

Null model analyses of small mammal community structure in tropical islands

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Abstract: Peer-reviewed papers on the community structure of small mammals (Rodentia and Soricomorpha) from the tropical islands across the world were reviewed. In order to detect non-random patterns in the various assemblages under study, the original datasets were re-analyzed using null models (two independent randomization algorithms for niche overlap) and Monte Carlo simulations. Non-random habitat niche partitioning was rarely observed in rodents, whereas it was the rule in soricomorphs. Aggregated use of habitat resources was occasionally detected in rodents. Thus, in agreement with expectations, our review revealed clear evidence for interspecific competition along the habitat niche axis in tropical island soricomorphs but not in rodents.

Resumen: Se revisaron artículos arbitrados sobre la estructura de las comunidades de mamíferos pequeños (Rodentia y Soricomorpha) de islas tropicales en todo el mundo. Para detectar patrones no aleatorios en los diferentes ensambles estudiados, los conjuntos de datos originales fueron reanalizados usando modelos nulos (dos algoritmos independientes de aleatorización para el solapamiento de nicho) y simulaciones de Monte Carlo. Entre los roedores se observó muy raramente una repartición no aleatoria del nicho de hábitat, mientras que ésta fue la norma en los soricomorfos. Ocasionalmente se detectó para los roedores el uso agregado de los recursos del hábitat. Por lo tanto, y en coincidencia con las expectativas, la revisión reveló una evidencia clara de la competencia interespecífica a lo largo del eje del nicho de hábitat en los soricomorfos de islas tropicales pero no en los roedores.

Resumo: Analisaram-se artigos científicos, revistos por pares, sobre a estrutura da comunidade de pequenos mamíferos (Rodentia e Soricomorpha) nas ilhas tropicais, em todo o mundo. Afim de detectar padrões não-aleatórios nas várias associações em estudo, os conjuntos de dados originais foram reanalisadas usando modelos nulos (dois algoritmos de casualização independentes para sobreposição de nicho) e simulações de Monte Carlo. A partição não-aleatória do nicho de habitat foi raramente observada em roedores, enquanto que era a regra nas toupeiras. O uso agregado dos recursos do habitat foi ocasionalmente detectado nos roedores. Assim, de acordo com as expectativas, a nossa análise revelou evidências claras para a competição interespecífica ao longo do eixo do nicho habitat em toupeiras nas ilhas tropicais, mas não em roedores.

Key words: Interspecific competition, Monte Carlo methods, null models, Rodentia, Soricomorpha, tropical islands.

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Introduction

There has been a considerable interest on the studies of community patterns and niche partitioning in recent years (Chesson 2000; Chase & Leibold 2003; Diamond & Case 1986; Pianka 1986; Tokeshi 1990). Several authors have used small mammals to analyse the interspecific interaction in the temperate region (Bowman *et al.* 2001; Price 1984). It is well established that interspecific competition should be stronger at tropical than at non-tropical latitudes because of the high number of co-occurring competitors (Schall & Pianka 1978). Hence, it is pertinent to study the occurrence and relative strength of inter-specific competition of small mammal communities in tropical regions (Amori & Luiselli 2011). Moreover, studies on the interspecific competition in tropical islands can be particularly intriguing, given that these island systems may have greater species diversity and many endemics and are often characterized by ephemeral resource availability, thus strengthening competitive relationships among sympatric organisms (Crowell & Pimm 1976; Connor & Simberloff 1983).

Though, a wide range of taxonomic groups have been studied in the tropical islands to address the ecological and evolutionary questions, very few reviews are published on niche partitioning. Likewise, there has been no attempt at analyzing the patterns of coexistence among small mammals in these islands. In this paper we focus on island rodents and soricomorphs, chosen especially because the dynamics of insular faunas are of high interest from an evolutionary and ecological standpoint. Animal populations on different islands, especially oceanic islands, are geographically and often genetically isolated, forming closed biological systems with reduced impacts from immigration. Thus, comparisons with patterns observed on small mammal communities from mainland scenarios can be particularly interesting. More specifically, we analyze various studies published in the peer-reviewed literature with the main aims of determining (i) whether the communities are non-randomly structured along the habitat niche axis, i.e., whether a niche partitioning pattern can be individuated along habitats, and (ii) whether there is any difference in the community patterns between rodents and soricomorphs. Our hypothesis is that, since soricomorphs are carnivorous whereas rodents are omnivorous, food resource should be likely more

limited for the species assemblages of shrews than for those of rodents (Pianka 1986). As a consequence of food limitation, sympatric organisms tend to partition habitat resource to minimize competition (Pianka 1986), hence it would be more likely to uncover habitat niche partitioning within island shrew communities than within rodent communities.

To explore these hypotheses, we used a suite of traditional and null model analyses. Null model analyses are particularly well suited for this type of meta-analyses because they allow simultaneous testing of community-based hypotheses also in heterogeneous datasets (Gotelli 2001; Gotelli & Graves 1996; Luiselli 2006, 2008a), as is typically the case of community ecology studies in tropical regions which are often based on divergent field and analytical methodologies.

Materials and methods

Data source and criteria for selection of published literature

For this study, we considered all the tropical islands occurring throughout the world. We obtained data from the literature by searching across ISI Web of Knowledge and Google Scholar (key words: small mammals, rodents, soricomorphs, insectivores, country name, islands, archipelagos, islets, Africa, Asia, South America, Australia). We selected for our re-analysis only articles with the following characteristics: (i) they present raw datasets with numbers of individuals captured in various habitat types being reported; (ii) they are based on specimens captured by standard methodology (i.e., only carefully explained trapping and not, for instance, opportunistic sightings or general surveys); and (iii) they report clear and unequivocal description of habitat types (for the list of literature sources see Appendix Table 1). Some studies, albeit interesting, did not provide this type of data (for instance, they presented figures without raw data), and hence were not considered for our study. Nonetheless, trap type (e.g., live traps and pitfalls), trapping design (transect vs. grid), bait heterogeneity, survey effort (expressed as trap/nights), traps on ground-above ground (trunks, canopy), were heterogeneously used across studies. However, details of some of these aspects were not explained in some of the reviewed studies, and hence were not taken into account in this review. Main habitat

categories considered in our re-analyses followed exactly the category subdivision utilized by the original authors. These categories were in some cases relative to different habitats at a same altitude, or different habitats along altitudinal gradients. Overall, we re-analyzed datasets for 6 communities of soricomorphs (from 3 islands: Madagascar, Luzon, and Taiwan) and for 12 communities of rodents (in 4 islands: Madagascar, Borneo, Luzon, and Taiwan).

Terminology

Raw data (= number of individuals trapped in each habitat type) given in the original literature sources were used to recalculate habitat niche breadths and niche overlaps. We defined and calculated (i) niche breadth of each species as in Simpson (1949); (ii) niche overlap between pairs of species as in Pianka (1986), with values yielding from 0.0 (no overlap between pair of species) to 1.0 (100 % overlap). We defined as (1) 'non-random niche partitioning' the structured condition of a given community in which interspecific competition was the main shaping force (Gotelli & Graves 1996, and see below); (2) 'aggregated use of a given resource' a non-random concentration of different species into a particular habitat type resource (for instance, within forests); (3) 'habitat (or resource) use' the frequency of utilization of the various habitat types by each species in a given community. Sampling sites were distinct localities as reported in the original sources. In order to be considered as independent, two sampling sites should have been located at least 10 km linear distance from each another.

Statistical analyses

We used EcoSim software (version 7.71; Acquired Intelligence Corp., Kesey-Bear; <http://garyentsminger.com/ecosim/index.htm>) to calculate overlap indices and generate Monte Carlo simulations. All other analyses were conducted using SPSS (SPSS 11.0 for Windows) and Statistica (Statistica 6.4 for Windows); all tests were two-tailed with alpha set at 0.05.

Each rodent community at each sampling site was considered independent and distinct from each sympatric soricomorph community. To evaluate whether each small mammal community was randomly structured, we contrasted the data matrix as provided in the original source with

random "pseudo-communities" generated by Monte Carlo simulations (Gotelli & Graves 1996). We parameterized records of individual data as present (in terms of habitat categories or altitudinal sectors available) or absent. Because too many zeroes in the matrices might distort error levels and thus too often reject structure, we used EcoSim to fix zeroes (Manly 1991).

We calculated Pianka's (1986) overlap formula for all communities based on the raw data provided in the original literature sources. In Pianka's formula, values close to 0 (no overlap) indicate resource partitioning and hence competitive structure, whereas values close to 1 (total overlap) indicate aggregated use of the available resources and hence no competition (Pianka 1986). In the original data matrices, each row represented a different species in the assemblage being analyzed, and each column represented a different habitat type category. We then randomized the original species utilization matrices from which Pianka's overlap was calculated by shuffling the original values among habitat resource states. In this way, we generated a number of random Monte-Carlo simulations (= null matrices) of the original observed matrix. Each of these null matrices was built using two randomization algorithms (RA2 and RA3) after Lawlor (1980). These algorithms are particularly robust for niche overlap studies (Gotelli & Graves 1996). RA2 replaces every cell in the matrix with a randomly chosen, uniform number between 0 and 1, retaining the 0 structure of the matrix. It is a useful algorithm when it is believed that, in the absence of species interactions, certain resource states are unavailable for each species, but there are no other constraints on resource utilization (Gotelli & Graves 1996). RA3 retains the niche breadth of each species, but randomizes which particular habitat resource states are utilized. It corresponds to a simple reshuffling of each row of the matrix. RA3 is to be used when the experimenters want to retain the amount of specialization for each species, but allow it to potentially use other resource states (Gotelli & Graves 1996). For each pair of species, 3×10^4 random Monte Carlo permutations were generated. This amount ensures that algorithm biases are avoided (Lehsten & Harmand 2006; Luiselli 2008a). Niche overlap values were calculated for each of these randomly generated matrices, and species-pair and community-summary statistics were computed

Table 1. Numbers of species/families of small mammals present in the various islands reviewed in this paper. The total number of species/families occurring in each island is also given. % = percent of species occurring in a given island that were detected in the original studies reviewed in this meta-analysis. References indicate the literature sources from which the total number of species/families occurring in each island were calculated.

Island	Rodentia			Soricomorpha			References
	Present in meta-analysis	Island's total species	%	Present in meta-analysis	Island's total species	%	
SPECIES LEVEL							
Madagascar	14	30	46.7	2	2	100	Garbutt (1999)
Luzon (Philippines)	22	30	73.3	2	2	100	Heaney <i>et al.</i> (1998)
Taiwan	12	19	63.2	4	9	44.4	Smith & Xie (2008)
Borneo	25	61	41	2	8	25	Wilson & Reeder (2005)
MEAN			56.1±14.9			67.4±38.5	
FAMILY LEVEL							
Madagascar	2	2	100	1	1	100	Garbutt (1999)
Luzon (Philippines)	1	3	33.3	1	1	100	Heaney <i>et al.</i> (1998)
Taiwan	3	3	100	1	2	50	Smith & Xie (2008)
Borneo	3	3	100	1	1	100	Wilson & Reeder (2005)
MEAN			83.3±33.3			87.5±25	

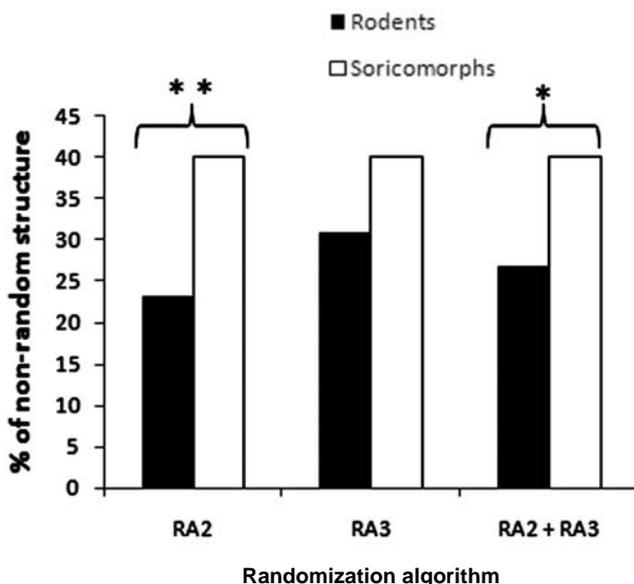


Fig. 1. Percent frequency of cases with non-random structure detected by null model analyses in the various studies reviewed in this paper, in relation to randomization algorithm used. Symbols: * = $P < 0.05$; ** = $P < 0.01$.

(Friggens & Brown 2005). Hence, we obtained a mean overlap value (with associated variance estimates) resulting from simulated null matrices. Overlap values from the observed dataset were then compared to the simulated mean overlap values. Non random structure was assumed when $P_{(\text{observed} \leq \text{expected})} \leq 0.05$ (Gotelli & Graves 1996). In all cases, equiprobable habitat resource use was assumed a priori in the analyses, unless a study explicitly reported resource availability data. Based on the $P_{(\text{observed} \leq \text{expected})}$ and $P_{(\text{observed} \geq \text{expected})}$ values with RA2 and/or RA3, we distinguished three cases: (i) when $P_{(\text{observed} \leq \text{expected})} < 0.05$, then the structure of the assemblage is non-random and competitively assembled; (ii) when both $P_{(\text{observed} \leq \text{expected})}$ and $P_{(\text{observed} \geq \text{expected})}$ are > 0.05 , then the structure is random; (iii) when $P_{(\text{observed} \geq \text{expected})} < 0.05$, then there is aggregated use of a particular habitat resource (Gotelli & Graves 1996; Luiselli 2008b).

Homoscedasticity and normality were verified by Levene's test and Kolmogorov-Smirnov test prior to applying parametric statistics. Differences in mean species richness per site between soricomorphs and rodents were assessed by

Student t-test. Differences among countries in mean species richness per site were tested by one-way Analysis of Variance (ANOVA). Differences in the frequency of study cases showing one of the three community patterns (random, non-random competitive, and aggregated use of resources) between soricomorphs and rodents were assessed by observed-versus-expected χ^2 test.

Results

The mean number of co-occurring species was 7.58 ± 4.4 (range 3 - 18) for rodents and 2.0 ± 0.9 species (range 1 - 4) for soricomorphs. Mean species richness per site was significantly higher in rodent than in soricomorph communities ($t = 3.76$, $df = 19$, $P = 0.0002$). The percent frequency of species occurring in a given island which are really present in the original sources (Table 1) was significantly higher in soricomorphs than in rodents (χ^2 test with $df = 1$, $P < 0.0001$). Over 80 % of the small mammal families occurring in the given islands was present in the original literature sources (Table 1), with no differences between soricomorphs and rodents (χ^2 test with $df = 1$, $P > 0.445$).

Non-random community structure was uncovered more frequently in soricomorphs than in rodents, and the difference was statistically significant at χ^2 test when RA2 was used as a randomization algorithm (Fig. 1). Among cases of non-random community structure, competitive structure was found in 75 % of cases ($n = 8$, see Table 2) and aggregated use of resource in 25 % of cases. It is noteworthy that the two cases of aggregated use of resources detected by our meta-analysis concerned rodents from Borneo and Luzon islands (Table 2), whereas in soricomorphs all cases of non-random community structures were clearly due to competitively-induced resource partitioning.

Discussion

Our study revealed some interesting patterns for community ecology of tropical island rodents, despite the limited data set available in the literature. Firstly, all the studies revealed that the island communities of rodents were richer in terms of number of species than the communities of island soricomorphs. This result is not unexpected, given that the species richness is overall higher in rodents than in soricomorphs, and indeed this evidence is consistent with patterns observed also

in mainland tropical communities of these animals (Amori & Luiselli 2011).

Non-random niche partitioning due to interspecific competition (i.e., $P_{(\text{observed} \leq \text{expected})} \leq 0.05$) was rarely uncovered across the studied assemblages of rodents, whereas it was the rule across island communities of soricomorphs. We suggest that this pattern derived from a relatively unlimited food resource available to rodents in tropical island habitats, whereas the same does not happen with resource availability for carnivorous soricomorphs. Since, in this study we examined only niche partitioning for habitat resources, non-random partitioning among sympatric species along other niche axes cannot be ruled out. The knowledge on interspecific competition of rodents in other regions of the world is still fragmentary, and the main conclusions are generally based on indirect evidence. For instance, since Grant's (1972) review, contiguous, allopatric distributions of rodent species have been interpreted as being the result of interspecific competition (Brown 1971), with evidence that two sympatric species may sometimes exhibit an inverse numerical relationship and an inverse spatial relationship (Norrdhal & Korpimaki 1993). On the contrary, in high latitude regions characterized by a lower number of sympatric species than in the tropics, rodents usually partition the habitat niche axis (Henttonen *et al.* 1977; Norrdhal & Korpimaki 1993). However, in tropical Australia, interspecific competition among sympatric rodents (and consequently niche structuring along habitat axis) was low inside a contiguous forest whereas it was strong within small isolated forest fragments (Lawrance 1994). Based on the present analysis, it is evident that competitive-mediated habitat partitioning does not usually occur among tropical island rodents. Data also suggest that on a couple of islands there is a non-random aggregated use of the forest habitat by sympatric rodents and that food availability within the forest habitat may be sufficiently high to allow the coexistence of a great number of species in this habitat type. It is possible that the aggregated use of the forest resource by small mammal species may be apparent, but that the various species indeed partition space at a lower scale, for instance selecting different microhabitats and soil types (Pianka 1986).

There also may be clumping of species in particular habitat and/or resource types despite strong competition because abundances of each species within these clumped habitat classes is low,

Table 2. Summary of the null model re-analyses on the available datasets for rodents and soricomorphs of tropical islands. Symbols: Observed index = mean of the Pianka's (1986) overlap indices calculated between pairs of species; mean simul = mean of the simulated Pianka's (1986) overlap formulas calculated after 30,000 Monte Carlo permutations of the original datasets; RA2 = randomization algorithm 2 (Lawlor 1980); RA3 = randomization algorithm 3 (Lawlor 1980).

Island	Observed index	RA3 mean simul	RA3 $P(\text{obs}<\text{exp})$	RA3 $P(\text{obs}>\text{exp})$	RA2 mean simul	RA2 $P(\text{obs}<\text{exp})$	RA2 $P(\text{obs}>\text{exp})$	Note
<i>Soricomorpha</i>								
Madagascar	0.507	0.317 (0.11)	0.784	0.216	0.507 (0.067)	0.469	0.531	no structure
Luzon (Philippines)	0.000	0.355 (0.09)	0.0088	0.999	0.351 (0.07)	0.0001	0.999	competitive structure
Taiwan	0.200	0.277 (0.0096)	0.223	0.777	0.189 (0.006)	0.627	0.373	no structure
Taiwan	0.360	0.500 (0.045)	0.311	0.689	0.414 (0.037)	0.405	0.595	no structure
Taiwan	0.189	0.373 (0.05)	0.225	0.775	0.635 (0.028)	0.002	0.998	competitive structure
Taiwan	0.099	0.373 (0.045)	0.024	0.976	0.429 (0.026)	0.017	0.983	competitive structure
<i>Rodentia</i>								
Madagascar	0.736	0.760 (0.001)	0.384	0.616	0.781 (0.004)	0.248	0.752	no structure
Luzon (Philippines)	0.348	0.386 (0.0008)	0.032	0.968	0.384 (0.0005)	0.062	0.938	competitive structure
Luzon (Philippines)	0.338	0.381 (0.0009)	0.016	0.984	0.367 (0.0005)	0.106	0.894	competitive structure
Luzon (Philippines)	0.469	0.329 (0.002)	0.992	0.008	0.442 (0.001)	0.786	0.214	aggregated use of resource
Taiwan	0.792	0.812 (0.0022)	0.401	0.599	0.842 (0.06)	0.262	0.738	no structure
Taiwan	0.309	0.338 (0.007)	0.421	0.579	0.371 (0.0033)	0.158	0.842	no structure
Taiwan	0.473	0.441 (0.004)	0.739	0.261	0.499 (0.002)	0.295	0.705	no structure
Taiwan	0.368	0.324 (0.0079)	0.745	0.255	0.464 (0.0039)	0.04	0.96	competitive structure
Taiwan	0.572	0.457 (0.008)	0.892	0.108	0.621 (0.008)	0.282	0.718	no structure
Borneo	0.637	0.650 (0.001)	0.497	0.503	0.661 (0.005)	0.377	0.623	no structure
Borneo	0.689	0.424 (0.0007)	0.999	0.001	0.563 (0.002)	0.999	0.001	aggregated use of resource
Borneo	0.463	0.567 (0.014)	0.293	0.707	0.522 (0.019)	0.360	0.640	no structure

relative to more dispersed habitat classes. This pattern was demonstrated for clumped distributions around particular body sizes (Holling 1992), and could not be totally ruled out in at least some of our study cases. Unfortunately, data on species' abundances are not available for tropical island forest rodent communities, and hence we could not test this possibility for the patterns observed.

Concerning soricomorphs, our study revealed that their communities are usually assembled by competition in tropical island ecosystems. This evidence does not mirror data for mainland communities of soricomorphs from Western Africa (Amori & Luiselli 2011) which are rarely organized through interspecific competition mechanisms. Hence, this study confirms the hypothesis that, particularly in island ecosystems, food resource should have been more limited for predators (i.e. soricomorphs in our study) than for herbivorous/omnivorous consumers (rodents), with non-random habitat niche partitioning occurring in the soricomorphs in order to minimize interspecific competition (Pianka 1986).

It is also important to discuss our results taking into consideration that cryptic species are the norm in tropical small mammals (Castiglia *et al.* 2006; May 1992). Hence, reliance on morphology alone can underestimate species richness. The conclusion on the lack of non-random community structure could be, at least partly, an artifact of deficient taxonomy. Thus, we strongly urge to combine ecological with genetic data when analyzing tropical island small mammal community structures in the future decades (see also Amori & Luiselli 2011 for a similar recommendation).

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(Received on 28.04.2011 and accepted after revisions, on 05.11.2011)

Appendix Table 1. List of the original literature sources from which data were re-analysed.

Island	References
Madagascar	<p>Goodman, S. M. & D. Rakotondravony. 2000. The effects of forest fragmentation and isolation on insectivorous small mammals (Lipotyphla) on the Central High Plateau of Madagascar. <i>Journal of Zoology (London)</i> 250: 193-200.</p> <p>Goodman, S. M., D. Rakotondravony, G. Schatz & L. Wilmé. 1996. Species richness of forest-dwelling birds, rodents and insectivores in a planted forest of native trees: a test case from the Ankaratra, Madagascar. <i>Ecotropica</i> 2: 109-120.</p> <p>Lehtonen, J. T., O. Mustonen, H. Ramiarinjanahary, J. Niemelä & H. Rita. 2001. Habitat use by endemic and introduced rodents along a gradient of forest disturbance in Madagascar. <i>Biodiversity and Conservation</i> 10: 1185-1202.</p>
Luzon (Philippines)	<p>Balete, D. S., L. R. Heaney, M. J. Veluz & E. A. Rickart. 2009. Diversity patterns of small mammals in the Zambales Mts., Luzon, Philippines. <i>Mammalian Biology</i> 74: 456-466.</p> <p>Rickart, E. A., L. R. Heaney, D. S. Balete & B. R. Tabaranza Jr. 2011. Small mammal diversity along an elevational gradient in northern Luzon, Philippines. <i>Mammalian Biology</i> 76: 12-21.</p>
Taiwan	<p>Ku, T. Y. & C. C. Lin. 1980. Abundance and distribution of field rodents in Taiwan. <i>Plant Protection Bulletin</i> 22: 397-420.</p> <p>Yu, H. T. 1994. Distribution and abundance of small mammals along a subtropical elevational gradient in central Taiwan. <i>Journal of Zoology (London)</i> 234: 577-600.</p>
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