



Species richness and structure of ant communities in a dynamic archipelago: effects of island area and age

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ABSTRACT

Aim To assess how ant species richness and structure of ant communities are influenced by island age (disturbance history) in a dynamic archipelago.

Location Cabra Corral dam, Salta Province, north-west Argentina (25°08' S, 65°20' W).

Methods Ant species richness on remaining fragments (islands) of a flooded forest was determined, as well as island area, isolation and age. Simple linear regressions were performed to assess relationships between ant species richness and those insular variables. Furthermore, a stepwise multiple linear regression analysis was conducted in order to determine the relative influence of each insular variable on ant species richness. Islands were categorized in two age classes (old and young) and co-occurrence analyses were applied within each class to evaluate changes in community structure because of interspecific competition.

Results Simple regression analyses indicated a moderate, positive effect of island area on ant species richness. Weak, marginally non-significant relationships were found between ant species richness and both island isolation and island age, showing the tendency for there to be a decrease in ant species richness with island isolation and that ant species richness might be higher in old islands. The multiple regression analysis indicated that island isolation and age had no significant effects on the number of ant species, island area being the only independent variable retained in the analysis. On the contrary, whereas a random pattern of species co-occurrence was found on young islands, ant communities in old islands showed a significantly negative pattern of species co-occurrence, suggesting that the effect of competition on community structure was stronger on older islands than on younger islands.

Main conclusions Island area was the most important variable explaining ant species richness on the islands of Cabra Corral dam. However, both island isolation and island age (or disturbance history) might also contribute to shape the observed community patterns. The present study also shows that island age significantly affects the strength with which interspecific interactions structure ant communities on islands.

Keywords

Ant communities, competitive exclusion, dynamic archipelago, disturbance, habitat fragmentation, island biogeography, island age, species assembly.

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INTRODUCTION

Studies on natural communities in oceanic archipelagoes or fragmented landscapes often address the following questions:

(1) does species richness depend on the area and isolation of islands? and (2) do species interactions play a key role in structuring communities on islands? Species–area and species–isolation relationships have been extensively analysed in several

insular systems since MacArthur & Wilson (1967) proposed the equilibrium model of insular biogeography. Most studies show that species richness increases with island area and decreases with degree of isolation (Lomolino, 1994; Hubbell, 1997 and references therein). The positive effect of island area on species richness has been mainly explained in three ways: (1) larger islands support higher population sizes than smaller ones, reducing the extinction risk of species (Preston, 1962), (2) habitat diversity increases with island area, causing a higher number of vacant niches on larger islands (Williams, 1964), and (3) the larger the island area, the higher the probability to be reached by the propagules of different species (Gilpin & Diamond, 1976). The negative effect of island isolation on species richness has been attributed to the differential dispersal ability of species in the source territory of colonists. Thus, species with lower dispersal ability would be poorly represented in more isolated islands (MacArthur & Wilson, 1967; Simberloff & Wilson, 1969). The second question, addressing the importance of biotic interactions in community structure, has been focused on the search of 'assembly rules'. The aim of these surveys is to propose models (rules) indicating how interspecific interactions – mainly competition – affect the structure of natural communities (Diamond, 1975; Fox, 2001). Although the usefulness of this approach is currently under discussion (see Keddy & Weiher, 2001), the methods used to assess patterns because of biotic interactions allow the comparison of the structure of species assemblages between environments (Gotelli & Ellison, 2002).

A remarkable point both in studies about insular biogeography and on assembly rules is that researchers usually assume that all niches on islands have been occupied and maximum species richness have been reached (Bush & Whittaker, 1991; Hubbell, 1997). This assumption is not verified in all archipelagos. Patch availability in fragmented landscapes can vary as a consequence of disturbance, generating dynamic archipelagos (Marquet & Velasco-Hernandez, 1997). In such insular systems, the persistence of viable populations and the successful colonization by new species also depend on another factor in addition to area and isolation: the patch age (Borges, 1999). Studies on community succession report greater primary productivity with time between perturbations (Sousa, 1984; del Moral & Jones, 2002). Likewise, it may be assumed that habitat availability for colonists increases with time. Therefore, we expect that the older the habitat patches or islands, the higher the species richness. On the contrary, island age may also influence the competitive structure of insular communities. Given that the rate of arrival of colonists may be positively related to island age, the number of vacant niches on islands should decrease with time (Simberloff & Wilson, 1970). Once all available niches are occupied, interspecific competition will increase with the continuous arrival of species (Simberloff & Wilson, 1970). On this basis, we hypothesize that the older the island, the higher the structural complexity because of competitive interactions. In other words, we expect that patterns of species co-occurrence would change from random patterns to negative patterns as patch age increases.

The objectives of this study were to determine the relationships between ant species richness and island area, isolation and age, and to compare the assembling of ant communities in islands of different age in a fragmented habitat in NW Argentina. Fragmentation was driven by landscape flood because of the construction of a dam and the remnant fragments (islands) have been disturbed by operational fluctuations in the level of water, generating a dynamic archipelago with islands of different age (different history of disturbance).

METHODS

Study system

Cabra Corral dam (25°08' S, 65°20' W) is located on Juramento River (Salta, Argentina). The climate is subtropical semiarid and the vegetation corresponds to a montane matorral (Cabrera, 1976). The dam was constructed in 1969 as part of a hydroelectric project. Topographically, the flooded valley shows hills reaching 1016–1100 m above sea level (m a.s.l.). Flooding finished in 1985 and the artificial lake reached a level of 1035 m a.s.l. and an area of 133 km² (Salfity, 1980). Four hills above 1035 m a.s.l. were isolated since 1985 forming a group of 'old islands' of different area (Table 1; islands 1, 2, 3 and 4). Old islands preserved relicts of the original vegetation. Although trees (mainly *Acacia* spp. and *Prosopis* spp.) dominated their plant communities, shrubs and forbs were well represented under canopy. The old islands were surrounded by water for 14 years when the ant sampling began in 1999. The level of water of the artificial lake decreased to 1025 m a.s.l. in 1997, and five new islands of different area emerged (Table 1; islands 5, 6, 7, 8 and 9). There were no trees on these 'young islands' and shrubs dominated plant communities. Young islands were 2 years old at the sampling date. Another group of islands emerged between 1999 and 2000, when the water level of the lake further decreased to 1016 m a.s.l. These islands were

Table 1 Ant species richness (S), island area (m²), island isolation (m, shortest distance between the island and the shoreline) and island age (years after the last disturbance), number of sampled quadrats (NQ) and quadrat number at which the plateau was reached in the species accumulation curves (NP) on islands of the artificial lake of Cabra Corral dam

Island	S	Area	Isolation	Age	NQ	NP
1	7	23786	250	14	22	11
2	16	42090	198	14	61	27
3	7	15363	143	14	35	9
4	18	625163	10	14	83	21
5	5	5498	167	2	18	10
6	8	52439	251	2	42	15
7	6	2486	732	2	9	5
8	7	2487	120	2	10	8
9	6	1686	198	2	8	5

only present during the dry season (spring–summer) and had no true ant communities (only one ant species, *Solenopsis invicta* Buren, the red fire ant, was recorded), hence they were not considered in the analyses.

The two island classes considered (old and young) differed not only in age (time elapsed from emergence to the sampling date) but also in their disturbance history. Whereas old islands are in fact undisturbed, relictual habitats, young islands suffered disturbance (flooding) during 12 years. Thus, age and disturbance are intrinsically linked variables in the study system, as has been the case in other studies (Wilcox, 1978). Although we chose to label islands as old and young, the discussion of results logically includes both age and disturbance issues.

Sampling

A single transect was laid out along the largest axis of each island and 1 × 1 m quadrats were drawn every 10 m to assess ant species richness. Ants within quadrats were collected applying a vacuum pump for 3–4 min, including ants below rocks or other objects. Species accumulation curves were performed for islands in order to assess if sampling efforts were adequate (Colwell & Coddington, 1994). Shoreline and forest surrounding the dam were considered ant species sources (mainland) for island re-colonization. Twenty-four starting points were randomly placed in the shoreline and 200 m-long transects were extended towards the forest. Ant sampling was performed with the same procedure used on islands. Collected individuals were identified using the keys proposed by Kusnezov (1978) and Hölldobler & Wilson (1990).

Insular variables

Island area and isolation were calculated from an aerial photograph (scale 1 : 10000 m) taken in January 1999, the last time that all islands had emerged before this study. Area (m²) was estimated as the planar surface of islands. Isolation of islands (m) was measured as the shortest distance between the islands and the shoreline. Island age was defined as described above: old (14 years) and young (2 years) islands.

Analyses

First, to determine whether island age and area were confounded variables in the analysis, i.e. that old islands were at the same time larger, we applied a *t*-test comparing island area (log-transformed) between old and young islands.

We initially performed simple regression analyses in order to assess separately the relationship between ant species richness and island area, isolation and age. Afterwards, a stepwise multiple linear regression analysis was used to determine the relative influence of each insular variable on ant species richness. All data were log-transformed to achieve normality.

In order to assess structural changes in ant communities because of species interactions, the C-score (Stone & Roberts, 1990, 1992) was chosen as a quantitative index of co-occurrence. The C-score is the average of ‘checkerboard units’ calculated for all the species pairs that occur at least once in the sample pool. A checkerboard unit is any sub-matrix of the form:

	Sample 1	Sample 2
Species 1	0	1
Species 2	1	0

or

	Sample 1	Sample 2
Species 1	1	0
Species 2	0	1

The number of checkerboard units (*CU*) for each species pair is calculated as $CU = (r_i - S)(r_j - S)$, where r_i and r_j are the numbers of islands on which species i and j were detected, and S is the number of islands containing both species. To analyse the influence of island age on community structure, islands were categorized in age classes (permanent and young islands) and a species co-occurrence matrix was constructed for each class (see Appendix S1 in Supplementary Material). A C-score value was computed from the matrix of each age class and it was contrasted against a C-score expected by chance (i.e. no interactions affect the species occurrence on islands). These expected values were computed as the average C-score of 1000 null communities simulated from the respective co-occurrence matrix. Null communities were constructed placing species randomly and independently of one another, but the probability of a particular island being ‘hit’ by a given species was weighted by the island area (this procedure makes the results obtained ‘safe’ from the hypothetical co-variation of island age and area described above). The relative area of islands determined the probability for a species to occur in a particular island (Gotelli & Entsminger, 2001). In competitively structured communities, the observed C-score should be significantly higher than the expected C-score (Stone & Roberts, 1992) because the C-score measures the tendency for species not to occur together. The reliability of checkerboard distribution as the simplest distributional pattern evidencing competitive exclusion was first discussed by Diamond (1975).

RESULTS

Species accumulation curves for all islands reached the plateau before the last quadrant, indicating an adequate sampling effort of ant richness (Table 1). Twenty-three ant species were detected on islands and *Solenopsis invicta*, the red fire ant, was the most common species. In the mainland, thirty-nine species were detected, and *S. invicta* was also the most common species (Table 2).

A marginally significant difference in area between old and young islands was found ($t = 2.384$, d.f. = 7, $P = 0.049$), old islands being slightly larger than young islands.

Subfamily	Species	Island	Mainland
Dolichoderine	<i>Biconomyrma brunnea</i> (Santschi) Kusnezov	2	21
	<i>Biconomyrma pulchella</i> (Santschi) Kusnezov	2	13
	<i>Conomyrma breviscapis</i> (Forel) Kusnezov	5	19
	<i>Conomyrma pyramica</i> (Roger) Kusnezov	8	15
	<i>Conomyrma wolffhüngeli</i> (Forel) Kusnezov	3	16
	<i>Forelius nigriventris</i> Forel	2	15
	<i>Iridomyrmex humilis</i> (Mayr) Kusnezov	6	19
	<i>Neoforelius tucumanus</i> Kusnezov	4	18
Formicinae	<i>Brachymyrmex physogaster</i> Kusnezov	3	6
	<i>Camponotus aguilerai</i> Kusnezov	0	11
	<i>Camponotus guayapa</i> Kusnezov	5	17
	<i>Camponotus leydigi</i> Forel	3	8
	<i>Camponotus substitutes</i> Emery	0	5
	<i>Camponotus yala</i> Kusnezov	2	5
	<i>Prenolepis fulva</i> Mayr	4	9
Myrmicinae	<i>Acromyrmex lobicornis</i> (Emery) Kusnezov	2	14
	<i>Acromyrmex rugosus</i> (F. Smith) Kusnezov	0	9
	<i>Acromyrmex striatus</i> (Roger) Kusnezov	1	7
	<i>Crematogaster guardiformis</i> Roger	7	19
	<i>Crematogaster iheringi</i> Forel	0	10
	<i>Monomorium pharaonis</i> (Linneanus) Kusnezov	0	11
	<i>Notomyrmex bidentatus</i> (Mayr) Kusnezov	3	20
	<i>Notomyrmex denticulatus</i> (Mayr) Kusnezov	0	9
	<i>Pheidole flavens</i> (Mayr) Kusnezov	0	8
	<i>Pogomyrmex cunicularius</i> (Mayr) Kusnezov	2	14
	<i>Rogeria foreli</i> (Emery) Kusnezov	0	3
	<i>Rogeria procera</i> (Emery) Kusnezov	3	18
	<i>Solenopsis andina</i> Santschi	0	1
	<i>Solenopsis invicta</i> Buren	9	24
	<i>Solenopsis nigrella</i> Emery	0	1
	<i>Solenopsis silvestrii</i> Emery	0	4
<i>Wasmania sulcaticeps</i> Emery	0	5	
Pseudomyrmicinae	<i>Pseudomyrmex gracilis</i> (Fabricius) Kusnezov	2	5
	<i>Pseudomyrmex pallida</i> F. Smith	1	13
Ecitoninae	<i>Labidus coecus</i> (Latreille) Kusnezov	0	6
Ponerinae	<i>Euponera fauveli</i> (Emery) Kusnezov	0	4
	<i>Ponera opaciceps</i> Mayr	0	2
Unidentified	Unidentified sp.(1)	1	5
	Unidentified sp.(2)	0	8

Table 2 Ant species on islands and the mainland. Number of islands (Island) and number of mainland transects (Mainland) on which each species was detected are shown

Simple regression analysis indicated a moderate, positive effect of island area on ant species richness ($F = 14.16$; d.f. = 7, $P < 0.01$, $r^2 = 0.67$) (Fig. 1a). A weak, marginally non-significant relationship was found between ant species richness and island isolation ($F = 5.021$, d.f. = 7, $P < 0.06$, $r^2 = 0.42$), showing the tendency of a decrease in ant species richness with isolation (Fig. 1b). Likewise, the number of ant species on islands showed a weak, marginally non-significant relationship with island age ($F = 5.04$, d.f. = 7, $P < 0.06$, $r^2 = 0.41$), suggesting that ant species richness might be higher in old islands (Fig. 1c). However, a stepwise multiple regression analysis indicated that island isolation and age had no significant effects on the number of ant species, island area being the only independent variable retained in the analysis.

The observed C-score for young islands (1.17) showed no difference with its expected value assuming random colonization by ant species [$1.19 (\pm 0.05 \text{ SD})$], indicating a random pattern of species co-occurrence [P (Observed > Expected) = 0.79]. In contrast, the C-score for old islands (1.41) was significantly higher than the value expected by chance [$1.36 (\pm 0.02 \text{ SD})$], suggesting a negative pattern of species co-occurrence [P (Observed > Expected) < 0.05].

DISCUSSION

Island area was the most important variable explaining ant species richness on the islands of Cabra Corral dam. A first explanation for this result could be based on the habitat diversity hypothesis, which assumes that large habitats have

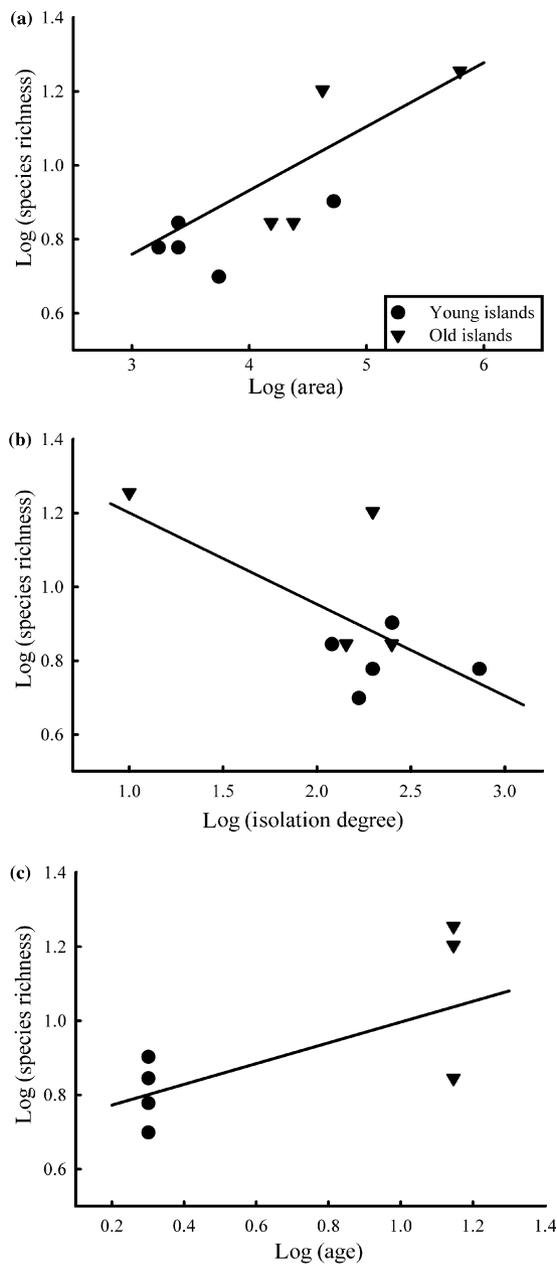


Figure 1 Relationships between ant species richness and island area (a), island isolation (b) and island age (c) on the archipelago of Cabra Corral dam. The lines shown correspond to linear regressions (see text for statistical results).

more niche opportunities than smaller ones (Williams, 1964). Species richness in ant communities is well known to be highly dependent on habitat diversity because several species have highly specialized habits and competitive hierarchies produce species segregation between patches of different quality (Hölldobler & Wilson, 1990; Samways *et al.*, 1997). Thus, larger islands could support more species because habitat availability for colonists increases with area. A second explanation for the observed positive effect of island area on ant species richness would consider the probability of islands

being found by dispersed ants, suggesting that larger islands have more species because their 'target area' is larger (Gilpin & Diamond, 1976). Thus, the probability of islands being 'hit' by dispersal propagules (i.e. gravid queens) would depend both on the intrinsic capacity of propagules to detect and reach available habitats and on island area. Likewise, the observed tendency of a negative effect of island isolation on ant species richness might be attributed to differential dispersion ability of the potential colonists from the mainland (MacArthur & Wilson, 1967). Poor dispersers from mainland cannot reach the farther islands, producing a decrease in species richness with island isolation (Simberloff & Wilson, 1969). Water is a very hostile matrix for insects lacking the ability to fly, which can only reach islands through external agents of dispersion (e.g. floating objects; Heatwole & Levins, 1972). In this study, sixteen ant species were detected only in the mainland. Although 14 of these species do have winged-queens (Kusnezov, 1978), they were not recorded on islands. This suggests that the dispersal capacity of these species is limited.

Island age (or island disturbance history) had a weak association with ant species richness in this archipelago. The tendency was that the longer the time since the last disturbance that affected the island, the higher the ant species richness. However, it should be noted that a marginally significant analysis showed that old islands are slightly larger than young islands, hence suggesting that island age and area are confounded variables. Nonetheless, keeping this caveat in mind, we consider that such a marginal result does not necessarily preclude the discussion of the observed tendency of a positive but weak effect of island age on ant richness. First, the longer the time since the emergence of islands, the higher the opportunity for ant species to reach the islands; the effects of island age are hence reduced to colonization probabilities through time. Secondly, development of plant communities on islands increases with time, increasing the primary productivity and the habitat heterogeneity for colonists. Therefore, island age might affect ant species richness by influencing habitat availability, as island area does. An earlier study addressing colonization patterns in Krakatau suggested that disturbance dynamics could be an important factor influencing species richness on islands (Bush & Whittaker, 1991). This study mainly discusses the effects of long-term disturbances, such as volcanic eruptions and hurricanes, on species richness in oceanic archipelagos. There is also evidence that lizard species distributions in Baja California are jointly affected by island area and island age (time since land bridges were submerged to form islands) in a time-scale of thousands of years (Wilcox, 1978). In the present study, for a smaller, dynamic archipelago, we suggest that short-term disturbances might also affect patterns of species richness.

Co-occurrence analyses indicated that island age may influence the structure of ant assemblages on the islands of Cabra Corral dam. The random pattern of co-occurrence found on young islands suggests that interspecific interactions have little effect on ant community structure. In contrast, the

negative pattern of co-occurrence observed on old islands indicates mutually exclusive distributions of ant species. These differences in the pattern of species distribution between young and old islands suggest that the time elapsed since patch formation may determine the importance of biotic interactions on community structure. Diamond (1975) proposed that mutually exclusive distributions of species among communities are caused by 'forbidden species combinations'. In other words, only certain species combinations are allowed to coexist on an island, while other combinations never occur, or at least are much less common, because of competitive exclusion (Fox, 2001). Results of the present study indicate that communities on old islands are competitively structured, agreeing with observations made on ant communities from highly productive habitats (Bestelmayer, 1997). Moreover, a meta-analysis has recently shown that, as a group, ants exhibit highly non-random patterns of co-occurrence (Gotelli & McCabe, 2002). The random pattern of species occurrence on young islands suggests that forbidden combinations between ant species were still not assembled due to the short time between island emergence and sampling date. The arrival of new species to young islands might produce competitively structured communities in the future, as has taken place on old islands.

The present study has shown that ant species richness in a dynamic archipelago is mainly determined by island area but both island isolation and island age (or disturbance history) might also contribute to shape the observed community patterns. Our results also indicate that island age significantly affects the strength with which interspecific interactions structure ant communities on islands. On this basis, we stress the importance of identifying how disturbance affects patch availability in fragmented landscapes when analysing community structure.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JBI1174/JBI1174sm.htm>

Appendix S1 Co-occurrence matrices for old and young islands of the artificial lake of the Cabra Corral dam.

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