The Effects of Matrix Properties on Ecological Processes Within Habitat Fragments
Or
Tilting at Windmills in Search of General Trends

Chris Terry

It is impossible to characterize all the ways that the matrix has been studied in a single paper. At best, this annotated bibliography will provide an introduction to a few of the paths that researchers have followed, particularly those that have looked at the relationship between the matrix and the species-area effect. It is grouped by theme, rather than author's last name.

A few papers searched for general trends. Here's one.

Debinski, D. M. and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology **14**(2): 342-355.

This comprehensive review paper examined 20 habitat/fragmentation experiments in terms of common hypothesis regarding the species area relationship, corridors, and density/abundance. Taken as a whole, the experiments had highly inconsistent results; only insects, which have short generation times, generally responded to fragmentation as predicted. The three long-term experiments did support prevailing theory more than the short-term experiments, which could indicate a "lag effect." However, such inconsistent results could also indicate the importance of the matrix in dampening fragmentation effects. I would call this required reading for anyone trying to understand how different taxa respond to fragmentation.

Much ecological research examines the species-area relationship. Here are a few studies that show how matrix effects can change the species-area relationship.

Anderson, W. B. and A. Wait. 2001. Subsidized island biogeography hypothesis: another new twist on an old theory. Ecology Letters **4**: 289-291.

This article presents a mathematical framework for understanding the effect of resource supplementation from the matrix into habitat fragments. Since small fragments have a higher edge/core ratio, they receive greater supplements per unit area than large fragments. Depending on the nature of the supplement, they could be more productive than larger fragments. The mathematics don't seem to have been used in terrestrial fragmentation studies, but the concept itself has made its way into a few papers.

Brotons, L., M. Monkkonen and J. L. Martin. 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. The American Naturalist **162**: 343-357.

This meta-study on boreal birds in Finland examines the species-area relationship in terms of four hypothesizes: the equilibrium theory of island biogeography, the resource concentration hypothesis, the density compensation hypothesis, and the matrix quality hypothesis. The researchers compared the species-area relationship of islands surrounded by water to mainland fragments surrounded by logged areas. They found that population density is higher on larger islands, consistent with the resource concentration hypothesis and Connor et al (2000). However, mainland fragments did not display the same trend, leading the researchers to conclude that the matrix somehow negates the density/area relationship by increasing the population density on smaller fragments. This means that comparing the patch area effect (PAE) across different matrix types may be problematic, which, as far as I can tell, is different from Connor et al (2000), who found a consistent correlation between patch area and population density.

Gibb, H. and D. F. Hochuli. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological Conservation **106**(1): 91-100.

This paper adds a new twist to the debate by claiming that insect assemblages on large versus small fragments in Australia are affected differently by urbanization. Although small and large fragments had similar species richness, the species assemblages were not the same (via ANOSIM on Bray-Curtis). Small fragment species assemblages were not subsets of large fragments, implying that changes occurred post-fragmentation. The researchers blamed this on fire-suppresion in small fragments, and the abiotic preferences of generalist ants. The researchers used the same total sampling effort on large and small fragments, a la "Connor and McCoy, 1979." If Connor were to read this paper today, would he consider this good experimental design?

Watson, J. E. M., R. J. Whittaker and D. Freudenberger. 2005. Bird community responses to habitat fragmentation: how consistent are they across landscapes? Journal of Biogeography **32**(8): 1353-1370.

This study tested the species-area and isolation hypothesis for birds in three different types of matrix: urban, suburban, and agricultural. Using an ANOVA, they found that species, and guilds, responded differently to patch area and isolation between landscape types. They also found that species richness was most sensitive to fragment area in the urban landscape, which is different than Gibb 2002, who found no relationship between area and insect species richness in urban areas. There were a few problems with this study, such as greater sampling effort in agricultural areas and the disregard of uncommon species. Still, it succeeds in showing the problems of generalizing species dynamics across different matrix types.

Wethered, R. and M. J. Lawes. 2003. Matrix effects on bird assemblages in fragmented Afromontane forests in South Africa. Biological Conservation **114**(3): 327-340.

This article also examined the species-area relationship for bird species in forest fragments embedded in different matrices: native grasslands and plantations. In this case, they found a non-significant relationship between species richness and fragment size in the plantation matrix, but a significant relationship in the grassland matrix. Investigating further, they found that total species richness per fragment size was lower in the plantation matrix than the grassland matrix. This is similar to Broton's conclusion, where a highly dissimilar matrix exacerbated a species-area effect. However, these birds are adapted to a naturally fragmented habitat (forest and grassland). Therefore, the authors concluded that increasing the ability of some birds ("generalists") to travel easily through the matrix may negatively impact rarer species.

Some studies evaluate the importance of landscape factors for individual species distributions.

Ohlenmuller, R., P. Bannister, K. J. M. Dickinson, S. Walker, B. J. Anderson and J. B. Wilson. 2004. Correlates of vascular plant species richenss in fragmented indigenous forests: assessing the role of local and regional factors. Community Ecology **5**(1): 45-54.

This article attempted to separate the importance of local versus regional factors for vascular plant species richness in New Zealand. This study is unique among the papers I reviewed because it does not assume, or require, heterogeneity of habitat fragments. Using "forward and backward stepwise variable selection based on Akaike Information Criterion", the authors found that species richness was most highly correlated with percent landuse type, though local factors were also important. However, each species set (native, woody, etc), responded slightly differently to each variable. Theoretically this is a good study, but I don't have the mathematical background to evaluate its methodology.

Soderstrom, B. and T. Part. 2000. Influence of landscape scale on farmland birds breeding in semi-natural pastures. Conservation Biology **14**(2): 522-533.

This study is slightly different than others in this paper. Rather than test the species-area relationship, it attempts to correlate the abundance of individual bird species with landscape characteristics. Specifically, the researchers measured the abundance of European birds that breed in (similar) old pastures within three different matrix types: forest, agricultural, and mixed. Though only a few species were significantly more abundant in one matrix type than another, regression showed that 78% of the bird species were significantly correlated with at least one landscape characteristic, usually percent of agricultural land. Oddly, all the species of concern were associated with forest, though most species were associated with agricultural land.

Other studies argue that the matrix confounds the data. If species that are present in both the matrix and the habitat patch are disregarded, fragmentation can be understood in terms of patch size and isolation.

Cook, W. M., K. T. Lane, B. L. Foster and R. D. Holt. 2002. Island theory, matrix effects and species richness patterns in habitat fragments. Ecology Letters **5**(5): 619-623.

This long-term experiment examines the effect of fragmentation on vegetative secondary succession in "old field patches," that are maintained in various sizes and configurations by mowing. The ANOVA on species richness in patches grouped by size and isolation was not significant, until the 34 species that were also present in the matrix were removed from the analysis. This was a very simple test, but it does show the danger of disregarding species that also exist in the matrix.

Godefroid, S. and N. Koedam. 2003. How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? Global Ecology and Biogeography **12**(4): 287-298.

This study of woodland remnants in Brussels Belgium had the same problem as the Cook (2002) paper. Patch isolation and area were not significant for species that were also present in the matrix. Like Cook, they removed these from the analysis and obtained the desired results. From a management perspective, I see some potential to conserve threatened species by deliberately planting them along city streets.

A few researchers have attempted to relate community composition in habitat fragments to "landscape metrics" that measure the heterogeneity of the landscape using GIS techniques. This subfield of matrix analysis may exhibit the least consensus of all.

Honnay, O., K. Piessens, W. V. Landuy, M. Hermy and H. Gulinck. 2003. Satellite based land use and landscape complexity indices as predictors for regional plant species diversity. Landscape and Urban Planning **63**: 241-250.

This paper analyzes floristic data across Northern Belgium using Fragstat and local variables. It fills a gap in the literature, since large scale ecological data seems to lag behind our ability to perform landscape analysis. They derived vegetation information from the Flora Database of Flanders (presence/absence only) then attempted to correlate species group (native, alien, assumed abiotic preferences, etc) to abiotic and landscape properties. They found that species richness, both native and invasive, was positively correlated with landscape diversity and urbanization, while degree of fragmentation was negatively correlated with total number of species, and native species. This led them to conclude that habitat diversity is more important than habitat fragmentation in the SLOSS debate, putting them on the side of Several Small.

Riitters, K. H., R. V. Oneill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones and B. L. Jackson. 1995. A Factor-Analysis of Landscape Pattern and Structure Metrics. Landscape Ecology **10**(1): 23-39.

This article doesn't directly deal with matrix properties or even ecology. I include it only because anyone seeking to understand how landscape metrics are calculated should be aware of this paper. The authors measured 55 different landscape metrics on 85 USGS maps (120X180km, raster grain size of 200m). They quickly reduced that number to 26 via correlation-coefficients, performed a PCA, and found 6 metrics that described 87% of the variation amongst the 26 metrics. The next step is to test these metrics at different resolutions, then link them to ecological processes. Sadly, this latter step does not yet show consistent results.

Tischendorf, L. 2001. Can landscape indices predict ecological processes consistently? Landscape Ecology **16**(3): 235-254.

This study follows previous work on neutral landscape models (NLM). NLM's, derived from percolation theory, use computer-generated habitat/matrix maps to test the effects of fragmentation on metapopulation models. Major researchers in this area include Fahrig, Tischendorf, With, and others. This study tests 26 landscape indices against dispersal patterns on both neutral landscape models and Landsat images. It attempts to derive general statistical relationships between behaviour patterns of species (generalist versus specialist) and landscape metrics. Overall, this study found that as-modeled, specialists are more sensitive to landscape structures such as fragment clumping and total habitat area. However, most of the landscape metrics do not respond consistently to variations in dispersal patterns. This is similar to the conclusions to other studies of landscape metrics across patterns, and is probably indicative of the fact that the study of landscape heterogeneity is still a "new" field. Tischendorf et al 2003 is a follow-up to this study.

Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. American Naturalist **158**(1): 87-99.

This excellent study on the ability of the matrix to impede movement between habitat fragments was performed in a naturally fragmented study system: butterflies that live in meadows surrounded by willow or conifer. Ricketts used a maximum likelihood estimation to test the null hypothesis that there is no difference in butterfly dispersal through conifer matrix versus willow matrix. He found that for four taxa, conifer is more resistant that willow. Two taxa exhibited no relationship between dispersal and matrix type. This highly-cited study provides a real-world basis for neutral landscape models, and explicitly integrates matrix qualities with the metapopulation paradigm.

Papers mentioned but not reviewed:

Connor, E.F. and E.D. McCoy. 1979. The statistics and biology of the species-area relationship. *American Naturalist* 113: 791-833.

Connor, E.F., A.C. Courtney, and J.M. Yoder. 2000. Individuals-area relationships: The relationship between animal population density and area. *Ecology* 81: 734-748.

Tischendorf, L., D.J. Bender, and L. Fahrig. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist species. Landscape Ecology 18: 41-50.