MINI-REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter?

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Recent reviews of evidence for plant metapopulation prevalence in nature have concluded that most species appear not to be arranged as metapopulations – hence other frameworks may be necessary for understanding large-scale, regional dynamics in plants. Separate but related paradigms from the disciplines of landscape ecology and metapopulation ecology exist for understanding patterns of regional population variation. The major models of both paradigms assume a binary landscape mosaic composed of "suitable habitat" and background "matrix." An important distinction between the two approaches is that metapopulation models essentially ignore features of the matrix. A binary approach to the landscape seems inappropriate for plants for several reasons. First, plants probably do not have a binary perception of the landscape, but rather respond to gradients of resource quality. Thus properties of patches, or the matrix per se, may be less important than the nature of the landscape mosaic, in particular as this is reflected in terms of connectivity. Secondly, many plants rely on a range of other agents for dispersal of pollen and seed, all of which are also affected by their environment in terms of connectivity. Furthermore the various components of the mosaic, including physical, spatial and functional elements can significantly influence plant movements. We review important effects of the matrix – via composition and configuration of habitat patches, extent of edges, patterns of land use, etc., upon plant populations.

We describe evidence supporting a general integration of metapopulation and landscape ecological approaches for understanding regional dynamics in plants, emphasizing notions of connectivity (traditionally measured in very different ways by metapopulation and landscape ecologists), and context, an emerging concept describing components of variability in the landscape from a species-specific perspective. Finally, we describe a functional landscape mosaic approach that treats structural and functional features of the landscape and show how these interact to determine the fate of plant populations.

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Ecological analysis at large spatial scales has emerged over the past decade as the subject of two, quite distinct sub-disciplines: metapopulation ecology and landscape ecology. The former provides one framework for understanding population dynamics – as consequences of migration, colonization, and extinction events in spatially structured habitats (Hanski and Gilpin 1997). In theory, metapopulations represent the organisms inhabiting regional landscapes – the reef fishes, grizzly bears, buttercups and butterflies, each experiencing its environment at unique, species-specific scales. At the same time, the study of landscape ecology considers a variety of subjects, including population dynamics, however its general goal is often summarized as the effects of landscape structure and spatial configuration on ecological processes (Tischendorf and Fahrig 2001, Turner et al. 2001).

The major theoretical models of both landscape ecology and metapopulation ecology assume a binary landscape, composed of "habitat" and "matrix" (i.e. the non-habitat surrounding native habitat patches, Wiens 1997). Metapopulation models have focussed almost exclusively on the habitat patch component, rather than the matrix (Ricketts 2001). An important distinction between the metapopulation approach and the spatially-explicit population approach of landscape ecology is that metapopulation models essentially ignore the characteristics of the non-habitat, or matrix portion of the landscape (Ims and Yoccoz 1997). In contrast, landscape models often assume that movement between patches depends on attributes of the matrix, which may influence dispersal mortality and/or movement direction (Tischendorf and Fahrig 2000a, 2001). At the same time, too much research in landscape ecology seems to focus more upon elements of spatial explicitness than on the biology of living organisms. Each of these emergent ecological sub-disciplines would seem to benefit from the integration of some of the approach of the other.

Plants differ from animals in several fundamental features of life history. In this paper we focus upon these features in plants to better understand patterns of regional variation. At all spatial scales, suitable environments are interspersed in a matrix of more or less inhospitable space (Eriksson and Ehrlén 2001). This means that for most plant species a fragmented habitat is the physical arena within which population dynamics, ecological processes, adaptation and evolution occur. As Eriksson and Ehrlén (2001) have shown, persistence of plants over the long term requires coping with temporally and spatially unpredictable resources. Many plant life-history features, including dispersal structures, seed dormancy, seed size and clonal propagation can be interpreted in this context – in conjunction with the rootedness of plants, necessary for capturing the diffuse water and mineral resources in the soil and of CO_2 in leaves. For example, the existence of long-lived life cycle stages (seeds, vegetative ramets) means that local populations may persist for a long time even though a patch has become unsuitable. Ehrlén and Eriksson (2003) argue that successful dispersal and recruitment in plant populations may be very sporadic and therefore recolonization is unlikely after local population extinction. In plants, dispersal over long distances may be governed by significant stochasticity. Moreover, while the definition of long distance may differ between species it is only infrequently more than a few hundred metres (Cain et al. 2000).

The over-riding importance of dispersal has long been recognized in influencing large scale patterns of distribution and geographic ranges in terrestrial plants (Reed et al. 2000). For plants, the mobility of the recruitment stage occurs primarily through dispersal of seeds or propagules, and via pollen movement (Bullock et al. 2002, Thompson et al. 2002). It is inherently difficult to track individual seeds as they disperse from a parent plant to their final site of deposition, and especially the rare, longer-distance events which are generally required for colonization of new habitat (Greene and Calogeropoulos 2002, Wang and Smith 2002). Such difficulties are doubly true for tracking pollen-mediated dispersal events (Dow and Ashley 1998, Waser et al. 2000). Understanding landscape matrix effects on connectivity, as it relates to large scale population dynamics, requires understanding the movements of those animals which disperse seeds, most commonly birds, mammals and ants (Chambers and MacMahon 1994), as well as the agents which move pollen.

As Raybould et al. (2002) have described, progeny fitness tends to be dependant on the distance between parents, so classical metapopulation biology may be sufficient. However, the extent of outcrossing may be an important confounding factor (Byers 1998, Waser et al. 2000, Greene and Calogeropoulos 2002). In animal-pollinated plants, reproductive success may be negatively related to the distance between flowering patches; several studies have documented lower success in isolated or fragmented populations (Aizen and Feinsinger 1994, Groom 2001). Furthermore, even when pollinators successfully travel long distances between patches, the quality of the pollen transferred may decline. For example, generalist pollinators may visit a variety of species when travelling longer distances, and heterospecific pollen may clog stigmas and lower reproductive success (Groom 2001).

There is an obvious acknowledgement of the importance of concepts of landscape ecology in the metapopulation literature (Hanski and Gilpin 1997). Yet it must also be reckoned that the major elements characterizing landscape ecology remain absent from metapopulation models, which are typically focused on idealized habitat in a featureless landscape (Wiens 1997). Wiens (1997) gave two reasons for the lack of integration. First,

metapopulation theory continues to be tied to a simplistic patch-matrix view of the landscape. Second, due to the challenges in quantifying complex spatial patterns, landscape ecology has not developed theoretically to a point that enables a body of metapopulation theory, which is already relatively complex, to encompass it. Here we will suggest that an integrative, landscape perspective promotes understanding of large-scale spatial dynamics in plants.

The matrix from a plant perspective

From a plant's perspective, there are several reasons why an integrated perspective on the landscape mosaic is important. When the distinction between habitat and non-habitat (matrix) is fairly clear, definition of distinct habitat patches is relatively uncomplicated and species dynamics may be described in terms of the properties of those patches (Thomas and Kunin 1999). For example, suitable habitat may be relatively easily defined for obligate epiphytes growing on tree trunks, or for hemiparasitic mistletoes growing in tree canopies. However for many other species, in particular those having relatively broad limits of physiological tolerance, there is often no clear distinction between habitat and matrix, and defining distinct habitat patches becomes difficult or impossible (Freckleton and Watkinson 2002). Assessment of 'empty' but suitable patches is even more difficult, and there are still only a few studies that have used experiments to estimate occupancy in plants (Ehrlén and Eriksson 2000).

Most plants probably respond to gradients of resource quality (With et al. 1997). For these species, suitable habitat lies along some environmental continuum, from optimal habitat, through suitable, and sub-optimal, with many biotic and abiotic parameters contributing toward suitability. Where a species does not perceive sharp and distinct boundaries, patch properties become less important and the nature of the overall landscape mosaic becomes increasingly significant in species' dynamics (Thomas and Kunin 1999).

It is perhaps not surprising then that a major conclusion from the several recent reviews of plant metapopulation prevalence in nature – by Husband and Barrett (1996), Bullock et al. (2002), and Freckleton and Watkinson (2002) – was that many plants appear not to be arranged as metapopulations. Hence other frameworks may be necessary to understand large-scale, regional dynamics in plants (and perhaps also other organisms, sharing relevant life history features). As Freckleton and Watkinson (2002) have described for plants, at the regional scale some species appear to exist as metapopulations in the classic sense, where regional persistence is governed by the processes of patch colonization, extinction and recolonization. However

according to Freckleton and Watkinson other species exist as regional ensembles, systems of essentially unconnected local populations persisting in an ill-defined mosaic of suitable and unsuitable habitat; while still others exist as spatially extended populations, essentially a single, extended population occupying large tracts of suitable habitat, but whose regional dynamics exist as a simple extension of local dynamics. We note that Ehrlén and Eriksson (2003) have recently argued that the typology of Freckleton and Watkinson (2002) may be interpreted as if local processes alone are sufficient to understand regional dynamics for most plant populations. Ehrlén and Eriksson (2003) state that the available evidence indicates local processes are insufficient for understanding regional dynamics in most plant species and suggest that metapopulation theory should be developed further as a tool for studies of plants, rather than being replaced by a new typology. Pannell and Obbard (2003) point out that the metapopulation terminology has been successfully adopted in evolutionary and population-genetic analysis of species that do not occupy readily identifiable habitat patches. In these analyses it is the discrete nature of the groups of organisms involved, rather than the discrete nature of the habitat patches, that affects important aspects of population genetics.

We support the conclusion of Freckleton and Watkinson (2002) that most plant populations appear not to be organised as metapopulations. However, like Ehrlén and Eriksson (2003), we do not find the new typology necessarily useful and suggest that the landscape mosaic approach we present here for understanding regional dynamics of plant populations benefits little from this pre-characterization of the nature of the regional dynamics. Rather, as Thomas and Kunin (1999) noted, many such labels might better be considered as points on continua, and in fact populations may exhibit elements of several categories, or their definition may be dependant on a particular spatial or temporal scale.

The assumption in metapopulation ecology that properties of the matrix are unimportant is probably only really true for terrestrial organisms inhabiting oceanic islands. This situation sits at one extreme of a continuum extending from situations such as these true islands, where the marine matrix is completely inhospitable and quite homogenous (Gilpin and Diamond 1980), through the (paradigmatic) metapopulation landscape where discrete habitat is separated by a homogenous matrix that is not suitable for colonization but is also not fatal to dispersers (Ims and Yoccoz 1997), and finally to continuous habitat in which the matrix nature is indistinguishable from the patch (Vandermeer and Carvajal 2001). One feature that distinguishes terrestrial habitat fragmentation from the true island model (of MacArthur and Wilson 1967) is that the matrix may, for some species, actually be hospitable to varying degrees.

In this case the matrix should have a strong influence on the between-patch processes of dispersal and colonization, as well as the within-patch processes of extinction, population growth and density dependence (Davies et al. 2001). The matrix has at least three potential roles in between-patch processes: (1) reducing or enhancing dispersal and colonization rates; (2) providing alternative, though possibly sub-optimal, habitat; and (3) as a source of novel invading species competing for patch space (Davies et al. 2001, Cook et al. 2002).

Characterizing the matrix: toward a functional mosaic approach

In principle, the matrix begins at the edge of a patch and is composed of an array of natural and anthropogenically-derived features which tend to act as barriers to, or conduits for, biotic movement. Researchers have sought to characterize and quantify the matrix in various ways. Of the many structural features of the landscape, corridors have received the greatest attention, mostly from conservation biologists (Wiens 2002b). Corridors through the matrix are thought generally to facilitate movement between patches within fragmented landscapes, and thus impact regional population dynamics by increasing gene flow, enabling re-establishment of locally extinct populations and increasing species diversity within otherwise isolated areas (Tewksbury et al. 2002). Contrary arguments have been raised, based primarily on the role that corridors may play in facilitating the spread of disease or disturbance, or the movements of predators or species of concern (Wiens 2002b). Characterizing the structure and function of corridors in the landscape is problematic (Beier and Noss 1998). Lidicker (1999) pointed out that difficulties arise due to an unclear definition of corridors, and proposed that corridors should be viewed functionally, as any narrowly delimited place in the environment that facilitates movement of organisms between patches, relative to the matrix. According to Lidicker, corridors should not be construed as linear strips of habitat independently supporting breeding populations of focal species, and they need not necessarily be of the same habitat quality as the patches they connect.

Regardless of whether corridors are effective or not as conduits for species movement in fragmented landscapes, a focus on corridors as the defining element of connectedness in a matrix tends to perpetuate the simplistic patch-matrix view of landscapes and obscures some of the richness of detail that characterises landscape mosaics (Wiens 2002b). "Connectivity" (in a general landscape ecology sense) is an aggregate property of the structural configuration and composition of elements in a landscape mosaic; it is the relative permeability of their boundaries to species (Wiens 2002b), and the success with which focal organisms move between particular patches without starving, being preyed upon or otherwise suffering mortality in the process of moving. Connectivity is a functional measure of landscape structure – the degree to which the landscape facilitates or impedes the movement of individuals among patches (Taylor et al. 1993). When a landscape is composed of habitat patches embedded in a matrix used only for dispersal of a particular species, the connectivity of that landscape is a combined result of landscape composition, landscape configuration and the ease of movement of individuals through the matrix (Taylor et al. 1993).

Although a boundary, or ecotone, may have properties of its own, the nature of a boundary is largely contextual, determined by the surrounding environment (Wiens 2002a). To capture this, the term 'landscape context' is becoming common in the literature, especially in studies of habitat fragmentation, although the meaning and method of characterization are not yet standard. "Context" determines the rate of immigration into a patch, through (1) the amount of occupied habitat in the area around the patch that is within the dispersal range of the organism; and (2) the quality of the intervening non-habitat area – the matrix – for survival and dispersing individuals (Fahrig 2001). Landscape context has been used in general to refer to the composition, and sometimes the configuration or arrangement, of landscape elements surrounding a particular focal habitat type (Forman 1995). Some authors (Gustafson 1998, Steffan-Dewenter et al. 2002) contend that the simple proportion of a habitat type in a landscape is nearly as important as many other, more complex, measures of heterogeneity since this compositional characteristic effectively determines the probable range of many configuration characteristics, including patch size and isolation distances (both of which are essential parameters in metapopulation ecology).

Lindenmayer et al. (1999) have used landscape context to characterize the contrast in the composition of the landscape that was included in, and surrounded, habitat patches of interest. Landscape context has also been categorized variously by the proportion of habitat types, and by the diversity of habitat types at a given spatial scale (Steffan-Dewenter et al. 2002), by the proportion of forest cover alone (Donovan et al. 1997), total cover of focal habitat type, and configuration, or spatial arrangement of focal habitat type (Mazerolle and Villard 1999).

Similarly, 'patch context' and 'gap context' have been used variously to describe the components of variability in surroundings, as an attribute of a habitat patch or gap. 'Gap context' seems to be an important determinant in the species composition of colonized gaps. Bullock et al. (2002) investigated gap colonization capacity in seven grassland species and showed that the number of seedlings colonizing a gap was correlated with the abundance of the species in the immediate neighbourhood of the gap. Dalling et al. (1998) reported a similar

relationship where, in forest gaps, composition was determined by the proximity of parents.

Several authors have drawn comparisons between ecological edges and cellular membranes or filters, noting that edges may be differentially permeable to ecological flows (Fagan et al. 1999). Habitat proximal to a patch may be more important in determining dispersal rates than habitat farther away, since proximal habitat must be crossed in order to migrate, whereas more distal habitat is less likely to lie within the realised migration route of any particular individual (Moilanen and Hanski 1998). Thus a further context-related variable having potentially important influences on movement of organisms or propagules is 'edge context'. Furthermore, the permeability of the edge itself may be just as important as the permeability of the environment between two patches in determining the probability of success of emigration or immigration. Patches may be bounded by an impenetrable boundary that dispersing individuals virtually never cross (i.e. a 'hard edge', such as the boundary between an urban subdivision and a remnant mature woodland), or a barrier that is very permeable to dispersers (i.e. a 'soft edge', Stamps et al. 1987), such as that between a mature forest patch and regrowth forest.

Effects of scale

Most ecological processes and interactions depend on spatial scales much larger than that of a single patch, and ecologists have become increasingly aware of the importance of linking spatial patterns with ecological processes at various scales (Thies et al. 2003). Problems of spatial scale generally pertain to issues of extent, grain and resolution of data collection or observation (Gustafson 1998). In practice, ecological studies tend to treat scale simplistically, prefacing it variously by patch-, landscape-, local-, regional-, small-, medium-, large-, fine-, individual-, population- or habitat-, for example, and rarely with reference to whether the scale is based on biological properties of the organisms, physical properties of the landscape or some interaction of the two.

Clearly, relevant spatial scale is species specific. Different species perceive a landscape at different scales (Keitt et al. 1997), and even related species respond to processes operating at different spatial scales. For example, landscape context influenced the abundance and distribution of solitary wild bees, bumble bees and honey bees at different spatial scales (Steffan-Dewenter et al. 2002). Furthermore, the same species might perceive its environment at different scales during different life stages. Plants of most species live parts of their lives at two different spatial scales: the relatively broad, dispersal scale of the seed and pollen grain, and the relatively fine scale of the sessile adult. For adults, day-to-day growth may depend only on immediate microsite conditions, such as light, water and soil nutrient levels. But reproductive success may depend on processes operating at broader scales, for example, pollen production of nearby males, for outcrossing plants, and movement of pollinators in the surrounding landscape (Kollmann 2000). Hence spatial scale is also process-specific. At the fine end of the spatial scale continuum, a fundamentally different set of processes (e.g. microsite selection) may be involved than at broader scales (e.g. dispersal capacity and colonization, abundance, and range of distribution, Bowers and Dooley 1999).

The temporal scale at which a landscape is observed can also have important implications for understanding long-term dynamics of some species since the landscape may change dramatically over the lifespan of a long-lived tree species. Jules and Shahani (2003) recently highlighted the importance of temporal changes in the matrix on within patch dynamics of plant species.

In terms of connectivity, where we are mostly concerned with problems of movement and mobility, scale must generally be defined by both the degree of vagility of the species in question, and the scale at which the species responds to landscape patterns. Proper analysis requires that the scale of measurement of the physical landscape and that of the organism's response fall within the same scale domain, or the region of the scale continuum over which patterns either do not change, or change monotonically with changes in scale (Wiens 1989).

Measuring connectivity

At present there is no commonly accepted measure of connectivity (Tischendorf and Fahrig 2000a). Metapopulation ecologists measure connectivity mostly at the patch scale, while landscape ecologists measure connectivity as a species-specific attribute of the landscape, and both camps use these measures in different ways. Yet as mentioned, the underlying process is the same: movement of individuals (here as ramets, seeds, or pollen) across a landscape (Tischendorf and Fahrig 2001). Despite the fact that terrestrial habitat patches tend to be surrounded by a complex mosaic of other landcover types (Forman 1995), which may differ in their resistance to the movement of individuals among patches, the landscape matrix has mostly been assumed to be uniform, and most connectivity measures in the literature of population ecology are based on simple nearest-neighbour distances (Moilanen and Neiminen 2002), or negative exponential distances with population size or area as weighting functions (Hanski 1999).

In metapopulation theory, movement success depends on the distance between patches and the inherent "dispersal ability" of an organism (as captured in the colonization rate parameter, Gustafson and Gardner 1996, Moilanen and Hanski 2001). Goodwin and Fahrig (2002) cogently showed that dispersal success is not only a function of an organism's dispersal ability but also

depends on particular attributes of the landscape, which may differentially impede movement and/or increase dispersal mortality. In fact, although it is widely held that species having high mobilities are more tolerant of habitat loss and fragmentation (due to the potential for increased colonization rates), the high emigration rates in these species may also increase the overall population mortality rate, by placing such individuals in a perilous matrix more frequently. Therefore, as Fahrig (2001) argued, the concept of dispersal ability may only be applicable in a species' optimal environment and not necessarily in a human-altered, fragmented landscape.

In landscape ecology models, movement through the landscape is assumed to depend on the interaction between characteristics of the matrix and the movement behaviour of the organism (Tischendorf and Fahrig 2000a). Tischendorf and Fahrig (2000a) examined the use and measurement of the term connectivity (in conjunction with either landscape, patch or habitat) in the literature and found a significant lack of consistency. In particular, connectivity was sometimes measured in a structural manner and sometimes in a functional manner; and it was sometimes simply equated with corridors, or with patch isolation, both of which the authors considered are only components of connectivity. In theoretical studies, connectivity has been estimated as dispersal success, i.e. the number of successful immigrants into habitat patches in a landscape, or as search time, the number of movement steps individuals require to find a new habitat (Tischendorf and Fahrig 2000b). More recently, Tischendorf and Fahrig (2000b) have proposed using the rate of immigration into equal-sized habitat cells in a landscape, as a measure for landscape connectivity that accounts for both within- and between-patch movement.

Incorporating the matrix in measures of connectivity

Movement between patches has been mostly thought of in terms of corridors (Tischendorf and Fahrig 2000a), however it is perhaps more usefully envisioned as a complex product of particular patch qualities (e.g. resistance to movement, or patch residence time), boundary properties, and context (Wiens 2002a). Ricketts (2001) conducted a mark-recapture study of a butterfly community inhabiting meadows in a naturally patchy landscape. Ricketts used a maximum likelihood technique to estimate the relative resistances of the two major matrix types (willow thicket and conifer forest) to butterfly taxa – thus for example, conifer was 3–12 times more resistant than willow to movement, for four of the six butterfly taxa studied. Ricketts's results suggest that the surrounding matrix may significantly influence the effective isolation of habitat patches, rendering them more or less isolated than simple distance would indicate.

For mobile organisms which tend to migrate only short distances between patches, resistance parameters may be relatively straight-forward to calculate and incorporate into metapopulation models. However measures of the effect of a heterogeneous matrix on migration or dispersal are not so easy to estimate for organisms such as plants – which rely on a variety of other organisms and agents (water, wind), to disperse propagules and gametes between patches.

Landscape ecologists have given considerable effort to quantifying the spatial composition and configuration of landscapes (Gustafson 1998). Patch-based measures portray features of particular patches, independent of their surroundings. Adjacency and contrast measures, for example, deal with what lies directly across the boundary of a given patch type. Indices such as semivariance, lacunarity and fractal dimension, characterise features of the landscape mosaic as a whole (Gustafson 1998). In terms of connectivity, measures of landscape spatial structure alone are not synonymous with measures of connectivity, although they are clearly related. Together with spatially-referenced records of biotic inventories or ecological variables of interest (e.g. population abundance, species richness values, species diversity), these measures can serve as probes to assess how landscapes affect ecological processes (Wiens 2002b). Landscape indices continue to be refined for different species in different circumstances at different scales, and there now exists a large array of metrics that have been used to relate landscape structure with ecological variables – with mixed success (Gustafson 1998). Ecologists have had some success in the prediction of ecological patterns such as abundance and diversity, from landscape and patch indices (Mazerolle and Villard 1999). However the difficulties associated with predicting the response of ecological entities to spatial pattern has led to few definitive tests, at the level of ecological processes (Gustafson 1998).

Clearly the incorporation of matrix effects into measures of connectivity is not straightforward and, despite the efforts of both metapopulation and landscape ecologists, there is still much to be accomplished before any benefit is realised in terms of the outcomes of theoretical models in these fields, and ultimately for predictions of regional dynamics and persistence of a species in fragmented landscapes. Landscape context, boundary effects and the matrix all importantly influence connectivity and ultimately individual success, as we try to show in the following.

Effect of landscape context on connectivity

Laurance et al. (2002) recently synthesized key findings over 22 years from the Biological Dynamics of Forest Fragments Project, in central Amazonia. Fragments

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surrounded by regrowth forest 5–10 m tall experienced less intensive changes in microclimate and had lower edge-related tree mortality than did similar fragments adjoined by cattle pastures. Edge avoidance by mixed-species bird flocks was also reduced when fragments were surrounded by regrowth rather than cattle pasture. Laurance et al. (2002) point out that several species of primates, antbirds, obligate flocking birds, and euglossine bees, all of which had disappeared soon after fragment isolation, recolonized fragments when regrowth regenerated in the surrounding landscape. Furthermore, some of the Amazonian matrix habitats were more suitable for rainforest fauna than others. Thus regrowth dominated by *Cecropia* trees, which tends to be tall and floristically diverse with a relatively closed canopy, was used by more rainforest bird, frog, and ant species than was more open *Vismia*-dominated regrowth (Laurance et al. 2002). In general, the more closely the matrix approximated the structure and microclimate of the primary forests, the more likely that fragmentation-sensitive species could use it. Fahrig (2001) estimated that under certain circumstances up to 58% less habitat was required for population persistence if a matrix of very low quality was converted to one of very high quality. These results indicate that the composition of the matrix can have a significant influence on fragment connectivity and functioning.

Many authors have demonstrated the effects of landscape context and connectivity in community structure (Pearson 1993, Holt 1997, Sisk et al. 1997). MacArthur and Wilson (1967) used surface area combined with age as the principle factors predicting species richness on oceanic islands. In terrestrial ecosystems, species diversity is also significantly affected by other landscape-level factors, beyond patch size (Lovett-Doust and Kuntz 2001, Lovett-Doust et al. 2003). The notion of "mass effect" has been used at the community level to describe how neighbouring communities influence species composition of a target community (Cantero et al. 1999). Similarly the "rescue effect" describes how occupied patches on the brink of extinction are rescued by immigrating dispersers from other occupied patches (Gotelli 1991). This occurs in a manner analogous to the way in which 'sink' populations are maintained at the population level, through dispersal from 'source' populations (Pulliam 1988), and how species presence is maintained in sub-optimal habitat in metapopulations (Holt 1997). Holt (1997) used variants of the Levins metapopulation model to examine the effect of spatial heterogeneity on community structure. Holt's theoretical results suggested that species having high occupancies in the abundant habitat (the matrix) had the potential to contribute disproportionately to species composition in the more sparse habitat (the patches), via a spillover effect. This effect has important implications for determining the effect of the matrix on biodiversity in fragmented landscapes.

Forest fragments are susceptible to "bombardment" of propagules from weedy plant species in the matrix vegetation, which may then be incorporated into the fragments community (Janzen 1986). Many authors have documented invasion of forest habitats from plant species in the matrix (Janzen 1983, Tabarelli et al. 1999, Cook et al. 2002). Coinciding with an increase in exotic species in Atlantic forest fragments, Tabarelli et al. (1999) described a decline in the relative number of species from plant families considered most important for vertebrate frugivores (Myrtaceae, Lauraceae, Rubiaceae and Sapotaceae). Although this study provided no data on abundance of these vertebrates, it is likely that decreases in the abundance and diversity of fleshy fruits will ultimately lead to an impoverished vertebrate community (Tabarelli et al. 1999). Changes in the abundance of seed predators can have significant impacts on plant populations in patches. For example, Curran et al. (1999) found that recruitment of canopy trees, mostly from the family Dipterocarpaceae, collapsed in the Gunung Palung National Park in western Borneo. During a masting event in 1998, dipterocarp recruitment in the park fell drastically because of an increase in seed predation by vertebrates that had moved into the park from surrounding degraded areas.

Effect of corridors and "stepping-stones" on connectivity

Corridors linking patches in fragmented landscapes may improve connectivity between patches and hence dispersal success for some species. The use of corridors enabling movement in the matrix habitat has received considerable attention, in particular for butterflies (Haddad 1999, 2000, Dover and Fry 2001), other insects (Hill 1995, Nicholls et al. 2001) and small mammals (Downes et al. 1997, Bolger et al. 2001, Coffman et al. 2001). These studies typically demonstrate that for some species in certain landscape contexts, corridors facilitated movement between patches, but were often not essential. Furthermore, the disparate response of species, even closely related taxa, is noteworthy (Bolger et al. 2001, Dover and Fry 2001).

Tewksbury et al. (2002) recently conducted a study linking the effects of corridors across an array of plant-animal interactions. They tested hypotheses of corridor function in an experimental landscape, by studying movements of butterflies and pollen and bird-dispersed seeds. Corridors were found to facilitate the movement of butterflies between connected patches. Pollen movement mirrored the movement of the butterflies, and a significantly greater proportion of flowers produced fruit in connected patches than in unconnected patches. Seeds

of the two species studied (large, fruiting shrubs, *Ilex vomitoria* and wax myrtle, *Myrica cerifera*) were more likely to be found in connected patches than unconnected ones. The study also demonstrated increases in fruit set and seed movement in connected patches across diverse sets of pollinators and seed dispersers, suggesting a potentially wide application.

Highly mobile species, such as birds and many insects, can move rapidly over extensive areas of fragmented landscapes, and for these species even small remnant patches of habitat may act as 'stepping stones' across the landscape and enhance movement (Fischer and Lindenmayer 2002, Lovett-Doust et al. 2003). Nason and Hamrick (1997) reported that small fragments and even single, lone trees may serve as important stepping stones for pollinator movement between larger patches of tropical forest. Solitary and isolated paddock trees in fragmented landscapes in Australia have been shown to serve as connecting landscape elements for a range of bird species (Fischer and Lindenmayer 2002), while several authors (Guevara and Laborde 1993, Luck and Daily 2003) have demonstrated the importance of free-standing trees in the surrounding matrix of tropical rain forest patches, as foci for seed deposition by birds. Thus connectivity may be improved between patches without necessity for a continual corridor between patches; rather, remnant habitat between patches may suffice to improve connectivity for relatively mobile species.

For particularly long-lived species, such as trees (where old age for many species may mean many decades, even centuries), the traditional definition of the matrix in the metapopulation paradigm (namely, habitat suitable for traversing but unsuitable for supporting breeding individuals, Wiens 1997) is often not appropriate. Levin (1995) reviewed the importance in highly modified habitats of isolated trees, or "reproductive outliers," to within-patch population dynamics. Levin suggested that these trees may serve as bridges between populations and concluded that, although isolated individuals may produce fewer seeds than do individuals located within inhabited patches, they may be a major source for pollen and seeds to nearby populations, retarding the divergence of local populations and forming nuclei for new populations. Few empirical studies have considered the importance to regional dynamics of trees residing in matrix habitat. Where these individuals have been considered, the results support the conclusion of Levin (1995), that they may contribute in a number of important ways to regional dynamics. For example, adult trees of *Symphonia globulifera* in pasture habitat have been shown to contribute most of the seedlings in nearby remnant forest patches, whereas remnant forest adults produced very few of the seedlings residing in their own patch (Aldrich and Hamrick 1998).

Effect of edges on connectivity

Edge effects are closely related to both landscape context and corridor effects on connectivity. Sisk et al. (1997) suggested that many matrix effects may actually manifest as edge effects. For example, landscape context should not be expected to have much impact on emigration for patches with relatively hard (impermeable) edges (as in, e.g. a forested patch adjacent to an industrial, or developed area). Consequences of disruptions to dispersal via edge permeabilities have long been linked to plant pollination and seed dispersal in fragmented landscapes. By disrupting or impeding movement of pollinators, edges having relatively high impermeability may restrict pollen flow and seed dispersal among plants in patches (Fagan et al. 1999).

Edge-mediated effects on seed dispersal and seed mortality may also be important in determining species composition, and successional patterns in patches (Fagan et al. 1999). In regions of remnant tropical forest surrounded by a harsher, modified environment, edge-related seed mortality may impede germination of native tree fauna at the expense of more edge-tolerant weedy species, so altering successional patterns and making fragmented forest even less similar to unfragmented forest (Janzen 1983). In temperate forests, extinction likelihoods may be greater due to decreased population sizes near habitat edges, as Jules (1998) concluded from his study of fragmentation effects on demography of the understory herb *Trillium ovatum*. The mechanism for the demographic change was likely a combination of reduced seed set and diminished survivorship of seeds and seedlings near edges.

Edge-related gradients in physical and biotic variables are likely to be less pronounced when the matrix is more similar in structure to that of the fragment (Gascon et al. 1999). Mesquita et al. (1999) reported that Amazonian forest fragments surrounded by pasture had significantly higher tree mortality than fragments adjoined by *Vismia* spp regrowth forest. Laurance et al. (2000) also reported disproportionate mortality of large canopy and emergent trees in Amazonian forest fragments following fragmentation.

Thus far, processes at population margins and zones of contact have generally been described in terms of the behaviour of 'one-dimensional' transect-like, mean field models (Antonovics et al. 2001). Such studies have used either 'connected lattice' models in one dimension (such as stepping-stone models in population genetics), or partial differential equations describing spatial change in abundance or gene frequency over one or two dimensions. Antonovics et al. (2001) recently used spatially explicit individual-based models to study the patterns and dynamics that develop in population margins as they expand into regions that become more and more unsuitable; at the same time they probed effects of plant pathogens. At the margins, local, short-lived, 'flame-like'

population patterns developed. While the local density of individuals at population margins initially prevented the invasion of disease into these margins, in the long term marginal populations and disease seemed to be sustained by complex colonization-extinction dynamics, where there was no clear gradient in pathogen abundance at the margin (Antonovics et al. 2001).

Effects of matrix land use

Biernacki et al. (unpubl.) investigated effects of land-use in the matrix surrounding a reserve of nearly a hundred designated natural areas along the 735 km Niagara Escarpment, a regional biodiversity hotspot in southern Ontario, Canada. Seven land-use categories were mapped in the matrix surrounding each natural area. Stepwise logistic regression techniques were used to identify factors influencing presence/absence, and size of the major biotic groups (including plants). Results showed that both the types of land-use and their proportions at different distances from the edge of each patch of natural area (at 0, 100, 250 and 500 m from the perimeter) had highly significant effects on species richness of biota.

In another study, Lovett-Doust et al. (2003) compared three general classes of ownership of natural area patches in Ontario, Canada – private, public, and mixed – in terms of both numbers and kinds of rare species measured for global and regional rarity. Land ownership had highly significant effects on rare species richness, including plants, with, in this case, more rare species occurring in publicly-owned patches than in privately owned ones, even after other factors, such as the size of the patch, were controlled statistically.

A functional mosaic approach

Plant population dynamics are often influenced by more than a patch/matrix model can account for. Many plants exist in situations where individuals are not clustered in their distribution and definition of distinct populations is problematic, and where suitable habitat patches are not easily delineated, but rather where gradients of habitat suitability more appropriately characterize the region. Here description of the landscape in terms of suitable patches and a homogenous matrix greatly over-simplifies reality, and an integrative, landscape-based approach to understanding regional scale dynamics is likely to be more valuable. Such a large, layered situation seems to lend itself to Forman's (2002) notion of a 'functional mosaic model' in which the landscape is composed of places influencing movement and flow of organisms.

To date, landscape context has been limited generally to the inclusion of such spatial parameters as habitat composition and configuration (Mazerolle and Villard 1999). Presumably, for plants, physical factors such as light intensity and moisture availability are important parameters. Other authors have taken a more functional approach (Forys and Humphrey 1999). For plants, the distribution of "safe sites" (sensu Harper 1977) for seed germination and seedling recruitment should be very important. Furthermore, populations of pollinators and seed dispersers will likely be necessary; factors associated with pathogens/parasites and competitors will all also likely be important functional variables. We suggest landscape connectivity be viewed as a composite of parameters occurring via structural context – including both physical and spatial parameters – as well as an array of functional context parameters (at both community and population levels). Table 1 outlines components of a landscape mosaic approach, and general parameters which should be considered in the parsing of landscape connectivity. Naturally the most important consideration is how the organism of interest perceives its environment, and at what scales, with suitable weighting of the most relevant components and metrics.

In order to further develop the mosaic approach, we support Thomas and Kunin's (1999) suggestion of a grid-based approach to mapping spatially structured

Table 1. Components of a landscape mosaic approach to connectivity: parameters of structural (physical and spatial) and functional (community level and population level) contexts in a landscape.

Structural		Functional	
Physical context	Spatial context	Community level	Population level
• Habitat nature and quality, extent of disturbance • Resource availability: mineral nutrients, light, water, etc • Climatic parameters • Soil types • Physical elements: landforms, waterbodies, roads, urban development • Land use/land cover	• Habitat composition • Habitat configuration • Habitat diversity: richness, evenness, dominance, similarity, etc. • Habitat dispersion, contagion • Edge extent	• Species richness • Fraction of habitat specialists • Invasibility • Soil mineralization • Successional trends • Biomass • Overall dynamics (turnover of individuals) • Resilience	• Density of conspecifics • Nearest neighbour distances, nearest potential mate distances • Plant sizes and size distribution • Density of pollinators, dispersal agents, predators, prey • Local extinctions, colonizations • Pollen availability • Seed production • Seedling recruitment

populations that do not adhere neatly to habitat/non-habitat delineations. This approach has several advantages when dealing with plant populations at regional scales. Employment of a spatial grid system avoids the need for a subjective definition of suitable habitat patches, and allows for an evaluation of the relative significance of different components of the landscape. This approach is also amenable to grid-based modeling and allows plant distributional data to be related to Geographic Information System data-sets. Many authors have demonstrated advantages of spatially explicit or spatially realistic grid-based models for assessing aspects of plant population and community dynamics (e.g. successional patterns: Hovestadt et al. 2000; tree species diversity patterns: Liu and Ashton 1999; competition: Coomes et al. 2002). Several other authors have recently described a gradient-based approach to viewing landscapes (McIntyre and Hobbs 1999, Theobald and Hobbs 1999, Lindenmayer et al. 2003). Gradients of habitat quality, which may be composed of several landscape structural and functional components, are mapped in a grid-based structure, giving a framework for interpreting a species response (e.g. dispersal, reproductive success) to the landscape (McIntyre and Hobbs 1999).

The matrix clearly is important in its effect on connectivity and population dynamics of species living in fragmented habitats. However we have argued that, for many plant species, patches of suitable habitat are not readily defined and, furthermore that plants likely respond to gradients of habitat suitability. Thus, by default, the matrix, or unsuitable habitat (as traditionally defined), is also difficult to discern, and nebulous. The advantage of the functional mosaic approach, when combined with division of the landscape into a grid, is that each cell within the grid can be described simply in terms of local population size and its structural and functional context, without the need to define explicitly patch and matrix habitat. In this sense, the answer to the question we pose in the title of this paper is, strictly, no – the matrix is not important, but neither is the patch – rather the nature of the composite landscape mosaic is the key determinant of the fate of plant populations.

Conclusions

A landscape is always heterogeneous at some spatial or temporal scale. Structurally it is a mosaic, with multiple sources, barriers, conduits, attractors, repellents, sinks, avoidance spots, and comfort places (Forman 2002). From an individual's perspective, it is a mosaic of food resources, grazing and predation risks, confrontations and competitions, and structural conditions. It is also a mosaic of land use, land ownership, management and jurisdiction. Treatment of the landscape as a mosaic,

with attention given to dominant features of the landscape context and how they interact, to determine the fate of populations has been eloquently advocated by landscape ecologists (Wiens 1997, 2002b, Forman 2002). As we have demonstrated, the empirical evidence continues to urge a more integrative perspective when considering regional population persistence, compared to that mostly employed in current metapopulation and landscape ecological approaches. Thus, in the words of Forman (2002): "We can now move beyond the stage of patches-in-an-inhospitable matrix, source and sink, and corridor-connecting-two-patches.....Why couldn't the patch-corridor-matrix model be enriched or even replaced by a functional mosaic model, in which the landscape is composed of such places portraying movements and flows?"

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