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Conceptual domain of the matrix in fragmented landscapes

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In extensively modified landscapes, how the matrix is managed determines many conservation outcomes. Recent publications revise popular conceptions of a homogeneous and static matrix, yet we still lack an adequate conceptual model of the matrix. Here, we identify three core effects that influence patch-dependent species, through impacts associated with movement and dispersal, resource availability and the abiotic environment. These core effects are modified by five 'dimensions': (i) spatial and (ii) temporal variation in matrix quality, (iii) spatial scale, (iv) temporal scale of matrix variation, and (v) adaptation. The conceptual domain of the matrix, defined as three core effects and their interaction with the five dimensions, provides a much-needed framework to underpin management of fragmented landscapes and highlights new research priorities.

A matrix focus is now both important and possible

Biodiversity conservation often focusses on patches of native vegetation in a surrounding matrix that is highly modified by agriculture or urbanisation [18, 19]. The patch-matrix model of landscapes [20] includes patches that are useful for conservation and the matrix in which the patches are embedded [21] (see Glossary). Assumptions underpinning the patch-matrix model are reasonable in many situations, particularly in fragmented and relictual landscapes where there are patch-dependent species [22-24]. However, the matrix surrounding remnant vegetation can have a strong influence on species occurrence and spatial dynamics [25, 26] and can be more important than the size and spatial arrangement of remnant patches [2, 27, 28]. The growth in knowledge about the matrix means it is now possible to develop a detailed synthesis of the mechanisms by which the matrix directly, or indirectly drives the distribution of patch-dependent species in space and time.

Not only is such a synthesis possible, it is also urgent. The nature of the matrix has profound implications for conserving biodiversity [28, 29]. Management of the matrix can limit or exacerbate the impacts of habitat loss and fragmentation [30]. Habitat loss and fragmentation are the biggest threat to biodiversity globally [31]. In highly modified landscapes, further loss of remnant vegetation is limited because most of it is already gone, or because what remains is legally protected [32, 33]. Where this is the case, modifying the matrix will be the major form of landscape change in the future, and will therefore likely be the main process influencing biodiversity conservation. There is now a pressing need for a comprehensive theoretical framework of the matrix to guide the way scientists and land managers think about matrix ecology.

While there has been much conceptual development in the habitat fragmentation literature [22, 26, 34], the concepts related to how the matrix influences patch-dependent species have not been thoroughly synthesised. In this review, we build on progress made within ecological sub-disciplines [25, 35, 36], and on research into edge-effects [37] and habitat fragmentation [26, 34], to describe the conceptual domain of the matrix in fragmented landscapes.

Our approach to understanding the conceptual domain of the matrix is to synthesise ideas from the empirical literature. However, instead of providing a list of matrix effects [e.g. 25, 35, 36, 38, 39], we illustrate relationships among mechanisms in a conceptual model. We demonstrate through the conceptual model that what previously were considered primary effects of the matrix are actually secondary outcomes of three 'core effects' (see Boxes 1 and 2). In the second part of our review we identify five influential 'dimensions' and show how these modify the way that core effects play out. The resulting conceptual model of the matrix can help to improve communication of matrix ideas, and guide future research, including research that addresses new questions about interactions between core effects and dimensions associated with time, space and adaptation.

Core effects of the matrix

After considering the range of effects that the matrix can have on patch-dependent species [using empirical literature, also canvased in numerous reviews: 19, 25, 34-36], we identified three fundamental ways that the matrix influences the spatial dynamics of populations and species occurrence in fragmented landscapes. The matrix can influence population persistence in fragmented systems through effects associated with (i) movement and dispersal; (ii) resource availability, and; (iii) the abiotic environment (Figure 1).

Movement and Dispersal. Matrix quality influences the outcome of movement into the matrix

Recent reviews report that movement between patches is enhanced as the matrix becomes structurally more similar to the remnant patches [40, 41]. For example, when pastures are replaced by tree plantations, colonisation of forest patches by forest specialists can increase [4]. However, the matrix can influence immigration and emigration in other ways. Sharp ecotonal boundaries between a patch and the matrix can cause individuals to cluster inside remnants ('fence effects') [1]. If a species does venture into the matrix, rapid movement through unfavourable habitat could enhance connectivity between separated habitat patches [42]. On the other hand, dispersal or movement between disjunct habitat patches might decline due to altered behaviour, or increased mortality [2, 5, 26, 43]. The influence of the matrix as a demographic sink has received little research attention, although in theory, density-independent emigration can increase the risk of local extinctions [44].

Resource availability. Matrix resources could aid patch-dependent species or support matrix specialists.

The role of the matrix as a resource base for species that invade remnant patches has long been understood [19] (Box 3). For example, red squirrel *Tamiasciurus hudsonicus* populations thrived on pine-seeds in Canadian pine plantations. Squirrels subsequently invaded remnant broad-leaf forest and ate Brown Creeper *Certhia americana* eggs, increasing the rate of nest failure of this patch-dependent bird [16]. On the other hand, if the right resources are provided, the matrix can be converted to habitat and desirable native species can live throughout the landscape [e.g. 45]. However, if species remain patch-dependent, they might nevertheless use resources within the matrix as a food subsidy [34]. With the possible exception of bees that can forage outside of the nesting patch [e.g. 14], evidence that patch-dependent species gather resources outside of the patch to support higher population densities inside the patch is limited [e.g. 46].

Abiotic environment. The matrix influences microclimate and disturbance regimes of patches. The physical structure of the matrix is often different from habitat patches and can alter the environmental conditions within patches [19, 37], particularly when treed landscapes are cleared [25]. Microclimatic changes associated with increased light and wind penetration can have far-reaching effects on patch-dependent species, increasing the risk of local extinction [7, 47]. In addition, species that prosper under the altered microclimate can colonise remnant vegetation and drive edge-sensitive species into the remnant core [37, 48].

Changes to disturbance regimes in the matrix can also affect patch-dependent species. Larger and more frequent fires can occur if there are more ignitions in the matrix [11], or when the fuel structure in the matrix is changed by forest logging [11, 49] or by invasive grasses [17]. Conversely, active fire suppression in matrix environments can reduce rates of natural disturbance in patches [3]. Altered microclimate and disturbance regimes can advantage some species, often invasive exotic species [6, 17], but disadvantage others, often species that depend on remnant vegetation [8]. Increased disturbance associated with urban or mining landscapes can also drive local extinctions in patches [9, 10].

Conceptualising matrix effects as stemming from three core effects (impacts associated with dispersal, resource availability, and the abiotic environment) provides a structure for identifying ecological pathways that influence abundance and population survival (Figure 1). For example, invasion of patches by new species has often been listed as an important effect of the matrix on patch-dependent species [19, 25, 35, 36]. However, our new conceptual model emphasises that such colonisation can be an indirect effect of any one of the three core effects (Box 2). Similarly, altered species interactions have been listed as one of four main effects of the matrix [38], but these too are a consequence of the three core effects (Box 1).

Our conceptual model of core effects (Figure 1) is a substantial heuristic advance, but we think there are five influential dimensions that also must be considered to define the conceptual domain of the matrix. In the next section, we outline how the core effects (Figure 1) depend on five modifying dimensions: (i) spatial variation in matrix quality; (ii) the spatial scale of the matrix and patches; (iii) temporal variation in matrix quality; (iv) longevity and demographic rates of species relative to the temporal scale of changes in the matrix, and; (v) adaptive (plastic or evolutionary) responses of species (Figure 2). Patch features, including size, shape and quality also influence the response of patch-dependent species to habitat loss and fragmentation (Box 4). However, consideration of patch effects is beyond the scope of our review and was recently examined in detail by Didham *et al.* [26].

Five dimensions modify how the core effects influence biodiversity

Spatial variation. The matrix is not spatially homogeneous

Although a spatially homogeneous matrix is often assumed in metapopulation and fragmentation research, many landscapes are characterised by a heterogeneous mix of land uses and habitat types [10, 25, 50]. By introducing variation into dispersal patterns, the structure and quality of a heterogeneous matrix can influence the degree of isolation of habitat patches [10, 27]. Matrix heterogeneity might also influence the extent and symmetry of dispersal which can lead to spatially-biased movement that differentially inhibits or facilitates the colonisation of particular habitat patches [51, 52]. Although practical ways have been developed to explore how spatial variation in matrix quality affects dispersal, empirical knowledge of matrix effects remains scarce [53].

Spatial variation in matrix quality will also lead to variation in microclimate conditions, imposing spatially variable edge effects [25, 54]. Furthermore, variation in matrix quality can affect taxa differently by providing contrasting resources. For example, Öckinger *et al.* [46] found higher butterfly species richness within grassland patches surrounded by a forest matrix, but higher species richness of hoverflies in grassland patches surrounded by arable land, reflecting differences in food resources for these species.

Spatial scale. The extent of the matrix influences its impacts on patch-dependent species

The spatial scale of the matrix, including geographic extent and distance between patches (see Glossary), has an important effect on patch-dependent species. The distance between patches is well understood to influence dispersal rates [55]. Because dispersal influences the probabilities of population extinction and recolonisation of patches [24], the effects of matrix scale on dispersal (i.e. longer distances between patches) can affect patch occupancy and mediate the operation of patchy populations, metapopulations or isolated populations in fragmented ecosystems [13].

The spatial extent of the matrix can also influence resource subsidisation and spill-over edge effects, although evidence for such effects is limited. If patch-dependent species exploit resources in the matrix [34], a proportionally greater area of matrix to patch could increase the relative abundance of such resources. However, movement limitation and satiation can prevent patch-based species from exploiting an ever-increasing amount of matrix. Spill-over of matrix-specialist predators or prey into patches [56] is influenced by the scale of the matrix and patches. Increasing the scale of the matrix increases the population size of matrix specialists, and can cause larger spill-over edge effects [16].

The influence of the spatial extent of the matrix on the abiotic environment of patches is likely to be more limited than the effects on dispersal and resources. Most edge studies disregard the scale of the adjacent matrix and so understanding of such effects is rudimentary. Narrow gaps like forest roads can have substantial abiotic edge effects [57]. The extent to which wider gaps have bigger effects and the scale at which effects plateau is yet to be established. The extent of the matrix could also influence the risk of fire, in circumstances where fires are more likely to start in agricultural lands [11].

Interactions between spatial scale and spatial variation in matrix quality can have important effects on populations in fragmented systems [58, 59]. By examining the extent to which changes in population size were synchronous, Powney *et al.* [58] found that matrix permeability to dispersal had the strongest effect on movement between patches at intermediate distances. In contrast, movement between patches was relatively insensitive to matrix type at short or long distances between patches. There has been limited direct study of how such interactions occur. However, the effects of matrix heterogeneity are most likely to be apparent on the spatial scale of individual movement behaviour [59] or the scale over which population synchrony occurs [58].

Temporal variation. The matrix is not static.

Many studies have examined dispersal through contrasting matrix types, with implications for how matrix permeability is likely to change over time. For example, bird dispersal through patch-matrix landscapes can increase or decline due to increases or loss of trees [60, 61]. However, there are few long-term studies that directly measure temporal trends in matrix use through time (but see Box 3). In one example, reintroducing fire to woodland in Missouri, USA, allowed collared lizards (*Crotaphytus collaris*) to disperse between glades and establish stable metapopulations [3]. Movement through the matrix can be influenced in other ways, including annual variation in crops planted in farming landscapes [62], and climatic cycles of rainfall and drought [15, 63].

Changes in dispersal are often driven by temporal changes in resources [61, 63, 64]. Temporal variation in the resource base might also lead to variation in resource subsidisation [34], but to date, the limited evidence for this is largely inferential.

Abiotic effects are highly dynamic [7] and change over time as a consequence of succession, seasonality, and changes in species composition, management and disturbance regimes. In abandoned pastures, forest can begin to re-establish, gradually reducing temperature, wind, moisture and light extremes experienced at forest edges [65]. Similar changes can take place seasonally in regions with distinct dry and wet seasons [66] or during droughts [67]. In addition, fire regimes change to become more extreme as exotic grasses invade new areas [68].

Temporal scale. Demographic and dispersal rates influence responses to changes in the matrix

Dispersal rate is a key trait determining the ability of species to exploit changes in the matrix [69]. For example, in poorly dispersing lichen species, forest succession through plantation harvest cycles can be too rapid for colonisation, particularly when the matrix is extensive [70]. Strong dispersers are in the best position to exploit short-term changes in matrix resources [71], while species with intermediate dispersal abilities could benefit most from longer-lasting temporal changes such as revegetation [69].

The ability to exploit resource pulses in the matrix also depends strongly on a species' life history characteristics. For example, hairy-footed gerbils *Gerbillurus paeba* of southern African savannas are dependent on grasslands embedded in an inhospitable shrubby matrix that is maintained by heavy grazing [15]. In years when extreme rainfall triggered unusually high grass growth, gerbil abundance and reproductive output in the (former) matrix increased markedly. The short generation time (3 months) and high fecundity (up to 6 young per litter) of the gerbils allowed them to exploit this short-term boom in seed supply [15]. In contrast, species with a low reproductive output, fixed seasonal breeding cycles, and low population growth rates are unlikely to respond strongly to pulses of food resources in the matrix [72]. Resource specialisation can also influence a species' ability to respond to changing resources in the matrix. Diet generalists can exploit food resource pulses better than specialists because specialisation on rare and ephemeral food sources is uncommon [72]. In contrast, where resources change gradually, dietary specialists can replace generalists as succession advances [73].

Short-term changes in the abiotic environment of patches can provide opportunities that are similar to short term resource pulses, but the ability of species to exploit such changes will depend on their life-history and dispersal abilities. For example, species with multiple generations within a year [74] or adequate dispersal [7] are able to exploit seasonal retreats of abiotic edge effects and expand the area that they occupy within a patch [66].

Adaptation. A species response to the matrix can change over time.

Plastic and evolutionary responses of species to the matrix are rarely considered, but have the potential to influence response pathways. Behavioural and morphological plasticity that increases or reduces flight is widely reported, particularly for insect species in fragmented landscapes [75-77]. Increased dispersal with fragmentation is advantageous when local extinction is common, but lower dispersal can be beneficial if there is low extinction risk and high dispersal mortality [75, 76]. Therefore, changes in the matrix that influence dispersal-related mortality [e.g. increased desiccation risk, 62], or extinction risk within patches [e.g.

changes in the matrix fire regime, 68] could apply selection pressure that drives changes in dispersal through the matrix over time, or invoke a rapid plastic response.

Species can also exhibit evolutionary or plastic responses to use resources within the matrix [e.g. forest dung beetles expanding through farmland by using cattle dung, 78]. Adaptive responses to changes in the abiotic environment are also possible [e.g. caterpillars adapted to survive in open farmland environments, 77]. Such effects, however, have not been widely investigated. Recent reviews of adaptation to global change indicate that, while such adaptation does occur, much remains to be learnt about the extent to which adaptation can mitigate negative effects of human-induced environmental change [75, 78, 79]. We nevertheless expect that adaptation (plastic or evolutionary) is an important phenomenon that influences how species respond to matrix conditions. It would not be surprising for the effects of a given matrix on a species to change, potentially over a small number of generations [75].

What can be achieved with the new conceptual model?

By defining the conceptual domain of the matrix (Figures 1, 2, Boxes 1, 4) and emphasising how core effects can be modified by the five dimensions, important new research priorities are now apparent (see Box 5 Outstanding Questions). Research addressing these questions has the potential to generate novel conservation strategies and improved understanding of ecological phenomena in fragmented landscapes. For example, when there is substantial spatial and temporal variation in matrix quality, it might be difficult for species to adapt to matrix conditions because selection pressures will be inconsistent [80]. This sets up a conundrum because managmenent recommendations to increase matrix heterogeneity [81] might also inhibit adaptation to a dominant matrix type. New research is also needed to understand the interaction of the temporal scale of changes in the matrix with other dimensions and core effects. For example, what are the trade-offs between dispersal ability, the temporal scale of changes in the matrix and the spatial extent of the matrix [70]? Related to this, do species have different responses to the same kind of temporal variation in the matrix (such as those caused by La Niña climate events) if those events also vary in temporal scale? Our conceptual model therefore provides a framework for developing research questions that lead to conditional predictions about matrix effects [82]. Combined with attempts to generalise across species by considering species traits [39, 41](Box 5), the framework can help to understand the circumstances in which particular effects might be expected.

Our framework also provides a new perspective to the old question of how the matrix might be manipulated to support patch-dependent species [28, 30, 83]. Previously, lists of possible approaches have been proposed, such as maintaining a certain proportion of forest cover of particular size [30], maintaining hedge-rows or reducing insecticide use [83]. Our conceptual framework means it is now possible for researchers and land managers to think about potential approaches in a structured way. What ephemeral management practices in the matrix would encourage dispersal across the landscape, provide additional resources for patch-dependent species, or increase the core-area of remnant patches? How extensive should a manipulation be to have these benefits? Using our conceptual model as a guide will help researchers to construct and test hypotheses that consider the range of ways that the matrix influences patch-dependent species.

Our conceptual model also enables rapid learning and an improved capacity to frame research about the matrix. It brings together the key phenomena through which the matrix acts on patch-dependent species; it highlights the three core effects (Figure 1), and how these effects are modified by five dimensions (Figure 2). In combination with considering patch features (Box 4) and species interactions (Box 1), the conceptual model provides a simple scheme for people who are new to the field to quickly comprehend these critical processes in fragmented landscapes. As a research planning tool, it stimulates new ways of framing hypotheses about the matrix, including drawing attention to novel interactions among the dimensions and core effects (Box 5).

The matrix in agricultural and urban landscapes is changing. Changes in the amount of tree cover, the prevalence of exotic plant and animal species, fire regimes and land-use intensity (among others) all contribute to making the matrix more or less hostile for patch-dependent species. These changes could make the conservation outlook more bleak as land use intensifies, for example, but matrix changes also provide opportunities to support species in patches. We trust that by defining the conceptual domain of the matrix, the opportunities and risks associated with matrix management can be better identified, understood and communicated. Ultimately, an improved understanding of the matrix will enable land management practices that help stem the ongoing decline of biodiversity.

Acknowledgements

Joern Fischer, Laura Prugh, anonymous reviewers and the editor provided valuable feedback on an earlier draft of our manuscript. Thanks to Clive Hilliker who prepared the figures and Nici Sweaney for her Nanangroe photograph.

Figure 1. Matrix core effects

The matrix can influence species abundance, community composition and ecological processes within patches of native vegetation through three core effects associated with (i) movement and dispersal, (ii) resources provided within the matrix, and (iii) the abiotic environment of patches. Individuals that move into the matrix can risk elevated mortality, with possible consequences for immigration rates and the population size of patch-dependent species. The matrix can also alter dispersal by acting as a barrier to emigration, or can promote dispersal leading to increased immigration. The matrix can provide resources that allow non-patch species to breed and subsequently spill over into patches. The matrix could also provide food supplementation to patch-based species. Resources within the matrix can also facilitate dispersal. The matrix can drive abiotic edge effects, altering moisture, light, and disturbance levels. Each of these effects can have consequences for individual species, and subsequently for community composition (see Box 2 for a more detailed description of some pathways and Box 1 for consideration of species interactions). Numbers indicate studies listed in the references that support parts of each pathway.

Figure 2. Five dimensions modify matrix core effects

The conceptual model of the matrix consists of the three core effects (detailed in Figure 1) whereby the matrix influences patch-dependent species through effects associated with movement and dispersal, resource availability, and the abiotic environment. Five dimensions modify the way the core effects influence patch-matrix dynamics; temporal variation and temporal scale, spatial variation and spatial scale, and adaptation. Although we portray these dimensions as stacked, this does not imply any priortity of effects (although difficult to draw, these could also be imagined as overlapping spheres encompassing the core effects, like electrons around an atom's nucleus). The blue arrow indicates that dimensions can act together, or can interact to influence the core effects. Although we emphasise phenomena related to the matrix, the importance of patch characteristics and species interactions are well established (Boxes 1, 4). For simplicity we have not attempted to draw all of the likely relationships between patches and the factors that influence the impact of the matrix on patch-dependent species.

Figure 1

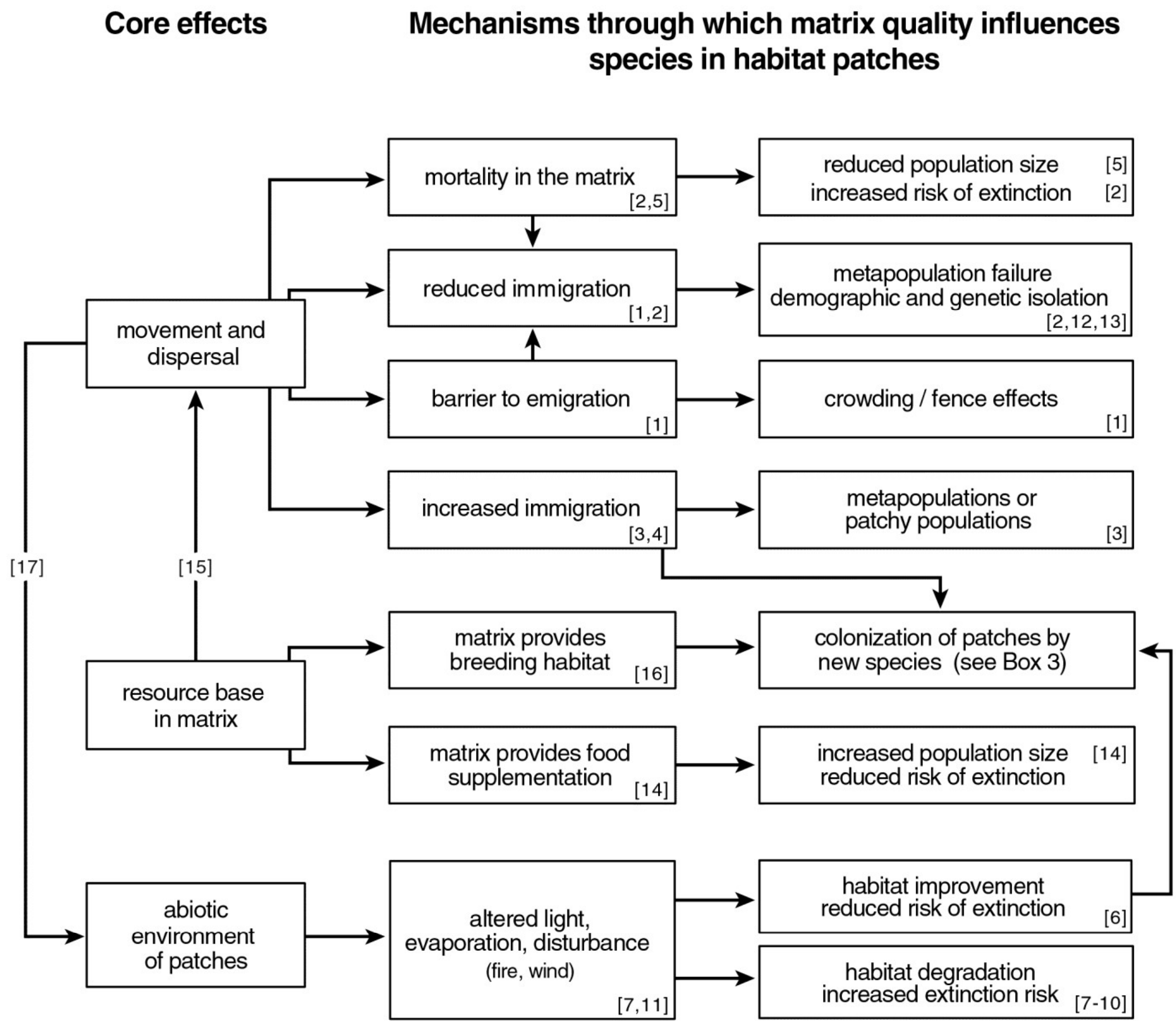
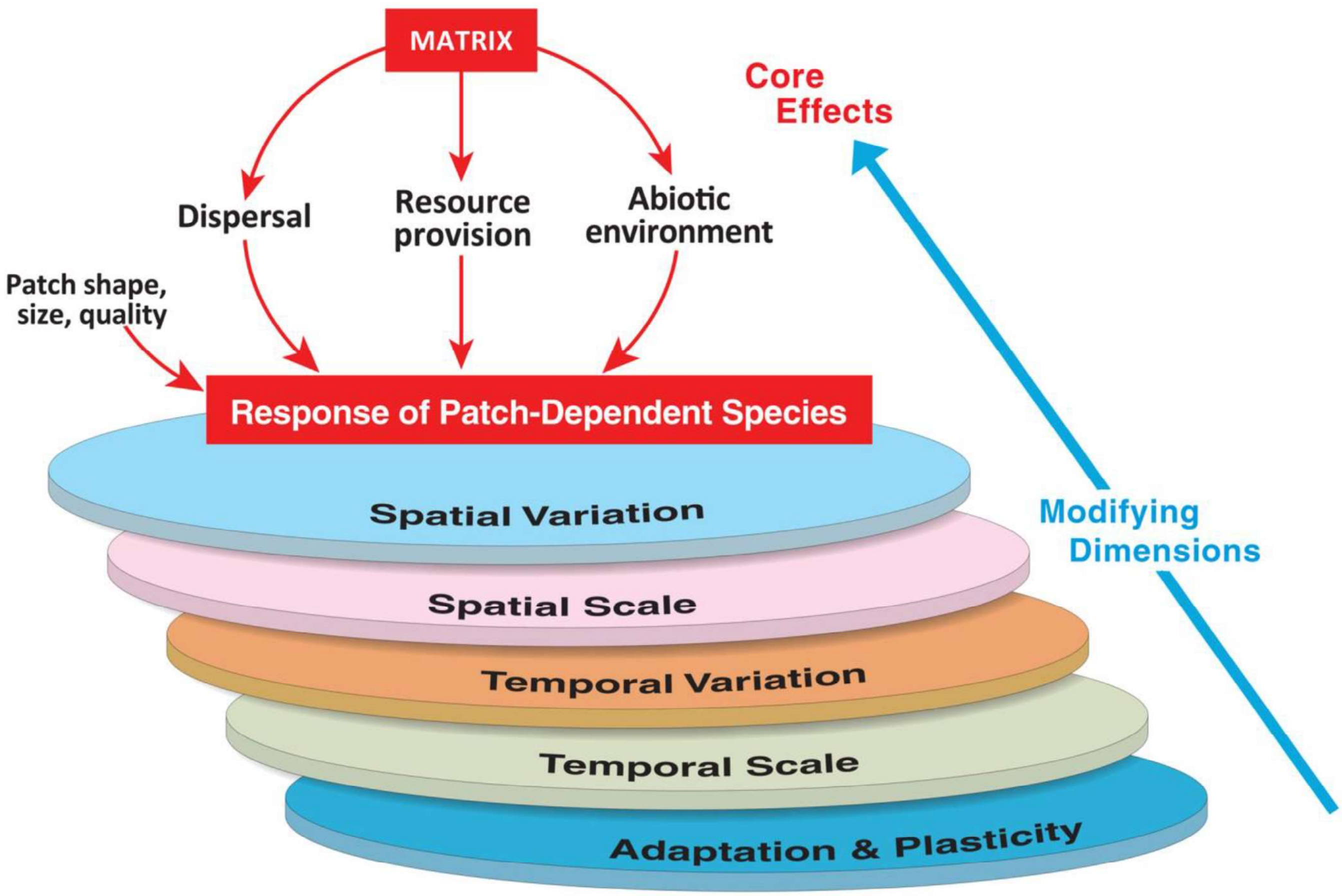

Core effects
Mechanisms through which matrix quality influences species in habitat patches
movement and dispersal
resource base in matrix
abiotic environment of patches
[17]
[15]
mortality in the matrix [2,5]
reduced immigration [1,2]
barrier to emigration [1]
increased immigration [3,4]
matrix provides breeding habitat [16]
matrix provides food supplementation [14]
altered light, evaporation, disturbance (fire, wind) [7,11]
reduced population size [5]
increased risk of extinction [2]
metapopulation failure
demographic and genetic isolation [2,12,13]
crowding / fence effects [1]
metapopulations or patchy populations [3]
colonization of patches by new species (see Box 3)
increased population size [14]
reduced risk of extinction
habitat improvement
reduced risk of extinction [6]
habitat degradation
increased extinction risk [7-10]

Figure 2


MATRIX
Core Effects
Dispersal
Resource provision
Abiotic environment
Patch shape, size, quality
Response of Patch-Dependent Species
Spatial Variation
Spatial Scale
Temporal Variation
Temporal Scale
Adaptation & Plasticity
Modifying Dimensions

Box 1. Species interactions

Species interactions are integral to every step of Figure 1 (as they are to the edge-effects conceptual model by Ries *et al.* [37] and the fragmentation conceptual model by Didham *et al.* [26]). A pathway that affects one strongly interacting species could drive changes in many other species, forming feedback loops through numerous different pathways. For example, Pita *et al.* [2] suggested that predators can occupy degraded matrix sites in Mediterranean farmland (matrix provides breeding habitat, Figure 1). The predators could inflict high dispersal mortality on patch-dependent Cabrera voles *Microtus cabrerae*, reducing patch occupancy where the matrix is highly modified. In another example, increasing resources in the matrix (seeds in wet years) enabled seed-eating rodents to forage widely throughout the landscape [84]. With rodents foraging beyond the patch, seed predation on hawthorn (*Crataegus monogyna*) within the patch was reduced, providing an opportunity for recruitment of this important structural species [84].

Competition-colonisation trade-offs or predator-prey patch dynamics [85] might also drive feedbacks between pathways in Figure 1. Where the matrix is highly permeable, a community could consist of strongly competing species because poorly dispersing but competitively dominant or predatory species can reach all sites. However, if the matrix offers strong resistance to dispersal, the community might consist of less competitive, but strongly dispersive species [86]. Our key point is that species interact. Therefore, the influence of the matrix on patch-dependent species could be indirect because the matrix influences the dispersal, resources or the abiotic environment of other species that depredate, out-compete or have some other interaction [pollination, fruit dispersal, 64, 87] with the patch-dependent species.

Box 2. New species colonise patches by multiple pathways

Invasion of patches by novel species is a widely recognised effect of the matrix on patch-dependent species [25, 35, 36]. However, by defining three core effects (Figure 1), our conceptual model puts colonisation of patches into a mechanistic context. Patch invasion could occur through pathways that stem from each core effect.

1. Dispersal. A particular matrix type might allow species to disperse more effectively, increasing colonisation rates. This mechanism is supported by studies of native species becoming more prevalent in patches surrounded by a matrix suitable for dispersal. For example, the Grand Skink *Oligosoma grande* from New Zealand occupies rocky outcrops in either a native tussock grass matrix, or a modified pasture matrix. Higher dispersal through the native matrix contributes to a more than doubling of patch occupancy [12]. In Argentina, invasion of forest patches by the introduced Red-bellied Squirrel *Callosciurus erythraeus* was facilitated by structural features within the matrix such as forested strips or fences [88].

2. Resource Provision. The matrix provides resources that support a wide range of species and these can spill over into patches of native vegetation to the disadvantage of patch-dependent species. For example, coffee plantations have received widespread attention as a matrix capable of supporting forest species [89], but these plantations also provide resources for pest species. In Mauritius, the Coffee Berry Moth *Prophantis smaragdina* moves from the matrix into adjacent rainforest, consuming the fruit and thereby reducing the reproductive success of the endemic dioecious shrub *Bertiera zaluzania* [90]. Such

spill-over edge-effects could be more widespread than is currently recognised in the literature [56, 90].

3. The abiotic environment. When habitat structure becomes more open and disturbed at edges of native vegetation patches, the altered abiotic conditions enables disturbance-favouring matrix species to invade patches, with consequences for patch-specialists [19, 37]. For example, in the USA, Amur Honeysuckle *Lonicera maackii* is a shade-intolerant invasive shrub occurring in disturbed areas and forest edges with sufficient light [91]. Invasion changed the microclimate which reduced amphibian abundance and diversity [48], along with effects on the invertebrate fauna [92].

Box 3. The Nanangroe Natural Experiment

Figure I. A changing matrix. Pines (*Pinus radiata*) were planted into grazing land beginning in 1998. The left plate shows soil mounds scoured into the farmland in preparation for planting. The trees have now grown into a dense plantation (right plate) which surrounds many remnant woodland patches. The pine matrix will continue to change through cycles of thinning, clearfelling and re-establishment. The dynamic matrix is likely to drive ongoing changes in the animal communities of woodland patches.

The Nanangroe Natural Experiment was designed to quantify the effects of temporal changes in the matrix on patch-dependent species in Australian temperate eucalypt woodlands [4]. The major temporal change in the matrix was the transformation of a former grazing landscape into one dominated by Radiata Pine (*Pinus radiata*) (Figure I) [93].

The Nanangroe study comprises 58 *Eucalyptus* woodland remnants surrounded by pine stands and a set of 58 matched woodland “control” sites on farmland where the surrounding areas are semi-cleared grazing paddocks. The experimental design is underpinned by a randomised and replicated patch selection procedure in which patches in four size classes and five woodland vegetation types were identified for study [93]. Vegetation cover and selected vertebrate species have been sampled on all sites every 1-2 years between 1998 and 2012, creating a high quality time series dataset.

For birds, a range of responses to the changing matrix have been observed in the Nanangroe study [4] and these illustrate some of the pathways emphasised in the conceptual model of core effects (Figure 1). Key responses to the changing matrix include: **(i)** new species were recruited to the landscape because the pine matrix provided breeding habitat (matrix provides breeding habitat, Figure 1); **(ii)** a "spill-over" process whereby some species which increased with the landscape transformation then "spilled over" from the pine matrix into adjacent woodland remnants (matrix provides breeding habitat leading to colonisation of patches by new species, Figure 1), and; **(iii)** a habitat-linked process in which some species' responses were associated with measured temporal changes in vegetation attributes as the patches responded to the changed abiotic conditions and management regime. For example, the ground-foraging Brown Treecreeper *Climacteris picumnus* declined with increasing ground-level vegetation cover [4] (habitat degradation leading to increased extinction risk, Figure 1). These examples underscore the array of responses that can occur as a result of temporal changes in matrix quality.

Box 4. The patch still matters

The matrix affects local populations through core effects associated with dispersal, the resource base and the abiotic environment, but patch dynamics are also strongly influenced by characteristics of the habitat patch itself. For example, does the patch offer high quality habitat for a species, leading to high intrinsic growth rate or is the patch a net sink [94]? How does the quality, size or shape of the patch influence the rate of emigration and immigration [95, 96]? How are the abiotic effects of the matrix mediated by patch shape [97]? The interaction of matrix and patch effects means that the same surrounding matrix could have a large or small effect on a population within a patch, depending on the species' demographic and dispersal response to patch quality, size and shape.

The dimensions that are important modifiers of the effects of the matrix (Figure 2) might also apply to patches. Habitat patches are not homogeneous and vary in quality over time [98]. The rate of change of habitat quality within patches could allow, for example, long-lived species to readily survive short-term changes in habitat quality [99]. Patch size is often important, but spatial scale issues are more relevant when considering a matrix with multiple embedded patches. Adaptation to survive in patches with altered abiotic environments, for example, might also help some patch-dependent species remain in fragmented landscapes [75]. While we emphasise the importance of matrix-related phenomena that influence patch-dependent species in this paper, patch characteristics remain important. Whether the matrix or the patch is more important for the persistence of a particular species can depend on the total amount of native vegetation in the landscape, and whether the matrix or the patch is most variable. For example, if the matrix is homogeneous and relatively static, patch features might be most important, and vice-versa [27].

Box 5. Outstanding Questions

Matrix resources

To what extent do resources outside habitat patches influence patch occupancy? In a metacommunity framework [85], does the species-sorting mechanism extend beyond the habitat patch? In a conservation context, can resource supplementation from the matrix be exploited by managers to maintain patch-dependent species?

Matrix mortality

Animals that venture into the matrix can have elevated death rates [5]. In what circumstances is the matrix a demographic sink and when might the sink be avoided by "fence effects" that discourage movement into the matrix?

Temporary connectivity and population boosts

Can management be temporarily altered during drought, during wet periods or seasonally (e.g. changing grazing levels, crop type, feral predator density) to facilitate dispersal or support population growth of patch-dependent species? Long term studies, spanning cycles of El Niño for example, are needed to solve these problems, in addition to experimental landscape manipulations.

Extent of the matrix

Does the extent of the matrix influence the depth of abiotic or spill-over edge effects? If it does, can the core-area of patches be increased by reducing matrix extent?

Interaction of extent and heterogeneity

Are there typically lower and upper limits to the extent of the matrix beyond which there is no effect of matrix quality on dispersal between patches? To explore the interaction between matrix scale and heterogeneity we need improved understanding of species' dispersal limits through different matrix types.

Interaction of extent and temporal scale

How does dispersal limit a species' ability to exploit matrix resources when the resources are temporary [70]? For example, when an exploitable food resource becomes available in the matrix, how far into the matrix can a patch-dependent species extend before the resource dries up?

Adaptation and potential conflict with other management

In what circumstances does adaptation have an important influence on species survival in extensively modified landscapes, and is adaptation hindered by measures, such as increasing heterogeneity [81], that are aimed at promoting a less hostile matrix?

Developing Generality

Greatest progress towards answering the questions raised in this section will be made if research simultaneously attempts to define the characteristics of species that have similar responses to the matrix, enabling generalisation [39, 41]. For example, if temporary resources are provided in the matrix, what are the traits of patch-dependent species that successfully exploit the resources?

Glossary

Matrix	The matrix is an extensive land-cover with different types of land-cover embedded within it (patches). The matrix does not provide for self-sustaining populations of some species, which are dependent upon the patches. The matrix therefore, includes the extensive land-cover types that patch-dependent species cannot sustainably live in. This definition means that what is the matrix for some species, or was the matrix at one time, might not be at other times [15] or for other species [16].
Patch	Patches are embedded within the matrix, have vegetation that is different from the matrix, and provide habitat for species that cannot live in the matrix. A patch must be defined from the species point of view, but this definition often coincides with a human point of view because many species depend on native vegetation and cannot live in cleared land or other matrix types.
Landscape	A spatial area with diameter substantially exceeding the dispersal distance of species of interest so that spatial dynamics among populations can occur, such as among populations in separate patches. In the context of human-dominated landscapes and species with dispersal distances of a few hundred to a few thousand meters, a landscape could reasonably be delineated as an area spanning 5-10 km.

Matrix scale	Scale can be considered in terms of the distance between patches, and the overall extent of the matrix (that is, does the matrix (with or without embedded patches) extend for a few km or a few hundred km?).
Matrix quality	Defined from a species point of view, and referring to the features of the matrix that influence dispersal, resource availability and abiotic edge effects.
Edge	The boundary between matrix and patch
Edge effect	An increase or decline in abundance or occurrence of a species near the edge, often in response to altered environmental conditions near the edge or as a result of the spill-over of matrix-based species or other resources into patches [see 37]
Dispersal	Movement of organisms across space [100]

References

1 Schtickzelle, N. and Baguette, M. (2003) Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *J. Anim. Ecol.* 72, 533-545

2 Pita, R., *et al.* (2007) Spatial population structure of the Cabrera vole in Mediterranean farmland: The relative role of patch and matrix effects. *Biol. Conserv.* 134, 383-392

3 Templeton, A.R., *et al.* (2011) The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92, 1736-1747

4 Lindenmayer, D.B., *et al.* (2008) Temporal changes in vertebrates during landscape transformation: a large-scale "natural experiment". *Ecol. Monogr.* 78, 567-590

5 Schwab, A.C. and Zandbergen, P.A. (2011) Vehicle-related mortality and road crossing behavior of the Florida panther. *Appl. Geogr.* 31, 859-870

6 Keeley, J.E. (2006) Fire management impacts on invasive plants in the western United States. *Conserv. Biol.* 20, 375-384

7 Lehtinen, R.M., *et al.* (2003) Edge effects and extinction proneness in a herpetofauna from Madagascar. *Biodivers. Conserv.* 12, 1357-1370

8 Urbina-Cardona, J.N., *et al.* (2006) Herpetofauna diversity and microenvironment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. *Biol. Conserv.* 132, 61-75

9 Williams, N.S.G., *et al.* (2006) Local extinction of grassland plants: The landscape matrix is more important than patch attributes. *Ecology* 87, 3000-3006

10 Kennedy, C.M., *et al.* (2011) Landscape matrix mediates occupancy dynamics of Neotropical avian insectivores. *Ecol. Appl.* 21, 1837-1850

11 Cochrane, M.A. and Barber, C.P. (2009) Climate change, human land use and future fires in the Amazon. *Global Change Biol.* 15, 601-612

12 Seddon, P.J., *et al.* (2011) Dynamics of an endangered New Zealand skink: accounting for incomplete detectability in estimating patch occupancy. *N. Z. J. Ecol.* 35, 247-253

13 Driscoll, D.A., *et al.* (2012) Spatial dynamics of the knob-tailed gecko Nephrurus stellatus in a fragmented agricultural landscape. *Landscape Ecol.* 27, 829-841

14 Hinners, S.J., *et al.* (2012) Roles of scale, matrix, and native habitat in supporting a diverse suburban pollinator assemblage. *Ecol. Appl.* 22, 1923-1935

15 Blaum, N. and Wichmann, M.C. (2007) Short-term transformation of matrix into hospitable habitat facilitates gene flow and mitigates fragmentation. *J. Anim. Ecol.* 76, 1116-1127

16 Poulin, J.-F. and Villard, M.-A. (2011) Edge effect and matrix influence on the nest survival of an old forest specialist, the Brown Creeper (Certhia americana). *Landscape Ecol.* 26, 911-922

17 D'Antonio, C.M. and Vitousek, P.M. (1992) Biological Invasions by Exotic Grasses, the Grass Fire Cycle, and Global Change. *Annu. Rev. Ecol. Syst.* 23, 63-87

18 Lindenmayer, D.B. and Fischer, J. (2006) *Habitat Fragmentation and Landscape Change. An ecological and conservation synthesis*. Island Press

19 Saunders, D.A., *et al.* (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5, 18-32

20 Forman, R.T.T. (1995) *Land mosaics. The ecology of landscapes and regions*. Cambridge University Press

21 Fahrig, L. and Merriam, G. (1994) Conservation of fragmented populations. *Conserv. Biol.* 8, 50-59

22 McIntyre, S. and Hobbs, R. (1999) A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conserv. Biol.* 13, 1282-1292

23 Driscoll, D.A. (2004) Extinction and outbreaks accompany fragmentation of a reptile community. *Ecol. Appl.* 14, 220-240

24 Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press

25 Kupfer, J.A.*, et al.* (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecol. Biogeogr.* 15, 8-20

26 Didham, R.K.*, et al.* (2012) Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* 121, 161-170

27 Bender, D.J. and Fahrig, L. (2005) Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology* 86, 1023-1033

28 Prugh, L.R.*, et al.* (2008) Effect of habitat area and isolation on fragmented animal populations. *Proc. Natl. Acad. Sci. USA.* 105, 20770-20775

29 Franklin, J.F. and Lindenmayer, D.B. (2009) Importance of matrix habitats in maintaining biological diversity. *Proc. Natl. Acad. Sci. USA.* 106, 349-350

30 Franklin, J.F. (1993) Preserving biodiversity - species, ecosystems, or landscapes. *Ecol. Appl.* 3, 202-205

31 Secretariat of the Convention on Biological Diversity (2010) *Global biodiversity outlook 3*.

32 Kyle, G. and Duncan, D.H. (2012) Arresting the rate of land clearing: Change in woody native vegetation cover in a changing agricultural landscape. *Landscape Urban Plann.* 106, 165-173

33 Bradshaw, C.J.A. (2012) Little left to lose: deforestation and forest degradation in Australia since European colonization. *J. Plant Ecol.* 5, 109-120

34 Ewers, R.M. and Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81, 117-142

35 Jules, E.S. and Shahani, P. (2003) A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. *Journal of vegetation science* 14, 459-464

36 Murphy, H.T. and Lovett-Doust, J. (2004) Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos* 105, 3-14

37 Ries, L., *et al.* (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.* 35, 491-522

38 Campbell, R.E., *et al.* (2011) Production land use alters edge response functions in remnant forest invertebrate communities. *Ecol. Appl.* 21, 3147-3161

39 Kennedy, C.M., *et al.* (2010) Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. *Ecol. Monogr.* 80, 651-669

40 Eycott, A.E. (2010) *Do landscape matrix features affect species movement? Systematic Review CEE 08-006*. Collaboration for Environmental Evidence; http://www.environmentalevidence.org/SR43.html

41 Prevedello, J.A. and Vieira, M.V. (2010) Does the type of matrix matter? A quantitative review of the evidence. *Biodivers. Conserv.* 19, 1205-1223

42 Kuefler, D., *et al.* (2010) The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology* 91, 944-950

43 Schooley, R.L. and Wiens, J.A. (2004) Movements of cactus bugs: patch transfers, matrix resistance, and edge permeability. *Landscape Ecol.* 19, 801-810

44 Hovestadt, T. and Poethke, H.J. (2006) The control of emigration and its consequences for the survival of populations. *Ecol. Model.* 190, 443-453

45 Karp, D.S.*, et al.* (2011) Resilience and stability in bird guilds across tropical countryside. *Proc. Natl. Acad. Sci. USA.* 108, 21134-21139

46 Ockinger, E.*, et al.* (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography* 35, 259-267

47 Ewers, R.M. and Didham, R.K. (2008) Pervasive impact of large-scale edge effects on a beetle community. *Proc Natl Acad Sci U S A* 105, 5426 - 5429

48 Watling, J.I.*, et al.* (2011) Invasive shrub alters native forest amphibian communities. *Biol. Conserv.* 144, 2597-2601

49 Lindenmayer, B.D.*, et al.* (2009) Effects of logging on fire regimes in moist forests. *Conservation Letters* 2, 271-277

50 Ramalho, C.E. and Hobbs, R.J. (2012) Time for a change: dynamic urban ecology. *Trends Ecol. Evol.* 27, 179-188

51 Gustafson, E.J. and Gardner, R.H. (1996) The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77, 94-107

52 Hudgens, B.R.*, et al.* (2012) How complex do models need to be to predict dispersal of threatened species through matrix habitats? *Ecol. Appl.* 22, 1701-1710

53 Zeller, K.A.*, et al.* (2012) Estimating landscape resistance to movement: a review. *Landscape Ecol.* 27, 777-797

54 Pinto, S.R.R.*, et al.* (2010) Landscape attributes drive complex spatial microclimate configuration of Brazilian Atlantic forest fragments. *Trop. Conserv. Sci.* 3, 389-402

55 Hill, J.K., *et al.* (1996) Effects of habitat patch size and isolation on dispersal by Hesperia comma butterflies: implications for metapopulation structure. *J. Anim. Ecol.* 65, 725-735

56 Rand, T.A., *et al.* (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9, 603-614

57 Delgado, J.D., *et al.* (2007) Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). *Landscape Urban Plann.* 81, 328-340

58 Powney, G.D., *et al.* (2011) Measuring functional connectivity using long-term monitoring data. *Methods Ecol. Evol.* 2, 527-533

59 Revilla, E., *et al.* (2004) Effects of matrix heterogeneity on animal dispersal: From individual behavior to metapopulation-level parameters. *Am. Nat.* 164, E130-E153

60 Tremblay, M.A. and St Clair, C.C. (2011) Permeability of a heterogeneous urban landscape to the movements of forest songbirds. *J. Appl. Ecol.* 48, 679-688

61 Manning, A.D., *et al.* (2006) Scattered trees are keystone structures - Implications for conservation. *Biol. Conserv.* 132, 311-321

62 Cosentino, B.J., *et al.* (2011) Connectivity of agroecosystems: dispersal costs can vary among crops. *Landscape Ecol.* 26, 371-379

63 Blaum, N., *et al.* (2012) Climate induced changes in matrix suitability explain gene flow in a fragmented landscape - the effect of interannual rainfall variability. *Ecography* 35, 650-660

64 Magrach, A., *et al.* (2012) Effects of Matrix Characteristics and Interpatch Distance on Functional Connectivity in Fragmented Temperate Rainforests. *Conserv. Biol.* 26, 238-247

65 Laurance, W.F., *et al.* (2011) The fate of Amazonian forest fragments: A 32-year investigation. *Biol. Conserv.* 144, 56-67

66 Hennenberg, K.J., *et al.* (2008) Detection of seasonal variability in microclimatic borders and ecotones between forest and savanna. *Basic Appl. Ecol.* 9, 275-285

67 Asbjornsen, H., *et al.* (2004) Synergistic responses of oak, pine and shrub seedlings to edge environments and drought in a fragmented tropical highland oak forest, Oaxaca, Mexico. *For. Ecol. Manage.* 192, 313-334

68 D'Antonio, C.M., *et al.* (2011) Long-term impacts of invasive grasses and subsequent fire in seasonally dry Hawaiian woodlands. *Ecol. Appl.* 21, 1617-1628

69 Donald, P.F. and Evans, A.D. (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *J. Appl. Ecol.* 43, 209-218

70 Boudreault, C., *et al.* (2012) Epiphytic lichen colonization in regenerating black spruce forest stands of clearcut origin. *For. Ecol. Manage.* 276, 247-258

71 Wilcock, H.R., *et al.* (2007) Landscape, habitat characteristics and the genetic population structure of two caddisflies. *Freshwat. Biol.* 52, 1907-1929

72 Ostfeld, R.S. and Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *T.R.E.E.* 15, 232-237

73 Alanen, E.-L., *et al.* (2011) Differential responses of bumblebees and diurnal Lepidoptera to vegetation succession in long-term set-aside. *J. Appl. Ecol.* 48, 1251-1259

74 Barbosa, O. and Marquet, P.A. (2002) Effects of forest fragmentation on the beetle assemblage at the relict forest of Fray Jorge, Chile. *Oecologia* 132, 296-306

75 Hanski, I. (2012) Eco-evolutionary dynamics in a changing world. *Ann. N. Y. Acad. Sci.* 1249, 1-17

76 Heidinger, I.M.M., *et al.* (2010) Patch connectivity and sand dynamics affect dispersal-related morphology of the blue-winged grasshopper Oedipoda caerulescens in coastal grey dunes. *Insect Conservation and Diversity* 3, 205-212

77 Merckx, T. and Van Dyck, H. (2006) Landscape structure and phenotypic plasticity in flight morphology in the butterfly Pararge aegeria. *Oikos* 113, 226-232

78 Tuomainen, U. and Candolin, U. (2011) Behavioural responses to human-induced environmental change. *Biological Reviews* 86, 640-657

79 Sih, A., *et al.* (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications* 4, 367-387

80 REX Consortium (2013) Heterogeneity of selection and the evolution of resistance. *Trends Ecol. Evol.* 28, 110-118

81 Shreeve, T.G. and Dennis, R.L.H. (2011) Landscape scale conservation: resources, behaviour, the matrix and opportunities. *J. Insect Conserv.* 15, 179-188

82 Driscoll, D.A. and Lindenmayer, B.D. (2012) Framework to improve the application of theory in ecology and conservation. *Ecol. Monogr.* 82, 129–147

83 Fahrig, L. (2001) How much habitat is enough? *Biol. Conserv.* 100, 65-74

84 Herrera, J.M., *et al.* (2011) Matrix effects on plant-frugivore and plant-predator interactions in forest fragments. *Landscape Ecol.* 26, 125-135

85 Leibold, M.A., *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601-613

86 Rodriguez, A., *et al.* (2007) Composition of an avian guild in spatially structured habitats supports a competition-colonization trade-off. *Proceedings of the Royal Society B-Biological Sciences* 274, 1403-1411

87 Taki, H., *et al.* (2011) Plantation vs. natural forest: Matrix quality determines pollinator abundance in crop fields. *Sci Rep* 1

88 Bridgman, L.J., *et al.* (2012) Short perceptual range and yet successful invasion of a fragmented landscape: the case of the red-bellied tree squirrel (Callosciurus erythraeus) in Argentina. *Landscape Ecol.* 27, 633-640

89 Philpott, S.M., *et al.* (2008) Biodiversity Loss in Latin American Coffee Landscapes: Review of the Evidence on Ants, Birds, and Trees. *Conserv. Biol.* 22, 1093-1105

90 Kaiser, C.N., *et al.* (2008) Exotic pest insects: another perspective on coffee and conservation. *Oryx* 42, 143-146

91 Watling, J.I. and Orrock, J.L. (2010) Measuring edge contrast using biotic criteria helps define edge effects on the density of an invasive plant. *Landscape Ecol.* 25, 69-78

92 McNeish, R.E., *et al.* (2012) Riparian forest invasion by a terrestrial shrub (Lonicera maackii) impacts aquatic biota and organic matter processing in headwater streams. *Biol. Invasions* 14, 1881-1893

93 Lindenmayer, D.B., *et al.* (2001) A prospective longitudinal study of landscape matrix effects on fauna in woodland remnants: experimental design and baseline data. *Biol. Conserv.* 101, 157-169

94 Sanderlin, J.S., *et al.* (2012) On valuing patches: estimating contributions to metapopulation growth with reverse-time capture-recapture modelling. *Proceedings of the Royal Society B-Biological Sciences* 279, 480-488

95 Pavlacky, D.C., Jr., *et al.* (2012) Anthropogenic landscape change promotes asymmetric dispersal and limits regional patch occupancy in a spatially structured bird population. *J. Anim. Ecol.* 81, 940-952

96 Nams, V.O. (2012) Shape of patch edges affects edge permeability for meadow voles. *Ecol. Appl.* 22, 1827-1837

97 Gonzalez-Moreno, P., *et al.* (2011) Is spatial structure the key to promote plant diversity in Mediterranean forest plantations? *Basic Appl. Ecol.* 12, 251-259

98 Mortelliti, A., *et al.* (2010) The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. *Oecologia* 163, 535-547

99 Williams, D.A., *et al.* (2007) Genetic diversity and spatial structure of a keystone species in fragmented pine rockland habitat. *Biol. Conserv.* 138, 256-268

100 Vellend, M. (2010) Conceptual synthesis in community ecology. *Q. Rev. Biol.* 85, 183-206