

Comparison and Origin of Forest and Grassland Ant Assemblages in the High Plateau of Madagascar (Hymenoptera: Formicidae)¹

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ABSTRACT

We assessed species richness and composition of ant assemblages in adjacent montane forest and secondary (anthropogenic) grassland habitats in the central plateau of Madagascar. We used five quantitative methods (leaf litter sifting, two types of pitfall traps, beating low vegetation, and soil digging) and compared methods within and across habitats. Sample-based and occurrence-based accumulation curves demonstrated that the efficiency of ant inventory methods is habitat specific. Litter sifting, however, was the single most efficient method in both habitats. Overall, our analyses of the relative efficiency of methods recommend the use of sifting and beating in the montane forest site, and sifting alone in the grassland site. In four of five methods, more species were collected in the grassland site (31 spp.) than in the forest site (26 spp.). Occurrence-based accumulation curves based on all methods demonstrated that species richness was similar in the two habitats, reaching a maximum difference of approximately one species. Only five species were shared between the grassland and forest sites. The presence of a high number of ant species restricted to the grassland site (18 spp.) is the first record of high endemism in this habitat in Madagascar and may have strong implications for the reconstruction of the natural vegetation types at the time humans arrived. Their presence suggests that a comparable open habitat, such as montane woodland, shrubland, or thicket, was present on Madagascar long before humans developed the secondary grasslands less than 2000 years ago. These results are contrary to the “classical hypothesis” that the central plateau was a continuous region of closed forest. These results support the hypothesis that the montane regions, including the central plateau, once contained areas of habitat with an open structure and that the endemic ants now found in the secondary grasslands were originally native to such a habitat.

RÉSUMÉ

La richesse en espèces et la composition des fourmis ont été inventoriées dans la forêt montagneuse du plateau central de Madagascar et dans la prairie secondaire adjacente. Cinq méthodes quantitatives ont été utilisées (tamisage des litières, deux types de trous-pièges, battage des végétations basses et lavage de terre). Nous avons comparé l'efficacité de ces méthodes dans chacun et entre les deux habitats. Les courbes d'accumulation d'espèces basées sur l'échantillon et sur l'occurrence ont montré que l'efficacité des méthodes d'inventaire de fourmis est habitat-dépendant. Cependant, le tamisage des litières se montrait la méthode la plus efficace dans les deux habitats. Nos analyses sur l'efficacité relative des méthodes recommandent l'utilisation combinée du tamisage des litières et du battage de végétation dans la forêt montagneuse, et l'utilisation seule du tamisage des litières dans la prairie secondaire. Dans quatre des cinq méthodes, plus d'espèces ont été collectées dans la prairie (31 spp.) que dans la forêt (26 spp.). Les courbes d'accumulation d'occurrence basées sur toutes les méthodes ont démontré que la richesse en espèces de ces deux habitats est similaire, atteignant seulement une différence maximale d'approximativement une espèce. Pourtant, seulement cinq espèces partageaient les deux habitats. La présence de plusieurs espèces de fourmis uniquement trouvées dans la prairie (18 spp.) est la première observation d'une forte endémicité de cet habitat et peut avoir une importante implication pour la restauration des types de végétation naturelle initiale de l'île. Leur présence suggère que des habitats ouverts similaires tels que les formations arbustives de montagnes et les fourrés, étaient présents à Madagascar longtemps avant la transformation de ces habitats en prairie secondaire par les humains. Ces résultats contredisent l'hypothèse classique qui avance que le plateau central a été uniquement composé d'une région de forêt dense. Ainsi, ces résultats supportent l'hypothèse que la région montagneuse contenant le plateau central, renfermait des habitats à structure ouverte et que les fourmis endémiques actuellement trouvées dans la prairie secondaire sont, à l'origine natives de ces habitats.

Key words: collection methods; deforestation; Formicidae; grassland; inventory design; Madagascar; tropical montane forest.

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SINCE HUMANS COLONIZED MADAGASCAR *ca* 1500–2000 years ago (MacPhee *et al.* 1985, Burney 1987a–c), it is estimated that more than 80 percent of Madagascar's original habitat has been destroyed (Du Puy & Moat 1996, 1998). Most of the island (*ca* 72% of the total land surface) is now composed of secondary (anthropogenic) grasslands, which are depauperate, dominated by pantropical species characteristic of disturbed settings, and burnt annually (Abraham *et al.* 1996, Lowry *et al.* 1997). The central plateau region of Madagascar, which includes the Ankazomivady region studied here, is now dominated by this extremely impoverished flora.

How, when, why, and to what extent the central plateau of Madagascar has been transformed from its primary vegetation since the arrival of humans have been of great interest and debate (reviewed in Gade 1996, Lowry *et al.* 1997). The arguments differ in their interpretation of the original vegetation type, but all conclude that fire was the dominant force in altering the vegetation. The central difference among the views is the extent to which grasslands were present when humans first started altering the environment. The so-called "classical hypothesis" holds that prior to human arrival, the central plateau of Madagascar was covered by essentially continuous, dense, climax forest (Perrier de la Bâthie 1921, 1936; Humbert 1927, 1949; MacPhee *et al.* 1985: 465; Burney 1987a: 130; Gade 1996). On the other hand, studies based on pollen core samples taken across the island argue that grasslands were present when humans arrived. One interpretation of the pollen core samples holds that the grassland vegetation occurring today is primarily a degraded form of this original climax vegetation, which consisted of open grassland areas devoid of any woody elements (MacPhee *et al.* 1985; Burney 1987a, b). A second interpretation based on pollen cores and other evidence suggests that open grasslands were not dominant when humans arrived but that grasses were present only as a minor component of the vegetation, which included forest and less densely wooded vegetation such as shrubland and thicket (Lowry *et al.* 1997). In this latter case, the secondary grasslands of today were once a mosaic of forest, thicket, and shrubland in which grasses were present.

Gade (1996) and Lowry *et al.* (1997) have summarized several lines of evidence supporting the idea that the central highlands of Madagascar were once forested (Gade 1996) or composed of forest, shrubland, and thicket (Lowry *et al.* 1997) and that the vast grasslands seen today resulted

from anthropogenic burning. One of the arguments for this scenario is based on known high levels of plant and animal endemism in other natural habitats in Madagascar, contrasted with low levels in grasslands. If the grasslands were ancient on Madagascar, Gade (1996) and Lowry *et al.* (1997) reasoned that a rich endemic herbaceous flora would have evolved. To further support this claim, Gade (1996) noted that the highlands of Madagascar today have none of the ecological complexity of East African savannas where plants and mammals show remarkable adaptations to fire. All living mammalian species on Madagascar are forest dwelling, and no amphibians or reptiles are known to be endemic to the secondary grassland areas (Gade 1996, Raxworthy & Nussbaum 1996). Furthermore, the absence of endemic amphibians and reptiles in the high plateau grasslands was used by Raxworthy and Nussbaum (1996) as strong evidence that the current grasslands are recent and artificial, and that the original vegetation and endemic herpetofauna have been lost. As a result, the secondary grassland habitat has been viewed as a bleak, sterile landscape with few endemic taxa. Since ants are successful invaders of disturbed habitats in Madagascar and throughout the world (Williams 1994, Fisher *et al.* 1998), the ant assemblages in these grassland habitats would be expected to show a similar pattern of low diversity and few endemics. We provide the first detailed account of the ant assemblages in grasslands of the high plateau and present evidence of high levels of endemism.

Our first objective addressed the need to develop efficient inventory methods for these habitat types. We used five quantitative methods (leaf litter sifting, two types of pitfall traps, beating low vegetation, and soil digging) and compared their relative efficiency within and across habitats. Our second objective was to compare the species richness and composition of ant assemblages in adjacent forest and grassland habitats in the central plateau of Madagascar. Specifically, we wanted to test the hypothesis that the ant fauna in the grassland would contain no or few endemics and be dominated by invasive exotics.

METHODS

STUDY SITES.—Ants were intensively surveyed in a montane forest block (Ankazomivady) and the adjacent exotic grassland between 6 and 15 January 1998. The two sites were located in the central high plateau of Madagascar in the province of Fia-

narantsoa. The forest block was recently (8–12 years ago) cut off from the extensive forest block to the east, which extends to the east and south toward Vohipara, Vohiparara, and Ranomafana (Ifandiana; Goodman *et al.* 1998). The inventories were conducted at the following sites: (1) Ankazomivady Forest site located 29 km SSW of Ambositra, 4.6 km SW of Ambalamanakana, 20°46.6'S, 47°09.9'E at 1700 m elevation. The forest had been selectively logged for large trees and showed numerous signs of use by zebu (*Bos indicus*), bamboo harvesting, and wood cutting. Goodman *et al.* (1998) provides a botanical description of the forest; (2) Grassland site located 28 km SSW of Ambositra, 4.1 km SW of Ambalamanakana, 20°46.5'S, 47°10.1'E at 1670 m elevation. The age of the grassland is difficult to determine but discussions with the elders in Ambalamanakana, a neighboring village, revealed that the grassland had been present for longer than 50 years and subjected to burning every few years.

SURVEY METHODS.—Five quantitative methods were used at the forest and grassland sites. Each method consisted of taking samples along a 250 m transect. Separate transect lines were used for each method, except for beating and sifting, which followed the same transect line. Transects were parallel and *ca* 10 m apart. The grassland transects ran perpendicular to the forest edge and began *ca* 100 m from the forest edge. The forest transects were located over 500 m from the forest edge.

(1) Pitfall traps (test tubes). Fifty pitfall traps were spaced at 5 m intervals along the transect. Pitfall traps consisted of test tubes (18 mm internal diam. \times 150 mm length) partly filled to a depth of *ca* 50 mm with soapy water and 5 percent ethylene glycol solution, which were inserted into PVC sleeves and buried with the rim flush to the soil surface. Traps were left in place for four days.

(2) Pitfall traps (cups). Fifty pitfall traps were spaced at 5 m intervals along the transect. Pitfall traps consisted of plastic cups (65 mm internal diam. \times 90 mm length) partly filled to a depth of *ca* 40 mm with soapy water and 5 percent ethylene glycol solution, which were buried with the rim flush to the soil surface. Traps were left in place for four days.

(3) Leaf litter sifting. Invertebrates were extracted from samples of leaf litter (leaf mold, rotten wood) using a modified form of the Winkler extractor (Fig. 2 in Fisher 1998). The leaf litter samples involved establishing 50 plots, each 1 m², at 5 m intervals along the transect line. The leaf litter

inside each plot was collected and sifted through a wire sieve of 1 cm grid size. Before sifting, the leaf litter material was chopped with a machete to disturb ant nests in small twigs and decayed logs. Ants and other invertebrates were extracted from the sifted litter during a 48-hour period in mini-Winkler sacks (for a detailed discussion of the mini-Winkler method, see Fisher 1998).

(4) Soil digging. Subterranean ants were collected from 25 soil samples, spaced 10 m apart along the transect line. Soil sampling methodology consisted of digging a 30 \times 30 \times 30 cm hole and searching the extracted soil for ants and ant brood. Small ants are difficult to discern in soil, but their white brood contrast well with the soil and facilitate location of nests.

(5) Beating low vegetation. Along the leaf litter transect, 25 beating stations were established 10 m apart. Ants on low vegetation and arboreal ants were sampled by holding a stretched 60 \times 60 cm white canvas platform below the undergrowth and beating the trunk of a tree (forest site) or clump vegetation (grassland site) three times with a stick. The dislodged ants that fell onto the canvas platform were placed in ethanol. This process was repeated six times for each of the 25 beating samples. Therefore, each beating sample consisted of six different plant subsamples, each beaten three times with a stick. The six beating subsamples were taken within a 5 m radius of the beating station along the transect.

Ants were also surveyed through general collecting, defined as any collection that was separate from the five quantitative transect methods, including searching in rotten logs and stumps, in dead and live branches, in bamboo, on low vegetation, under canopy moss and epiphytes, and under stones.

DATA ANALYSIS.—Our analyses are divided into two parts: (1) evaluation of inventory design: efficiency, cost (effort), and completeness of inventory methods; and (2) comparison of ant species richness and composition in grassland and forest sites. Only records of ant workers were used in data analysis since the presence of queens or males in samples does not necessarily signify the establishment of a colony of that species within the transect habitat type.

Our analyses of inventory design (efficiency, effort, and completeness) and number of species collected are based on visual inspection of the shape and magnitude of species accumulation curves. Comparison of measured species richness without reference to accumulation curves is not meaningful

even when a standardized sampling effort is employed (Colwell & Coddington 1994, Gotelli & Colwell 2001). We used two types of accumulation curves to address the two types of objectives. To analyze inventory design, species accumulation was plotted as a function of both the number of samples taken and the number of species occurrences (see below). For comparing relative community species richness in the two habitats, species accumulation was plotted as a function of the number of species occurrences. These two types of accumulation curves evaluate two different aspects of the inventory process.

Species accumulation curves plotted as a function of the number of samples is a measure of species density, the number of species per unit of sample effort, and may not reflect species richness (Gotelli & Colwell 2001). If habitats differ in density of individuals, or if two habitats differ in structure in a way that influences the effectiveness of a particular sampling method, then species accumulation curves plotted as a function of number of samples may not reflect the actual species richness of the community. For example, high density habitats will need less sampling effort than low density habitats to reach equal levels of completeness. Although not always appropriate for comparing relative species richness, we used sample-based accumulation curves as a tool to evaluate sampling design and effort. Effort in this case was the time and cost to collect a unit sample in the field. This is useful when comparing methods or evaluating the number of species captured with each succeeding sample.

The cost of an ant inventory involves both fieldwork and laboratory processing effort. The cost of processing samples is strongly related to the number of individuals captured (which requires mounting representatives of each species). An efficient method collects a high number of species with a low number of occurrences per species. As outlined in Fisher (1999a), we compared the relative cost of processing species from each method using accumulation curves plotted as a function of the number of occurrences.

We also used occurrence-based accumulation curves to compare species richness between habitats. Gotelli and Colwell (2001) argue that to compare species richness, species accumulation curves should be plotted as a function of individuals instead of number of samples. Ants, like other social insects, pose a problem since they are colonial. Because it is impossible to count colonies in beating and leaf litter sampling methods, a compromise is

to use number of occurrences (the total number of times a species is captured independently in the samples, ignoring the number of individuals of a species in any one sample).

Since the form of the species accumulation curve can depend on the ordering of samples (Palmer 1990, Colwell & Coddington 1994), all curves were smoothed through the process of randomization. Sample order was randomized 100 times and means were computed for each succeeding station using the program EstimateS (R. K. Colwell, pers. comm.).

The complementarity of methods was evaluated separately for each habitat using the combined accumulation curve method outlined in Longino and Colwell (1997). The five individual method curves were compared to (1) ten two-method curves, (2) ten three-method curves, (3) five four-method curves, and (4) one five-method curve. Accumulation curves were plotted as a function of both the number of samples and the number of species occurrences. Interpretation of the combined curves involves visual inspection of the rate and magnitude of species accumulation. For example, if each method singly collects a distinct portion of the fauna, then the combined curve will be steeper than the single method curves. Such a result indicates that the methods are complementary and not redundant. If the combined curve coincides or falls below the single method curves, then the methods capture a similar assemblage of species.

To evaluate the similarity of the grassland site and forest site to other faunas, we compared results with two forest sites in the Réserve Naturelle Intégrale (RNI) d'Andringitra (1680 and 1800–2050 m) located *ca* 160 km to the south and two sites in the Réserve Spéciale (RS) d'Anjanaharibe-Sud (1565 and 1985 m) located *ca* 710 km to the north.

RESULTS

EFFICACY OF INVENTORY METHODS.—Species accumulation curves of observed species plotted as a function of the number of samples and number of species occurrences for all methods combined showed decreased species accrual with increased sampling, but did not reach an asymptote (Fig. 1). For methods analyzed separately, however, most species accumulation curves were still rising steeply at the end of each transect (Figs. 2 and 3). Visual inspection of species accumulation curves showed that litter sifting had a higher rate of species accumulation than all other methods (Figs. 2 and 3).

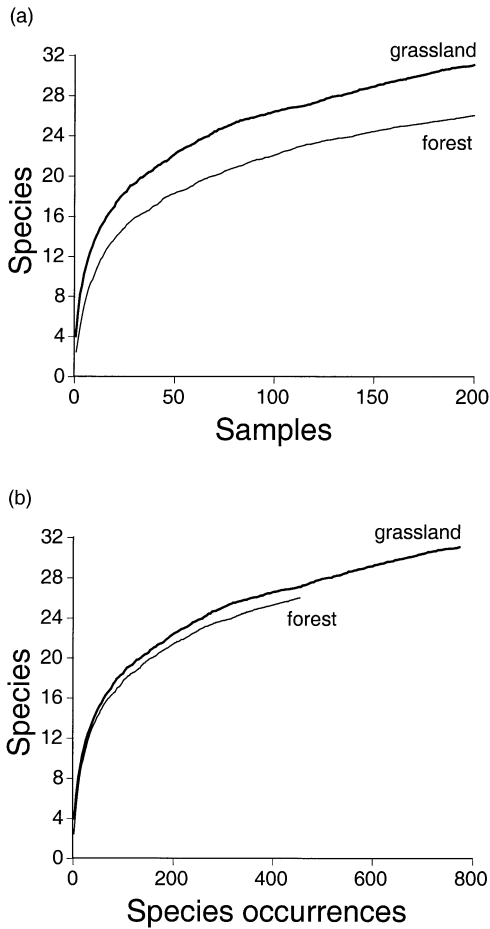


FIGURE 1. Assessment of ant species richness for forest and grassland sites based on all five methods. The species accumulation curves plot the observed number of species as a function of the number of: (a) samples taken (200 total samples) and (b) species occurrences. Curves are plotted from the means of 100 randomizations of sample accumulation order.

Accumulation curves of the sifting method were still increasing at the end of the transect in the grassland site, but showed little increase after ten samples in the forest site (Figs. 2 and 3). The total number of species collected was greatest for litter sifting in both habitats.

For methods other than litter sifting, the total number of species collected and the steepness of the accumulation curve depended on habitat and on the *x*-axis of the accumulation curve (Figs. 2 and 3). Within the grassland site, the shape of the sample-based and occurrence-based curves was similar (Fig. 2). In contrast, the forest had low species occurrences in all methods but sifting (Fig. 3).

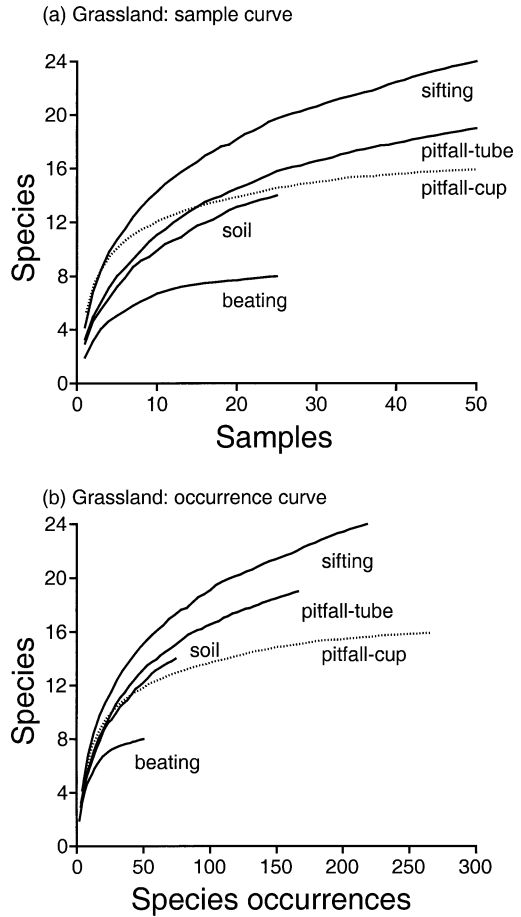


FIGURE 2. Efficiency of different collecting methods in the grassland site based on smoothed species accumulation curves of observed species. See text for explanation of collecting methods. The species accumulation curve in each chart plots the observed number of species as a function of the number of: (a) stations sampled and (b) species occurrences. Curves are plotted from the means of 100 randomizations of sample accumulation order. Litter samples have the highest rate of species accumulation in both charts.

Also, the few occurrences recorded in beating were diverse, resulting in a steeper occurrence-based curve relative to the sample-based curve. The relative ranking of methods between habits also differed. Compared to grassland, beating was more efficient in forests, while pitfall tubes were less efficient.

In the grassland habitat, sifting + tubes and sifting + tubes + soil were the most successful combinations, but were only a slight improvement over the single method of sifting (Fig. 4a). Sifting alone was as efficient and productive as any com-

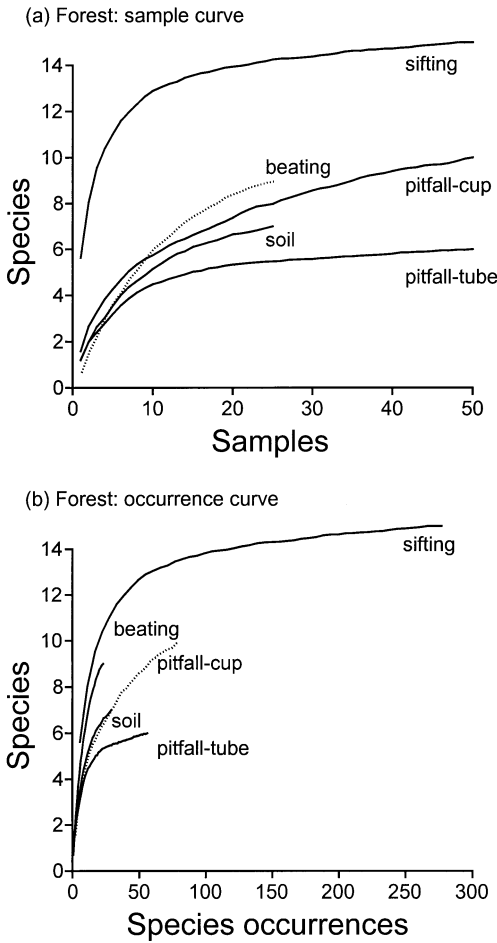


FIGURE 3. Efficiency of different collecting methods in the forest site based on smoothed species accumulation curves of observed species. See text for explanation of collecting methods. The species accumulation curve in each chart plots the observed number of species as a function of the number of: (a) stations sampled and (b) species occurrences. Curves are plotted from the means of 100 randomizations of sample accumulation order. Litter samples have the highest rate of species accumulation in both charts. The basal portions of the soil and pitfall cup curves almost perfectly coincide and thus are indistinguishable.

bination of methods. The most redundant, least productive combination was sifting and beating. In forest habitat, combined methods were far more efficient, with a steeper species accumulation curve than any method considered singly (Fig. 4b). In the forest, sifting and beating was the most effective two-method combination, and sifting + beating + cups was the best three-method combination (Fig.

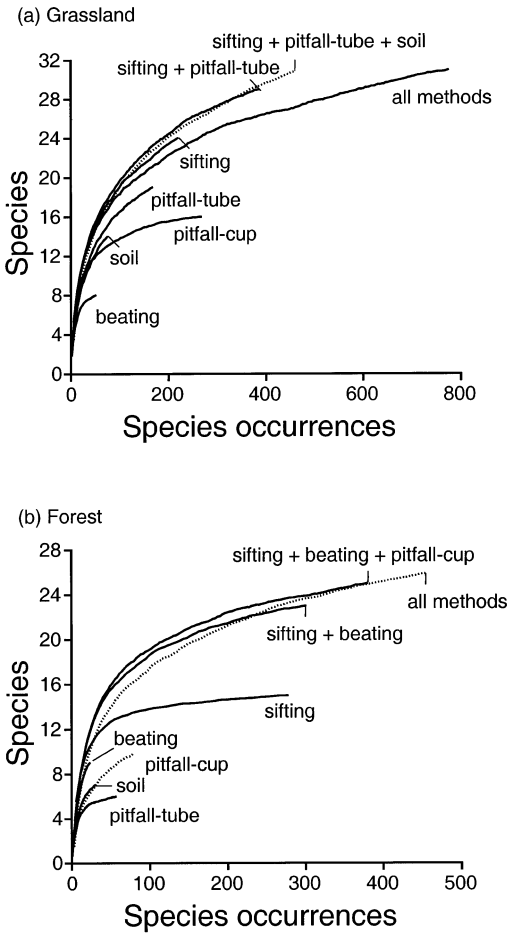


FIGURE 4. Efficiency of different combinations of methods in the (a) grassland and (b) forest sites. Only the most efficient two-method, three-method, and five-method curves are shown. The species accumulation curve in each chart plots the observed number of species as a function of the number of species occurrences. Curves are plotted from the means of 100 randomizations of sample accumulation order. In the forest site, the basal portions of the soil and pitfall cup curves almost perfectly coincide and thus are indistinguishable.

4b). The least productive combination was sifting and soil.

Although different methods collected the same species within a habitat, the abundance, measured as number of occurrences of these species, often differed considerably from one method to the next (Table 1). For example, in the forest site, *Pheidole* sp. 6 and *Tetramorium* sp. 10 had a high number of occurrences in the 50 litter samples (31 and 36, respectively) while the 50 cup and 50 tube pitfall samples for both species had an occurrence of less

than 6. Even though pitfall tubes collected more species than cups in the grassland site (19 vs. 16), the total number of occurrences for all species was greater in cups than tubes (Fig. 2; 266 vs. 166).

COMPARISON OF GRASSLAND AND FOREST ANT RICHNESS AND COMPOSITION.—The grassland and forest sites yielded a total of 19 genera and 59 species from general collections, leaf litter, pitfall, soil, and beating methods (Table 1). This included the first record of the ant genus *Anoplolepis* in Madagascar. Separated by habitat, 15 genera and 33 species were collected in the Ankazomivady grassland site and 12 genera and 31 species were found in the adjacent forest site.

Each quantitative method collected more species in the grassland than the forest site, except for beating, which collected one more species in the forest than in grassland (Figs. 2 and 3). The total number of species collected from all five quantitative methods in the grassland was also greater (31 spp.) than in the forest (26 spp.). An analysis of species richness for grassland and forest sites using species accumulation curves, however, suggests that the differences in number of species is caused by a species density effect, and not a community-level difference in species richness (Fig. 1). When observed species is plotted as a function of species occurrences, the habitats show almost identical species richness, differing only by one species (Fig. 1b).

COMPARISON WITH OTHER FAUNAS.—All 31 species collected in the forest site are thought to be endemic to Madagascar and its neighboring islands. Of these 31 species, 6 are known from this forest only. The forest site shared only 5 species with the grassland site. Compared to four additional montane forest sites surveyed in Madagascar (RNI d'Andringitra, Fisher 1996; RS d'Anjanaharibe-Sud, Fisher 1998), the Ankazomivady forest site shared the most species with the RNI d'Andringitra 1680 m site (11 spp.), which is closer (160 km south) than the RS d'Anjanaharibe-Sud (710 km north; Table 2).

Of the 33 species in the grassland site, 28 are thought to be endemic to Madagascar. Of the 33 species in the grassland site, 18 are known only from the Ankazomivady grassland site. Of the remaining species, 5 species are shared with the Ankazomivady forest site only; 5 species are known from other forest sites in Madagascar, and 5 species also occur outside of Madagascar (3 spp. are exotics common to disturbed tropical habitats around the

world: *Pyramica mandibularis*, *Cardiocondyla emeryi*, and *Tetramorium albipes*; 2 spp. are widespread in Africa and in Madagascar: *Pachycondyla ambigua* and *Cardiocondyla shuckardi*).

DISCUSSION

EVALUATION AND COMPARISON OF COLLECTING METHODS.—An important issue in conservation biology is understanding landscape-level patterns of diversity. These data are essential to developing rigorous conservation plans for a region. Most research to date has focused on providing vertebrate data for conservation assessment. Due to a lack of appropriate collection methods, invertebrates are often excluded from terrestrial inventories despite their importance in ecosystem functioning and ability to elucidate fine-scale levels of diversity (Fisher 1999a, Delabie *et al.* 2000).

A critical issue associated with invertebrate inventories is determining the method that is the most appropriate for each habitat type. Sampling methods do not collect all species equally well (Longino & Colwell 1997, Fisher 1999a). Ants nest and forage in the soil, litter (leaf mold, rotten wood), rotting logs, dead branches, on the ground surface, and on vegetation. Nest site location and the proportion of time spent foraging in these habitats help determine the species-specific probability of capture for each type of inventory method employed. Ant species that are rare in pitfall and leaf litter collections may be arboreal nesters, which only occasionally forage on the forest floor and may be abundant in canopy samples (Longino & Colwell 1997). The decision to employ one or more techniques in a given habitat requires information on the number or kind of species obtained based on a standardized sampling unit or number of individuals. Species with a low probability of capture using one method may be more efficiently surveyed by changing methods, not by more intensive sampling with the same methods.

This study evaluated five quantitative methods to survey ants in forest and grassland habitats. The results demonstrated that litter sifting was the most efficient method to capture ant species in both forest and grassland habitats (Figs. 2 and 3). Litter sifting collected 58 and 77 percent of the total number of species captured by all five quantitative methods in the forest and grassland habitats, respectively. This is the first published record to demonstrate the efficiency of the litter sifting technique in grassland habitats.

The optimal combination of sampling methods

TABLE 1. Species list of ants for collections in the forest and grassland based on leaf litter sifting (L), cup pitfall traps (PF cups), test tube pitfall traps (PF tubes), beating (Beat), soil digging (Soil), and general collecting (G). Abundance measured as the number of occurrences (number of samples in which each species was recorded for each inventory method; 50 samples of PF and L, 25 samples of Beat and Soil). Based on all methods, 31 species were recorded in the Forest site, and 33 species in the Grassland site. Out of the 59 species collected in both habitats, 5 species were shared between habitats (shared taxa in bold).

| Species | Ankazomivady Forest | | | | | | Grassland | | | | | |
|----------------------------------|---------------------|--------|---------|------|------|---|-----------|--------|---------|------|------|---|
| | L | PF cup | PF tube | Beat | Soil | G | L | PF cup | PF tube | Beat | Soil | G |
| <i>Anoplolepis</i> sp. 01 | | 1 | | 2 | | | | | | | | |
| <i>Apbaenogaster swammerdami</i> | | | | | | | 3 | 42 | 10 | | | + |
| <i>Camponotus</i> sp. 14 | | | | | | | | | | | | + |
| <i>Camponotus</i> sp. 50 | | | | | | | 1 | 5 | 4 | 6 | | + |
| <i>Camponotus</i> sp. 51 | | | | | | + | | | | | | + |
| <i>Camponotus</i> sp. 55 | | | | | | | | | | | | + |
| <i>Camponotus</i> sp. 56 | | | | | | + | | 6 | 3 | | | + |
| <i>Cardiocondyla emeryi</i> | | | | | | | 5 | 1 | 3 | 1 | 1 | |
| <i>C. shuckardi</i> | | | | | | | | 9 | 1 | | 1 | |
| <i>Cerapachys</i> sp. 08 | 10 | | | | 1 | | | | | | | |
| <i>Cerapachys</i> sp. 26 | | | | | | | | | 1 | | | |
| <i>Cerapachys</i> sp. 27 | | | | | | | 3 | | 1 | | | |
| <i>Crematogaster lobata</i> | | | | 3 | | + | | | | | | |
| <i>C. schenki</i> | | | | 2 | | + | | | | | | |
| <i>Crematogaster</i> sp. 01 | | | | | | + | | | | | | |
| <i>Crematogaster</i> sp. 19 | | | | | | + | | | | | | |
| <i>Hypoponera</i> sp. 01 | 34 | 1 | | | | | 1 | | | | | |
| <i>Hypoponera</i> sp. 08 | 13 | | | | | | 1 | | | | | |
| <i>Hypoponera</i> sp. 10 | 14 | | | | | | | | | | | |
| <i>Hypoponera</i> sp. 11 | 21 | | 1 | | 5 | | | | | | | |
| <i>Hypoponera</i> sp. 60 | | | | | | | | | | | 2 | |
| <i>Leptothorax</i> sp. 06 | | | | 6 | | | | | | | | |
| <i>Leptothorax</i> sp. 07 | | | | 1 | | | | | | | | |
| <i>Leptothorax</i> sp. 08 | | | | 2 | | + | | | | | | |
| <i>Monomorium</i> sp. 10 | 2 | 2 | | | | | | | | | | |
| <i>Monomorium</i> sp. 50 | | | | | | | 18 | 37 | 26 | 4 | 5 | |
| <i>Monomorium</i> sp. 51 | | | | | | | 13 | 10 | 3 | | 3 | + |
| <i>Monomorium</i> sp. 52 | 15 | | | 2 | | + | | | | | | |
| <i>Oligomyrmex</i> sp. 1 | | | | | | | 14 | | | | 1 | |
| <i>Pachycondyla ambigua</i> | | | | | | | 3 | 2 | 1 | | 2 | + |
| <i>Paratrechina</i> sp. 1 | | | | | | | 3 | 25 | 18 | 3 | 9 | + |
| <i>Pheidole</i> sp. 02 | | 14 | 8 | | | | | | | | | |
| <i>Pheidole</i> sp. 06 | 31 | 5 | 4 | | 2 | | 1 | | | | | |
| <i>Pheidole</i> sp. 09 | 49 | 34 | 29 | | 14 | + | 4 | | | | | |
| <i>Pheidole</i> sp. 100 | | | | | | | 44 | 48 | 49 | 8 | 19 | + |
| <i>Pheidole</i> sp. 101 | | | | | | | 29 | 23 | 6 | | 18 | + |
| <i>Plagiolepis</i> sp. 03 | | | | 4 | | | | | | | | |
| <i>Plagiolepis</i> sp. 04 | | | | | | | 13 | 8 | 2 | 20 | | + |
| <i>Prionopelta</i> sp. 07 | | | | | | | 1 | | | | | |
| <i>Pyramica mandibularis</i> | | | | | | | 1 | | | | | |
| <i>P. tathula</i> | | | | | | | 4 | | | | | |
| <i>Strumigenys abdera</i> | 6 | | | | | | | | | | | |
| <i>S. adsita</i> | | | | | | | | | | | 1 | |
| <i>S. manga</i> | | | | | 1 | | | | | | | |
| <i>S. milae</i> | | | | | | | 2 | | | | | |
| <i>S. sphaera</i> | 29 | | | | 3 | | | | | | | |
| <i>S. sylvaini</i> | 7 | 2 | | | | | | | | | | |
| <i>S. tegar</i> | 1 | | | | | | | | | | | |
| <i>S. toma</i> | | | | | | | 1 | | | | | |
| <i>Technomyrmex albipes</i> | | | | | | | 17 | | 1 | 2 | 3 | + |
| <i>Tetramorium schaufussi</i> | | | | | | + | | | | | | |

TABLE 1. *Continued.*

| Species | Ankazomivady Forest | | | | | | Grassland | | | | | |
|---------------------------|---------------------|--------|---------|------|------|----|-----------|--------|---------|------|------|----|
| | L | PF cup | PF tube | Beat | Soil | G | L | PF cup | PF tube | Beat | Soil | G |
| <i>Tetramorium</i> sp. 01 | | 1 | | | | | | | | | | |
| <i>Tetramorium</i> sp. 10 | 36 | 3 | 6 | | | | | | | | | |
| <i>Tetramorium</i> sp. 14 | 9 | 16 | 8 | | 3 | + | | | | | | |
| <i>Tetramorium</i> sp. 61 | | | | | | | 24 | 13 | 10 | 6 | 7 | + |
| <i>Tetramorium</i> sp. 62 | | | | | | | 12 | 33 | 21 | | 2 | + |
| <i>Tetramorium</i> sp. 63 | | | | | | | | 2 | 2 | | | |
| <i>Tetramorium</i> sp. 64 | | | | | | | | 2 | 4 | | | |
| Undescribed genus sp. 06 | | | | 1 | | | | | | | | |
| Total Species | 15 | 10 | 6 | 9 | 7 | 11 | 24 | 16 | 19 | 8 | 14 | 14 |

for maximizing the number and rate of species captured in grassland and forest, however, was different. For the grassland site, sifting and pitfall traps were the most productive combination, collecting 94 percent of the species captured using all five quantitative methods, while sifting alone captured 77 percent. In the forest, sifting and beating were the best combination, collecting 88 percent of the species captured using all five quantitative methods, while sifting alone captured 58 percent. The structural difference in grassland and forest plant communities is probably the main factor affecting efficiency of beating and pitfall traps in each habitat. It is not surprising that beating low vegetation in

grassland sites was completely redundant with leaf litter sifting because of the overall height and structural complexity of beaten foliage.

Even though sifting and pitfall traps were the most productive combination of methods in the grassland site, occurrence-based accumulation curves do not strongly support the use of pitfall traps (Fig. 4a). The shape of the sifting accumulation curve is almost identical to the pitfall trap curve. Pitfall traps have also been shown to be a relatively ineffective tool in sampling ants in wet forest habitats (Fisher 1999a). Based on an analysis of 14 inventories in rain forest of Madagascar, pitfall traps collected few species and were redundant

TABLE 2. *Species collected at Ankazomivady grassland (Ank-G) and forest (Ank-F) sites that were also captured at four other inventoried forest sites. For each site, records are based on pitfall and leaf litter transects, and general collections. (And: Réserve Naturelle Intégrale d'Andringitra; Anj: Réserve Spéciale d'Anjanaharibe-Sud).*

| Species | Ank-G 1670 m | Ank-F 1700 m | And 1680 m | And | | |
|---------------------------------|-----------------|-----------------|---------------|----------------|---------------|---------------|
| | | | | 1800–2050 m | Anj 1565 m | Anj 1985 m |
| <i>Camponotus</i> sp. 14 | + | | | + | | |
| <i>Crematogaster</i> sp. 01 | | + | | + | | |
| <i>Hypoponera</i> sp. 01 | + | + | + | + | + | |
| <i>Hypoponera</i> sp. 10 | | + | + | + | | |
| <i>Hypoponera</i> sp. 11 | | + | + | | + | |
| <i>Leptothorax</i> sp. 07 | | + | | + | | |
| <i>Monomorium</i> sp. 52 | | + | | + | | |
| <i>Paratrechina</i> sp. 01 | + | | | + | + | |
| <i>Pheidole</i> sp. 02 | | + | + | | | |
| <i>Pheidole</i> sp. 06 | + | + | + | | | |
| <i>Pheidole</i> sp. 09 | + | + | + | + | | |
| <i>Pheidole</i> sp. 100 | + | | | + | | |
| <i>Strumigenys sphaera</i> | | + | + | | | |
| <i>S. sylvaini</i> | | + | + | | | |
| <i>Tetramorium</i> sp. 01 | | + | + | + | | |
| <i>Tetramorium</i> sp. 10 | | + | + | | | |
| <i>Tetramorium</i> sp. 14 | | + | + | | + | |
| Total species collected at site | 33 | 31 | 32 | 31 | 55 | 10 |
| Species shared with Ank-G | | 5 | 3 | 5 | 2 | 0 |
| Species shared with Ank-F | 5 | | 11 | 7 | 2 | 2 |

with respect to litter samples, collecting few new species not collected by the litter sifting method (Fisher 1999a). Additional studies in dry forest habitats of Madagascar, which include areas of open ground, showed that pitfall traps are more useful (Fisher & Razafimandimby 1997). Likewise, in the present study, pitfall traps performed slightly better in grassland habitats than in wet forest habitats (Fig. 4). Nonetheless, in the grassland site, sifting alone performed just as efficiently as any combination of methods, including sifting and pitfall (Fig. 4a). In general, these studies suggest that pitfall trap performance does increase in open habitats but should not be included in inventories if sifting can be effectively employed. Pitfall traps may be most appropriate in habitats that lack the necessary organic matter for sifting, such as deserts.

Overall, based on this study of five methods, sifting and beating are the recommended methods to survey forest habitats in Madagascar, while sifting alone is the best method to survey mesic grasslands.

COMPARISON OF GRASSLAND AND FOREST ANT ASSEMBLAGES.—The similarity of grassland and forest richness was an unexpected result. Expectations were of a relatively rich forest and a depauperate grassland. Several factors may be acting to increase richness in grasslands relative to forest in this montane site. Low diversity in montane forest sites has been well documented in Madagascar (Fisher 1996, 1998, 1999a, b). Species richness of ants in forest habitats peaks at mid-elevation (*ca* 800 m) and declines rapidly at higher elevations. The decrease in species richness with elevation is hypothesized to reflect climatic variables, mainly the reduction of radiant energy with increasing elevation (Brown 1973, Fisher 1996). Montane grassland habitats may support relatively high ant diversity at the same elevation because the grassland litter layer receives more radiant heat during fog-free periods. In a similar study in South Africa, in Natal Province at 1350 m, a comparison of grassland and montane forest revealed greater ant diversity in grassland habitat than in the adjacent forest block (B. Fisher, pers. obs.).

The grassland and forest sites surveyed in the present study shared very few species (5 spp.). An additional five species from the grassland site were also shared with other forest sites on the island. The difference in ant assemblages between grassland and forest sites may be the result of the structural differences (*i.e.*, absence of trees in the grassland sites) rather than the presence of specific plant

species or edaphic conditions. Trees have been shown to cause most of the environmental discontinuities occurring at the forest/secondary grassland interface (Belsky & Amundson 1992). By intercepting rain and solar radiation, trees reduce the amount of water and light reaching the ground layer (Belsky & Amundson 1992). Consequently, soil temperatures and potential evapotranspiration are higher in grasslands. These fundamental environmental disparities may preclude the occurrence of similar ant assemblages in the two surveyed habitats. Habitat-associated ant assemblages comprise species adapted to the microclimate within their particular habitat; hence, it is not surprising that there was little overlap in the two ant faunas. The grassland habitat, however, could share species with native montane thickets, shrublands, or woodlands in Madagascar, which have a similar open structure and lack a closed canopy (see below).

ORIGIN OF GRASSLAND ANTS.—The central plateau region of Madagascar, which includes the Ankazomivady forest studied here, is now dominated by an extremely impoverished flora. The secondary grasslands characteristically have fewer than 20 species of grasses at a given site, and often fewer than 12. The dominant species at a site are widespread and often pantropical, fire-resistant grasses. Their low taxonomic diversity is in sharp contrast to the comparatively high floristic richness of native grasslands elsewhere in the world (Lowry *et al.* 1997). In addition to low species diversity, fewer than 10 percent of the grassland species are endemic and confined to grasslands (Koechlin *et al.* 1974, Gade 1996, Lowry *et al.* 1997). The angiosperm flora across all habitats, however, has more than 80 percent endemism at the species level (Lowry *et al.* 1997; G. Schatz, pers. comm.).

The origin of 18 ant species known only from this grassland at Ankazomivady is an enigma. We are not aware of any other published accounts of high endemism for any taxon in secondary grasslands of Madagascar. The contradiction of the ant data is rather puzzling but may have strong implications for the reconstruction of the natural vegetation types at the time humans arrived. The presence of endemic ants in the grassland site suggests that a comparable habitat, at least structurally (*i.e.*, lacking a closed canopy and with open areas), was present on Madagascar long before humans developed the secondary grasslands. These results are contrary to the "classic hypothesis that Madagascar, including the central plateau, was a continuous region of forest" (Burney 1996, 1997; Gade 1996).

We propose that the montane regions, including the central plateau, once contained areas of habitat with a similar open structure to the present day grasslands, and that the endemic ants now found in the secondary grasslands were originally native to this habitat. The most likely open habitats are montane woodlands, shrublands, and thickets, which are ericoid-, graminoid-, and composite-dominated. Woodland, thicket, and shrubland differ in the density of woody plants, and the degree of canopy cover and height (see White 1983 for detailed descriptions).

Montane woodlands, shrublands, and thickets on Madagascar today are restricted to the highest mountain ranges (above 2000 m) but may have been more widespread. Recent palynological studies throughout the island have indicated a dynamic environmental history during the Pleistocene (Burney 1996, 1997). Burney (1996, 1997) has hypothesized that during the Last Glacial Maximum, the montane thickets and shrublands of Madagascar may have flourished. They may have extended down to elevations of *ca* 1000 m. As a result, vast areas of shrubland and thickets may have been part of the evolutionary history of Madagascar. The surviving remnants of tapia (Sarcolaenaceae: *Uapaca bujeri*) woodlands and montane ericoid thickets have not been surveyed for ants, but in the light of this study this will be a necessary exercise. The endemic grassland ants captured in this study may be found in these habitats. Whereas the woody elements of these native habitats were unable to withstand the frequent fires, endemic ants may have persisted in the secondary grasslands by virtue of being ground nesters. Of note, the plants that do persist the longest tend to be geophytes with most of the storage tissue below ground (G. Schatz, pers. comm.).

Subfossil evidence from lemurs also suggests that structurally open habitats were present on Madagascar before the arrival of humans (Abraham *et al.* 1996). The extinct family of Archaeolemuridae has been described as being equivalent to the baboons (*Papio* spp.) found throughout mainland Africa (Mittermeier *et al.* 1994). One member of this family, *Hadropithecus*, is known from Holocene subfossil sites in southern and central Madagascar. *Hadropithecus* is thought to have been similar to the present-day gelada (*Theropithecus gelada*), which is a specialized terrestrial primate that feeds on grass blades and rhizomes in the open grasslands of Ethiopia (Mittermeier *et al.* 1994, Godfrey *et al.* 1997).

An alternative hypothesis is that grassland ant species colonized from forest habitats. The 18 grassland-restricted species could represent formerly localized forest species that have recently colonized grasslands. These species may appear to be restricted to grasslands simply because they have not yet been collected in their native and localized forest habitats. In this study, 10 of the 33 species from the Ankazomivady grassland site have already been collected at other forest sites. This hypothesis predicts that with more studies on Madagascar, most of the 18 localized grassland species will be found in other forest sites. Although it is difficult to rule out this hypothesis completely, a much greater number of species from the Ankazomivady forest site (25 of 31 spp.) is known from other forest sites. Our knowledge of montane ant assemblages, therefore, does not strongly support this hypothesis.

Sample-based and occurrence-based accumulation curves demonstrate that the efficiency of ant inventory methods is habitat-specific. The leaf litter sampling method, however, had the greatest rate and magnitude of species capture in both habitats and should be included in ant surveys in forest and grassland habits. Beating should also be combined with sifting in forest habitats. The high level of endemism of grassland ants suggests that an open habitat (montane woodland, shrubland, or thicket) existed before humans arrived *ca* 2000 years ago. To account for the unique ant fauna, we propose that the habitat was extensive and extant long enough to evolve endemic taxa. The present-day grassland ants would have been native to this habitat. The next step is to survey the ants in remnant patches of these native montane open habitats.

This study highlights the urgent need to map biodiversity in Madagascar. Given the current levels of habitat loss and continued high rates of deforestation, this map is vital for effective conservation practices on the island. In basic sciences, this map is needed to understand the complex historical factors that have shaped the origin and evolution of the remarkable fauna and flora of Madagascar. Now is the time to document and analyze biodiversity within the island before the chance is lost forever.

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