



Available online at:

<http://www.italian-journal-of-mammalogy.it/article/view/12350/pdf>

doi:10.4404/hystrix-28.2-12350

Research Article

Understanding the long term consequences of fragmentation: lessons from the bats of Bijagós (Guinea-Bissau, West Africa)

Ana RAINHO*, Jorge M. PALMEIRIM

¹ Centre for Ecology, Evolution and Environmental Changes and Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal**Keywords:**

bat assemblages
Bijagós islands
Guinea-Bissau
Long-term fragmentation

Article history:

Received: 25 January 2017
Accepted: 16 March 2017

Acknowledgements

We would like to thank Cláudia Franco, Mónica Sousa, Rui Rebelo, Hamilton Monteiro, Cristina Schwarz da Silva, Quintino Tchanchalan, Castro Barbosa and all the park guards, staff and other colleagues that collected or helped us collecting data. We would also like to thank Paulo Catry, Aissa Regala and Alfredo Simão da Silva for the support and for giving us the opportunity to work in the Parque Nacional Marinho João Vieira e Poilão.

To Prof. Ulrich Weber we thank the help provided in sorting out some issues in the analysis of pairwise patterns of species co-occurrence. Constructive comments by an anonymous referee greatly helped to improve this manuscript.

This study was partly funded by the Instituto para a Biodiversidade e Áreas Protegidas and MAVA Foundation pour la Nature. AR was supported by a postdoctoral fellowship from the Portuguese Foundation for Science and Technology (SFRH/BPD/101983/2014).

Abstract

The Bijagós archipelago consists of about 80 land-bridge islands located just off the coast of Guinea-Bissau (West Africa). The current faunas of such land-bridge archipelagoes reflect the isolation resulting from the fragmentation of the original coastal plains, caused by sea level rise about 11000 years ago. Therefore, they represent a unique opportunity to study long-term consequences of natural habitat fragmentation, analogous to the ongoing fragmentation processes caused by Man.

We sampled and analyzed the bat assemblages of eight Bijagós islands and two nearby coastal regions to understand how insularity shaped island assemblages, and evaluate the potential impacts of fragmentation on African bat assemblages. Rarefaction using Chao2 estimator indicated that total species richness on Bijagós is only about 1/5 of that on the coast. Cluster and correspondence analyses demonstrated that bat faunas of different islands are quite similar, and not a random set of the mainland species assemblage. Moreover, trait analysis indicated that islands assemblages are composed by generalist and abundant species; presumably only generalist species can attain island population sizes viable in the long-term.

The observed species depletion resulting from long-term isolation in Bijagós is much more accentuated than that observed in recent fragments, corroborating the view that such fragments are still losing species. Our results indicate that, despite the high mobility of bats, even relatively large fragments are unable to sustain viable populations of most species and that the impacts are worse in the case of rarer species. Most ongoing fragmentation resulting from habitat destruction involves matrices with a lower contrast than water, and this may lessen impacts. However, at least in the case of high contrast matrices, currently fragmented landscapes are likely to continue losing species, and thus the true, long-term, impacts of fragmentation shall likely be worse than those so far reported.

Introduction

A major challenge in ecology is to understand the main drivers of species' assembly patterns and structure. This is of particular interest in insular systems; as a result of their discrete, manageable, replicated and somehow simplified nature, islands assemblages are the base of a great number of ecological theories, concepts and insights in the functioning of ecosystems (see Whittaker and Fernández-Palacios, 2007 for a synthesis). The understanding of the determinants of species assemblages is not only interesting per se but also to predict and manage the impacts on natural systems when assemblages experience perturbation and habitat loss.

Human-induced destruction and degradation of natural habitats are generally regarded as the greatest threats to tropical ecosystems (Sala et al., 2000; Laurance et al., 2014). They typically lead to habitat fragmentation, the division of the original habitat into smaller fragments or "islands" separated by a matrix of modified habitat. Here, the fate of taxa will be ruled largely by the resilience of their populations (Lindenmayer and Fischer, 2006).

Studies of long-term effects of fragmentation on biodiversity are thus critical (Haddad et al., 2015; Meyer et al., 2016), and naturally fragmented systems, like land-bridge archipelagos, provide opportunities to understand and predict the long-term consequences of habitat fragmentation. Natural land-bridge islands are islands that were once connected to the mainland and could then be freely colonized by its species.

Fragmentation usually occurred at the time of sea level rise (Newmark, 1987).

The Bijagós archipelago is an exceptional theatre in which to investigate the long-term effect of fragmentation on animal assemblages. It is composed of more than 80 islands and islets, located in the delta of the river Geba, up to 70 km off the coast of Guinea-Bissau (West Africa). The isolation of these islands presumably dates from the Holocene marine transgression (ca. 11000 years before present; Alves et al., 2015).

Bats are considered a good model for evaluating fragmentation issues, as they are taxonomically and ecologically diverse and highly mobile, showing potential to move over extensive areas, even if fragmented (Meyer and Kalko, 2008b). Additionally, bats play crucial roles in ecosystem functioning, either as pollinators, seed dispersers or predators, so changes in their diversity and abundance may alter ecological processes and have impacts on the survival of other species (Lindenmayer and Fischer, 2006). Despite this importance of bats and the growing attention of researchers to the problems of fragmentation, to our knowledge, no studies focused the effect of fragmentation on African bats.

A growing number of studies have assessed the effects of fragmentation on tropical taxa, including bats, but most have been conducted in the Neotropics (e.g. Haddad et al., 2015; Meyer et al., 2016; Rocha et al., 2017). The great majority of them studied recently formed, non-natural fragmented systems, and thus their results reflect the species short- to medium-term response to fragmentation (Haddad et al., 2015).

Species persistence in fragmented landscapes is strongly affected by the level of permeability of the matrix that surrounds the fragments.

*Corresponding author

Email address: amrainho@fc.ul.pt (Ana RAINHO)

Although bats have excellent dispersal abilities, even over water (Cosson et al., 1999a), sea water is one of the most unsuitable and least permeable habitats for them, so a matrix of sea water represents a worse-case scenario in terms of fragmentation effects (Cosson et al., 1999b; Meyer and Kalko, 2008b). We predicted that, overall, the bat assemblages in the Bijagós island “fragments” would be affected by the syndromes of isolation described in manmade landscape fragments, further accentuated by the water matrix and by the longer period of isolation of the islands.

We studied the bat assemblages of the Bijagós islands and those of nearby mainland areas to understand how insularity has shaped island assemblages, and to evaluate the impacts of fragmentation on African bat assemblages. The following specific questions were addressed: (i) How are bat species richness and abundance affected by isolation in the Bijagós? (ii) Are species assemblages similar among islands? (iii) How is the species composition of island assemblages different from assemblages on the coastal mainland? (iv) Which species traits make bats capable of sustaining isolation? Finally, the contribution of the results to the understanding of long-term consequences of habitat fragmentation on animal species assemblages is discussed.

Methods

Study sites

Guinea-Bissau is located on the west coast of Africa, between Senegal and the Republic of Guinea (10°55'–12°45' N and 13°37'–16°43' W) (Fig. 1). Generally flat, its maximum altitude is just 269 m asl. The climate is Sudano-Guinean with two seasons; a rainy season between June and October and a dry season between November and May. Most of the country receives 1500–2000 mm of rain annually, but the south is wetter with rainfall averaging over 2000 mm. Monthly average temperature in Bissau, the country’s capital, ranges from 25 °C to 28 °C.

We surveyed bats in three regions (Fig. 1): the Bijagós archipelago and two regions on the mainland coast:

- The region of Cacheu corresponds roughly to the area of the Cacheu Mangroves Natural Park (PNTC), located at the extreme northwest of the mainland and including both banks of the river Cacheu estuary. It includes 30000 ha of mangroves as well as mud- and sandbanks, semi-dry woodland, palm forest, savanna and agricultural land (BirdLife International, 2016b).
- The Cantanhez Forests National Park (PNFC) is located in the southernmost part of the country and encompasses both banks of the river Cacine estuary. This is the wettest region of Guinea-Bissau, reaching an annual precipitation of 2600 mm. It includes most of the remaining areas of semi-humid forest in the country, farmland, river flood-plains, mangroves and areas of savanna (BirdLife International, 2016a).

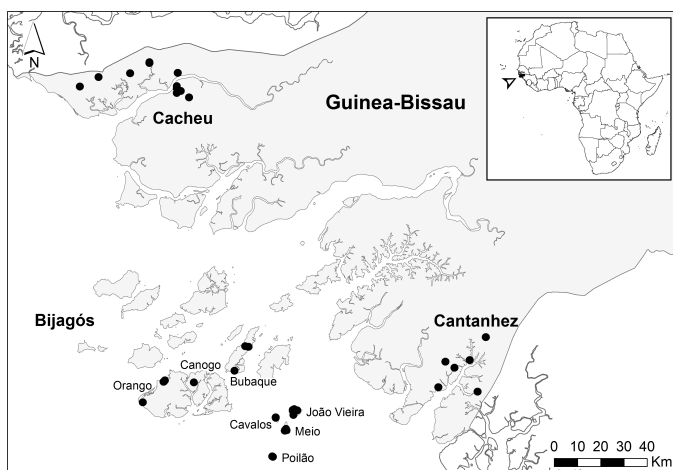


Figure 1 – Map of Guinea-Bissau, showing the sites sampled in Cacheu, Cantanhez and in the Bijagós islands.

- The Bijagós archipelago is composed of 88 islands and islets surrounded by a vast intertidal area of open mudflat and mangrove. Seven islands were surveyed during this study (Fig. 1):
 - Bubaque located in the centre of the archipelago;
 - Orango and Canogo both in the Orango National Park (PNO); and
 - João Vieira, Meio, Cavalos and Poilão, all part of in João Vieira / Poilão Marine National Park (PNMJVP) in the south-east of the archipelago.

All sampled islands are mostly covered by forest, coastal wooded savanna, palm forests, mangroves and other flooded areas.

Data collection

Bat data was obtained during several field surveys all carried out during the dry season. The survey in Cacheu was conducted in 1998 (Rainho and Franco, 2001), and that of Cantanhez in 2007 (Rainho et al., 2007). In the Bijagós archipelago, Bubaque, Orango and Canogo were surveyed in 1997 and 1998 (Rainho and Franco, 2001), and the four islands of the PNMJVP in 2015 (Rainho et al. unpublished data).

Mist nets were set for no more than two consecutive nights at each site to reduce net avoidance by bats (Marques et al., 2013). Most nets were set on poles near ground level or slightly above the surrounding vegetation in each region’s main habitats, including wetlands, when available. Nets were generally open from sunset to midnight, but on some nights they were re-opened before sunrise, from about 4:30 to 6:30 (see capture effort at each site in Tab. S1).

Captured individuals were sexed, measured, identified and released. Species identifications were based on published keys (Hill, 1963; Rosevear, 1965; Hayman and Hill, 1971; Robbins et al., 1985; Van Cakenberghe and De Vree, 1985; Bergmans, 1988, 1989, 1997; Bouchard, 1998) and taxonomy follows Simmons (2005).

Captures were done under license of the responsible regulatory authority in Guinea-Bissau, the Institute for Biodiversity and Protected Areas (IBAP).

Statistical analysis

Species richness estimates for the archipelago and the coastal regions of Guinea-Bissau were obtained using the Chao2 estimator and unconditional 95% confidence intervals on incidence data (Gotelli and Coldwell, 2011). Calculations were made using EstimateS software (v. 9.1.0, Colwell, 2013).

Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis with Jaccard distances was used for classifying (a) sampled sites according to the presence of the various bat species, and (b) species according to their sites of occurrence. The cophenetic correlation coefficient was then used as a measure of goodness of fit, assessing how faithfully each dendrogram preserves the pairwise distances between the original unmodeled data points (Saraçlı et al., 2013). Correspondence analysis, which provides a joint ordination of species and sites, was used to help understanding how species assemblages are organized. These analyses were performed with PAST software (v. 3.12, Hammer et al., 2001).

We used Spearman correlation to test the relationships between species richness and island size, distance to the mainland and distance to the nearest island. Islands ranged in size from Poilão (0.43 km²) to Orango (261 km²) (Embaló et al., 2008a,b). Distance to mainland is less variable ranging from 29 km for João Vieira to 73.5 km for Orango. The distance to the nearest island ranged from 0.46 km between Orango and Canogo to 11.6 km in the case of Poilão (see Tab. S1). Correlation analyses were performed with the package Hmisc in R (R Core Team, 2016).

Several species traits have been suggested to influence the ability of species to colonize and survive in fragmented habitats (e.g. Henle et al., 2004; Barbaro and Van Halder, 2009; Öckinger et al., 2010; Franzén et al., 2012). Here we evaluated the potential influence of species abundance, rarity, dispersal power and body size, traits that are likely to be relevant to bats (Cosson et al., 1999b).

There is no reliable way to measure population density of bats, so we used an index of relative abundance, following the procedure by Arita (1993): first all species were ranked by the total number of netted individuals; the rank of each species was then divided by the number of species captured at each site. Finally, for each species, we averaged this index for all localities in which it was detected, thus obtaining a rough estimate of overall local abundance. Each species was also ranked by its prevalence, defined as the proportion of sampled sites in which the species was recorded. However, local abundance and prevalence indices were highly correlated (Spearman correlation, $r_s=0.91$, $n=26$, $p<0.001$), so we used the local abundance index as a proxy of occurrence (Arita, 1993).

The traits body size and dispersal power of each species were estimated using body mass and wing characteristics (wing loading and aspect ratio). These were calculated using measurements of the specimens that we captured or from information in the literature (Rosevear, 1965; Robbins et al., 1985; Norberg and Rayner, 1987; Jacobs and Barclay, 2009; Monadjem et al., 2010; Happold and Happold, 2013). No information on wing characteristics was found for *Epomops buettikoferi* and *Glauconycteris poensis*, so measurements from closely related species were used (*Epomops franqueti* and *Glauconycteris variegata*). Body mass was used to classify species according to size. Dispersal ability in bats is at least partly dependent on wing morphology (Norberg and Rayner, 1987; Meyer et al., 2009). We followed Happold and Happold (2013) and classified each species wing loading and aspect ratio from 1 (very low) to 5 (very high). Due to the different range of sizes, the threshold values used in defining classes were different for Pteropodid species, so they were analysed separately (Happold and Happold, 2013). Furthermore, the wing loading of *Eidolon helvum* and *Hypsiphatius monstrosus* proved to be extremely high so they were classified as 6. Species dispersal power was quantified by adding the values of wing loading and aspect ratio, giving greater weight to the latter (Happold and Happold, 2013).

To compare the traits body size and dispersal power of island species assemblages with those on the mainland, we first ranked all species according to each trait. Wilcoxon-Mann-Whitney tests were then used to verify if the median of the trait ranks on the island assemblage is different from the median of the traits in the mainland. These analyses were performed in R.

To test for evidence of competition in the structuring of island bat assemblage, we used the checkerboard score (C-score) as an index of co-occurrence (Stone and Roberts, 1990; Gotelli, 2000). The C-score metric has proved to be very robust, particularly for small or middle-sized matrices; it is based on the number of checkerboard units in the matrix and varies between 0 (maximally aggregated) to a maximum of $R_A R_B$ (maximally segregated with no shared sites), where R is the row total for species A and B , respectively (Gotelli and Ulrich, 2012). We simulated the presence-absence data of each species across all sampled sites in the islands (see Tab. 1) in 5000 random “pseudo-assemblage” matrices generated by Monte Carlo methods (Gotelli and Graves, 1996) and using a randomization algorithm that preserves the observed row and column totals (fixed-fixed). This analysis was performed in the EcoSimR package (version 0.1.0) developed by Gotelli and Ellison (2013), in R. Taking that the C-score represents an average calculated over all possible species pairs, the analysis of which individual species pairs show aggregation or segregation may provide further insight into the structure of the assemblage (Gotelli and Ulrich, 2012). Additionally, the analysis of each pair of species provides insight into the performance of the C-score metrics (Ulrich and Gotelli, 2013). Pairwise patterns of species co-occurrence were analysed using C-score and a fixed-fixed matrix randomization algorithm in the program Pairs (Ulrich, 2008).

A significance level of 0.05 was used in all analyses.

Results

Species richness

A total of 296 bats were captured with mist nets, comprising 26 species, 15 genera, and 6 families. Seventeen species were recorded in

Cacheu, 15 in Cantanhez but only eight in Bijagós. Two additional species, of the families Molossidae and Hipposideridae, are known to occur in some of the islands. However, they were not considered in this paper because their species identity has not been confirmed and they were recorded acoustically, a method that was not used in all sites.

Overall, average capture success ($\pm 95\%$ confidence intervals) was 0.61 (± 0.24) bats per 12 m mist net hour (b/h) for all sites. Capture success in Bijagós (0.42 ± 0.18 b/h) was considerably lower than in Cacheu (0.71 ± 0.56 b/h) and Cantanhez (0.81 ± 0.6 b/h). However, the capture success of the eight species known to occur both in the mainland and in the Bijagós was very similar in all regions (0.47 ± 0.66 b/h in Cantanhez and 0.40 ± 0.19 b/h in Cacheu).

Species richness in the mainland was several times higher than in the islands, with no overlap between the 95% confidence intervals of the Chao2 estimator (mainland: 37 (29, 67) and islands: 8 (8, 10)).

No significant correlation was found between species richness and island area (Spearman correlation, $r=0.09$, $n=7$, $p=0.85$), distance to the mainland ($r=-0.13$, $n=7$, $p=0.79$) and distance to the nearest island ($r=0.18$, $n=7$, $p=0.71$). Furthermore, no significant correlation was found between island richness and island sampling effort ($r=0.48$, $n=7$, $p=0.27$).

Assemblage composition

Cluster analysis on the dissimilarities among sites using presence-absence of bat species (Fig. 2A) revealed a good adjustment to the data

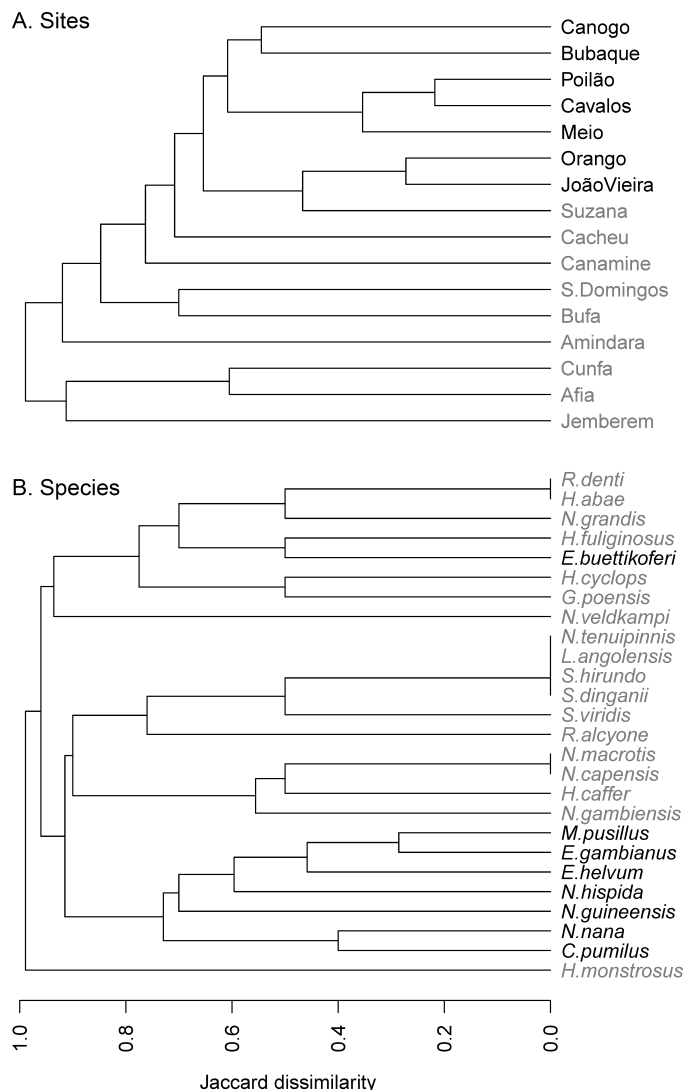


Figure 2 – UPGMA dendrogram (using Jaccard similarity) index on the dissimilarities A) among studied sites in terms of presence-absence of the various bat species and B) among species present on the studied sites. Sites and species present in islands are labeled in black.

(cophen. correl.=0.87). Three sites from Cantanhez form a separate cluster, but the dendrogram of all the remaining sites on the mainland shows “chaining”, with each sampled site linked to the next by a slightly lower tie bar, which suggests a gradient of dissimilarity or nestedness across mainland sites. The islands sites form a single cluster, which only includes one site on the mainland, Suzana. This confirms that species composition is quite similar among islands and distinct from that of the assemblages on the mainland. No clustering patterns relating to island size or distance to coastline are evident.

The UPGMA dendrogram of species (cophen. correl.=0.88; Fig. 2B) shows all the species present in the Bijagós islands aggregated in one branch. *E. buettikoferi* is the exception to this pattern; although occurring on the islands, this species is included in a separate branch that comprises species that have a higher affinity to forested areas, like *Hipposideros fuliginosus*, *H. cyclops* or *G. poensis*, and thus occur mainly in the well forested region of Cantanhez. The two central clusters include mostly species that were recorded in the dryer region of Cacheu. *H. monstrosus* shows up as an outlier to this pattern.

Characteristics of the species present on islands

The correspondence analysis (37.9% of explained variation, Fig. 3) shows all the islands sites forming a tight group, thus confirming the similarity in species composition among islands.

The species that occur on islands occupy positions very close to the center of the space defined by the first axes, suggesting that they are generalist widespread species. That is the case of *Epomophorus gambianus* (recorded in 81% of the sampled sites), *Micropteropus pusillus* (69%), *E. helvum* (50%) and *Nycteris hispida* (50%), which are ubiquitous species in Guinea-Bissau (Rainho and Franco, 2001).

The comparison between the medians of traits in the islands assemblages with those of the mainland assemblages confirmed this pattern — the island assemblages consists of species that are among the most common in the region (Tab. 1). Species abundance shows up as a very important trait facilitating the presence on islands. No statistically significant differences were found in the other traits analyzed; species body size and dispersal potential did not differ between island and mainland assemblages. This result is illustrated by the presence in

the islands of *Neoromicia nana* and *N. hispida*, which are among the smallest and potentially less vagile species.

The co-occurrence analysis indicates that competition is not important in the structuring of the bat assemblage in the islands (C-score observed: 1.00, simulated: 0.94, $p=0.307$). The species pairwise analysis supports this result by detecting no significant pairs in the islands, which indicates that neither negative nor positive interspecific interactions are major drivers in the occurrence of the bat species among islands.

Discussion

How does insularity affect bat abundance and species richness in the Bijagós islands?

Our results demonstrate that bat species richness in the Bijagós islands is several times lower than in the mainland and shows that insularity has important consequences on the composition of species assemblages.

Thousands of years since the formation of the islands, due to the post glaciations rise in the sea level, their species assemblages are likely to be the result of long-term fragmentation; it is plausible to consider that both bat assemblages and associated ecological interactions have reached an equilibrium (but see Heaney, 2000).

Lower species richness is a common pattern both in oceanic (e.g. Triantis et al., 2015) and in recently formed land-bridge tropical islands (see the review by Jones et al., 2016 for reservoir islands). Published information on land-bridge archipelagos focus on recently formed systems (<100 years), generally created by flooding in a reservoir. These studies also show that the already impoverished assemblages continue to sustain richness declines (Jones et al., 2016). This seems to be true even for the oldest (≈ 100 yo) and large islands such as Barro Colorado, and in spite of the conservation efforts made in the area.

The time since the creation of the island or fragment seems to be a major driver in defining species richness (Triantis et al., 2015; Jones et al., 2016), but other geographical characteristics are often considered as important mediators in species richness patterns (Lomolino and Weiser, 2001; Frick et al., 2008; Meyer and Kalko, 2008a; Yu et al., 2012). This is the case of island area, isolation, specific patterns of fragmentation and habitat quality and diversity.

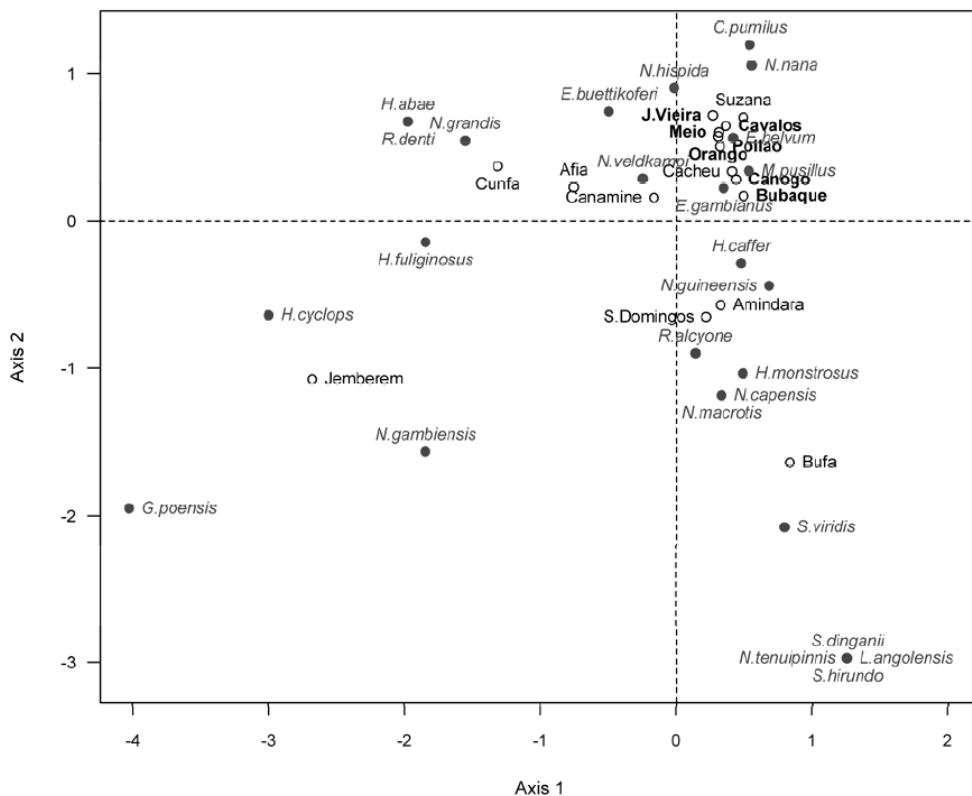


Figure 3 – Correspondence analysis of sampled sites (open dots) and species (black dots) using species presence-absence. Sites in islands are shown in bold.

Table 1 – Median values of the trait ranks of species present on islands and mainland, and significance of Wilcoxon-Mann-Whitney's comparison between the two assemblages.

	Median [range]		Wilcoxon-Mann-Whitney test		
	Islands	Mainland	U	p	Sig.
Abundance	21.5 [16–26]	13.5 [1–26]	41.0	0.011	**
Body size	15.0 [1–25]	13.5 [1–26]	99.0	0.855	n.s.
Dispersal power:					
Pteropodid	4.8 [1–5.5]	3.3 [1–5.5]	10.0	0.739	n.s.
Other species	8.0 [1.5–20]	8.0 [1.5–20]	44.5	0.744	n.s.

The habitats available in the islands are quite diverse, but they are dominated by open dry-woodland or savanna-like habitats. Semi-humid forest is also present on some islands but in small areas and this may contribute to explain the absence of species generally associated with humid-forests, such as *G. poensis* or *H. monstrosus* (Happold and Happold, 2013). The scarcity of this habitat may also justify the greater similarity of the assemblages of the islands with those of the dryer region of Cacheu than with the more humid Cantanhez (Fig. 3). Furthermore, the absence of caves in the islands surely limits the occurrence of species like *Rhinolophus denti* or *Hipposideros abae* that depend on underground roosts (Rodríguez-Durán, 2010; Happold and Happold, 2013). Despite these differences, the range of habitats available on the islands is overall quite similar to that on the coastal areas, so it is unlikely that habitat diversity explains much of the difference in species richness.

The lack of a significant relationship between species richness and island area or isolation in our data should be interpreted with care; it may be to some extent due to the inclusion of islands with incomplete inventories, or to relatively small sample sizes. However, it is worth noting that there is still no consensus on how area and isolation affect bat species richness in fragments or in near shore islands. While some studies reveal a weak or no effect of size and isolation (Cosson et al., 1999a) others show that at least one of these variables is influential (e.g. Estrada et al., 1993; Frick et al., 2008; Meyer and Kalko, 2008a). Several reasons may justify these different results: the composition and traits of species in the mainland assemblage (Franzén et al., 2012), island (in)stability (Willig et al., 2010), methodological issues and undetected species (Nichols et al., 1998; Kunz et al., 2009), numerical and statistical issues in data analysis (Bunnfeld and Phillimore, 2012) and island age (Triantis et al., 2015; Jones et al., 2016). Several authors suggested that the decline in bat species richness in larger islands is just delayed and the differences in species richness between small and large islands are mediated by the time since their formation (e.g. Cosson et al., 1999a; Jones et al., 2016).

The long time since the isolation of Bijagós islands may thus have contributed to the observed lack of clear association between richness and both island size and level of isolation. However, a study with more complete inventories and including more Bijagós islands is likely to reveal that islands that are either very close to the mainland harbor more bat species and the smallest islands fewer species.

As observed in bat assemblages of other insular systems (e.g. Cosson et al., 1999a), species composition and richness levels are quite similar in many of the sampled islands. In this context, it is unsurprising that co-occurrence analyses did not provide evidence that assemblage composition on Bijagós islands is structured by negative interspecific interactions. The similarity of bat assemblages in multiple islands (see Fig. 2A and 3) indicates that the assemblages are not random; the occurrence of species in the islands is determined by common ecological or life-history traits.

The major reduction in species richness is not the only consequence of isolation on the Bijagós bat assemblages. Assuming that mist net capture rate is roughly proportional to overall bat abundance, we can conclude that abundance in the islands is about half of that on the coastal mainland. However, the abundance of the eight species captured on the islands is similar to that of the same set of species on the mainland. This indicates that the reduced overall abundance is due to the many species that are absent on the islands but present on the coast.

Our data did not show any evidence of an overall “density compensation” i.e. an increase in the abundance of island species as a consequence of an overall poorer assemblage. This phenomenon is common in islands and it is thought to result from a lowering of interspecific competition (Henry et al., 2007; Whittaker and Fernández-Palacios, 2007). The absence of density compensation suggests that the missing species were not close competitors of the species present in the islands, or that the latter have some level of competitive advantage (Russo et al., 2014).

Which species manage to maintain populations on the islands?

It is well known that not all species respond equally to habitat fragmentation and this variability in species' response is likely to be explained by life-history traits (e.g. Henle et al., 2004; Öckinger et al., 2010).

Contrarily to what has been reported in several studies in the Neotropics (e.g. Cosson et al., 1999a; Meyer and Kalko, 2008b) our data did not suggest that body size and dispersal potential of species are important determinants of their occurrence in Bijagós. In fact, many bat species present in Guinea-Bissau that are known to be able to disperse over water (see Juste and Ibañez, 1994a,b) were not found in the archipelago.

However, we found that not all bat species in the mainland have an equal probability of succeeding to maintain viable populations on the islands. The species that succeeded in the Bijagós are generalists characterized by high abundance/prevalence. When the Bijagós were connected to the mainland their bat assemblages were certainly richer, and in the thousands of years since the islands were formed dispersers of many species must have arrived there from the mainland. How can we explain that so many of those species failed to establish viable populations, while this relatively small group of abundant/widespread species succeeded? The answer seems to lay in the fact that the latter are more resistant to fragmentation; their greater capacity to maintain populations in fragmented habitats may have several explanations, not mutually exclusive. Species that are abundant and widespread on the mainland are likely to depend on abundant resources; if these resources are also abundant on the island then this allows local populations to reach a large enough size to be viable in the long-term. In contrast, rare bat species are likely to specialize on scarce resources, which on small islands may only sustain small populations, not viable in the long-term. A second explanation for the greater success of common species on islands is the greater likelihood of the arrival of dispersing individuals. Species that are common in the coastal regions are more likely to send such dispersing individuals to the islands, and thus allow the recovery of island populations that are declining or extirpated.

Long-term consequences of fragmentation on bat assemblages

Marine land-bridge islands are fragments that resulted from natural processes, but the consequences of these processes are analogous to the long-term consequences of the ongoing fragmentation caused by humans. Our study in the Bijagós land-bridge archipelago clearly shows that a major reduction of species diversity is a likely long-term consequence of habitat fragmentation. Even in large islands, located fairly close to the mainland, the richness of bat assemblages are a fraction of that of the nearby coast. One of the studied islands, Orango, has a

surface of 261 km², and is separated by narrow channels from two islands that, combined, cover a similar surface. But even this area, which is greater than that of most protected areas in West Africa, was insufficient to prevent the loss of most of the bat species that presumably harbored before isolation.

Several short-term studies with a variety of vertebrate groups have found an overall richness decline in recently formed fragments and an extinction debt is predicted both for small and large islands (e.g. Cosson et al., 1999b; Jones et al., 2016). Our study confirms this prediction, showing that, in the long-term few bat species are capable of maintaining viable populations in fragmented systems. It is thus evident that the species richness declines reported in most studies are an underestimate of the real, long-term, losses due fragmentation. In fact, the degree of bat species impoverishment observed in the Bijagós is much greater than that reported in any short-term studies (see Jones et al., 2016).

An impoverishment of the species assemblages is not the only negative consequence of fragmentation. Our results in the Bijagós archipelago suggest that the species that survive in the long-term in fragmented systems are mainly abundant and widespread species; rarer species usually do not survive, even in relatively large fragments. This suggests that long-term fragmentation has a disproportionate impact on species of greater conservation concern.

A dramatic reduction in bat species richness due to long-term fragmentation, as that observed in his study, is also likely to have significant negative consequences in terms of ecosystem functioning on the fragmented landscape, such as those reported elsewhere (e.g. McConkey and Drake, 2006). In fact, the few species of bats that persist on the islands are unlikely to fulfill all the ecosystem roles performed by the rich species assemblages that live in similar habitats on the mainland.

The Bijagós are true islands, and thus surrounded by a high contrast matrix, so in terms of isolation they may represent a worst case scenario for fragmentation. Lower contrast matrices (e.g. degraded vegetation) may result in lower species' loss. However, our results show that the long-term consequences of fragmentation are likely to be substantially worse than those that have been reported from short-term examples (see Jones et al., 2016). Our study is focused on bats, which are highly mobile animals with a good capacity to reach habitat fragments across unsuitable habitat (Estrada et al., 1993; Meyer and Kalko, 2008b). The impact of long-term fragmentation on less mobile animal groups is likely to be greater than on bats, although mobility is not the only factor influencing those impacts (Bowne and Bowers, 2004; Gibson et al., 2013).

Habitat fragmentation is a threat to biodiversity all over the world (Lindenmayer and Fischer, 2006; Haddad et al., 2015) and Africa is no exception. The explosive growth of its human population and the consequent expansion of farmland are resulting in a dramatic fragmentation of natural areas, which is likely to persist in the long-term. To make the preservation of biodiversity compatible with the needs of livelihoods, it is thus necessary to minimize the consequences of fragmentation by promoting efficient and less land demanding agricultural practices, land uses with low contrast with natural habitats, and preserving connectivity elements in the landscapes. ☞

References

Alves P.H., Silva T.P., Figueiredo M.O., Ramalhal F.J., 2015. Laterites da Guiné-Bissau: morfologia e geodiversidade. In: Abreu M.M., Fangueiro D., Santos E.S. (Eds.) O Solo na Investigação Científica em Portugal. ISAPress, Lisboa. 5–8. [In Portuguese]

Arita H.T., 1993. Rarity in Neotropical Bats – Correlations with Phylogeny, Diet, and Body-Mass. *Ecol Appl.* 3(3): 506–517.

Barbaro L., Van Halder I., 2009. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography* 32(2): 321–333.

Bergmans W., 1988. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 1. General introduction; material and methods; results: the genus *Epomorphus* Bennett, 1836. *Beaufortia* 38(5): 75–146.

Bergmans W., 1989. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 2. The genera *Micropteropus* Matschie, 1899, *Epomops* Gray, 1870, *Hypsignathus* H. Allen, 1861, *Nanonycteris* Matschie, 1899, and *Plerotes* Andersen, 1910. *Beaufortia* 39(4): 89–153.

Bergmans W., 1997. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 5. The genera *Lissonycteris* Andersen, 1912, *Myonycteris* Matschie, 1899 and *Megaloglossus* Pagenstecher, 1885; general remarks and conclusions; annex: Key to all species. *Beaufortia* 47(2): 11–90.

BirdLife International, 2016a. Important Bird and Biodiversity Area factsheet: Cantanhez forests. Downloaded from <http://www.birdlife.org> on 05/07/2016.

BirdLife International, 2016b. Important Bird and Biodiversity Area factsheet: Rio Cacheu. Downloaded from <http://www.birdlife.org> on 05/07/2016.

Bouchard S., 1998. *Tadarida pumila*. *Mammalian Species*. 574: 1–6.

Bowne D.R., Bowers M.A., 2004. Interpatch movements in spatially structured populations: a literature review. *Landsc Ecol.* 19(1): 1–20.

Bunnefeld N., Phillimore A.B., 2012. Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. *Ecography*. 35(1): 15–22. doi:10.1111/j.1600-0587.2011.07078.x

Colwell R., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's guide and application. Downloaded from <http://viceroy.colorado.edu/estimates/> on 12/12/2016.

Cosson J.F., Pons J.M., Masson D., 1999a. Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *J Trop Ecol.* 15: 515–534.

Cosson J.F., Ringuet S., Claessens O., de Massary J.C., Dalecky A., Villiers J.F., Granjon L., Pons J.M., 1999b. Ecological changes in recent land-bridge islands in French Guiana, with emphasis on vertebrate communities. *Biol Conserv.* 91(2–3): 213–222.

Embaló D.S., Silva A.S., Barbosa C., 2008a. Plano de Gestão do Parque Nacional Marinho de João Vieira e Poilão. Instituto para a Biodiversidade e Áreas Protegidas. Bissau. Available at <http://www.ibapgbissau.org/index.php/pnmjvp> [In Portuguese]

Embaló D.S., Silva A.S., Silva A., Pereira A.F., 2008b. Plano de gestão do Parque Nacional de Orango (2008–2018). Instituto para a Biodiversidade e Áreas Protegidas. Bissau. Available at <http://www.ibapgbissau.org/index.php/pno> [In Portuguese]

Estrada A., Coates-Estrada R., Merritt J.D., 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography* 16(4): 309–318.

Franzén M., Schweiger O., Betzholtz P.-E., 2012. Species-Area relationships are controlled by species traits. *PLoS ONE* 7(5): e37359 doi:10.1371/journal.pone.0037359

Frick W.F., Hayes J.P., Heady P.A. III, 2008. Island biogeography of bats in Baja California, Mexico: patterns of bat species richness in a near-shore archipelago. *J Biogeogr.* 35(2): 353–364.

Gibson L., Lynam A.J., Bradshaw C.J., He F., Bickford D.P., Woodruff D.S., Bumrungsri S., Laurance W.F., 2013. Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science* 341(6153): 1508–1510.

Gotelli N.J., 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81(9): 2606–2621. doi:10.2307/177478

Gotelli N.J., Colwell R.K., 2011. Estimating species richness. In: Magurran A.E., McGill B.J. (Eds.) *Biological diversity: frontiers in measurement and assessment*, vol 12. Oxford University Press, Oxford. 39–54.

Gotelli N.J., Ellison A.M., 2013. *EcoSimR: Null Models for Ecology*. Retrieved from <https://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html> on 12/12/2016.

Gotelli N.J., Graves G.R., 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, DC.

Gotelli N.J., Ulrich W., 2012. Statistical challenges in null model analysis. *Oikos* 121(2): 171–180. doi:10.1111/j.1600-0706.2011.20301.x

Haddad N.M., Brudvig L.A., Clobert J., Davies K.F., Gonzalez A., Holt R.D., Lovejoy T.E., Sexton J.O., Austin M.P., Collins C.D., Cook W.M., Damschen E.I., Ewers R.M., Foster B.L., Jenkins C.N., King A.J., Laurance W.F., Levey D.J., Margules C.R., Melbourne B.A., Nicholls A.O., Orrock J.L., Song D.-X., Townshend J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1(2): e1500052 doi:10.1126/sciadv.1500052

Hammer Ø., Harper D.A.T., Ryan P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Paleontol Electron* 4(1): 9.

Happold M., Happold D.C.D., (Eds.) 2013. *Mammals of Africa, Vol. IV: Hedgehogs, Shrews and Bats*. Bloomsbury Publishing, London.

Hayman R., Hill J.E., 1971. Order Chiroptera. In: Setzer J.M.H.W. (Ed.) *The Mammals of Africa. An Identification Manual Part 1*, vol 2. Smithsonian Institution Press, Washington, D.C. 1–73.

Heaney L.R., 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Glob Ecol Biogeogr.* 9(1): 59–74. doi:10.1046/j.1365-2699.2000.00163.x

Henle K., Davies K.F., Kleyer M., Margules C., Settle J., 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* 13(1): 207–251.

Henry M., Cosson J.-F., Pons J.-M., 2007. Abundance may be a misleading indicator of fragmentation sensitivity: The case of fig-eating bats. *Biol Conserv.* 139(3–4): 462–467. doi:10.1016/j.biocon.2007.06.024

Hill J.E., 1963. A revision of the genus *Hipposideros*. *British Museum (Natural History)*.

Jacobs D.S., Barclay R.M., 2009. Niche differentiation in two sympatric sibling bat species, *Scotophilus dinganii* and *Scotophilus mhlangani*. *J Mammal.* 90(4): 879–887.

Jones L.L., Bunnefeld N., Jump A.S., Peres C.A., Dent D.H., 2016. Extinction debt on reservoir land-bridge islands. *Biol Conserv.* 199: 75–83. doi:10.1016/j.biocon.2016.04.036

Juste J.B., Ibáñez C., 1994a. Bats of the Gulf of Guinea islands: faunal composition and origins. *Biodivers. Conserv.* 3(9): 837–850.

Juste J.B., Ibáñez C., 1994b. Contribution to the knowledge of the bat fauna of Bioko island, Equatorial Guinea (Central Africa). *Z. Säugetierkunde* 59: 274–281.

Kunz T., Hodgkinson R., Weise C., 2009. Methods of capturing and handling bats. In: Kunz T., Parsons S. (Eds.) *Ecological and behavioral methods for the study of bats*. The John Hopkins University Press, Baltimore. 3–35.

Laurance W.F., Sayer J., Cassman K.G., 2014. Agricultural expansion and its impacts on tropical nature. *Trends Ecol Evol.* 29(2): 107–116. doi:10.1016/j.tree.2013.12.001

Lindenmayer D.B., Fischer J., 2006. *Habitat fragmentation and landscape change: an ecological and conservation synthesis*. Island Press, Washington, DC.

Lomolino M., Weiser M., 2001. Towards a more general species-area relationship: diversity on all islands, great and small. *J Biogeogr.* 28(4): 431–445.

Marques J.T., Pereira M.J.R., Marques T.A., Santos C.D., Santana J., Beja P., Palmeirim J.M., 2013. Optimizing sampling design to deal with mist-net avoidance in Amazonian birds and bats. *PLoS ONE*. 8(9):e74505. doi:10.1371/journal.pone.0074505

McConkey K.R., Drake D.R., 2006. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology* 87(2): 271–276.

Meyer C.F.J., Kalko E.K.V., 2008a. Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns. *Divers Distrib.* 14(4): 644–654.

- Meyer C.F.J., Kalko E.K.V., 2008b. Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. *J Biogeogr.* 35(9): 1711–1726. doi:10.1111/j.1365-2699.2008.01916.x
- Meyer C.F.J., Kalko E.K.V., Kerth G., 2009. Small-Scale Fragmentation Effects on Local Genetic Diversity in Two Phyllostomid Bats with Different Dispersal Abilities in Panama. *Biotropica* 41(1): 95–102.
- Meyer C.F., Struebig M.J., Willig M.R., 2016. Responses of Tropical Bats to Habitat Fragmentation, Logging, and Deforestation. In: Voigt C.C., Kingston T., (Eds.) *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham. 63–103.
- Monadjem A., Taylor P.J., Cotterill W., Schoeman M., 2010. *Bats of southern and central Africa: a biogeographic and taxonomic synthesis*. Wits University Press, Johannesburg.
- Newmark W.D., 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* 325(6103): 430–432.
- Nichols J.D., Boulinier T., Hines J.E., Pollock K.H., Sauer J.R., 1998. Inference Methods for Spatial Variation in Species Richness and Community Composition When Not All Species Are Detected. *Conserv Biol.* 12(6): 1390–1398.
- Norberg U.M., Rayner J.M.V., 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences.* 316(1179): 335–427.
- Öckinger E., Schweiger O., Crist T.O., Debinski D.M., Krauss J., Kuussaari M., Petersen J.D., Pöyry J., Settele J., Summerville K.S., 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecol Lett.* 13(8): 969–979.
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing. Available at www.R-project.org
- Rainho A., Franco C., 2001. *Morcegos da Guiné-Bissau. Um contributo para o seu conhecimento*. Coleção Técnica. ICN, Lisboa. [In Portuguese]
- Rainho A., Sousa M., Monteiro H., da Silva C.S., Palmeirim J.M., 2007. *Morcegos e aves das florestas de Cantanhez e Cacine*. IBAP, ICNB & CBA. Bissau. [In Portuguese]
- Robbins C., De Vree F., Van Cakenberghe V., 1985. A systematic revision of the African bat genus *Scotophilus* (Vespertilionidae). *Zoologische Wetenschappen* 246: 53–84.
- Rocha R., López-Baucells A., Farneda F.Z., Groenenberg M., Bobrowiec P.E.D., Cabeza M., Palmeirim J.M., Meyer C.F.J., 2017. Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects. *Landsc Ecol.* 32: 31–45.
- Rodríguez-Durán A., 2010. Bat assemblages in the West Indies: the role of caves. In: *Island bats: evolution, ecology, and conservation*. University of Chicago Press, Chicago, IL. 265–280.
- Rosevear D.R., 1965. *The Bats of West Africa*. Trustees of the British Museum, London.
- Russo D., Di Febbraro M., Rebelo H., Mucedda M., Cistrone L., Agnelli P., De Pasquale P.P., Martinoli A., Scaravelli D., Spilinga C., Bosso L., 2014. What Story Does Geographic Separation of Insular Bats Tell? A Case Study on Sardinian Rhinolophids. *PLOS One.* 9(10): e110894. doi:10.1371/journal.pone.0110894
- Sala O.E., Stuart Chapin F. III, Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Hueneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M.N., Poff N.L., Sykes M.T., Walker B.H., Walker M., Wall D.H., 2000. Global Biodiversity Scenarios for the Year 2100. *Science* 287(5459): 1770–1774.
- Saraçlı S., Doğan N., Doğan İ., 2013. Comparison of hierarchical cluster analysis methods by cophenetic correlation. *Journal of Inequalities and Applications* 2013(1): 1–8.
- Simmons N.B., 2005. Order Chiroptera. In: Wilson D.E., Reeder D.M. (Eds.) *Mammal species of the world: a taxonomic and geographic reference*, vol 1. The Johns Hopkins University Press, Baltimore. 31–529.
- Stone L., Roberts A., 1990. The checkerboard score and species distributions. *Oecologia* 85(1): 74–79.
- Triantis K.A., Economo E.P., Guilhaumon F., Ricklefs R.E., 2015. Diversity regulation at macro-scales: species richness on oceanic archipelagos. *Glob Ecol Biogeogr.* 24(5): 594–605.
- Ulrich W., 2008. Pairs — a FORTRAN program for studying pair-wise species associations in ecological matrices. Available at: www.keib.umk.pl/pairs
- Ulrich W., Gotelli N.J., 2013. Pattern detection in null model analysis. *Oikos* 122(1): 2–18.
- Van Cakenberghe V., De Vree F., 1985. Systematics of African *Nycteris* (Mammalia: Chiroptera). *Proceedings of the International Symposium on African Vertebrates, Bonn.* 53–90.
- Whittaker R.J., Fernández-Palacios J.M., 2007. *Island biogeography: ecology, evolution, and conservation*. Oxford University Press.
- Willig M.R., Presley S.J., Bloch C.P., Genoways H.H., 2010. Macroecology of Caribbean bats: effects of area, elevation, latitude, and hurricane-induced disturbance. In: *Island bats: evolution, ecology, and conservation*. University of Chicago Press, Chicago, IL. 216–264.
- Yu M., Hu G., Feeley K.J., Wu J., Ding P., 2012. Richness and composition of plants and birds on land-bridge islands: effects of island attributes and differential responses of species groups. *J Biogeogr.* 39(6): 1124–1133.

Associate Editor: D. Russo

Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplemental S1 List of surveyed sites, with habitat and capture effort per site.