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Small-island effect in snake communities on islands of an inundated lake: The need to include zeroes

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Abstract

The small-island effect (SIE), i.e. the pattern that species richness on islands below a certain threshold area varies independently of area, has become a widely accepted part of the theoretical framework of island biogeography and biodiversity research. However, because very few previously published datasets include islands without species, the role of $S = 0$ in generating the SIE is rarely examined. Here, we tested the role of $S = 0$ in generating the SIE for the first time by using snake data collected on 48 islands in the Thousand Island Lake, China. To determine the role of $S = 0$ in generating the SIE, we used regression analysis and path analysis to conduct separate analyses for all the islands (including islands with no snake records) and for the 29 islands inhabited by snakes. When including islands with no snakes, model selection based on AIC_c identified the left-horizontal SIE model as the most parsimonious model. When excluding islands with no snakes, model selection based on AIC_c identified the simple logarithm model without an SIE as the best model. Path analysis detected an SIE for the full dataset, but none for the dataset excluding islands with no snakes. Our results suggest that $S = 0$ plays an important role in generating the SIE and excluding islands with no snakes can lead to erroneously not detecting an SIE when in fact an SIE exists. We conclude that, for the robust detection of the SIE, islands with no species should not be excluded in future studies.

Zusammenfassung

Der ‘small-island-effect’ (SIE), d.h., der Befund, dass der Artenreichtum auf Inseln mit einer Fläche unterhalb eines bestimmten Schwellenwerts unabhängig von der Inselfläche variiert, ist zu einem weithin akzeptierten Teil des theoretischen Gebäudes der Insel-Biogeographie und der Biodiversitätsforschung geworden. Da indessen nur sehr wenige publizierte Datensätze Inseln ohne Arten einschließen, ist die Funktion von S = 0 beim Zustandekommen des SIE selten untersucht worden. Hier testeten wir erstmalig diese Funktion mit einem Datensatz über die Schlangen auf 48 Inseln im Qiandao-Stausee (China).

Wir benutzten Regressionsanalysen und Pfadanalysen und nahmen getrennte Analysen für alle Inseln (d.h. einschließlich der Inseln mit S = 0) und nur die 29 von Schlangen bewohnten Inseln vor. Wenn die Inseln ohne Schlangen

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einbezogen wurden, identifizierten wir mit AIC_c das links-horizontale SIE-Modell als das sparsamste Modell. Wenn die Inseln ohne Schlangen weggelassen wurden, war ein einfaches logarithmisches Modell ohne SIE das beste Modell. Die Pfadanalyse entdeckte einen SIE für den vollen Datensatz, aber keinen SIE für den reduzierten Datensatz. Unsere Ergebnisse legen nahe, dass S = 0 eine wichtige Rolle bei der Bildung eines SIE spielt und dass die Nichtberücksichtigung von Inseln ohne Schlangen dazu führen kann, dass kein SIE entdeckt wird, obwohl er tatsächlich existiert. Wir schließen, dass bei zukünftigen Untersuchungen für die belastbare Identifizierung des SIE Inseln ohne Arten nicht eliminiert werden sollten.

Keywords: Breakpoint regression; Landbridge archipelago; Multimodel inference; Path analysis; Logarithm function; Minimum area requirement (MAR); Species–area relationship; Thousand Island Lake

Introduction

The small-island effect (hereafter SIE) is a cryptic pattern that has been largely ignored by most ecologists and biogeographers in the species–area relationship studies prior to 2000 (Lomolino, 2000; Lomolino & Weiser, 2001). The SIE occurs when species richness (S) on islands below a certain threshold area varies more or less independently of area (A) (Lomolino, 2000; Triantis et al., 2006). Although the pattern was first described almost 50 years ago (Niering, 1963; Whitehead & Jones, 1969), SIE studies only became popular after Lomolino and Weiser (2001) applied the breakpoint regression model for the first time to identify SIEs statistically. Ever since, the SIE is becoming more and more part of the theoretical framework of island biogeography and biodiversity research (Gentile & Argano, 2005; Triantis et al., 2006; Whittaker & Fernandez-Palacios, 2007; Dengler, 2010; Wang et al., 2012a).

However, there are still serious debates over how to test for SIEs and whether they occur at all (Burns, McHardy, & Pledger, 2009; Dengler, 2010; Tjørve & Tjørve, 2011; Triantis & Sfenthourakis, 2012). The methods for the detection of SIEs often are flawed in one way or another, including not accounting for model complexity, not comparing all relevant models, not including islands with no species, and ignoring the effects of logarithmic data transformations and habitat diversity on generating SIEs (Triantis et al., 2006; Burns et al., 2009; Dengler, 2010). All these methodological shortcomings have drawn some attention and have been somewhat well addressed (e.g. Triantis et al., 2006; Burns et al., 2009; Sfenthourakis & Triantis, 2009; Dengler, 2010), except the role of $S = 0$ (islands with no species) in generating the SIE.

Whether or not we should include islands with no species ($S = 0$) is an important issue in SIE studies in particular (Dengler, 2010; Morrison, 2014), and in species–area relationship studies in general (Williams, 1996). In most previous studies, islands with no species are simply excluded probably because such islands cause trouble when fitting a power model ($S = cA^z$, where c is the intercept and z is the slope) in its linearized form since log(0) is undefined (Dengler, 2010). However, islands with no species should not be excluded at least for two reasons. First, $S = 0$ is within the normal range of the variation of species richness, especially on small islands (Williams, 1996; Morrison, 2011). Second, from a statistical perspective, the exclusion of islands with no species would bias the parameter estimate of c, z, and S (Williams, 1996), thus likely lead to the erroneous detection of SIEs (Dengler, 2010). However, because of the paucity of studies reporting islands without species (Dengler, 2010), the role of $S = 0$ in generating SIEs remains obscure.

In this study, we tested the role of $S = 0$ in generating SIEs for the first time using snake data from islands created by the inundation of the Thousand Island Lake, China. We used two broad sets of analyses, i.e. regression analyses and path analyses, to detect the SIE. First, we used an information–theoretic multimodel inference approach to compare the fit of a logarithm model without an SIE with two breakpoint regression models with SIEs (Dengler, 2010). Second, we used a method based on path analysis (Fattorini, 2006a) that simultaneously incorporates island area and habitat diversity into detecting the SIE (Triantis et al., 2006). We hypothesized that the exclusion of islands with no species would influence the detection of the SIE because towards the far-left, the shape of the species–area curve is mostly determined by the increasing fraction of islands with no species (Williams, 1996; Dengler, 2009).

Materials and methods

Study sites

The Thousand Island Lake (29°22′–29°50′N, 118°34′–119°15′E) is a large man-made hydroelectric reservoir formed in 1959 by the damming of the Xinanjiang River in Zhejiang Province, China (Wang, Zhang, Feeley, Jiang, & Ding, 2009). Construction of the Xinanjiang dam inundated an area of 573 km^2 when the water reached its final level (108 m a.s.l.), creating 1078 landbridge islands larger than 0.25 ha out of former hilltops (Wang, Bao, Yu, Xu, & Ding, 2010). The total land area of the archipelago is 409 km^2. Forests on islands were clear cut before the creation of the dam (Wang et al., 2012a). The major vegetation on the islands is thus now a successional forest dominated by