

Subsidized Island Biogeography Hypothesis: another new twist on an old theory

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Abstract

We present a new hypothesis for predicting and describing patterns of species diversity on small islands and habitat fragments. We have modified the traditional island biogeography equilibrium theory to incorporate the influence of spatial subsidies from the surrounding matrix, which vary among islands and habitat fragments, on species diversities. The modification indicates three possible directions for the effects of spatial subsidies on diversity, which depend on where the focal community falls on the hypothesized unimodal curve of the productivity–diversity relationship. The idea is novel because no recent syntheses of productivity–diversity–area relationships examine the role of allochthonous resources on recipient communities' diversity patterns.

Keywords

Diversity, island biogeography, productivity, spatial subsidies, species richness.

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INTRODUCTION

In an effort to explain and predict diversity patterns on isolated islands and in habitat fragments, ecologists often return to MacArthur & Wilson's (1967) equilibrium theory of island biogeography (IB) and its many supplements (e.g. MacArthur *et al.* 1972; Root 1973; Kareiva 1983; Kohn & Walsh 1994; Connor *et al.* 2000). We propose another supplement based on allochthonous inputs to islands to explain diversity patterns on very small islands (< 3 km²), which often do not fit the standard species–area curve that explains many larger island systems so well. Our conceptual model synthesizes MacArthur and Wilson's IB theory with the hypothesized unimodal curve that Rosenzweig (1995), Huston (1994) and others have used to describe the productivity (P)–diversity (D) relationship.

The traditional IB equilibrium theory predicts increasing immigration of new species coupled with decreasing extinction as a function of island area until species richness reaches an equilibrium point (S) that is lower than the total species pool for the adjacent mainland. Smaller and more remote islands would have lower immigration rates and possibly higher extinction rates, and thus have smaller S (equilibrium diversity). One assumption of IB theory is that population densities remain constant across island size. If this is not valid, as Connor *et al.* (2000) suggested, and densities vary over island size, then the log–log relationship between

diversity and island area may not be linear. For example, small islands often have much higher productivity (defined as the rate at which energy flows through a system, Rosenzweig 1995) per unit area than large islands, which would lead to higher population densities (Polis & Hurd 1995) and lower extinction rates (Preston 1962). Lower extinction rates in productive sites could then lead to higher diversity. Alternatively, higher productivity might lead to stronger competitive dominance by a few species, and thus higher extinction rates of competitive subordinates. Therefore, small islands may have higher or lower diversity than expected based on just their colonization–extinction rates.

Relationships between island size and productivity suggest that small islands have more resources per unit area than large islands in the same area (Polis & Hurd 1996). In effect, if islands receive material from the surrounding system, these subsidies will have a greater relative impact on island inhabitants when the edge:interior ratio is greater, as it is on small islands. Therefore, smaller islands may have greater total productivity per unit area when considering the combined *in situ* and allochthonous resources. This concept was well developed and supported by Polis & Hurd (1995, 1996) and Anderson & Polis (1998) on desert islands of the Gulf of California, where they demonstrated that marine subsidies increased population densities of many terrestrial arthropod consumers. In addition, the effects of spatial subsidies on population dynamics and community

interactions have been documented in several systems (see Polis *et al.* 1997). What is still relatively unknown, however, but may be possible to predict with old and new theories and models, and with existing data, is how allochthonous resources affect diversity of recipient communities in island systems.

Two recent papers provide a mathematical basis for integrating productivity, diversity and area, although neither explicitly incorporates subsidies into their measures of productivity. Dodson *et al.* (2000) proposed a linear model for species richness that synthesized productivity and area as components of the model, but they did not specify the mathematical relationship between productivity and area, nor did they explicitly consider subsidies in their review of productivity–diversity–area data from lakes. Pastor *et al.* (1996) examined relationships between richness and productivity as a function of area sampled in grass and sedge-dominated meadows. Both Dodson *et al.* (2000) and Pastor *et al.* (1996) eloquently discuss how the P–D relationship varies as a function of area. We are interested in how the species–area relationship varies as a function of productivity. Finally, He & Legendre (1996) provided a synthesis of three species–area models, where inclusion of subsidies as a mechanism may help explain deviations of fit of exponential, power and logistic species–area models among area samplings of different size ranges.

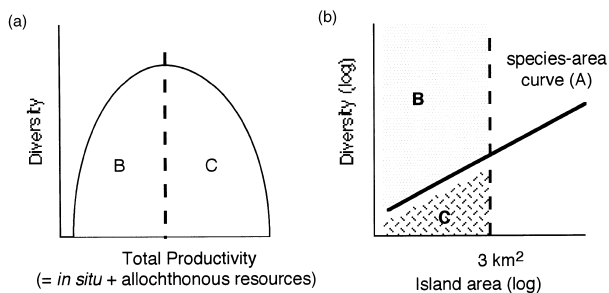


Figure 1 (a) The standard unimodal (or quadratic) curve for the relationship between productivity and diversity. The ascending section of the curve is labelled B, and corresponds to the B range in (b). The descending section of the curve is labelled C, and corresponds to the C range in (b). The traditional species–area curve (line A in b) based on size alone predicts a linear relationship for log-transformed area and richness data, such that $\log S = \log c + z \log X$, where S is species richness, c is a constant, z is the slope and X is island area. In the small island range of the line A ($< 3 \text{ km}^2$), allochthonous resources may increase the productivity in a way that alters diversity. Where the focal group falls in the curve from (a) will determine whether the slope of line A increases or decreases relative to A.

To facilitate examining or understanding if spatial subsidies increase or decrease diversity, or neither, we propose a conceptual model that integrates the P–D hypothesis with the species–area curve (Fig. 1). Our model suggests that the relationship between subsidies, island size and diversity depends on where each taxonomic or trophic group of interest currently falls on the hypothesized P–D unimodal curve (Fig. 1a). The model considers only the section of the line that encompasses small islands that are significantly influenced by allochthonous resources, and suggests that the slope of that section of line will vary from the slope that encompasses larger islands in a direction that is a function of where the focal group is in the P–D relationship.

We provide a hypothetical illustration of our conceptual model. Vascular plant diversity on small islands that receive no subsidies will fall on the line with the same slope and y -intercept as the points from larger islands (line A in Fig. 1b). However, when small islands receive nutrients from the ocean that stimulate plant growth, those nutrients affect diversity in two possible ways. First, if plants are on the ascending side of the P–D curve where richness increases with an increase in productivity, the slope (z) of the species–area curve for those islands will decrease relative to A (B range in Fig. 1a, b). If plants are on the descending side of the P–D curve where richness decreases with increasing productivity, z for those islands will increase relative to A (C range in Fig. 1a, b). The degree to which the slope will change will be a function of the kurtosis of the P–D curve for that taxon because the steeper the P–D relationship, the more strongly the subsidized productivity of an island will affect its diversity. Both altered curves must eventually approach the origin, as an island with zero area will have zero species (B range), and negative diversity is not possible for small islands with high productivity (C range). As islands increase in size, the effect of subsidies becomes less important for population density and thus diversity, so the slope eventually approaches that of larger islands where subsidies are unimportant.

An empirical example where this theory may explain deviation from the species–area curve is found in Case & Cody (1983). According to Cody *et al.* (1983), plant diversity on islands in the Gulf of California fits a species area curve where $z \approx 0.25$. However, diversity for each of the smallest islands ($< 3 \text{ km}^2$) falls below the curve. Cody *et al.* (1983) explain the deviation as a lack of appropriate habitat and catchment area for less xeric species on small islands. However, unpublished data collected by W. Anderson and G. Polis on very small islands in this region suggest a different explanation. Small islands with similar topography and substrate but with different patterns of seabird guano input exhibit different patterns of plant diversity. Those islands without guano inputs have up to four times higher

plant diversity than islands with guano inputs. Small islands without guano fall along the $z \approx 0.25$ species–area line, while those with guano fall below the line. Although the identities of all the small islands presented in Cody *et al.* (1983) are not known, those that are explicitly named (and fall below the curve) are densely inhabited by seabirds.

One way to recognize this pattern in new or existing data is to examine the residuals of the species–area curve of empirical data to see if variation in diversity is higher at the small end of the curve than at the large end. If it is, then subsidies on small islands may be important factors altering the diversity pattern in either direction. Once the pattern emerges, deviant islands (or fragments, lakes, etc.) can be examined for the presence of subsidies that might have significant effects on the recipient groups of interest. Also, experimental resource additions to unsubsidized islands followed by long-term monitoring of diversity responses would provide data on the role of subsidies in island diversity patterns. These methods could rule out or integrate the many alternative mechanistic hypotheses that have been proposed previously or may arise subsequently (e.g. predator absence, habitat heterogeneity).

Various syntheses of diversity–area–productivity relationships have proven fruitful (e.g. Dodson *et al.* 2000, Connor *et al.* 2000), but none consider the effects of subsidies on diversity patterns. Although we do not wish to discount numerous other explanations for deviations from species–area curves in log–log space, we believe subsidies may be important factors affecting diversity patterns. We would like to add them as a possible explanation for previously unexplained divergences at the small island or patch end of the species–area curve, and invite ecologists with appropriate species–area data to test this idea.

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BIOSKETCH

Wendy B. Anderson is a community ecologist interested in the effects of marine materials on island ecosystems. She focuses on plant physiological responses to marine materials, which might influence community structure.

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