

The Prominent Role of the Matrix in Ecology, Evolution, and Conservation

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Keywords

countryside biogeography, edge effect, land use, landscape resistance, spatial ecology

Abstract

As the Anthropocene proceeds, the matrix in which remaining habitats are embedded is an increasingly dominant component of altered landscapes. The matrix appears to have diverse and far-reaching effects, yet our understanding of the causes and consequences of these effects remains limited. We first synthesize the broad range of perspectives on the matrix, provide a generalized framing that captures these perspectives, and propose hypotheses for how and why the matrix matters for ecological and evolutionary processes. We then summarize evidence for these hypotheses from experiments in which the matrix was manipulated. Nearly all experiments revealed matrix effects, including changes in local spillover, individual movement and dispersal, and use of resources in the matrix. Finally, we discuss how the matrix has been, and should be, incorporated into conservation and management and suggest future issues to advance research on and applications of the matrix in ecology, evolution, and conservation.

INTRODUCTION

Matrix: land use, cover, and/or environmental conditions that differ from either species' habitat or reference/natural conditions

Patch: an area that differs from its surroundings; often assumed to provide habitat for species that cannot persist in the matrix

Habitat: resources and conditions present in an area that produce occupancy, survival, and reproduction by a given organism (a species-specific concept)

Edge: the boundary between patch types or between the matrix and a patch

Matrix effects: changes that occur in habitat or across land uses due to variation in the matrix

A traveler to Manaus, Brazil, in the mid-1980s, looking out her window after flying across seemingly endless tracts of dark green rain forest, would have been startled to see a Mondrian-like landscape: patches of dark green, varying in size, separated by a matrix of much lighter color (**Figure 1a**). What she would have been looking at was the celebrated habitat fragmentation experiment initiated by Thomas Lovejoy (Lovejoy et al. 1984), based on principles of island biogeography that emphasized the area and degree of isolation of habitat patches, akin to islands in an ocean. The patches were experimental remnants of original forest; the matrix was cattle pasture. As expected, species loss was greatest on smaller patches (Laurance et al. 2002). Some decades later, a visitor flying over would see darker matrix surrounding those fragments (**Figure 1a**). In the intervening years, the matrix had ceased to be used for cattle ranching and had slowly regenerated to secondary forest dominated by either *Cecropia* or *Vismia* (**Figure 1a**). Some species that were lost had returned, and the species least likely to disappear in the patches were those found living in and using the matrix to some degree (Gascon et al. 1999). These long-term results clearly demonstrate that the nature of the matrix separating remaining habitat matters greatly for biodiversity in the Anthropocene (Stouffer et al. 2006).

Across the planet, the matrix has become an increasingly pervasive feature of contemporary landscapes. Human land use has transformed 75–95% of the Earth's ice-free land area (Ellis 2021). Cropland now comprises approximately 10% of the planet's land surface area, and much of the planet's remaining forest occurs within 1 km of an edge that borders the matrix (Haddad et al. 2015, Potapov et al. 2022). Indeed, human-modified lands are encroaching on all natural biomes (Hansen et al. 2022). The velocity of land-use change is rapid and dynamic, with 1.25×10^6 km² and 1.42×10^6 km² global increases in croplands and built areas, respectively, between 2000 and 2020 (**Figure 1b**) (Potapov et al. 2022). These changes in land use are creating a spatially pervasive and temporally dynamic matrix in which fragments of remaining natural areas are embedded.

Clearly, the matrix matters. While theory employed to understand human land-use effects on biodiversity initially ignored the matrix, focusing instead on the spatial, island-like attributes of remnant habitat patches (reviewed in Matthews 2021), there is increasing empirical evidence from global syntheses that the matrix can have effects as strong as or stronger than the spatial attributes of habitat patches. For instance, the surrounding matrix explained more variation than did patch area and isolation in occurrences of 785 animal species across the planet (Prugh et al. 2008). Based on 283 populations, investigations incorporating the matrix reported greater effects of isolation on species abundance and occupancy than did investigations ignoring the surrounding matrix (Watling et al. 2011). More recently, an analysis of 4,426 terrestrial mammals indicated that matrix characteristics may be more influential than habitat loss in extinction risk (Ramirez-Delgado et al. 2022). There is also increasing evidence that the matrix can alter evolutionary processes, restricting gene flow and altering population differentiation across both short and long timescales (Balkenhol et al. 2016, Brusquetti et al. 2023, Jacob et al. 2020).

Although matrix effects appear ubiquitous, our understanding of these effects remains limited. Some local effects of the matrix are well understood (e.g., Blitzer et al. 2012), yet our knowledge of matrix effects has been slow to move beyond the phrase “the matrix matters” (Ricketts 2001) to understand when, why, and where—and by how much—the matrix governs ecological and evolutionary dynamics. Generalized conservation strategies that embrace the matrix and its effects have been slow to emerge (but see Donald & Evans 2006). Experiments manipulating the matrix to address mechanisms that influence biodiversity are rare (Haynes & Cronin 2004), and theory encompassing the matrix remains underdeveloped in comparison to the vast theory developed to interpret other aspects of landscape change (e.g., Flather & Bevers 2002, Rybicki et al. 2020).

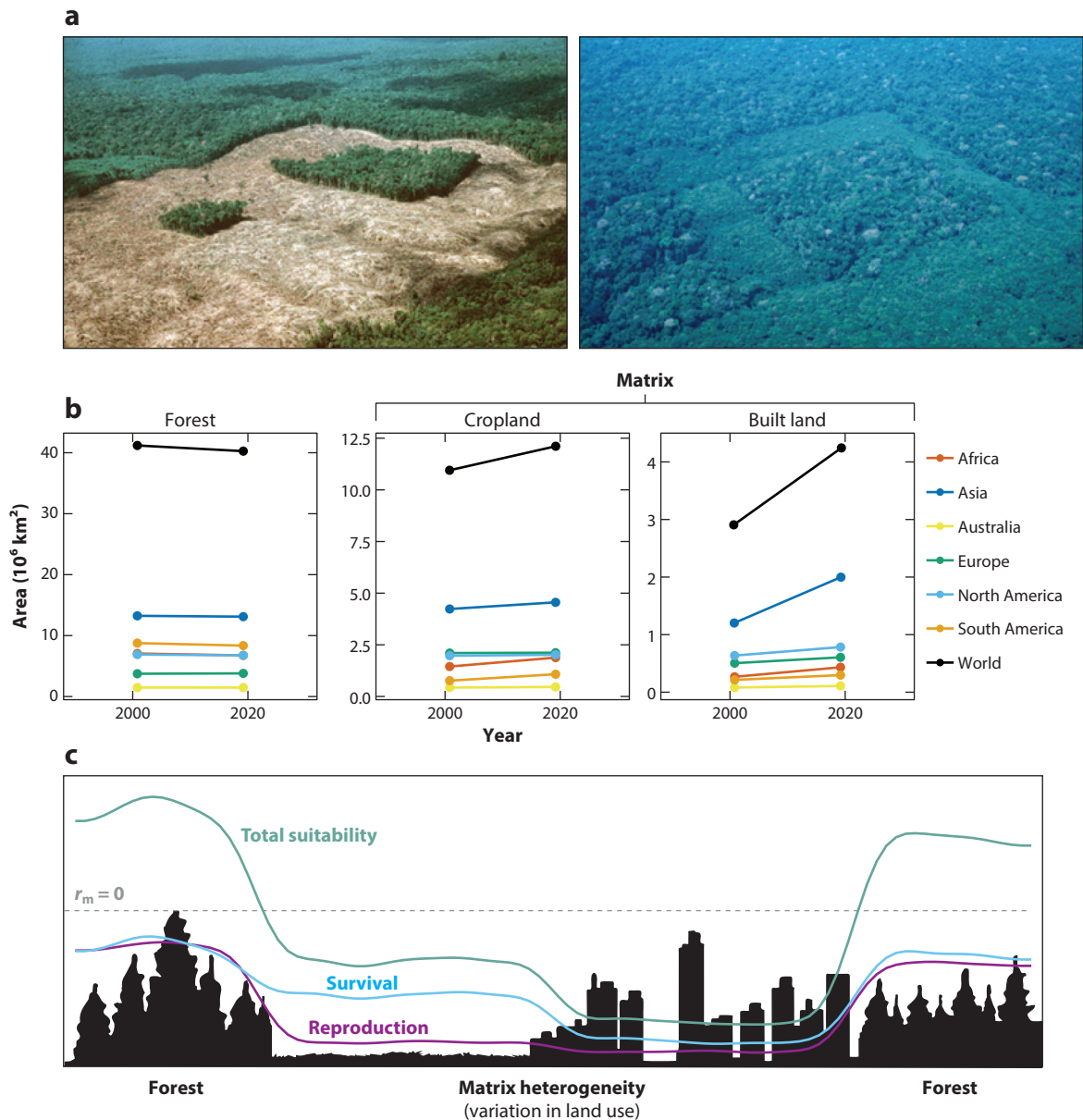


Figure 1

The increasingly pervasive role of the matrix in ecology, evolution, and conservation. (a) Natural ecosystems across the world, such as grasslands, forests, and wetlands, are now embedded in a matrix that can vary in structure. Patches from the Biological Dynamics of Forest Fragments project are shown as an example; the two photos were taken decades apart, emphasizing how the matrix can change over time. (b) Most matrix land uses, such as cropland and built (e.g., urban) areas, are increasing across the planet. (c) Variation in land uses outside of habitat for a species can alter both survival and reproduction, leading to changes in the intrinsic rate of increase (r_m) and expectations for total suitability. Often, the matrix is assumed to vary in its propensity for survival and movement (not shown), but reproduction is assumed to be negligible. Panel *a* (left) adapted with permission from Ferraz et al. (2007). Photo in panel *a* (right) provided by E. Bruna. Panel *b* adapted with permission from Potapov et al. (2022).

We synthesize our current knowledge of matrix effects and their relevance for ecology, evolution, and conservation. We first synthesize the range of extant perspectives on the matrix and its effects and provide a unified framing that captures these diverse perspectives. We identify theoretical developments that provide key hypotheses for why the matrix may (or may not) matter. We then discuss the underappreciated role of the matrix in evolutionary dynamics and summarize the experimental evidence for matrix effects on ecological and evolutionary outcomes. Finally, we highlight the broad scope and implications of the matrix in conservation and management and end by identifying future issues to advance our understanding of matrix effects and their relevance to conservation.

THE SCOPE OF THE MATRIX CONCEPT

In recent decades, the matrix has been defined and interpreted in several ways. Research on habitat loss and fragmentation, land-use change, agroecology, forest regeneration, and population genetics applies principles related to the matrix (Balkenhol et al. 2016, Frishkoff et al. 2019, Mesquita 2000, Pereira et al. 2004), although these fields envision the matrix and its relevance in different ways. Here, we identify commonalities across these perspectives to advance and unify applications of matrix concepts. To do so, we revisit descriptions of what is considered to be the matrix and how it may generate matrix effects.

One group of perspectives and definitions stems from the matrix being defined from a species-centric view. As such, the matrix is defined in reference to species' habitat requirements: The matrix is simply all nonhabitat for that species (Lindenmayer & Franklin 2002). This matrix definition is thus contingent on the definition of habitat itself, which of course differs among species (Hall et al. 1997). What constitutes habitat and therefore nonhabitat? Perhaps the most common definition of habitat is “the resources and conditions present in an area that produce occupancy—including survival and reproduction—by a given organism” (Hall et al. 1997, p. 175). In this context, the matrix is often assumed to be locations where species cannot successfully reproduce, or, at least, reproduction occurs at a greatly lowered rate (**Figure 1c**) (Cronin 2007, Wiegand et al. 2005). This definition of matrix emphasizing a lack of reproduction is justified by two considerations. First, when the focus is on birth, immigration, death, and emigration rates, most locations in a landscape likely permit nonzero survival and movement probability per unit time such that using survival and movement data alone cannot distinguish matrix from habitat. Second, by focusing on a lack of reproduction in the matrix, habitat can be categorized as a source or a sink (Loreau et al. 2013), such that both sources and sinks are distinct from the matrix (Wiegand et al. 2005, Yamaura et al. 2022). In this way, a sink is assumed to support some reproduction but with overall growth rates that are not sufficient to prevent population decline in the absence of immigration, whereas the matrix does not support reproduction, and individuals are often assumed to be transients moving through, but not settling in, the matrix. This perspective is prevalent in animal ecology and theoretical models of the matrix.

A second group of perspectives stems from interpreting the matrix without respect to individual species. These perspectives build from land-use concepts and landscape-centered views. Land-use and land-cover perspectives tend to define the matrix as nonfocal land-cover types or elements in the landscape (Kupfer et al. 2006), sometimes described by the dominant plant species or functional groups, such as in the context of forest regeneration (Mesquita 2000). There is an explicit focus on one primary land-cover type implicitly assumed to be a reference natural ecosystem (e.g., tallgrass prairie), and the matrix is any land use or land cover that does not belong to the focal land cover. A related definition focuses on entire landscapes, defining the matrix as the most dominant land-cover type other than the focal land-cover type (Turner &

DEVELOPMENT OF CONCEPTUAL MODELS OF THE MATRIX

Conceptualizations of the matrix have moved over time from uniform and discrete to more variable and continuous (Matthews 2021). Matrix concepts emerged from island biogeography and the application of an island model to landscapes. This simple model considered only discrete patches of a focal cover type, ignoring all other variation in land cover. Extensions considered land use surrounding patches and their impacts on demography within patches (Gascon et al. 1999, Perfecto & Vandermeer 2010). Countryside biogeography also emerged to address variation in land use (Daily et al. 2001), although some argue it is simply a matrix-explicit extension of island biogeography (Driscoll et al. 2019).

The past 15 years have seen greater focus on continuous gradients across entire landscapes. The continuum and related gradient models emphasize that landscapes are a combination of several continuous environmental gradients (Cushman et al. 2010, Fischer & Lindenmayer 2006). These models abandon the habitat–nonhabitat dichotomy, such that focal habitats or landcovers and the matrix are also deemphasized. Nonetheless, these models share a strong focus on species-specific niche and habitat concepts. Given the duality of the matrix with habitat, the matrix is implicitly enconced in these conceptual models, although it is currently underappreciated.

Gardner 2015). This perspective is often emphasized in plant ecology, landscape ecology, and ecosystem science.

Both perspectives define the matrix by contrast to something else, be it a focal land type, environmental condition, or species' habitat. By defining the matrix based on reference conditions, differences between any particular environment and the natural condition (a structural perspective) or species' requirements (a functional perspective) provide comparative measures across many issues related to matrix effects. For instance, land-use investigations that may not invoke matrix concepts still use, and indeed often require, reference land covers to fully evaluate impacts (e.g., Jones et al. 2022). Such land-use investigations are pervasive and necessary for interpreting the nature of land-use effects on biodiversity. Taken together, we define the matrix as land use and/or environmental conditions that differ from either species habitat or reference/natural conditions.

This definition helps resolve some terminological issues and connect related ideas across a broad swath of sciences (see the sidebar titled Development of Conceptual Models of the Matrix). For example, Frishkoff et al. (2019) argue that the matrix term becomes problematic for species strongly associated with human-modified land covers. The species-centric perspective included in our definition would consider these human-modified land covers as habitat, not the matrix, in such situations and so helps resolve this issue. Moreover, our definition highlights that any investigation where land uses are contrasted against a reference or baseline condition would fall within the domain of understanding matrix effects (e.g., Pereira et al. 2004).

Several related terms describing matrix attributes (or features) naturally emerge from this general definition. Matrix heterogeneity describes variation in the matrix, which can be characterized based on structural (i.e., physical properties of the environment) or functional heterogeneity (i.e., biological processes that may differentially affect species) (Fahrig et al. 2011). Heterogeneity can be due to spatial or temporal variation in landscape composition or configuration (**Figure 2**). Commonly considered sources of heterogeneity include matrix contrast, similarity, permeability, resistance, and quality; these features can alter key processes and can be considered functional attributes of the matrix (**Figure 2**). Matrix effects can describe changes that occur in habitat or across land uses that arise from matrix heterogeneity, such as changes in species occurrence in

Matrix

heterogeneity:

the landscape-scale variability in one or more matrix attributes, which results from variation in both matrix composition and configuration

Matrix similarity:

the similarity between the matrix and habitat in terms of structure or function

Matrix permeability:

the extent to which the matrix is conducive to movement

Matrix resistance:

the extent to which the matrix is a barrier to movement

Matrix quality:

the extent to which the matrix is conducive to individual vital rates

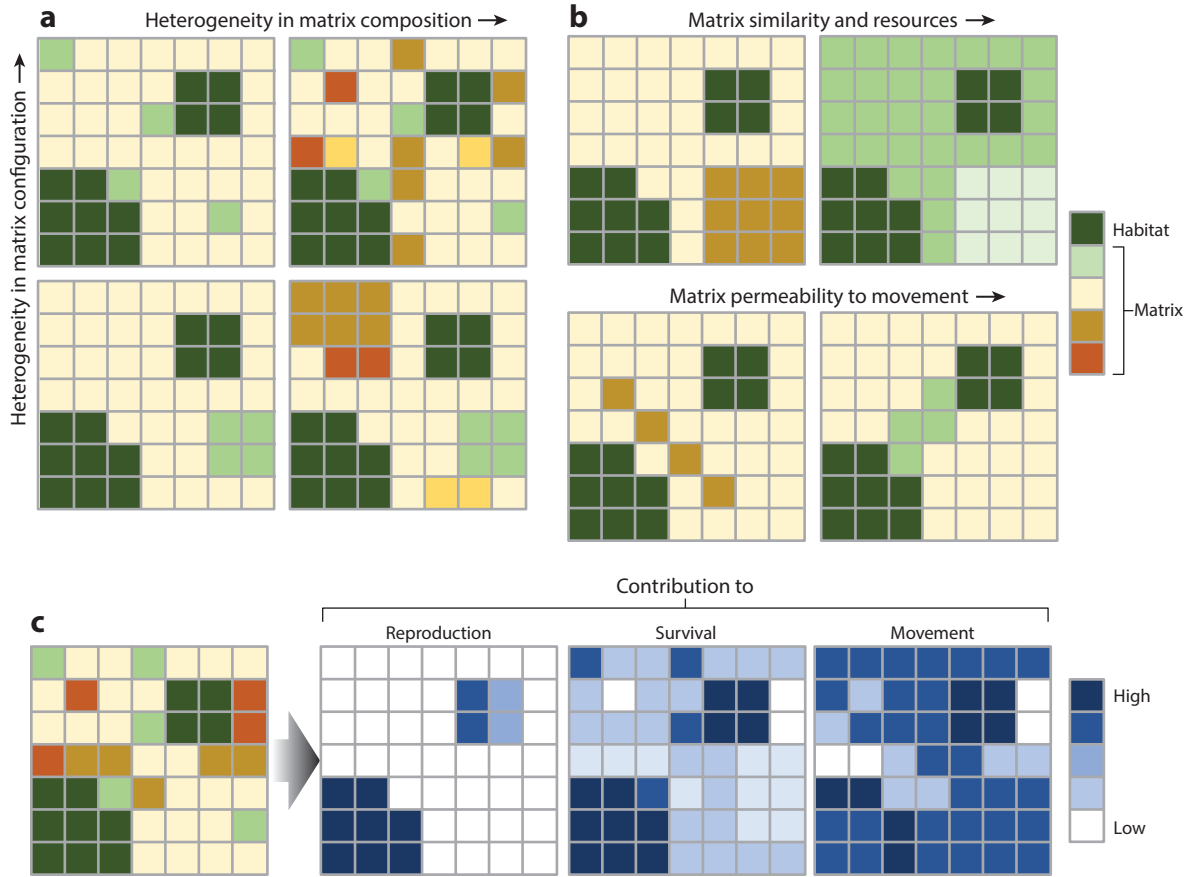


Figure 2

Attributes of the matrix can be described based on (a) structural and (b) functional heterogeneity, which ultimately may alter (c) how the matrix contributes to the demography and movement of species and ecosystem processes. Structural heterogeneity describes the physical pattern of the matrix, in terms of composition and configuration. Functional heterogeneity describes variation in how the matrix can influence ecological or evolutionary processes, such as variation due to resource availability (e.g., matrix similarity or complementarity) and movement permeability (e.g., degree of resistance).

fragments surrounded by different matrix types (Prugh et al. 2008) or changes in movement paths within the matrix due to variation in matrix permeability (Eycott et al. 2012).

HOW THE MATRIX INFLUENCES ECOLOGICAL PROCESSES

The matrix can impact ecological processes in many ways. Some of these processes have been identified under the rubric of different problems in ecology and conservation (e.g., edge effects, land-use effects, forest regeneration), such that there is a growing need to synthesize empirical and theoretical insights to identify key hypotheses for where, when, and why the matrix matters. Mechanisms and hypotheses can be organized based on three factors: (a) the scales at which variation in the matrix impacts populations and communities, (b) the biological processes (e.g., demography, movement, species interactions) by which those effects operate, and (c) the matrix attributes that drive effects.

Matrix type:

a description of the classification of land use or land cover in the matrix

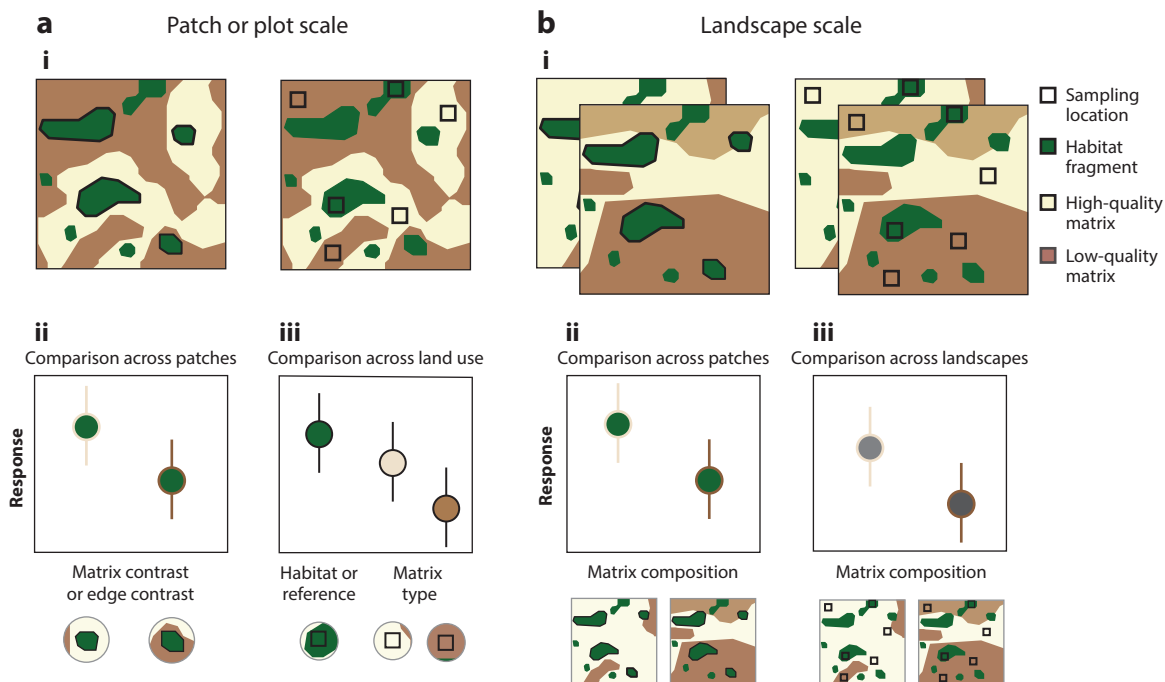


Figure 3

Matrix effects at the patch and landscape scales. (*a, i*) At the patch (or plot) scale, matrix effects are often interpreted in two ways. (*ii*) First, patches or fragments are contrasted to interpret how the surrounding matrix may influence patches, often in terms of matrix contrast. In this scenario, responses within the matrix are not considered. (*iii*) Second, tests across plots or patches in both habitat patches or fragments and the matrix are considered. This scenario is often applied in land-use investigations. In both cases, the sampled areas are shown as black outlined polygons. (*b, i*) At the landscape scale, matrix effects can also be compared in two ways: (*ii*) changes across multiple habitat patches or fragments or (*iii*) changes across habitat and matrix land uses in landscapes with different matrix attributes. In these situations, responses are typically pooled (e.g., summed, averaged) across sampling locations within landscapes, and attributes such as matrix composition or configuration are considered.

Mechanisms for potential matrix effects have been elucidated at the patch and landscape scales (**Figure 3**). Patch-scale processes largely reflect effects driven by local variation in the matrix surrounding patches, often referred to as edge-type or edge-contrast effects (Ries et al. 2017, Sisk et al. 1997). Landscape-scale mechanisms tend to focus on movement processes and how variation in the matrix, such as matrix configuration, may alter expectations regarding movement between patches (Kennedy & Marra 2010, Ricketts 2001). Landscape-scale mechanisms also focus on the emergent properties that may arise from changes at both patch and landscape scales (e.g., as expectations for metapopulation viability driven by overall variation in between-patch dispersal) (Vandermeer & Carvajal 2001).

Understanding mechanisms at different scales is critical for three reasons. First, the scale at which mechanisms operate alters expectations for where matrix effects arise across landscapes and the spatial extent of such effects. Second, mechanisms can interact across scales. For instance, mechanisms at the patch scale that foster emigration (e.g., Haynes et al. 2007) increase the number of individuals experiencing landscape variation in the matrix. Similarly, landscape-scale mechanisms can alter local population sizes, potentially altering pressures to disperse. Third, conservation strategies should take into account the scale at which matrix effects operate (see the section titled Conservation that Embraces the Matrix).

Edge type:

a description of the classification of land use, land cover, or environmental condition adjacent to a habitat or patch

Edge contrast:

the structural difference between the matrix and the adjacent patch

Matrix configuration:

the spatial arrangement of matrix types or attributes in a landscape

Matrix composition:
the amount or
proportion of matrix
types or attributes in a
landscape

At each scale, the biological mechanisms by which matrix effects operate often occur in two general, and sometimes interdependent, ways (Driscoll et al. 2013). First, matrix heterogeneity can alter resource availability and environmental conditions both within patches (e.g., edge-contrast effects) and in the matrix itself. When the matrix provides resources (e.g., food, conditions for plant establishment), individuals should use the matrix more frequently. Resources can supplement or complement those found in habitat, providing similar or different resources, respectively (Dunning et al. 1992, Ries et al. 2004). Such changes can affect demography and species interactions. For instance, the matrix can sustain natural enemies, which penetrate into habitat fragments to various extents and inflict damage on prey or hosts (e.g., Bitters et al. 2022, Robinson et al. 1995). Second, the matrix may alter movement (e.g., emigration, immigration), acting as either a barrier or facilitator of movement (Eycott et al. 2012). In a related way, properties of the matrix can also alter the cues available about recipient patches, thereby altering the information landscape for dispersing individuals (Sweaney et al. 2022). One way in which the matrix can alter movement is through altering the mortality risk of dispersers, thus blending these two biological mechanisms (Fletcher et al. 2019). Changes in movement can also be mediated by other species, as might be the case for plants with animal-dispersed seeds or microbes dispersed via hosts (Murphy & Lovett-Doust 2004).

In addition, matrix heterogeneity can be characterized in several ways (**Figure 2**) and these attributes may lead to different mechanisms of matrix effects. For instance, the spatial configuration of the matrix should alter movement patterns and affect genetic differentiation across space (Cushman et al. 2012). Variation in matrix composition may alter matrix quality, impacting survival (Chetcuti et al. 2021). Matrix similarity to focal habitats or land cover can drive the magnitude of matrix effects (Eycott et al. 2012, Prevedello & Vieira 2010). Temporal variation in the matrix from succession and forest regeneration can also have dramatic effects in some landscapes (Jakovac et al. 2021), which has been highlighted in long-term fragmentation experiments (Bitters et al. 2022, Gascon et al. 1999, Haddad et al. 2015). Based on these factors, we identified five core hypotheses for how the matrix matters (**Table 1**) that operate at local and landscape scales.

Local-Scale Hypotheses for Matrix Effects

At the patch scale, two core hypotheses have been proposed: the spillover hypothesis and the ecosystem decay hypothesis (**Table 1**). The spillover hypothesis describes the idea that the movements of materials, energy, or individuals spill over across the patch–matrix boundary, and matrix contrast may alter the magnitude, extent, and direction of spillover (Blitzer et al. 2012). The idea of spillover in a matrix context arose from models of edge effects, which may vary depending on the matrix contrast relative to habitat or based on the extent to which the matrix provides complementary resources (edge complementation) (Ries et al. 2004). For instance, spillover may create cross-boundary subsidies or spillover predation (e.g., predators from the adjacent matrix consuming prey in patches), depending on which species or individuals move locally across the patch–matrix boundary (Rand et al. 2006). A related idea is that the matrix can sometimes impede spillover, generating a fence effect on movement out of patches, typically driven by matrix contrast (Kuefler et al. 2010).

The ecosystem decay hypothesis describes the idea that harsh matrix conditions surrounding habitat patches can alter the local environment within patches (Driscoll et al. 2013), ultimately lowering the fitness and/or demography of organisms within patches (Chase et al. 2020, Laurance et al. 2002, Lovejoy et al. 1984). Driscoll et al. (2013) emphasize that the matrix can alter the abiotic environment within remaining habitat patches, and such changes can then lead to variation in resources and the species remaining in patches (Ries et al. 2004). It is often assumed that these

Table 1 Core hypotheses for matrix effects and their mechanisms

Scale	Hypothesis	Rationale	Mechanisms	Relevant matrix attributes
Patch	Spillover	The matrix adjacent to patches alters the flow of materials, energy, or individuals into or out of patches	Localized movement, edge complementation	Permeability, contrast, quality
	Ecosystem decay	The matrix adjacent to patches alters the environment within patches by altering resources and/or species interactions	Resources, interactions	Quality, contrast
Landscape	Movement trajectory	The matrix alters the speed and direction of movement across a landscape	Movement	Permeability, configuration
	Dispersal filter	The matrix alters the rate and/or success of movement between patches, via altering emigration rates, successful movement during transience, or immigration success	Movement, mortality	Permeability, quality
	Resource availability	The matrix can provide resources to individuals outside of patches, leading to higher abundances of species in landscapes with high-quality matrix	Landscape supplementation, complementation	Quality, heterogeneity, similarity

changes lead to decay or degradation relative to reference conditions (Chase et al. 2020), although degradation may or may not occur (Driscoll et al. 2013). Taken together, this hypothesis assumes that the matrix can alter patch quality and lead to wholesale changes in species' or communities' responses inside patches or habitat fragments (Prevedello & Vieira 2010). This hypothesis is indirect (see **Supplemental Table 1**) because other matrix processes could contribute to ecosystem decay within patches; therefore, predictions regarding how different matrix attributes influence species or communities are less clear than those arising from the spillover hypothesis.

Supplemental Material >

Landscape-Scale Hypotheses for Matrix Effects

At the landscape scale, three core hypotheses capture many specific ideas in spatial ecology: the movement trajectory, dispersal filter, and resource availability hypotheses (**Table 1**). The movement trajectory hypothesis states that matrix resistance (or conversely, permeability) determines movement paths and speed for dispersers (reviewed in Zeller et al. 2012), such that matrix configuration largely drives movement routes (Cushman et al. 2012). Differential resistance has been attributed to physical impediment to movement (Cline & Hunter 2014), perceived predation risk (Winandy et al. 2019), or additional resources tempting dispersers to linger longer in the matrix (Harmon-Threatt & Anderson 2023). More structurally open matrix types may facilitate more directed movement paths leading to more efficient dispersal (Crone et al. 2019, Russell et al. 2007) and might increase transmission of informational cues (e.g., visual, auditory) to greater distances.

The dispersal filter hypothesis states that the matrix can alter the rate and identity of the individuals that successfully disperse between patches because the matrix alters dispersal mortality (Vandermeer & Carvajal 2001). This hypothesis combines the movement of individuals and their survival while moving through different matrix types (Fletcher et al. 2019); it differs from the movement trajectory hypothesis because it includes a demographic component that focuses on

Countryside:
an intermixing of
human habitations,
agricultural lands, and
remnant natural lands
in a landscape

variation in dispersal failure rather than simply how the matrix alters the routes that dispersers take. Dispersal success is driven by matrix quality, which can alter metapopulation persistence via changes in colonization rates (Vandermeer & Carvajal 2001). Interspecific variation in dispersal success can also lead to dispersal filtering at the community level (Leite et al. 2022).

The resource availability hypothesis states that the type or quality of the matrix can increase population sizes in landscapes due to the additional resources provided by high-quality matrix (Driscoll et al. 2013). Additional resources can, in some cases, result in the matrix (defined from a structural perspective) in effect being habitat for some species (see the section titled The Scope of the Matrix Concept). This hypothesis is related to the landscape supplementation and landscape complementation processes that occur when individuals move between the focal habitat and the matrix, for example, breeding in habitat but foraging in the matrix (Dunning et al. 1992). The resource availability hypothesis is often implicit in investigations of land use and countryside biogeography, as variation in land use has the potential to alter the palette of resources available to organisms across landscapes.

Interactions Among Hypotheses and Other Environmental Changes

These core hypotheses can act alone or in concert. For example, the matrix trap hypothesis combines ideas regarding the movement trajectory and dispersal filter hypotheses (Vasudev et al. 2015). According to the trap hypothesis, a highly permeable but inhospitable matrix results in high mortality risk, such that the matrix can effectively be an ecological and even evolutionary trap because of maladaptive decisions made by individuals (Schlaepfer et al. 2002).

In addition, matrix effects have been hypothesized to interact with other types of landscape change, particularly habitat loss and fragmentation (Bender & Fahrig 2005, Chetcuti et al. 2021, Leite et al. 2022, Yamaura et al. 2022) and climate change (Nowakowski et al. 2017, Tourani et al. 2023). Matrix effects are often predicted to increase with habitat loss and fragmentation because loss and fragmentation can cause more individuals to be exposed to matrix conditions. Decreased patch size from loss and/or fragmentation may lead to the remaining habitat being more affected by patch-scale matrix processes, while the effects of increased interpatch distances may be more influenced by landscape-scale matrix processes. Land uses in the matrix can also alter microclimate conditions (e.g., Nowakowski et al. 2017), such that matrix heterogeneity can amplify or attenuate the effects of climate change in the remaining habitat.

THE MATRIX AND EVOLUTIONARY PROCESSES

The matrix mechanisms outlined above for ecological processes may have evolutionary consequences (**Figure 4**), although the role of the matrix in evolution is less well studied and understood. Cheptou et al. (2017) document how habitat loss and fragmentation might alter selection on life histories and species traits because of changes in dispersal, environmental variability, and population size. We argue that the matrix has a role to play in evolution beyond just those of habitat loss and fragmentation. Some evolutionary processes have been considered in terms of the matrix, such as how the matrix alters gene flow in landscape genetics studies (Balkenhol et al. 2016), but in general, evolutionary issues have received scant attention. Below, we detail how the matrix can impact multiple evolutionary processes, organized by the scale at which mechanisms operate.

Local-Scale Evolutionary Outcomes

The two local-scale hypotheses—spillover and ecosystem decay—focus on the consequences of conditions within patches that are modified by the matrix nearby. The most direct of these effects

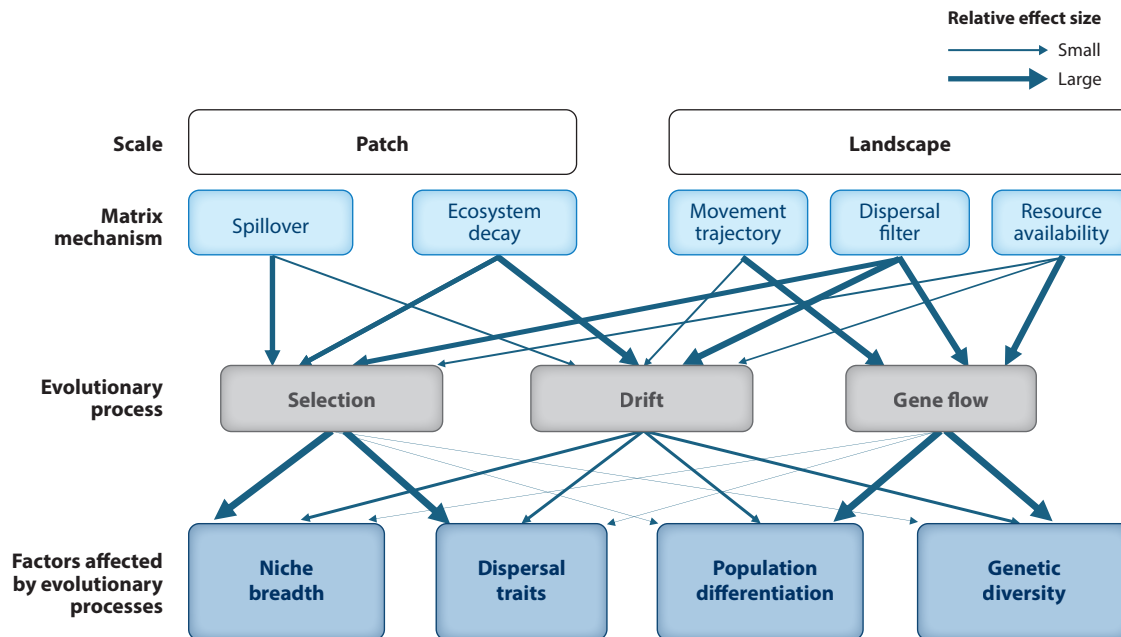


Figure 4

Matrix hypotheses and their potential impact on evolutionary processes. Hypotheses are organized by the spatial scale at which they act. The evolutionary processes they shape combine in complex ways to change characteristics of populations living in fragmented landscapes. Commonly measured characteristics of species are listed at the bottom. Arrow weights indicate the expected relative effect of the hypotheses on evolutionary processes and that of evolutionary processes on characteristics of populations.

relates to how the matrix can alter selective regimes in fragmented landscapes (Cheptou et al. 2017).

The spillover hypothesis has the potential to alter evolutionary processes because it predicts that material in the matrix spills over into the remaining habitat patches, which can alter environmental conditions and species composition. For instance, spillover of species that are common in matrix environments, and uncommon in habitat prior to land change, can lead to a variety of novel selection pressures. For mobile species, selection may favor reduced use of patch edges and therefore lead to lower rates of emigration, patch-boundary crossing, and gene flow (Martin & Fahrig 2015). For less mobile species, tolerance and avoidance adaptations might be more likely to be selected. Adaptation to conditions at patch edges that are more similar to matrix conditions because of spillover may facilitate evolution toward using the matrix as habitat, an idea conceptually similar to issues in niche evolution and the evolution of range limits (Holt 2009), although at decidedly smaller spatial scales.

The ecosystem decay hypothesis predicts that demographic performance of species depends on local matrix contrast and composition, which can also alter selection pressures. For example, common observations in fragmented landscapes are that species are lost locally and communities shift in structure more markedly in habitat with higher contrast matrix (Betts et al. 2019, Gascon et al. 1999). For some species, these local-scale changes represent decay because the species lost are mutualists, pollinators, or dispersers or because communities shift in favor of natural enemies and nonnative or generalist competitors (Legrand et al. 2017). We expect such changes to favor more generalist interactors, such as generalist plant pollinators (Hagen et al. 2012), or select for increased tolerance to predation and competition.

Ecosystem decay may also reduce the efficacy of selection because it predicts lower population abundance and occupancy patterns at both local and landscape scales (Bender & Fahrig 2005, Ramirez-Delgado et al. 2022). As such, effective population sizes are likely to decline under ecosystem decay and thus increase the potential for genetic drift. For instance, transformation of the matrix via urbanization can speed up drift, leading to nonadaptive evolution (Miles et al. 2019). Despite this potential, testing the effects of the matrix on effective population size and resulting genetic diversity remains rare, as most studies to date have focused on landscape-scale patterns of genetic differentiation between populations rather than variation in genetic diversity within and among patches (DiLeo & Wagner 2016).

Landscape-Scale Evolutionary Outcomes

Landscape-scale hypotheses lead to predictions about matrix effects that influence dispersal or the effects of matrix experienced by many individuals beyond focal patches. These effects may change selection across entire landscapes, alter gene flow, and modulate the effects of genetic drift (Figure 4).

The movement trajectory hypothesis predicts that changes in connectivity arising from matrix heterogeneity should influence gene flow among populations (Balkenhol et al. 2016, Manel et al. 2003). For example, gene flow in black bears (*Ursus americanus*) in the Pacific Northwest was better explained by human land cover than natural barriers or isolation by distance (Cushman et al. 2006). Changes in movement trajectories may also indirectly influence local population density and relatedness within patches that shift the influence of genetic drift and the accumulation of mutational load.

Matrix conditions enhance the overall costs of dispersal under the dispersal filter hypothesis because mortality during dispersal is elevated under certain matrix conditions. A first prediction of this enhanced dispersal cost is that gene flow should be reduced at the landscape scale, reducing genetic connectivity among patches (Fletcher et al. 2022, Nagylaki 2015). This hypothesis differs in its predictions regarding gene flow from the movement trajectory hypothesis, which focuses on spatial patterns of gene flow rather than total reductions in gene flow across landscapes. Higher dispersal costs may tip the scales from dispersal being adaptive to being maladaptive (Fahrig 2007, Nowicki et al. 2014), further reducing gene flow. For example, individuals of the weedy plant species *Crepis sancta* lost more seeds in urban areas than in rural areas because much dispersal was to concrete surfaces where there is effectively no chance of establishment (Cheptou et al. 2008). Differential dispersal mortality was sufficient to explain the evolution of reduced dispersal over 5–12 generations in this situation. Similarly, populations of ciliates in microcosms evolved lower dispersal propensity overall and more directed movement when dispersal occurred in harsh matrix environments (Jacob et al. 2020). However, depending on the genetic variation in dispersal ability, the severity of the filter, and the importance of dispersal for fitness, dispersal mortality might also favor those genotypes that have better than average dispersal (Winandy et al. 2019).

An interesting evolutionary tweak to the dispersal filter hypothesis is that the filter may apply to traits not directly related to dispersal. Because gene flow requires the movement of alleles between local populations, which requires not only movement but successful reproduction, filtering can arise based on both movement and the likelihood of reproduction after immigration. Successfully dispersing genotypes that are poorly adapted or fail to find mates in the postdispersal environment (Vasudev & Fletcher 2016) may nonetheless be evolutionarily filtered if patches vary in resources or costs accumulate for dispersers. In addition, traits that are correlated with dispersal (i.e., dispersal syndromes) are indirectly filtered (Cote et al. 2017). For example, traits with greater survival in the matrix might represent generalized adaptations for life in the matrix and may trade

off with fitness in remnant patches or the ability to find mates, especially if sexual traits are costly during dispersal.

The resource availability hypothesis suggests that novel resources may be available in some matrix conditions, such that selection might favor greater use of the matrix where these resources are available, with concomitant changes in movement to access these resources. Matrix with high similarity to focal habitats represents a large potential source of resources, which some genotypes may exploit better than others. Especially near habitat boundaries, these resources may be more available (as implied by the spillover hypothesis), and in this way, adaptation to the edge environment may be a prerequisite for adaptation to the matrix itself, possibly with a trade-off in the ability to use habitat. In doing so, such changes can lead to niche evolution via changes in niche breadth (Cheptou et al. 2017).

Interactions Among Mechanisms

Evolutionary change from the matrix may be driven ultimately by several mechanisms. Multiple processes can operate simultaneously, altering effective population size and the efficacy of selection versus drift. For instance, ecosystem decay and dispersal filters reduce the effective population size because they imply elevated mortality and lower reproduction, but altered movement trajectories could also lead to local declines in population size if trajectories lead to high emigration but low immigration. As such, these mechanisms in combination should elevate the effect of drift and the erosion of genetic variability (Vandergast et al. 2007). For example, high genetic load occurs in isolated populations of the Glanville fritillary butterfly (*Melitaea cinxia*), which increases extinction risk for these populations (Mattila et al. 2012).

Landscape-scale mechanisms influencing gene flow may interact with local-scale matrix mechanisms influencing selection (Cheptou et al. 2017). Local selection may have less of an effect on evolution in the face of high gene flow from other areas of the landscape. In such cases, selection may instead favor strategies that are well adapted on average among the connected patches. Local selection may have a greater effect under weak gene flow, such as when dispersal filters and low matrix permeability inhibit movement. While these interactions are plausible based on the theory of adaptation in spatially heterogeneous environments (Cheptou et al. 2017), these ideas remain poorly tested in relation to matrix effects.

Interactions between matrix mechanisms rely on complex combinations of local adaptation, genetic drift, and inbreeding depression, and so understanding how the matrix alters gene flow and resulting genetic differentiation is important (Fletcher et al. 2022, Marcus et al. 2021, McRae 2006). Ecological and evolutionary processes can also feed back on each other, leading to eco-evolutionary dynamics from the matrix (Legrand et al. 2017).

EXPERIMENTAL EVIDENCE FOR MATRIX EFFECTS ON ECOLOGICAL AND EVOLUTIONARY PROCESSES

The extent of empirical evidence for these core hypotheses and mechanisms affecting ecology and evolution remains unclear. Most evidence for matrix effects comes from observational studies (Prevedello & Vieira 2010, Prugh et al. 2008, Ramirez-Delgado et al. 2022, Watling et al. 2011). It is thus challenging to interpret why patterns of matrix effects arise. We compiled the experimental evidence that exists for matrix effects to identify hypotheses with weak or strong support and highlight those hypotheses that demand further study.

To find experiments that manipulated the matrix, we searched Web of Science (for search terms and related details, see the **Supplemental Appendix**). From this search, we reviewed 2,048 articles, identifying 39 articles reporting experiments (27 unique experiments, 189 tests) that manipulated the matrix to understand its potential effects (**Supplemental Table 2**). We

Supplemental Material >

summarized experimental results based on (a) the type of response being tested, (b) whether responses were measured in the matrix or the focal land cover (or both), (c) the scale of the manipulation and analysis (patch versus landscape) (Fletcher et al. 2023), (d) the hypotheses addressed, (e) whether tests of hypotheses were direct versus indirect (see **Supplemental Table 1**), (f) the attributes of the matrix being manipulated, (g) whether effects of the matrix were observed, and (h) whether the level of matrix similarity to the reference conditions explained the direction of observed effects. We focused on matrix similarity because it has been previously emphasized as an important attribute to explain matrix effects (Eycott et al. 2012, Prevedello & Vieira 2010). We did not attempt to use meta-analyses because the experimental designs and objectives varied considerably among studies. For more details, see the **Supplemental Appendix**.

Experiments varied in taxa, habitat, and scale (**Supplemental Table 2**). Most experiments were on arthropods or amphibians and conducted in grassland or forest biomes (**Supplemental Table 2**). The most common response variables were abundances and related distribution metrics (e.g., occupancy), whereas demography was rarely measured (**Figure 5a,b**). Nearly all experiments (96%) focused on ecological responses; only one experiment was conducted in the context of evolutionary outcomes (Jacob et al. 2020), and it focused on selection on dispersal phenotypes. Only 17% of tests measured responses in both habitat and matrix; 51% of responses were measured only in habitat. Overall, most studies manipulated the matrix at the patch (or plot) scale rather than across entire landscapes composed of multiple patches of habitat and/or matrix (landscape scale) (**Figure 5c**).

Across all experimental studies, there was substantial evidence for matrix effects: 38 of 39 (97%) articles and 122 of 189 (65%) tests found evidence for matrix effects. Overall, there was less frequent support for matrix effects at the patch scale (63% of tests) rather than across landscapes (69%) (**Figure 5c**) and for effects on diversity metrics (59%) than on population-level metrics (demography, 80%; abundance, 69%) (**Figure 5d**).

There was substantial variation in the number of tests and support for hypotheses. The ecosystem decay and resource availability hypotheses were the most frequently assessed; the dispersal filter hypothesis was the least (**Figure 5e**). The movement trajectory hypothesis had the most frequent support (82% of tests found effects of the matrix on movement paths). While there is overwhelming evidence that the matrix alters movement trajectories, the ways in which it does so are highly variable. For instance, evidence that more open or harsher matrix types increase movement velocity and decrease turning angles was found in some experiments (e.g., Nakano et al. 2018) but not others (e.g., Zajitschek et al. 2012). The spillover hypothesis had moderate support (59% of tests found evidence for spillover). For example, experimental removal of forest cover surrounding riparian zones altered stream flow and increased nutrient inputs (Dodds et al. 2023). Tests of the ecosystem decay hypothesis had moderate support (68%), but the tests were largely indirect, in that occupancy, abundance, or richness was measured in patches rather than demographic rates or ecosystem changes, which can arise from ecosystem decay (Lindenmayer et al. 2009). While this hypothesis operates at the patch scale, several landscape-scale experiments summarized patch responses across multiple patches within landscapes (**Figure 5b**). The dispersal filter hypothesis is commonly assumed in theoretical models of matrix effects (Vandermeer & Carvajal 2001, Yamaura et al. 2022), yet it had the weakest support (46% of tests found evidence for dispersal filtering). Direct tests of the dispersal filter hypothesis were less common than indirect tests (7 versus 17 tests, respectively) but were much more likely to provide support for this hypothesis (86% of direct versus 29% of indirect tests found support). This suggests that dispersal filtering may be more pervasive than currently recognized. The resource availability hypothesis was also commonly tested and had moderate support (64%). Although this hypothesis is based on landscape-scale variation, many of these tests occurred at the local scale, with responses being

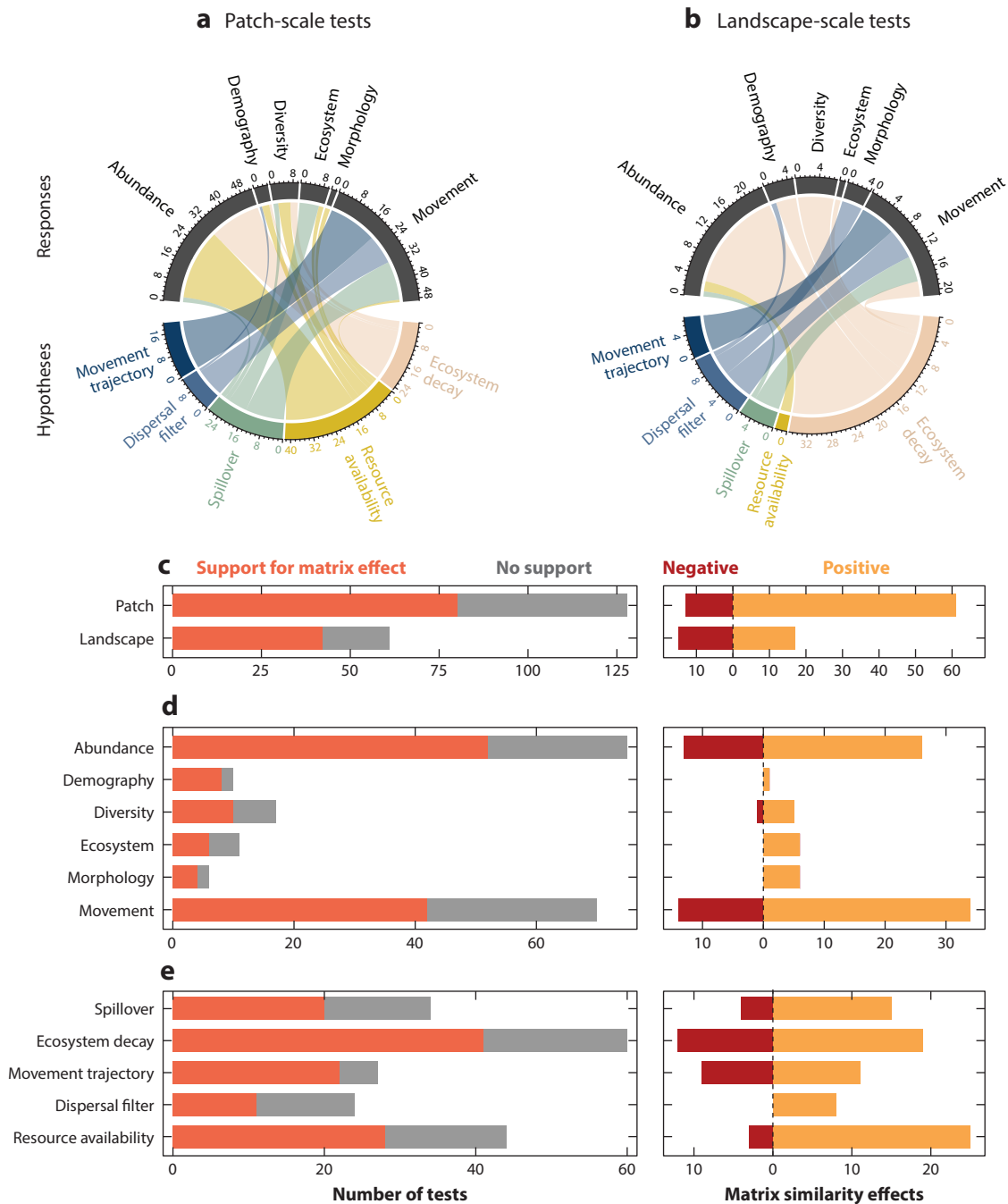


Figure 5

A summary of experimental tests of matrix effects. Chord diagrams highlight tests of hypotheses based on different response types at the (a) patch (or plot) and (b) landscape scale of the manipulations. The support for effects of the matrix by (c) the scale of the manipulation, (d) the response type, and (e) the core hypotheses. For panels c–e, the left side shows the number of tests, whereas the right side shows the direction of the observed effects based on matrix similarity. Positive responses indicate when greater similarity in matrix conditions corresponded with greater similarity in responses to the reference.

compared among plots with different land uses (**Figure 5a**). These experiments rarely measured resources directly, and thus nearly all tests of this hypothesis were indirect.

Most experiments focused on manipulating matrix types, and investigators emphasized that these types were relevant to matrix quality or permeability, based largely on the similarity of the matrix type to the reference (e.g., habitat). There were consistently more frequent positive effects of matrix similarity than negative effects, where positive responses reflect situations where greater similarity in matrix conditions corresponded with greater similarity in responses to the reference. Yet the magnitude of this difference varied by response type, scale, and hypothesis (**Figure 5c–e**). Among the response types, movement responses were the most variable (26 positive, 13 negative); this variation appeared driven by movement trajectories being facilitated in more open matrices that were sometimes less similar to the reference habitat (Eycott et al. 2012). Patch-scale effects were more variable than landscape effects. Among the hypotheses, the magnitude of differences was greatest for the dispersal filter (8 positive, 0 negative responses) and resource availability (25 positive, 3 negative) hypotheses. These results point to matrix similarity being a repeatable and consistent attribute explaining variation in matrix effects, particularly for mechanisms linked to supplemental resources or mortality risk (Eycott et al. 2012, Prevedello & Vieira 2010).

In general, landscape-scale experiments often focused on interactions of matrix effects with manipulation of fragmentation and/or habitat loss (e.g., Haynes et al. 2007). Seven articles manipulated the matrix and habitat amount and/or fragmentation, testing for potential independent and/or interactive effects. Notably, matrix effects were more commonly observed than effects of either habitat amount or fragmentation in these experiments. Interactions were variable: Some experiments emphasized that the effect of matrix type was greater in less fragmented landscapes (Astrom & Part 2013), whereas other experiments suggested the effect was larger in more fragmented landscapes (Goodsell & Connell 2008). The reason(s) for such discrepancies are unclear, though we note that these experiments were largely restricted to manipulations of a few habitat patches and included limited variation in the matrix over short time periods. More experiments are needed that span greater variation in both habitat and matrix conditions across multiple generations.

These experimental results illustrate the prominent role of the matrix in influencing ecological processes. Experimental studies on evolutionary processes were rare, but the one experiment we identified emphasizes the potential for the matrix to alter selection on movement-related phenotypes (Jacob et al. 2020). Some hypotheses and mechanisms for matrix effects remain poorly tested, particularly those related to the ecosystem decay and resource subsidy hypotheses. While limited sample sizes and publication biases may make some results equivocal, the pervasive matrix effects shown in these experiments mirror those of global syntheses of observational studies (Prugh et al. 2008, Ramirez-Delgado et al. 2022, Watling et al. 2011). A wider range of experiments spanning a greater variety of biomes and taxa are needed to understand the generality of matrix effects. Tests that contrast the relative role of different hypotheses are largely lacking but would be helpful for interpreting how these processes operate simultaneously in nature. Measuring different types of responses, such as demographic and community-level responses, to changing matrix conditions is needed to interpret linkages among mechanisms operating at different levels of organization. As yet, there is limited connection between such experiments and formal theory about population and community responses to landscape heterogeneity.

CONSERVATION THAT EMBRACES THE MATRIX

Long-standing goals for conservation are to maintain populations and biological diversity, each of which depends on ecological and evolutionary processes that can be influenced by the matrix.

Many conservation strategies embrace the matrix in their design and implementation. In addition, some management strategies within the matrix are not viewed as such but simply as strategies for increasing biodiversity in agricultural landscapes, urban areas, or other human-modified environments (Kremen & Merenlender 2018). By incorporating matrix concepts more firmly into these strategies, there is the potential to gain greater conservation benefits. An understanding of how the matrix matters based on the hypotheses we have provided can be useful, as it can guide ecological and evolutionary targets for effective conservation. Our hypotheses about matrix effects arise at two spatial scales, each of which emphasizes different potential conservation actions.

Local-Scale Strategies

Local spillover is often managed, either to promote or limit flow across the patch–matrix boundary. For instance, promoting spillover of wildlife into matrix lands such as agriculture can foster ecosystem services including pollination and pest control for crops (Rand et al. 2006). Spillover from the matrix into habitat can also have important conservation implications. When organisms such as pollinating insects have habitat requirements that vary across life stages (Jules & Shahani 2003), access to high-quality foraging resources within the adjacent matrix can meet this need and promote the pollination of native plants (Blitzer et al. 2012).

Reducing spillover by creating hard barriers between patches and the matrix, such as fencing, is a common management tool that may prevent wildlife from accessing the matrix when the risk of mortality or conflict is high. Such strategies are often used around protected areas. Organisms targeted for poaching can be protected by fencing and human guards that keep them within designated protected habitat areas, prohibiting access to a matrix where risk of capture or death is high (Hayward & Kerley 2009). Crop raiding by taxa such as elephants and primates and livestock predation by large carnivores are also causes of conflict and wildlife persecution that can be mitigated by physically restricting the movement of wildlife into the matrix to prevent access to agricultural resources (Mackenzie & Ahabyona 2012).

Managing the surrounding matrix to reduce edge contrast and increase resource similarity to habitats is a conservation strategy that may buffer detrimental matrix effects arising from ecosystem decay. Such management strategies can increase the effective habitat area and potential population sizes for species (Jules & Shahani 2003, Tabarelli & Gascon 2005) or reduce the mortality of sessile individuals (Mesquita et al. 1999). This principle can be applied within managed lands to increase their utility as habitat or in areas surrounding protected lands to increase the available core area. For example, removing woody edges bordering grasslands can increase the effective area of habitat for grassland specialists and improve population vital rates (Ellison et al. 2013). By increasing the effective area and population sizes of target species, these strategies can reduce the long-term likelihood of extinction and the loss of genetic diversity.

Landscape-Scale Strategies

Across entire landscapes, we identify three general strategies that can be implemented in management: increasing connectivity, increasing matrix quality, and improving matrix provisioning of resources. These strategies often emphasize restoration and rewilding of the matrix (Donald & Evans 2006, Mesquita 2000).

Conservation strategies increasingly call for improving connectivity by managing the matrix permeability of lands to facilitate movement. Wildlife movement through the matrix is particularly critical to conservation under climate change, which must account for species range shifts, novel species assemblages, and evolutionary adaptation to novel climate conditions (Heller & Zavaleta 2009). Promoting connectivity among metapopulations has long been a conservation

goal (e.g., the one-migrant-per-generation rule), as the flow of selectively advantageous alleles throughout a metapopulation is essential to species persistence under environmental change (Mills & Allendorf 1996). Practitioners may increase matrix permeability to facilitate movement or strategically channel the movement of wildlife through the matrix. For instance, matrix lands with low movement resistance may be leveraged to protect pathways of gene flow and facilitate range shifts under climate change (Littlefield et al. 2017).

Management strategies for increasing matrix permeability can involve increasing the similarity of the vegetation structure between the matrix and habitat, reducing anthropogenic chemical inputs (e.g., fertilizers, pesticides), and removing invasive species (Tabarelli & Gascon 2005). Reducing the mortality risk for organisms moving through the matrix may also be achieved in a variety of ways. For example, cooperative efforts to have lights-out events in urban areas across the United States during bird migration is a tactic to reduce light pollution-induced mortality for nocturnally migrating birds (Horton et al. 2019). Similarly, other approaches aimed at reducing mortality during migration, such as reducing wind farm collisions and window collisions by bats and birds (Marques et al. 2014), point to the broad scope of matrix management. By enhancing matrix permeability, species may also be more likely to move and adapt to a changing climate (Littlefield et al. 2017).

The flow of individuals through the matrix may be channeled to reduce the incidence of human-wildlife conflict. Wildlife corridor construction can facilitate functional connectivity through a heavily anthropogenic matrix. Corridors such as highway overpasses can mitigate the expenses and injury risks associated with wildlife-vehicle collisions—collisions with deer alone cause over \$1 billion in damage annually across the United States (Gilbert et al. 2017). Managing movement through the matrix does not preclude anthropogenic land uses such as industrial agriculture. For instance, novel approaches recommend aligning plantation rows with animal movement patterns to facilitate the flow of organisms between habitat patches in a directed way (Doherty & Driscoll 2018).

Improving matrix quality and resource availability are other strategies for promoting landscape-scale biodiversity (Donald & Evans 2006). Human-dominated matrix lands can be managed to sustain diversity outside protected habitat, as emphasized in countryside biogeography and agroecology (Daily et al. 2001, Kremen & Merenlender 2018). However, methods for improving resource availability in the matrix are highly context dependent. For agricultural land uses, land-sharing strategies emphasize practicing wildlife-friendly agriculture both to boost local biodiversity and to improve ecosystem services to crop production (Fischer et al. 2014). Examples of successful wildlife-friendly farming techniques include planting native trees in shade-grown coffee plantations and allowing native plants to grow in hedgerows and field margins without pesticide use (e.g., Pywell et al. 2012). Urban and residential areas can be managed to improve resources in the matrix. Many styles of residential development retain mature trees and therefore a greater proportion of the predevelopment vegetation community and structure than other types of anthropogenic landcover (Brady et al. 2009). Coupled with social efforts to replace lawns with native vegetation and pollinator gardens, such as the US National Wildlife Federation's residential habitat certification program (<https://certifiedwildlifehabitat.nwf.org/>), residential areas may provide opportunities for active conservation of similar resources and structure to habitat patches (Brady et al. 2009).

Integrating Matrix and Habitat Management Across Scales

Matrix effects are often contingent on other aspects of environmental change, such as habitat loss, fragmentation, and climate change (Fletcher et al. 2014, Leite et al. 2022, Ramirez-Delgado et al.

2022). We argue that matrix management should be treated as complementary rather than mutually exclusive to habitat protection measures to arrive at holistic approaches for place-based conservation (Kremen & Merenlender 2018). As some matrix management strategies aim to restore habitat from the matrix while others aim to connect existing habitats or fragments by improving the matrix for movement (Brennan et al. 2022, Fischer et al. 2014), placing matrix conservation explicitly in the context of maintaining habitat across landscapes is essential. Aligning conservation in the matrix (e.g., modifying agricultural strategies to promote biodiversity) with conservation policies focused on natural areas is needed in order for whole-landscape conservation to address both ecological and evolutionary goals (Hodge et al. 2015).

CONCLUSIONS

The matrix is an increasingly dominant feature of landscapes, and its effects are extensive. Our synthesis highlights how matrix concepts pertain to a wide range of topics in ecology, evolution, and conservation. The overwhelming evidence for matrix effects documented here demands greater development of theory and efforts for understanding the causes and consequences of matrix effects.

FUTURE ISSUES

1. Matrix concepts need to be integrated into investigations on how land-use variation matters for biodiversity. Currently, investigations on land use suffer from the lack of a generalized conceptual framework with which to interpret biodiversity effects, yet many existing frameworks implicitly share matrix concepts in their development (e.g., Daily et al. 2001, Fischer et al. 2014).
2. More investigations are needed in both habitat and the matrix itself, as studies on matrix effects often interpret matrix effects based only on responses within habitat fragments regarding how they are affected by the surrounding landscape matrix. Greater insight can be made by directly assessing responses in the matrix.
3. As increasing evidence mounts highlighting the fact that matrix similarity can help explain variation in matrix effects (**Figure 5**) (Eycott et al. 2012, Prevedello & Vieira 2010), quantitative assessments of different aspects of matrix similarity and its effects are needed. Such assessments may also help identify the situations in which other attributes (e.g., matrix complementarity, resistance) are necessary for reliably predicting matrix effects.
4. A better understanding of the temporal dynamics of the matrix is needed. Such dynamics can play out over long time periods and can alter several model predictions (Matthews 2021, Zeller et al. 2020).
5. Understanding evolutionary effects of the matrix on both selection and drift processes will complement the current focus on gene flow and genetic differentiation to better anticipate overall evolutionary impacts. This information will improve understanding of contemporary evolution, eco-evolutionary dynamics under rapid environmental change, evolutionary rescue in a landscape context, and management strategies built from evolutionary principles.
6. Generalized, scale-dependent approaches for effective management of the matrix alongside habitat for the persistence of biodiversity will deliver more effective whole-landscape conservation.

DISCLOSURE STATEMENT

E.C.T. is a member of the Bedfordshire, Cambridgeshire, and Northamptonshire Wildlife Trust, which does conservation work on landscape restoration; E.C.T. also holds active grants in South-east Asia and the United Kingdom, investigating conservation management options, including in habitat that could be described as matrix. The other authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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