

LETTER

Island theory, matrix effects and species richness patterns in habitat fragments

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Abstract

Island biogeography theory, created initially to study diversity patterns on islands, is often applied to habitat fragments. A key but largely untested assumption of this application of theory is that landscape matrix species composition is non-overlapping with that of the islands. We tested this assumption in successional old field patches in a closely mowed matrix, and because our patches are appropriately viewed as sets of contiguous habitat units we studied patterns of species richness per unit area. Previous studies at our site did not find that diversity patterns on patch 'islands' conformed to predictions of island biogeography theory. Our results indicate that when matrix species are removed from the patch samples, diversity patterns conform better to theory. We suggest that classical island theory remains an appropriate tool to study diversity patterns in fragmented habitats, but that allowances should be made for spill-over colonization of 'islands' from the 'sea'.

Keywords

Habitat fragmentation, island biogeography theory, landscape matrix, plant succession, species richness patterns.

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INTRODUCTION

The theory of island biogeography (IBT) of MacArthur & Wilson (1967) has been one of the most influential conceptual constructs in ecology. This paradigm continues to develop, and in many directions (e.g. McGuinness 1984; Gascon & Lovejoy 1998; Brown & Lomolino 2000; Gonzalez 2000; Lomolino 2000; Anderson & Wait 2001), including the interpretation of diversity patterns in heterogeneous and fragmented landscapes. One motivation for developing IBT was the observation that the species–area relationship among islands varying in size is stronger than is the relationship among similarly sized nested samples within continuous habitats (e.g. on continents). If the scaling of richness to sample area is the same among islands and continents, then local community richness per unit area should be elevated as a function of island size (see Fig. 1; Holt 1993; Rosenzweig 1995). MacArthur & Wilson (1967; p.16) conjectured that this elevated richness arises from the 'spill-over' of transient species among distinct habitats, permitted by the elevated immigration rates enjoyed by sample areas embedded in larger regions. Holt (1992) extended this insight, suggesting that it is useful to view

islands as sets of contiguous habitat units, connected by within-island dispersal; roughly speaking, island size is proportional to the number of such units. If within-island dispersal elevates local colonization rates into each unit, and/or decreases local extinction rates, species richness per unit area should tend to increase with island size (see also Kelly *et al.* 1989; Hart & Horwitz 1991). In a landscape context, however, this effect can be clouded by 'spill-over' into habitat patches from the surrounding matrix.

Island theory has often been applied to conservation questions in terrestrial systems comprised of anthropogenic (or natural) habitat patches set into a sharply contrasting matrix (Harris 1984; Fahrig & Merriam 1994; Harrison 1999; Zschokke *et al.* 2000). The utility of this approach rests upon the degree to which the basic premise of IBT – namely, the existence of discrete habitat units spatially separated from sources of colonists – is realized. Thus, IBT as applied to fragmented landscapes assumes that the matrix separating habitat islands is inhospitable, much as the sea is to colonists of oceanic islands, and so does not contain species or processes relevant to the study at hand (Lomolino 2000). However, there is increasing recognition that the matrix in fragmented landscapes can potentially influence

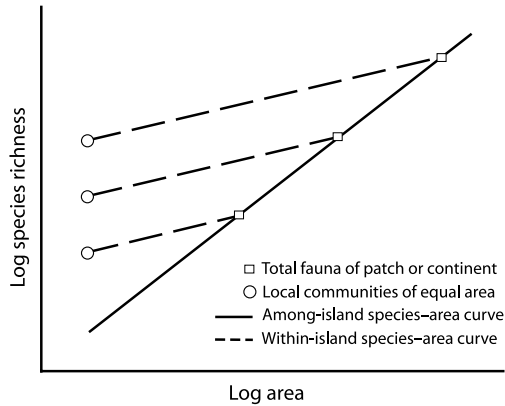


Figure 1 Two kinds of species–area curves, after Holt (1993). The total species pool of an island (which is assumed to depend upon its total area) and the number of species found within a sample area on an island are both described by power laws. Given that the slope describing the increase in species richness within an island is lower than that describing the increase in richness between islands, local communities increase in richness with increasing area.

species abundance or composition in the embedded patches (Holt 1997; Gascon & Lovejoy 1998; Ås 1999; Harrison 1999; Hobbs 2001; but see Anderson & Wait 2001; Davies *et al.* 2001).

The phenomenon of secondary succession resembles island colonization, in that it often involves colonists entering a community from propagule sources at varying distances (Glenn-Lewin *et al.* 1992; Miles & Walton 1993). Holt *et al.* (1995) suggested a conceptual framework examining the implications of these spatial processes for succession theory. They predicted that for isolated patches undergoing succession, large habitat patches and those near

propagule sources should have greater species richness (particularly early in succession) than do patches which are small or distant. Different patterns may emerge for non-isolated patches.

Some of the patterns predicted for isolated patches (area and distance effects in habitat ‘islands’) have been observed for individual species (Yao *et al.* 1999) and guilds (Bascompte & Rodríguez 2001). Contrary to theoretical expectations, however, the most thorough study to date of diversity patterns in patchy landscapes undergoing succession found little evidence that local species richness varied predictably with patch size or position during early secondary succession (Holt *et al.* 1995). In this paper we revisit this system and examine the influence of the matrix upon interpretation of richness patterns in the successional patches. We demonstrate that matrix effects can obscure spatial patterns that conform to the general expectations of IBT.

METHODS

The study site and design is shown in Fig. 2. Since 1984, an array of three patch sizes (4 × 8 m, 12 × 24 m, 50 × 100 m), arranged into 50 × 100 m clusters, have been maintained by frequent mowing of the interstitial matrix (Robinson *et al.* 1992; Holt *et al.* 1995) (Fig. 2). (Because medium-sized patches contain barely half the number of sampled quadrats of large and small patches, and are less well-dispersed in space, this study excludes data from medium patches.) Since establishment, the patches have undergone secondary succession. The plant community dynamics are monitored in permanent 1 m² quadrats. To characterize the matrix community, in July 2001 110 of these quadrats were established in the matrix, midway

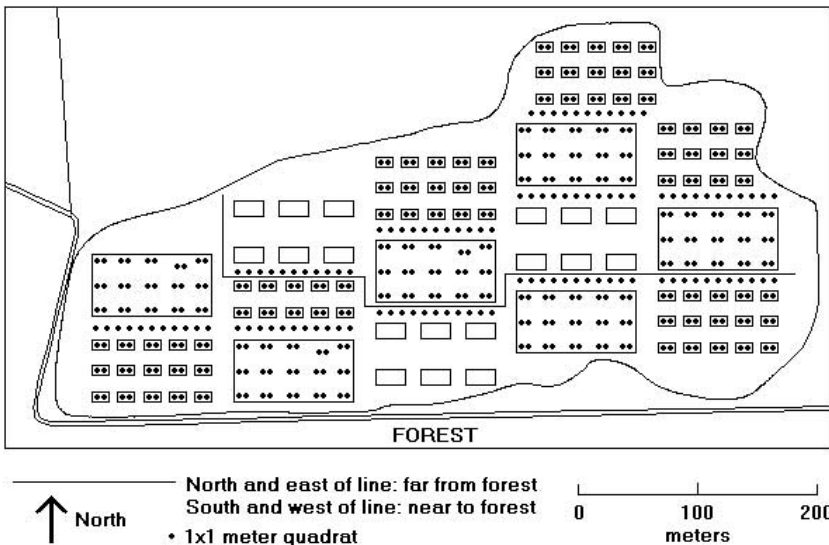


Figure 2 Diagrammatic map of Kansas Fragmentation Study, Nelson Environmental Study Area, University of Kansas Field Station and Ecological Reserves, located in southern Jefferson County in eastern Kansas, USA.

between patch clusters (Fig. 2). Plant species composition and cover were measured for each quadrat, and then cumulated for all matrix quadrats and patch quadrats. Each quadrat was assigned as being near or far from the forest (see Fig. 2). Our patch sample consists of 90 near-large, 80 near-small, 90 far-large, and 84 far-small quadrats.

To gauge the influence of matrix species on diversity patterns in the experimental patches, we performed two-way ANOVAs (predictor variables: patch size and distance from forest) on total species richness within patch quadrats, and on species richness in the same quadrats after eliminating species also found in the matrix. We performed two-way ANOVAs (same predictor variables) on cumulative species richness per patch cluster (15 small patches, or one large patch), with and without matrix species. Finally, we used one-way ANOVAs to compare the species richness in quadrats on edges and interiors of large patches ($N = 132$, $N = 48$, respectively) and quadrats on small patches ($N = 164$), with and without matrix species.

RESULTS

The matrix was dominated by grasses and low-lying forbs (total 60 species). The patches were heterogeneous, including both old field vegetation and thickets dominated by woody plants. Introduced grass species were common to both habitat types. One hundred and forty-six species occurred in the experimental patches; 35 of these were shared with the matrix.

The ANOVA on total species richness per m^2 in the patches detected no effect of patch size, a marginal trend towards greater richness in near patches, and a significant interaction (Table 1). There was no detectable difference in species richness by distance for large patches, but small patches near the forest had greater richness than small patches far from the forest. Quadrats on near patches

averaged 12.51 species \pm a standard error of 0.30, far 11.81 \pm 0.28, large 12.15 \pm 0.28 and small 12.16 \pm 0.31. However, when species that also occur in the matrix were removed from the patch community lists, the subsequent two-way ANOVA detected significantly greater richness in near patches, again no significant trend towards greater species richness in large patches, and no interaction (Table 1). Quadrats on near patches then averaged 6.86 species \pm a standard error of 0.18, far 5.72 \pm 0.16, large 6.44 \pm 0.18 and small 6.15 \pm 0.17. A similar analysis performed on cumulative species per patch cluster (six large patches and four clusters of small patches) found qualitatively similar results.

Quadrats had similar richness, whether they were on the edge or interior of large patches or on small patches, when all species were included (interior 12.04 species per quadrat \pm standard error of 0.53, edge 12.19 \pm 0.33, small patches 12.16 \pm 0.31, ANOVA $F = 0.03$, d.f. = 2, $P = 0.974$). By contrast, quadrats on large patch interiors had greater richness than did either edge or small patch quadrats, when matrix species were excluded (interior 7.08 \pm 0.33, edge 6.16 \pm 0.21, small patches 6.15 \pm 0.17, ANOVA $F = 3.45$, d.f. = 2, $P = 0.033$). Thus, matrix species were relatively richer in small patches or edge quadrats than in large patch interiors.

DISCUSSION

If successional patches were figurative islands in a sea of inhospitable mowed matrix, the expectation (looking at the patches of this system through the lens of classical island theory) would be no overlap in species composition between the two habitats, and a pattern in which species richness is comparatively high in large patches and in those near to the adjacent forest.

However, substantial overlap exists between the matrix and patch communities in this successional landscape; 35

Table 1 Results of two-way ANOVAs testing the effects of patch size and distance on average species richness per quadrat, performed with and without matrix species included.

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
All species included					
Patch size	1	0.08	0.08	0.01	0.940
Near/far	1	47.71	47.71	3.34	0.069
Interaction	1	97.84	97.84	6.84	0.009
Error	340	4863.37	14.30		
Total	343	5009.00			
Matrix species removed					
Patch size	1	5.11	5.11	1.03	0.312
Near/far	1	111.99	111.99	22.54	< 0.001
Interaction	1	1.02	1.02	0.21	0.650
Error	340	1689.63	4.97		
Total	343	1807.75			

species were shared by both habitats, accounting for 24% of the total species assemblage in the experimental patches, and 58% of the matrix assemblage. When species occurring in the matrix were removed from the patch samples, patterns became stronger and more similar to those expected from island theory (Table 1). Specifically, a nonsignificant effect of distance to the forest became highly significant, the overall effect of patch size upon local species richness became more pronounced (particularly when comparing interiors of large patches to small patches), and a significant interaction between the two landscape parameters disappeared. It appears that the total amount of variation present in the system decreased dramatically once matrix species were removed from the system, and much of the variance included in the significant interaction in the first ANOVA was transferred to the primary effects in the second ANOVA. Both of these statistical patterns are consistent with the interpretation that matrix species masked underlying patch size and distance effects. While habitat fragmentation has been shown to affect the population structure and dynamics of particular species in this system (Diffendorfer *et al.* 1995; Yao *et al.* 1999), the results presented here provide the best evidence to date that fragmentation also has noticeable effects on patterns of species diversity during succession.

In effect, matrix species contribute 'noise' to the species richness data set at our site, masking a more general pattern of greater species accumulation in large than small, and near than far, patches over the previous 6 years (W.M. Cook, unpublished result). We believe that a number of different processes are integrated in producing these patterns. Succession is underway in our system. If there tends to be an increase in species richness during the initial stages of succession, and succession takes place more rapidly on near and large patches, this could lead to the patterns we discerned once matrix species were removed. Moreover, edge effects on species richness are evident in our system. The 'spill-over' from the matrix into the patches should be spatially mediated, and hence more prevalent in small patches or on edges of large patches, as indeed we observed. Diffuse competition from 'spill-over' matrix species could then depress the richness of species restricted to the patches, and should differentially do so near the edges of large patches and on small patches. Finally, if species colonize a patch and then show localized spread (e.g. due to clonal growth), interior quadrats can have an enhanced colonization rate (due to within-patch, short-distance dispersal, Holt 1992), compared to quadrats at edges or on small patches, leading to the observed higher richness at interior sites.

In the spirit of other recent comments on the future of IBT (Brown & Lomolino 2000; Lomolino 2000; Anderson & Wait 2001), we suggest that further refinements of the

paradigm are necessary to adapt and broaden the theory. For island biogeography theory to be applied to terrestrial habitat 'islands' which are heterogeneous and subject to edge effects, methodological allowances need to be made for the likelihood that species can colonize the 'islands' from the sea. Our results suggest that 'spill-over' of matrix species may obscure real patch size and distance effects for species dependent solely on the patches, which are the analytical goals of many conservation studies in fragmented terrestrial systems.

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