BCI) in Panama. Richards & Coley (2007), on the other hand, found the number of ants on understory vegetation was significantly higher in treefall gaps than in adjacent intact forest understories on BCI, but they did not examine species richness or assemblage composition. To our knowledge, these two studies are the only ones to have examined the immediate response of ants to treefall gap disturbances in tropical systems, and no study

has examined how ant assemblages respond to regeneration in treefall gap disturbances along a chronosequence in a tropical forest.

In this study, we considered the effects of treefall gap disturbances on leaf-litter ant assemblages in a Neotropical montane cloud forest and asked a series of inter-related questions: (1) Do species richness, number of workers, 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 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 m^2) 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 Monteverde Cloud Forest Preserve (MCFP) in west-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) and is at an elevation of ~1500 m. Annual rainfall near the MCFP averages 2450 mm/yr although actual precipitation is 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 R. Lawton and colleagues (Lawton & Putz 1988, Lawton 1990, Daniels & Lawton 1991). During this annual census, treefall gaps are identified roughly following 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 all larger than $80m^2$ and comprised a chronosequence from less than one year old to greater than twelve years old (two gaps were < 1 yr old; two were 1-2 yr old; two were 2-3 yr old; two were 3-4 yr old; two were 4-5 yr old; two were 10-12 yr old). The paired intact sites were located ~25 m in a random direction away from the gap edge and were at least 25 m away from any other known gap in the study area.

BIOTIC SAMPLING.–We sampled leaf litter ants using two standard collecting techniques. First, we sampled the ground-foraging fauna using baits. In the center of each paired gap and intact forest plot, we established a 4 × 4 grid of 16 bait stations spaced 2 m apart. Each bait station was a laminated 3 × 5 index card baited with approximately 2-4 ml of canned tuna in oil. Paired gap and intact sites were baited on the same day between 0900-1200 h. One hour after placing the baits, we tallied the number of baits occupied at each site and collected all of the ants. The ants were then transported to the lab for enumeration and identification.

We recognize that baits are often dominated by mass recruiting species and can be a biased method of sampling because baiting often under samples cryptic ants, trophic specialists, and subordinate ant species (Fisher 1999). Therefore, we also used mini-Winkler samplers to extract ants from the leaf litter. At each gap and paired intact site, we collected leaf litter from four 1-m^2 quadrats from each 36-m^2 plot. We chopped the leaf litter inside each 1-m^2 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-m^2 quadrat that did not fit through the mesh were inspected for colonies. The concentrated fine leaf litter from each of the 1-m^2 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 baiting and mini-Winkler samples were counted and assigned to a morphospecies or identified to species where

possible. Voucher species are stored in N. Sanders's ant collection at the University of Tennessee.

ABIOTIC VARIABLES.–At each gap and paired forest site, we recorded insolation, leaf litter temperature, and soil moisture to examine whether any of these factors was related to ant species richness and worker abundance. We estimated insolation (Global Site Factor [GSF]) by taking hemispherical photographs in the middle of each gap and intact site with a Nikon 5400 camera with a fish-eye lens under uniform conditions (overcast sky between 0900 -1400). 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, UK). 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 180º 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 each of the 16 baiting stations within each gap and intact forest site following baiting but 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 16 baiting stations following baiting but 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 analysis.

STATISTICAL ANALYSES.–To address whether species richness, worker number and species composition differed between ant assemblages in treefall gaps and adjacent intact forest sites, we compared the cumulative observed species richness and cumulative observed worker number from baits and mini-Winkler samples from each site between gap and paired intact sites using paired *t*-tests. Because mini-Winkler samples and baits can yield different components of the fauna, we also compared the observed richness sampled by mini-Winkler samplers in treefall gaps to richness sampled by mini-Winkler samplers in forests and then we compared species richness of ants attracted to baits in the gaps to species richness of ants attracted to baits in the forest. We again used paired *t*-tests for both analyses.

Observed species richness may mirror actual species richness. But 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 (Version 7.5, R.K. Colwell, http://purl.oclc.org/estimates) to calculate the 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 using the formula:

$S_{Chao2} = S_{Obs} + (Q_1^2/2Q_2)$

where S_{Obs} is the observed number of species in each sample, Q_1 is the number of species

that occur in only one sample, and Q_2 is the number of species that occur in two samples. All paired data were tested to determine if the differences between pairs were normally distributed and the Wilcoxon signed-rank test was used if this assumption was violated.

To compare ant assemblage composition between gaps and intact forests, we constructed a matrix of pairwise comparisons among sites based on the Sørenson similarity index using PRIMER v6 (*Primer-E Ltd. Plymouth)*. Because 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 v6 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 while 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 then used analysis of similarity (ANOSIM) in PRIMER v6 to test for differences in *a priori*-defined groups (gap vs. intact) and randomly generated groups in ordination space. ANOSIM is a nonparametric 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 while 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 pair 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.

As potential explanatory variables for differences seen in the ant assemblages, we examined whether insolation, soil moisture, and leaf litter temperature differed between treefall gaps and adjacent intact forest using paired *t*-tests. Again, all paired data were tested to determine if the differences between pairs were normally distributed and the Wilcoxon signed-rank test was used if this assumption was violated. We also examined how insolation, soil moisture, and leaf litter temperature change as gaps age by plotting each abiotic variable against age using linear regression analyses.

To examine whether abiotic variables influenced estimated species richness in gaps and intact forest sites both separately and in combination we performed stepwise regressions with the abiotic variables insolation, soil moisture, and leaf litter temperature as potential predictors of the Chao2 estimate of ant species richness. Gap age was also considered as a potential predictor of the Chao2 estimated ant species richness when gaps were considered separately. Additionally, when estimated species richness in gap and

intact sites were considered separately we used estimated species richness in the paired gap or intact site as a potential predictor to control for landscape-level heterogeneity in species richness. All of the potential predictors were checked for collinearity and if collinearity was detected the variable least correlated with estimated species richness was excluded. The criterion for inclusion of a variable into the model was $P < 0.15$.

RESULTS

In total, 5,547 worker ants were collected using both baiting and mini-Winkler sampling techniques. From the twelve paired gap and intact sites, 38 morphospecies (hereafter referred to as species) from 20 genera were collected. Three subfamilies of ants were represented: Myrmicinae, Formicinae, and Ponerinae. In total, 3,108 ants were collected from baiting samples representing 14 species from 8 genera, and 2,426 worker ants were collected from mini-Winkler samples representing 36 species from 20 genera.

BAITING SAMPLES.–A total of 14 species were collected along the treefall gap chronosequence and 11 species were collected in the intact forest sites (Table 1; all tables and figures are located in the appendix) from baiting samples. Of the total number of individuals collected using baiting, 82.4 percent were of the genus *Pheidole*, and 13.3 percent were in the genus *Solenopsis*. The remaining 3.3 percent of the total was distributed among 6 species in 6 genera. Two additional genera represented more than 1 percent of individuals, *Paratrechina* with 2.5 percent and *Gnamptogenys* with 1.5 percent.

MINI-WINKLER SAMPLES.–A total of 36 species were collected along the treefall gap chronosequence and 28 species were collected in the intact forest sites using mini-Winkler extractors (Table 2). Of the total number of individuals collected using mini-Winkler extraction 26.9 percent were of the genus *Pheidole*, 15.6 percent were in the genus *Paratrechina*, 15.1 percent were in the genus *Stenamma*, and 13.6 percent were in

the genus *Solenopsis*. The remaining 28.8 percent of the total was distributed among 24 species in 16 genera. None of the remaining 16 genera accounted for more than 8 percent of the individuals collected although seven additional genera represented more than 1 percent of individuals, *Neivamyrmex* with 5.2 percent, *Adelomyrmex* with 4.2 percent, *Cyphomyrmex* with 1.9 percent, *Eurhopalothrix* with 2.3 percent, *Strumigenys* with 7.8 percent, *Gnamptogenys* with 4.6 percent, and *Hypoponera* with 1.4 percent.

The total observed species richness (the cumulative total observed species richness from baits + observed species richness Winkler samples) was 1.1 × higher in gaps than in adjacent intact forest understories ($t = 2.03$, $P = 0.07$; Fig. 1). However, analyzed separately neither the observed species richness sampled by baits nor the number of species collected with mini-Winkler samples differed between gap and intact sites (baits: $t = 0.09$, $P = 0.93$; mini-Winklers: $t = 16.5$, $P = 0.15$; Fig. 1). The Chao2 estimated species richness based on mini-Winkler was 1.3 × higher in gaps than in adjacent intact forest ($t = 3.07$, $P = 0.01$; Fig. 1). Worker number (collected from mini-Winklers) did not differ between gap and paired intact sites ($t = 0.11$, $P = 0.91$). Assemblage composition did not differ between gap and intact sites (Incidence: ANOSIM, global R = -0.014, $P = 0.56$, Fig. 2), and ant assemblages in gaps did not become more similar to those in adjacent intact forests as gaps age (Fig. 3).

Although ant assemblages differed little between gaps and intact sites, the same was not true for microenvironmental conditions. Insolation was 2.2 × greater ($t = 5.47$, $P < 0.01$; Fig. 4A), soil moisture was 27 percent lower ($t = 1.79$, $P = 0.01$; Fig. 4B), and leaf litter temperature ($t = 2.19$, $P = 0.05$; Fig. 4C) was 3 percent higher in gaps than in

adjacent intact forest sites. Insolation was significantly negatively correlated with gap age ($r^2 = 0.49$, $P = 0.01$; Fig. 4D). However, there was not a significant relationship between volumetric water content ($r^2 = 0.23$, $P = 0.11$; Fig. 4E) or surface temperature ($r^2 = 0.05$, $P = 0.5$; Fig. 4F) and gap age.

In the combined stepwise regression for gaps and intact forest sites soil moisture was the only significant predictor of the Chao2 estimate of species richness and it was negatively related to species richness ($r^2 = 0.28$, $P = 0.01$, Fig. 5). Similarly, in the stepwise regression for intact sites alone, soil moisture was significantly negatively related to estimated species richness ($r^2 = 0.35$, $P = 0.04$). In the stepwise regression for gap sites alone, gap age was excluded as a possible predictor of estimated species richness due to collinearity with total available light and soil moisture. The only significant predictor of estimated species richness in gap sites was the estimated species richness at the paired intact site. The estimated species richness in the intact site was positively related to estimated species richness in the gap site ($r^2 = 0.30$, $P = 0.07$).

DISCUSSION

Our study demonstrates that litter ant assemblages in the Monteverde Cloud Forest Preserve (MCFP) are affected, albeit weakly, by treefall gap disturbances. Although, Feener and Schupp (1998) found no difference in ant species richness between young gaps and intact forest sites in a lowland tropical forest across all seasons, we found significantly higher estimated ant species richness in gaps across a tree fall gap chronosequence during the wet season in a tropical montane forest. The increase in estimated species richness in gaps was not simply a result of increased ant abundance in gaps. In our study, as in Feener and Schupp's (1998) study, neither worker number nor species composition of ground litter ants differed consistently between gap and intact forest sites.

Feener and Schupp (1998) outlined three environmental features, which may change in a forest when a tree falls and have 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 abioitic 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). Treefall gaps in the MCFP, during the wet season, represent patches of habitat on the forest floor that have higher insolation levels and surface temperatures and lower soil moisture levels than intact forest sites. Temperature is thought to be one of the primary determinants of ant activity and nest site distribution (Hölldobler & Wilson 1990). Andersen (1995) considers low temperature to be the principal abiotic stress influencing the structure of ant assemblages and low-temperature stress is high in cool shaded habitats, such as tropical montane forests. Thus, higher temperatures in gaps might mean more suitable nest sites and higher rates of foraging activity in gaps as compared to intact forest understories, which might in turn lead to higher species richness.

However, while temperature and insolation levels did differ between gap and intact sites estimated ant species richness was not tightly correlated with either of these abiotic variables. Instead, our results indicate that species richness across all sites was *negatively* related to soil moisture in the MCFP. In the lowland tropics, ant abundance and species richness are generally positively related to soil moisture (Levings 1983, Levings & Windsor 1983). Why might ant species richness in the cloud forests of Monteverde be negatively related to soil moisture? Olson (1994) examined the distribution of leaf litter invertebrates, including ants, along an elevational gradient in Panama and found that the number of individuals and species richness declined as forests transitioned from premontane rainforest to lower montane rainforests between 1250 m

and 1500 m. This reduction in ant species richness and abundance in lower montane rainforest as compared to premontane rainforest has been attributed to cooler temperatures, reduced insolation, and consistently high leaf litter and soil moisture in lower montane rainforest, which results from the persistent immersion of these forests in cloud. Waterlogged soils and substrates may inhibit the decomposition of leaf litter resulting in reduced nutrient availability for invertebrate populations (Olson 1994). Thus, we might expect dryer sites such as gaps to harbor more species than intact forest understories, in exceptionally wet forests such as those found in the MCFP.

Estimated species richness in the paired intact forest site was the only significant predictor of estimated species richness in gap sites. This suggests that the spatial variation in ant species richness in the MCFP is also influenced by landscape-level processes, which operate at larger spatial scales than those occurring between treefall gaps and intact forest understories. Other large-scale abiotic processes that might influence ant species richness in tropical systems may include variation in edaphic or topographic conditions as demonstrated by Levings (1983) and suggested by Feener & Schupp (1998).

We found no differences in species composition between gap and intact forest sites although litter ant assemblages in the MCFP do exhibit vertical stratification; litter ant assemblages in the canopy are distinct from litter ant assemblages on the forest floor (Longino & Nadkarni 1990). One of the possible factors driving this vertical stratification is the more dramatic and fluctuating moisture conditions that canopy organic material experiences as compared to ground organic material (Bohlman et al. 1995). Likewise, the

forest floor of gap sites likely experiences more daily and seasonal variation in insolation, soil moisture, and temperature than do intact forest sites. Therefore, if differences in the abiotic environment on the forest floor as compared to the forest canopy are driving the vertical stratification of ant assemblages in the MCFP, it is reasonable to assume that differences in the abiotic environment between gap and intact sites might also drive differences in ant assemblage composition on the forest floor. Further, arboreal ant species might persist in the crowns of recent tree falls since gaps, much like forest canopies, represent patches of habitat were insolation and temperature are higher and soil moisture is lower than in intact forest understory. However, we saw no evidence that previously identified canopy specialists species (Longino & Nadkarni 1990) in the MCFP persist in recent tree falls.

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 ant species 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 (Andersen 1995, Hölldobler & Wilson 1990). The fact that we observed no significant change in assemblage composition or increase in similarity between habitats following disturbance supports this supposition. Further, 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 stress-related and occur through modifications to the microclimate on the forest floor (Andersen 1995). The establishment and persistence of ant species in a given area is a complex

interplay of various different patch-generating mechanisms, including treefall gap disturbances (Levings 1983, Feener & Schupp 1998). Our study demonstrates that ant assemblages in the MCFP are weakly affected by the formation of treefall gaps, through their impact on soil moisture and temperature levels on the forest floor. However, the spatial variation in species richness is also influenced by landscape-level processes, which operate at larger spatial scales than those occurring between treefall gaps and intact forest understories.

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APPENDIX

Table 1. Species by site matrix from baiting samples. For each site the total number of workers and species richness is shown

Age	12		10		5		5		4		4		3		3		2		2		1		1		
Species	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	
Brachymyrmex santschii	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paratrechina sp.1	10	0	6	4	1	0	4	0	29	0	0	1	0	3	0	1	0	0	5	0	0	12	2	1	
Cyphomyrmex salvini	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Pheidole sp.1	291	55	130	172	37	97	21	0	78	36	42	1	58	118	37	38	10	2	55	61	0	131	52	16	
Pheidole sp.2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Pheidole sp.3	0	0	24	4	0	47	10	1	7	7	0	0	7	15	83	4	32	1	0	0	0	35	0	19	
Pheidole sp.4	82	52	70	8	69	45	55	6	0	0	0	0	1	0	1	0	0	27	0	0	0	64	5	0	
Pheidole sp.5	0	0	5	0	0	0	168	0	5	5	0	0	3	0	0	0	0	0	0	0	0	0	0	6	
Pheidole sp.6	0	0	0	0	47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Solenopsis sp.1	1	1	14	1	1	46	0	0	8	18	0	0	0	48	0	0	0	0	8	0	0	24	17	15	
Solenopsis sp.2	0	1	0	0	0	0	96	5	2	0	15	0	0	7	0	0	0	0	0	0	0	0	84	0	
Stenamma sp.2 (cf. felixi)	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Pachycondyla aenescens	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	
Gnamptogenys sp.1 (cf. strigata)	1	10	2	0	1	0	0	0	7	5	2	0	5	2	0	1	0	0	0	0	0	2	2	5	
Total # of workers	386	119	259	189	156	235	354	12	136	72	59	2	75	193	121	44	42	30	68	61	0	271	162	62	
Species Richness	6	5	9	5	6	4	6	3	7	6	3	2	6	6	3	4	2	3	3	2	0	8	6	6	

Table 2. Species by site matrix from mini-Winkler samples. For each site the total number of workers and species richness is shown.

Age	12		10		5		5		4		4		3		3		2		2		1		1	
Species	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I
Neivamyrmex sumichrasti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	125	0	0	0	0	0	0	0
Brachymyrmex santschii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Paratrechina sp.1	16	0	16	51	23	17	3	1	14	0	0	0	17	100	0	50	17	35	0	0	1	19	0	0
Acromyrmex coronatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Adelomyrmex brevispinosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Adelomyrmex tristani	0	0	14	6	4	1	0	0	3	4	2	3	1	31	0	1	4	6	5	6	0	10	0	0
Cyphomyrmex salvini	0	0	0	5	0	8	0	0	1	0	7	1	0	8	1	0	3	0	0	0	5	6	0	0
Eurhopalothrix (cf. JTL-01)	0	0	13	1	6	2	0	0	2	0	2	0	1	6	0	0	3	2	1	4	2	12	0	0
Octostruma (cf. rugiferoides)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp.1	1	27	33	50	22	16	24	23	12	7	16	6	6	24	4	24	22	17	20	7	48	48	3	2
Pheidole sp.2	0	0	0	0	0	0	1	3	0	0	7	0	0	1	0	0	0	0	0	0	0	0	0	0
Pheidole sp.3	0	0	8	6	131	2	0	2	1	0	2	0	1	0	0	1	7	0	0	0	1	0	0	0
Pheidole sp.4	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp.5	4	0	3	0	1	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	2	0	0	0
Pyramica (cf. dontopagis)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0
Pyramica (cf. schulzi)	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Solenopsis sp.1	13	31	15	23	34	17	11	9	14	2	10	7	4	27	3	5	1	1	9	0	6	64	5	5
Solenopsis sp.2	0	3	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	4
Solenopsis sp.3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenamma sp. (cf. schmidt)	60	41	3	4	5	0	43	16	14	8	26	3	0	4	3	2	3	3	17	1	61	12	7	2
Stenamma sp.2 (cf. felixi)	0	0	16	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Stenamma sp.3 (cf. JTL-019)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	1	0	0
Strumigenys sp.1	1	3	5	9	2	27	0	7	1	5	8	1	0	24	1	0	4	1	17	15	5	29	4	6
Strumigenys sp.2 (cf. biolleyi)	0	0	4	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Strymigenys sp.3	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4	0	0
Wasmannia (cf. auropunctata)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Table 2, cont. Species by site matrix from mini-Winkler samples. For each site the total number of workers and species richness is shown

Age	12		10		5		5		4		4		3		3		2		2		1		1	
Species	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I	G	I
Discothyrea (cf. horni)	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnamptogenys (cf. interrupta)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Gnamptogenys (cf. strigata)	3	10	15	7	6	4	4	3	8	8	7	5	0	2	1	0	2	1	1	0	3	0	5	15
Hypoponera sp.1	2	0	1	2	1	0	0	0	1	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0
Hypoponera sp.2	0	1	4	7	0	2	1	0	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hypoponera sp.3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla aenescens	0	0	0	0	1	2	1	0	0	0	1	0	0	2	0	1	0	2	1	0	0	3	0	0
Pachycondyla sp.2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proceratium (cf. convexiceps)	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Simopelta (cf. JTL-03)	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total # of workers	100	118	152	173	239	105	89	67	74	41	93	28	32	230	16	85	197	72	73	33	140	209	26	34
Species Richness	8	9	16	14	15	15	9	10	13	10	15	9	8	12	7	8	14	11	10	5	15	12	7	6

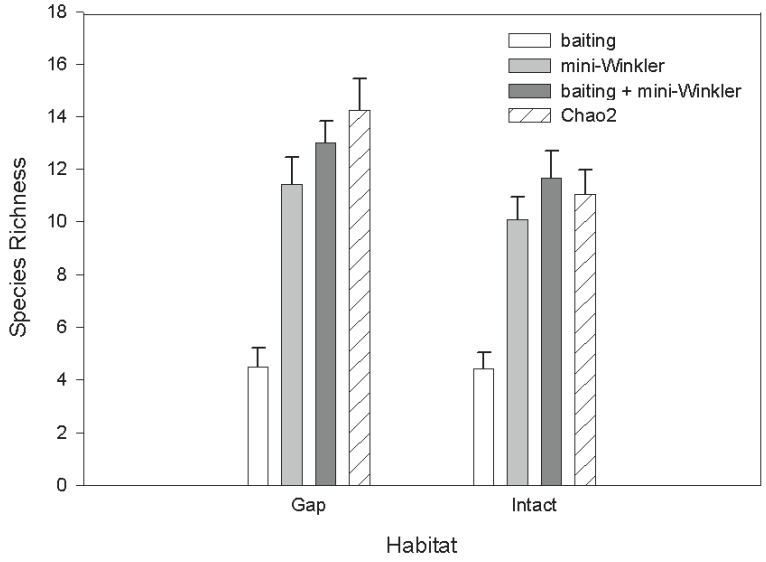

FIGURE 1. The mean (±SE) observed species richness from (baits, mini-Winkler, baits + mini-Winkler) and estimated species richness (Chao2) across all sites in each habitat.

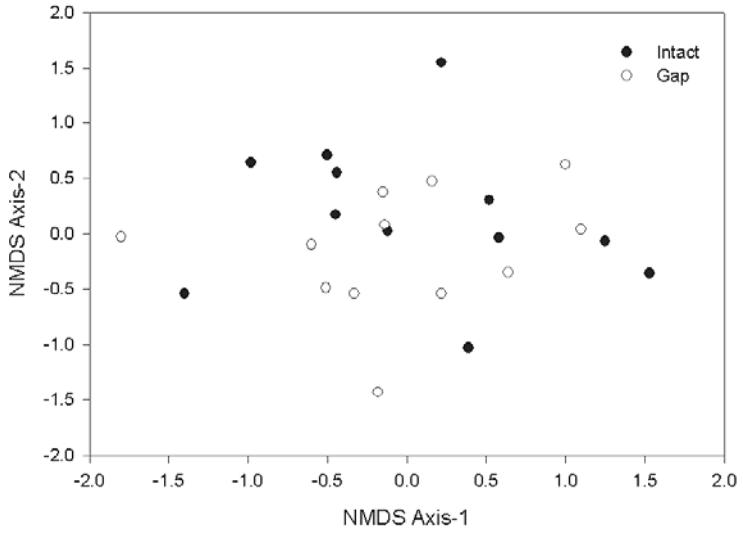

FIGURE 2. Incidence-based ordination. Non-metric multidimensional scaling ordination of leaf litter ant assemblage composition in gap and intact sites using presence-absence data. Ant assemblage composition does not differ significantly between gap and intact sites (ANOSIM, global R = -0.014, *P* = 0.56)

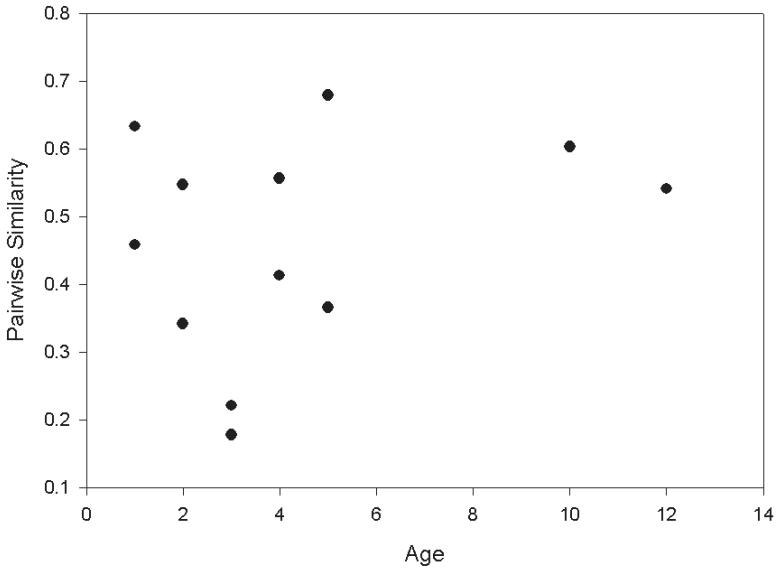

FIGURE 3. Assemblage similarity does not increase between paired gap and intact sites as gap sites age.

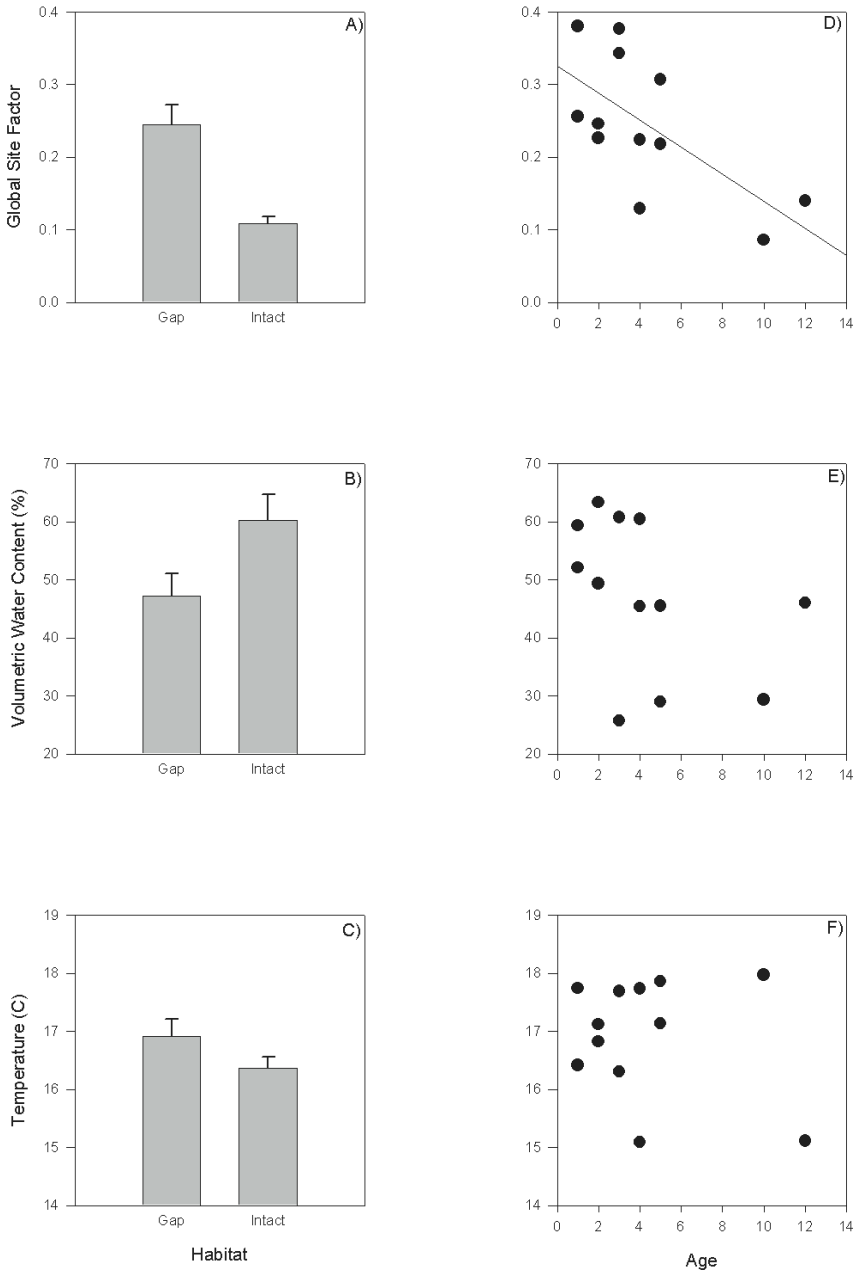

FIGURE 4. Difference in abiotic variables between habitats and along the gap chronosequence. Difference in A) insolation, B) soil moisture, and C) temperature between habitats and change in D) insolation, E) soil moisture, F) and temperature along treefall gap chronosequence.

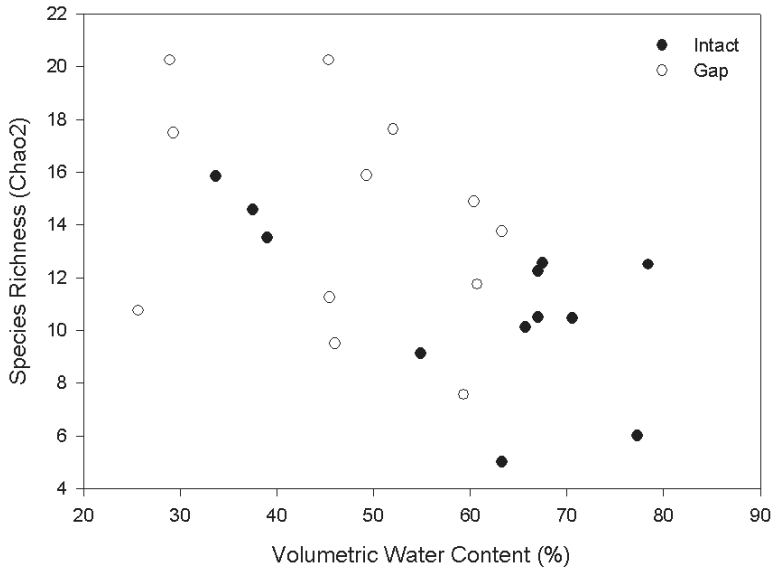

FIGURE 5. Relationship between estimated species richness and soil moisture. Estimated species richness (mini-Winklers) is significantly negatively related to soil moisture when both gap and intact sites are considered together ($r^2 = 0.28$, P = 0.01).

VITA

Margaret Patrick was born in Jacksonville, Alabama, on May 3, 1981. In 2003, She received a B.S. degree in Zoology from Auburn University. She began attending the University of Tennessee in 2006 and received a M.S. degree in Ecology and Evolutionary Biology with a minor in Environmental Policy in 2008. In August 2008, she will start working towards a Ph.D. in the Geography department at the University of Tennessee.