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# Variation in Species and Trophic Composition of Insect Communities in Puerto Rico[1]

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## ABSTRACT

Insects are important participants in many ecosystem processes, but the effects of anthropogenic and natural disturbances on insect communities have been poorly studied. To describe how disturbances affect insect communities, we addressed two questions: Do insect communities return to a pre-hurricane composition? And how do insect communities change during succession? To answer these questions, we studied insect communities in a chronosequence of two abandoned pastures (5 yr and 32 yr) and a mature forest (>80 yr) that were recently disturbed by two hurricanes (Hurricane Hugo, 1989; Hurricane Georges, 1998). Although insect abundance and richness fluctuated during the study, all sites returned to pre-hurricane (Hurricane Georges) abundance and richness in less than one year. All trophic categories present before Hurricane Georges were present after the hurricane, but richness within categories fluctuated greatly. Insect richness did not increase during succession; the 5 yr site had the highest richness, the >80 yr site had an intermediate richness, and the 32 yr site the lowest. Nevertheless, the species composition of the two forested sites was different in comparison to the 5 yr site. These results suggest that trophic structure varies little in time and space, but the species composition within each trophic category is highly variable.

## RESUMEN

Los insectos participan en muchos de los procesos de los ecosistemas, sin embargo pocos estudios se han investigado el efecto que tienen las perturbaciones naturales y antropogénicas sobre las comunidades de insectos. Para describir cómo estas perturbaciones afectan a las comunidades de insectos, nos planteamos dos preguntas: regresan las comunidades de insectos a la composición previa despúes de un huracán? Y cómo cambian las comunidades de insectos durante la sucesión? Para contestar estas preguntas, estudiamos las comunidades de insectos en una cronosecuencia de dos pastizales abandonados (5 años y 32 años) y un bosque maduro (>80 años) que fueron recientemente perturbados por dos huracanes (Huracán Hugo, 1989; Huracán Georges, 1998). Aunque la abundancia y riqueza de insectos fluctuó durante el estudio, todos los sitios recuperaron los niveles prehuracán (Huracán Georges) en menos de un año. Todas las categorías tróficas presentes antes del Huracán Georges siguieron presentes después del huracán, pero la riqueza dentro de las categorías fluctuó ampliamente. La riqueza de insectos no aumentó durante la sucesión; el sitio de 5 años tuvo la riqueza más alta, el sitio de >80 años tuvo una riqueza intermedia, y el sitio de 32 años tuvo la riqueza más baja. Sin embargo, la composición de especies de los dos sitios de bosque fue diferente en comparación al sitio de 5 años. Estos resultados sugieren que la estructura trófica varía poco en tiempo y espacio, pero la composición de especies de las categorías tróficas es muy variable.

*Key words:* *abandoned pastures; disturbance; Hurricane Georges; insect community structure; insect diversity; Puerto Rico.*

Plant species richness and structural diversity increase with succession, and as a consequence late successional stages have a greater diversity of resources and habitats that promote insect richness (Murdoch *et al.* 1972, Southwood *et al.* 1979). Natural and anthropogenic disturbances alter the structure of habitats by changing the composition and abundance of the vegetation (Garrison & Willig 1996, Pfeiffer 1996). For example, treefall gaps change plant species composition by increasing the abundance of pioneers (Denslow 1980). Hurricanes can cause complete defoliation, and branch- and treefalls, but often there is little change in the composition of plant communities (Lawrence 1996). Anthropogenic disturbances such as deforestation followed by agriculture remove the aboveground biomass, which leads to a loss of the upper soil layers (Begon *et al.* 1990) and greatly reduces the recovery potential of these sites. These disturbances redistribute resources (Shure & Phillips 1991), change animal movement patterns (McIntyre & Wiens 1999), and thus change insect diversity and species composition (Klein 1989).

Although the insect community is crucial in the process of plant succession, few studies have

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described the recovery of insect communities following natural or anthropogenic disturbances (Schowalter & Ganio 1999). Insects play an important role in the recovery of vegetation mainly through decomposition, pollination, and herbivory. Decomposition by insects is important because they initiate the breakdown of litter and accelerate the rate of nutrient release to the soil (Pfeiffer 1996). Insect pollinators, mainly bees and butterflies, are important for gene flow in flowering plants and influence genetic diversity in plant communities (Huffaker & Rabb 1984). Herbivore insects can reduce the area for photosynthesis, and decrease plant primary productivity, but their activity can also stimulate nutrient cycling (Mattson & Addy 1975, Schowalter 1995). These examples illustrate the tight relationship between insects and plants, and thus suggest that any change in the plant community should produce a change in the insect community.

The response of insect communities to disturbance is highly variable because changes in a habitat may increase resources for some species or reduce resources for others. For example, hurricanes have diverse effects on the vegetation because they produce landslides, floods, large amounts of fallen wood, and large open areas in the canopy (Lawrence 1996, Walker *et al.* 1996). Insect species may disappear from a disturbed habitat as a result of local extinction of their resources (Willig & Camilo 1991). On the other hand, populations of some Lepidoptera larvae that feed on new foliage of early successional vegetation increased dramatically after Hurricane Hugo (Torres 1992).

To study the effects of natural and anthropogenic disturbances, we compared insect communities before and after Hurricane Georges (September 1998) in a chronosequence of two abandoned pastures (5 yr and 32 yr) and a mature forest (>80 yr) in the Luquillo Experimental Forest (Puerto Rico). Specifically, we addressed the following two questions: (1) Do insect communities return to a pre-hurricane composition (within-site variation)? The recovery of the insect community will depend on how the hurricane affected the vegetation within each successional stage. Hurricane effects are stronger in older forests because the canopy is heterogeneous and subjected to more wind-related damage, which leads to more fallen trees (Barberena-Arias 2000). As a consequence, there is a greater change in resources and habitats in older forests compared with younger forests. If abundance and richness are used to characterize the insect community, we would expect a more rapid recovery in the younger sites in comparison with older sites. The number of trophic categories present before Hurricane Georges should not change after the hurricane, but their richness should vary among pre-hurricane and post-hurricane censuses. Specifically, insects depending on decomposing material such as litter should increase (*e.g.*, detritivores), while insects that depend on leaves and flowers should decrease. (2) How do insect communities change during succession (among-site variation)? During succession, insect richness should increase as plant richness and structural diversity increase. The largest difference in species composition should be between the herbaceous-dominated young site and the two older forested sites. The three sites should share the majority of the trophic categories, but the older site should have the highest richness within each trophic category. The effects of Hurricane Georges varied among the successional stages, and we expected that the older site would lose a greater proportion of its insect diversity compared with younger forests. As a consequence, the recovery of pre-hurricane richness and species composition should be slower in the older site.

# METHODS

STUDY AREA.—The study sites were located in the Sabana area of the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18°17'N, 65°42'W; Fig. 1). The area occurs in the subtropical wet forest zone, which has an annual rainfall range of 2000 to 4000 mm (Ewel & Whitmore 1973). A chronosequence of three sites was established. The two younger sites were pastures that had been abandoned for 5 and 32 years and the older site (>80 yr) had little human disturbance during the last 80 years (Aide *et al.* 1995). In addition to the effects of past human disturbances, these sites have been recently disturbed by two severe hurricanes, Hugo (1989) and Georges (1998).

The 5 yr site was dominated by grasses and ferns, but also included scattered shrubs, mainly *Miconia prasina* (Melastomataceae). The 32 yr site was dominated by *Myrcia splendens* (Myrtaceae). Other common tree species were *Syzygium jambos* (Myrtaceae), *M. prasina* (Melastomataceae), *Tabebuia heterophylla* (Bignoniaceae), and *Palicourea riparia* (Rubiaceae; Aide *et al.* 1995). These species have created a closed canopy (12 m height) that reduces the growth of grass and fern species. The >80 yr site was dominated by *Ficus citrifolia* and *Cecropia schreberiana* (Moraceae), mixed with

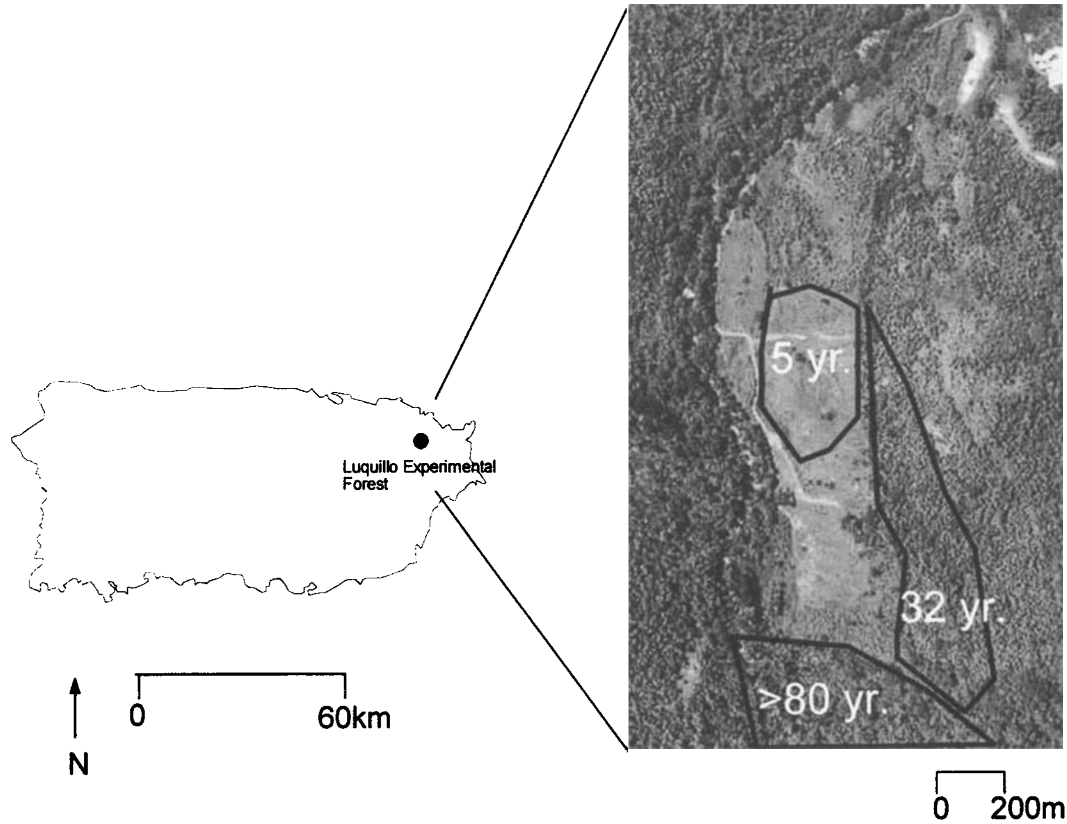


FIGURE 1. Location of the three study sites (5 yr, 32 yr, and >80 yr) in Puerto Rico, within the Luquillo Experimental Forest.

*Psychotria brachiata, P. berteriana* (Rubiaceae), *Prestoea montana* (Palmae), *Piper glabrescens* (Piperaceae), and *Casearia arborea* (Flacourtiaceae; Aide *et al.* 1995). Before Hurricane Georges there was a closed canopy *ca* 20 m in height with scattered gaps that had been created by Hurricane Hugo.

During the study period, the structure of all sites changed. In the 5 yr site, Hurricane Georges caused little change but there was an increase in shrub cover. The structure of the 32 yr and >80 yr sites was more affected by the hurricane. In the 32 yr site, Hurricane Georges caused some treefalls and canopy gaps (17.68 $m^2$/ha of fallen wood, Barberena-Arias 2000), increasing litter and woody debris, but there continued to be little understory vegetation. The >80 yr site suffered more extensive damage due to Hurricane Georges (67.8 $m^2$/ha of fallen wood; Barberena-Arias 2000), which created larger canopy gaps favoring the growth of herbaceous vegetation (*e.g.*, grasses) in the understory. By the end of the study, the canopy in the >80 yr site was closing and the herbaceous vegetation was dying.

DATA COLLECTION.—Insects were surveyed five times: before Hurricane Georges in June 1998 (census 1); after the hurricane in October 1998 (census 2); March 1999 (census 3); July 1999 (census 4); and October 1999 (census 5). At each survey, four different sampling methods were used: litter sampling, malaise trap, interception trap, and pitfall trap baited with human feces. Four litter samples (30 × 30 cm each) were collected in each site and were placed in a Berlese funnel for 24 hours. This sampling method collects insects that have a small movement range. One malaise trap was left for 24 hours (in each site) in order to collect insects that fly upwards when they collide with the trap. One interception trap was left for 24 hours. The trap consisted of mosquito netting 1.65 (width) × 1.2 m (height), with the bottom ending in a canal of soapy water. This trap collects

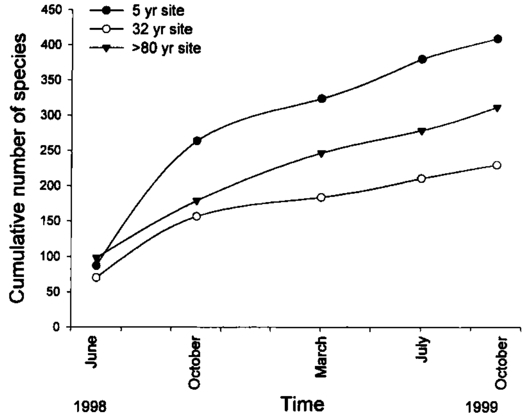


FIGURE 2. Species/sampling curves for the three sites during the five censuses. Data are the total number of morphospecies collected with the four sampling methods.

flying insects that fall once they collide with the trap. Five pitfall traps baited with human feces were placed in the soil at each site and were retrieved after 24 hours. This trap collected walking and coprophagous insects. In each site, litter samples were separated by 20 m, and pitfall traps were also separated by 20 m. Each trap was located at least 20 m from the edge of the site.

To determine species composition, all adult insects were identified to family and assigned to a morphospecies. In addition, each morphospecies was assigned to a trophic category according to the food habit of adults as determined by the group's natural history (Borror *et al.* 1989), morphology, and the trap in which it was collected (Table 1). Individuals in the order Collembola were identified and grouped by family, because differences between species and between life stages are difficult to determine.

DATA ANALYSIS.—Species/sampling curves were constructed for each site. Two Friedman two-way analyses of variance were used to determine the effect of site age (5 yr, 32 yr, and >80 yr) on abundance and insect richness, using censuses as replicates. A non-metric multidimensional scaling ordination (NMDS) was used to compare the species composition at each site in each census (Clarke 1993, Philippi *et al.* 1998, Talley & Levin 1999). The matrix for the NMDS was based on the Sørensen dissimilarity index, calculated using presence/absence of each morphospecies in each site at each census. In addition, given that more than 50 percent of the species were Diptera (347 of 610), a second matrix without Diptera was analyzed. The multi-response permutation procedure (MRPP; PC-ORD 1999) was used to determine if differences were significant among sites (age) and time (censuses), for species and trophic composition.

## RESULTS

MORPHOSPECIES ABUNDANCE AND RICHNESS.—A total of 13,126 individuals was collected in the five censuses at the three sites. These individuals were classified into 616 morphospecies and 17 orders (Table 1). Diptera had the highest number of morphospecies (347), followed by Hymenoptera (72) and Lepidoptera (71). In addition, the species/sampling curves, for each site, continued to increase at the end of the study (Fig. 2).

There was no significant age effect on insect abundance (Friedman statistic = 2.8, df = 2, $P$ = 0.25), but it fluctuated greatly within each site (June 1998–October 1999; Fig. 3). Before Hurricane Georges (June 1998), the abundance varied between 500 and 1000 individuals per site. In the census immediately after the hurricane, insect abundance increased by 200 to 400 percent in all sites, from 495 to 2275 in the 5 yr site, from 932 to 2267 in the 32 yr site, and from 768 to 2337 in the >80 yr site. With the exception of a small peak in July 1999 in the 5 yr site, the abundance returned to pre-hurricane levels in the last three censuses (March, July, and October 1999).

There was a significant age effect on insect richness (*i.e.*, sites; Friedman statistic = 8.4, df = 2, $P$ = 0.01; Fig. 3). A total of 409 morphospecies was collected in the 5 yr site, 230 in the 32 yr site, and 312 in the >80 yr site; in addition, in the four post-hurricane censuses, the 32 yr site had the lowest richness and the 5 yr site had the highest. Before Hurricane Georges, richness varied between 50 and 100 morphospecies in all sites. In the 5 yr and 32 yr sites, richness increased dramatically immediately after the hurricane but returned to pre-hurricane levels in the last three censuses. In the >80 yr site, richness varied little among censuses.

TROPHIC CATEGORIES.—Among the 16 trophic categories, the 3 richest categories were plant exudates (179 spp.), licking (78 spp.), and nectarivore (75 spp.; Table 1). There was little variation in the total number of trophic categories through time and among sites, but the number of morphospecies within trophic categories varied greatly (Table 2). Before Hurricane Georges, the total number of morphospecies in each trophic category within sites varied between 0 and 29 morphospecies, while af-

of morphospecies, by order, assigned to each of the 16 trophic categories. Trophic categories were created to group morphospecies that exploit res
categories were assigned according to the group's natural history, the morphospecies morphology, and the trap in which it was collected.*

| | Insect orders | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| gories | Diptera | Hymenoptera | Lepidoptera | Coleoptera | Homoptera | Hemiptera | Collembola | Psocoptera | Orthoptera | Thysanoptera | Isoptera | Ephemeroptera | Dermaptera | Diplura | Blattaria | Odonata | Stre sip- tera |
| | 151 | 28 | | | | | | | | | | | | | | | |
| | 78 | | | | | | | | | | | | | | | | |
| | 2 | 2 | 71 | | | | | | | | | | | | | | |
| | 31 | 9 | | 15 | | 1 | | | | | | | 2 | | | 1 | |
| | 47 | | | | | | | | | | | 3 | | | | | |
| ıs | | | | | 35 | 8 | | | | | | | | | | | |
| | | 33 | | | | | | | | | | | | | 2 | | |
| | 33 | | | | | | | | | | | | | | | | |
| ous | | | | 17 | | | | | 4 | 4 | | | | | | | |
| | | | | 2 | | | 5 | 5 | | | 3 | | | 2 | | | |
| | 5 | | | 4 | | | | | | | | | | | | | |
| ıs | | | | 2 | | | | | | | | | | | | | |
| | | | | 2 | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | 1 |
| | | | | 1 | | | | | | | | | | | | | |
| | | | | 1 | | | | | | | | | | | | | |
| ıorphospecies | 347 | 72 | 71 | 44 | 35 | 9 | 5 | 5 | 4 | 4 | 3 | 3 | 2 | 2 | 2 | 1 | 1 |

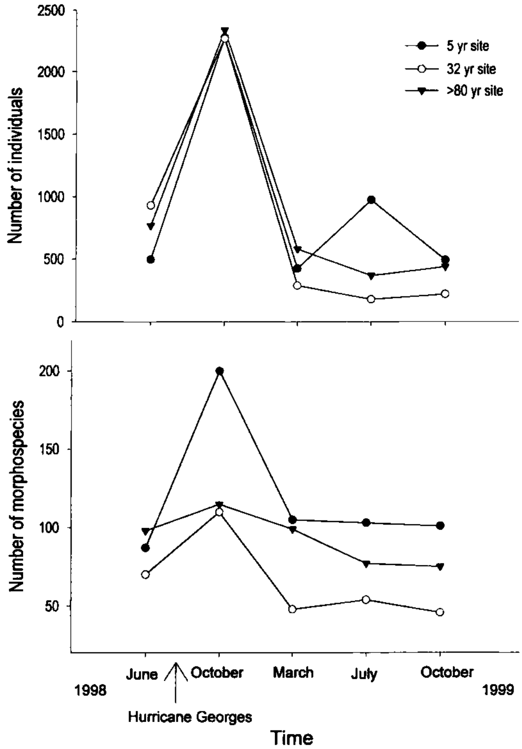


FIGURE 3. Fluctuations in (a) abundance and (b) richness of insects from June 1998 to October 1999 in the three sites. Note that Hurricane Georges passed over these sites on 21 September 1998.

ter the hurricane, the range increased to between 0 and 66 morphospecies. In the 5 yr site, the number of species in the plant exudates category increased from 9 to 66 morphospecies after the hurricane, while the richness of nectarivores decreased from 29 to 8 morphospecies. In the 32 yr site, the number of morphospecies in the plant exudates category doubled and the number of licking morphospecies increased from 0 to 16. By the end of the study, in the 5 yr site, the richness of the plant exudates category decreased to levels similar to June 1998, and in the 32 yr site, richness of plant exudates and licking categories also decreased to pre-hurricane levels. In the >80 yr site, richness within trophic categories showed little variation through time, in comparison with the 5 yr and 32 yr sites.

SPECIES AND TROPHIC COMPOSITION.—Of a total of 213 morphospecies collected in all sites in the first census, only 18 of these morphospecies persisted (*i.e.*, were captured in at least three of the four post-hurricane censuses; Table 3). Two morphospecies, *Wasmannia auropunctata* and *Solenopsis* spp. (Formicidae), occurred in all sites and in all censuses. In the 5 yr site, there were 8 persistent morphospecies. Most were Diptera collected in the malaise and interception traps. In the 32 yr and >80 yr sites, there were 8 and 10 persistent morphospecies, respectively, mostly Hymenoptera and Coleoptera, collected in pitfall traps and litter samples.

There were significant effects of age (site; MRPP, $P < 0.01$) and time (census) (MRPP, $P << 0.01$) on insect species composition (Fig. 4). When all Diptera (>50% percent of the species) were excluded from the analysis, there continued to be significant effects of age (MRPP, $P = 0.003$) and time (MRPP, $P = 0.006$; Fig. 4). In the NMDS there was no overlap in species composition trajectory of the 5 yr site with the trajectories of the 32 yr and >80 yr sites. In addition, when the 5 yr site was excluded from the analysis, the species composition between the 32 yr and >80 yr sites was not different (MRPP, $P = 0.25$), suggesting that the age effect was due to a different species composition in the 5 yr site. Through time, species composition trajectories in all sites moved in the same direction, resulting in different species composition between census 1 and census 5 (Fig. 4). In census 1, the three sites shared 9 species (2 Formicidae, 2 Collembola, 3 Homoptera, 1 Coleoptera, and 1 Hemiptera), and in census 5, there were 16 shared species. Only 2 species (Formicidae) were common to all sites in census 1 and census 5. The remaining 15 species (11 Diptera, 4 Fomicidae, and 1 Homoptera) shared in census 5 were responsible for the common trajectory of the three sites. In census 2, the three sites shared 28 species (22 Diptera, 3 Formicidae, 1 Collembola, and 2 Homoptera), and in censuses 3 and 4, the sites shared 7 species (6 Diptera and 1 Homoptera) and 8 species (4 Formicidae, 1 Collembola, 2 Diptera, and 1 Coleoptera), respectively.

There was also a significant effect of time (MRPP, $P = 0.03$) and age (MRPP, $P = 0.01$) on trophic composition. In all sites, during all censuses, there was little variation in the number of trophic categories present (11–14; Table 2). Nevertheless, richness within trophic categories varied during the study period. In all sites, the number of species assigned to plant exudates, licking, predator, and vestigial mouthparts increased in the first census after the hurricane. In contrast, richness of nectarivores in the 32 yr and >80 yr sites remained similar to pre-hurricane levels, but decreased in the 5 yr site. By the end of the study period, richness within trophic categories in the 32 yr and >80 yr sites was similar to June 1998; however, in the 5

of trophic categories in each site at each census. Data were collected before Hurricane Georges (September 21, 1998) and in June 1998 (ce
e, data were collected in October 1998 (2), March 1999 (3), July 1999 (4), and October 1999 (5).

| | Censuses | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5 yr site | | | | | 32 yr site | | | | | >80 yr si | | |
| | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 |
| | 9 | 66 | 29 | 31 | 15 | 13 | 27 | 9 | 7 | 8 | 22 | 30 | 18 |
| | 4 | 31 | 20 | 21 | 20 | | 16 | 4 | 4 | 2 | 4 | 11 | 13 |
| | 29 | 8 | 15 | 8 | 8 | 2 | 3 | 5 | 3 | 3 | 5 | 6 | 17 |
| | 7 | 22 | 19 | 12 | 12 | 3 | 11 | 4 | 7 | 5 | 4 | 6 | 11 |
| | 4 | 23 | 7 | 5 | 11 | 8 | 12 | 7 | 4 | 6 | 10 | 13 | 9 |
| us | 12 | 14 | 4 | 7 | 11 | 10 | 11 | 3 | 5 | 2 | 9 | 6 | 8 |
| | 7 | 12 | 2 | 9 | 7 | 10 | 11 | 4 | 9 | 9 | 10 | 6 | 4 |
| | 7 | 13 | 3 | 3 | 10 | 5 | 9 | 1 | 4 | 6 | 11 | 13 | 1 |
| ous | 3 | 4 | 1 | 1 | 1 | 8 | 5 | 3 | 5 | 2 | 7 | 5 | 5 |
| | 2 | 2 | | 2 | 2 | 5 | 3 | 5 | 2 | 1 | 9 | 8 | 2 |
| | 1 | 4 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | | 2 | 4 | 3 |
| us | 1 | | | | | | | | | | 1 | | |
| | | | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| | | | | 1 | | | | | | | 1 | | 1 |
| | | | | | | 1 | | | | | | | |
| | 1 | | | | | | | | | | | | |
| ophic categories | 13 | 11 | 11 | 13 | 12 | 12 | 12 | 12 | 12 | 11 | 14 | 12 | 13 |
| orphospecies | 87 | 199 | 104 | 102 | 99 | 68 | 111 | 48 | 53 | 46 | 97 | 110 | 94 |

TABLE 3. *Morphospecies that persisted through the study period in a given site and sampling method. Only species that were collected in three of the four post-hurricane censuses are shown.*

| | | Sampling methods | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Malaise | | | Interception | | | Pitfall | | | Litter samples | | |
| Morphospecies | Sites | 5 yr | 32 yr | >80 yr | 5 yr | 32 yr | >80 yr | 5 yr | 32 yr | >80 yr | 5 yr | 32 yr | >80 yr |
| Order | Family | | | | | | | | | | | | |
| Coleoptera | Scolytidae | | | x | | | | | | | | x | |
| Collembola | Entomobryidae | | x | | | | | | | | | x | x |
| Diptera | Simuliidae | x | | | x | | | | | | | | |
| Diptera | Dolichopodidae | x | | | | | | | | | | | |
| Diptera | Dolichopodidae | x | | | | | | | | | | | |
| Homoptera | Cicadellidae | x | | | | | | | | | | | |
| Homoptera | Cicadellidae | | | x | | | | | | | | | |
| Diptera | Tipulidae | | | x | | | | | | | | | |
| Hymenoptera | Formicidae | | | | x | | | | | | | | |
| Diptera | Dolichopodidae | | | | x | | | | | | | | |
| Homoptera | Delphacidae | | | | x | | | | | | | | |
| Hymenoptera | Formicidae | | | | | | | x | | x | x | x | x |
| Coleoptera | Staphylinidae | | | | | | | x | x | x | | | |
| Coleoptera | Scarabaeidae | | | | | | | | x | x | | | |
| Hymenoptera | Formicidae | | | | | | | | | | | x | x |
| Hymenoptera | Formicidae | | | | | | | | | | | x | x |
| Collembola | Poduridae | | | | | | | | | | | x | x |

yr site, richness continued to be high, resulting in an age effect.

## DISCUSSION

One year after Hurricane Georges, richness in all sites returned to pre-hurricane levels and trophic categories remained similar; but within each site, species composition was very different in comparison with the initial composition. Changes in habitat structure appear to be the major factor influencing these changes in the insect community.

The 5 yr site was the least affected by Hurricane Georges. The major change in structure was an increase in shrub cover, following the typical pattern of regeneration in abandoned pastures (Aide *et al.* 2000). This site, however, continued to be dominated by grasses and was a high light, high temperature environment. At the beginning of the study, the 32 yr site was a closed canopy forest with low plant diversity, dominated by *M. splendens* (Aide *et al.* 1995). Hurricane Georges created many small canopy gaps, but there was no dramatic increase in the cover of herbaceous species. Of the three sites, the >80 yr site suffered the most damage. Before Hurricane Georges, there were some canopy gaps from Hurricane Hugo, but the canopy was mostly closed. After Hurricane Georges, the canopy was completely open and there was a dramatic increase in herbaceous vegetation. In addition, both forested sites experienced almost complete defoliation, dramatically increasing the standing crop of litter and delaying the production of new leaves and flowers (Lawrence 1996). Furthermore, the study area occurs in a landscape dominated by secondary forests (Thomlinson *et al.* 1996) that experienced similar levels of defoliation, and thus, there was an enormous amount of decomposing material in the landscape. These changes in the habitat clearly affected the composition of the insect community.

Although insect communities fluctuate seasonally with changes in humidity, temperature, and food availability (Wolda 1978, Holl 1995, Garrison & Willig 1996, Stewart & Woolbright 1996), they can also respond rapidly to resource pulses following disturbances (Torres 1992). Disturbances change the abundance and distribution of resources and can greatly modify the microhabitats used by insects (Huffaker & Rabb 1984, Shelly 1988, Didham *et al.* 1996, Garrison & Willig 1996, Reagan *et al.* 1996). For example, in this study the increase in litter and decomposing material resulted in a dramatic increase in dipteran species because this is the major food resource of the larvae (McAlpine *et al.* 1981, Borror *et al.* 1989). The diversity of other groups, such as Homoptera, Coleoptera, and Lepidoptera, declined because the production of

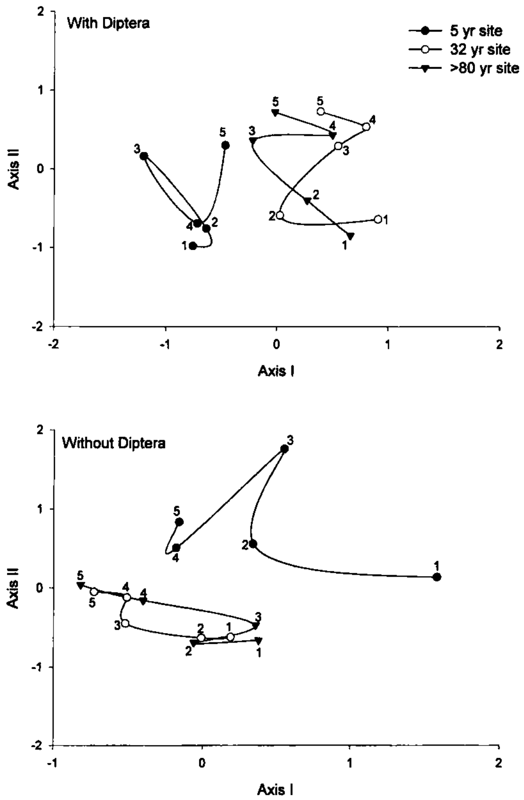


FIGURE 4. NMDS ordination of species composition trajectories with and without Diptera through time for each site. Numbers represent the five censuses.

leaves and flowers (*i.e.,* nectar), important resources for these organisms, takes longer to recover (Lawrence 1996).

Changes in the insect community in the 5 yr site were mainly due to the high light environment that influences insect behavior (Herrera 1995) by attracting flying insects. Although richness returned to pre-hurricane levels by the end of the study, there was a dramatic peak immediately after the hurricane. The majority of new species were Diptera in the plant exudates, licking, and vestigial mouthparts trophic categories that develop mainly on decomposing material. As the resource was depleted, richness dropped and the species composition changed. In this site, there were 24 dipteran species in census 1 and 68 dipteran species in census 5. The majority of these species feed on decaying vegetation as larvae, which was much greater in the forested sites, and thus, adults were migrating from forested sites into the high light environment (Frouz 1999, Frouz & Paoletti 2000).

As in the 5 yr site, the 32 yr site had a peak in richness immediately after the hurricane and then the richness decreased to pre-hurricane levels. The increase immediately after the hurricane was due to the increase in the plant exudates and licking trophic categories, mainly Diptera. In contrast, richness of sucking and chewing phytophagous insects decreased after the hurricane, probably due to the low availability of leaves and flowers (Lawrence 1996). This site had the lowest richness, possible due to high dominance of a single tree species, *M. splendens* (Aide *et al.* 1995). Furthermore, the hurricane did not create large enough canopy gaps to increase the cover of herbaceous species, as in the older site. In the 32 yr site, the persistent species were litter insects, suggesting that although litter quality and quantity change after a hurricane (Pfeiffer 1996), the litter habitat persisted. Nevertheless, species composition was different between census 1 and census 5, suggesting that although habitat structure did not change significantly, the impact of the hurricane on resources in adjacent areas may have contributed to this change.

The >80 yr site was the most affected by Hurricane Georges, which changed the plant community from a habitat dominated by woody vegetation to a habitat with increased herbaceous cover. This change in the vegetation resulted in a greater variety of resources and habitats that may promote insect richness. Nevertheless, although habitat structure and availability of resources changed during the study, species richness varied little among the different censuses. In addition, trophic categories that included dipterans increased following the hurricane, while sucking and chewing phytophagous trophic categories decreased; but these changes were smaller in comparison with the 5 yr and 32 yr sites. The small increase in categories that group dipterans was possibly due to the migration of adults to high light, high temperature habitats, and the small decrease in herbivore categories may have been due to the growth of herbaceous vegetation that increased the availability of green leaves. As in the 32 yr site, the majority of the persistent species were litter insect; nevertheless, species composition varied greatly among censuses, reflecting changes in plant species composition.

Although we expected a more rapid recovery in the younger sites, all sites returned to similar pre-hurricane richness in less than one year, suggesting that the input of resources from the hurricane was depleted. In all sites, species composition was different between June 1998 and October 1999, possibly due to changes in habitat structure and also seasonality (Stewart & Woolbright 1996). If seasonality explained the majority of the variability, however, one would expect the two October censuses (1998 and 1999) to be similar. The different species composition between these censuses reinforces the idea that the hurricane caused strong vegetation changes that resulted in very different insect communities within a site. Species composition between the 5 yr and >80 yr sites was more similar at the end of the study in comparison with the initial composition. In the first census, there were 6 species (2 Hymenoptera, 1 Coleoptera, and 3 Diptera) shared only by the 5 yr and >80 yr sites, and in the last census, there were 17 species (1 Hymenoptera, 2 Lepidoptera and 14 Diptera) shared between these sites. This suggests that the development of larvae in the >80 yr site and the migration of adults to the 5 yr site resulted in greater similarities in insect species composition.

During succession (among-site variation), richness of insects did not increase, trophic composition was similar, and species composition was different between open and forested habitats. Richness was highest in the early successional stage (5 yr site; an area of low diversity of woody plants) and lowest in the intermediate stage (32 yr site), suggesting that although habitat structure is an important determinant of insect diversity, insects with high dispersal ability (*i.e.*, Diptera) may contribute to large changes in insect communities because they move over wide spatial ranges tracking their resources. The number of trophic categories was similar among successional stages, but their richness varied greatly. In the 5 yr site, these changes were mainly due to migration of species into the high light, high temperature habitat, while in the >80 yr site, these changes were most likely associated with the effects of the hurricane (*e.g.*, vegetation and litter dynamics). Other studies have also found that the number of trophic categories varies little in time and space, but their richness is highly variable (Moran & Southwood 1982, Southwood *et al.* 1982). The species composition was different between early and late successional stages, suggesting that in the 5 yr site, the combination of increasing structural complexity and high light conditions result in a unique insect community, while the more similar habitat structure of the two forested sites resulted in similar resources and microhabitats that promote a similar species composition. These results suggest that although insect species participating in ecosystem processes are highly variable through time and space, the redundancy of trophic composition ensures that the processes continue to occur.

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