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Sampling Ground-dwelling Ants: Case Studies from the World's Rain Forests

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and Ted Schultz



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The cover illustration was drawn by Nicolette Layover and depicts the soil-dwelling ant *Melophorus majeri* Agosti, an unusual member of this genus, that has only been found at two heathland localities in the extreme south of Western Australia.

Chapter 4 - Ant inventories along elevational gradients in tropical wet forests in Eastern Madagascar

Brian L. Fisher

Introduction

Inventory methods designed to permit rapid, replicable, and quantitative sampling of the leaf litter ant fauna were used to investigate altitudinal and latitudinal patterns in ant diversity in wet tropical forests in eastern Madagascar. A total of 14 inventories were conducted at four regional sites. I discuss the nature of leaf litter ant assemblages in Madagascar and present summary information on species richness, species accumulation curves, and species turnover. Detailed discussions of the species collected, their relative abundance, faunal similarity, species turnover, and the efficacy of inventory methods are presented in Fisher (1996a, 1998, 1999a).

Methods

Study sites

Elevational gradients were surveyed at four localities in eastern Madagascar (Figure 1):

- (1) Réserve Naturelle Intégrale (RNI) d'Andohahela. 24°33'–34'S, 46°48' - 49'E; elevational sites surveyed: 400, 800, and 1250 m.
- (2) RNI d'Andringitra, 22°12'–14'S, 46°58'– 47°01'E; elevational sites surveyed: 785, 825, 1275, and 1680 m.
- (3) Western Masoala Peninsula, 15°34'–41'S, 49°57'–50°00'E; elevational sites surveyed: 25, 425, and 800 m.
- (4) Réserve Spéciale (RS) d'Anjanaharibe-Sud, 14°45'S, 49°26'–30'E; elevational sites surveyed: 875, 1200, 1565, and 1985 m.

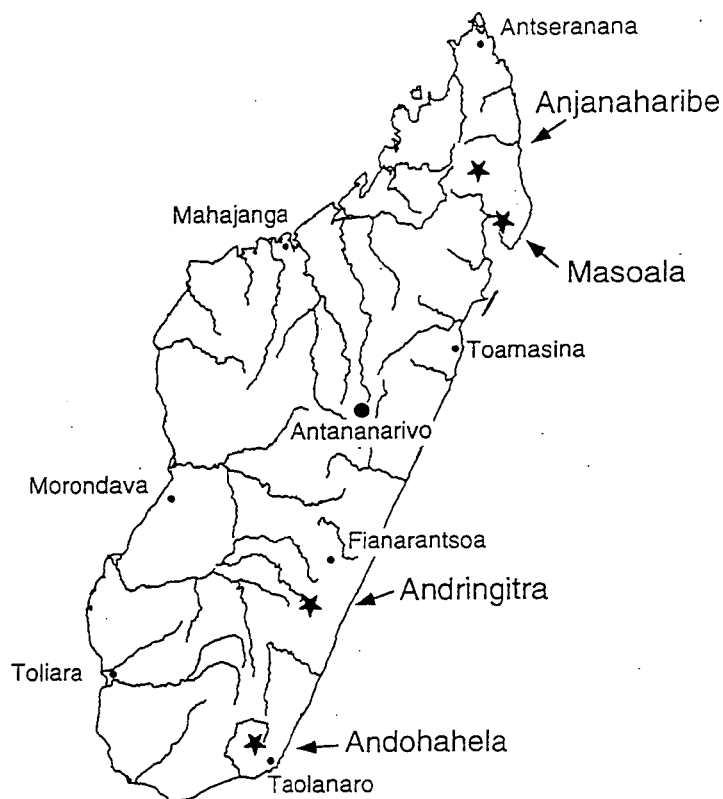


Figure 1. Inventory sites in eastern Madagascar: Réserve Naturelle Intégrale (RNI) d'Andohahela, RNI d'Andringitra, Western Masoala Peninsula, Réserve Spéciale d'Anjanaharibe-Sud.

At each elevational site, the survey method used 50 pitfalls and 50 leaf litter samples (Winkler), in parallel lines 10 m apart, along a 250 m transect. Pitfall traps were placed and leaf litter samples gathered every 5 m along the transect. Further details are found in Fisher (1996a, 1998, 1999a, and J. Delabie et al. in the accompanying book).

Data analysis

Only records of ant workers were used in data analysis. To assess the completeness of the survey for the elevations sampled, I plotted cumulative species per sample curves for each elevation. Species accumulation was plotted as a function of the number of leaf litter and pitfall trap samples taken. For the analysis, each leaf litter sample was paired with the

adjacent pitfall sample, collectively termed a *station sample*. Species-accumulation curves for the 50 stations per transect, as well as incidence-based coverage estimator (ICE) and first-order jackknife estimates of the total number of species in the local community from which the samples were taken, are plotted for each succeeding station sample. Detailed descriptions of these methods of analysis are found in Fisher (1996a, 1998, 1999a, 1999b) and J. Delabie et in the accompanying book.

Complementarity (the distinctness or dissimilarity) of the ant assemblages (sensu Colwell and Coddington 1994) at different elevations was assessed using an index of species turnover. Beta-diversity (species turnover between elevations) was calculated using beta-2 developed by Harrison et al. (1992): $\text{beta-2} = (S/a_{\text{max}}) - 1$, where S = the total number of species in the two elevations combined, and a_{max} = the maximum value of alpha-diversity (i.e., number of species) among the elevations compared.

Results and Discussion

From all sampling methods, I collected and identified 128,677 ants comprising 36 genera and 471 species. These included 2032 queens and 780 males. Leaf litter and pitfall methods yielded 117,044 worker ants belonging to 30 genera and 381 species. The relative prevalence of the different subfamilies in the leaf litter and pitfall samples is shown in Table 1. The fauna is dominated by the Myrmicinae, followed by the Ponerinae. The 8 most dominant ant genera comprised 77% of the species in leaf litter and pitfall samples (Table 2).

Table 1. The total number and percentage of species per subfamily based on worker ants collected from pitfall and leaf litter samples in the four localities.

Subfamily	Total species	%
Myrmicinae	234	62.4
Ponerinae	93	24.4
Formicinae	30	7.9
Cerapachyinae	18	4.7
Dolichoderinae	3	0.8
Pseudomyrmecinae	3	0.8

Table 2. The eight dominant ant genera, representing 80% (304 species) of all species collected from pitfall and leaf litter samples in the four localities.

Genus	Total Species	%
<i>Pheidole</i>	68	17.8
<i>Strumigenys</i>	51	13.4
<i>Tetramorium</i>	51	13.4
<i>Hypoponera</i>	50	13.1
<i>Monomorium</i>	36	9.4
<i>Camponotus</i>	21	5.5
<i>Cerapachys</i>	18	4.7
<i>Crematogaster</i>	9	2.4
<i>Leptogenys</i>	9	2.4
<i>Paratrechina</i>	8	2.1
<i>Discothyrea</i>	6	1.6
<i>Proceratium</i>	6	1.6
<i>Madamorium</i>	5	1.3
<i>Smithistruma</i>	5	1.3
<i>Amblyopone</i>	5	1.3
<i>Pachycondyla</i>	5	1.3
<i>Prionopelta</i>	5	1.3
<i>Oligomyrmex</i>	4	1.0
<i>Mystrium</i>	4	1.0
<i>Technomyrmex</i>	3	0.8
<i>Tetraoponera</i>	3	0.8
<i>Plagiolepis</i>	1	0.3
<i>Aphaenogaster</i>	1	0.3
<i>Eutetramorium</i>	1	0.3
<i>Kyidris</i>	1	0.3
<i>Leptothorax</i>	1	0.3
<i>Pilotrochus</i>	1	0.3
<i>Anochetus</i>	1	0.3
<i>Odontomachus</i>	1	0.3
<i>Platythyrea</i>	1	0.3
Total	381	

Because of its long isolation from other land masses, the level of endemism of ant species on Madagascar is high. For the island, 90% of the valid specific and subspecific ant taxa are endemic (Fisher 1996b, 1997). For the relatively undisturbed wet forest localities surveyed, endemism is close to 100% (Fisher 1996a, 1998, 1999a). The ant fauna of Madagascar, however, is incompletely known, with two-thirds of the 1000 estimated species

on the island thought to be undescribed (Fisher 1997). As an extreme example, of the 51 species of *Strumigenys* collected in the four localities (Table 2), 50 are undescribed.

Species accumulation curves demonstrate the efficacy of the leaf litter and pitfall methods in sampling the majority of the ants in the leaf litter (Fisher 1999b). Species accumulation curves for observed, ICE, and jackknife estimates showed a decrease in the rate of species accumulation, but were still increasing slowly. For example, accumulation curves for the 825 m site on the Masoala Peninsula, the most species rich site, are presented in Figure 2 (for plots of other elevations and localities, see Fisher 1996a, 1998, 1999a). These curves indicate that within the area of the survey, the technique employed collected the majority of ants foraging and living in the leaf litter in the area encompassed by the 250 m transect, and that with increased sampling effort using the same methods (i.e., adding more pitfall and litter stations) in the same area, only marginal increases in species richness would be attained. Additional collecting methods, or a survey in a different area or season at the same elevation, would most likely collect additional species. Nevertheless, these results show that the inventory techniques used in this study provide sufficient sampling for statistical estimation and comparison of species richness, and comparison of faunal similarity and species turnover.

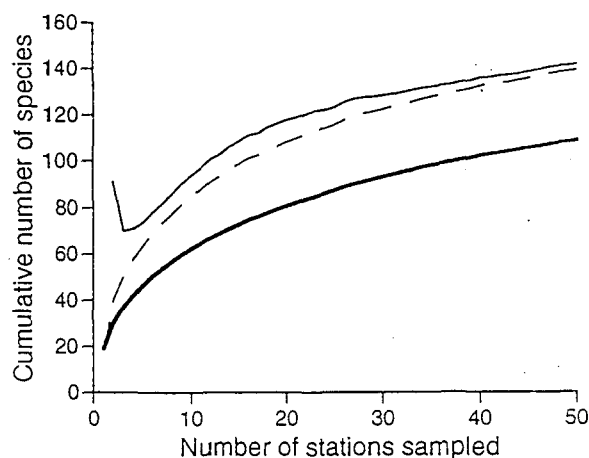


Figure 2. Assessment of leaf litter ant sampling technique for the most species rich site: 825 m on the Masoala Peninsula. The lower species accumulation curve (thick line) plots the observed number of species as a function of the number of stations sampled. The upper curves display the non-parametric first order jackknife (dashed line) and the incidence-based coverage estimator, ICE (solid line), estimated total species richness based on successively larger numbers of samples from the data set. Curves are plotted from the means of 100 randomizations of sample accumulation order.

An alternative approach to evaluating the efficacy of the sampling methods in terms of completeness of sampling (i.e., accumulation curves), would be to ask what minimum number of collections would be necessary to provide the same relative ranking of species richness among elevations as shown in Figure 3. Do pitfall samples alone show the same mid-elevation peak? Not at all localities. For example, within the Masoala Peninsula locality, the 825 m site had the lowest number of species recorded from pitfalls. Species accumulation curves for pitfall samples are still rising rapidly after 50 samples, which suggests that pitfall samples in this study do not provide sufficient sampling for comparison among elevations. It is also possible that pitfalls sample a different subset of the ant fauna, which may not show a mid-elevation peak. In tropical dry forest sites, the pitfall trap method collects a greater number of individuals and species (Fisher and Razafimandimby 1997). For mini-Winkler samples, the same relative ranking in observed species richness was reached and maintained after 25 samples. A smaller number of leaf litter samples will produce a more incomplete species list necessary for complementarity studies, but fewer samples may be appropriate for addressing questions on patterns of species richness.

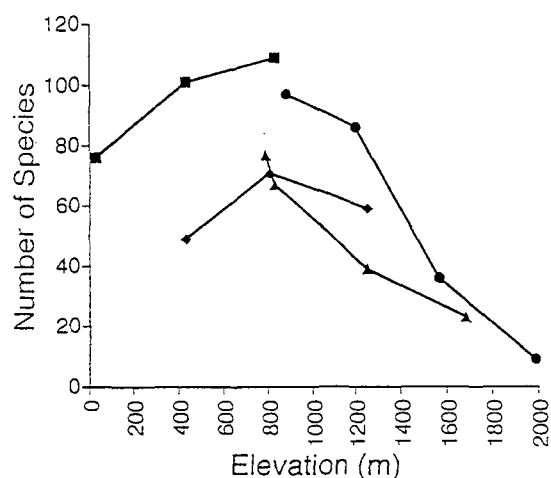


Figure 3. The number of ant species as a function of elevation. Data are from pitfall and mini-Winkler samples from the RNI d'Andohahela (F), the RNI d'Andringitra (H), the Masoala Peninsula (B), and the RS d'Anjanaharibe-Sud (J).

Species richness did not decrease monotonically as a function of elevation. Species richness peaked at mid-elevations (Figure 3). Along an elevational gradient, the peak in species richness at mid-elevations is thought to be the result of the mixing of two distinct,

lower and montane forest assemblages (see below; Fisher 1998). After the mid-elevation peak, species richness declined rapidly, reaching a minimum of nine species at 1985 m. This rapid decrease in species richness probably reflects climatic variables, mainly the reduction of radiant energy (Brown 1973; Fisher 1996a) and resultant decreasing primary productivity (Rosenzweig and Abramsky 1993). For ants in montane forests, the most important factor regulating colony survival may be clouds and high humidity which prevent bright sunlight from raising the ground temperature toward the optimal level for larval development and for worker foraging activities.

Faunal similarity and beta-diversity measures suggest a division of the ant fauna into two communities, one occurring in lowland forests ≤ 875 m and the other in montane forests ≥ 1200 m. For example, species turnover calculated using beta-2 was greatest at mid-elevation (Figure 4). Similar patterns were found using the Jaccard and Morisita Indices (Fisher 1996a, 1998, 1999a).

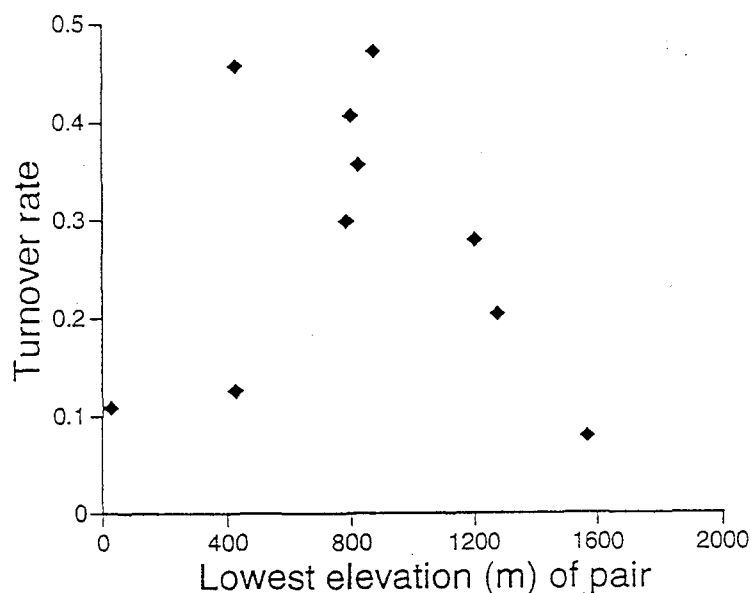


Figure 4. Species turnover rate between adjacent elevational sites along the gradient calculated using the Beta-2 Index of Harrison et al. (1992). Adjacent elevations are separated by approximately 400 m. The lowest elevation in the comparison is plotted. Data are from pitfall and mini-Winkler samples from all localities.

Conclusions

These studies demonstrate that effective methods to inventory hyperdiverse groups like ants are possible, and that results from inventories can make important contributions towards understanding landscape-level patterns of invertebrate biodiversity. In addition, the specimens collected in ant inventories in Madagascar are invaluable for future studies of the systematics, evolution, and biogeography of Malagasy ants.

By comparison with data on other biotic groups, these inventories will permit the analysis of how species composition and diversity change with altitude and latitude. These comparative data are important for understanding intertaxon differences in diversity patterns, which should be factors critical for developing a conservation strategy based on diversity.

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