ACTA BIOLÓGICA COLOMBIANA

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Facultad de Ciencias Departamento de Biología Sede Bogotá



NOTA BREVE / SHORT NOTE

FCOLOGÍA

TEST OF THE ISLAND BIOGEOGRAPHY THEORY ON **BOULDERS IN A SEAGRASS BED**

Test de la teoría de biogeografía de islas con piedras en una pradera de pastos marinos

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Received: 10th September 2019, Returned for revision: 27th May 2019, Accepted: 17th June 2020. Associate Editor: Valeria Pizarro.

Citation/Citar este artículo como: Rincón AMP, Gómez V, García CB. Test of the island biogeography theory on boulders in a seagrass bed. Acta Biol Colomb. 2021;26(1):131-134. Doi: http://dx.doi.org/10.15446/abc.v26n1.82188

ABSTRACT

We used shore boulders that had been previously colonized, and were scattered in a seagrass bed as models for islands. We tested two predictions of Island Biogeography theory: (1) small boulders harbored fewer species than large boulders, and (2) small boulders had higher rates of extinction than large boulders, as reflected in higher faunal replacement variability. We detected a definite relation between species richness and boulder size although not for all statistical models. We did not confirm higher compositional variability in small boulders.

Keywords: colonization, extinction, habitat size, island, species richness.

RESUMEN

Utilizando piedras litorales dispersas colonizadas en una pradera de pastos marinos se probaron dos predicciones de la teoría de biogeografía de islas, donde (1) las piedras pequeñas tendrán menos especies que las grandes, y (2) las piedras pequeñas tendrán tasas mayores de extinción que las grandes reflejado en una mayor variabilidad en el reemplazamiento de especies. Se encontró una relación bien definida entre el tamaño de las rocas y el número de especies pero no para todos los modelos estadísticos. No se confirmó una mayor variabilidad composicional en las piedras pequeñas que en las grandes.

Palabras clave: colonización, extinción, islas, riqueza de especies, tamaño de hábitat.



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The Theory of Island Biogeography postulates that (1) the probability that a species that reaches an island is inversely proportional to the distance to the source; (2) the probability that a species reaches an island is directly proportional to the size of the island (Arrehenius, 1921; Patiño *et al.*, 2017); and (3) the probability of extinction of a species on an island is a function of the island size because small islands would harbor small populations that are prone to local extinction versus larger islands that would harbor large populations and hence be less prone to local extinction. A corollary of the last postulate is that there is a dynamic process of colonization and extinction on islands regulated by the first two postulates and these islands have a corresponding equilibrium point, i.e., an equilibrium (balanced) number of species (MacArthur and Wilson, 1967).

In this research we tested predictions of the island biogeography theory of McArthur and Wilson in a marine setting using as a model colonized shore boulders in a range of sizes acting as islands. We predicted that (1) large boulders have more species than small boulders, and (2) extinction rates on small boulders is higher than on large boulders. Since boulders are basically exposed to the same environment gradients and are part of the same seascape, we assumed that the source of colonists is the same for all of them, thus distance from a source is not a factor in boulder species richness.

The study site was Isla Arena in Colombia (10°8'42" N, 75°43'40" W, Islas del Rosario archipelago). Isla Arena is surrounded by a well-developed seagrass bed, predominantly consisting of *Thalassia testudinum* (K.D. Koenig 1805). Scattered among the shoots of *T. testudinum* boulders of sedimentary and coralline origin are common. The boulders are colonized by a number of mobile and sessile species on the underside. On May 1, 2019, the Isla Arena seagrass bed

was visited and 16 boulders were chosen along four transects parallel to the beach, at depths of about 0.3 m - 2 m and their species richness were determined. One large boulder was excluded from the analysis because, according to field notes, it harbored only one species (*Molpadida* sp, a holothurian), which is probably a mistake. Taxonomic identifications were carried out *in situ* with the aid of visual keys to genus level. Because no genus exhibited more than one species, we considered the count of genera equivalent to the count of species. We measured the width and length of the underside of the boulders. The boulder underside areas ranged from 196 cm² to 2520 cm² with a mean of 654 cm² (± 585 cm², s.d.).

To test the hypothesis that large boulders have more species than small boulders, a number of statistical models were fitted to the data with species richness as the dependent variable and area of boulder underside as the independent variable (Table 1). This analysis was performed with the software Rwizard (Guisande *et al.*, 2014).

The hypothesis that extinction rate is higher in small boulders (n= 8, mean size 324 cm² ± 60 cm², s.d.) than in large boulders (n=7, mean size 1031 cm² ± 696 cm², sd.) implies that the replacement component of beta diversity (Baselga, 2010; 2017) must be higher for small than for large boulders. In order to test this hypothesis, the boulders were distributed into two size groups as defined above, and the dispersion of the replacement component of beta diversity compared. The expectation is that small boulders will show higher species replacement dispersion while large boulders will be more uniform. For this purpose we used the R packages betapart (beta.pair function, Jaccard dissimilarity, Baselga *et al.*, 2018) and vegan (betadisper function, Oksanen *et al.*, 2019).

Table 1. Statistical models used for exploring the species-area-relationship (SAR) on shore boulders in the Colombian Caribbean Sea. The s-curve model is not included because it was heteroscedastic (studentized Breusch-Pagan test, p<0.05). All other models complied with the assumptions (Lilliefors, Durbin-Watson and studentized Breuch-Pagan tests, p<0.05). S is species richness, A is area in cm². Other letters refer to the coefficients. * models that detect a statistically significant SAR relationship.

Model	Formula	R ²	p-value	
Linear	S = a + z * A	0.25	0.06	
Logarithmic	$S = e^{a + \frac{z}{A}}$	0.38	0.01*	
Power	$S = a * A^z$	0.33	0.02*	
Exponential	$S = a * e^{z^* A}$	0.22	0.06	
Quadratic	$S = a + z * A + c * A^2$	0.39	0.05	
Cubic	$S = a + z * A + c * A^2 + d * A^3$	0.43	0.09	
Inverse	$S = a + \frac{z}{A}$	0.38	0.01*	

Appendix 1 shows a synthesis of boulder biota. Species richness is high with 49 species inhabiting boulders. This number is a low limit of boulder diversity because sampling was restricted to shallow depth, to a small shore section, to a limited boulder size range, and to a limited number of boulders. Species are patchily distributed on the boulders with many appearing just one time and none appearing on all the boulders (Appendix 1).

Table 1 shows the statistical models fitted in order to describe the species-area-relationship on shore boulders. The logarithmic, power, and inverse models identify a statistical significant relation between richness and area (p<0.05) while the other models do not (Table 1, Fig. 1). However, the variance in richness attributable to area is low, less than 40 % (Table 1).

The question as to which statistical model fits better or is more adequate for describing the species-area-relation (SAR) has been posed before. For instance, Drira et al. (2019) after examining 13 SAR functions, concludes that no single formulation fitted all SAR scenarios. In our research it is clear that SAR is detectable in tropical seagrass bed shore boulders in the size range investigated but not by any statistical model (Table 1). Interestingly, the power model discovered by Arrhenius (1921), which is the classical formulation for the study of SAR, was valid for our setting (Table 1) in line with findings by Drira et al. (2019).

The levels of species richness variance explanation by valid models were below 40 % (Table 1). So more than 60 % of the species richness variation must be attributable to other biological and non-biological causes. The small sample (16 boulders), inaccuracies in taxa identification, incomplete counting of species on the boulders, inaccuracies on boulder dimension measurements, and inaccuracies measuring the actual habitat area offered by individual boulders, (i.e. the

area comprised by irregularities such as crevices or cavities on the undersides of the boulders or a combination of these), may qualify as non-biological factors not taken into account and that have influence on the variance of the species richness.

Species composition does not differ from small to large boulders. The same suit of species is found on both boulder sizes (principal coordinates analysis not shown). Analysis of variance to formally test whether there is a difference in heterogeneity was not statistically significant (ANOVA, p > 0.05) suggesting that patterns of species replacement among boulders are the same regardless of boulder size, at least at this spatial scale. Thus, we detected no effect of colonization and extinction rates on boulder species richness mediated by the size of the boulders. A possible reason for this may be lack of a stronger contrast in size of boulders. It seems more plausible, however, that the potential monopolization of space by colonial species had the same influence on both the small and large boulders, and many of the species appeared just one time regardless of boulder size, thus decoupling richness from area.

ACKNOWLEDGMENTS

The Universidad Nacional de Colombia provided funding for this field work. Fellow students of the course "Fundamentos de Biología y Ecología Marina", first semester, 2019, Departamento de Biología, Universidad Nacional de Colombia, helped with sampling.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

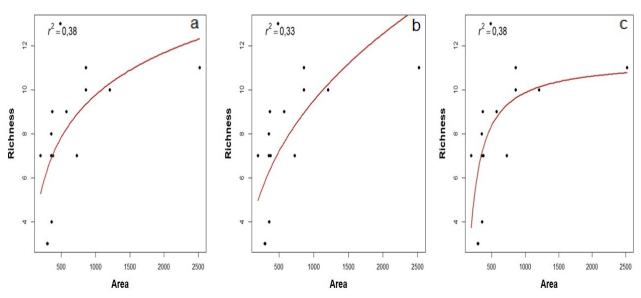


Figure 1. Statistical models fitted to boulder species richness-size data. Logarithmic (a), power (b) and inverse (c) models detected a significant relation (p<0.05) between species richness and boulder size. Other models (not shown, see text) did not distinguished from random effects.

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