LEAF-LITTER INHABITANTS OF A BRAZILIAN PEPPER STAND IN EVERGLADES NATIONAL PARK

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ABSTRACT

Brazilian pepper (Schinus terebinthifolius Raddi) is the focus of a major restoration project in Everglades National Park, and here I have attempted to broaden our understanding of this plant and the phenomenon of its invasion. Brazilian pepper leaf litter fauna (especially ants but also beetles, wasps, centipedes, millipedes, isopods, and collembola) was compared to that of hammock and pineland. The abundance of certain species in the different habitats was consistent with previous records of habitat preference and confirmed Brazilian pepper leaf litter as a high-moisture habitat. In addition, two species collected here were not previously known from the Everglades: Strumigenys rogeri Emery and S. lanuginosa Wheeler, W. M. Hammock leaf litter had more ant species, more beetle families, and more wasp families than Brazilian pepper. Rank-abundance plots for all three habitats were either log-series or log-normal distributions, but the sample size was too small to discriminate. K-series plots showed ants in Brazilian pepper to be more diverse than in pineland but slightly
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less diverse than in hammock. Brazilian pepper is more likely to harbor exotic ants than native habitats (52% versus 36% of species were exotic respectively), and exotic ants are more likely to be found in both hammock and Brazilian pepper than in only one or the other (67% of species found in both habitats were exotic).

Key Words: Everglades, ants, Brazilian pepper, *Schinus*, *Strumigenys*, exotic, Formicidae

**RESUMEN**

La pimienta de Brasil (Brazil pepper; *Schinus terebinthifolius* Radii) es el foco de atención de un amplio proyecto de restauración en el Everglades National Park. En este trabajo he intentado ampliar nuestro conocimiento de esta planta y el fenómeno de su invasión. La fauna que habita en la hojarasca de la pimienta de Brasil (principalmente hormigas, pero también escarabajos, avispas, cienpiés, milpiés, isópodos y collembo) se comparó con aquella de los hábitats tipo "hammock" y "pineland". La abundancia de ciertas especies en los diferentes hábitats fue consistente con registros previos de la preferencia de hábitat y confirmaron a la hojarasca de la pimienta de Brasil como un hábitat de alta humedad. Además, se colectaron dos especies del Everglades no conocidas previamente: *Strumigenys rogeri* Emery y *S. lanuginosa* Wheeler, W. M. La hojarasca del hammock tuvo mayor cantidad de especies de hormigas, más familias de escarabajos y más familias de avispas que la de la pimienta de Brasil. Mapas de abundancia por jerarquía de los tres hábitats tuvieron distribuciones logarítmicas en serie o normales, aunque el tamaño de muestra empleado fue demasiado pequeño para diferenciar entre los dos tipos. Mapas de tipo serie K (k-series) mostraron que las hormigas en la pimienta de Brasil tuvieron mayor diversidad que en el hábitat tipo pineland, pero que su diversidad fue menor en comparación con el hábitat tipo hammock. La pimienta de Brasil es más propensa a albergar hormigas exóticas que los hábitats nativos (52% vs. 36% de las especies fueron exóticas, respectivamente) y es más probable encontrar hormigas exóticas en los hábitats tipo hammock y de pimienta de Brasil combinados que en uno solo de ellos (67% de las especies encontradas en ambos hábitats fueron exóticas).
grow into dense thickets prevents most other plants from entering Brazilian pepper thickets. A significant Brazilian pepper stand in the Everglades (commonly called the “Hole-in-the-Donut”) consists of about half of 4000 hectares of abandoned agricultural land on Long Pine Key. This area was farmed from the early 1900s, and after rock plowing was introduced in the 1950s, various parts were farmed and abandoned up to the 1970s. The restoration plan for the Hole-in-the-Donut consists mainly of razing the Brazilian pepper down to unplowed limestone; test plots have shown that this technique produces wetland prairie relatively free of Brazilian pepper seedlings (Jones & Doren 1997).

My goal in this study was to understand the Brazilian pepper area in more detail than previously known. This may seem odd, given that the Hole-in-the-Donut is scheduled to be destroyed and does not constitute native habitat, but there are theoretical and site-specific reasons for such a study. First, the extent to which the Hole-in-the-Donut area is dominated by Brazilian pepper is extreme in size, intensity, and persistence. Profiling this area and understanding how it interacts with its surrounding native habitat may lend insight to other areas of exotic invasion and even native habitats and species. Second, the outcome of the Hole-in-the-Donut restoration, while likely to be wetland prairie, cannot be predicted with complete certainty. There may be subtle differences between the restored area and native prairie that persist long after the project is completed, such as the presence or absence of species that were present or absent when it was dominated by Brazilian pepper. In this study I analyze the leaf-litter fauna (primarily ants) from the Hole-in-the-Donut, and I compare it to native leaf litter. I address three questions: (1) What is the microfauna of Brazilian pepper leaf litter, (2) What does this fauna indicate about the nature of Brazilian pepper leaf litter, and (3) What is the relationship between native and exotic ants and native and Brazilian pepper habitats?

**MATERIALS AND METHODS**

All work was done on Long Pine Key in Everglades National Park, Dade Co., FL between 13 August and 21 December 1996. Samples were processed at the Dan Beard Research Center in Everglades National Park, and voucher specimens are currently property of the Everglades Museum.

The main goal was to compare the abundance and diversity of ants and other small arthropods in Brazilian pepper, hardwood hammock, and to lesser degree, rocky pineland leaf litter. I also wanted to describe the nature of Brazilian pepper and hammock leaf litter, including moisture content. These sampling efforts were divided into two phases: a General Survey and Quantitative Sampling.

The General Survey was conducted by taking Burlese funnel samples from Brazilian pepper, hardwood hammock, and rocky pineland. Each sample consisted of a full one-gallon plastic sealable bag of leaf litter. On each date four samples were taken, with each sample taken 1 to 2 meters from the others. An effort was made on subsequent visits to the same habitat to use different access roads and paths than before, until most areas within each habitat on Long Pine Key had been visited. Each sample was sifted through a coarse screen, which removed rocks, large sticks, and whole leaves. Sticks were broken open and sifted before discarding. The remaining debris was placed in a Burlese funnel and dried for approximately 24 hours. After drying, the extracted arthropods were identified and pinned. Four samples were taken on each of the following dates: Brazilian pepper—August 14, 23, 26, 28, 31, September 6, 23, October 2 and 3; Hammock—August 17, 23, 27, September 19 and 26; Pineland—August 13, 20, 21, 29, September 2, 4, and 11.
Quantitative Sampling methods resembled the General Survey in that all samples consisted of a one-gallon bag of leaf litter, and an attempt was made to collect from as many different areas within each habitat on Long Pine Key as possible (but not in pineland). The goal of this phase was to compare Brazilian pepper and hammock leaf litter quantitatively, so the samples were paired to minimize the effect of superfluous variables, such as weather, and they were analyzed in more detail after each collection. During each sampling trip, two samples were taken from two different Brazilian pepper locations, and two were taken from two different hammock locations. Ten trips were made, yielding 40 separate samples. An effort was made to sample at least three meters into the Brazilian pepper stands and as far from roads as possible into hammocks. The samples were weighed to the nearest gram and placed, unsifted, into Burrese funnels. After 24 hours, the dried samples were removed, weighed again, and the number of ants (identified to species), beetles (identified to family), parasitic wasps (identified to family), centipedes (Chilopoda), millipedes (Diplopoda), isopods, and collembola were counted.

Diversity and Abundance

Rank-abundance and k-series plots were plotted from the following two data sets: (1) a combination of General Survey and Quantitative Sampling for pineland, Brazilian pepper, and hammock in which the appearance of a species in a sample constituted one incidence datum (because the numbers of individuals per species per sample were not counted in the General Survey), and (2) the Quantitative Sampling data. Rank-abundance plots juxtapose the abundance of each species (on a log scale) against the abundance rank of each species (most abundant first). As discussed by Magurran (1988), rank-abundance plots usually conform to one of four distributions: geometric, log-series, log-normal, or "broken stick." In this study the sample size was too small to perform goodness-of-fit tests, but hypothetical geometric and "broken stick" rank-abundance curves were drawn for the Quantitative Sampling data for comparison; they represent the two extremes between a harsh or empty habitat where incoming species occupy the same percentage of remaining niche space as previous settlers (most geometric distributions) and situations where closely related species evenly share a single resource (most "broken stick" distributions). Hypothetical geometric curves in this paper are based on the assumption that arriving species use 50% of the available niche space. K-series plots show the cumulative abundance versus the rank (on a log scale); higher k-series curves indicate a smaller number of species and/or a greater dominance by the most abundant species than lower curves. In addition, combined data on hymenopteran and coleopteran families were compared.

Density and Clustering

Quantitative Sampling data were used to calculate density measurements (number of individuals per 100 grams of dry leaf litter) for ants, millipedes, centipedes, isopods, and collembola. Density measurements were compared using t-tests, and density data were plotted versus moisture content of leaf litter to search for correlations between density and moisture for both ants and non-insects. These data were analyzed by comparing the density in samples above the median moisture content with the density in samples below the median moisture content using Mann-Whitney U tests, done separately for data from hammock and Brazilian pepper habitats.

The average number of individuals of each species per sample was divided into the variance to produce a measure of clustering for each ant species and non-insects.
RESULTS

Leaf-Litter Characteristics

Brazilian pepper leaf litter consisted more of sticks than leaves. It was about three to four centimeters deep in most areas, and it sat on a layer of hard-packed soil mixed with broken limestone. A dense network of pencil-sized roots was in the soil. Most sticks in the litter were smaller than 1 cm in diameter, but larger sticks (1 to 4 cm diameter) were in deeper piles. Larger pieces of debris (to 7 cm diameter) were found at the base of the largest Brazilian pepper trees. In some areas the sticks seemed to be hollowed before falling, and termite galleries could be seen in dead twigs still attached to the plants. Brazilian pepper leaf litter contrasted sharply with hammock leaf litter, which was thick and soft. In the hammock large logs were also common, and the range in leaf sizes was, of course, much greater. Brazilian pepper leaf litter collected during the quantitative sampling had a higher water content than hammock leaf litter (40.22% versus 33.70%; p = 0.04; t-test). Brazilian pepper litter moisture also tended to be more variable (0.018 versus 0.0094; p = 0.09; F-test).

Diversity and Abundance

At the end of both the General Survey and Quantitative Sampling, hammock leaf litter had a larger number of ant species (23), followed by Brazilian pepper (20) and then pine land (9) (Table 1). There were no ant species unique to the pine land, but four native species were found only in the pine land and the hammock. Seven species were found only in the hammock, and eight were only in the Brazilian pepper. *Pheidole merens* Wheeler was significantly more abundant in the Brazilian pepper than the hammock at the Bonferoni-corrected alpha value of 0.0016 (Chi-squared, df = 1). *Solenopsis abdita* Thompson was more common in the hammock than the Brazilian pepper. Despite the larger number of species collected from hammock habitat in general, there was no clear difference in the evenness of these species when compared to Brazilian pepper.

Rank-abundance plots for Brazilian pepper and hammock are very similar, and neither habitat has a geometric or “broken stick” distribution (Figs. 1 & 2). Histograms based on these distributions could represent log-series curves or log-normal curves with small sample sizes (Fig. 2). The k-series curves—which incorporate both the number and evenness of species—shows Brazilian pepper to be more diverse than pine land and slightly less diverse than hammock (Fig. 3).

For the combined General Survey and Quantitative Sampling data, 52% of all ant species were exotics. For just native habitat (hammock and pine land), 36% of the species were exotic. Of species found in both native habitat and Brazilian pepper, 67% were exotic, and of species found only in Brazilian pepper, 55% were exotic.

I collected more families of parasitic wasps and beetles from the hammock than the pine land or Brazilian pepper. The hammock had five families of wasps: *Aphelin-
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idae, Ceraphronidae, Diapriidae, Encrytidae, and Eulophidae. The pineland and Brazilian pepper samples had wasps only from the family Scelionidae. Hammock also had more families of beetles (13) than pineland (9) or Brazilian pepper (8). Representatives of the following families of beetles were found exclusively in the hammock: Cryptophagidae, Helodidae, Nitidulidae, Scolytidae, Scymaenidae, and Tenebrionidae. The pineland produced the only Chrysomelids, and the Brazilian pepper had the only Dytiscids. Hydraenids, and Hydrophilids were found exclusively in the pineland and Brazilian pepper.

Density and Clustering

The average density of ants in Brazilian pepper samples (16 ± SD25 per 100g dry litter; n = 20) was not significantly different from ant density in hammock (27 ± SD32; n = 20; p > 0.05; t-test). Broken down by species, the number of individuals per 100 grams of hammock leaf litter varied from 0.066 (Brachymyrmex minutus Forel) to 7.4 (Solenopsis abdita), and in Brazilian pepper leaf litter it ranged from 0.056 (Paratrechina bourbonica (Forel)) to 5.9 (Paratrechina guatemalensis (Forel)). The densities for ant species were not significantly correlated with the water content of the leaf litter. Still, Hypoponera opaceps (Mayr) and Strumogenys rogeri were generally found in higher-moisture leaf litter (41% and 39% moisture respectively) than Cyphomyrmex ramosus (Spinola), Solenopsis tennesensis Smith, M. R., and Brachymyrmex minutus (all 25%).

Millipede density did not differ between Brazilian pepper and hammock, but it was more variable in the hammock (p < 0.0001; F-test; Table 2). Centipedes were more dense (p < 0.0017; t-test) and more variable (p < 0.0001; F-test) in the hammock. Millipedes tended to be denser in high-moisture leaf litter in both the hammock and Brazilian pepper (p < 0.025; Mann-Whitney U test; Bonferoni-corrected alpha = 0.0125). Centipedes did not vary significantly with moisture content in Brazilian pepper or hammock. Isopods tended to be denser in wetter hammock leaf litter (p < 0.05), but collembola were not significantly correlated with water content in the hammock or Brazilian pepper.

Most ants and non-ant arthropods were clumped. In the hammock, those species most evenly distributed were Aphaenogaster miamiana Wheeler, Brachymyrmex minutus, Cyphomyrmex ramosus, Monomorium floricola (Jerdon), and Paratrechina longicornis (Latreille). In Brazilian pepper, Hypoponera opaceps, Odontomachus ruginodus Wheeler, Paratrechina bourbonica, and the centipedes showed the most even distributions. In the hammock, the most clumped species were Crematogaster minutissima Mayr (variance/mean ratio = 58) and Solenopsis abdita (57). In the Brazilian pepper, the most clumped species were Paratrechina guatemalensis (30) and Strumigenys rogeri (21).

DISCUSSION

Two items deserve clarification before going further. First, it is important to remember that this study pertains to leaf-litter inhabitants only, since some common Everglades ants such as Pseudomyrmex gracilis (Fab.), Crematogaster arkinsonii Wheeler, W. M., and C. aeshemeadi Mayr, etc. are noticeably absent. A study of insects on Brazilian pepper foliage in Lee Co., FL by Cassani (1986) documents an ant fauna that, while also highly exotic (>25%), contains species not found in this study. Second, the pineland samples are shown only briefly in the results, for they are difficult to
Table 1. Ant species collected from the general survey and quantitative sampling. For each species its status as a native or exotic is indicated, along with the percentage of samples from each habitat in which it was found (H = Hammock, P = Pine land, and B = Brazilian Pepper). The Hammock and Brazilian Pepper samples are compared using X² tests (H vs B). P-values less than 0.0016 are significant (**); P-values at the less-conservative level of 0.05 are also shown (*). Next are comments by Ferster and Prusak (1994) and Deyrup et al. (1998).

<table>
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<tr>
<th>Species</th>
<th>Native?</th>
<th>H</th>
<th>P</th>
<th>B</th>
<th>p</th>
<th>Ferster &amp; Prusak 1994¹</th>
<th>Deyrup et al. 1988</th>
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<td>41</td>
<td>3</td>
<td>8</td>
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<td>6</td>
<td>2</td>
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¹Ferster and Prusak (1994) categorized collections by seven habitat types: hardwood hammock, rocky pineland, coastal prairie, mangrove, wetland prairie, disturbed, and freshwater slough. Their notes on habitat preference are repeated here, some of which are originally from Koptur (1992), Smith (1930 and 1933) and Wheeler (1932).
²Taxonomically unresolved (Deyrup et al. 1988).
³Trager (1984); lives in a variety of habitats.
⁴Known to invade native and disturbed habitats swiftly.
⁵Twig and vine nester.
⁶One dealate found in this study.
⁷Trager (1994) reports it from flooded, disturbed areas devoid of other ants.
⁸Aggressive invader of moist areas (Deyrup & Trager 1984).
TABLE 1. (CONTINUED) Ant species collected from the general survey and quantitative sampling. For each species its status as a native or exotic is indicated, along with the percentage of samples from each habitat in which it was found (H = Hammock, P = Pineland, and B = Brazilian Pepper). The Hammock and Brazilian Pepper samples are compared using $X^2$ tests (H vs B). P-values less than 0.0016 are significant (**); P-values at the less-conservative level of 0.05 are also shown (*). Next are comments by Ferster and Prusak (1994) and Deyrup et al. (1998).

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<td>3</td>
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</table>

¹Ferster and Prusak (1994) categorized collections by seven habitat types: hardwood hammock, rocky pineland, coastal prairie, mangrove, wetland prairie, disturbed, and freshwater slough. Their notes on habitat preference are repeated here, some of which are originally from Koptur (1992), Smith (1930 and 1933) and Wheeler (1932).

²Trager (1984) reports it from semiopen and secondary habitats.

³Taxonomically unresolved (Deyrup et al. 1988).

⁴Trager (1984): lives in a variety of habitats.

⁵Known to invade native and disturbed habitats swiftly.

⁶Twig and vine nester.

⁷One dealate found in this study.

⁸Trager (1994) reports it from flooded, disturbed areas devoid of other ants.

⁹Aggressive invader of moist areas (Deyrup & Trager 1984).
### Table 1. (Continued) Ant Species Collected from the General Survey and Quantitative Sampling. For each species, its status as a native or exotic is indicated, along with the percentage of samples from each habitat in which it was found (H = Hammock, P = Pineland, and B = Brazilian Pepper). The Hammock and Brazilian Pepper samples are compared using χ² tests (H vs B). P-values less than 0.0016 are significant (**); P-values at the less-conservative level of 0.05 are also shown (*). Next are comments by Ferster and Prusak (1994) and Deyrup et al. (1998).

<table>
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</tr>
</thead>
<tbody>
<tr>
<td>Paratrechina bourbonica&lt;sup&gt;a&lt;/sup&gt;</td>
<td>no</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>not pineland or coastal prairie</td>
<td></td>
<td>disturbed areas only</td>
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<tr>
<td>Solenopsis invicta</td>
<td>no</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>not slough</td>
<td></td>
<td>moist shaded areas</td>
</tr>
<tr>
<td>Strumigenys louisianae</td>
<td>yes</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>pineland and slough</td>
<td></td>
<td>moist, shaded leaf litter</td>
</tr>
<tr>
<td>Strumigenys rogeri&lt;sup&gt;b&lt;/sup&gt;</td>
<td>no</td>
<td>0</td>
<td>0</td>
<td>22</td>
<td>*</td>
<td>not previously recorded</td>
<td>not collected</td>
</tr>
</tbody>
</table>

<sup>a</sup>Ferster and Prusak (1994) categorized collections by seven habitat types: hardwood hammock, rocky pineland, coastal prairie, mangrove, wetland prairie, disturbed, and freshwater slough. Their notes on habitat preference are repeated here, some of which are originally from Koptur (1992), Smith (1930 and 1933) and Wheeler (1932).

<sup>b</sup>Trager (1984) reports it from semiopen and secondary habitats.

<sup>c</sup>Taxonomically unresolved (Deyrup et al. 1988).

<sup>d</sup>Trager (1984): lives in a variety of habitats.

<sup>e</sup>Known to invade native and disturbed habitats swiftly.

<sup>f</sup>Twig and vine nester.

<sup>g</sup>One dealate found in this study.

<sup>h</sup>Trager (1994) reports it from flooded, disturbed areas devoid of other ants.

<sup>i</sup>Aggressive invader of moist areas (Deyrup & Trager 1984).
standardize and not sources of large amounts of data. This is because "leaf litter" in the rocky pinelands is often non-existent. (I finally began taking litter from around solution holes and where it had accumulated near fallen trees. This is why the beetles from the pinelands include both very common and large families as well as ones that are found mostly near water.)

Brazilian pepper vs. Hammock Leaf Litter

Brazilian pepper leaf litter seems more likely to become saturated and dried than hammock leaf litter. This could be caused by the greater openness of the Brazilian pepper canopy relative to hammock. Also, it seems likely that because Brazilian pepper leaf litter lies directly on hard-packed soil and rock, it is more likely to be submerged during rainstorms than hammock leaf litter, which sits on top of more absorbent material.

Overall, Brazilian pepper ants and their relative abundance are consistent with high moisture. The only ant species found in both hammock and Brazilian pepper but found significantly more frequently in Brazilian pepper, *Pheidole moerens* Wheeler, is known to favor mesic forests. The only two species found frequently in Brazilian pepper and not at all in hammock, *Hypoponera opaciceps*, and *Strumigenys rogeri*, are known inhabitants of wet areas. The brazilian pepper beetle list is also consistent with high moisture: the only beetle family found in exclusively in Brazilian pepper was Dytiscidae, commonly known as "predaceous diving beetles." In addition, the only two beetle families found here in both the Brazilian pepper and pineland are also water-loving families: Hydraenidae and Hydrophilidae.

Although no ant densities correlated with water content, millipedes showed a strong preference for wetter leaf litter, and isopods preferred moisture content be-

![Fig. 1. Rank-abundance curves for combined General Survey and Quantitative Sampling ant data.](image-url)
tween Brazilian pepper and hammock. Centipedes were almost totally absent from Brazilian pepper leaf litter, and the lack of any correlation between centipede density and moisture content in the hammock suggests that they avoid Brazilian pepper for some reason other than moisture. Collembola showed no trends at all, but the fact that I did not identify collembola any more specifically may hide important trends at the family or species level.

Being a social animal, it is not surprising that ants are usually clumped. The few low variance-to-mean ratios probably indicate rare colonies and far-ranging foragers. Uncommon species with large, roaming workers (Aphaenogaster miamiana, Odontomachus ruginodus, Hypoponera opaciceps, and Paratrechina bourbonica), had small variance to mean ratios, as did centipedes.

Fig. 2. Rank-abundance curve for hammock Quantitative Sampling ant data (II) for Hammock (A) and Brazilian Pepper (B) leaf litter. The same number of individuals and species were used to construct hypothetical distributions that conform to the “broken stick” (I) and the geometric (III) model. The inset histogram shows the number of species found in different abundance categories (log base 2). The histogram would be a normal curve if the distribution were a log-normal curve with a large sample size.
Ant Anomalies

*Strumigenys rogeri* and *S. lanuginosa* have not previously been found in Everglades National Park. *Strumigenys rogeri* is a common tropical exotic from Africa, and its restriction to wet areas may confine it to Brazilian pepper at Everglades National Park. Deyrup and Trager (1984) report *S. rogeri* in extremely dense populations in moist bayheads at Archbold Biological Station, and I have seen it in high densities along marshy trails on the Eastern Florida coast. An aggressive invader, *S. rogeri* shares its moist habitat preference with *S. louisianae*, a native species. Why *S. rogeri* was not found in the moist litter around pineland solution holes is an interesting question. As for *S. lanuginosa*, it has not been collected in South Florida with enough frequency to establish a habitat correlation.

Two species collected here made somewhat surprising appearances in hammock, *Odontomachus ruginodus* and *Monomorium floricola* (Jerdon). In the Everglades, neither species has previously been collected in hammock, and *O. ruginodus* has not been
Clouse: Ants in Brazilian Pepper Leaf Litter

collected in pineland before (Ferster & Prusak 1994). Collecting *O. ruginodus* in pineland is somewhat consistent with its habit of frequenting open areas, although often those areas are also disturbed (e.g., roadsides). It is difficult to discern any pattern to *M. floricola*'s habitat, being that it has now been collected in slough, pineland, hammock, and disturbed habitats. As an exotic, its ability to occupy several different Everglades habitats with ease is disturbing.

Diversity

More extensive ant, beetle, and wasp lists for hammocks make the native forests appear more diverse than Brazilian pepper. Inasmuch as k-series plots encapsulate diversity, in this study they show that hammock ants are slightly more diverse than Brazilian pepper. The crossing of the curves seems minor enough to ignore, especially since it happens at the appearance of *Paratrechina guatemalensis*, the first- or second-most abundant species in each habitat. However, the Brazilian pepper fauna is not merely a subset of that of the native habitat, for some species seem to prefer or only survive in Brazilian pepper leaf litter. This phenomenon is also documented by Curnutt (1989) in a study of breeding birds in the Hole-in-the-Donut: even though Curnutt lists a smaller number of species in Brazilian pepper relative to the number in native habitat, the Red-winged Blackbird and Common Yellowthroat are far more common in the Brazilian pepper. It could also be argued that the reason why more ant species were found in the hammock is simply because I found more ants there, and the rank-abundance curves further emphasize the similarity between hammock and Brazilian pepper. My inability to discriminate between a log-series and log-normal curve for each habitat is probably no great loss of information: the biological meaning of these two distributions is debated, and together they seem to represent the majority of stable, complex communities (Magurran 1988).

Regardless of diversity measures, however, Brazilian pepper is clearly an inhospitable habitat for native ants. Even though I found only two fewer native species in the Brazilian pepper than in the hammock during Quantitative Sampling, I found only 16

Table 2. The mean densities and their variance for non-insects from the Quantitative Sampling (number per 100g leaf litter). P-values less than 0.0125 (*) are considered significant.

<table>
<thead>
<tr>
<th></th>
<th>mean</th>
<th>variance</th>
<th>t-test</th>
<th>F-test</th>
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<tr>
<td><strong>Millipedes</strong></td>
<td>1.20</td>
<td>4.50</td>
<td>0.13</td>
<td>0.05</td>
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<td></td>
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<td></td>
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<td>0.84</td>
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<tr>
<td><strong>Centipedes</strong></td>
<td>1.81</td>
<td>0.14</td>
<td>0.0017*</td>
<td>0.04</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td><strong>Isopods</strong></td>
<td>6.00</td>
<td>4.70</td>
<td>0.29</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.41</td>
</tr>
<tr>
<td><strong>Collembola</strong></td>
<td>72.40</td>
<td>97.60</td>
<td>0.29</td>
<td>38.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>74.40</td>
</tr>
</tbody>
</table>

TABLE 2. THE MEAN DENSITIES AND THEIR VARIANCE FOR NON-INSECTS FROM THE QUANTITATIVE SAMPLING (NUMBER PER 100G LEAF LITTER). P-VALUES LESS THAN 0.0125 (*) ARE CONSIDERED SIGNIFICANT.
native individuals in the Brazilian pepper (as opposed to 194 in the hammock). Even if one found a larger number of native species in the Brazilian pepper, the fact any one ant has a 5% chance of being native in the Brazilian pepper (as opposed to 54% in the hammock) is cause for concern.

The rise in diversity caused by the inclusion of exotic species has been called the “mall effect” by Deyrup (pers. comm.) and “Macdonaldization” by Lövel (1997). The analogy of the “mall effect” is that a small town may have a sudden increase in the diversity of retail stores by building a mall, but they are the same stores one might see anywhere else in the country, like popular fast-food outlets. Similarly, the invasion of exotic ants enhances diversity in many Everglades habitats. Lövel shows that this process is homogenizing the biosphere, and he points out that even though exotics have led to small-scale increases in diversity (e.g., in New Zealand) exotic invasion could cause a 50% decrease in global biodiversity. Thus part of the problem with exotic invasion is that although exotics may maintain or increase local diversity (as they are added to and in some cases replace existing species), they will ultimately lower the number of species counted on a global scale.

The more fundamental problem with exotic invasion is that regardless of how it changes the total number of species and their evenness, the fact that the historical assemblage of species is altered has a destabilizing effect. The main role of Brazilian pepper in this process is equivalent to a keystone species (Deyrup, pers. comm.), a term (like “diversity”) that usually carries positive connotations but is actually neutral. Under Brazilian pepper branches thrives a microfauna more diverse than that found in pineland and not much less diverse than hammock. However, the Brazilian pepper community is not as native as in hammock, and the Hole-in-the-Donut area serves as a safe refuge for exotics that would otherwise not have such a strong foothold in the heart of native habitat. It is easy to imagine a scenario in which natural Everglades disturbances (e.g., hurricanes and fire) are followed by quicker and more thorough invasions by Brazilian pepper and its associates than if they were not already entrenched in the park.

The important question now is not whether exotic invasions pose a major threat to endemic communities and global biodiversity, but how can we stop them in the face of increasing human mobility. It is difficult to imagine a solution to the ant invasion (or other invasions among fish, reptiles, etc.) that is surgical enough to remove only the exotics but does not involve the resource-consuming process of finding a specific nemesis for each pest species. Moreover, as shown here, some exotics establish whole new species assemblages, which are also quite exotic.

ACKNOWLEDGMENTS

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REFERENCES CITED

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