

NESTED SUBSETS AND PARTITION PATTERNS IN ANT ASSEMBLAGES (HYMENOPTERA, FORMICIDAE) OF COLOMBIAN DRY FOREST FRAGMENTS

INGE ARMBRECHT, IRENE TISCHER, & PATRICIA CHACON

Departamentos de Biología y Estadística, Universidad del Valle, Cali, Valle,
Apartado Aereo 25360, Cali, Colombia

Abstract.—We analyzed the conservation status of ant assemblages in seven dry forest fragments located in the Cauca River valley in southwestern Colombia, by means of nested subsets techniques which are applicable in situations where a fragmented landscape can be compared with an archipelago. Ant communities were intensively sampled between 1994 and 1995 in all forests as well as in their surrounding matrices (i.e., neighboring agricultural lands). From 123 ant species found, 63 species were captured only in the forest habitat and 60 ant species in both forests and matrices (“habitat generalist”). No significant species-area relation was found. Monte Carlo simulations and N index showed a significant nesting for “habitat generalist” ant species. The opposite was true for the ant species limited to forests: we found a pattern of extreme non-nestedness (i.e., the opposite of nestedness pattern), which cannot be explained in terms of random effects. This led us to amplify the nested subsets analysis by the concept of “partition pattern” which describes a scheme, where species found on one island of an archipelago are not likely to be found on any other one. The relevance of partition identification in conservation biology is obvious: in a partitioned archipelago, it is essential to protect all component islands. Each one possesses a fauna not repeated in the whole archipelago. Destroying this fauna means extinguishing it in the whole archipelago.

Key Words.—Insecta, Dry forest, Formicidae, fragmentation, nested subsets.

One of the main issues in conservation biology is the widespread transformation of natural land for human use, resulting in the fragmentation and insularization of many formerly continuous habitats (Cutler 1991). Although Colombia has been regarded as a megadiverse country (Brown 1989) with various biotic endemic centers (Terborgh & Winter 1983), it is being affected by an extensive destruction of its tropical forest. The Andean region, where most of the Colombian population is concentrated, is the zone most affected by human action (Saavedra & Freese 1986) with the consequent fragmentation of ecosystems. The dry tropical forest, as found in the interandean valleys, is the most endangered habitat of all the major lowland tropical forests (Janzen 1988). Slash and burn agriculture formerly applied to this fertile land, and the recent advance of extensive fire-managed sugar cane monocultures, have contributed to the progressive destruction of these tropical dry forests.

A fragmented landscape such as the one just described, can be compared with an oceanic archipelago, in which the patches of suitable habitat could be considered “islands”, surrounded by an “ocean” of anthropogenic matrix. Although this assumption is fundamental for the application of island biogeography to conservation, it has to be handled carefully, because the mainland habitat islands are separated in reality by other habitats and are not completely isolated. Thus, depending on the matrix surrounding a particular remnant, some species may not be isolated at all, but others may be trapped as if they were embedded in actually “isolated islands” (Doak & Mills 1994).

In many natural and anthropogenic habitats, the fauna of the archipelago tends

to form nested subsets (Cutler 1991). This pattern, termed "nested subset model" by Patterson and Atmar (1986), arises in an archipelago when species occurring on species-poor islands are mere subsets of the species living on islands richer in biota. Nested subset analysis tests for patterns between species identities and the numbers of species occurring on different islands (Doak & Mills 1994). A nested pattern has been variously attributed to both selective immigration and selective extinction (Cutler 1991).

If a nested subsets model fits in a situation with a strong species-area relation, it supports the argument that a large reserve, rather than many small ones, preserves more vulnerable biota. However, a nested subsets pattern does not necessarily imply that a predictable extinction sequence will result from shrinking remnant size and it is quite possible to have a nested subset and no significant species-area relationship or vice versa, as argued by Doak and Mills (1994). The power of nested subsets techniques is that they support statements concerning predictability of species lost or colonizations, in an ordered sequence from the species-rich to species-poor remnants (Doak & Mills 1994).

Due to their ubiquity, abundance and their importance in energy and matter transfer in tropical terrestrial ecosystems, arthropods, especially insects, have been proven a valuable tool in studies of conservation biology (Kremen et al. 1993). Ants (Hymenoptera: Formicidae) have been proposed as bioindicators of species diversity (Andersen & Majer 1991, Roth et al. 1994), disturbance (Brown 1989, Olson 1991, Burbidge et al. 1992, Majer 1992) and successional stages or ecosystem rehabilitation (Majer 1983, 1985; Mackay & Vinson 1989).

This paper analyzes the conservation status of ant assemblages in seven dry forest fragments located in the same river valley in southwestern side Colombia, by means of nested subsets techniques. We discuss new insights concerning the application and interpretation of Patterson and Atmar's nested subsets index.

MATERIALS AND METHODS

Study area.—The study was carried out in the Cauca Valley, an alluvial valley formed by the Cauca River. The valley is about 220 km long and 10–20 km wide (coordinates 30°5', 5°05' N and 76°04', 76°30' W) with an extension of about 421,000 ha. It is between 900–1000 m above sea level. Its soils are of extraordinary fertility, and its climatic conditions are very appropriate to agricultural use: the average temperature is about 24° C. There are two rainy seasons (March–May, September–November), each followed by a dry season. The mean annual rainfalls range between 1000 and 2000 mm. According to the Holdridge classification system, this region is designated as tropical dry forest (Espinal 1967).

It is known from anecdotal sources that this valley was once covered by continuous and extensive, closed canopy forests (Alvarez & Kattan 1995) which rapidly retreated after the Spaniards' colonization. Simultaneously, extensive crop and cattle fields and also numerous settlements appeared in this landscape. By 1957, the forest area reduction was severe, only 25,320 ha of the valley were covered by forest. Only 29 years later, this forest area was further reduced by 66% (Corporación Autónoma Regional del Valle del Cauca 1990).

Today, the valley is almost totally dominated by sugar cane and other crops and by pastures (Alvarez-López & Kattán 1995). The intensive fragmentation left only small isolated forests, with extensions between 1 and 15 ha. They are of

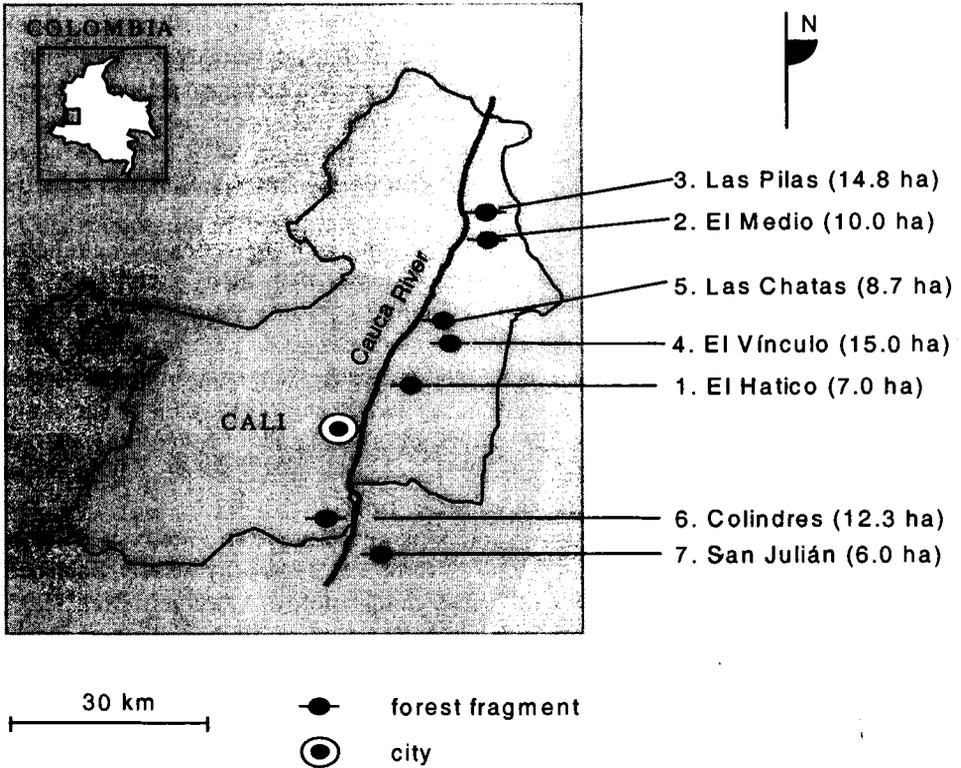


Figure 1. Localization of the study sites. The forest fragments are ordered according to species richness of ants: 1 denotes the richest fragment. Forest area is denoted in parenthesis.

secondary growth, with 20–40 m high canopies, in which species such as *Laetia americana* L., *Guadua angustifolia* Kunth, *Xylopia ligustrifolia* Humboldt & Bonpland ex Dunal and *Anacardium excelsum* (Bertero & Balb. Ex Kunth) dominate. The common biographic history allows us to consider the region as an archipelago of forest remnants embedded in a ocean-like anthropogenic “matrix”, term defined by Samways (1994) as “the most extensive and continuous portion of a landscape, which often surrounds a fragment of different nature”.

In this study we selected seven dry forest fragments along Cauca river valley (Fig. 1). It is important to state here that there was neither transition zone nor ecotone in any of the fragments studied.

Sampling.—Ant assemblages were sampled twice in each forest fragment and its corresponding matrix. The first sampling set was conducted at three-week intervals between August and September 1994 and the second was carried out between January and February 1995.

Sampling in the forest fragments and their surrounding matrix was done according to Armbrrecht (1995). In brief, four 100 m long transects were designated, two inside the forest fragment beginning 20 m inside from the forest edge, and two in matrices beginning 20 m outside the border. The transects inside the forest were parallel to each other, but perpendicular to the forest border. The transects in the matrix were located in the same way, along the same lines.

Ten equidistant, 10 m separated stations were labeled along each transect. At each station, the following procedures were carried out: firstly, three tuna bait traps (i.e., 5 g tuna-in-oil on 7×10 cm piece of paper) were installed in different places (10 cm underground, on the soil surface and attached to a tree trunk at 1.70 m height). Also a pitfall trap (i.e., a plastic glass 6 cm diameter, containing a 1:1 alcohol-water mixture) was set up at each station to trap falling ants. Both tuna baits and pitfall traps were left out for four h. In addition, a total of 50 liters/transect (5 liters/station) of forest litter was collected and sifted with a Winkler sac. Ants caught in the sifted material were separated in the laboratory. Finally, eight h of visual scrutiny and manual capture were performed along all transects (10–15 min/station), searching for ants in the different microhabitats. The total sampling effort in a forest and its surrounding matrix included a total of 320 hours of pitfall trapping, 880 hours of tuna baits attraction, 80 samples of litter and 16 person-hours of manual collection.

Ants were determined taxonomically to genus level according to Holldobler and Wilson (1990), Mackay and Vinson (1989), and Jaffé et al. (1993). Specific level was assessed by specialists from different U.S. and Colombian Institutions (see acknowledgment). Voucher specimens are deposited at the "Museo de Entomología de la Universidad del Valle", Cali, Colombia.

Data Analysis.—The geographic separation of the selected forest fragments allowed us to use the nested subsets principle in the analysis concerning biological conservation. The nested subsets concept is based on the richness of each island, i.e., number of species. The distribution of species in a group of islands follows a nested subsets pattern if the species of a poorer island can always be found on the richer ones (Patterson 1987).

Obviously, it is not probable to find a pure nested subsets pattern in an archipelago, so it is necessary to define an index which allows an evaluation of how close a given pattern of species is to a nested subsets pattern. There are various alternative indices (see for instance Patterson & Atmar 1986, Cutler 1991, Wright & Reeves 1992). We used the index of unexpected absences described in Patterson and Atmar (1986). The difficulty with all definitions is that these indices are not normalized; that is, the specific structure of the archipelago and the number of species found do affect the absolute size of the index. In order to judge the closeness of a pattern to nestedness, Patterson and Atmar (1986) proposed calculating the indices of a number of random patterns and comparing their probability distribution with the index of the observed pattern.

There are different possibilities for simulating the required random patterns. Patterson and Atmar (1986) proposed the following: the simulation algorithm called RANDOM0 generates the given number of species, supposing a uniform distribution of the number of species per island. In RANDOM1, the distribution of species per island follows the observed richness. Obviously, RANDOM1 is closer to the real situation, and can therefore be considered more reliable.

We implemented a modified version of the Monte Carlo algorithm proposed by Patterson and Atmar (1986) to reduce the computing time to 1000 simulations to a few seconds.

The procedure for determining the index of unexpected absences (N), which we used to evaluate the observed and simulated patterns of species, is the following: the islands are ranked in order of richness and the species, in order of their

frequency of occurrences. Using this order, the presence-absence matrix is constructed. For each species, the poorest island containing it is found, and the number of absences in all richer islands is determined (the unexpected absences). This number is a measure of how strictly this species follows the conservation principle. In a pure conservation pattern, one would not expect any absences. The index N , the sum of the unexpected absences of all species, describes the deviation of the observed pattern from a completely nested one.

We found it convenient to standardize the index N of unexpected absences (as emphasized by Cutler 1991, Wright & Reeves 1992, Cook 1995). We standardized the probability distribution function of the simulated N indices, dividing them by the standard deviation and subtracting the mean value. By the same operation, applied to the calculated N index of the studied archipelago, we obtained the standardized index \tilde{N} . Based on the Monte Carlo simulation process, the index \tilde{N} is independent of the specific matrix structure and density. It is therefore possible to compare evaluations of different archipelagos, evaluations of one archipelago in different instances, or as in our case, subgroups of species found in the archipelago.

Using the standardized index \tilde{N} it is easy to interpret the nestedness of a pattern. Values near 0 indicate a complete random pattern, the more negative the values, the more significant is the nested pattern. High positive values indicate a pattern which is significantly not random.

The following statistics for the simulated N indices were determined: total mean, variance, standard deviation and highest and lowest values. *t*-tests (Zar 1984) were used to assess the probability of the calculated N index being the result of a normal distribution of values.

RESULTS

We recorded 3006 capture events, 69.7% of them in the forest transects, 30.3% in the matrix. One capture event refers to an ant species captured by any of the methods described above regardless the number of workers collected. We found a total of 136 different ant species. After excluding the species present only in the matrix, which are of no relevance in our study, we counted a total of 123 ant species; 63 species were captured only in the forest and 60 were captured in both forest and matrix. The appendix shows the presence-absence matrix for species in each of the forest fragments. No significant correlation in the species-area relationship was found for the fragments ($r = 0.11$; $n = 7$; $P > 0.5$).

Figure 2 shows the species saturation curves for all species sampled, as well as forest and matrix habitats separately. As recommended by Longino and Colwell (1997), we included all sampling methods. The curves show stabilization after $\frac{2}{3}$ of the total capture events, thus confirming sufficiency of our sampling effort (Armbrecht & Ulloa-Chacon 1999).

The nesting index N was calculated and Monte Carlo simulations type RANDOM0 and RANDOM1 were done. Here we will discuss only the results obtained by simulation using RANDOM1; the results using RANDOM0 are similar, but slightly weaker. The index of unexpected absences is quite near the mean value obtained by 1000 simulations, indicating that the pattern found can be explained by mere randomness (Table 1).

Given the separate surveys in forests and the surrounding fields, we were able

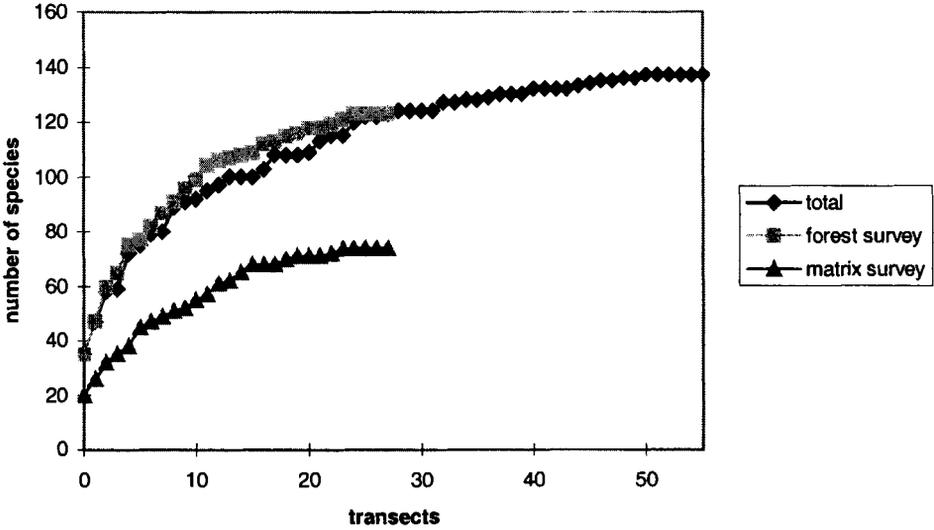


Figure 2. Saturation curves for species sampled in the forest and matrix transects (total), in the forest transects only (forest survey) and in the surrounding matrix only (matrix survey). Data from different transects were ordered randomizing individual fragment transects. Note that the “total” curve is less steep initially than “forest survey” because the accumulation of species slows down initially due to the effect of the less rich matrices included in this group.

to analyze separately the group of ant species found only in the forest (exclusive forest habitat species) and those present in both forest and matrix (“habitat generalist” species) (Table 1). The behaviors of these two groups are completely contrary: the group of species present in the forest and its surrounding matrix present a nested pattern. The group of exclusive forest habitat species does not follow a nested subsets scheme, but neither is the pattern completely random. We found a value of the unexpected absence index which is significantly above the mean value ($P = 0.01$). We term this pattern, characterized by a significant non-nestedness, a partition pattern. The species which contributed most to the high N

Table 1. Summary of the nestedness analysis of all ant species found in the study (first row), and the two subgroups in which we divided it: “habitat generalists” and “exclusive forest species”. N is the observed index of unexpected absences. \bar{N} is the standardized index proposed by us, in which values near 0 indicate a complete random pattern (see text). Additionally we report the mean value, standard deviation, maximum and minimum obtained in the Monte Carlo simulation of 1000 archipelagos, using RANDOM1. P refers to the probability that the observed values could be explained by randomness.

Group	Actual data			Monte Carlo simulation				
	Spp.	N	\bar{N}	Mean N	S.D.	Min	Max	P<
All species	123	247	0.43	241.0	13.89	192	283	0.67
“Habitat generalist” species*	60	80	-2.23	99.1	6.55	66	122	0.013
Exclusive forest habitat species**	63	105	4.30	78.0	6.28	54	107	0.99

* Refer to ant species found both in forests and matrices

** Refer to ant species found only inside forests.

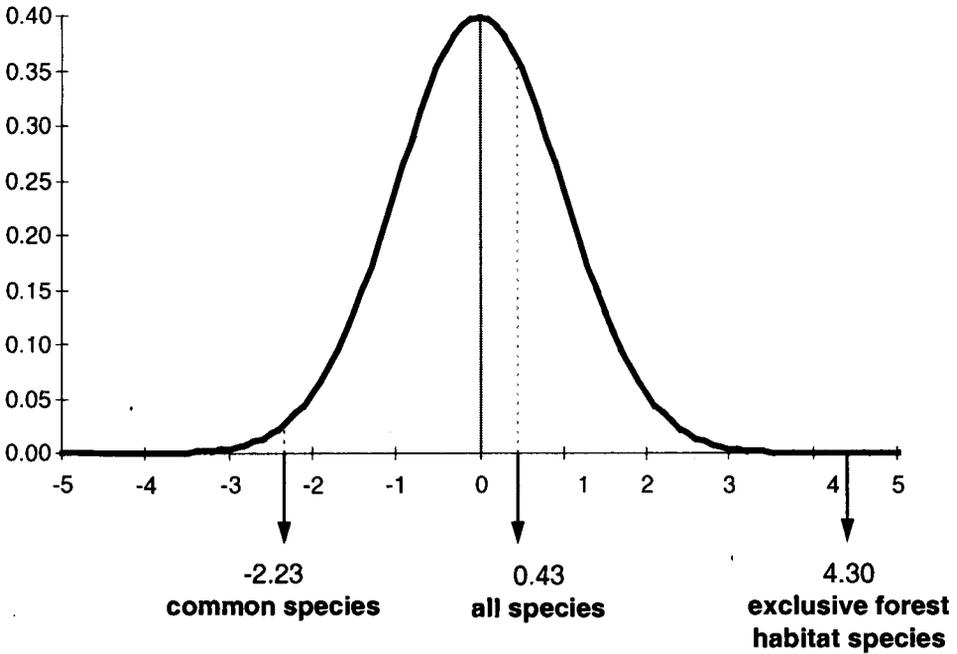


Figure 3. Standardized normal distribution of \bar{N} showing the values for the three group combinations of ant species analyzed in the study.

index are the ones which are present in only one forest. They explain 66.7% (70 of 105) of the unexpected absences.

In order to show the contrary behaviors of the two groups we standardized the normal distributions of the simulated indices and the observed index of the different combination groups (Fig. 3). The random pattern shown by the combinations of all species can thus be explained by the superposition of the two groups: the nested group of "habitat generalist" species and the group of exclusive forest habitat species, which is significantly not nested.

DISCUSSION

The Concepts of Nestedness and Partition.—Species of an archipelago follow a nested subsets pattern if those species present on the poorer islands are also present on the richer ones. In this case, the index N of unexpected absences is significantly below the value expected in a completely random pattern. Nestedness could be explained by extinction (i.e., Brown & Gibson 1983, Patterson & Atmar 1986, Patterson 1987) or colonization (Darlington 1957, Simberloff & Wilson 1967) in a "nested way". When assumptions are met (Atmar & Patterson 1993), the species of an archipelago follow a predictable scheme of extinction if there is a sequence of species ordered according to their susceptibility to extinction. Species present a scheme of selected immigration, if they have followed a predictable "colonization program" possibly determined by selected dispersal. In both cases, the nested pattern of species in the archipelago can be attributed to the conditions of the islands: they must follow a scheme whereby the habitat "capacity" for supporting ant species diminishes in a sequential order from the

species-rich to the species-poor island (that means, the habitats also follow a nested pattern).

Here we would like to develop a concept to apply in a situation where a partition pattern is found, that is, a pattern of significant non-nestedness. Nestedness means that the species occurring on the poorer islands are all present on the richer ones. The extreme opposite situation is a partition pattern, where each species occurs on only one island. A nested pattern presents a very low index of unexpected absences; the index for partition schemes is very high. This means that a partition pattern could not be explained as random variation. There must be an explanation, as for nested structures.

The reason why real archipelagos or habitat fragments show a partitioned fauna can, in analogy to the nested case, be attributed to their ecological and geographical conditions. In the case of partition, that means, that habitat conditions present in one island, will not occur on other ones: they are mutually exclusive. Alternatively, the priority of access to an establishment site can give a forest ant species a competitive advantage because of greater colony size. Therefore, the ants species left in forest fragments are apt to be most successful in replacing themselves, especially if establishment of outsiders is restricted by low rates of colonization by habitat specialists because of the low quality of the matrix. Consequently, each fragment conserves its special fauna. The implications for conservation are serious: if one of the habitat islands disappears, the remnant fauna will also disappear, because it is only present in this single island.

Implications for the Situation Studied.—We assume that before fragmentation each ant species in the forest had the same probability of being present in any part of the continuously wooded geographical Cauca River valley. If all the fragments had the same history, the largest fragment would have retained more species. The lack of a significant correlation in the species-area relationship may be due to the fact that the seven wooded fragments are about the same size (6–15 ha), but present a large variation in the number of ant species. Thus, the richest forest (El Hatico) with 67 species, has nearly double fauna of the poorest forest (San Julian) with only 34 species (Appendix).

For the analysis of the nesting for the species common to both forest and matrix (“habitat generalists”), we consider the forest plus its nearest matrix as the island, because the samples were taken no further than 150 m away from the forest borderline. The result is a highly significant nestedness. Following Doak and Mills (1994), it is important to consider that island fragments are separated from other terrestrial communities by habitats that might be occupiable by the species under study. Therefore, depending on the type of matrix surrounding the fragments, some species will not really be isolated, but others will be trapped, with the matrix acting as a barrier equivalent to oceanic islands. As a working hypothesis, we propose that the agricultural practices of the matrix, which includes the progressive utilization of land to single crop farming explain the extinctions (or the fail of successful colonizations). For instance, it has been shown for coffee crops that high quality agricultural matrices sustain more associated biodiversity than low quality ones (Perfecto & Snelling 1995, Perfecto et al. 1996). Forests which have been protected throughout generations and which are surrounded by the richest matrices (for example, El Hatico, El Medio) had also the richest ant faunas. We suggest that those species which accept a wide range of living conditions are able

to immigrate from the surrounding fields and pastures to the forest-matrix fragments and that they are colonizing new areas in a predictable sequence. The pattern found for "habitat generalists" ants may therefore indicate that the fragments are true isolates, from the viewpoint of very low rates of colonization by ants across the intervening matrix. We suggest that a sustainable management of the agricultural landscape can be the key for biodiversity conservation.

Contrary to the group of species found in forest and matrix, in the group of species exclusively occurring in forest, a partition pattern was found, indicating that each forest preserves its own species. Thus, many species living in forests with few species are not found in forests with many species. How can this pattern be explained? One possibility is that demographic rarity has affected the geographic rarity. However, if this had been the case, one would expect a purely random pattern (Doak & Mills 1994), not the partition pattern we found. An alternative explanation for this pattern is that throughout the process of fragmentation microhabitats and communities of the different fragments have turned out to be mutually exclusive, so that each forest sustains a particular forest ant fauna that is almost isolated by "low quality" matrices. The important conclusion from the partition pattern found is that if any of these forest fragments disappears, an important portion of rare, exclusive forest ant species will disappear with it. Moreover, ants, as bioindicators, may reflect biodiversity in other taxa like invertebrates or plants (Majer 1983), so that the danger of local extinction may extend to an even broader range of organisms. In this heavily fragmented distribution, each forest remnant, be it large or small, constitutes a refuge for preserving biodiversity.

General Remarks.—The concept of nestedness should be supplemented by the concept of partition, a pattern where the N index is higher than it would be expected from a random process. A partitioned pattern means that many species are found in only one island, more than could be expected in a random scheme. This means, that all the islands in the archipelago deserve special attention. Only protection of the archipelago as a whole can lead to the conservation of fauna.

We found it helpful to standardize the index of unexpected absences, N, in order to allow comparison among different groups of species on an archipelago (or even among archipelagos) with respect to nestedness or partition. The standardization uses means and standard deviations of the simulated indices, thus compensating for the effects of size and density of the presence-absence matrix.

It is important to keep in mind that results of nested subsets analysis could be ambiguous if the subgroups involved present nested as well as partitioned patterns. The results for the whole group are thus only the superposition of the evaluations of the subgroups. In studies, that intend to apply nestedness analysis, it is very important to include intensive sampling of the matrix. The findings of the present paper depend highly on the possibility of distinguishing species of an exclusive forest habitat and species found in the surrounding fields as well.

ACKNOWLEDGMENT

We thank W. P. Mackay, University of Texas; J.J. Longino, Estación Biológica La Selva, Costa Rica; R. J. Hampton, Long Beach; H. G. Fowler Instituto de Biociencias, Brazil; F. Fernandez Instituto Humboldt, Colombia and J. F. Watkins, Baylor U., Texas for determination of ant species. J. Colmenares, V. Peñaranda

and M. Cuervo helped with the samplings and two unidentified reviewers for invaluable comments and corrections. This study was funded by the program in conservation of the Wildlife Conservation Society, GEA and the Federation of Superior Education of Colombia; the "José Celestino Mutis" fund of the "Financiera Eléctrica Nacional" of Colombia; and the "Universidad del Valle", Cali. The "Corporación Autónoma Regional del Valle del Cauca" allowed us to visit the forest fragments.

LITERATURE CITED

- Alvarez-López, H. & G. Kattan. 1995. Notes on the conservation status of resident diurnal raptors of the middle Cauca valley, Colombia. *Bird Conserv. Internal.*, 5: 137–144.
- Andersen, A. N. & J. D. Majer. 1991. The structure and biogeography of rain forest ant communities in the Kimberley region of northwestern Australia. pp. 333–346. *In* McKenzie N. L., R. B. Johnston & P. G. Kendrick, (eds.). *Kimberley Rainforests*. Surrey Beatty & Sons, Chipping Norton, Australia.
- Armbrecht, I. 1995. Comparación de la mirmecofauna en fragmentos boscosos del valle geográfico del río Cauca, Colombia. *Bol. Mus. Entomol. Universidad del Valle*, 3: 1–10.
- Armbrecht, I & P. Ulloa-Chacon. 1999. Rareza y diversidad de hormigas en fragmentos de bosque seco colombianos y sus matrices. *Biotropica*, 31: 546–653.
- Atmar, W. & B. D. Patterson. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 96: 373–382.
- Brown, J. H. & A. C. Gibson. 1983. *Biogeography*. C. V. Mosby Company, St. Louis, Missouri.
- Brown, K. Jr. 1989. The conservation of neotropical environments. Insects as indicators. pp. 354–404. *In* Collins, N. M. & J. A. Thomas, (eds.). *The conservation of insects and their habitats*. 15th Symposium of Royal Entomological Society of London. Academic Press, Hartcourt Brace Jovanovich.
- Burbidge, A. H., K. Leicester, S. McDavitt & J. D. Majer. 1992. Ants as indicators of disturbance at Yanchep National Park, Western Australia. *J. Roy. Soc. West. Aust.*, 75: 89–95.
- Cook, R. R. 1995. The relationship between nested subsets, habitat subdivision and species diversity. *Oecologia*, 101: 204–210.
- Corporación Autónoma Regional del Valle del Cauca, CVC. 1990. Informe 90-7. Comparación de la cobertura de bosques y humedales entre 1957 y 1986, con delimitación de las comunidades naturales críticas en el valle geográfico del río Cauca. Cali, Valle, Colombia.
- Cutler, A. 1991. Nested faunas and extinction in fragmented habitats. *Cons. Biol.*, 5: 496–505.
- Darlington, P. J. Jr. 1957. *Zoogeography: the geographical distribution of animals*. John Wiley & Sons, New York.
- Doak, D. F. & L. S. Mills 1994. A useful role for theory in conservation. *Ecology*, 75: 615–626.
- Espinal, L. S. 1967. *Apuntes sobre ecología colombiana*. Universidad del Valle, Cali, Colombia.
- Holldobler, B. & E. O. Wilson. 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts.
- Jaffe, K., J. Latke & E. Pérez. 1993. *El mundo de las hormigas*. Equinoccio Ediciones. Universidad Simon Bolivar, Venezuela.
- Janzen, D. H. 1988. Tropical dry forest, the most endangered major tropical ecosystems. pp. 130–137. *In* Wilson, E. O. (ed.). *Biodiversity*. National Academy Press, Washington D.C.
- Kremen, C. R., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss & M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Cons. Biol.*, 7: 796–808.
- Longino, J. T. & R. K. Colwell: 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecol. Applic.*, 7: 1263–1278.
- Mackay, W. P. & S. V. Vinson. 1989. A guide to the species identification of the new world ants. *Sociobiology*, 16: 3–47.
- Majer, J. D. 1983. Ants: bio-indicators of minesite rehabilitation, land use and land conservation. *Environ. Manag.*, 7: 375–383.
- Majer, J. D. 1985. Recolonization by ants of rehabilitated Mineral sand mines on North Stradbroke Island, Queensland with particular reference to seed removal. *Aust. J. Ecol.*, 10: 31–48.
- Majer, J. D. 1992. Ant recolonization of rehabilitated bauxite mines of Pocos de Caldas, Brazil. *J. Trop. Ecol.*, 8: 97–108.

- Olson, D. 1991. A comparison of the efficacy of litter sifting and pitfall traps for sampling leaf litter ants (Hymenoptera: Formicidae) in a wet forest, Costa Rica. *Biotropica*, 32: 166–172.
- Patterson, B. D. 1987. The principle of nested subsets and its implications for biological conservation. *Cons. Biol.*, 1: 323–334.
- Patterson, B. D. & W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linnean Soc.*, 28: 65–82.
- Perfecto, I. & R. Snelling. 1995. Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecol. Appl.*, 5: 1084–1097.
- Perfecto, I., R. A. Rice, R. Greenberg & M. E. Van der Vort. 1996. Shade coffee: a disappearing refuge for biodiversity. *Bioscience*, 46: 598–608.
- Roth, D. S., I. Perfecto & B. Rathcke. 1994. The effects of management systems on ground foraging ant diversity in Costa Rica. *Ecol. Appl.*, 4: 423–436.
- Saavedra, C. J. & C. Freese. 1986. Prioridades biológicas de conservación en los Andes tropicales. *Parques*, 11: 8–11.
- Samways, M. J. 1994. *Insect conservation biology*. Chapman & Hall, London.
- Saunders, D. A., R. J. Hobbs & C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Cons. Biol.*, 5: 18–32.
- Simberloff, D. & J. L. Martin 1991. Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. *Ornis Fennica*, 68: 178–192.
- Simberloff, S. D. & E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, 50: 278–296.
- Terborgh, J. & B. Winter. 1983. A method for sitting parks and reserves with special reference to Colombia and Ecuador. *Biol. Cons.*, 27: 45–58.
- Wright, D. H. & J. H. Reeves. 1992. On the meaning and measurement of nestedness of species assemblages. *Oecologia*, 92: 416–428.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice Hall, New Jersey.

Received 21 Apr 2000; Accepted 4 Oct 2001.

Appendix. Presence-absence matrix of the ant species in the seven sites (the forest fragment and its surroundings). The species labeled with "f" were found exclusively inside the forest (exclusive forest habitat) and not in its surrounding matrix. That is, they are exclusive forest habitat species as defined in the paper. Species without labeling were captured at least one time each in both the forest and matrix. Forests are ordered by richness, and ant species are ordered according to their presence from the richest to the poorest forests. 1: El Hatico, 2: El Medio, 3: Las Pilas, 4: El Vínculo, 5: Las Chatas, 6: Colindres, 7: San Julián.

Scientific name and code assigned during the study	Forest only	forest fragments						
		1	2	3	4	5	6	7
<u>Wasmannia auropunctata</u>		x	x	x	x	x	x	x
Myr-04 <u>Solenopsis</u> ("Diplorhoptrum")		x	x	x	x	x	x	x
<u>Crematogaster</u> sp.		x	x	x	x	x	x	x
Myr-08 <u>Solenopsis</u> ("Diplorhoptrum")		x	x	x	x	x	x	x
<u>Camponotus novogranadensis</u>		x	x	x	x	x	x	x
<u>Camponotus crassus</u>		x	x	x	x	x	x	x
<u>Pseudomyrmex oculatus</u>		x	x	x	x	x	x	x
<u>Pseudomyrmex boopis</u>		x	x	x	x	x	x	x
<u>Pseudomyrmex elongatus</u>		x	x	x	x	x	x	x
<u>Paratrechina ca. pubens</u>		x	x	x	x			x
For-13 <u>Camponotus</u> sp.		x	x	x	x			x
<u>Brachymyrmex heeri</u>		x	x	x		x	x	x
<u>Pheidole sussanae</u>		x	x	x		x	x	x
<u>Cephalotes maculatus</u>		x	x		x	x	x	x
<u>Cyphomyrmex rimosus</u>		x	x	x	x			x
<u>Atta cephalotes</u>		x	x	x	x			x
Myr-03 <u>Pheidole</u> sp.		x	x		x		x	x
Myr-32 <u>Pheidole</u> sp.				x	x		x	x
Pon-10 <u>Hypoponera</u> sp.	f		x	x	x		x	x
Dol-06 <u>Linepithema</u> sp.		x	x			x	x	x
<u>Crematogaster curvispinosa</u>	f	x				x	x	x
<u>Pseudomyrmex gracilis</u>		x	x			x		x
<u>Pseudomyrmex pallens</u>	f	x	x				x	x
<u>Strumigenys eggersi</u>	f		x	x	x			x
Pon-09 <u>Hypoponera</u> sp.	f			x		x		x
Dol-01 <u>Azteca</u> sp.	f	x			x			x
<u>Dolichoderus lutosus</u>	f	x				x		x
<u>Cephalotes minutus</u>						x		x
<u>Crematogaster distans</u>	f			x				x
For-11 <u>Camponotus</u> sp.	f	x						x

Appendix. Continued.

Scientific name and code assigned during the study	Forest only	Forest fragments						
		1	2	3	4	5	6	7
<u>Pseudomyrmex kuenckeli</u> .	f			x			x	
Myr-56 <u>Crematogaster (Orthocrema) sp.</u>	f					x		x
Myr-10 <u>Cephalotes sp.</u>	f							x
Myr-43 <u>Cephalotes sp.</u>	f							x
Myr-14 <u>Pheidole sp.</u>		x	x	x	x			x
<u>Pachycondyla constricta</u>	f	x	x	x	x			x
<u>Procryptocerus hylaeus</u>		x		x		x	x	
Dol-03 <u>Azteca sp.</u>		x			x	x	x	
<u>Crematogaster acuta</u>		x	x					x
Pon-13 <u>Pachycondyla n. sp.</u>	f	x				x	x	
<u>Linepithema dispertitum</u>		x	x					x
Pse-10 <u>Pseudomyrmex sp.</u>				x	x			x
Myr-18 <u>Trachymyrmex sp.</u>	f			x				x
Myr-23 <u>Cephalotes (Paracryptocerus)</u>	f	x						x
<u>Pseudomyrmex rochai</u>	f	x						x
<u>Pachycondyla obscuricornis</u>	f	x						x
For-05 <u>Camponotus</u>	f					x		x
Dol-07 <u>Azteca</u>	f			x				x
<u>Crematogaster ampla</u>								x
<u>Cardiocondyla nuda</u>	f							x
<u>Pachycondyla harpax</u>	f							x
Pon-15 <u>Pachycondyla sp.</u>	f							x
Dol-13 <u>Azteca sp.</u>								x
<u>Labidus coecus</u>			x	x	x	x		
<u>Azteca velox</u>				x	x	x		
<u>Leptothorax echinatinopis</u>				x	x	x		
<u>Leptothorax pleuriticus</u>	f	x		x		x		
<u>Solenopsis geminata</u>		x				x		
<u>Leptothorax sp.</u>				x		x		
<u>Pachycondyla foetida</u>	f	x				x		
<u>Camponotus abdominalis</u>	f	x				x		
Dol-12 <u>Azteca sp.</u>	f	x				x		
<u>Pseudomyrmex ita</u>								x
Pse-15 <u>Pseudomyrmex sp.</u>	f					x		
<u>Pseudomyrmex lissus</u>	f					x		
<u>Camponotus bidens</u>	f					x		
<u>Pachycondyla impressa</u>		x	x	x	x			
<u>Crematogaster evallans</u>			x	x	x			
Myr-13 <u>Solenopsis ("Diplorhoptum") sp.</u>			x	x	x			
<u>Megalomyrmex drifti</u>	f	x	x		x			
Myr-02 <u>Pheidole (flavens group) sp.</u>			x		x			
Myr-36 <u>Pheidole (biconstricta group) sp.</u>				x	x			
Myr-46 <u>Pheidole sp.</u>	f	x			x			
Myr-52 <u>Pheidole (Trachypheidole) sp.</u>		x			x			
Myr-59 <u>Solenopsis sp.</u>			x		x			
Myr-63 <u>Strumigenys sp.</u>	f			x	x			
<u>Odontomachus chelifera</u>		x			x			
Myr-15 <u>Cephalotes sp.</u>	f				x			

Appendix. Continued.

Scientific name and code assigned during the study	Forest only	Forest fragments						
		1	2	3	4	5	6	7
<u>Strumigenys smithii</u>	f				x			
<u>Octostruma balzani</u>	f				x			
<u>Gnamptogenys striatula</u>	f				x			
Dol-16 <u>Tapinoma</u> sp.	f				x			
Myr-31 <u>Pheidole (Hendecapheidole)</u> sp.		x	x	x				
Myr-37 <u>Pheidole (biconstricta group)</u> sp.	f	x		x				
Myr-47 <u>Pheidole</u> sp.	f	x		x				
<u>Sericomyrmex amabilis</u>	f	x		x				
Myr-42 <u>Pheidole</u> sp.	f	x		x				
<u>Dolichoderus bispinosus</u>		x		x				
Myr-33 <u>Solenopsis</u> sp.				x				
Myr-39 <u>Leptothorax (Nesomyrmex)</u> sp.				x				
<u>Acanthognathus brevicornis</u>	f			x				
Pon-14 <u>Pachycondyla</u> sp.	f			x				
For-10 <u>Brachymyrmex</u> sp.	f			x				
For-16 <u>Brachymyrmex</u> sp.				x				
For-17 <u>Camponotus</u> sp.	f			x				
Dol-10 <u>Azteca</u> sp.	f			x				
For-06 <u>Paratrechina</u> sp.		x	x					
For-08 <u>Camponotus (Tanaemyrmex)</u> sp.	f	x	x					
For-19 <u>Brachymyrmex</u> sp.		x	x					
Dol-04 <u>Azteca</u> sp.		x	x					
<u>Gnamptogenys annulata</u>	f	x	x					
Myr-25 <u>Crematogaster (Orthocrema)</u> sp.				x				
Myr-27 <u>Pheidole (Macropheidole)</u> sp.	f			x				
<u>Pseudomyrmex flavidulus</u>				x				
Myr-29 <u>Monomorium</u> sp.	f			x				
Myr-35 <u>Pheidole</u> sp.				x				
Myr-60 <u>Rogeria</u> sp.				x				
<u>Prionopelta antillana</u>	f			x				
<u>Gnamptogenys horni</u>	f			x				
<u>Pseudomyrmex termitarius</u>	f			x				
For-09 <u>Camponotus (Myrmobrachys?)</u>				x				
Dol-15 <u>Linepithema</u> sp.	f			x				
<u>Pseudomyrmex tenuissimus</u>	f	x						
<u>Pseudomyrmex levivertex</u>		x						
Myr-48 <u>Pheidole</u> sp.		x						
Myr-50 <u>Strumigenys</u> sp.	f	x						
<u>Myocepurus smithii</u>		x						
Myr-57 <u>Strumigenys</u>	f	x						
Myr-65 <u>Solenopsis (Diplorhoptrum)</u> sp.	f	x						
Myr-66 <u>Pheidole</u>	f	x						
For-18 <u>Paratrechina</u>	f	x						
<u>Linepithema humile</u>		x						
For-20 <u>Camponotus</u> sp.	f	x						
Total		67	53	50	41	38	37	34