Changes in Ant Species Richness and Composition During Plant Secondary Succession in Puerto Rico

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Abstract.—In general, faunal diversity increases with forest age; therefore, we predict that ant species richness in secondary forests will increase during succession and species composition will vary among different stages of succession. To test this hypothesis we describe the ant communities from five chronosequences comprised of forests that varied in the time lapsed since abandonment (i.e. 0-5 yr, 25-35 yr, and >60 yr). In each site, ants were sampled using baited traps, pitfall traps, and litter sampling. Ants were identified to species and species abundance per sample was recorded. A total of 21 ant species were collected. In all chronosequences, the 25-35 yr secondary forests had the highest ant richness. During this stage of succession, these forests have resources and microhabitats representative of both early successional forest (0-5 yr) and older successional forest (>60 yr). Thus, the ant species composition included both open-habitat and forest ant species. However, the overall composition of the 25-35 yr secondary forests displayed greater similarity to the composition of the >60 yr secondary forests. Similar results were obtained when we included two additional chronosequences and limited the analysis to litter ants. These results suggest that site age is a major force driving ant diversity and composition during plant secondary succession in Puerto Rico.

Keywords.—arboreal ants, litter ants, Puerto Rico, species composition, species richness, succession

Introduction

Humans have transformed large areas of forests into agricultural lands. Occasionally these lands are abandoned, thereby allowing the process of secondary succession to occur. In many tropical systems, secondary succession can result in a rapid recovery of woody species richness (Aide et al., 1995) and an increase in structural complexity (Connell and Slatyer, 1977). This in turn increases the availability of habitats and resources for organisms (Murdoch et al., 1972). For example, the increase in richness of woody vegetation in abandoned pastures in Puerto Rico (Aide et al., 1995) increased the quantity and richness of litter, which was correlated with an increase in litter insect richness (Barberena-Arias and Aide, 2003).

The recovery of ant communities is important because they participate in many ecosystem processes, such as seed dispersal, predation and decomposition (Torres and Medina-Gaud, 1998), and can therefore influence the pattern of forest recovery (Didham et al., 1996). For example, ants can have an enormous impact on soil characteristics, vegetation, and other organisms in a community (Hölldobler and Wilson, 1990; Andersen, 1991; Torres and Medina-Gaud, 1998). Ants can improve conditions for plant growth (Torres and Medina-Gaud, 1998) by exposing nutrients and minerals (Hölldobler and Wilson, 1990; Martin and Gershuny, 1992; Hoyt, 1997), mixing soil and thereby improving aeration (Hölldobler and Wilson, 1990; Hölldobler and Wilson, 1995; Hoyt, 1997; Agosti et al., 2000), and by accelerating water drainage (Hoyt, 1997). But ants can also eliminate plants around the nesting area (Hölldobler and Wilson, 1990). For example, leaf-cutting ants can eat more than 250 kg of leaves per year (Fowler et al., 1990) and thus also influence the spatial distribution of nutrients because the areas where they

deposit nest debris/fresh plant material have higher nutrient concentrations than the surrounding soil (Torres et al., 1999). This evidence highlights the importance of ants in influencing plant dynamics. However, changes in plant richness and structure can also influence the ant community.

During succession, the increase in vegetation cover changes the environmental conditions (e.g. temperature, shaded areas, soil moisture and amount of litter) (Lubertazzi and Tschinkel, 2003), which in turn affects the ant community. Because each ant species has particular physiological and behavioral characteristics that allow them to utilize a particular habitat, slight changes in microhabitat conditions can shift the ant community composition (Sanders and Gordon, 2000). For example, ant diversity decreased in hammock forest stands in the Florida Everglades after being invaded by the Brazilian pepper tree because of a change in the litter microhabitat conditions (Clouse, 1999).

During the early 1900s, agricultural lands dominated the island of Puerto Rico (Birdsey and Weaver, 1987). Later, as a result of changes in the economy during the 1950s, agricultural lands were progressively abandoned. This resulted in an increase of secondary forests (Dietz, 1986; Birdsey and Weaver, 1987). Forest cover has increased from approximately 5% in 1940 to >35% in 1985 (Birdsey and Weaver, 1987). The result is a mosaic of secondary forests that provides the opportunity to study the recovery of ant communities. Although ants participate in many ecosystem processes, few studies have described ant community changes during secondary succession in the Caribbean. We predict that during plant secondary succession, ant species richness will increase with site age and ant species composition will vary among sites in different stages of vegetation recovery. To test this hypothesis, we present two data sets. The first data set, "Ant community", focuses on the entire community by including data on litter as well as epigeal and arboreal ant species from three chronosequences (Sabana, Carite and Luquillo). The second data set, "Litter ants", covers a large geographic area (e.g.five chrono-

sequences from (Sabana, Carite, Luquillo, Ciales, and Utuado). However, the analyses are restricted to only ant species sampled in the litter.

MATERIAL AND METHODS

Ant community

Study sites.—The study sites were located in the Sabana and Carite regions of Puerto Rico in the subtropical wet forest life zone (Ewel and Whitmore, 1973). Within each region, a chronosequence of three secondary forests was selected. The chronosequences included: a 0-5 yr secondary forest, a 25-35 yr secondary forest, and a >60 yr secondary forest.

The 0-5 yr and 25-35 yr forests are abandoned pastures (Aide et al., 1995, Pascarella et al., 2000) while the older forests are >60 yr secondary forests with dense vegetation. The 0-5 yr secondary forests have an open canopy and are dominated by grasses, the 25-35 yr secondary forests have a semi open canopy and some understory vegetation, and the >60 yr secondary forests have a closed canopy and scarce understory vegetation. In the Sabana region one of the common pioneer species is *Cecropia schreberiana* (Moraceae) (Guariguata, 1990), and the dominant trees are *Dacryodes excelsa* (Burseraceae), *Manilkara bidentata* (Sapotaceae) and *Sloanea berteriana* (Elaeocarpaceae) (Brown et al., 1983; Ewel and Whitmore, 1973). In the Carite region, the dominant trees species are *Spathodea campanulata* (Bignoniaceae), *Caesaria sylvestris* (Flacourtiaceae) and *C. guianensis*. *Prestoea montana* (Aracaceae) was the most common species in the >60 yr secondary forest (Pascarella et al., 2000).

A rapid assessment in an additional chronosequence (Luquillo) was done to verify the results of the successional study. The Luquillo sites occur in the subtropical moist forest life zone, and were similar in age and structure to those of Sabana and Carite. In addition, to characterize differences in microclimate among forests of different ages, in June 2001, temperature at 30 cm aboveground was measured. The 0-5 yr secondary forest had the highest maxi-

mum temperature (36°C) and the greatest range in temperature (22.8°C-36°C). The range of temperature in the 25-35 yr (22°C-30°C) and >60 yr secondary forests (23°C-29°C) was much less in comparison with the 0-5 yr secondary forest, and the maximum temperature in the 25-35 yr secondary forest was slightly higher (0.5-1.0°) than that of the >60 yr secondary forest.

Data collection.—The ant communities in Sabana and Carite were collected in five monthly censuses between February and July 2000. In each site and during each census, samples were collected along two transects, and the orientation position of each transect was changed to increase site coverage. In each transect three sampling points, separated by 8 m, were established. At each sampling point, three sampling methods were used: one litter sample (30 × 30 cm) was collected, one ground petri dish containing tuna fish, peanut butter and honey was left for 45 minutes, and one arboreal trap containing tuna fish was placed on a nearby tree at a height of 2 m and was left for 45 minutes. The arboreal traps were small plastic containers (3 cm in diameter) with 2 mm mesh. Arboreal traps were not used in the 0-5 yr secondary forest because there were no large trees. Litter samples were placed in a Berlese funnel for 24 hours. In the laboratory, individuals were identified, counted, and stored in alcohol. Ants were identified to species by Dr. Juan Torres. With this design, during each census, we collected 18 samples per site (6 replicates/method × 3 methods) except for the 0-5 yr secondary forests where arboreal traps were not used (6 replicates/method × 2 methods). Each site was censused five times for a total of 90 samples (18 samples × 5 times) from each 25-35 yr and >60 yr secondary forest, and 60 samples (12 samples × 5 times) from each 0-5 yr secondary forest.

The rapid assessment in the Luquillo chronosequence was conducted on March 10, 2001. The total number of litter samples, and baited and arboreal traps was the same as the cumulative number of samples from the 5 censuses in the Sabana and Carite chronosequences.

Statistical analyses.—A Kruskal-Wallis one-way ANOVA (Statistix7, 2000) was used to determine the effect of site age (0-5 yr, 25-35 yr, >60 yr) and region (Sabana, Carite, Luquillo) on ant richness. A nonmetric multidimensional scaling analysis (NMDS) was used to discriminate sites based on species composition. NMDS uses ranked distances to linearize relationships between species. In addition, community composition data sets are not independent, and thus do not meet the assumptions required for other multivariate analyses (e.g., Canonical, Correspondence, Detrended, or Principal Component analyses) (McCune and Grace, 2002). Due to the high variability in species abundance, this analysis was based on Sorensen's dissimilarity index using presence/absence data. This analysis was done using PC-ORD (1999) with a random starting, the number of runs with real data was 15, the number of iterations was 500, and the stability criterion was 0.005. In addition, a Multi-Response Permutation Procedure (MRPP) was used to determine the differences among predefined groups. We tested differences due to age and region on ant composition. This test is a nonparametric test similar to Anosim (McCune and Grace, 2002), and was also based on Sorensen dissimilarity index.

Litter ants

Study sites.—The study sites included the three chronosequences previously described, and two additional chronosequences in Ciales and Utuado that were similar to those described for Sabana and Carite (Rivera and Aide 1998, Marcano et al., 2002).

Data collection.—This section includes data of litter ants collected as described earlier (2000 collection), and data collected in Sabana, Carite, Ciales and Utuado during 1998-1999 (Barberena-Arias 2000, Barberena-Arias and Aide 2003). Both, the 2000 collection and the 1998-1999 collection followed a similar procedure using Berlese funnels, and the time allowed for ant extraction was 24 hrs and 48 hrs, respectively. Ants are mobile enough to respond quickly to the temperature and humidity gradients

created within the extraction funnel, as a consequence, the majority of species will be collected in the first 24 hrs (Barberena-Arias et al. unpubl.) resulting in no different ant diversity between the two collections due to different extraction times.

Statistical analysis.—We used a Kruskal-Wallis one-way ANOVA to determine the effect of site age (0-5 yr, 25-35 yr and >60 yr secondary forests) and region (Carite, Sabana, Luquillo, Ciales and Utuado) on ant richness. An NMDS analysis was used to discriminate sites based on species composition, using the Sorensen index based on presence/absence of species on each site. The parameters were the same as for the successional hypothesis. In addition, a MRPP test was used to determine differences in species composition due to age and region (data from the 1998-99 and 2000 samples in the same chronosequence were pooled).

<center>RESULTS</center>

Ant community

A total of 19 species were collected in the three chronosequences from Carite, Sabana and Luquillo (Table 1). *Wasmannia auropunctata, Brachymyrmex heeri, Tapinoma melanocephalum, Pheidole moerens,* and *Linepithema mellea* were collected in all traps (Table 1). *Cardiocondyla emeryi* and *Tapinoma melanocephalum* are introduced Old World species and the other 17 species are native to Puerto Rico (Snelling and Torres, in litt.). *Wasmannia auropunctata, Strumigenys rogeri, B. heeri* and *Solenopsis corticalis* occurred in all nine sites. *Pheidole fallax, Pheidole subarmata* and *Cardiochondyla emeryi* were unique to 0-5 yr secondary forests, and *L. mellea, Odontomachus ruginodis, Cyphomyrmex minutus, Hypoponera opaciceps,* and *Solenopis azteca* were collected exclusively from older secondary forests (Table 1).

The total cumulative number of species collected in Sabana and Carite ranged from 9 to 13, and from 11 to 14, respectively (Fig. 1). In Sabana, the species/sample curves for the 0-5 yr and >60 yr secondary forests reached a plateau after three

samples, and for the 25-35 yr secondary forest a plateau was reached after four samples. In Carite, the curves continued to increase at the end of the study, suggesting that additional sampling may have detected more species. There was no statistical difference in ant species number due to site age (Kruskal-Wallis = 4.99, P = 0.08) or region (Kruskal-Wallis = 2.11, P = 0.34) (Fig. 1). However, there was a trend for a highest number of species in 25-35 yr secondary forests in all regions and a similar number of species between 0-5 yr and >60 yr secondary forests. The rapid assessment in the Luquillo chronosequence showed a similar pattern of richness, with the highest richness in the 25-35 yr secondary forest (Fig. 1).

There was a significant age effect on species composition (MRPP, A = 0.16, p = 0.01), but no regional effect (MRPP, A = −0.05, p = 0.75) (Fig. 2). Axis I explained 31.2% and Axis II explained 24.2% of the variance. These axes had 76.3% orthogonality. When the 0-5 yr secondary forests were excluded from the analysis, there was no difference in the species composition between the 25-35 yr and >60 yr secondary forests (MRPP, A = 0.001, p = 0.47). The difference in species composition between the young (0-5 yr) and older (i.e. 25-35 yr and >60 yr) forest sites was due to three unique species (*Pheidole subarmata, P. fallax* and *Cardioncondyla emeryi*) in the young sites and five species that were absent from the young sites but shared by the two older forest stages (Table 1).

Litter ants

A total of 18 species were collected from litter samples from the five chronosequences (Table 2). The most common species were *Wasmannia auropunctata, Solenopsis corticalis, Tapinoma melanocephalum,* and *Strumigenys rogeri. Monomorium ebeninum* was unique to 0-5 yr secondary forests, and *O. ruginodis, C. minutus, L. mellea, Platythyrea punctata* and *S. azteca* were only collected in 25-35 yr and >60 yr secondary forests.

The number of species ranged from 3 to 9 in the 0-5 yr secondary forests, from 7 to 12

TABLE 1. Ant species present in three chronosequences (young, intermediate and old secondary forests) from three regions in Puerto Rico (Carite, Sabana and Luquillo). The trap type where each species was collected is indicated by L = litter, P = baited petri dish, A = arboreal bait. Following Snelling and Torres (unpubl.), we classified ants as introduced (I) or native (N).

| Species (classification)	Trap			Carite			Sabana			Luquillo		
				Young	Intermediate	Old	Young	Intermediate	Old	Young	Intermediate	Old
Wasmannia auropunctata (N)	L	P	A	x	x	x	x	x	x	x	x	x
Strumigenys rogeri (N)	L			x	x	x	x	x	x	x	x	x
Brachymyrmex heeri (N)	L	P	A	x	x	x	x	x	x	x	x	x
Solenopsis corticalis (N)	L	P		x	x	x	x	x	x	x	x	x
Tapinoma melanocephalum (I)	L	P	A	x	x	x	x	x	x	x	x	
Pheidole moerens (N)	L	P	A	x	x	x	x	x	x	x	x	
Solenopsis geminata (N)	L	P		x	x	x	x	x		x	x	
Paratrechina steinheili (N)	L	P		x		x	x	x	x	x	x	x
Anochetus mayri (N)	L	P			x	x	x	x			x	x
Linepithema mellea (N)	L	P	A		x	x		x	x		x	x
Odontomachus ruginodis (N)	L	P						x	x		x	x
Cyphomyrmex minutus (N)	L				x	x		x	x			
Leptothorax sp. (N)		P			x			x		x		
Pheidole fallax (N)		P		x								
Monomorium ebeninum (N)	L	P		x	x					x	x	x
Pheidole subarmata (N)		P		x								
Cardiocondyla emeryi (I)		P		x								
Hypoponera opaciceps (N)	L				x							
Solenopsis azteca (N)	L				x							
Total in each site				12	14	11	9	13	10	10	12	9
Total in each region					18			13			13	
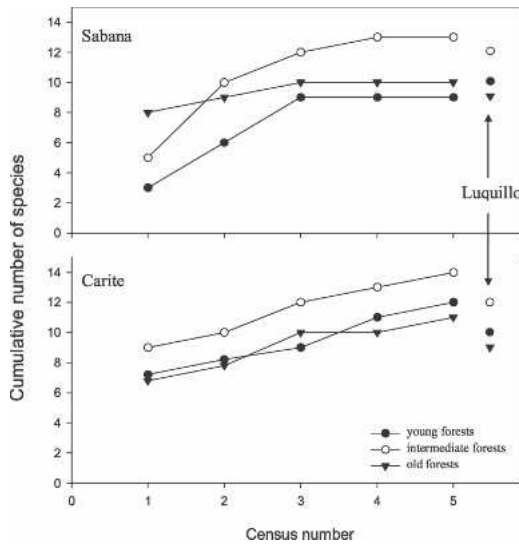
FIG. 1. Cumulative number of ant species in the three types of secondary forest in Carite and Sabana. The number of species in the rapid assessment in Luquillo is indicated by dots at the right side of the figure. Young forests represent the 0 – 5 yr sites, intermediate forests represent the 25-35 yr forests, and the old forests represent the >60 yr sites.

in the 25-35 yr secondary forests, and from 8 to 9 in the >60 yr secondary forests (Table 2). There was a significant age effect on the number of species (Kruskal-Wallis = 8.55,
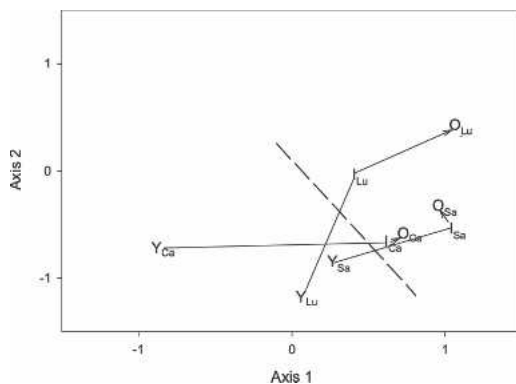

FIG. 2. NMDS plot ordination of sites within regions. Upper case letters indicate site age (Y: 0-5 yr, I: 25-35 yr, O: >60 yr), and lower case letters indicate region (Sa: Sabana, ca: Carite, Lu: Luquillo). The arrow indicates the direction of succession, and the dashed line indicates the two groups that resulted from the MRPP analysis: 0-5 yr secondary forests and 25-35 yr/ >60 yr secondary forests.

df = 2, P = 0.01) but there was no regional effect (Kruskal-Wallis = 6.99, df = 6, p = 0.32). The age effect was due to the low richness in the 0-5 yr secondary forests and a trend for the highest number of species to be in the 25-35 yr secondary forests.

There was a significant effect of age (A = 0.10, p = 0.0007), but no effect of region (A = 0.037, p = 0.18) on ant species composition (Fig. 3). Axis I explained 38.7% and Axis II 22.7% of the variance. These axes had 99.7% orthogonality. When the 0-5 yr secondary forests were excluded from the analysis, the species composition between 25-35 yr and >60 yr secondary forests was not different (MRPP, A = 0.16, p = 0.27). The difference in species composition between the young (0-5 yr) and older (i.e. 25-35 yr and >60 yr) forests sites was due to one unique species (*Monomorium ebeninum*) in the young sites and five species that were absent from the young sites and shared by the two older forest stages (Table 2).

DISCUSSION

Successional trends in the ant community

We predicted that ant species richness would increase in response to an increase in structural complexity and that richness would be highest in the >60 yr secondary forests. However, it was found that richness was highest in the 25-35 yr secondary forests (Table 1). These forests have microhabitat characteristics of 0-5 yr secondary forests (e.g. areas of high light and herbaceous vegetation) and of >60 yr secondary forests (e.g. trees, closed canopy, and leaf litter), suggesting that they have a greater diversity of the microhabitats and resources that are good predictors of ant diversity (Torres and Snelling, 1997). Similar results have been observed in secondary forests on abandoned bauxite mines in Brazil, where habitats with greater plant structural diversity tended to have higher ant species richness (Majer, 1992).

Ant species composition also varied among the forests in different stages of succession. The most obvious difference was between the young forest sites (0-5 yr) and

TABLE 2. Litter ant species in Sabana, Carite, Utuado, Ciales and Luquillo. The 1998-1999 collections are reported in Barberena-Arias (2000). Upper case letters indicate Y: 0-5 yr secondary forests, I: 25-35 yr secondary forests, O: >60 yr secondary forests.

| Species	Sabana 98-99			Sabana 2000			Carite 98-99			Carite 2000			Utuado 98-99			Ciales 98-99			Luquillo 2000		
	Y	I	O	Y	I	O	Y	I	O	Y	I	O	Y	I	O	Y	I	O	Y	I	O
Wasmannia auropunctata	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Solenopsis corticalis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x
Strumigenys rogeri	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x
Tapinoma melanocephalum	x	x	x	x	x	x			x	x	x	x	x	x	x		x			x	
Pheidole moerens	x		x	x	x	x		x	x	x	x	x	x	x	x		x	x		x	
Paratrechina steinheili			x	x	x	x	x		x			x	x	x	x	x	x		x		x
Odontomachus ruginodis		x	x		x	x			x					x	x		x	x		x	x
Hypoponera opacipeps		x					x	x			x			x	x		x	x			
Cyphomyrmex minutus					x	x		x	x		x	x			x		x	x			
Solenopsis geminata				x				x		x	x		x						x		
Brachymyrmex heeri			x	x	x	x															x
Pheidole sp.	x								x								x	x			
Morfo 571										x	x	x		x							
Monomorium ebeninum										x									x		
Anochetus mayri				x	x						x									x	x
Linepithema mellea											x	x								x	x
Platythyrea punctata		x																			
Solenopsis azteca											x										
Total in site	6	7	8	9	10	9	5	7	9	8	12	9	6	9	9	3	10	8	6	8	8
Total in region		11			11			11			14			11			10			12	
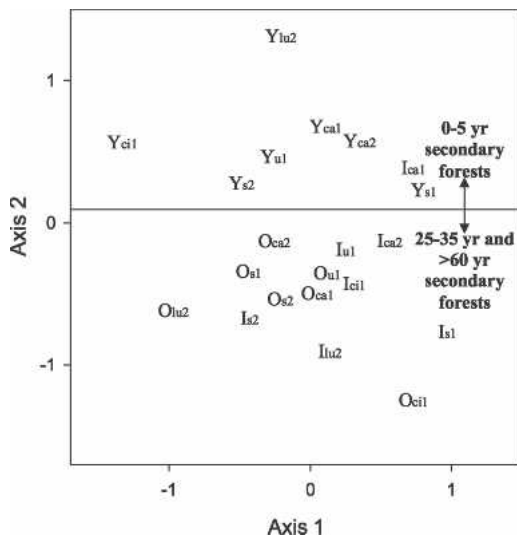
FIG. 3. NMDS ordination plot of sites based on the species composition of litter ants. Site age is indicated by upper case letters (Y: 0-5 yr, I: 25-35 yr, O: >60 yr), regions by lower case letters (s: Sabana, ca: Carite, u: Utuado, ci: Ciales, lu: Luquillo) and collections by numbers (1: 1998-1999 and 2: 2000).

the older sites (25-35 yr and >60 yr). Three ant species, *Pheidole fallax*, *P. subarmata* and *C. emeryi*, were unique to the young secondary forests. These species mainly occur in areas with high temperatures, such as pastures or agricultural lands (Torres, 1984a), suggesting that their presence in the recently abandoned sites is due to their presence prior to abandonment. Because these sites are open habitats with scattered woody vegetation (Aide et al., 1995) and higher temperatures (see site description), there are still microhabitats appropriate for these species. But, as forest succession proceeds, plant diversity and composition (Aide et al., 1995) and environmental conditions change and this is reflected as a shift in ant community composition. Specifically, the previously mentioned species are not present in the older sites and yet a few forest-specialist species appear (e.g. *L. mellea*, *C. minutus*, *O. ruginodis*, *H. opaciceps* and *S. azteca*). *Linepithema mellea* is an arboreal species, *C. minutus* feeds on fungus grown on caterpillar "feces" and nests under rotten logs and stumps (Snelling and Torres, pers. comm.), and *O. ruginodis* and *H. opaciceps* are sensitive to high tempera-

tures (Torres, 1984b). These microhabitat conditions and resources occur in the 25-35 yr and >60 yr secondary forests but are rarely present in the 0-5 yr secondary forests. Our analysis did not detect significant differences between the intermediate and older forest sites, suggesting that the ant community can recover composition in approximately 25 yr.

Successional trends in litter ants

As in the entire ant community, litter ant richness tended to be highest in the 25-35 yr forests. However, the major difference among the different forests was in their species composition. The young sites (0-5 yr) had a different composition in comparison with the intermediate (25-35 yr) and old sites (>60 yr). The young sites contained one unique species, *Monomorium ebininum*. The major difference was that all species collected in the 25-35 yr secondary forests were also collected in >60 yr secondary forests. Furthermore, five species (*O. ruginodis*, *C. minutus*, *L. mellea*, *P. punctata* and *S. azteca*) that were collected in the intermediate and older sites were absent from the younger sites. These species have habitat or resource needs that are not met in the recently abandoned sites. When sufficient forest cover was available (such as in 25-35 yr), these species began colonizing these sites. For example, *O. ruginodis* prefers low temperature areas, *C. minutus* nests on rotten logs, *L. mellea* is an arboreal species, *P. punctata* nests in forest litter and prefers shaded locations, and *S. azteca* nests in litter and decaying organic matter.

The similarity between the intermediate and older sites, and their difference with the younger site suggests that variation in the quantity and types of resources and microhabitats are influencing the species present in the different stages of succession. This observation is supported by the difference in the quantity of litter in the forest age classes (0-5 yr—mean litter mass 97 g/m^2; 25-35 yr—404 g/m^2; >60 yr—421 g/m^2, Barberena-Arias and Aide, 2003), where there is a four-fold increase in litter from the young sites to the intermediate sites but little difference between the inter-

mediate and older sites. This large change in litter quantity will change the microclimatic conditions (Lubertazzi and Tschinkel, 2003; Clouse, 1999) and greatly increase the habitat structural complexity (McGlynn and Kirksey, 2000) for litter ants.

CONCLUSIONS

Presently, Puerto Rico is a mosaic of secondary forests (Aide et al., 2000), with the different forest types providing different combinations of resources and microhabitats for ants. Both the ant community and the litter ant data sets suggest a rapid recovery of the ant community during secondary succession because after approximately 25-35 yr of forest recovery, the ant community was very similar to that of the old forest sites. The majority of ant species collected in this study appear to be generalist as most species occurred in the majority of sites. However, there are species that were restricted to old forest areas. These results suggest that old forest areas are important reservoirs of ant species and that these areas play an important role as the source of species to colonize recovering areas. Furthermore, these results also suggest that cutting secondary forests before ~30 yr of recovery threatens ant diversity in Puerto Rico. As a consequence, it is important to include both of these areas in management practices for conservation so that ant diversity is maintained in Puerto Rico.

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