



Island biogeography and metapopulation dynamics of Bahamian ants

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Abstract

Aim I examined the island biogeography and metapopulation dynamics of ants inhabiting two archipelagos of small Bahamian islands. Of particular interest were measurement and comparison of turnover rates, examination of variation in relative population abundances, and the effect of a hurricane force disturbance on the ant fauna of these small islands.

Location Archipelagos of small islands in the central Exumas and near the northeast coast of Andros, Bahamas.

Methods Ants occupying small islands were surveyed using tuna and honey baits. I surveyed ninety-three islands in the Exumas in 1998 and fifty-eight islands at Andros in 1999, to compare with earlier surveys in both regions. The proportions of baits occupied were used as a measure of relative population abundance. A subset of seventeen small islands in the Exumas was surveyed in 1999 in the aftermath of Hurricane Floyd.

Results Mean annual relative turnover rates were low: $<2.5\%$ year⁻¹ on a per island basis, and $<7\%$ year⁻¹ on a per species basis. Rates of immigration and extinction were similar, although immigrations exceeded extinctions in some comparisons. Relative population abundances of the two most common ant species varied inversely with each other. One species revealed a strong positive correlation with recent rainfall, whereas another varied strongly inversely. No extinctions of ants occurred on the seventeen small islands surveyed after Hurricane Floyd.

Main conclusions Ants were found to be ubiquitous in this system, occurring on almost all vegetated islands. Ant populations were persistent over the period of study, and species rarely became extinct or colonized islands. The few instances of turnover observed appeared to occur randomly with respect to physical island characteristics. The correlational data suggest an interaction of interspecific competition and precipitation affect relative population abundances. Ants were found to be resistant to hurricane-force disturbances. In the short term (one decade), the ant fauna of these islands appears to be in a state of static equilibrium, although non-equilibrium dynamics may better characterize the system over longer time periods (several decades).

Keywords

Bahamas, Formicidae, hurricane, species turnover.

INTRODUCTION

The equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967) provided a pioneering quantitative approach to the study of fragmented populations (but see

Brown & Lomolino, 1989). This body of theory has inspired many investigations of insular biotas (reviewed in Williamson, 1981; Rosenzweig, 1995; Brown & Lomolino, 1998; Whittaker, 1998), although numerous criticisms have been levied against the simple equilibrium model (e.g. Gilbert, 1980; Williamson, 1989; Whittaker, 1998).

The related concept of the metapopulation (Levins, 1969, 1970) provided an alternate theoretical underpinning for investigations of insular populations, focusing on the

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archipelago-wide immigration-extinction dynamics of one or a few species, rather than species number on a single island. In the last decade, a paradigm shift in the study of fragmented populations has occurred, in which metapopulation theory (e.g. Gilpin & Hanski, 1991; Hanski & Gilpin, 1997) has replaced the equilibrium theory of island biogeography as the dominant theoretical approach (Hanski & Simberloff, 1997). A complementary analysis (Ouborg, 1993; Morrison, 1997a, 1998a; Vidal *et al.*, 2000), however, may elucidate more about fragmented populations than either approach alone.

Recently, a call for a new paradigm of island biogeography has been issued (Global Ecology & Biogeography, 2000). A crucial question in modern island biogeography theory is whether islands ever actually reach a state of equilibrium, or whether the frequency of disturbance is too great (Whittaker, 1995, 2000). A major challenge to resolving this issue is obtaining data sets of sufficient temporal and spatial scales. With the possible exception of butterfly metapopulations, which have been relatively well studied (Thomas & Hanski, 1997), data on invertebrate persistence in very small habitat fragments remains scarce (Abensperg-Traun & Smith, 1999). Furthermore, a large proportion of existing studies have focused on species that exhibit relatively high rates of turnover (e.g. Schoener, 1983, 1991; Bengtsson, 1991).

Previously, I reported results of a 5-year study of the ants occupying an archipelago of small islands in the central Bahamas (Morrison, 1998a). Here I present additional results from subsequent work on small Bahamian islands across two archipelagos, from a data set that now spans almost a decade. This paper addresses the following aspects of this insular ant fauna: (1) How frequently do ants turn over on these small islands, and how does this vary spatially and temporally? (2) How do relative population abundances of ants vary with biotic and abiotic factors? and (3) What effects do hurricane-strength disturbances have on the ant populations occupying these small islands?

METHODS

Study sites

This study was conducted on small islands in the central Exumas and near the northeast coast of Andros, Bahamas. In the Exumas, the study area included the 13.5 km island chain between O'Briens Cay to the north and Bitter Guana Cay to the south. The study area at Andros included the small islands lying offshore the main island of Andros, between Nicholls Town to the north and Staniard Creek to the south (see maps in Morrison, 1997a).

All islands with a vegetated area < 1000 m² were surveyed, with the exception of 'outer islands' in the Exumas that occurred in deep water and were mostly denuded by wave action. Islands with more than 1000 m² of vegetated area were not surveyed because species with small populations could have been overlooked.

In the Exumas, I surveyed ninety-three vegetated islands in May 1998. All islands had been surveyed last in May 1994, and most had been surveyed at annual intervals in the four preceding years (see Morrison, 1998a). At Andros, I surveyed a total of fifty-eight islands in April – May 1999. Forty-eight islands were vegetated, and ten lacked vegetation. Forty-six of the vegetated islands had been surveyed previously for ants in 1990.

On 14, September 1999, Hurricane Floyd, a strong category 4 storm, passed c.100 km NE of the Exumas archipelago. Conditions in the study area approximated a class 2 hurricane. The rise in sea level in the immediate vicinity of the islands as a result of the hurricane was estimated to be at least 1.5 m, based upon debris washed up on nearby islands and interviews with natives. During 25–30 September, 1999, I re-surveyed seventeen of the smallest and lowest vegetated islands in the Exumas, to compare with surveys conducted in May 1998. The vegetated areas of the islands ranged from 0.2 to 474.6 m², and elevations ranged from 0.55 to 2.74 m.

Survey methodology

Baits of tuna and honey were used to attract the diurnally active ant species inhabiting these islands. Baits were placed uniformly over each island, the number of baits being proportional to the log(area) of the island, and ranging from a minimum of six on the smallest to a maximum of fifty on the largest. Approximately 1 g of finely ground tuna in vegetable oil (to provide proteins and lipids) and 1 g of honey (to provide carbohydrates) were placed in Petri dishes 58 mm in diameter. The Petri dishes (painted white) prevented the oil from soaking into the ground and facilitated ant identification at baits. The sides of the Petri dishes (approximately 9 mm tall) were roughened with sandpaper to allow ants to crawl easily over them, and were not observed to be a barrier to any species.

The baits were left out for 45 min, at which time the ant species present at the baits were recorded. All surveys were conducted between 8:00 am and 6:00 pm. Negative interspecific interactions sometimes resulted in workers of one species being excluded from within the Petri dishes, but not from the immediate vicinity of the baits. I recorded both species that were within Petri dishes (with direct access to baits) and species around the perimeter that were prevented access to the Petri dishes by other species. Thus, all species that were attracted to the baits were sampled. The methods employed were exactly the same as those used in previous surveys (see Morrison, 1998a).

Because relatively few ant species inhabit these islands, accurate field identification of most species was possible. Specimens of morphologically similar congeners were collected and later identified in the lab to verify field identifications. Slight variations in coloration and eye size in *Brachymyrmex obscurior* Forel indicate that more than one species may exist under this name, but the observed differences were not pronounced enough to allow separation into distinct morphospecies. Thus if the populations

identified as *B. obscurior* do contain cryptic species, turnover for this group may be greater than the values reported here. Until this genus is thoroughly revised, however, this issue cannot be entirely resolved. Reference specimens have been placed in the Bohart Museum of Entomology at the University of California at Davis.

Calculation of turnover

Turnover may be calculated on a per island basis [the MacArthur & Wilson (1967) island biogeographical approach] or on a per species basis [a metapopulation approach; see Morrison (1997a, 1998a)]. The following formula was used to calculate the turnover:

$$\text{Relative turnover} = [(I + E)/(S_1 + S_2)] \times 100$$

When turnover was calculated on a per island basis, S_1 and S_2 were the number of species on an island in surveys 1 and 2, respectively; I was the number of new species immigrating to the island between surveys; and E was the number of species becoming extinct on the island between surveys. When turnover was calculated on a per species basis, S_1 and S_2 were the number of islands on which a particular species was present at the beginning and end, respectively, of a survey interval; I was the number of islands on which the species was found at the end of the survey interval but not at the beginning; and E was the number of islands on which the species was found at the beginning of the survey interval but not at the end. Because surveys were conducted at intervals of 4 or 8 years, turnover rates were divided by the number of years between censuses to obtain annual relative turnover (see Schoener, 1988 for a discussion of turnover rate calculation).

In the Exumas, some species were not attracted to baits consistently and thus were characterized by pseudoturnover (*sensu* Lynch & Johnson, 1974), an inflation of turnover rates resulting from species actually present but missed in a census. Pseudoturnover was quantified in an earlier study and found to be zero for most species (Morrison, 1998a). The species that exhibited pseudoturnover were those that found and recruited to food resources at very short distances from the colony (Morrison, 1995). If such species were rare on an island, they may not have found or recruited to any of the baits. All species for which pseudoturnover was nonzero were excluded from the analyses presented here, with the exception of *Pheidole punctatissima* Mayr. Pseudoturnover in this relatively common species was found to be approximately one-third of observed turnover (Morrison, 1998a). Thus turnover on a per island basis was calculated with and without *P. punctatissima*. Another *Pheidole* species, *P. moerens* Wheeler, was present on the small islands near Andros. No pseudoturnover estimates were available for this species, and turnover rates at Andros were calculated including and excluding *P. moerens*.

Statistical analyses

To determine whether certain physical or biological characteristics of islands were associated with the occurrence of

turnover, I conducted a series of *t*-tests. Four different island characteristics were evaluated in separate tests: vegetated area, distance from the nearest large island, elevation and number of plant species. All variables were log-transformed to normalize the distributions. For each characteristic, I tested whether islands on which turnover occurred were significantly different than islands on which turnover did not occur. Thus four separate *t*-tests of each island characteristic were conducted for both the Exumas and Andros archipelagos.

In the Exumas, I tested whether islands that experienced immigrations were significantly different than islands on which no immigrations occurred, and whether islands that experienced extinctions were significantly different than islands on which no extinctions occurred. Immigrations and extinctions were not tested separately at Andros because too few turnover events occurred. All recorded turnover events spanning the periods of 1990–98 for the Exumas, 1990–99 for Andros were included in the analyses.

I compared relative population abundances of ants with Pearson correlation coefficients, based on the proportion of baits occupied. Data on bait occupancy from 1991 to 1994 (see Morrison, 1998a) and 1998 were analysed. To determine whether *B. obscurior* occupied fewer baits on islands with higher ant species richnesses, a one-way analysis of variance (ANOVA) was used. Proportions of baits occupied were arc-sine square-root transformed prior to statistical analyses. The Tukey method with a family confidence level of 0.95 (Neter *et al.*, 1985) was used to make multiple comparisons of factor level means.

To evaluate correlations of rainfall with relative population abundance, data were obtained from the Perry Institute for Marine Science Caribbean Marine Research Center data base for two weather stations, one on Warderick Wells (*c.* 25 km North of the study area) and one on Lee Stocking Island (*c.* 50 km South of the study area). Rainfall data were averaged between the two stations unless data from only one station was available. Rainfall data were not available for 1998, so correlations of rainfall and relative ant abundance were performed for the 4 years, 1991–94.

Whenever multiple comparisons of the same type were made over multiple years, the sequential Bonferroni method was used to control the group-wide Type I error rate (Rice, 1989). StatView 5.0.1 was used for all analyses.

RESULTS

Ants were present on eighty-eight of the ninety-three vegetated islands surveyed in the Exumas, and on twenty-one of the forty-eight vegetated islands surveyed at Andros. Twenty-one of the forty-eight vegetated islands at Andros were low-lying, apparently washed over completely by high tides and contained only salt-tolerant species growing in or near the intertidal zone [red mangrove, *Rhizophora mangle* L.; white mangrove, *Laguncularia racemosa* (L.) Gaertn. f.; black mangrove, *Avicennia germinans* (L.) L.; saltwort, *Batis maritima* L. and glasswort, *Salicornia virginica* L.]. If these twenty-one islands are excluded, twenty-one of the

twenty-seven vegetated islands at Andros were inhabited by ants in 1999. No ants were found on the ten non-vegetated islands at Andros.

In the Exumas, only the smallest vegetated islands ($< 3.7 \text{ m}^2$ vegetated area) lacked ants. Vegetated areas of islands with ants were larger than those without ants [227.2 ± 267.7 vs. $1.4 \pm 0.6 \text{ m}^2$ (mean \pm SD), respectively; $t = 5.97$, $P = 0.0001$, d.f. = 91, two-tailed t -test following a log transformation of vegetated areas]. At Andros, all islands with a vegetated area (excluding the five intertidal plant species above) $> 92 \text{ m}^2$ supported ants. As in the Exumas, vegetated areas of islands with ants were larger than those without [399.9 ± 542.1 vs. $34.1 \pm 38.5 \text{ m}^2$ (mean \pm SD), respectively; $t = 3.2$, $P = 0.003$, d.f. = 35].

Turnover

On a per island basis, mean annual relative turnover for all ants in the Exumas for the 4-year period 1994–98 was $1.30\% \text{ year}^{-1}$ (0.71 excluding *P. punctatissima*) (Table 1). This compares with a mean annual relative turnover rate of $2.41\% \text{ year}^{-1}$ (1.71 excluding *P. punctatissima*) for this same archipelago for the 4-year period 1990–94 (see Morrison, 1998a). Thus, turnover for the period 1994–98 was approximately half that observed in 1990–94, which was a significant difference ($P = 0.049$ and 0.042 , including and excluding *P. punctatissima*, respectively; Mann–Whitney tests). Turnover in both time periods, however, was low in an absolute sense (always $< 2.5\% \text{ year}^{-1}$).

Immigrations outnumbered extinctions in the Exumas from 1994 to 1998 by almost 2 : 1 when all ant species are considered (Table 1). If *P. punctatissima* was dropped from the analysis, however, immigration and extinction rates were equivalent. For 1990–94, immigrations outnumbered extinctions by a 5 : 3 ratio, including or excluding *P. punctatissima*.

At Andros, mean annual relative turnover for the 9-year interval 1990–99 was $1.41\% \text{ year}^{-1}$ (1.11 excluding *P. moerens*). These rates were similar to those observed in the Exumas (Mann–Whitney tests; $P = 0.29$ and 0.14 , including and excluding *Pheidole* spp., respectively; after considering all turnover events in the Exumas over a single 1990–98 interval). Immigrations exceeded extinctions whether or not *P. moerens* was excluded (Table 1).

On a per species basis, turnover rates varied among species, but in an absolute sense were low, ranging from 0 to $6.25\% \text{ year}^{-1}$ (Table 2). For all species occurring in the Exumas, turnover rates from 1994 to 1998 were lower than or equal to those from 1990 to 1994. Turnover rates of the two species found in both archipelagos, *B. obscurior* and *Dorymyrmex pyramicus* Roger, were similar between the two regions.

The occurrence of turnover was not associated with any of the physical or biological characteristics of the islands tested, for either the Exumas or Andros (t -tests, $P > 0.05$ for all). Additionally, in the Exumas, the occurrence of immigrations or extinctions were not associated with any of the island characteristics tested (t -tests, $P > 0.05$ for all). Thus, turnover appeared to occur randomly with respect to the island characteristics examined.

Population correlations

The relative abundances of the two most common species, *B. obscurior* and *D. pyramicus*, on islands where both existed, were significantly inversely correlated in 2 of 5 years (4 of 5 before correction for multiple comparisons; Table 3). Overall, the relative abundance of the most common species, *B. obscurior*, generally decreased as a function of the number of ant species on an island. Significant differences were found in all 5 years (Table 4).

Summing over all islands in each year, a comparison of mean relative abundances of *B. obscurior* and *D. pyramicus* for all islands on which they coexisted over 5 years also revealed a negative correlation ($r = -0.882$, $P = 0.048$). For the 4 years 1991–94, the mean relative abundance of *B. obscurior* on all islands on which it existed was positively correlated with rainfall over the three previous months ($r = 0.95$, $P = 0.05$). Conversely, mean relative abundance of *D. pyramicus* was negatively correlated with rainfall over the three previous months ($r = -0.98$, $P = 0.02$).

Effects of disturbance

Most of the seventeen small islands surveyed days after Hurricane Floyd revealed moderate to severe damage to the vegetation because of the hurricane seas or winds

Table 1 Turnover, immigration, and extinction rates calculated on a per island basis. Turnover rates are given as mean \pm SD; units are $\% \text{ year}^{-1}$. Immigration and extinction rates are absolute (number for species island $^{-1}$ year $^{-1}$)

Time period	Number of cays	Turnover (relative)	Turnover (annual)	Immigration rate	Extinction rate
Exumas					
1994–98	88	5.21 ± 11.80	1.30 ± 2.95	0.13	0.07
without <i>P. punctatissima</i>		2.84 ± 9.86	0.71 ± 2.47	0.05	0.05
1990–94 ¹	86	9.63 ± 16.95	2.41 ± 4.24	0.21	0.13
without <i>P. punctatissima</i>		6.82 ± 16.07	1.71 ± 4.02	0.13	0.08
Andros					
1990–99	20	12.67 ± 16.17	1.41 ± 1.80	0.25	0.20
without <i>P. moerens</i>		10.00 ± 15.67	1.11 ± 1.74	0.15	0.20

¹ From Morrison (1998).

Table 2 Turnover rates on a per species basis. unites are % year⁻¹

Species	Turnover (1994–98) (relative)	Turnover (1994–98) (annual)	Turnover (1990–94) ¹ (annual)
Exumas			
<i>Brachymyrmex obscurior</i> Forel	0.00	0.00	0.12
<i>Dorymyrmex pyramicus</i> Roger	8.47	2.12	4.00
<i>Forelius pruinosus</i> Roger	0.00	0.00	8.33
<i>Pseudomyrmex cubaensis</i> Forel	1.11	2.78	8.33
<i>Brachymyrmex minutus</i> Forel	14.29	3.57	10.71
<i>Monomorium floricola</i> Jerdon	20.00	5.00	5.00
<i>Pheidole punctatissima</i> ² Mayr	25.00	6.25	16.67
Andros ³			
<i>Brachymyrmex obscurior</i> Forel	0.00	0.00	
<i>Dorymyrmex pyramicus</i> Roger	38.46	4.27	

¹From Morrison (1998).²After correction for pseudoturnover [see Morrison (1998)].³The turnover interval for Andros is from 1990–99.

(L. W. Morrison, in review). The thin layer of soil was washed or blown away in many places, and marine vegetation and coral were found on the highest points of some of the islands. It appeared that all small islands surveyed were completely washed over by the sea in the storm. Despite the damage, no ant species went extinct on any of the islands. The proportion of baits occupied decreased from 0.69 ± 0.20 to 0.32 ± 0.20 (mean \pm SD;

$P = 0.0001$, d.f. = 17, two-tailed paired t -test) from May 1998 to September 1999. A decrease in *B. obscurior* relative abundance between May and September, however, was documented in both 1998 and 1999 in this archipelago (L. W. Morrison, in review). Thus the low bait occupancy immediately after the hurricane may reflect a seasonal trend rather than an effect of the hurricane.

Table 3 Correlations between proportions of baits occupied by *Brachymyrmex obscurior* Forel and *Dorymyrmex pyramicus* Roger for five different years. n = the number of islands on which both species coexisted in each year

Year	r	P	n
1991	-0.09	0.065	27
1992	-0.47	0.018	25
1993	-0.67	0.0001*	27
1994	-0.51	0.006*	28
1998	-0.41	0.032	28

* Significant ($P < 0.05$) using the sequential Bonferroni method (five comparisons).**Table 4** Proportion of baits occupied by *B. obscurior* Forel (mean \pm SD), according to the total number of ant species attracted to baits on an island, by year. All islands are averaged together in each year. '# Spp' = total number of species on an island including *B. obscurior*. 'n' = number of islands. Different letters indicate significant differences by the Tukey method of multiple comparisons with a family confidence level of 0.95 following a one-way ANOVA (Neter *et al.* 1985)

# Spp.	1991	1992	1993	1994	1998
One	51.6 \pm 22.3 A	52.0 \pm 24.2 A	69.2 \pm 18.6 A	64.3 \pm 20.2 A	70.9 \pm 16.8 A
Two	38.9 \pm 21.2 B	33.8 \pm 16.4 B	48.5 \pm 20.8 B	46.6 \pm 21.7 B	51.4 \pm 21.7 B
Three	30.4 \pm 18.9 B	21.7 \pm 15.2 B	43.0 \pm 22.6 B	38.6 \pm 14.7 BC	51.1 \pm 18.9 AB
Four +	15.8 \pm 6.1 B	34.0 \pm 8.5 B	24.8 \pm 12.4 B	21.7 \pm 13.6 C	19.0 \pm 13.7 C
F	5.70	8.32	12.23	13.34	13.99
P	0.0014*	0.0001*	0.0001*	0.0001*	0.0001*
n	86	86	90	86	88

* Significant ($P < 0.05$) using the sequential Bonferroni method (five comparisons).

DISCUSSION

Distribution patterns

Ants are a ubiquitous component of the fauna of small Bahamian islands (see also Morrison, 1998b). Ants were found to be present on almost all vegetated islands in both archipelagos, and only islands with very small vegetated areas lacked ants. Ants were not found on any of the ten islands at Andros without vegetation. This is consistent with a previous survey of forty non-vegetated islands in the Exumas that all lacked ants (Morrison, 1998a). Thus, the presence of vegetation, and moreover a certain threshold size of vegetated area, appears to be a necessary precursor before ants can colonize these islands. The fact that this threshold size was larger for

Andros than the Exumas is likely because of the fact that the islands surveyed at Andros were lower than those in the Exumas (Morrison, 1997a), and were subject to a greater degree of flooding from large waves or high tides.

The prerequisite of a certain size of vegetated area, which may vary among archipelagos, is an example of 'colonization rules' as proposed by Vepsäläinen & Pisarski (1982), in which ants can only colonize an island if it possesses the appropriate habitat types or other species. Apparently not all ant species require terrestrial vegetation to colonize oceanic islands, however (Heatwole, 1971; Heatwole *et al.*, 1981).

Turnover

The metapopulation approach to insular turnover is the per species equivalent to the (classic island biogeography theory) MacArthur & Wilson (1963, 1967). The utility of the former is that it allows for comparisons of the immigration–extinction dynamics among individual species, while the latter may be more valuable in comparisons among different higher level taxa or archipelagos (e.g. Schoener, 1983). The simultaneous use of both approaches may more completely elucidate the overall immigration–extinction dynamics in insular systems, as demonstrated here.

In the Bahamas archipelagos, ant populations were extremely persistent over time. The low rates of turnover observed were similar between the two archipelagos. More turnover occurred in the Exumas in the 1990–94 interval compared with the 1994–98 interval. Turnover varied among individual ant species, yet overall turnover rates were low in an absolute sense, particularly when compared with turnover documented for other arthropods (e.g. Schoener, 1983). Immigrations and extinctions appeared to occur at random in relation to the most obvious physical island characteristics. Rates of immigration and extinction were similar, although immigrations exceeded extinctions in some comparisons.

Few other studies have evaluated turnover of ants on oceanic islands. Goldstein (1975), in a study of small islands near Connecticut, reported a relatively high average turnover rate of 33% year⁻¹ on a per island basis (46% year⁻¹ on a per species basis). These rates were derived from a very small sample size, however. Only six islands were visited, with a 1-year interval between surveys.

Levins *et al.* (1973) also reported a high rate of turnover for ants on small islands near Puerto Rico, although their turnover calculations are derived from only two islands that were surveyed more than once. Torres & Snelling (1997) revisited twenty-one of the islands that were surveyed by Levins *et al.* (1973) *c.* 18 years later, and reported that immigrations outnumbered extinctions by a factor of 4.7. Torres & Snelling (1997) state that their surveys were probably more thorough than those of Levins *et al.* (1973), but posit that the differences are too great to result completely from sampling error and that the ants of the Puerto Rican bank may exemplify a non-equilibrium case.

Increased sampling effort often leads to increases in known species number of ants on oceanic islands (Morrison,

1996, 1997b). Such variation in sampling intensity by different investigators using different methodologies in the context of a turnover study frequently results in pseudoturnover [i.e. species that are actually present but overlooked in a survey (*sensu* Lynch & Johnson, 1974)]. Pseudoturnover is one of the many problems that are known to plague studies of species turnover (summarized in Morrison, 1998a), and several authors have criticized inappropriate methodologies in such studies (Lynch & Johnson, 1974; Gilbert, 1980; Abbott, 1983; Nilsson & Nilsson, 1983, 1985).

In contrast, the surveys of Bahamian ants described here, spanning over 100 islands in two archipelagos over almost a decade, encompasses by far the broadest spatiotemporal dimensions of any ant (or almost any other organism) study, in which all surveys were conducted by the same investigator using the same methodologies. Thus, the potential for pseudoturnover was low, and furthermore was quantified in an earlier study and found to be 0 for most species (Morrison, 1998a). Because immigrations occur so infrequently, survey intervals of 4–5 years appear to be sufficient to avoid cryptoturnover [undetected immigrations and extinctions occurring between surveys (*sensu* Lynch & Johnson, 1974)] in this system.

Population correlations

The strong inverse correlations of relative population abundance between *B. obscurior* and *D. pyramicus* may be the result of interspecific interactions, to some extent. Interspecific competition is known to be an important force structuring ant communities in general (Hölldobler & Wilson, 1990 and references therein), and elsewhere I have experimentally documented interspecific competition between these two species (Morrison, 1995). Likewise, the decline in *B. obscurior* populations as species number on an island increases may be because of diffuse competition (MacArthur, 1972).

Relative population abundances of *B. obscurior* and *D. pyramicus* were strongly correlated with recent rainfall. It is logical that most terrestrial life on these small, rocky islands would benefit from fresh water, yet it is not clear why the relative abundance of *D. pyramicus* would be negatively correlated with precipitation. Because *B. obscurior* is dominant to *D. pyramicus* at rich food resources (Morrison, 1995), it is possible that *B. obscurior* directly benefits from higher rainfall and, as *B. obscurior* populations increase, competing *D. pyramicus* populations decline.

Thus, population abundances of *B. obscurior* and *D. pyramicus* appear to be affected by an interaction of interspecific competition and precipitation. These forces are apparently not strong enough, however, to result in many extinctions.

Effects of disturbance

The ant fauna of these small islands is surprisingly resistant to disturbances caused by tropical storms of hurricane force. No ant populations went extinct on any of the seventeen

very small islands surveyed immediately after Hurricane Floyd. The ability to resist such disturbances varies among the flora and fauna inhabiting this region. For example, no plant species were observed to go extinct on a larger set of thirty islands in the same archipelago (including the subset of seventeen surveyed for ants; L. W. Morrison, in review). A similar disturbance (Hurricane Lili) in nearby Great Exuma, however, resulted in mass extinctions of lizards and web spiders on small islands (Spiller *et al.*, 1998). Ants that nest in cavities in the limestone, as well as the underground root systems of plants, would receive much greater protection in a hurricane than would web spiders and lizards (which sleep in the trees). A survey of the ants on the same small islands surveyed by Spiller *et al.* (1998) near Great Exuma conducted after Hurricane Lili did not reveal evidence of such strong effects on ants, as ants were present on all vegetated islands surveyed (L. W. Morrison, unpublished data). Some species of ants may have gone extinct on some islands, although this cannot be determined with certainty as no survey data prior to the hurricane exist.

The mechanism by which ants are able to survive such storms is not known. All the islands surveyed are primarily composed of limestone. Because the ants nest within chambers of the limestone, it is possible that they are able to block off the entrance tunnels or otherwise remain below ground in air-filled chambers while waves wash over the tops of the islands. Unfortunately, islands composed of a sandy substrate were not available for comparisons.

It is possible that extinctions of ants on these islands could occur eventually, if the destructive effects of the hurricane (i.e. damage to plants and loss of soil) cause a long-term diminishment of the ant's food supply. This will be evaluated in a future survey.

CONCLUSIONS

A data set now spanning almost a decade is beginning to reveal the long-term metapopulation dynamics of the ant species inhabiting these small islands. Immigrations and extinctions are relatively rare events in this system. These two processes appear to occur at similar rates, although immigrations were observed to exceed extinctions at times.

In an attempt to classify the different types of insular turnover dynamics, Whittaker (1998, 2000) characterized species turnover along two axes: the first axis specifies the degree to which the system is in equilibrium, and the second indicates whether the system is dynamic or static. In this scheme, over a time period of a decade (or less), the ant fauna of these small Bahamian islands would appear to fall near the region of 'static equilibrium'.

It is conceivable, however, that over longer periods of time direct hits by large (category 4 or 5) hurricanes could scour all the soil and plant life from these small islands, setting the system back to an early successional stage. Over decades, species numbers may rise very slowly, but never reach a true equilibrium before the next major hurricane. In this scenario, the turnover dynamics of these small islands may fall nearer the non-equilibrium region of Whittaker's scheme.

Detection of processes operating over such long time scales will necessarily require data spanning decades. From such a perspective, the data presented here represent merely a baseline for future work.

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BIOSKETCH

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