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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': spatial and temporal variation in matrix quality; spatial scale; temporal scale of matrix variation; and adaptation. The conceptual domain of the matrix, defined as three core effects and their interaction with these 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 focuses on patches of native vegetation in a surrounding matrix that is highly modified by agriculture or urbanisation [1,2]. The patch–matrix model of landscapes [3] includes patches that are useful for conservation and the matrix in which the patches are embedded [4] (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 [5–7]. However, the matrix surrounding remnant vegetation can have a strong influence on species occurrence and spatial dynamics [8,9] and can be more important than the size and spatial arrangement of remnant patches [10–12]. The growth in knowledge about the matrix means that 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, but it is also urgent. The nature of the matrix has profound implications for conserving biodiversity [12,13]. Management of the matrix can limit or exacerbate the impacts of habitat loss and fragmentation [14], which are the biggest threat to biodiversity globally [15]. 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 [16,17]. Where this is the case, modifying the matrix will be the major form of landscape change in the future and, therefore, will 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 in which scientists and land managers think about matrix ecology.

Although there has been much conceptual development in the habitat fragmentation literature [5,9,18], 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 [8,19,20], and from research into edge effects [21] and habitat fragmentation [9,18], 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

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Glossary

Dispersal : movement of organisms across space [83].

Edge : the boundary between the matrix and the 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 spillover of matrix-based species or other resources into patches [21].

Landscape : a spatial area with a 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 : an extensive land cover with different types of land cover embedded within it (i.e., patches). The matrix does not provide for self-sustaining populations of some species, which are dependent upon the patches. Therefore, the matrix 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 [61] or for other species [32].

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.

Matrix 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?].

Patch : an area embedded within the matrix that has vegetation that is different from the matrix, and provides 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.

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Box 1. Species interactions

Species interactions are integral to every step of Figure 1 (main text), as they are to the edge-effects conceptual model by Ries *et al.* [21] and the fragmentation conceptual model by Didham *et al.* [9]. 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.* [10] suggested that predators occupy degraded matrix sites in Mediterranean farmland (matrix provides breeding habitat, Figure 1, main text). 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 (main text). Where the matrix is highly permeable, a community could comprise 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 comprise 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, outcompete, or have some other interaction (e.g., pollination or fruit dispersal, [63,87]) 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 [8,19,20]. However, by defining three core effects (Figure 1, main text), our conceptual model puts colonisation of patches into a mechanistic context. Patch invasion could occur through pathways that stem from each core effect.

Dispersal
A particular matrix type might enable 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 [88]. 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 [89].

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 [90], but they 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* [91]. Such spillover edge effects could be more widespread than is currently recognised in the literature [54,89].
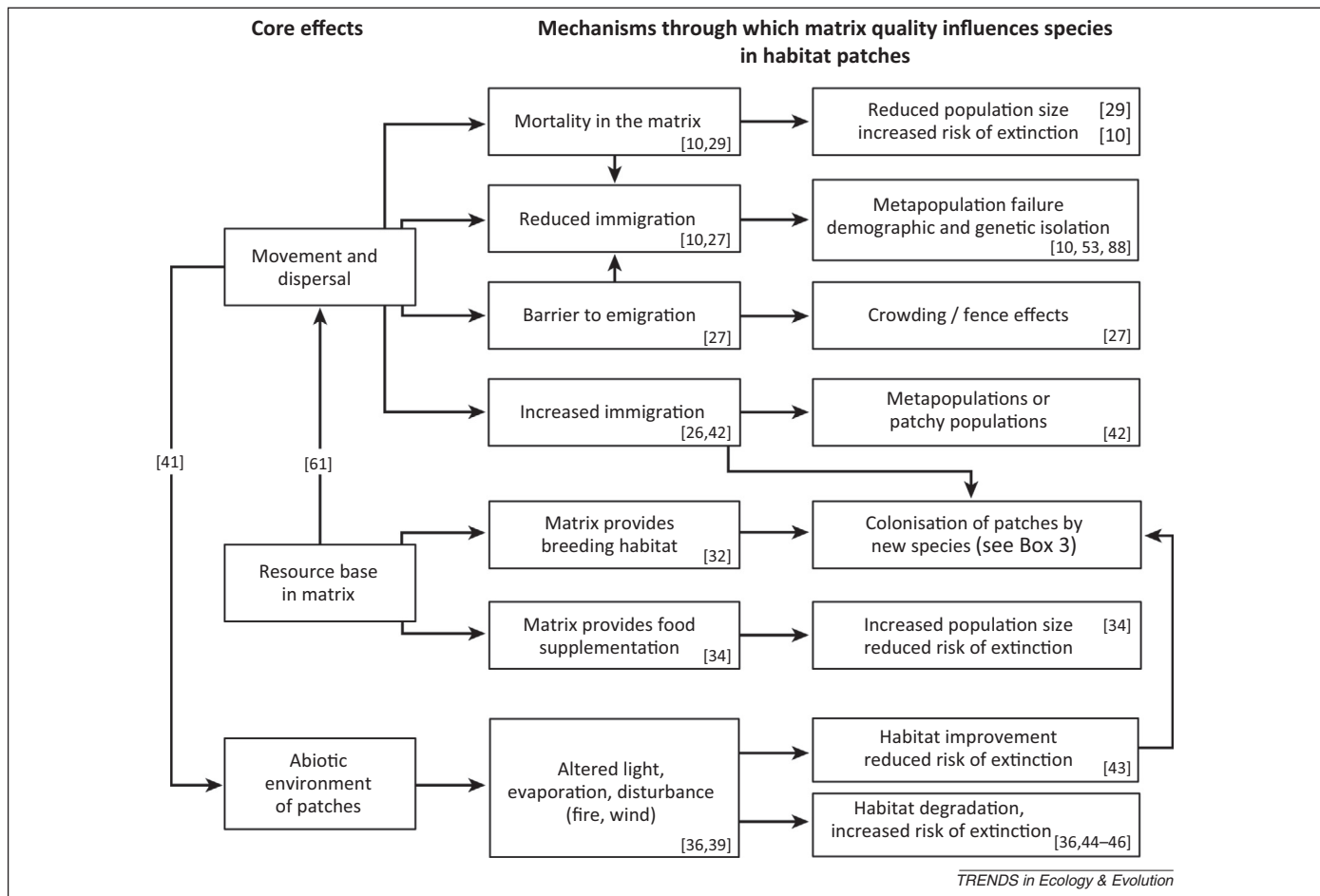
The abiotic environment
When habitat structure becomes more open and disturbed at edges of native vegetation patches, the altered abiotic conditions enables disturbance-favouring matrix species to invade patches, with consequences for patch specialists [2,21]. For example, in the USA, Amur honeysuckle (*Lonicera maackii*) is a shade-intolerant invasive shrub occurring in disturbed areas and forest edges with sufficient light [92]. Invasion changed the microclimate, which reduced amphibian abundance and diversity [38], along with effects on the invertebrate fauna [93].

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effects (e.g. [8,19,20,22,23]), we illustrate relations among mechanisms in a conceptual model. We demonstrate through the conceptual model that what previously were considered primary effects of the matrix are in fact secondary outcomes of three 'core effects' (Boxes 1 and 2). In the second part of our review, we identify five influential 'dimensions' and show how these modify the way in which 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 canvassed in numerous reviews [2,8,18–20]), we identified three fundamental ways in which 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 [24,25]. For example, when pastures are replaced by tree plantations, colonisation of

forest patches by forest specialists can increase [26]. 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') [27]. If a species does venture into the matrix, rapid movement through unfavourable habitat could enhance connectivity between separated habitat patches [28]. By contrast, dispersal or movement between disjunct habitat patches might decline due to altered behaviour or increased mortality [9,10,29,30]. 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 [31].

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 [2] (Box 3). For example, red squirrel (*Tamiasciurus hudsonicus*) populations thrived on pine seeds in Canadian pine plantations. The squirrels subsequently invaded

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 enable nonpatch 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 in square brackets indicate references that support parts of each pathway.

remnant broad-leaf forest and ate brown creeper (*Certhia americana*) eggs, increasing the rate of nest failure of this patch-dependent bird [32]. By contrast, if the right resources are provided, the matrix can be converted to habitat and desirable native species can live throughout the landscape (e.g., [33]). However, if species remain patch dependent, they might use resources within the matrix as a food subsidy [18]. With the possible exception of bees that can forage outside of the nesting patch (e.g., [34]), evidence that patch-dependent species gather resources outside of the patch to support higher population densities inside the patch is limited (e.g., [35]).

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 [2,21], particularly when treed landscapes are cleared [8]. Microclimatic changes associated with increased light and wind penetration can have far-reaching effects on patch-dependent species, increasing the risk of local extinction [36,37]. In addition, species

that prosper under the altered microclimate can colonise remnant vegetation and drive edge-sensitive species into the remnant core [21,38].

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 [39], or when the fuel structure in the matrix is changed by forest logging [39,40] or by invasive grasses [41]. Conversely, active fire suppression in matrix environments can reduce rates of natural disturbance in patches [42]. Altered microclimate and disturbance regimes can advantage some species, often invasive exotic species [41,43], but disadvantage others, often species that depend on remnant vegetation [44]. Increased disturbance associated with urban or mining landscapes can also drive local extinctions in patches [45,46].

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

Box 3. The Nanangroe natural experiment

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 [26]. 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) [94].

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 semicleared 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 [94]. Vegetation cover and selected vertebrate species were sampled on all sites every 1–2 years between 1998 and 2012, creating a high-quality time-series data set.

For birds, a range of responses to the changing matrix have been observed in the Nanangroe study [26] and these illustrate some of the pathways emphasised in the conceptual model of core effects (Figure 1, main text). 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, main text); (ii) a 'spillover' process, whereby some species that 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, main text); and (iii) a habitat-linked process in which the responses of some species 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, main text). These examples underscore the array of responses that can occur as a result of temporal changes in matrix quality.
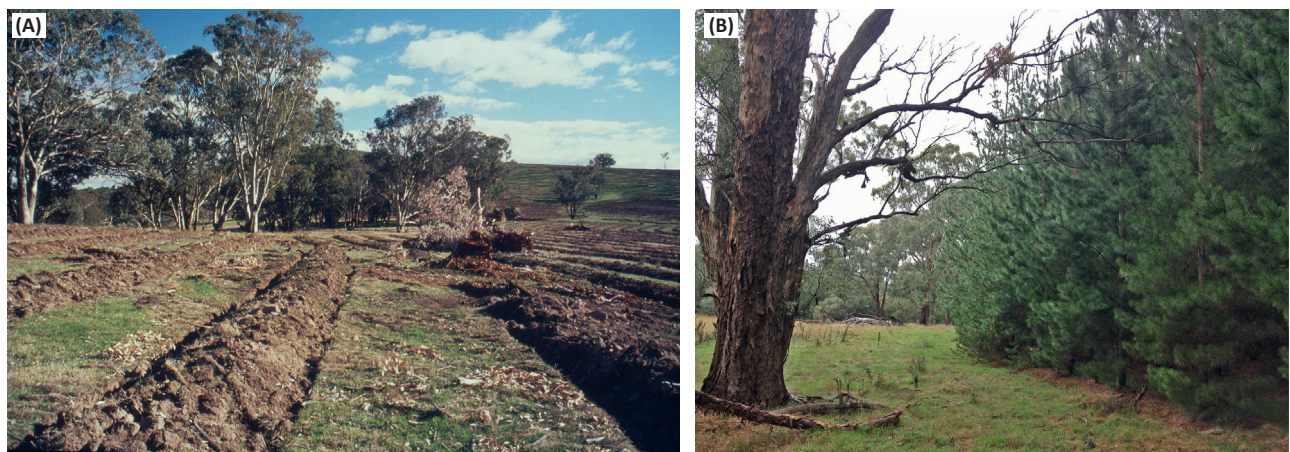
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Figure I. A changing matrix. Pines (*Pinus radiata*) were planted into grazing land beginning in 1998. **(A)** shows soil mounds scoured into the farmland in preparation for planting. The trees have now grown into a dense plantation **(B)** which surrounds 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.

as an important effect of the matrix on patch-dependent species [2,8,19,20]. 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 [22], 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 that there are five influential dimensions that must also 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.* [9].

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 [8,46,47]. By introducing variation into dispersal patterns, the structure and quality of a heterogeneous matrix can influence the degree of isolation of habitat patches [11,46]. 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 [48,49]. Although practical ways have been developed to explore how spatial variation in matrix quality affects dispersal, empirical knowledge of matrix effects remains scarce [50].

Spatial variation in matrix quality will also lead to variation in microclimate conditions, imposing spatially variable edge effects [8,51]. Furthermore, variation in matrix quality can affect taxa differently by providing contrasting resources. For example, Öckinger *et al.* [35] found higher butterfly species richness within grassland
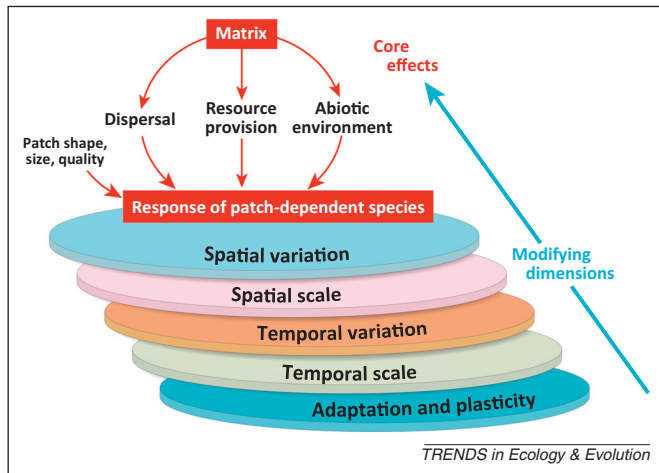
Figure 2. Five dimensions modify matrix core effects. The conceptual model of the matrix comprises the three core effects (Figure 1, main text) whereby the matrix influences patch-dependent species through effects associated with movement and dispersal, resource availability, and the abiotic environment. Five dimensions modify the way in which 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 priority of effects (although difficult to draw, these could be imagined as overlapping spheres encompassing the core effects, similar to electrons around the nucleus of an atom). 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 and 4, main text). For simplicity, we have not attempted to draw all of the likely relations between patches and the factors that influence the impact of the matrix on patch-dependent species.

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 [95]? How does the quality, size, or shape of the patch influence the rate of emigration and immigration [96,97]? How are the abiotic effects of the matrix mediated by patch shape [98]? 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 demographic and dispersal response of the species to patch quality, size, and shape.

The dimensions that are important modifiers of the effects of the matrix (Figure 2, main text) might also apply to patches. Habitat patches are not homogeneous and vary in quality over time [99]. The rate of change of habitat quality within patches could enable, for example, long-lived species to survive readily short-term changes in habitat quality [100]. 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 [74]. Although we emphasise the importance of matrix-related phenomena that influence patch-dependent species in this review, 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 [11].

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patches surrounded by a forest matrix, but higher species richness of hoverflies in grassland patches surrounded by arable land, reflecting differences in the food resources of 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, has an important effect on patch-dependent species. The distance between patches is well understood to influence dispersal rates [52]. Because dispersal influences the probabilities of population extinction and recolonisation of patches [7], 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 [53].

The spatial extent of the matrix can also influence resource subsidisation and spillover edge effects, although evidence for such effects is limited. If patch-dependent species exploit resources in the matrix [18], a proportionally greater area of matrix to patch could increase the relative abundance of such resources. However, movement limitation and satiation might prevent patch-based species from exploiting an ever-increasing amount of matrix. Spillover of matrix-specialist predators or prey into patches [54] 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 spillover edge effects [32].

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, thus, understanding of such effects is rudimentary. Narrow gaps such as forest roads can have substantial abiotic edge effects [55]. 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 [39].

Interactions between spatial scale and spatial variation in matrix quality can have important effects on populations in fragmented systems [56,57]. By examining the extent to which changes in population size were synchronous, Powney *et al.* [56] found that matrix permeability to dispersal had the strongest effect on movement between patches at intermediate distances. By 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 [57] or the scale over which population synchrony occurs [56].

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 in, or loss of, trees [58,59]. 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, enabled collared lizards (*Crotaphytus collaris*) to

disperse between glades and establish stable metapopulations [42]. Other causes of temporal variation in dispersal through the matrix have included annual variation in crops planted in farming landscapes [60], and climatic cycles of rainfall and drought [61,62].

Changes in dispersal are often driven by temporal changes in resources [59,62,63]. Temporal variation in the resource base might also lead to variation in resource subsidisation [18], but to date, the limited evidence for this is largely inferential.

Abiotic effects are highly dynamic [36] 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 [64]. Similar changes can take place seasonally in regions with distinct dry and wet seasons [65], or during droughts [66]. In addition, fire regimes change to become more extreme as exotic grasses invade new areas [67].

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 [68]. 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 [69]. Strong dispersers are in the best position to exploit short-term changes in matrix resources [70], whereas species with intermediate dispersal abilities could benefit most from longer-lasting temporal changes, such as revegetation [68].

The ability to exploit resource pulses in the matrix also depends strongly on the life-history characteristics of a species. For example, hairy-footed gerbils (*Gerbillurus paeba*) of southern African savannahs are dependent on grasslands embedded in an inhospitable shrubby matrix that is maintained by heavy grazing [61]. 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 six young per litter) of the gerbils enabled them to exploit this short-term boom in seed supply [61]. By 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 [71]. Resource specialisation can also influence the ability of a species to respond to changing resources in the matrix. Diet generalists can exploit food resource pulses better than can specialists because specialisation on rare and ephemeral food sources is uncommon [71]. By contrast, where resources change gradually, dietary specialists can replace generalists as succession advances [72].

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 [73] or adequate dispersal [36] are able to exploit seasonal retreats of abiotic edge effects and expand the area that they occupy within a patch [65].

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 [74–76]. 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 [74,75]. Therefore, changes in the matrix that influence dispersal-related mortality (e.g., increased desiccation risk [60]), or extinction risk within patches (e.g., changes in the matrix fire regime [67]) 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 [76]). Adaptive responses to changes in the abiotic environment are also possible (e.g., caterpillars adapted to survive in open farmland environments [77]). However, such effects have not been widely investigated. Recent reviews of adaptation to global change indicate that, although such adaptation does occur, much remains to be learnt about the extent to which it can mitigate the negative effects of human-induced environmental change [74,77,78]. Nevertheless, we 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 [74].

What can be achieved with the new conceptual model?

By defining the conceptual domain of the matrix (Figures 1 and 2; Boxes 1 and 4) and emphasising how core effects can be modified by the five dimensions, important new research priorities are now apparent (Box 5). 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 [79]. This sets up a conundrum because management recommendations to increase matrix heterogeneity [80] 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 [69]? 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? Therefore, our

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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 [29]. 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, wet periods, or seasonally (e.g., changing grazing levels, crop type, or 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 spillover 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 the dispersal limits of species through different matrix types.

Interaction of extent and temporal scale
How does dispersal limit the ability of a species to exploit matrix resources when the resources are temporary [69]? 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 [80], that are aimed at promoting a less hostile matrix?

Developing generality
Greatest progress towards answering the questions raised here will be made if research attempts simultaneously to define the characteristics of species that have similar responses to the matrix, enabling generalisation [23,25]. For example, if temporary resources are provided in the matrix, what are the traits of patch-dependent species that successfully exploit the resources?

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conceptual model provides a framework for developing research questions that lead to conditional predictions about matrix effects [81]. Combined with attempts to generalise across species by considering species traits [23,25] (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 [12,14,82]. Previously, lists of possible approaches have been proposed, such as maintaining a certain proportion of forest cover of particular size [14], maintaining hedgerows, or reducing insecticide use [82]. Our conceptual framework means that 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 researchers who are new to the field to comprehend quickly 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.

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