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5 **Conceptual domain of the matrix in fragmented landscapes**

6

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12

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

23

24 **A matrix focus is now both important and possible**

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

36

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

47

48 While there has been much conceptual development in the habitat fragmentation literature [22,
49 26, 34], the concepts related to how the matrix influences patch-dependent species have not been
50 thoroughly synthesised. In this review, we build on progress made within ecological sub-
51 disciplines [25, 35, 36], and on research into edge-effects [37] and habitat fragmentation [26,
52 34], to describe the conceptual domain of the matrix in fragmented landscapes.

53

54 Our approach to understanding the conceptual domain of the matrix is to synthesise ideas from
55 the empirical literature. However, instead of providing a list of matrix effects [e.g. 25, 35, 36,
56 38, 39], we illustrate relationships among mechanisms in a conceptual model. We demonstrate
57 through the conceptual model that what previously were considered primary effects of the matrix
58 are actually secondary outcomes of three 'core effects' (see Boxes 1 and 2). In the second part of
59 our review we identify five influential 'dimensions' and show how these modify the way that core
60 effects play out. The resulting conceptual model of the matrix can help to improve
61 communication of matrix ideas, and guide future research, including research that addresses new
62 questions about interactions between core effects and dimensions associated with time, space and
63 adaptation.

64

65 **Core effects of the matrix**

66 After considering the range of effects that the matrix can have on patch-dependent species [using
67 empirical literature, also canvassed in numerous reviews: 19, 25, 34-36], we identified three
68 fundamental ways that the matrix influences the spatial dynamics of populations and species
69 occurrence in fragmented landscapes. The matrix can influence population persistence in

70 fragmented systems through effects associated with (i) movement and dispersal; (ii) resource
71 availability, and; (iii) the abiotic environment (Figure 1).

72

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

74 Recent reviews report that movement between patches is enhanced as the matrix becomes

75 structurally more similar to the remnant patches [40, 41]. For example, when pastures are

76 replaced by tree plantations, colonisation of forest patches by forest specialists can increase [4].

77 However, the matrix can influence immigration and emigration in other ways. Sharp ecotonal

78 boundaries between a patch and the matrix can cause individuals to cluster inside remnants

79 ('fence effects') [1]. If a species does venture into the matrix, rapid movement through

80 unfavourable habitat could enhance connectivity between separated habitat patches [42]. On the

81 other hand, dispersal or movement between disjunct habitat patches might decline due to altered

82 behaviour, or increased mortality [2, 5, 26, 43]. The influence of the matrix as a demographic

83 sink has received little research attention, although in theory, density-independent emigration can

84 increase the risk of local extinctions [44].

85

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

87 *specialists.*

88 The role of the matrix as a resource base for species that invade remnant patches has long been

89 understood [19] (Box 3). For example, red squirrel *Tamiasciurus hudsonicus* populations thrived

90 on pine-seeds in Canadian pine plantations. Squirrels subsequently invaded remnant broad-leaf

91 forest and ate Brown Creeper *Certhia americana* eggs, increasing the rate of nest failure of this

92 patch-dependent bird [16]. On the other hand, if the right resources are provided, the matrix can

93 be converted to habitat and desirable native species can live throughout the landscape [e.g. 45].
94 However, if species remain patch-dependent, they might nevertheless use resources within the
95 matrix as a food subsidy [34]. With the possible exception of bees that can forage outside of the
96 nesting patch [e.g. 14], evidence that patch-dependent species gather resources outside of the
97 patch to support higher population densities inside the patch is limited [e.g. 46].

98

99 *Abiotic environment. The matrix influences microclimate and disturbance regimes of patches.*

100 The physical structure of the matrix is often different from habitat patches and can alter the
101 environmental conditions within patches [19, 37], particularly when treed landscapes are cleared
102 [25]. Microclimatic changes associated with increased light and wind penetration can have far-
103 reaching effects on patch-dependent species, increasing the risk of local extinction [7, 47]. In
104 addition, species that prosper under the altered microclimate can colonise remnant vegetation
105 and drive edge-sensitive species into the remnant core [37, 48].

106

107 Changes to disturbance regimes in the matrix can also affect patch-dependent species. Larger
108 and more frequent fires can occur if there are more ignitions in the matrix [11], or when the fuel
109 structure in the matrix is changed by forest logging [11, 49] or by invasive grasses [17].

110 Conversely, active fire suppression in matrix environments can reduce rates of natural
111 disturbance in patches [3]. Altered microclimate and disturbance regimes can advantage some
112 species, often invasive exotic species [6, 17], but disadvantage others, often species that depend
113 on remnant vegetation [8]. Increased disturbance associated with urban or mining landscapes can
114 also drive local extinctions in patches [9, 10].

115

116 Conceptualising matrix effects as stemming from three core effects (impacts associated with
117 dispersal, resource availability, and the abiotic environment) provides a structure for identifying
118 ecological pathways that influence abundance and population survival (Figure 1). For example,
119 invasion of patches by new species has often been listed as an important effect of the matrix on
120 patch-dependent species [19, 25, 35, 36]. However, our new conceptual model emphasises that
121 such colonisation can be an indirect effect of any one of the three core effects (Box 2).
122 Similarly, altered species interactions have been listed as one of four main effects of the matrix
123 [38], but these too are a consequence of the three core effects (Box 1).

124

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

135

136

137 **Five dimensions modify how the core effects influence biodiversity**

138 *Spatial variation. The matrix is not spatially homogeneous*

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

148
149 Spatial variation in matrix quality will also lead to variation in microclimate conditions,
150 imposing spatially variable edge effects [25, 54]. Furthermore, variation in matrix quality can
151 affect taxa differently by providing contrasting resources. For example, Öckinger *et al.* [46]
152 found higher butterfly species richness within grassland patches surrounded by a forest matrix,
153 but higher species richness of hoverflies in grassland patches surrounded by arable land,
154 reflecting differences in food resources for these species.

155
156
157 *Spatial scale. The extent of the matrix influences its impacts on patch-dependent species*
158 The spatial scale of the matrix, including geographic extent and distance between patches (see
159 Glossary), has an important effect on patch-dependent species. The distance between patches is
160 well understood to influence dispersal rates [55]. Because dispersal influences the probabilities
161 of population extinction and recolonisation of patches [24], the effects of matrix scale on

162 dispersal (i.e. longer distances between patches) can affect patch occupancy and mediate the
163 operation of patchy populations, metapopulations or isolated populations in fragmented
164 ecosystems [13].

165
166 The spatial extent of the matrix can also influence resource subsidisation and spill-over edge
167 effects, although evidence for such effects is limited. If patch-dependent species exploit
168 resources in the matrix [34], a proportionally greater area of matrix to patch could increase the
169 relative abundance of such resources. However, movement limitation and satiation can prevent
170 patch-based species from exploiting an ever-increasing amount of matrix. Spill-over of matrix-
171 specialist predators or prey into patches [56] is influenced by the scale of the matrix and patches.
172 Increasing the scale of the matrix increases the population size of matrix specialists, and can
173 cause larger spill-over edge effects [16].

174
175 The influence of the spatial extent of the matrix on the abiotic environment of patches is likely to
176 be more limited than the effects on dispersal and resources. Most edge studies disregard the
177 scale of the adjacent matrix and so understanding of such effects is rudimentary. Narrow gaps
178 like forest roads can have substantial abiotic edge effects [57]. The extent to which wider gaps
179 have bigger effects and the scale at which effects plateau is yet to be established. The extent of
180 the matrix could also influence the risk of fire, in circumstances where fires are more likely to
181 start in agricultural lands [11].

182
183 Interactions between spatial scale and spatial variation in matrix quality can have important
184 effects on populations in fragmented systems [58, 59]. By examining the extent to which changes

185 in population size were synchronous, Powney *et al.* [58] found that matrix permeability to
186 dispersal had the strongest effect on movement between patches at intermediate distances. In
187 contrast, movement between patches was relatively insensitive to matrix type at short or long
188 distances between patches. There has been limited direct study of how such interactions occur.
189 However, the effects of matrix heterogeneity are most likely to be apparent on the spatial scale of
190 individual movement behaviour [59] or the scale over which population synchrony occurs [58].

191

192

193 *Temporal variation. The matrix is not static.*

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

203

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

207

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

214

215

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

217 Dispersal rate is a key trait determining the ability of species to exploit changes in the matrix

218 [69]. For example, in poorly dispersing lichen species, forest succession through plantation

219 harvest cycles can be too rapid for colonisation, particularly when the matrix is extensive [70].

220 Strong dispersers are in the best position to exploit short-term changes in matrix resources [71],

221 while species with intermediate dispersal abilities could benefit most from longer-lasting

222 temporal changes such as revegetation [69].

223

224 The ability to exploit resource pulses in the matrix also depends strongly on a species' life history

225 characteristics. For example, hairy-footed gerbils *Gerbillurus paeba* of southern African

226 savannas are dependent on grasslands embedded in an inhospitable shrubby matrix that is

227 maintained by heavy grazing [15]. In years when extreme rainfall triggered unusually high grass

228 growth, gerbil abundance and reproductive output in the (former) matrix increased markedly.

229 The short generation time (3 months) and high fecundity (up to 6 young per litter) of the gerbils

230 allowed them to exploit this short-term boom in seed supply [15]. In contrast, species with a low

231 reproductive output, fixed seasonal breeding cycles, and low population growth rates are unlikely
232 to respond strongly to pulses of food resources in the matrix [72]. Resource specialisation can
233 also influence a species' ability to respond to changing resources in the matrix. Diet generalists
234 can exploit food resource pulses better than specialists because specialisation on rare and
235 ephemeral food sources is uncommon [72]. In contrast, where resources change gradually,
236 dietary specialists can replace generalists as succession advances [73].

237

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

243

244

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

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

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

255
256 Species can also exhibit evolutionary or plastic responses to use resources within the matrix [e.g.
257 forest dung beetles expanding through farmland by using cattle dung, 78]. Adaptive responses to
258 changes in the abiotic environment are also possible [e.g. caterpillars adapted to survive in open
259 farmland environments, 77]. Such effects, however, have not been widely investigated. Recent
260 reviews of adaptation to global change indicate that, while such adaptation does occur, much
261 remains to be learnt about the extent to which adaptation can mitigate negative effects of human-
262 induced environmental change [75, 78, 79]. We nevertheless expect that adaptation (plastic or
263 evolutionary) is an important phenomenon that influences how species respond to matrix
264 conditions. It would not be surprising for the effects of a given matrix on a species to change,
265 potentially over a small number of generations [75].

266

267

268 **What can be achieved with the new conceptual model?**

269

270 By defining the conceptual domain of the matrix (Figures 1, 2, Boxes 1, 4) and emphasising how
271 core effects can be modified by the five dimensions, important new research priorities are now
272 apparent (see Box 5 Outstanding Questions). Research addressing these questions has the
273 potential to generate novel conservation strategies and improved understanding of ecological
274 phenomena in fragmented landscapes. For example, when there is substantial spatial and
275 temporal variation in matrix quality, it might be difficult for species to adapt to matrix conditions

276 because selection pressures will be inconsistent [80]. This sets up a conundrum because
277 management recommendations to increase matrix heterogeneity [81] might also inhibit
278 adaptation to a dominant matrix type. New research is also needed to understand the interaction
279 of the temporal scale of changes in the matrix with other dimensions and core effects. For
280 example, what are the trade-offs between dispersal ability, the temporal scale of changes in the
281 matrix and the spatial extent of the matrix [70]? Related to this, do species have different
282 responses to the same kind of temporal variation in the matrix (such as those caused by La Niña
283 climate events) if those events also vary in temporal scale? Our conceptual model therefore
284 provides a framework for developing research questions that lead to conditional predictions
285 about matrix effects [82]. Combined with attempts to generalise across species by considering
286 species traits [39, 41](Box 5), the framework can help to understand the circumstances in which
287 particular effects might be expected.

288

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

298 and test hypotheses that consider the range of ways that the matrix influences patch-dependent
299 species.

300

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

309

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

319

320

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323 an earlier draft of our manuscript. Thanks to Clive Hilliker who prepared the figures and Nici
324 Sweaney for her Nanangroe photograph.

325

326

327

328 Figure 1. Matrix core effects

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

343

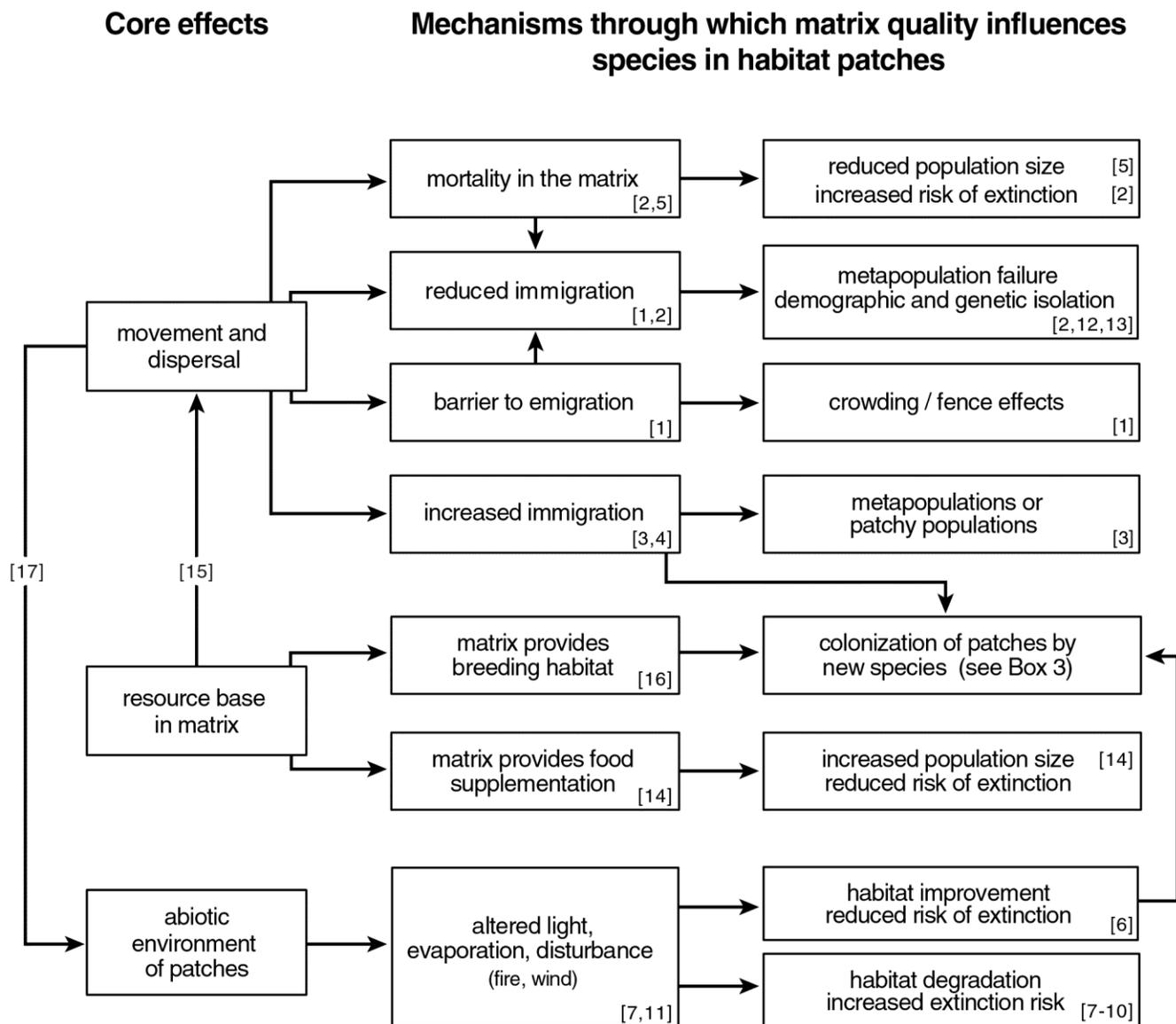
344 Figure 2. Five dimensions modify matrix core effects

345 The conceptual model of the matrix consists of the three core effects (detailed in Figure 1)
346 whereby the matrix influences patch-dependent species through effects associated with
347 movement and dispersal, resource availability, and the abiotic environment. Five dimensions
348 modify the way the core effects influence patch-matrix dynamics; temporal variation and
349 temporal scale, spatial variation and spatial scale, and adaptation. Although we portray these

350 dimensions as stacked, this does not imply any priority of effects (although difficult to draw,
351 these could also be imagined as overlapping spheres encompassing the core effects, like
352 electrons around an atom's nucleus). The blue arrow indicates that dimensions can act together,
353 or can interact to influence the core effects. Although we emphasise phenomena related to the
354 matrix, the importance of patch characteristics and species interactions are well established
355 (Boxes 1, 4). For simplicity we have not attempted to draw all of the likely relationships between
356 patches and the factors that influence the impact of the matrix on patch-dependent species.
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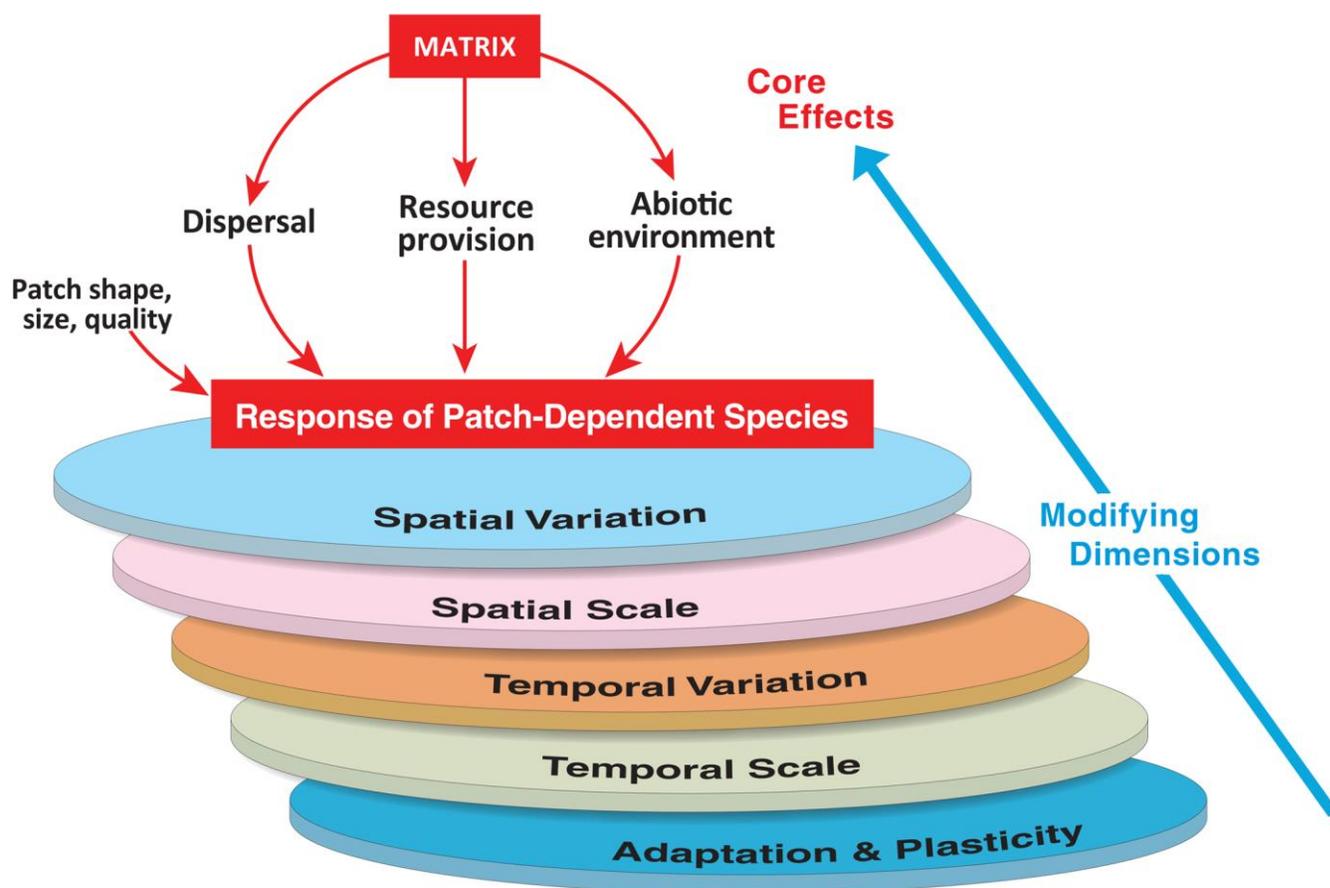
Figure 1



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Figure 2



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375

376 **Box 1. Species interactions**

377 Species interactions are integral to every step of Figure 1 (as they are to the edge-effects
378 conceptual model by Ries *et al.* [37] and the fragmentation conceptual model by Didham *et al.*
379 [26]). A pathway that affects one strongly interacting species could drive changes in many other
380 species, forming feedback loops through numerous different pathways. For example, Pita *et al.*
381 [2] suggested that predators can occupy degraded matrix sites in Mediterranean farmland (matrix
382 provides breeding habitat, Figure 1). The predators could inflict high dispersal mortality on
383 patch-dependent Cabrera voles *Microtus cabreræ*, reducing patch occupancy where the matrix is
384 highly modified. In another example, increasing resources in the matrix (seeds in wet years)
385 enabled seed-eating rodents to forage widely throughout the landscape [84]. With rodents
386 foraging beyond the patch, seed predation on hawthorn (*Crataegus monogyna*) within the patch
387 was reduced, providing an opportunity for recruitment of this important structural species [84].
388
389 Competition-colonisation trade-offs or predator-prey patch dynamics [85] might also drive
390 feedbacks between pathways in Figure 1. Where the matrix is highly permeable, a community
391 could consist of strongly competing species because poorly dispersing but competitively
392 dominant or predatory species can reach all sites. However, if the matrix offers strong resistance
393 to dispersal, the community might consist of less competitive, but strongly dispersive species
394 [86]. Our key point is that species interact. Therefore, the influence of the matrix on patch-
395 dependent species could be indirect because the matrix influences the dispersal, resources or the
396 abiotic environment of other species that depredate, out-compete or have some other interaction
397 [pollination, fruit dispersal, 64, 87] with the patch-dependent species.

398

399 **Box 2. New species colonise patches by multiple pathways**

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

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

413
414 2. Resource Provision. The matrix provides resources that support a wide range of species
415 and these can spill over into patches of native vegetation to the disadvantage of patch-
416 dependent species. For example, coffee plantations have received widespread attention as
417 a matrix capable of supporting forest species [89], but these plantations also provide
418 resources for pest species. In Mauritius, the Coffee Berry Moth *Prophantis smaragdina*
419 moves from the matrix into adjacent rainforest, consuming the fruit and thereby reducing
420 the reproductive success of the endemic dioecious shrub *Bertiera zaluzania* [90]. Such

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

423

424 3. The abiotic environment. When habitat structure becomes more open and disturbed at
425 edges of native vegetation patches, the altered abiotic conditions enables disturbance-
426 favouring matrix species to invade patches, with consequences for patch-specialists [19,
427 37]. For example, in the USA, Amur Honeysuckle *Lonicera maackii* is a shade-intolerant
428 invasive shrub occurring in disturbed areas and forest edges with sufficient light [91].
429 Invasion changed the microclimate which reduced amphibian abundance and diversity
430 [48], along with effects on the invertebrate fauna [92].

431

432

433 **Box 3. The Nanangroe Natural Experiment**

434



435

436 Figure I. A changing matrix. Pines (*Pinus radiata*) were planted into grazing land beginning in

437 1998. The left plate shows soil mounds scoured into the farmland in preparation for planting.

438 The trees have now grown into a dense plantation (right plate) which surrounds many remnant

439 woodland patches. The pine matrix will continue to change through cycles of thinning,

440 clearfelling and re-establishment. The dynamic matrix is likely to drive ongoing changes in the

441 animal communities of woodland patches.

442

443

444 The Nanangroe Natural Experiment was designed to quantify the effects of temporal changes in

445 the matrix on patch-dependent species in Australian temperate eucalypt woodlands [4]. The

446 major temporal change in the matrix was the transformation of a former grazing landscape into

447 one dominated by Radiata Pine (*Pinus radiata*) (Figure I) [93].

448

449 The Nanangroe study comprises 58 *Eucalyptus* woodland remnants surrounded by pine stands

450 and a set of 58 matched woodland “control” sites on farmland where the surrounding areas are

451 semi-cleared grazing paddocks. The experimental design is underpinned by a randomised and
452 replicated patch selection procedure in which patches in four size classes and five woodland
453 vegetation types were identified for study [93]. Vegetation cover and selected vertebrate species
454 have been sampled on all sites every 1-2 years between 1998 and 2012, creating a high quality
455 time series dataset.

456
457 For birds, a range of responses to the changing matrix have been observed in the Nanangro
458 study [4] and these illustrate some of the pathways emphasised in the conceptual model of core
459 effects (Figure 1). Key responses to the changing matrix include: **(i)** new species were recruited
460 to the landscape because the pine matrix provided breeding habitat (matrix provides breeding
461 habitat, Figure 1); **(ii)** a “spill-over” process whereby some species which increased with the
462 landscape transformation then “spilled over” from the pine matrix into adjacent woodland
463 remnants (matrix provides breeding habitat leading to colonisation of patches by new species,
464 Figure 1), and; **(iii)** a habitat-linked process in which some species’ responses were associated
465 with measured temporal changes in vegetation attributes as the patches responded to the changed
466 abiotic conditions and management regime. For example, the ground-foraging Brown
467 Treecreeper *Climacteris picumnus* declined with increasing ground-level vegetation cover [4]
468 (habitat degradation leading to increased extinction risk, Figure 1). These examples underscore
469 the array of responses that can occur as a result of temporal changes in matrix quality.
470

471 **Box 4. The patch still matters**

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

481

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

493 the matrix is homogeneous and relatively static, patch features might be most important, and
494 vice-versa [27].

495

496 **Box 5. Outstanding Questions**

497 **Matrix resources**

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

502

503 **Matrix mortality**

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

507

508 **Temporary connectivity and population boosts**

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

514

515 **Extent of the matrix**

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

518

519 **Interaction of extent and heterogeneity**

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

524

525 **Interaction of extent and temporal scale**

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

530

531 **Adaptation and potential conflict with other management**

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

535

536 **Developing Generality**

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

541

542 **Glossary**

543

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

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

544

545

546 **References**

- 547 1 Schtickzelle, N. and Baguette, M. (2003) Behavioural responses to habitat patch boundaries
548 restrict dispersal and generate emigration-patch area relationships in fragmented landscapes.
549 *J. Anim. Ecol.* 72, 533-545
- 550 2 Pita, R., *et al.* (2007) Spatial population structure of the Cabrera vole in Mediterranean
551 farmland: The relative role of patch and matrix effects. *Biol. Conserv.* 134, 383-392
- 552 3 Templeton, A.R., *et al.* (2011) The transition from isolated patches to a metapopulation in the
553 eastern collared lizard in response to prescribed fires. *Ecology* 92, 1736-1747
- 554 4 Lindenmayer, D.B., *et al.* (2008) Temporal changes in vertebrates during landscape
555 transformation: a large-scale "natural experiment". *Ecol. Monogr.* 78, 567-590
- 556 5 Schwab, A.C. and Zandbergen, P.A. (2011) Vehicle-related mortality and road crossing
557 behavior of the Florida panther. *Appl. Geogr.* 31, 859-870
- 558 6 Keeley, J.E. (2006) Fire management impacts on invasive plants in the western United States.
559 *Conserv. Biol.* 20, 375-384
- 560 7 Lehtinen, R.M., *et al.* (2003) Edge effects and extinction proneness in a herpetofauna from
561 Madagascar. *Biodivers. Conserv.* 12, 1357-1370
- 562 8 Urbina-Cardona, J.N., *et al.* (2006) Herpetofauna diversity and microenvironment correlates
563 across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas
564 Biosphere Reserve of Veracruz, Mexico. *Biol. Conserv.* 132, 61-75
- 565 9 Williams, N.S.G., *et al.* (2006) Local extinction of grassland plants: The landscape matrix is
566 more important than patch attributes. *Ecology* 87, 3000-3006
- 567 10 Kennedy, C.M., *et al.* (2011) Landscape matrix mediates occupancy dynamics of Neotropical
568 avian insectivores. *Ecol. Appl.* 21, 1837-1850

- 569 11 Cochrane, M.A. and Barber, C.P. (2009) Climate change, human land use and future fires in
570 the Amazon. *Global Change Biol.* 15, 601-612
- 571 12 Seddon, P.J., *et al.* (2011) Dynamics of an endangered New Zealand skink: accounting for
572 incomplete detectability in estimating patch occupancy. *N. Z. J. Ecol.* 35, 247-253
- 573 13 Driscoll, D.A., *et al.* (2012) Spatial dynamics of the knob-tailed gecko *Nephurus stellatus* in
574 a fragmented agricultural landscape. *Landscape Ecol.* 27, 829-841
- 575 14 Hinnners, S.J., *et al.* (2012) Roles of scale, matrix, and native habitat in supporting a diverse
576 suburban pollinator assemblage. *Ecol. Appl.* 22, 1923-1935
- 577 15 Blaum, N. and Wichmann, M.C. (2007) Short-term transformation of matrix into hospitable
578 habitat facilitates gene flow and mitigates fragmentation. *J. Anim. Ecol.* 76, 1116-1127
- 579 16 Poulin, J.-F. and Villard, M.-A. (2011) Edge effect and matrix influence on the nest survival
580 of an old forest specialist, the Brown Creeper (*Certhia americana*). *Landscape Ecol.* 26, 911-
581 922
- 582 17 D'Antonio, C.M. and Vitousek, P.M. (1992) Biological Invasions by Exotic Grasses, the
583 Grass Fire Cycle, and Global Change. *Annu. Rev. Ecol. Syst.* 23, 63-87
- 584 18 Lindenmayer, D.B. and Fischer, J. (2006) *Habitat Fragmentation and Landscape Change. An*
585 *ecological and conservation synthesis.* Island Press
- 586 19 Saunders, D.A., *et al.* (1991) Biological consequences of ecosystem fragmentation: a review.
587 *Conserv. Biol.* 5, 18-32
- 588 20 Forman, R.T.T. (1995) *Land mosaics. The ecology of landscapes and regions.* Cambridge
589 University Press
- 590 21 Fahrig, L. and Merriam, G. (1994) Conservation of fragmented populations. *Conserv. Biol.* 8,
591 50-59

- 592 22 McIntyre, S. and Hobbs, R. (1999) A framework for conceptualizing human effects on
593 landscapes and its relevance to management and research models. *Conserv. Biol.* 13, 1282-
594 1292
- 595 23 Driscoll, D.A. (2004) Extinction and outbreaks accompany fragmentation of a reptile
596 community. *Ecol. Appl.* 14, 220-240
- 597 24 Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press
- 598 25 Kupfer, J.A., *et al.* (2006) Not seeing the ocean for the islands: the mediating influence of
599 matrix-based processes on forest fragmentation effects. *Global Ecol. Biogeogr.* 15, 8-20
- 600 26 Didham, R.K., *et al.* (2012) Rethinking the conceptual foundations of habitat fragmentation
601 research. *Oikos* 121, 161-170
- 602 27 Bender, D.J. and Fahrig, L. (2005) Matrix structure obscures the relationship between
603 interpatch movement and patch size and isolation. *Ecology* 86, 1023-1033
- 604 28 Prugh, L.R., *et al.* (2008) Effect of habitat area and isolation on fragmented animal
605 populations. *Proc. Natl. Acad. Sci. USA.* 105, 20770-20775
- 606 29 Franklin, J.F. and Lindenmayer, D.B. (2009) Importance of matrix habitats in maintaining
607 biological diversity. *Proc. Natl. Acad. Sci. USA.* 106, 349-350
- 608 30 Franklin, J.F. (1993) Preserving biodiversity - species, ecosystems, or landscapes. *Ecol. Appl.*
609 3, 202-205
- 610 31 Secretariat of the Convention on Biological Diversity (2010) *Global biodiversity outlook 3*.
- 611 32 Kyle, G. and Duncan, D.H. (2012) Arresting the rate of land clearing: Change in woody
612 native vegetation cover in a changing agricultural landscape. *Landscape Urban Plann.* 106,
613 165-173

- 614 33 Bradshaw, C.J.A. (2012) Little left to lose: deforestation and forest degradation in Australia
615 since European colonization. *J. Plant Ecol.* 5, 109-120
- 616 34 Ewers, R.M. and Didham, R.K. (2006) Confounding factors in the detection of species
617 responses to habitat fragmentation. *Biological Reviews* 81, 117-142
- 618 35 Jules, E.S. and Shahani, P. (2003) A broader ecological context to habitat fragmentation: Why
619 matrix habitat is more important than we thought. *Journal of vegetation science* 14, 459-464
- 620 36 Murphy, H.T. and Lovett-Doust, J. (2004) Context and connectivity in plant metapopulations
621 and landscape mosaics: does the matrix matter? *Oikos* 105, 3-14
- 622 37 Ries, L., *et al.* (2004) Ecological responses to habitat edges: mechanisms, models, and
623 variability explained. *Annu. Rev. Ecol. Evol. Syst.* 35, 491-522
- 624 38 Campbell, R.E., *et al.* (2011) Production land use alters edge response functions in remnant
625 forest invertebrate communities. *Ecol. Appl.* 21, 3147-3161
- 626 39 Kennedy, C.M., *et al.* (2010) Landscape matrix and species traits mediate responses of
627 Neotropical resident birds to forest fragmentation in Jamaica. *Ecol. Monogr.* 80, 651-669
- 628 40 Eycott, A.E. (2010) *Do landscape matrix features affect species movement? Systematic*
629 *Review CEE 08-006*. Collaboration for Environmental Evidence;
630 <http://www.environmentalevidence.org/SR43.html>
- 631 41 Prevedello, J.A. and Vieira, M.V. (2010) Does the type of matrix matter? A quantitative
632 review of the evidence. *Biodivers. Conserv.* 19, 1205-1223
- 633 42 Kuefler, D., *et al.* (2010) The conflicting role of matrix habitats as conduits and barriers for
634 dispersal. *Ecology* 91, 944-950
- 635 43 Schooley, R.L. and Wiens, J.A. (2004) Movements of cactus bugs: patch transfers, matrix
636 resistance, and edge permeability. *Landscape Ecol.* 19, 801-810

- 637 44 Hovestadt, T. and Poethke, H.J. (2006) The control of emigration and its consequences for the
638 survival of populations. *Ecol. Model.* 190, 443-453
- 639 45 Karp, D.S., *et al.* (2011) Resilience and stability in bird guilds across tropical countryside.
640 *Proc. Natl. Acad. Sci. USA.* 108, 21134-21139
- 641 46 Ockinger, E., *et al.* (2012) Landscape matrix modifies richness of plants and insects in
642 grassland fragments. *Ecography* 35, 259-267
- 643 47 Ewers, R.M. and Didham, R.K. (2008) Pervasive impact of large-scale edge effects on a
644 beetle community. *Proc Natl Acad Sci U S A* 105, 5426 - 5429
- 645 48 Watling, J.I., *et al.* (2011) Invasive shrub alters native forest amphibian communities. *Biol.*
646 *Conserv.* 144, 2597-2601
- 647 49 Lindenmayer, B.D., *et al.* (2009) Effects of logging on fire regimes in moist forests.
648 *Conservation Letters* 2, 271-277
- 649 50 Ramalho, C.E. and Hobbs, R.J. (2012) Time for a change: dynamic urban ecology. *Trends*
650 *Ecol. Evol.* 27, 179-188
- 651 51 Gustafson, E.J. and Gardner, R.H. (1996) The effect of landscape heterogeneity on the
652 probability of patch colonization. *Ecology* 77, 94-107
- 653 52 Hudgens, B.R., *et al.* (2012) How complex do models need to be to predict dispersal of
654 threatened species through matrix habitats? *Ecol. Appl.* 22, 1701-1710
- 655 53 Zeller, K.A., *et al.* (2012) Estimating landscape resistance to movement: a review. *Landscape*
656 *Ecol.* 27, 777-797
- 657 54 Pinto, S.R.R., *et al.* (2010) Landscape attributes drive complex spatial microclimate
658 configuration of Brazilian Atlantic forest fragments. *Trop. Conserv. Sci.* 3, 389-402

- 659 55 Hill, J.K., *et al.* (1996) Effects of habitat patch size and isolation on dispersal by Hesperia
660 comma butterflies: implications for metapopulation structure. *J. Anim. Ecol.* 65, 725-735
- 661 56 Rand, T.A., *et al.* (2006) Spillover edge effects: the dispersal of agriculturally subsidized
662 insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9, 603-614
- 663 57 Delgado, J.D., *et al.* (2007) Edge effects of roads on temperature, light, canopy cover, and
664 canopy height in laurel and pine forests (Tenerife, Canary Islands). *Landscape Urban Plann.*
665 81, 328-340
- 666 58 Powney, G.D., *et al.* (2011) Measuring functional connectivity using long-term monitoring
667 data. *Methods Ecol. Evol.* 2, 527-533
- 668 59 Revilla, E., *et al.* (2004) Effects of matrix heterogeneity on animal dispersal: From individual
669 behavior to metapopulation-level parameters. *Am. Nat.* 164, E130-E153
- 670 60 Tremblay, M.A. and St Clair, C.C. (2011) Permeability of a heterogeneous urban landscape to
671 the movements of forest songbirds. *J. Appl. Ecol.* 48, 679-688
- 672 61 Manning, A.D., *et al.* (2006) Scattered trees are keystone structures - Implications for
673 conservation. *Biol. Conserv.* 132, 311-321
- 674 62 Cosentino, B.J., *et al.* (2011) Connectivity of agroecosystems: dispersal costs can vary among
675 crops. *Landscape Ecol.* 26, 371-379
- 676 63 Blaum, N., *et al.* (2012) Climate induced changes in matrix suitability explain gene flow in a
677 fragmented landscape - the effect of interannual rainfall variability. *Ecography* 35, 650-660
- 678 64 Magrach, A., *et al.* (2012) Effects of Matrix Characteristics and Interpatch Distance on
679 Functional Connectivity in Fragmented Temperate Rainforests. *Conserv. Biol.* 26, 238-247
- 680 65 Laurance, W.F., *et al.* (2011) The fate of Amazonian forest fragments: A 32-year
681 investigation. *Biol. Conserv.* 144, 56-67

- 682 66 Hennenberg, K.J., *et al.* (2008) Detection of seasonal variability in microclimatic borders and
683 ecotones between forest and savanna. *Basic Appl. Ecol.* 9, 275-285
- 684 67 Asbjornsen, H., *et al.* (2004) Synergistic responses of oak, pine and shrub seedlings to edge
685 environments and drought in a fragmented tropical highland oak forest, Oaxaca, Mexico.
686 *For. Ecol. Manage.* 192, 313-334
- 687 68 D'Antonio, C.M., *et al.* (2011) Long-term impacts of invasive grasses and subsequent fire in
688 seasonally dry Hawaiian woodlands. *Ecol. Appl.* 21, 1617-1628
- 689 69 Donald, P.F. and Evans, A.D. (2006) Habitat connectivity and matrix restoration: the wider
690 implications of agri-environment schemes. *J. Appl. Ecol.* 43, 209-218
- 691 70 Boudreault, C., *et al.* (2012) Epiphytic lichen colonization in regenerating black spruce forest
692 stands of clearcut origin. *For. Ecol. Manage.* 276, 247-258
- 693 71 Wilcock, H.R., *et al.* (2007) Landscape, habitat characteristics and the genetic population
694 structure of two caddisflies. *Freshwat. Biol.* 52, 1907-1929
- 695 72 Ostfeld, R.S. and Keesing, F. (2000) Pulsed resources and community dynamics of consumers
696 in terrestrial ecosystems. *T.R.E.E.* 15, 232-237
- 697 73 Alanen, E.-L., *et al.* (2011) Differential responses of bumblebees and diurnal Lepidoptera to
698 vegetation succession in long-term set-aside. *J. Appl. Ecol.* 48, 1251-1259
- 699 74 Barbosa, O. and Marquet, P.A. (2002) Effects of forest fragmentation on the beetle
700 assemblage at the relict forest of Fray Jorge, Chile. *Oecologia* 132, 296-306
- 701 75 Hanski, I. (2012) Eco-evolutionary dynamics in a changing world. *Ann. N. Y. Acad. Sci.* 1249,
702 1-17

- 703 76 Heidinger, I.M.M., *et al.* (2010) Patch connectivity and sand dynamics affect dispersal-related
704 morphology of the blue-winged grasshopper *Oedipoda caerulescens* in coastal grey dunes.
705 *Insect Conservation and Diversity* 3, 205-212
- 706 77 Merckx, T. and Van Dyck, H. (2006) Landscape structure and phenotypic plasticity in flight
707 morphology in the butterfly *Pararge aegeria*. *Oikos* 113, 226-232
- 708 78 Tuomainen, U. and Candolin, U. (2011) Behavioural responses to human-induced
709 environmental change. *Biological Reviews* 86, 640-657
- 710 79 Sih, A., *et al.* (2011) Evolution and behavioural responses to human-induced rapid
711 environmental change. *Evolutionary Applications* 4, 367-387
- 712 80 REX Consortium (2013) Heterogeneity of selection and the evolution of resistance. *Trends*
713 *Ecol. Evol.* 28, 110-118
- 714 81 Shreeve, T.G. and Dennis, R.L.H. (2011) Landscape scale conservation: resources, behaviour,
715 the matrix and opportunities. *J. Insect Conserv.* 15, 179-188
- 716 82 Driscoll, D.A. and Lindenmayer, B.D. (2012) Framework to improve the application of
717 theory in ecology and conservation. *Ecol. Monogr.* 82, 129–147
- 718 83 Fahrig, L. (2001) How much habitat is enough? *Biol. Conserv.* 100, 65-74
- 719 84 Herrera, J.M., *et al.* (2011) Matrix effects on plant-frugivore and plant-predator interactions in
720 forest fragments. *Landscape Ecol.* 26, 125-135
- 721 85 Leibold, M.A., *et al.* (2004) The metacommunity concept: a framework for multi-scale
722 community ecology. *Ecol. Lett.* 7, 601-613
- 723 86 Rodriguez, A., *et al.* (2007) Composition of an avian guild in spatially structured habitats
724 supports a competition-colonization trade-off. *Proceedings of the Royal Society B-Biological*
725 *Sciences* 274, 1403-1411

- 726 87 Taki, H., *et al.* (2011) Plantation vs. natural forest: Matrix quality determines pollinator
727 abundance in crop fields. *Sci Rep* 1
- 728 88 Bridgman, L.J., *et al.* (2012) Short perceptual range and yet successful invasion of a
729 fragmented landscape: the case of the red-bellied tree squirrel (*Callosciurus erythraeus*) in
730 Argentina. *Landscape Ecol.* 27, 633-640
- 731 89 Philpott, S.M., *et al.* (2008) Biodiversity Loss in Latin American Coffee Landscapes: Review
732 of the Evidence on Ants, Birds, and Trees. *Conserv. Biol.* 22, 1093-1105
- 733 90 Kaiser, C.N., *et al.* (2008) Exotic pest insects: another perspective on coffee and conservation.
734 *Oryx* 42, 143-146
- 735 91 Watling, J.I. and Orrock, J.L. (2010) Measuring edge contrast using biotic criteria helps
736 define edge effects on the density of an invasive plant. *Landscape Ecol.* 25, 69-78
- 737 92 McNeish, R.E., *et al.* (2012) Riparian forest invasion by a terrestrial shrub (*Lonicera maackii*)
738 impacts aquatic biota and organic matter processing in headwater streams. *Biol. Invasions*
739 14, 1881-1893
- 740 93 Lindenmayer, D.B., *et al.* (2001) A prospective longitudinal study of landscape matrix effects
741 on fauna in woodland remnants: experimental design and baseline data. *Biol. Conserv.* 101,
742 157-169
- 743 94 Sanderlin, J.S., *et al.* (2012) On valuing patches: estimating contributions to metapopulation
744 growth with reverse-time capture-recapture modelling. *Proceedings of the Royal Society B-*
745 *Biological Sciences* 279, 480-488
- 746 95 Pavlacky, D.C., Jr., *et al.* (2012) Anthropogenic landscape change promotes asymmetric
747 dispersal and limits regional patch occupancy in a spatially structured bird population. *J.*
748 *Anim. Ecol.* 81, 940-952

- 749 96 Nams, V.O. (2012) Shape of patch edges affects edge permeability for meadow voles. *Ecol.*
750 *Appl.* 22, 1827-1837
- 751 97 Gonzalez-Moreno, P., *et al.* (2011) Is spatial structure the key to promote plant diversity in
752 Mediterranean forest plantations? *Basic Appl. Ecol.* 12, 251-259
- 753 98 Mortelliti, A., *et al.* (2010) The role of habitat quality in fragmented landscapes: a conceptual
754 overview and prospectus for future research. *Oecologia* 163, 535-547
- 755 99 Williams, D.A., *et al.* (2007) Genetic diversity and spatial structure of a keystone species in
756 fragmented pine rockland habitat. *Biol. Conserv.* 138, 256-268
- 757 100 Vellend, M. (2010) Conceptual synthesis in community ecology. *Q. Rev. Biol.* 85, 183-206