

## Forum

# A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought

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**Abstract.** Consequences of habitat fragmentation have garnered much attention over the past few decades. The resulting literature has been useful for understanding how land-use changes influence population viability and community structure, but we are still hampered by a major aspect of the conceptual framework within which most fragmentation work arises. Specifically, habitat between fragments ('matrix') is usually treated as uniform and ecologically irrelevant. However, recent work on animals shows that matrix habitat can profoundly influence within-fragment dynamics. We review related evidence for plants. Various matrix types (e.g. clear-cutting, agriculture, or urbanization) can act in different ways to alter resource availability and movement of pollinators, seed dispersers, and herbivores. Inclusion of matrix qualities in fragmentation studies is further complicated since most matrices are not static; sites in which timber harvesting or agriculture occur develop through succession or change as crops are rotated, respectively, such that their influence on within-fragment processes vary temporally. Also, many plants are not restricted to remnants of original habitat. Using studies of forest understory plants, we summarize work showing how diversity can change significantly through time in matrix. Understanding the persistence of a species across fragmented landscapes will require more attention to matrix habitat, and to the species utilizing the matrix.

**Keywords:** Clear-cut logging; Extinction; Habitat remnant; Patch dynamics; Plant population viability; Succession; Understorey vegetation.

## Introduction

Over the short history of conservation biology, the paradigm of habitat fragmentation and its population and community effects has acquired ever-increasing importance as a unifying concept with which to understand the genesis and solution of conservation problems. Habitat fragmentation engenders images of once contiguous landscapes being destroyed piece by piece – the original habitat reduced in size and converted to isolated remnants of habitat surrounded by

new types of habitat, such as agricultural fields, urban development, and roads. There is no question that the many effects of fragmentation have the potential to be harmful; species restricted to remnant fragments can experience increased extinction risks due to a multitude of changes, including reduced population sizes, decreased gene flow, and changes in interspecific interactions that influence demographic rates (Young & Clarke 2000; McGarigal & Cushman 2002). Conservation efforts have benefited enormously from both theoretical and empirical work on these effects of fragmentation.

Both the power of the pioneering research on fragmentation – as well as its ultimate shortcomings – lie in its roots in island biogeography and metapopulation theory. In their simplest forms, these theories have allowed ecologists working in terrestrial systems to treat their study regions, such as forested landscapes, as one would treat an island archipelago in an ocean. The predictions developed are simple and elegant: fragments that are relatively small and/or isolated should experience reduced immigration rates, harbour populations with elevated extinction probabilities, and eventually contain fewer species (Simberloff 1988; Doak & Mills 1994). Fragments of remnant habitat are considered analogous to islands, and, importantly, all of the newly created area between fragments (termed 'matrix') is analogous to ocean, an area treated as ecologically uniform and thus unimportant for the fate of populations within fragments (Ricketts 2001; Vandermeer & Carvajal 2001). Specifically, because dispersal between fragments has usually been treated as a function of fragment size and isolation distance alone, ecologists have focused their attention solely on fragments of habitat, ignoring characteristics of the 'ocean' component of their systems.

Recently, there has been a growing realization of the importance of matrix quality in governing the dynamics of population and community-level processes in fragmented landscapes (e.g. Gustafson & Gardner 1996; Vandermeer & Perfecto 1997; Fahrig 2001; Vandermeer & Carvajal 2001).

Under these newer models of fragmentation, the matrix is not viewed as one kind of habitat, but rather as an array of different habitat types (e.g. urban developments, farms, clear-cuttings, etc.). The ecological qualities of matrix have the potential to influence migration rates between fragments, the movement of pollen, and the quality and extent of edge effects into fragments. Consequently, within-fragment dynamics will vary as a function of the matrix types surrounding individual fragments.

Several empirical studies of animals support the importance of matrix quality in fragmented landscapes (e.g. Andr  n 1995; Sisk et al. 1997; Daily et al. 2001; Bayne & Hobson 2002). Ricketts (2001), for instance, demonstrated that the movement of some butterfly species between meadow patches can be strongly influenced by the type of intervening matrix habitat (i.e. willow thicket or conifer forest). Franklin et al. (2000) showed that the owl *Strix occidentalis* in northwestern California has greater fitness in areas with a mosaic of old-growth forest interspersed in a matrix of other vegetation types than in areas composed solely of old-growth. The type of matrix habitat can also influence the diversity (Sisk et al. 1997), survival (Bayne & Hobson 2002), and nesting success (Bayne & Hobson 1997) of passerine birds in remaining fragments.

There is a growing literature documenting a diversity of ways in which matrix landscapes can strongly impact plant populations at specific life history stages. However, little work has directly tested the role of matrix quality in governing overall plant population persistence or community structure. Still, effects on particular life stages likely scale up to larger effects on population health. Here, we review this literature, and suggest that further research is needed. Furthermore, we argue that the inclusion of temporal changes in matrix quality in fragmentation research will add a layer of complexity not yet discussed in recent work. Most matrix habitats are constantly changing through time (e.g. successional changes), such that effective long-term models of fragmented landscapes require a highly dynamic view of the matrix.

We first discuss how characteristics of different matrix types can influence plant life history components for which there is appropriate data. Specifically, we discuss the mechanisms by which matrix quality can affect pollination, seed set, herbivory, and seed predation. Although effects of matrix on other interactions (e.g. seed dispersal) are likely, we were unable to find any work exploring these effects. We also review work that is suggestive of matrix influences at the population level, and infer likely community-level implications; our review is limited to only highly replicated studies, with two exceptions where replication across sites was not possible due to species rarity (noted in text). Next, we show that temporal changes in vegetation within matrix habitats are likely to be of critical importance in fragmented regions. Finally, we make recommendations about how these data should be used to influence future research.

### The influence of matrix quality on within-fragment dynamics

The fragility of plant-pollinator mutualisms has received much attention in recent years, as there has been growing concern over pollinator declines and subsequent reproductive failure of plant populations. Matrix habitat alteration has been identified as one of the potential drivers of a 'pollination crisis' (Kearns et al. 1998; Buchmann & Nahban 1996; Cane & Tepedino 2001). For instance, reduced pollinator communities due to urbanization of the surrounding landscape were suspected to cause significant seed set reduction in a reintroduced population of an endangered salt marsh plant in California, where hand pollination of *Cordylanthus maritimus* ssp. *maritimus* increased seed capsule set by 89% in 1992 and 52% in 1993 (Parsons & Zedler 1997; note these hand pollinations could only be conducted at one site). Such substantial effects on reproduction would quite likely have strong impacts on population health, but they may even impact the evolutionary trajectories of plant populations. For example, in studying the endangered heterostylous *Primula sieboldii* in Japan, Washitani et al. (1994) found that only one genet, with a rare short homostyle morph, was able to successfully set seed (via self-pollination) in the absence of pollinators; further, both of the other style morphs were found to be pollinator limited, as artificial hand pollination increased seed set in pin flowers by > 780%, and in thrum flowers by 1700%. Washitani (1996) later predicted that the observed shortage of pollinators, most likely due to the increasing urbanization of lands surrounding the reserve in which *P. sieboldii* occurs, exerts a strong enough selective pressure to outweigh the costs of inbreeding depression, potentially leading to elimination of the less self-fertilizing style morphs from the population.

There are three primary mechanisms by which altering matrix habitat may influence the availability of pollinators in fragments, with cascading effects on the plant species that rely on them for pollination services. First is the problem of 'partial habitats' (Dunning et al. 1992): the pollinator may require different habitats at different stages in its life history, and disrupting any of the resources that it requires may have strong effects on pollinator population size. This problem has been highlighted by Westrich (1989), who detailed the phenomenal complexity and specificity of nesting versus foraging requirements of various solitary bees. Secondly, in some cases (certainly in the case of timber harvest in forests) matrix alteration results in an abundance of new or augmented plant populations competing for visitation by some of the same pollinators. If these plants offer greater nectar or pollen rewards, they may be preferred and the competing species within the nearby fragments rejected; conversely, as demonstrated by work on bordercrops in agro-ecological systems (Lagerl  f et al. 1992), the additional lure provided

by flowering plants in the nearby matrix may serve to augment pollinator numbers and increase pollination rates of plants in remnant patches (i.e., crop fields). Note that in these situations, it is important to also consider the issue of pollinator effectiveness (Kunin 1993): an effective pollinator must not only visit a plant, but must also be faithful enough to that species to transfer significant amounts of conspecific pollen.

The third mechanism by which pollinator communities may be affected by matrix composition is through the 'permeability' of the lands separating habitat patches. Several theoretical models address the likelihood of this problem (Stamps et al. 1987; Gardner et al. 1989), and recent empirical work has documented this effect in insect taxa, with some habitats being less traversable than others by butterflies (Roland 2000; Ricketts 2001) and damselflies (Pither & Taylor 1998). Though little field research has addressed this issue for other insect species (Cane 2001), it is likely that bees and other pollinators would be similarly affected. For example, Westerbergh & Saura (1994) found that *Silene dioica* populations surrounded by open pine and birch forest experienced higher rates of gene flow than populations surrounded by dense spruce forest. Because anthropogenic movement of seed through this landscape is very unlikely, they concluded that restricted movement of bumblebee and fly pollinators through the spruce matrix was responsible for lower genetic diversity.

The composition of the matrix landscape may affect herbivory patterns as well. There is a rich literature in agro-ecology regarding the role of border crops in drawing natural enemies of herbivorous insect pests into crop field 'fragments' (reviewed in Altieri 1993). Work on natural enemies of California vineyard pests has demonstrated that the matrix landscape can play a role similar to border crops by providing partial habitat. For example, egg parasitoids (*Anagrus*) of grape leafhoppers, notorious crop pests in California vineyards, are known to overwinter in French prune trees, which are frequently planted adjacent to vineyards to maintain populations of *Anagrus*. However, Corbett & Rosenheim (1996) found that the French prune tree refuges contributed 1% and 34% of the early-season *Anagrus* population in the two vineyards that they studied. The remaining *Anagrus* individuals found at each of these vineyards came from overwintering sites in the surrounding matrix lands, outside of the cultivated French prune tree system. This result highlights the importance of the matrix landscape in maintaining and determining trophic relationships, in particular when one or more of the players requires multiple habitats to complete its life cycle.

Variation in matrix habitat may affect seed predation in similar ways to those discussed above regarding herbivory: higher-level trophic interactions may regulate numbers of seed predators, and thus rates of seed predation.

For example, demographic rates of predators may be elevated in some matrix, thus increasing population sizes and, consequently, overall predation rates in adjacent fragments (Jules & Rathcke 1999; Tallmon et al. in press). Curran et al. (1999) found drastic effects of logging in matrix surrounding a national park in Borneo on dipterocarp trees within the park. Dipterocarps in this area engage in landscape-level interspecific mast synchrony. Mast-fruiting in this taxon generally serves to preoccupy seed-predators with foraging in some areas, while elevating dipterocarp recruitment in other areas (Curran & Leighton 2000). However, intensive logging of dipterocarps in the surrounding landscape has increased seed predator abundance such that dipterocarp trees within the protected area experience consistent reproductive failure (Curran et al. 1999; Curran & Webb 2000).

With the diversity of ways in which matrix lands may affect different stages of a plant's life history, it is difficult to imagine that these effects do not combine to create strong consequences for plant population health in habitat fragments. While no work has directly demonstrated matrix effects on plant population health to date, a study of regional turnover in populations of serpentine seep plants by Harrison et al. is suggestive (2000). They conducted a three-year survey of 132 serpentine seeps in a 4200 ha area, noting population densities of five serpentine endemic plant species at each seep. Pairing this work with data from surveys conducted 15 years prior, they found that populations that were more isolated from conspecifics were more likely to go extinct, a result that may be driven by the 'rescue effect': lower rates of recolonization are thought to result in higher extinction rates for more isolated sub-populations (Brown & Kodric-Brown 1977). However, they additionally found that populations that did go extinct were significantly closer to human disturbance in the surrounding matrix lands than populations that persisted. While this correlational work does not directly identify a mechanism that is responsible for this pattern, it does point toward matrix effects on population health.

The role of matrix in fragmented landscapes is not as simple as we have portrayed using our limited set of examples. It is important to bear in mind that while some matrix habitats will have deleterious effects on plant populations, others may have positive overall effects – and also that the same matrix landscape may influence plant populations in both positive and negative ways. For example, Steffan-Dewenter et al. (2002) found counterbalancing effects of matrix habitat on *Centaurea jacea*, such that the positive effects of increased pollinator visitation with increased semi-natural habitat in the matrix landscape were offset by the negative effects of increased numbers of seed predators. Such complex relationships will make it difficult to tease apart the various effects of matrix habitat on plant populations.

### Temporal changes in the matrix

While the quality of the matrix can have significant consequences for fragmented populations, it would be a mistake to assume that these influences stay constant through time. Contrary to classical paradigms in conservation ecology, few fragmented landscapes are comprised of 'fixed' matrix types. Rather, most habitat converted to matrix will continue to change, either by natural or anthropogenic influences, after its initial conversion. For instance, many areas in tropical South America experience timber harvest followed by one of three scenarios: (1) abandonment and re-growth of forests, (2) conversion to agriculture, or (3) conversion to agriculture followed by abandonment (Carroll et al. 1990; Rudel & Horowitz 1993). Likewise, matrix landscapes in the Pacific Northwest of North America often experience periodic logging with continual growth and change between harvests (Franklin et al. 1996).

There are two reasons why temporal changes in matrix are important. Most obviously, because matrix quality can influence within-fragment dynamics, these effects may change as the matrix changes. For instance, as a forest regenerates after timber harvesting, the permeability of the matrix for pollinators or seed dispersers may be altered. The second reason is of equal importance for understanding the long-term persistence of a species in fragmented landscapes, and is comprised of two parts. First, at least at some points in its changing condition, the matrix landscape often harbours sizeable plant populations, in contrast to the traditional model of fragmentation which suggests that species considered in fragmentation studies will be entirely restricted to fragments. Second, remnants of original habitat are often rare or non-existent across large areas, such that a species' persistence may depend entirely on its ability to utilize matrix. In this latter case, the landscape can be thought of as one in which every site within the area is converted to some initial condition (e.g. a clear-cutting) and then allowed to develop for a certain amount of time (e.g. until the next harvest). In landscapes representing this model, global persistence across the landscape depends on a plant's ability to colonize matrix habitats at a rate that mitigates the effects of constant site conversions across the landscape, or to persist in the matrix habitats at some low density until more favourable habitat conditions return.

Extending the context of fragmentation studies to include temporal changes in matrix quality on within-fragment and within-matrix and landscape-level dynamics requires information on vegetation changes through time. Fortunately, there is a rich history of ecological research on the relationship between forest age and plant community composition (e.g. MacLean & Wiens 1977; Peterken & Game 1984; Halpern 1989; Duffy & Meier 1992). For the sake of brevity, we discuss only temporal changes in forest understory flora that accompany post-logging regeneration.

There has been considerable debate over the response of

understory vegetation to timber harvesting (Johnson et al. 1993; Duffy 1993; Matlack 1994), and responses are likely to be system-specific (Halpern & Spies 1995). Nonetheless, some conclusions can be reached. First, a number of studies have tracked understory composition in fixed-plots, starting prior to timber harvest and sampling for several years to several decades afterwards (e.g. Dyrness 1973; Halpern 1989; Schoonmaker & McKee 1988; Roberts & Zhu 2002). In Pacific Northwest forests, understory plant species frequently exhibit significant declines following timber harvest, although these declines are quite short-lived; most understory plants are resilient to clear-cutting and recover to pre-harvest levels in matrix during the study period (Halpern & Spies 1995). Unfortunately, these studies are limited to relatively short-term studies in sites that have been harvested less than ca. 40 yr before present. As an alternative, ecologists have frequently assessed chronosequences of forest ages or compared older forests with post-harvest forests of various ages (e.g. Whitney & Foster 1988). These studies show significant differences in understory plant communities related to the age of regenerating forest. Peterken & Game (1984) found that richness of vascular plants in ancient woods (400+ yr old) was significantly greater than in recent woods (< 400 yr) in Great Britain. Similar results were found by Dzwonko & Loster (1989) in woodlands of the Carpathian foothills of eastern Europe, and by Honnay et al. (1999) in forests of Belgium. Halpern & Spies (1995) studied young (30-79 yr), mature (80-190), and old-growth (130-900 yr) forests in the Pacific Northwest. In general, their results support a model in which diversity is initially high after clear-cutting, declines to its lowest point when the forest canopy closes, and begins to increase to its highest point (in old-growth) once light-gaps begin to open the canopy.

The studies we describe above are relevant for fragmented landscapes in several ways. First, while it is obvious that temporal changes in the matrix resulting from the development of, for example, increased forest structure may be important for permeability of the matrix, there are also more subtle changes that may be critical. Temporal changes in understory plants in the matrix will alter floral resources, host availability for herbivores, and propagule abundance, among other factors that might influence the connectivity of remnant fragments. Second, the wealth of understory diversity seen in matrix forest habitats shows clearly that matrix does not usually fit the 'ocean' analogy in the island-ocean model. For the many plants found in both remnant fragments and matrix habitat, understanding their landscape-wide persistence can only be attained by study of population dynamics in both matrix and fragments, rather than in fragments alone.



## Synthesis and Conclusions

Although traditional concepts of habitat fragmentation have generally ignored the quality of matrix in governing the abundance of species across landscapes, there is ample evidence to suggest that increased study of matrix is necessary. In particular, little attention has been paid to the role of matrix habitat for plants. The various matrix types in which fragments are embedded can have very different influences on within-fragment dynamics, including both positive and negative effects on life history processes and population viability. The lack of studies on these influences has limited our general understanding of how fragmentation may affect biological diversity.

While plants and matrix have not been studied directly, the need for increased attention to matrix, in general, has been discussed by others (e.g. Gustafson & Gardner 1996; Fahrig 2001; Ricketts 2001; Vandermeer & Carvajal 2001). We suggest, however, that enriching the traditional island-ocean theories of fragmentation with concepts of matrix quality can still oversimplify the real landscape. Because the matrix at any given location is often changing in time, its influence on within-fragment dynamics has the potential to change as well. Temporal changes in the matrix can alter matrix effects on within-fragment dynamics and can alter the abundance and persistence of species not restricted to fragments. The changes are most likely to be important in areas where vegetation develops relatively quickly after initial conversion to matrix, and where there is little original habitat left.

Our review suggests that studies of plants in fragmented habitat should follow several avenues. First, studies should continue to focus on within-patch dynamics, as they have for several decades, but they should add measures of matrix quality to the usual list of explanatory variables. Second, studies should be purposely designed to understand the differential effects of matrix types on isolated populations in fragments, and to detect the temporal variation of these effects. Finally, more focus is needed on plants that are not entirely restricted to remnants of the original habitat. For these plants, it will be crucial to understand how these species persist in matrix, how much time is required for population sizes to recover, and what mechanisms drive population trajectories. Clearly, shifting our view of fragmented landscapes toward the full inclusion of matrix in our conceptual models is a positive step in applied ecology.

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