Biogeography of Puerto Rican ants: a non-equilibrium case?

JUAN A. TORRES

Department of Biology, PO Box 23360, University of Puerto Rico, San Juan, Puerto Rico 00931-3360 and International Institute for Tropical Forestry, USDA Forest Service, PO Box 25000, Río Piedras, Puerto Rico 00928-2500, USA

ROY R. SNELLING

Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, CA 90007, USA

Ants were studied on Puerto Rico and 44 islands surrounding Puerto Rico. Habitat diversity was the best predictor of the number of species per island and the distributions of species followed a nested subset pattern. The number of extinctions per island was low, approximately 1–2 extinctions per island in a period of 18 years, and the rates of colonization seem to be greater than the extinction rates. Ant dynamics on these islands do not seem to support the basic MacArthur and Wilson model of island biogeography. The MacArthur and Wilson equilibrium is based on the notion that species are interchangeable, but some extinctions and colonizations can change the composition and number of species drastically.

Keywords: Caribbean; insects; island; equilibrium; extinction; tropics.

Introduction

The theory of island biogeography (MacArthur and Wilson, 1967) tries to predict the number of species on an island using mainly area and distance from the mainland as the independent variables. The theory predicts that the number of species on an island represents the balance between the colonization and extinction rates. The equilibrium does not imply that the species number is a fixed equilibrium value, rather a stationary probability distribution with certain variance (Diamond and Gilpin, 1980). For mobile species, an equilibrium should be reached quickly, but for species with limited dispersal power, an equilibrium may require periods equalling those of major geological or evolutionary events (Case and Cody, 1987). To test the theory on a given island, it is necessary to demonstrate the existence of an equilibrium in species numbers and the existence of species turnover as a steady ongoing process (Gilbert, 1980; Murphy, 1983). The existence of an equilibrium implies that extinction and colonization rates are relatively constant over time. Many researchers incorrectly assume that the existence of a significant species area curve for a group of islands validates the theory (Simberloff, 1974; Gilbert, 1980), and often it is assumed that the islands are at equilibrium: the average of the species number on several censuses is used to calculate the equilibrium value (see Heatwole and Levins, 1973).

The MacArthur and Wilson theory postulates that within a biogeographic region, the differences in species composition are mainly due to stochastic factors (Thomson and Gilligan, 1983; Whittaker, 1992; Simberloff, 1994). The existence of an equilibrium does not depend on any biological interactions: in the case of linear immigration and extinction

curves, the implicit assumption is made that biological interactions are absent. Curvilinear extinction and immigration curves result when the assumption of species as independent entities is relaxed, species differ in colonization abilities, or interference among species increases as species number grows (MacArthur and Wilson, 1967), but it is assumed that the rates depend only on species number and not on the identity of the species. In a model of island biogeography based on strong interspecific interactions, multiple configurations (species sets) may be possible, and changes from one equilibrium number to another are predicted. Predictions from the MacArthur and Wilson model are expected when species interactions are weak, some species substitute for others, and communities are stable over geological time (Case and Cody, 1983).

Whittaker (1992, 1995) criticized the equilibrium framework as an explanation for the changes in several taxonomic groups on Krakatau Island, pointing out the importance of succession and disturbance in determining species number. Monotonic changes in the environment (deterministic factors) can be so great that they can explain the biotic change observed, but the theory does not postulate a constant environment. The predictions of the model are upheld if the probabilities of catastrophic events are constant and frequent with respect to the time scale of the study (Simberloff, 1976). Also, the original MacArthur and Wilson (1967) stochastic model has been criticized on grounds that turnover is insignificant, involves the same set of ephemeral species, and that some extinctions simply represent the comings and goings of individuals of widely ranging single populations or perhaps peripheral populations in a source–sink system (Simberloff, 1976, 1994; Williamson, 1989; Whittaker, 1995). Habitat requirements and interspecific interactions have been presented as alternatives to the equilibrium model to explain species composition (Lack, 1976; Simberloff, 1994). In addition, historical legacy models consider immigrations as coming in one great wave in the past and then ceasing; extinctions are not considered very important (Case and Cody, 1983).

The ant fauna of Puerto Rico is relatively well known, having been studied during this century by Wheeler (1908), Smith (1936), Levins *et al.* (1973), Culver (1974), Lavigne (1977), Torres (1984a, b) Torres and Snelling (1992), and Snelling and Torres (in preparation). This knowledge provides an opportunity to investigate some of the hypotheses that have been proposed to explain the distributions of organisms on islands. In this study we will (i) describe the distribution and the factors responsible for the distribution of ants on the Puerto Rican bank, (ii) determine the extinction and colonization rates on these islands, and (iii) see if the dynamics of ants are in accord with the basic MacArthur and Wilson (1967) model of island biogeography.

Methods

We sampled ants during 1981–83 on the island of Puerto Rico (8865 km^2, max. elevation 1338 m) and on 44 small islands and keys that surround Puerto Rico. The total number of species from the Puerto Rican bank is 87 (Snelling and Torres, in preparation). The islands surrounding Puerto Rico range in size from 0.000023 km^2 to 134.6 km^2, and in elevation from under water at high tide to 30l m above sea level. Puerto Rico is the easternmost of the islands comprising the Greater Antilles. The conditions for growth on these islands are classified into six life zones (Ewel and Whitmore, 1973). The Subtropical Moist Forest occupies 58% of the island of Puerto Rico, the subtropical Wet Forest about 23%, and the Subtropical Dry Forest about 18% of the island. The combined Subtropical Rain Forest,

Lower Montane Wet Forest, and Lower Montane Rain Forest life zones occupy about 1% of Puerto Rico. The small islands and keys are all in the Subtropical Dry Forest life zone, as are the islands of Culebra, Caja de Muertos, and Mona. Both Subtropical Dry Forest and Subtropical Moist Forest life zones are present on Vieques.

During the survey, we searched for whole ant colonies by overturning stones, logs and other objects lying on the ground; by breaking tree stumps, logs, branches and dead twigs; and by examining the soil for nests. Active searching methods also included removing dead bark from live trees, and litter from the soil to uncover cryptic nests. In addition, ants were collected in transects (numbers proportional to the size of the islands) containing tuna fish or honey as baits (every 3 m) laid on soil and vegetation. Passive search methods (which were more efficient for finding cryptic ant species) included the laying of 5 to 20 pitfall traps (number depended on the size of the island) that were left in the field for 24 hours, and the collection of leaf litter samples of approximately 4 litres (from 2 to 20 samples, depending on the amount of leaf litter on the island). Leaf litter samples were sifted after returning to the laboratory. We have found that sifting dry litter is more efficient in the extraction of ants than Berlese funnel extraction using a heat source. Active searching was continued on the small islands until 1.5 hours of intensive searching did not yield any new species. Most of the small islands were actively surveyed within a full field day (8 hours). Active searching on the large islands (e.g., Caja de Muertos, Mona, Vieques and Culebra) took at least 3 days and was completed after more than 6 hours of searching did not yield new species. The sampling schemes varied because of habitat differences among the islands and keys, i.e. islands lying below sea level were not sampled with pitfalls or by sifting leaf litter. Considering the complementarity and redundancy of the different methods to sample ants (Romero and Jaffe, 1989), we think the total number of species reported in this study should be close to a complete census for the majority of the islands. Because of old problems in the taxonomy of the ants in *Odontomachus*, *Pachycondyla* and *Camponotus ustus* group (Snelling and Torres, in preparation), and in order to make this study comparable with previous ones, we did not separate these groups into species. Presently the Puerto Rican bank has two species of *Odontomachus* and *Pachycondyla*, and three in the *Camponotus ustus* group.

For each island we determined the straight-line distance in km from the island to the nearest point on Puerto Rico, the maximum height – a possible indicator of microclimate diversity (from topographic maps), the area and the number of habitat types. Areas were determined either by planimetry or from published records (Anonymous, 1979; Cardona, 1985). Habitat diversity, defined as the number of habitat types, was recorded in each visit or extracted from the literature (Puerto Rican Department of Natural Resources and Research Planning Institute, 1984). The following habitats were recognized: sandy beach, rocky shore (gravel beach, cobble beach, and rip rap boulders), short herbaceous vegetation (halophytic herbs, rhizomaceous grasses and creeping vines near the coast), tall herbaceous vegetation (over two feet – generally inland), shrubs and scrub, dry forest, mangroves, dry semi-evergreen forest, moist forest, and wet forest (rain forest).

We tested ant distributions to determine if they conform to a non-random pattern (nestedness) with the Wilcoxon 2-sample statistic (Patterson, 1987; Simberloff and Martin, 1991). To estimate turnover of species we used the surveys by Wheeler (1908), Ramos (1946), and Levins *et al.* (1964–68 unpublished, the raw data of the publication by Levins *et al.*, 1973). The list of ant species in Ramos (1946) is a compilation from previous works and his findings. It is difficult to know how complete the Ramos survey was, because he

did not present details about collecting methods. Levins *et al.* (1973) searched for ants by sifting leaf litter, baiting, overturning stones and logs, and breaking twigs. Although Levins (pers. com.) regards their ant census as a good one, he considers the possibility of small errors because of the participation in some occasions of students with little experience. We consider that the number of species recorded by Levins *et al.* for the island of Culebra is incomplete (their number of species is far from those of the survey by Wheeler (1908) and our survey), but we kept the information from the island of Culebra to have an estimate of the extinction of those species collected by them. Because the completeness of previous sampling schemes by Levins *et al.* (1964–68 – published in 1973) and Ramos (1946) is unknown, we have more confidence about extinction than about colonization estimates. Any species found by them and not by us can be considered a real extinction. Nonetheless a species absent in their records and present in ours can represent a species missed during their surveys or a real colonization. We have been working for the past 18 years on a taxonomic revision of the ants of Puerto Rico, and this fact has enabled us to avoid erroneously recording extinctions and colonizations because of misidentifications. Species misidentifications could result in pseudoextinctions and pseudocolonization, while the number of species does not change (in perfect agreement with the MacArthur and Wilson model).

Results

Species distributions

The number of recognized species ranged from 0 to 71 with a median of 8 per island. Most species were found on a few islands (see Appendix). Half of the species occupied three or fewer islands (including Puerto Rico) and five or fewer if Puerto Rico is excluded. Only six species were found on more than half the islands. The species with the widest distributions were the ones that nest in wood (Table 1). Wood nesting species can inhabit islands with no soil, and they can colonize the islands by drifting on wood. Another characteristic of the most widely distributed species was the possession of multiple queens (polygynous) per nest. Polygynous species have a greater probability that a group of workers arriving on an island by drift contains a fertile queen.

The ant species distribution followed a nested pattern (Appendix). Although *Leptothorax albispina*, *Tetramorium lanuginosum*, *Quadristruma emmae*, and *Pheidole susannae* were found on relatively large islands, their distributions tend to be unpredictable and they were absent from the largest island, Puerto Rico.

Table 1. Nesting preferences of the most widely distributed ant species

Species	Number of islands	Nesting sites
Crematogaster steinheili	40	wood
Monomorium floricola	34	wood
Paratrechina longicornis	29	soil, wood
Solenopsis geminata	27	soil, wood
Tapinoma melanocephalum	25	wood
Cardiocondyla emeryi	22	soil
Camponotus spp.	21	wood
Solenopsis globularia	20	soil

A stepwise multiple regression with species number as the dependent variable and area, number of habitats, height, and distance as independent variables was conducted with the variables untransformed and log transformed (log x + 0.01). Since height in the untransformed data was correlated with area (r = 0.73, P < 0.01) and habitat diversity (r = 0.67, P < 0.01), we used a P to enter of 0.05 and a tolerance of 0.10 to reduce the possibility of constructing multicolinear models which tend to have unstable regression coefficients (Wilkinson *et al.*, 1992). For the untransformed data the assumptions of the regression model (errors normally distributed with constant variance and independent) were met with good agreement, and the number of habitats was the only variable with a significant coefficient ($\hat{b}$ = 2.98, t = 12.85, df = 1, P < 0.001) (R^2 = 0.80, N = 44). There were two Cook's distances with a high value in the untransformed data regression, but deleting them did not affect any conclusions or levels of significance. Since we measure distance as the shortest distance from an island to Puerto Rico, there is the possibility that some islands could serve as stepping stones, reducing the real degree of isolation for some islands. To explore this possibility we conducted the regression model removing the small islands that were close to the large islands of Culebra, Vieques, and St Thomas. In this way, we eliminated the possibility that these large islands have served as secondary sources of colonizers for the small islands. Even with this modification, distance did not enter into the model as a significant variable. For the log-transformed data, the only significant coefficient was the one associated with area ($\hat{b}$ = 0.47, t = 9.17, df = 1, P < 0.001) (R^2 = 0.67, N = 44), but the assumptions of the regression model (errors normally distributed with constant variance and independent) were not met. Not only was the R^2 lower in the log transformed data, but the independent variables height, area and habitat diversity were highly correlated.

Species turnover

We found 21 islands in common between the study by Levins *et al.* (1973) and ours (Table 2). We found a greater number of species on each island except for the islands of Palominitos and Caracoles. Most of the islands had a low extinction rate, with the exception of the island of Palominitos. These extinctions may be underestimates (Diamond and May, 1977; Boeklen and Simberloff, 1986), since it is likely that ant species could be lost and regained during the approximately 18 years between censuses. The reduction in species from 12 to 4 and the extinction of ten species and colonization by only two species argues against an equilibrium in species number for Palominitos (Table 3). The following species have experienced the highest (in three islands) number of extinctions: *Monomorium floricola*, *Tapinoma melanocephalum*, *Camponotus* spp. and *Solenopsis globularia*. All these species belong to the group of widely distributed species (Table 1).

When we compared the data from Ramos (18 species) with ours (31 species – Torres and Snelling, 1992), we found that only *Monomorium pharaonis* was not present in our collections. This is the only extinction among those species recorded by Ramos (1946) on Mona Island in a period of 36 years. *Monomorium pharaonis* is mostly associated with human structures, and during our survey we did not search the buildings for ants. Maybe *M. pharaonis* is still present on Mona Island.

The survey conducted by Wheeler (1908) on the islands of Culebra and Culebrita provides another opportunity to estimate species turnover (Tables 4–5). Wheeler found 26 species (the most abundant, the fire ant, *Solenopsis geminata*) during his visit to Culebra in 1906, and we found 33 ant species in 1982. We have some doubts about Wheeler's record

Table 2. Number of species, extinctions, and possible colonizations in the islands common to the Levins *et al.* study and this study

Island	Total species (Levins *et al.*)	Total species (this study)	Extinctions	Possible colonizations
Caballo Blanco	1	3	0	2
Cabeza de Perro	9	17	1	9
Caracoles	3	2	2	1
Cayo Congo	4	12	1	9
Cayo Diablo	6	7	1	2
Cayo don Luis	5	5	2	2
Cayo Enmedio	1	2	1	2
Cayo Majimo	2	2	1	1
Cayo Norte	6	17	1	12
Cayo Ratones	10	17	2[a]	9
Culebra	11	33	2[b]	24
Culebrita	5	16	0	11
Icacos	10	26	2[a]	18
Inner Brass	8	17	1[c]	10[c]
Isla la Gata	2	4	0	2
Laurel	1	3	0	2
Palominitos	12	4	10	2
Palominos	13	24	1	12
Piñerito	1	8	1	8
Piñero	7	12	2	7
Turrumote	2	3	0	1
Total			31	146

[a] Assuming that *Anochetus kempfi* is extinct, a species difficult to collect.
[b] Considering *Pheidole megacephala* as a valid identification by Levins *et al.*
[c] Considering that *Pheidole moerens* is a misidentification of *P. transversostriata* by Levins *et al.*

of *Paratrechina vividula* as being present on Culebra. Removing *P.vividula* from the species list, we have 5 extinctions and 12 colonizations. In the case of Culebrita, Wheeler found that *Pheidole megacephala* was 'in full possession to the exclusion of every other ant'. In our visit, we found 16 species with *P. megacephala* restricted to a small patch in the centre of the island. *Solenopsis geminata* and *Pheidole susannae* were abundant, especially foraging on the vegetation on Culebrita. Both islands were far from equilibrium and indicate an increase in the number of species.

Discussion

Ant distributions

Habitat diversity was the best predictor of the number of species per island. Area was not as good a predictor as habitat diversity. Also, untransformed data better explained the variation in species numbers and better followed the assumptions of the multiple regression model. This is in harmony with the findings of Weissman and Rentz (1976) in which untransformed variables explain a greater variation of the distribution of the grasshoppers and their relatives on the California Channel Islands. Traditionally, log transformations

Table 3. Ant species found (+) on Palominitos in different time intervals

Species	Levins *et al*. (1964)	this study (1981)
Brachymyrmex heeri	+	–
Brachymyrmex obscurior	+	–
Camponotus spp.	+	–
Cardiocondyla emeryi[a]	+	–
Crematogaster steinheili	+	–
Dorymyrmex sp.	–	+
Monomorium floricola[a]	+	+
Paratrechina longicornis[a]	+	–
Pheidole moerens	+	–
Solenopsis geminata	+	+
Solenopsis globularia	+	–
Tapinoma melanocephalum[a]	+	–
Tetramorium simillimum[a]	+	–
Wasmannia auropunctata	–	+

[a] Introduced Old World species.

have been employed in biogeographic studies, but caution should be taken because greater correlations among independent variables could arise, affecting the results of regression analysis. Also, caution needs to be taken to avoid confusing the best fitting model with the real one (Wilkinson *et al*., 1992). MacArthur and Wilson (1967) pointed out that area allows a large enough sample of habitats, and in the absence of information on diversity of habitats they turned to island areas. Area is correlated with environmental diversity (Weissman and Rentz, 1976; Mühlenberg *et al*., 1977), which exerts a more direct effect on species numbers.

Area has been found to be a bad predictor of ant species number on other islands. Virgin Gorda, with an area 23 times greater than that of Thatch key, has a lower ant diversity (Pressick and Herbst, 1973). Goldstein (1975) found that plant area was a better predictor than total area, although not as good as the diversity of exposure (temperature regime) of the habitats, and that ant exclusions were due to habitat inadequacy. In addition, the similar range of habitat types on the Canary Islands, despite their size differences, controls the number of lizard species (Case and Cody, 1983).

Distance to Puerto Rico did not appear important in determining total number of species. Probably distance was important in determining the distribution of some individual species like *Wasmannia auropunctata* and the species found only in Puerto Rico, but species that are absent from the islands and present in Puerto Rico make no contribution to the regression equation. Since the distances of most of the islands to Puerto Rico are small, it is possible that queens can fly easily to these islands, explaining in part the absence of a distance effect. Similarly, Goldstein (1975) does not find an isolation by distance effect on the ants of Thimble Islands, nor do Mühlenberg *et al*. (1977) in the spiders of the Seychelles.

The importance of passive transport (in wood drift) in the distribution of species can be seen in the case of *Monomorium floricola*, whose queens have lost the ability to fly (queens and ergatoids) and which was nevertheless found on 34 of the islands. The fungus grower ants *Cyphomyrmex minutus* and *Mycocepurus smithi* have similar food habits and environmental tolerances, except that *C. minutus* can nest in wood or inside decomposing

Table 4. Ant species present (+) on Culebra in different censuses

Species	Wheeler (1906)	this study (1982)
Anochetus kempfi	+	−
Brachymyrmex heeri	+	+
Brachymyrmex obscurior	−	+
Camponotus sexguttatus	+	+
Camponotus spp.	+	+
Cardiocondyla emeryi[a]	+	+
Cardiocondyla nuda[a]	−	+
Cardiocondyla venustula[a]	+	+
Crematogaster steinheili	+	+
Cyphomyrmex minutus	+	+
Hypoponera opaciceps	+	+
Hypoponera opacior	−	+
Leptothorax albispina	+	−
Monomorium ebeninum	+	+
Monomorium floricola[a]	+	+
Monomorium pharaonis[a]	+	−
Monomorium subcoecum[a]	−	+
Myrmelachista ramulorum	+	+
Odontomachus spp.	−	+
Pachycondyla stigma	+	−
Paratrechina longicornis[a]	+	+
Paratrechina steinheili	−	+
Paratrechina vividula[a,b]	+	−
Pheidole fallax	+	+
Pheidole moerens	+	+
Pheidole subarmata	−	+
Pheidole susannae	−	+
Rogeria carinata	−	+
Solenopsis corticalis	−	+
Solenopsis geminata	+	+
Solenopsis globularia	+	+
Strumigenys gundlachi	−	+
Tapinoma melanocephalum[a]	+	+
Tetramorium bicarinatum[a]	+	−
Tetramorium caldarium[a]	−	+
Tetramorium lanuginosum[a]	−	+
Tetramorium simillimum[a]	+	+
Trachymyrmex jamaicensis	+	+
Wasmannia auropunctata	+	+
Total	26	33

[a] Introduced Old World species.
[b] Probably misidentification by Wheeler.

Table 5. Ant species found (+) on Culebrita in different time intervals

Species	Wheeler (1906)	Levins *et al.*	this study (1982)
Brachymyrmex heeri	–	+	+
Brachymyrmex obscurior	–	–	+
Camponotus spp.	–	–	+
Cardiocondyla emeryi[a]	–	–	+
Cardiocondyla nuda[a]	–	–	+
Crematogaster steinheili	–	+	+
Cyphomyrmex minutus	–	–	+
Monomorium floricola[a]	–	+	+
Paratrechina longicornis[a]	–	–	+
Pheidole fallax	–	–	+
Pheidole megacephala[a]	+	+	+
Pheidole susannae	–	–	+
Solenopsis geminata	–	+	+
Solenopsis globularia	–	–	+
Tapinoma melanocephalum[a]	–	–	+
Tetramorium lanuginosum[a]	–	–	+
Total	1	5	16

[a] Introduced Old World species.

organic matter, and *M. smithi* nests only in soil (Torres, 1984a, 1989). This difference in nesting behaviour could explain the distribution of *C. minutus* in 15 islands around Puerto Rico and the absence of *M. smithi* from the small islands. The distribution of these fungus grower ants was similar to that reported from keys and small islands adjacent to Cuba (Fontenla, 1993a, b).

Monomorium ebeninum* and *Monomorium floricola* have similar ecology (Torres, 1984a); they nest in wood and queens are ergatoids, but *M. ebeninum* was found on 9 islands compared to 34 for *M. floricola*. *M. ebeninum* was sympatric with *M. floricola* in all the islands that it inhabits; these *Monomorium* species did not have complementary distributions that would suggest competitive exclusion. It is difficult to present a deterministic explanation for the large difference in the distribution of these two wood nesting *Monomorium* species. Similar to the pattern in Puerto Rico, *Monomorium floricola* has a broader distribution than *M. ebeninum*, and *M. pharaonis* is rare in the keys and islands adjacent to Cuba (Fontenla 1993a, b).

Wasmannia auropunctata* was found on only four of the islands adjacent to Puerto Rico. Also, *W. auropunctata* was rare in the Florida Keys (Deyrup and Trager, 1986; Deyrup *et al.*, 1988; Deyrup, 1992) and was present on only 2 of 15 islands studied by Fontenla (1993a, b) on Cuba. Similar to Puerto Rico, most Ponerinae were found on a few islands surrounding Cuba, and the Dacetini ants were rare in the Florida Keys.

The majority of the species found on the islands around Puerto Rico inhabit coastal habitats, human modified environments, or open habitats; many of them are tropical tramp species. Many of the endemic species are confined to the wet forest of the island of Puerto Rico and were absent from the small islands that surround Puerto Rico. Similar to the situation in Puerto Rico, most species in the keys and islands around Cuba and on the Florida Keys are introduced or widespread ant species (Deyrup and Trager, 1986; Deyrup

et al., 1988; Deyrup, 1992; Fontenla, 1993a, b). On Puerto Rico, ant distributions are correlated with the temperature tolerance of the species: species that do not tolerate high temperatures tend to be found on larger islands, high-temperature-tolerant species on smaller islands, and broadly temperature tolerant species spread over both (Levins *et al.*, 1973; Torres, 1984a).

The frequency of occurrence of species on different islands did not provide a complete picture of the relationships among ant species. Although we did not quantify species abundances explicitly, it was easy to observe that some islands were dominated by species whose dominance was difficult to explain. Dutchman's Cap, Cayo del Agua, and María Langa were dominated by the crazy ant, *Paratrechina longicornis*, even though these islands were inhabited by aggressive competitors like *Solenopsis geminata* (Torres, 1984a, b). Maybe there was a priority effect operating on these islands as found in mangrove islands by Cole (1983). There were islands where the dominant species change in the different parts of the islands. This was observed even on small islands where the environment was apparently quite homogeneous. In addition, there were species like *Pheidole fallax* that were present on many islands in low abundance but in high abundance on only one island. Similar patterns of ant distributions have been observed in the Florida Keys (Deyrup, 1992). Most island biogeography studies do not take species abundance into account and can give incomplete representations of the ecological interactions on islands.

Nestedness

This nested pattern (see Appendix) in the distribution of ants was the result of the addition of species as the number of habitats increases with the size of the island. The smallest islands are devoid of supratidal soil and have only arboreal species (*Tapinoma melanocephalum*, *Monomorium floricola*, *Crematogaster steinheili*, *Camponotus* spp, etc.). The presence of dry soil permits the colonization by soil nesting species like *Pheidole*, *Cardiocondyla*, *Solenopsis*, etc. On larger islands there is the development of moist forests, and species that need a cooler habitat appear. The species adapted to wet conditions were found only on Puerto Rico, where the topography allows the development of rain forests.

A nested pattern is to be expected from a non-interactive species model (resource coupled; Case and Cody, 1987) and is in contradiction to the idea that each island fauna constitutes a random draw of a mainland species pool (Patterson, 1987; Whittaker, 1992). Nested subsets indicate that there are few ecological substitutes among the island species: a given sized island supports a given species set with few alternatives (Cody, 1983). Non-conformance to a nested pattern could be due to habitat differences, interspecific competition, and equilibrium turnover (Simberloff and Levin, 1985; Simberloff and Martin, 1991). In our study, the conformance of these ant distributions to a nested subset pattern was correlated with the increase in the number of habitats as area increases and with the absence of complementary distribution patterns. Similarly, in the Florida Keys, most ant species apparently occur wherever their preferred habitat is available and the larger number of species on the larger islands is correlated with a greater diversity of habitats (Deyrup *et al.*, 1988).

Extinction and turnover

Although we recognize the possibility of sampling errors in the survey by Levins *et al.* (1964–68), the increase in number of species is so great as to be due to more than improved sampling and cannot easily be dismissed as a sampling artifact. The differences are such that

we think the colonization rates on these islands were far greater than extinction rates (apparent colonizations were 4.7 times more common than the extinctions). Many of the species found by us (and not by Levins *et al.*) are so easy to detect that we doubt that, if they had been present, they would have been detected by them. The data from Culebra and Culebrita collected by Wheeler also point toward an increase in the number of ant species. In 18 years of searching for ants in the island of Puerto Rico we have recorded only one apparent extinction, *Tetramorium lucayanum*. However, during this century *Solenopsis wagneri*, *Cerapachys biroi*, *Trachymyrmex jamaicensis* and *Wasmannia sigmoidea* have colonized Puerto Rico. There is the possibility that *Gnamptogenys striatula*, *Leptogenys pubiceps*, *Monomorium subcoecum*, *Pheidole cocciphaga* and *Solenopsis succinea*, are recent arrivals to Puerto Rico. Clearly there is an indication of a non-equilibrium situation.

A non-equilibrium situation is common in several insect studies. In Hawaii the extinction rates of collembollan species seem to be greater than the colonization rates (Christiansen and Bellinger, 1994). The extinction rates for endemics are higher than for exemic species, and there is a low rate of successful introduction of exemics to the Hawaiian islands. On Krakatau, the butterfly colonization rate is greater than the extinction rate, the extinction rate is low, and there is no evidence of an approach to equilibrium (Thornton *et al.*, 1993). Similarly, the Hymenoptera (excluding ants) are increasing in numbers on Krakatau (Seiki and Takuya, 1992) and the number of ant species has more than doubled in approximately 20 years in the Florida Keys (Deyrup *et al.*, 1988). Also, Heatwole and Levins (1973) found a higher extinction (0.78/yr) than colonization (0.04/yr) rate of ants on Cayo Ahogado, but they did not separate transient species from established ones.

We found low extinction rates in ants compared to the 1.5 extinctions of arthropods per year after the defaunated mangrove islands attained an equilibrium (Simberloff, 1976). The higher number of extinctions in the mangrove islands could be explained by the small size of these islands and by the fact that Simberloff's study involved all the arthropods, and we studied only a subset of the arthropods. On Mona island to the west of Puerto Rico, Terborgh and Faaborg (1973) found two bird extinctions and three colonizations in a period of 71 years, indicating an even lower extinction rate than those observed during the present study. Goldstein (1975) found a high turnover of ants, but most was pseudoturnover (the extinction of an established single colony which was unable to reproduce because the habitats were marginal for ants).

The study of island biotas has overemphasized the number of species and ignored the identity of the species. One of the simplifications of the MacArthur–Wilson model is that it treats the species as interchangeable. Nevertheless, the invasions of the fire ant *Solenopsis wagneri*, *Wasmannia auropunctata*, *Pheidole megacephala* and *Linepithema humile* have resulted in drastic reductions in the number of species in continental and insular areas (Erickson, 1971; Clark *et al.*, 1982; Hölldobler and Wilson, 1990; Porter and Savignano, 1990; Ulloa and Cherix, 1990; Haines *et al.*, 1993; Reimer, 1993). The effects of these colonizations contradict the axiom of one colonization balanced by one extinction. In the same vein, the extinction of a successful colonizer could leave niche space for the colonization of the island by several other species. The larger number of extinctions in Palominitos could be the result of the colonization of this small island by *Wasmannia auropunctata* (the most common ant at the tuna fish baits) (Clark *et al.*, 1982, Lubin, 1984, but see Tennant, 1993).

The changes in the ant fauna of Culebrita have been quite drastic. The only species present in 1906 (Wheeler, 1908) was *Pheidole megacephala*, an exemic polygynous species

with unicolonial populations that spreads by the budding off of workers accompanied by inseminated queens. Unicolonial ant species are notable for their high local abundance and the degree to which they dominate the environment (Pressick and Herbst, 1973). Smith (1936) reported fighting on numerous occasions between *P. megacephala* and the fire ant *Solenopsis geminata* in Puerto Rico. It is possible that the invasion of Culebrita by *Solenopsis geminata* was the factor responsible for the drastic changes in species numbers. A specialized aggressive ant species that eliminates a species with a broader niche could leave empty niche space that subdominant species could occupy. In sugar cane fields in Cuba, the average number of species that co-occur with *P. megacephala* is 2.8, with *S. geminata* 4.7 and with *W. auropunctata* 4.8 (Fontenla, 1992). *Solenopsis geminata* could coexist with species displaced by *W. auropunctata*, and it is a good competitor against *W. auropunctata* (Lubin, 1984). One problem with species that substitute budding for the nuptial flights is the corresponding decrease in the power of active dispersal (Wilson, 1971), which could hinder the re-establishment of a species once it has been eliminated from a site. Experimental introductions of *Pheidole megacephala* on islands inhabited by the fire ant *Solenopsis geminata* and *Crematogaster steinheili* show that *P. megacephala* is unable to establish once the island is occupied by these species (Levins and Heatwole, 1973).

Drastic changes in ant communities seem to be a common phenomenon when some species are substituted. Room (1971) and Majer (1976a) found that a community of non-dominant ants was associated with each dominant ant in a combination that reduced interspecific competition, and when a dominant ant species was replaced in cocoa farms, there was a change in the associated ant community to that more characteristic of the invading ant (Majer 1976b). Fox and Fox (1982) found, in a successional sequence in Australian heathland, that the changes in dominant species were abrupt and correlated with changes in the associated ant species. In addition, in Hawaii when the Argentine ant *Linepithema humile* started to gain new territory and *Pheidole megacephala* vanished, other ant species were found in areas previously occupied by *P. megacephala* (Fluker and Beardsley, 1970).

It is possible that the rise of human visitors to some of these islands could have increased the amount of food for some ant species, but the effect of increase of food on species coexistence needs further investigation. For example, the harvester ant *Pogonomyrmex californicus* increased its density as a consequence of the additional food resources (provided by river rafters, and the abundance of blackflies) in the new shore created after the construction of the Glen Canyon Dam in the Colorado River. The floods of 1983 eliminated the harvester ants from the new high-water zone, but ant numbers have not returned to pre-flood levels despite high levels of food (Carothers and Brown, 1991). Mona Island is the farthest island from Puerto Rico, and the ant community consists of 4–5 species in the interior part of the island, but species increase in the areas near human settlements. The areas near the settlements are located in the wetter parts of the island and exhibit the tallest vegetation. It is possible that humans play a role in the distribution of ants on Mona Island, but alternatively hermit crabs, which were very abundant on the island, may be responsible for the low number of ant species in the interior of the island. In the interior of Mona Island hermit crabs arrived at a tuna fish bait faster than ants. Also, on the small islands of Icacos and Cabeza de Perro, lizards *(Ameiva exul)* and hermit crabs were so abundant that it was very difficult to study ants by using tuna fish and we had to switch to honey to avoid the interference of lizards and hermit crabs. It is possible that ants were suffering competition from lizards and hermit crabs that have become accustomed to feed on the dead animals that arrive on these small islands.

In conclusion, for some of these islands, the existence of an equilibrium was not supported and extinctions were low. Most of the species have a narrow distribution and habitat diversity was the most important predictor of the total number of species. Field experiments are needed to establish the importance of biotic interactions and priority effects in the determination of species numbers on these islands.

Acknowledgements

References

Anonymous (1979) *Inventario de cayos e islotes de Puerto Rico*. Department of Natural Resources, San Juan.

Boecklen, W.J. and Simberloff, D. (1986) Area-based extinction models in conservation. In *Dynamics of extinction* (D.K. Elliot, ed.) pp. 247–76. John Wiley and Sons. Inc.

Cardona, W.A. (1985) *Islotes de Borinquen: notas para la historia*. Oficina Estatal de Preservación Histórica. San Juan.

Carothers, S.W. and Brown, B.T. (1991) *The Colorado River through Grand Canyon*. Tucson: The University of Arizona Press.

Case, T.J. and Cody, M.L. (1983) Synthesis: pattern and processes in island biogeography. In *Island biogeography in the Sea of Cortéz* (T.J. Case and M.L. Cody, eds) pp. 307–41. Berkeley: University of California Press.

Case, T.J. and Cody, M.L. (1987) Testing theories of island biogeography. *Amer. Sci.* **75**, 402–11.

Christiansen, K. and Bellinger P. (1994) Biogeography of Hawaiian Collembolla: the simple principles and complex reality. *Oriental Insects* **28**, 309–51.

Clark, D.B., Guayasamín, C., Pazmiño, O., Donoso, C. and Páez, Y. (1982) The tramp ant *Wasmannia auropunctata*: autecology and effects on ant diversity and distribution on Santa Cruz island, Galapagos. *Biotropica* **14**, 196–207.

Cody, M.L. (1983) The land birds. In *Island biogeography in the Sea of Cortéz* (T.J. Case and M.L. Cody, eds) pp. 210–45. Berkeley: University of California Press.

Cole, B.J. (1983) Assembly of mangrove ant communities: patterns of geographical distribution. *J. Anim. Ecol.* **52**, 339–47.

Culver, D.C. (1974) Species packing in Caribbean and north temperate ant communities. *Ecology* **55**, 974–88.

Deyrup, M.A. (1992) Exotic ants of the Florida keys. In *Proceedings of the fourth symposium on the natural history of the Bahamas* (W. Hardy, ed.) pp. 15–22. Bahamas: Bahamian Field Station Ltd.

Deyrup, M.A. and Trager, J. (1986) Ants of the Archbold Biological Station, Highlands County, Florida (Hymenoptera: Formicidae). *Florida Entomologist* **69**, 206–28.

Deyrup, M.A., Carlin, N., Trager, J. and Umphrey, G. (1988) A review of the ants of the Florida keys. *Florida Entomologist* **71**, 163–76.

Diamond, J.M. and Gilpin, M.E. (1980) Turnover noise: contribution to variance in species number and prediction from immigration and extinction curves. *Amer. Natural.* **115**, 884–9.

Diamond, J.M. and May, R.M. (1977) Species turnover rates on islands: dependence on census interval. *Science* **197**, 266–70.

Erickson, J.M. (1971) The displacement of native ant species by the introduced Argentine ant, *Iridomyrmex humilis* (Mayr). *Psyche* **78**, 257–66.

Ewel, J.J. and Whitmore, J.L. (1973) *The ecological life zones of Puerto Rico and the U.S. Virgin Islands*. USDA Forest Service Research Paper ITF-18.

Fluker, S.S. and Beardsley, J.W. (1970) Sympatric associations of three ants: *Iridomyrmex humilis*, *Pheidole megacephala*, and *Anoplolepis longipes* in Hawaii. *Ann. Entomol. Soc. Amer.* **63**, 1290–6

Fontenla, J.L. (1992) Mirmecofauna de la caña de azúcar en Cuba. Aspectos biogeográficos. *Ciencias Biológicas* **25**, 61–75.

Fontenla, J.L. (1993a) Mirmecofauna de Isla Juventud y de algunos cayos del archipiélago cubano. *Poeyana* **444**, 1–7.

Fontenla, J.L. (1993b) Composición y estructura de comunidades de hormigas en un sistema de formaciones vegetales costeras. *Poeyana* **441**, 1–19.

Fox, M.D. and Fox, B.J. (1982) Evidence for interspecific competition influencing ant species diversity in a regenerating heathland. In *Ant-plant interactions in Australia*. (R.C. Buckley, ed.) pp.99–110. The Hague: Dr. W. Junk Publishers.

Gilbert, F.S. (1980) The equilibrium theory of island biogeography: fact or fiction? *Journal of Biogeography* **7**, 209–35.

Goldstein, E.L. (1975) Island biogeography of ants. *Evolution* **29**, 750–62.

Haines, I.H., Haines, J.B. and Cherrett, J.M. (1993) The impact and control of the crazy ant, *Anoplolepis longipes* (Jerd.), in the Seychelles. In *Exotic ants: biology, impact, and control of introduced species* (D.F. Williams, ed.) pp.206–218. Boulder: Westview Press, Inc.

Heatwole, H. and Levins, R. (1973) Biogeography of the Puerto Rican bank: species-turnover on a small cay, Cayo Ahogado. *Ecology* **54**(5), 1042–55.

Hölldobler, B. and Wilson, E.O. (1990) *The ants*. Cambridge: Harvard University Press.

Lack, D. (1976) *Island biology illustrated by the land birds of Jamaica*. Oxford: Blackwell Scientific publications.

Lavigne, R.J. (1977) Notes on the ants of Luquillo Forest, Puerto Rico (Hymenoptera: Formicidae). *Proceedings Entomological Society of Washington* **79**, 216–37.

Levins, R. and Heatwole, H. (1973) Biogeography of the Puerto Rican bank: introduction of species onto Palominitos Island. *Ecology* **54**, 1056–64.

Levins, R., Pressick, M.L. and Heatwole, H. (1973) Coexistence patterns in insular ants. *Amer. Sci.* **61**(4), 463–72.

Lubin, Y.D. (1984) Changes in the native fauna of the Galapagos Islands following invasion by the little red fire ant *Wasmannia auropunctata*. *Biol. J. Linn. Soc.* **21**, 229–42.

MacArthur, R.H. and Wilson, E.O. (1967) *The theory of island biogeography*. New Jersey: Princeton University Press.

Majer, J.D. (1976a) The maintenance of the ant mosaic in Ghana cocoa farms. *J. Appl. Ecol.* **13**(1), 123–44.

Majer, J.D. (1976b) The influence of ants and ant manipulation on the cocoa farm fauna. *J. Appl. Ecol.* **13**(1), 157–75.

Mühlenberg, M., Leipold, D., Mader, H.J. and Steinhauer, B. (1977) Island ecology of arthropods I: diversity, niches, and resources on some Seychelles Islands. *Oecologia* **29**, 117–34.

Murphy, R. (1983) The reptiles: origins and evolution. In *Island biogeography in the Sea of Cortéz*. (T.J. Case and M.L. Cody, eds) pp. 130–158. Berkeley: University of California Press.

Patterson, B.D. (1987) The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* **1**(4), 323–34.

Porter, S.D. and Savignano, D.A. (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* **71**, 2095–106.

Pressick, M.L. and Herbst, E. (1973) Distribution of ants on St. John, Virgin Islands. *Caribbean Journal of Science* **13**(3–4), 187–97.

Puerto Rican Department of Natural Resources and Research Planning Institute (1984) *Sensitivity of coastal environments and wildlife to spilled oil. PR a coastal atlas*. San Juan, PR.

Ramos, J.A. (1946) The insects of Mona Island (West Indies). *Journal of Agriculture of the University of Puerto Rico* **30**, 1–74.

Reimer, N.J. (1993) Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. In *Exotic ants: biology, impact, and control of introduced species.* (D.F. Williams, ed.) pp. 11–22. Boulder: Westview *Press, Inc.*

Romero, H. and Jaffe, K. (1989) A comparison of methods for sampling ants (Hymenoptera, Formicidae) in savannas. *Biotropica* **21**, 348–52.

Room, P.M. (1971) The relative distribution of ant species in Ghana's cocoa farms. *J. Anim. Ecol.* **40**, 735–51.

Seiki, Y. and Takuya, A. (1992) Recolonization of the Krakataus by Hymenoptera and Isoptera (Insecta). *GeoJournal* **28**, 213–18.

Simberloff, D. (1974) Equilibrium theory of island biogeography and ecology. *Ann. Rev. Ecol.* **5**, 161–82.

Simberloff, D. (1976) Species turnover and equilibrium island biogeography. *Science* **194**, 572–8.

Simberloff, D. (1994) Conservation biology and the unique fragility of island ecosystems. In *The fourth California islands symposium: update on the status of resources.* (W. L. Halvorson and G.J. Maender, eds) pp. 1–10. Santa Barbara: Santa Barbara Museum of Natural History.

Simberloff, D. and Levin, B. (1985) Predictable sequences of species loss with decreasing island area-land birds in two archipelagoes. *New Zealand J. Ecol.* **8**, 11–20.

Simberloff, D. and Martin, J.L. (1991) Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. *Ornis Fennica* **68**, 178–92.

Smith, M.R. (1936) The ants of Puerto Rico. *Journal of Agriculture of the University of Puerto Rico* **20**(4), 819–75.

Tennant, L.E. (1993) The ecology of *Wasmannia auropunctata* in primary tropical rainforest in Costa Rica and Panamá. In *Exotic ants.* (D.F. Williams, ed.) pp. 80–90. Boulder: Westview Press, Inc.

Terborgh, J. and Faaborg, J. (1973) Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *Auk* **90**, 759–79.

Thomson, D. and Gilligan, M. (1983) The rocky-shore fishes. In *Island biogeography in the Sea of Cortéz.* (T.J. Case and M.L. Cody, eds) pp. 98–129. Berkeley: University of California Press.

Thornton, I.W.B., Zann, R.A. and Balen, S. (1993) Colonization of Rakata (Krakatau Is.) by non-migrant land birds from 1883 to 1992 and implications for the value of island equilibrium theory. *Journal of Biogeography* **20**, 441–52.

Torres, J.A. (1984a) Niches and coexistence of ant communities in Puerto Rico: repeated patterns. *Biotropica* **16**, 284–95.

Torres, J.A. (1984b) Diversity and distribution of ant communities in Puerto Rico. *Biotropica* **16**, 296–303.

Torres, J.A. (1989) The status of the fungi-grower ants (Hymenoptera: Formicidae) in Puerto Rico and adjacent islands. *Journal of Agriculture of the University of Puerto Rico* **73**, 401–3.

Torres, J.A. and Snelling, R.R. (1992) Los himenópteros de Mona. *Acta Científica* **6**, 87–102.

Ulloa, P. and Cherix, D. (1990) The little fire ant *Wasmannia auropunctata* (R.) (Hymenoptera: Formicidae). In *Applied Myrmecology.* (R.K. Vander Meer, K. Jaffe and A. Cedeno, eds) pp. 281–289. Boulder: Westview Press.

Weissman, D.B. and Rentz, D.C. (1976) Zoogeography of the grasshoppers and their relatives (Orthoptera) on the California Channel Islands. *Journal of Biogeography* **3**, 105–14.

Wheeler, W.M. (1908) The ants of Porto Rico and the Virgin Islands. *Bull. Amer. Mus. Nat. Hist.* **24**, 117–58.

Whittaker, R.J. (1992) Stochasticism and determinism in island ecology. *Journal of Biogeography* **19**, 587–91.

Whittaker, R.J. (1995) Disturbed island ecology. *TREE* **10**, 421–5.

Wilkinson, L., Hill, M. and Vang, E. (1992) *SYSTAT: Statistic, Version 5.2.* Evanston, IL: SYSTAT, Inc.

Williamson, M. (1989) The MacArthur and Wilson theory today: true but trivial. *Journal of Biogeography* **16**, 3–4.

Wilson, E.O. (1971) *The insect societies.* Cambridge: Harvard University Press.

Appendix

Table A.1 List of ants present (1) on each of the 45 islands. Z refers to the Wilcoxon score. Islands were ranked by area. For the locations of the islands see Heatwole *et al.* (1981). Atoll Research Bulletin 1–68.

Islands	Enrique 1V	Enrique V	Lado Laurel	Enmedio	Laurel	Piñerito	Enrique VI	Jalovita	Cayo Majimo	Lado Chivas	Palominitos	Enrique VII	Caracoles	Caballo Blanco	Cayo del Agua	Isla La Gata	Turrumote	Cayo Vieques	María Langa II	Cayo Bayo
*Cardiocondyla emeryi**						1								1						
Camponotus spp.														1				1		
Solenopsis geminata						1					1			1						
Pheidole fallax																				
Cyphomyrmex minutus						1														
*Paratrechina longicornis**								1	1	1				1	1				1	1
*Cardiocondyla nuda**																				1
Monomorium ebeninum																				
*Tapinoma melanocephalum**					1	1							1							1
Pheidole moerens																				
*Monomorium floricola**	1					1				1	1			1	1	1	1	1		1
Brachymyrmex heeri																			1	
Solenopsis globularia															1	1			1	1
Odontomachus spp.																		1	1	
Myrmelachista ramulorum																				
Brachymyrmex obscurior						1							1							
*Tetramorium bicarinatum**																				
*Tetramorium simillimum**						1														
Solenopsis pygmaea					1															
Hypoponera opacior																				
*Tetramorium caldarium**																				
Trachymyrmex jamaicensis																				
Pheidole subarmata																				
Dorymyrmex sp.											1									
Strumygenys gundlachi																				
Crematogaster steinheili	1	1	1	1	1	1	1				1	1	1	1	1	1	1	1		
Leptothorax albispina																				
Hypoponera opaciceps																				
Camponotus sexguttatus																				
*Pheidole megacephala**																				
Solenopsis corticalis																				
Wasmannia auropunctata											1									
Pheidole cocciphaga																				
Paratrechina steinheili																				

Cayo Conejo	Cayo Don Luis	Cayo Ratones	Isla Chivas	Cayo Diablo	María Langa I	Cayo de Afuera	Cayo Caribe	Cabeza de Perro	Dutchmans' Cap	Lobos n. Culebra	Congo n. St. John	Palominos	Isla Cuevas	Inner Brass	Icacos	Culebrita	Cayo Norte	Luis Peña	Piñero	Caja de Muertos	Culebra	Mona	Vieques	Puerto Rico	N
	1		1	1	1				1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	−4.90
	1	1	1			1	1	1				1	1	1	1	1	1	1	1	1	1	1	1	1	−4.84
1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	−4.84
					1	1					1	1	1	1	1	1	1			1	1		1	1	−4.61
					1	1		1			1	1	1	1	1	1	1			1	1		1	1	−4.38
	1	1	1	1	1	1	1	1	1			1	1	1	1	1	1	1	1	1	1	1	1	1	−4.26
	1				1						1			1	1	1				1	1		1	1	−4.03
								1						1	1		1	1		1	1		1	1	−4.02
1	1	1	1		1	1	1	1		1		1		1	1	1	1	1	1	1	1	1	1	1	−3.76
	1	1				1				1		1			1	1				1	1	1	1	1	−3.75
1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	−3.71
1		1	1	1		1	1	1		1	1	1			1	1	1	1		1	1		1	1	−3.66
1		1	1		1	1		1				1	1		1	1	1		1	1	1	1	1	1	−3.56
	1				1	1	1			1		1	1	1					1	1	1	1	1	1	−3.41
	1											1		1		1	1			1	1			1	−3.41
			1	1				1	1		1	1		1	1		1			1	1		1	1	−3.41
												1	1			1		1		1		1		1	−3.27
	1											1	1	1			1			1	1	1	1	1	−3.24
							1	1		1	1		1		1		1		1	1		1		1	−3.11
	1													1						1	1	1		1	−3.07
																	1			1	1			1	−3.07
1								1			1		1						1	1	1			1	−3.03
					1					1		1			1					1			1	1	−2.97
1			1		1	1				1	1	1			1				1		1	1	1	1	−2.93
					1							1			1						1	1		1	−2.89
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	−2.81
	1													1			1	1	1	1	1			1	−2.80
				1		1				1		1									1	1		1	−2.70
										1		1			1						1			1	−2.60
															1								1	1	−2.59
															1		1			1				1	−2.59
																				1	1	1		1	−2.42
														1					1					1	−2.41
										1	1										1			1	−2.39

Islands	Enrique 1V	Enrique V	Lado Laurel	Enmedio	Laurel	Piñerito	Enrique VI	Jalovita	Cayo Majimo	Lado Chivas	Palominitos	Enrique VII	Caracoles	Caballo Blanco	Cayo del Agua	Isla La Gata	Turrumote	Cayo Vieques	María Langa II	Cayo Bayo
*Monomorium pharaonis**																				
Pachycondyla stigma																				
Tapinoma litorale																				
Solenopsis n. sp.																				
Platythyrea punctata																				
*Monomorium subcoecum**																				
Leptothorax torrei																				
*Monomorium destructor**																				
Rogeria carinata																				
*Cardiocondyla venustula**																	1			
*Tetramorium lanuginosum**																				
*Quadristruma emmae**																				
Smithistruma margaritae																				
Pheidole susannae																				
Solenopsis azteca																				
Anochetus kempfi																				
Anochetus mayri																				
Pseudomyrmex simplex													1							
*Hypoponera punctatissima**																				
Linepithema mellea																				
Myrmelachista n. sp.																				
Paratrechina myops																				
Paratrechina cisipa																				
Paratrechina pubens																				
Paratrechina n. sp.																				
Eurhopalothrix gravis																				
Leptothorax isabellae																				
Mycocepurus smithi																				
Pheidole exigua																				
Pheidole sculptior																				
Rogeria foreli																				
Strumigenys eggersi																				
Strumigenys louisianae																				
Strumigenys rogeri																				
Wasmannia sigmoidea																				
Amblyopone falcata																				
Gnamptogenys striatula																				
Leptogenys pubiceps																				
*Cerapachys biroi**																				
Solenopsis wagneri																				
*Cardiocondyla ectopia**																				
Mycetophylax conformis																				
Pheidole transversostriata																				

* Introduced Old World species.

Cayo Conejo	Cayo Don Luis	Cayo Ratones	Isla Chivas	Cayo Diablo	María Langa I	Cayo de Afuera	Cayo Caribe	Cabeza de Perro	Dutchmans' Cap	Lobos n. Culebra	Congo n. St. John	Palominos	Isla Cuevas	Inner Brass	Icacos	Culebrita	Cayo Norte	Luis Peña	Piñero	Caja de Muertos	Culebra	Mona	Vieques	Puerto Rico	N
																							1	1	−2.36
																							1	1	−2.36
																						1		1	−2.31
																						1		1	−2.31
																						1		1	−2.31
																					1			1	−2.25
																				1				1	−2.20
																				1				1	−2.20
		1				1												1			1			1	−2.20
																					1		1	1	−2.19
													1	1						1					−2.09
								1				1						1		1					−2.03
														1										1	−1.92
											1				1					1					−1.91
								1							1									1	−1.86
								1					1											1	−1.82
								1				1												1	−1.72
													1							1				1	−1.71
											1													1	−1.70
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
																								1	−1.69
							1																	1	−1.48
																				1					−1.38
1																								1	−1.21
															1										−0.92