The Theory of the Matrix

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Traditional models of fragmentation identify three components of the land mosaic: the patch, corridor, and matrix. A patch is defined as a continuous area of habitat with the necessary resources for the persistence of a population. A corridor allows passage from patch to patch, but cannot support individuals over the long term. The matrix consists the remaining landscape components and is considered ecologically irrelevant, homogeneous, and hostile. In fact, when island biogeography theory (MacArthur and Wilson, 1967) is applied to terrestrial ecology, patches are considered as the islands and the matrix is conceptualized as the ocean, where individuals entering the matrix effectively “drown” (Cook et al., 2002). The matrix is considered a biological sink and, as featureless background, is ignored.

Traditional fragmentation theory also includes the concept that fragments that are smaller and further apart support fewer species and have reduced immigration rates and elevated extinction rates. This concept is particularly captured by metapopulation theory (Levins, 1969), where regional persistence of metapopulations is believed to be governed by patch colonization, extinction, and recolonization. Metapopulation theory states that decreased patch size increases the risk of local extinction, and increased distance between patches decreases colonization (Murphy and Lovett-Doust, 2004). Movement success of an organism depends on distance between patches and a constant, species-specific dispersal ability. Metapopulation theory defines the matrix as habitat suitable for traversing, but unsuitable for supporting breeding individuals (Wiens,
The concept of a binary classification of the landscape into habitat patches and non-habitat matrix is also included.

In the past few years, research results have instigated a profound paradigm shift in how the matrix is characterized. Rather than classifying the landscape into binary habitat/non-habitat categories, the landscape is viewed as a continuum that organisms perceive as a gradient in resources. Fischer et al. (2004) proposed a conceptual model of habitat contours to capture species responses to the landscape. They envisioned habitat suitability contour maps for each species that, when overlaid, may define patches at an ecosystem level. In this new paradigm, patches are still defined as optimal habitat, but the matrix is now defined as an array of different habitat types that contribute to the overall quality of the matrix (Jules and Shahani, 2003).

By characterizing the matrix, the new paradigm also recognizes the influences the matrix exerts over the landscape. The quality of the matrix can affect the rate of migration between fragments, influence within-fragment dynamics, and provide alternate, though suboptimal, habitat. Migration between patches should no longer be considered a constant, species-specific trait. For example, the movement behavior of goldenrod beetles varied between land cover types and could almost completely be described by the structural complexity of the matrix (Goodwin and Fahrig, 2002). Matrix heterogeneity explained 53% of the variance in interpatch connectivity for lynx (Revilla et al., 2004). Ricketts (2001) found that different matrix types had different relative resistances to movement for four of six butterfly taxa studied. Therefore, dispersal cannot be considered a function of distance alone, but must include the permeability of the matrix. This is also an important influence on within-fragment dynamics. Since migration or colonization is no longer a function of distance alone, fragments must be characterized
in terms of “effective isolation” (Ricketts, 2001). This implies that, due to matrix effects, patches are more or less isolated than distance alone predicts.

Another important implication for within-fragment dynamics is the effect of the matrix on extinction rates. In the rainforest of southern Costa Rica, isolated trees in the matrix produce most of the seedlings in remnant forest patches, reducing the extinction rate within the fragment and maintaining continuous forest levels (Aldrich and Hamrick, 1998). Spill-over colonization was also documented in old field patches by plants in a closely mowed matrix (Cook et al., 2002). Carroll et al. (2004) found that as the quality of the matrix decreased, protected areas needed to be larger and more connected to sustain populations of grizzly bear and gray wolf. The contribution of matrix individuals to the persistence of patches cannot be ignored.

The third effect is that the matrix may provide alternate, though suboptimal, habitat for patch species. Rather than being completely inhospitable, matrix habitat supported rainforest trees and old field plants (Aldrich and Hamrick, 1998; Cook et al., 2002). Prairie voles were found to utilize the matrix extensively, and, in fact, their use increased with increasing fragmentation (Cook et al., 2004). It has been noted that the global persistence of a species across a landscape may depend on its ability to persist in the matrix at some low density until more favorable habitat conditions return (Jules and Shahani, 2003). Therefore, rather than being a biological sink, the matrix may represent a refuge, if not a biological source.

Recognizing the advances that have been made by including the matrix as an independent variable, the most forward-thinking paper argued strongly for also including temporal changes of matrix quality in fragmentation research (Jules and Shahani, 2003).
The authors suggest that by not considering the temporal context of the landscape, a layer of complexity is still being lost. This may be particularly relevant for the matrix which, at some point in time, was converted from patch habitat, creating the fragmented landscape. Drawing on the rich history of successional theory, this paper is an important reminder that natural or anthropogenic influences continue to operate on fragmented landscapes, changing the matrix and the effects it exerts. Monitoring studies that characterize the status of the landscape over time may be the best means to fully capture the ecological processes of the matrix.

Annotated Bibliography


The authors studied the reproductive contribution of isolated trees in the pasture matrix to remnant forest patches in the rainforest of southern Costa Rica. By evaluating genetic signatures, they found that adults in the pasture produced most of the seedlings in remnant forests (68.0%) whereas adults within the remnant patches produced few of their own seedlings (4.6%). They also discovered that a small subset of adults in the pasture population was dominating seedling production and that many of these seedlings were being self-fertilized, creating a genetic bottleneck. This study demonstrates that even though the matrix may not support reproductively viable populations, individuals can exist in the matrix, and, in fact, can significantly affect the life history parameters of patch populations. Seedlings from the matrix are reducing the extinction rate within nearby patches, and if they were removed, the patch density would fall below continuous forest levels. Therefore, without the spill-over colonization from matrix individuals, the remnant forest patches may become further fragmented.


In this study, the authors examined the relevance of island biogeography theory to mammal carnivore sustainability within protected-area networks. Specifically, they studied the effect of matrix quality on the population vitality of wolves and grizzly bears in three different subregions that represented a continuum of landscape contexts, from parks as semi-isolated islands surrounded by low quality matrix, to parks on the margin of continuously inhabited range, to parks embedded within a relatively benign matrix. They found that as the contrast between the park and the landscape matrix increased, the amount of park area and connectivity needed to sustain populations increased. The spatially explicit population modeling suggests that the protected-area network of the Rocky Mountains is not sufficient to support the persistence of large carnivores in a patch-matrix model of island biogeography theory. Interestingly, the authors found that the persistence of the patch-dependent species (grizzly bear) increased more with
doubling of connectivity than with doubling of patch size. As a result, they suggest that planning focus on ensuring functional connectivity in a broader landscape context (i.e., maintaining a high quality matrix).


This study tested the assumption of island biogeography theory that species richness increases with island area (species-area relationship). They found that this assumption was only true if there was no overlap in species composition between the patch and the matrix. When species were found in both environments, a spill-over colonization effect obscured the theoretical pattern. The authors state that this spill-over effect confounds conservation studies by obscuring “real” patch size and distance effects for patch-dependent species and that matrix species are simply “noise.” While this is a valid conclusion, this statement reveals an inherent bias of the authors toward patch obligate species rather than biodiversity. If they are interested in conservation planning for particular species, then species richness is not the correct metric for characterizing the landscape. However, if they are interested in sustaining viable populations of all species within patches, or maintaining biodiversity, then the contributions of individuals from the matrix should be appreciated.


The authors tested the concept in fragmentation theory that population density decreases with decreasing patch size. Using trapping methods, they found that prairie voles (*Microtus ochrogaster*) used the matrix extensively, and that their use increased with increasing fragmentation. Therefore, since population density estimates have patch area as a denominator, voles show a negative density-area relationship (i.e., higher population density with smaller patch area). The authors suggest that this pattern is problematic for conservation planning since it suggests that smaller patches support higher population densities. While this conclusion is counterintuitive to fragmentation theory, it reinforces the importance of the matrix for this species, both as alternate habitat and for maintaining patch populations. It also adds to the literature that species respond differently to the matrix, and that model systems, such as the *Microtus* spp., should be implemented carefully.

**Driscoll, Don A. 2005. Is the matrix a sea? Habitat specificity in a naturally fragmented landscape. Ecological Entomology 30: 8-16.**

This study tested the assumption of island biogeography and metapopulation theory that landscapes can be divided into binary classes of habitat patch and non-habitat matrix. The authors studied beetle abundance and species richness in three habitat types, rainforest and eucalypt forest (patches) and buttongrass sedgeland (matrix), using pitfall traps. They found that approximately 60% of the species they captured displayed habitat specificity for forested landscape, suggesting that for at least 40% of species, island biogeography and metapopulation theory are not relevant. This study demonstrates that traditional patch-matrix definitions are not appropriate for all species. The matrix does not always act as a biological sink, but may provide alternate habitat. It is interesting to
note that the authors defined patch and matrix based on vegetation cover rather than life history traits of the species. It would be interesting to determine if alternate delineations of patch and matrix would produce results that followed traditional theory. Further analysis of the species-specific requirements for maintaining reproductive populations may be necessary to fully understand interaction between the landscape structure and individual species.


This paper presents a possible next step in the successional line of conceptual landscape models. From island biogeography theory that classified land as either habitat or non-habitat to McIntyre and Barrett’s (1992) variegation model that recognized gradients in habitat suitability, this paper takes the next step in characterizing the landscape as a map of overlaid habitat suitability contours for different species. In addition, it emphasizes that habitat is species-specific and argues that landscape models should focus on individual responses rather than classifying habitat based on vegetation cover. There are many advantages to a habitat contour map, including the communicative power of explaining why entire landscapes need to be managed instead of certain patches and the ability to display ecological complexity. However, it would seem almost impossible to create habitat suitability maps for each species in a region, raising the question of which species to include in the model and why. In addition, the amount of data and analysis needed to sufficiently characterize habitat for each species is not trivial. For example, the authors surveyed more than 150 sites in order to use logistic regression to relate greater glider presence to habitat attributes. Therefore, while this may be an excellent theoretical tool, the quantitative inputs may be unattainable.


This study investigated the effects of different matrix types, different edge types, and distant resource patches on the movement behavior of adult goldenrod beetles. The authors tracked the movement of 30 adult beetles through the following three land cover types: goldenrod, netting over cut vegetation, and cut vegetation. The netting was low in food availability, like the cut vegetation, but high in structural complexity, like the goldenrod. They also assessed the responses of beetles to distant goldenrod plants and to all combinations of patch edges. Beetles did not respond to distant goldenrod plants or to different edge types, but did have different movement behaviors in the cut vegetation than they did in the goldenrod and netting. This is an important conclusion because dispersal ability is often considered a constant, species-specific trait. This study shows that the interaction between the matrix and an organism’s movement behavior will dictate movement ability. Therefore, the matrix may affect local distributions, local population dynamics, and persistence of regional metapopulations by influencing the movement ability of the species.

Haynes and Cronin conducted a meta-analysis to evaluate whether the hypothesis that matrix composition affects dispersal has been adequately tested. They suggest that patch quality and the type of surrounding matrix often co-vary, flawing conclusions that the matrix affects dispersal. Of the eleven studies they found, five provided evidence that the matrix effects on dispersal were not due to confounding effects of patch quality. They suggest that future studies measure movement rates within each matrix type or experimentally control or manipulate patch quality, in order to address landscape-matrix questions. This paper is an important reminder of the complexity of the interaction between organisms and the landscape, and that what humans perceive as causative agents may merely be circumstantial correlations that are not truly driving ecological processes. In order to make the strong conclusion of cause and effect, direct evidence of reactions to single variables is necessary, a very difficult threshold to meet in environmental studies.

This discussion paper contrasts the traditional theories of fragmentation (island biogeography and metapopulation theory) with recent studies demonstrating the importance of the matrix. In newer fragmentation models, the matrix is an array of different habitat types with the potential to influence migration rates, the movement of pollen, the quality and extent of edge effects in fragments, and within-fragment dynamics. The authors challenge researchers to take the next step, however, arguing that temporal changes in matrix quality can alter matrix effects and that unless this temporal component is included in studies, the concepts of matrix quality will still oversimplify the real landscape. This is an important point for landscape ecology, particularly in regards to the matrix which is often not in equilibrium. Natural or anthropogenic influences continue to alter the matrix after the initial conversion from habitat. Recognizing the temporal nature of the matrix, in addition to its quality, will broaden the findings of matrix effects within the landscape.

This paper is a review of the important effects of the matrix on the regional dynamics of plants. Since it appears that plants are not arranged as metapopulations, the authors suggest a new paradigm combining the species-specific aspects of metapopulation theory (i.e., idealized habitat in a featureless landscape) with landscape ecology (i.e., the effects of landscape structure and spatial configuration on ecological processes). Termed the functional mosaic model (after Forman, 2002), they consider the matrix a key component in landscape connectivity, which they define as a composite of structural context (physical and spatial parameters) and functional context (community and population level parameters). By evaluating these parameters within each cell of a grid, the landscape is classified as a gradient without needing to explicitly define patch and matrix habitat. Similar to other concepts, this approach attempts to capture ecological complexity in a composite mosaic, so that landscape pattern is linked with ecological processes. While this is a review paper with no specific recommendations for implementing this approach, it is a call to action for an integrative perspective that combines landscape ecology and population dynamics, and provides a list of parameters to consider.
Thirty Iberian lynx were captured and radio-tagged in southwestern Spain. Lynx were located at two temporal scales, hourly and daily. Movement properties were estimated using the Euclidean distance moved per hour, the net Euclidean distance between first and last location, the total distance moved during the period of activity, and the movement directionality. An individual-based spatially explicit simulation model based on the observed movement properties at the intraday temporal scale was created and tested. The authors found that movement capacity (the duration of a dispersal event) explained 27% of the variance in interpatch connectivity, while matrix heterogeneity explained an additional 53% of the variance. Therefore, habitat distribution was more important than interpatch distance in determining the connectivity between subpopulations. As mentioned by Ricketts (2001), there is an “effective isolation” that makes patches more or less isolated than simple distance would indicate. This study is an excellent model for landscape ecology because it considered both the spatial and temporal resolution of the analyses and how lynx were interacting with the landscape at different scales.


This study tested the hypothesis that the matrix affects migration and extinction rates by observing a butterfly community inhabiting meadow patches surrounded by the following two contrasting matrix types: conifer forest and willow thicket. Using mark-recapture studies of 21 species of meadow obligates, Ricketts tested the null hypothesis that dispersal was a function of distance alone, that emigration rate was not related to the vegetational composition of patch edges, and that emigration and immigration rates were not related to meadow quality. Movement was not affected by edge composition or meadow quality; however, he did find that different matrix types had different relative resistances for four of the six taxa studied. He termed this phenomenon “effective isolation,” the fact that patches are more or less isolated than simple distance would imply. Another important conclusion was that limited generalizations of the effect of the matrix on migration rates could be made, suggesting that the resistance of a matrix type will be species-specific.


This paper provided excellent background on the historical context of island biogeography and metapopulation theory and the transformation of the concept of the matrix over time. The authors conducted intense modeling efforts to determine the degree to which the matrix approximates these classic theories. I had particular difficulty with the models because they all assumed that individuals that did not move out of the matrix during the time step following when they entered the matrix would die. This assumption led to the conclusion that there is a general tendency toward extinction of the fragment population as the quality of the matrix increases, since animals were more likely to enter the matrix as its quality increased. It would have been more appropriate to
have the sink properties of the matrix fluctuate with the quality of the matrix. While the background theory of the paper is substantial, the usefulness of the models or their results is questionable.

Additional References

