1    Faster movement in non-habitat matrix

2    promotes range shifts in heterogeneous landscapes

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20    **Running title:** Matrix quality and range expansion

21    **Key words:** invasions, area restricted search, Baltimore checkerspot butterfly, climate change,

22    edge behavior, integrodifference equation, range expansion

23   **Abstract:** Ecologists often assume that range expansion will be fastest in landscapes composed

24   entirely of the highest quality habitat. Theoretical models, however, show that range expansion

25   depends on both habitat quality and habitat-specific movement rates.  Using data from 78 species

26   in 70 studies, we find that animals typically have faster movement through lower-quality

27   environments (73% of published cases).  Therefore, if we want to manage landscapes for range

28   expansion, there is a tradeoff between promoting movement with non-hostile matrix, and

29   promoting population growth with high-quality habitat.   We illustrate how this tradeoff plays

30   out using an exemplar species, the Baltimore checkerspot butterfly.  For this species, we

31   calculate that the expected rate of range expansion is fastest in landscapes with ~15% high-

32   quality habitat.  Behavioral responses to non-habitat matrix have often been documented in

33   animal populations, but rarely included in empirical predictions of range expansion.  Considering

34   movement behavior could change land planning priorities from focus on high-quality habitat

35   only to integrating high- and low-quality land cover types, and evaluating the costs and benefits

36   of different matrix land covers for range expansion.

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**Introduction**

Theoretical ecologists have a rich tradition of using mathematical models to explain and predict the rate of invasions into newly encountered or available habitat (see, e.g., Skellam 1951, Andow et al. 1990, Clark et al. 1998, Hastings et al. 2005). This area of research is longstanding, and is now of particular interest in the context of climate change, and the potential for species to shift their ranges to track suitable habitat and climate conditions (Hill et al. 2001, Wilson et al. 2009, MacDonald and Lutscher 2018). Climate change has been implicated in the rapidly accelerating pace of species extinctions (Urban 2015), but these extinctions could be partly moderated by managing landscapes in ways that maximize species' ability to shift their ranges as suitable habitats shift poleward and/or upward (Vos et al. 2008). To date, landscape management strategies to promote range expansion, e.g., agri-environment schemes to incorporate resources for wildlife into semi-natural landscapes (Donald & Evans 2006, Kleijn et al. 2011, Kleijn & Sutherland 2013), have been based largely on practical knowledge of species' habitat needs, and have not been linked tightly to ecological theory. In part, this gap exists because classic models of range expansion do not include spatial heterogeneity, whereas habitat quality at local scales, and the resulting spatial heterogeneity at landscape scales, are the primary targets of land management.

In this paper, we evaluate how landscape composition affects range expansion, using recent extensions of longstanding theories of invasion dynamics to heterogeneous landscapes (Musgrave & Lutscher 2014, Lutscher & Musgrave 2017). Our work is motivated by theoretical results and empirical patterns that point to an underappreciated role of matrix land cover types for range expansion. In homogeneous landscapes, simple reaction-diffusion models predict that range expansion increases with the product of the population growth rate and movement

62  (measured as rate of diffusion) (Skellam 1951). The intuitively appealing principle that both

63  higher growth rates and faster movement increase range expansion applies under a variety of

64  more complicated models and assumptions (e.g., Shigesada et al. 1986, Maciel & Lutscher

65  2013), possibly also moderated by a species' preference for different habitat types at patch edges

66  (Musgrave & Lutscher 2014).  Common starting assumptions for predicting range expansion in

67  heterogeneous landscapes are that movement occurs primarily through high-quality habitat, and

68  that the habitat type that confers the highest growth rate (e.g., high-quality habitat from a

69  demographic perspective) is also best for movement (e.g., Johnson 1992, Hill et al. 2001, Opdam

70  2004).  If this were the case, then range expansion would be fastest through homogeneous

71  landscapes composed of 100% high-quality habitat.

72        However, two empirical patterns suggest that the relationship between movement and

73  habitat quality, and, therefore, the relationship between landscape composition and range

74  expansion, is more complicated.  First, although many animals show preference for higher

75  quality habitat at patch interfaces, this preference is rarely perfect.  In many animal populations,

76  a substantial minority of individuals leave high-quality habitat at patch edges, e.g., 10% of bush

77  crickets released at edges between grassland habitat and forest matrix entered the forest

78  (compared to a null expectation of 50%; Kindvall 1999) and 20% of scarce large blue butterflies

79  released at edges between meadow habitat and forest matrix left into the forest (Skorka et al.

80  2013).  Therefore, the nature of the matrix, and of movement through the matrix, may contribute

81  significantly to rates of range expansion (cf. Ricketts 2001).

82        Second, at least some animal species move more quickly through lower quality land

83  cover types.  For example, Schultz (1998) quantified Fender's blue butterfly movement using

84  diffusion coefficients; Fender's blues moved 0.6 $m^2$/sec in host plant habitat patches, and 8.6

85  m$^2$/sec in prairie matrix with no host plants.  Similarly, Kuefler et al. (2010) measured squared

86  displacement of a wetland butterfly, the Appalachian brown, across multiple habitat types; these

87  butterflies moved 467 m$^2$/5-sec interval in upland fields (matrix), compared to 105 m$^2$/5-sec

88  interval in wetlands (habitat).  More generally, area-restricted search, in which animals move

89  more slowly in areas where they encounter more resources, is a common movement syndrome in

90  foraging predators (Kareiva and Odell 1988).  All else being equal, slower movement causes

91  animals to spend more time in a particular land cover type (Turchin 1991, Schultz et al. 2017),

92  which suggests a general fitness advantage of slower movement in higher-quality habitat.

93      If some proportion of animals leave high-quality habitat and move more quickly through

94  the matrix than through high-quality habitat, this creates a tradeoff for land managers between

95  increasing population growth by increasing the proportion of high-quality habitat and increasing

96  movement by increasing the proportion of non-hostile matrix on the landscape. Two past

97  modeling studies have shown that the presence of matrix on the landscape can sometimes

98  enhance range expansion: Lutscher and Musgrave (2017) calculated range expansion using an

99  integrodifference equation model; they found that, for a range of realistic parameter values for

100 emerald ash borer, ash-free "barrier zones" could increase rates of ash borer invasion.  Bocedi et

101 al. (2014) explored general simulation models (not tuned to any particular organism) that

102 assumed animals had a dispersal phase in which they searched for habitat patches until they

103 either found suitable habitat for settling or died.  They found that landscapes with relatively

104 small proportions of high-quality habitat could lead to the most rapid rates of range expansion, as

105 long as mortality in the matrix was not too high.  However, it is not clear from these two

106 modeling studies whether there is generally an empirical tradeoff between faster movement and

107 higher demographic quality among land cover types, or whether this tradeoff translates into

108     faster range expansion rates in heterogeneous landscapes for real species, given the demographic

109     costs.

110         Here, we evaluate this tradeoff empirically in two ways: First, we test whether animals

111     generally tend to move more quickly or more slowly through lower-quality habitat (i.e., matrix)

112     land cover types than through high-quality habitat, by compiling data from past studies that

113     independently estimated habitat quality and movement. A negative relationship between

114     movement and habitat quality is necessary (although not sufficient) for a habitat-quality /

115     movement tradeoff to exist in relation to range expansion. Second, we calculate the expected

116     rate of range expansion, i.e., the net effect of the habitat-quality / movement tradeoff, for a focal

117     species, the Baltimore checkerspot butterfly (*Euphydryas phaeton*), across a range of landscape

118     scenarios. (Notably, recent theoretical advances (Musgrave and Lutscher 2014) allow us to

119     calculate expected rates of range expansion in heterogeneous environments, rather than building

120     simulation models.) This case study allows us to evaluate conditions under which an increase in

121     the percentage of matrix land cover leads to an increased rate of range expansion, despite

122     reduced population growth, because of faster moment in matrix, using parameters measured

123     across four land cover types in natural populations (Brown and Crone 2016, Brown et al.

124     2017a&b). Together, the two parts of this paper (1) show that a habitat-quality / movement

125     tradeoff is common in natural populations, (2) illustrate a straightforward method for calculating

126     the balance of this tradeoff from field data, and (3) demonstrate that, for real populations,

127     landscape heterogeneity is likely to promote range expansion.

128

129     **Empirical patterns of movement**

130     *Methods:*

131        We compiled an initial list of 267 movement studies conducted in heterogeneous

132    environments by searching for papers that cited classic studies of movement in heterogeneous

133    environments and papers cited within. In addition, we searched Web of Science for all papers

134    that used the terms "Area Restricted Search", "Residence Index", and papers within ecology and

135    biology journals that used the term "diffusion." We screened these papers for studies that

136    included estimates of movement measured as net distance moved per time (or a response variable

137    that related monotonically to the rate of net displacement) in at least two habitat types, as well as

138    independent estimates of habitat quality for these habitat types, as indicated by demographic

139    rates such birth or death rates, food density, and/or population growth rates. We excluded studies

140    in which habitat quality was assumed but not measured (e.g., assuming suburban versus natural

141    areas represent "low" and "high" quality, respectively), in which habitat quality was inferred

142    from movement behavior (e.g., foraging behavior of pelagic birds as an indicator of prey

143    density), or if the measured movement metric confounded net displacement with other aspects of

144    behavior such as preference at patch boundaries (e.g., studies of residence time in patches could

145    reflect slower movement *or* higher preference at patch boundaries). Based on these criteria, we

146    retained 70 of the original 267 studies (listed in Appendix 1). We divided cases into categories

147    for which (1) movement was faster in higher-quality habitat, (2) no preference or unclear pattern,

148    and (3) movement was faster in lower-quality habitat. We compiled taxonomic data (Phylum,

149    Class, Order, Family, Genus, Species) for these 78 species (https://www.itis.gov/; accessed

150    November 2017).

151        We evaluated the potential effects of phylogeny on the relationship between habitat

152    quality and movement using binomial family, logit link, generalized linear mixed models

153    (GLMMs) with various metrics of taxonomy (combinations of Phylum, Order, Class and/or

154    Family) as random effects. Because binomial models require yes/no responses, these analyses

155    included only the studies that could be classified as faster movement in higher vs. lower quality

156    habitat; ten species with unclear patterns were not included in GLMMs. We used intercept-only

157    models (with taxonomic random effects) to compare the proportion of studies with faster versus

158    slower movement in lower quality environments, and tested whether the proportion of "faster"

159    studies differed significantly from 0.5, i.e., whether the value of the intercept on a logit scale

160    differed significantly from 0. Models were implemented using the lme4 package (Bates et al.

161    2015) in R (R Core Team 2016).  We evaluated taxonomic effects by comparing model AICs.

162    We did not pursue further phylogenetic analyses because of the complete lack of taxonomic

163    effects (see *Results* below), and the large breadth of phylogenetic distance included in our set of

164    studies, e.g., the single representative of Division Myxomycota (Kingdom Fungi) would have

165    especially high leverage.

166         We found no evidence for taxonomic patterns (see *Results*). Therefore, we estimated the

167    proportion of studies in each category (faster in higher-quality, no pattern, faster in lower-

168    quality) using ordinal multinomial logistical regression ('polr' function in the MASS package

169    (Venables & Ripley 2002) in R). Confidence limits were obtained by parametric bootstrapping,

170    i.e., 95% quantiles of 1000 simulated data sets obtained by applying the 'sim' function to the

171    original model, re-analyzed with the 'polr' function.

172

173    ***Results***

174         We found 70 studies comparing movement in high- and low-quality habitat types for 78

175    species from seven Phyla and one Division. Studies were heavily biased toward arthropods and

176    vertebrates, especially in the Lepidoptera (butterflies and moths) and Coleoptera (beetles) insect

orders, and in the Aves (birds) and Mammalia (mammals) vertebrate classes (Appendix S2: Tables S1 & S2). Four families, all in the class Insecta, were represented by more than two studies; three Lepidoptera families (Nymphalidae (8 studies), Pieridae (6 studies) and Papilionidae (3 studies) and one Coleoptera family (Chrysomelidae (4 studies)). Four species were represented by two studies (*Brachionus calyciflorus*, *Euphydryas anicia*, *Plebejus icarioides fenderii*, *Protaphorura armata*, *Tetranychus urticae*). Only one genus (the Nymphalid butterfly *Euphydryas*) was represented by more than three studies, and, in addition to the two-study species above, four genera (*Calopteryx, Morus, Phyllotreta, Selasphorus*) were represented in two studies. For analysis, we used each species within each study as the unit of observation. Conclusions changed only slightly if we randomly chose one species from each study for inclusion in the analysis.

There was no apparent effect of taxonomy on the proportion of studies with faster movement in low-quality habitat (Appendix S3: Table S1). GLMMs with random effects of Phylum, Class, Order and/or Family never improved model AICs relative to a simple GLM with no taxonomic structure. Because of their limited replication within units, Genus and Species were not included as taxonomic levels in GLMMs. Preliminary evaluation of these models indicated overparameterization.  Furthermore, estimates of variance among Phyla and Classes were 0. In the GLMM with all four taxonomic levels included, the variance estimates for Phylum, Class, and Family were 0, and the model was identical to the Order-only model. Of the 68 cases with a clear directional response, 83.8% showed faster net movement (diffusion or related metrics) in lower-quality environments (binomial family, logit link GLM; 95% CI: 73.9-91.3%, test for difference from 50%: $Z = 5.00$, $P < 0.001$).  Analysis of all studies (including unclear responses) with multinomial models showed that 73% (95% CI = 62.1-82.1%) of cases

200     had faster movement in low- than high-quality environments, and only 14% (95% CI = 7.7-

201     28.1%) had faster movement in high-quality environments (Fig. 1).

202

**Predicting range expansion in heterogeneous landscapes**

*General approach:*

205     Our literature review demonstrates that animals tend to move faster through lower-quality

206     land cover types.  However, heterogeneous landscapes facilitate movement only when the

207     benefits of faster movement outweigh the demographic costs of lower-quality habitat, and when

208     animals enter the matrix frequently enough to experience these benefits.  To explore how this

209     tradeoff plays out, we calculate the balance of habitat-quality / movement tradeoffs, using field

210     data from an exemplar species, the Baltimore checkerspot, across four land cover types.

211     Specifically, we used a spatially heterogeneous integrodifference equation (IDE) model

212     to calculate the expected rate of range expansion in landscapes consisting of high-quality habitat

213     in combination with one of three matrix types. In addition to including key aspects of spatial

214     heterogeneity, IDEs separate the time scales of different demographic processes, unlike

215     traditional differential or difference equation models (Powell and Zimmerman 2004).

216     Specifically, we used the model presented by Musgrave and Lutscher (2014), adjusted for

217     butterfly life history (see Appendix S4), and solved over a 1-dimensional, periodic landscape

218     (Fig. 2) to calculate range expansion of the Baltimore checkerspot butterfly under a range of

219     landscape scenarios.  This IDE model captures key aspects of butterfly biology, including

220     preference at patch interfaces.

221     We chose a periodic landscape as a general approach for modeling heterogeneous

222     environments for several reasons. First, this simplified landscape leads to a tractable model; the

223  solution is an analytical calculation, not a numerical simulation.  Second, the rate of range

224  expansion starting from a point in a 1-dimensional landscape is the same as the rate of expansion

225  starting from a line in a 2-dimensional landscape composed of parallel stripes of habitat

226  (Shigesada et al. 1986) (Fig. 2). A line is a reasonable first approximation of an altitudinal or

227  poleward range limit, so the approximation is particularly appropriate in the context of species'

228  range expansions with climate change. Third, periodic landscapes are characterized by only two,

229  ecologically meaningful, parameters: the length of the period and the proportion of high-quality

230  habitat (or, equivalently, the widths of parallel stripes of habitat of types 1 and 2). Exploration of

231  alternative landscape configurations may be a fruitful area of research, but, to date, these have

232  not led to general mathematical solutions (Kinezaki et al. 2010). Hence, rates of range expansion

233  would need to be solved numerically over specific landscape configurations. Given their

234  analytical tractability, periodic landscapes are a useful starting configuration for assessing rates

235  of range expansion when the specific landscape context is unknown, or might be variable.

236       The calculation of spread rates in this model is based on habitat-specific, density-

237  independent growth. Negative density dependence does not affect rates of range expansion under

238  most conditions (van den Bosch et al. 1990, Sullivan et al. 2017). Positive density dependence

239  (Allee effects) generally leads to more restrictive conditions for invasion (Dewhirst & Lutscher

240  2009, Musgrave et al. 2015).  Density dependent movement can also affect rates of range

241  expansion (Altwegg et al. 2013, Bocedi et al. 2014).  Further study of both could be a productive

242  area for future research, although density dependence, especially Allee effects, can also be very

243  difficult to quantify in natural populations (Liermann & Hilborn 1997).  Parameters for our case

244  study (described in *Model parameterization & implementation*, below) were estimated during a

245    period of rapid and monotonic population growth (2013-2015, see Crone 2018), so are likely to

246    represent conditions at the front of an invading population.

247

248    ***Study system***

249           The Baltimore checkerspot is a univoltine meadow species that has in recent decades

250    been decreasing in abundance in southern portions of its range (Frye et al. 2013) and increasing

251    in more northern locations (Breed et al. 2013).  In addition to simply having available data, the

252    Baltimore checkerspot is interesting as a case study because different matrix land cover types

253    show different features that might promote range expansion.  Specifically, we (Brown et al.

254    2017b) divided the landscape into four land-cover types in which we measured demography and

255    movement. These were high-quality habitat (open meadow areas with a high density of host

256    plants and nectar resources) and three land cover types we here refer to as matrix: sink habitat

257    that could not support a population in isolation (i.e., low-quality habitat with lower densities of

258    host plants and nectar sources), open matrix (structurally similar meadows with very few

259    resources, e.g., hayfields), and forests (structurally dissimilar areas without host plants and with

260    few nectar sources) (Brown et al. 2017b). Relative to high-quality habitat, butterflies moved

261    faster through all matrix types, but movement was fastest through open matrix (Table 1).

262    Reproduction was possible (though not sufficient to balance mortality) in sink habitat but not in

263    other matrix land cover types.  Finally, butterflies showed preference for high-quality habitat and

264    other open land cover types at forest boundaries, but no preference at habitat/sink or habitat/open

265    interfaces.

266

267    ***Model parameterization & implementation***

268    We use the "case S" for interface conditions from Musgrave & Lutscher (2014), in which

269    rates of diffusion while moving differ between two patch types, but the proportion of time flying

270    does not (based on empirical differences in parameter values for Baltimore checkerspot; Brown

271    et al. 2017b). Therefore, range expansion is described by the following dispersion relation, which

272    relates the asymptotic rate of range expansion, $c$, to an unknown shape parameter, $s$, as a function

273    of species-specific vital rates (survival, reproduction, and movement, defined below):

$$\kappa_s \sinh(q_1 l_1) \sinh(q_2 l_2) + \cosh(q_1 l_1) \cosh(q_2 l_2) - \cosh(sl) = 0 \qquad (1)$$

274    In this equation $l_1$ is the width of stripes of land cover type 1, $l_2$ is the width of stripes of land

275    cover type 2, the habitat period is $l = l_1 + l_2$ , $\kappa_s = \frac{D_1 q_1^2 + D_2 (q_2 \bar{z})^2}{2 \bar{z} q_1 q_2 \sqrt{D_1 D_2}}$, and $q_i = \mu_1 \sqrt{(1 - e^{-sc} \hat{r}_i)}$.

276    To calculate rates of population expansion in heterogeneous environments, we minimized

277    eq(1) as a function of $s$ with respect to $c$ (see, e.g., Shigesada et al. 1986, Musgrave and Lutscher

278    2014). We used field-estimated values of the parameters for habitat-specific diffusion ($D_i$),

279    reproductive rate ($\hat{r}_i$), edge preference, ($\bar{z}$), and mortality, ($m_i$). [$\mu_i$ is the inverse of average

280    dispersal distance, calculated from mortality and diffusion as described in (4) below.] Values of

281    these parameters (see Table 1) were measured in field studies (Brown and Crone 2016, Brown et.

282    al 2017a&b) as described briefly here:

283    (1) Habitat-specific diffusion coefficients, $D_1$ and $D_2$, were measured by following individual

284       flight paths, and using Kareiva and Shigesada's equation for approximating correlated

285       random walks with diffusion (Brown & Crone 2016, Brown et al. 2017b).

286    (2) Realized population growth rates, $\hat{r}_1$ and $\hat{r}_2$, were measured by calculating the habitat-

287       specific ratio of eggs per adult, multiplied by the probability that eggs survive to eclose as

288       mature females. In this system, females mate soon after eclosion (E. Crone & L. Brown, *pers*

289       *obs.*), and we see no evidence of mate limitation. For models presented here, we use the

290    conservative lower estimate of fecundity presented by Brown and Crone (2016), not their

291    higher estimate corrected for finite patch size in our (large) study site.

292  (3) Preference at patch edges, $\bar{z}$, is calculated from the proportion of butterflies that choose

293    habitat type 2 when exactly at patch boundaries; (1+z)/2 is the proportion choosing habitat

294    type 2, and $\bar{z} = \frac{1-z}{1+z}$. We estimated this preference by releasing butterflies at habitat

295    boundaries, and recording their location after fixed distances. Fixed-diameter edge circles are

296    a common metric of preference at patch edges in butterfly field studies (Schultz 1998,

297    Kuefler et al. 2010). However, they are an approximation of the exact edge preference as

298    assumed by Musgrave and Lutscher (2014) and earlier mathematical models (Ovaskainen &

299    Cornell 2013) because field observations over discrete intervals of time or space may be

300    influenced by rates of movement in each habitat type, as well as preference when exactly at

301    the edge. This bias appeared to be small in our system (E. Crone, *pers. obs.*), e.g., we did not

302    observe animals crossing back and forth over the edge while waiting for them to leave the

303    circles.

304  (4) Average lifetime dispersal distances, $\frac{1}{\mu_1}$ and $\frac{1}{\mu_2}$, were calculated from habitat-specific

305    movement and loss rates, where loss occurrs due to mortality and, possibly, settling of

306    dispersing individuals. We assume that butterflies move and lay eggs at a constant (though

307    possibly habitat-specific) rate throughout their life cycle (McIntire et al. 2007, Brown &

308    Crone 2016), an assumption based largely on field observations, but also on the fact that the

309    nutrients in butterfly eggs come from resources consumed as an adult, as well as resources

310    consumed as a larva (O'Brien et al. 2004). Therefore, the rate of loss is due only to mortality

311    of adult butterflies, and the average dispersal distance, $\frac{1}{\mu_i} = \sqrt{\frac{D_i}{m_i}}$, where $D_i$ and $m_i$ are

312    habitat-specific diffusion and mortality rates, respectively. To obtain appropriate units for this

313    ratio, daily survival from capture-recapture data were converted to survival per seconds of

314    time during daily activity (Brown & Crone 2016). Our estimate of loss during dispersal

315    includes only loss due to mortality, in contrast to Musgrave and Lutscher (2014), who

316    included loss due to settling of dispersing propagules as well as to mortality. However, the

317    same dispersion relation holds when parameterized in terms of average dispersal distance (as

318    derived in Appendix S4), emphasizing the generality of the original result.

319         Using these parameters, we calculated spread rates through heterogeneous landscapes

320    consisting of high-quality habitat combined with each of the different matrix land cover types.

321    We varied the proportion of high quality habitat from 0-50%, and solved the equation for

322    landscape periods of 0.5, 1, 5, and 10 km.  Our baseline projections assumed that adult survival

323    was the same in all land cover types, based on Baltimore checkerspot field observations. For

324    comparison, we explored this assumption by calculating rates of range expansion in scenarios

325    where survival, as well as fecundity, was reduced in the matrix.

326

327    ***Model predictions***

328         Patterns of range expansion were generally similar across different spatial scales of

329    environmental heterogeneity (Appendix S5: Fig. S1).  As expected from general analyses of this

330    model (Musgrave and Lutscher 2014), the rate of invasion increased with increasing landscape

331    period (Appendix S5: Fig. S1).  However, this effect was modest and did not change the

332    qualitative effects of landscape heterogeneity or matrix composition. Therefore, we focus

333    comparison of matrix types on the model solved for a 1-km period landscape (Fig. 3).

334         Baltimore checkerspot range expansion was generally fastest in landscapes composed of

335    high-quality habitat and open matrix. As long as the landscape consisted of at least 3% high-

336    quality habitat, range expansion was faster in a heterogeneous habitat-open matrix landscape

337    than homogeneous high-quality habitat alone (Fig. 3). The optimal combination for range

338    expansion was ~15% high-quality habitat; adding more high-quality habitat beyond this point

339    gradually reduced the rate of range expansion (Fig. 3A).  Below 3% high-quality habitat, matrix

340    type altered the outer limits of whether populations would expand or go extinct, but rates of

341    range expansion depended much more on the amount of high-quality habitat than the matrix type

342    (Fig. 3B).  In landscapes with < 1% high-quality habitat, range expansion was faster when the

343    landscape included forest matrix than sink or open matrix because edge preference at forest

344    edges prevented individuals from leaving habitat and spending too much time in the matrix (Fig.

345    3B). Low-quality sink habitat increased range expansion only in landscapes with >10% high-

346    quality habitat, and was never the matrix type with the fastest rate of invasion. However,

347    populations were able to persist (rates of range expansion > 0) in more highly degraded

348    landscapes if the matrix was sink habitat than if it was open matrix (persistence thresholds of

349    0.5% and 1% high-quality habitat, respectively).  In these conditions, the benefits of limited

350    reproduction in sink habitat outweighed the benefits of faster movement through open matrix.

351         Over a wide range of lower survival values in matrix, Baltimore checkerspot range

352    expansion was faster in heterogeneous landscapes composed of 15% high-quality habitat and

353    85% open matrix landscapes than in 100% high-quality habitat (Fig. 4).  For the observed rate of

354    diffusion in open matrix, range expansion was faster in heterogeneous landscapes over all

355    realistic survival values.

356

357    **Discussion**

358    In an era of unprecedented pressures on land, both the empirical pattern of faster

359    movement in lower quality habitat and the checkerspot case study suggest the positive message

360    that range expansion can occur through landscapes with a low proportion of high-quality habitat.

361    For example, in the past, urban/suburban areas have often been written off as impermeable to

362    wildlife.  Nonetheless, European cities have, on average, 19% green space (range 2-46%) (Fuller

363    & Gaston 2009), and major US cities range from 19-69% green space (Richardson et al. 2012).

364    At the present time, this greenspace is probably mostly wildlife-unfriendly, e.g., traditional lawns

365    and non-native ornamentals.  Replacing some of this green space with native plants has high

366    conservation potential for insects and other human-friendly wildlife species, especially if the

367    goal is to make landscapes permeable for range shifts.  More generally, in urban/suburban and

368    agricultural areas, providing strategic "stepping stones" of very high-quality habitat (at 1-5%

369    land cover) could be a much more feasible way to make landscapes permeable to wildlife than

370    attempting to create continuous areas of high-quality habitat.

371    Although 1-5% high-quality habitat sounds achievable in many contexts, this calculation

372    assumes that high-quality habitat is well-understood and restored and/or maintained to remain

373    high quality (which is not always the case in protected areas, cf. Jones et al. 2018).  In addition,

374    narrow specialist species such as Baltimore checkerspots perceive only a fraction of their biotope

375    (wet meadows with host and nectar plants, within prairie) as highly suitable.  Overall, only about

376    5-10% of historic habitat remains for many of the most threatened habitat types such as upland

377    prairies and wetlands (Hoekstra et al. 2010), and habitat loss is widely cited as a leading cause of

378    species endangerment and extinction (e.g., Mazor et al. 2018). Therefore, in many cases, habitat

379    restoration may be needed to achieve the >1% high-quality habitat needed for range expansion

380    by species like the Baltimore checkerspot.  Furthermore, effects of partial habitat restoration

381    could be unpredictable. For example, many agri-environment restoration schemes include only

382    some of the resources required for species persistence, e.g., food resources but not breeding

383    habitat for pollinators and birds (Kleijn et al. 2011).  There is a risk that these, like Baltimore

384    checkerspot sink habitat, would trigger slower movement without sufficiently boosting

385    population growth, leading to a reduced net impact on range expansion. Finally, we remind

386    readers that optimal landscapes for range expansion are not the same as optimal landscapes for

387    persistence (Hodgson et al. 2011).  Population growth rates generally increase with the amount

388    of high-quality habitat (see Musgrave and Lutscher 2014 for mathematical analysis of this

389    relationship).  Therefore, there is also a tradeoff between managing landscapes for population

390    size if the environment is stationary vs. managing landscapes for connectivity and range

391    expansion.

392         For a given amount of high-quality habitat, the Baltimore checkerspot case study also

393    illustrates that rates of range expansion can vary widely with different matrix land cover types.

394    This conclusion contrasts with past studies of species range shifts that typically focus on the

395    spatial distribution of suitable habitat (Hill et al. 2001), but rarely on the nature of the matrix

396    land cover types or vital rates (e.g., survival and movement) in the matrix. Our results emphasize

397    the importance of understanding how movement differs among land cover types.  For example,

398    "resistance" estimated by the number of animals moving through a particular habitat type

399    (Ricketts 2001) reflects both the tendency for animals to enter a land cover type at edges and

400    their rate of movement through that land cover type (Kuefler et al. 2010).  These two attributes

401    have different effects on range expansion (see eq (1), Musgrave and Lutscher 2014, Lutscher and

402    Musgrave 2017, and contrast "forest" and "sink" habitat types in this study, which have very

403    similar movement rates, but differ in demography and edge behavior, in Fig 3).

404 Together, the potential benefits and costs of landscape heterogeneity point to the need to

405 assess the habitat-quality / movement tradeoff using demographic and movement data for target

406 species, in relation to existing land cover and/or proposed restoration schemes.  The Baltimore

407 checkerspot may be an unusual species, in that it has a very high population growth potential (8-

408 fold increase per year) and highly habitat-dependent movement (15-fold difference between open

409 matrix and high-quality habitat).  It would be useful to compare this case study to others, but, at

410 the present time, there are few other species for which habitat-specific movement and vital rates

411 have been measured throughout the life cycle.  Ecologists often assume that spatial population

412 models are prohibitively data intensive (see, e.g., Saura et al. 2014).  However, all of the relevant

413 parameters have been measured individually for a variety of taxa and land cover types:

414 movement (1000's of taxa; Kays et al. 2015), survival and reproduction (1000's of taxa;

415 Salguero-Gomez et al. 2014, 2016), and, to a lesser extent, preferences at edges (e.g., Kuefler et

416 al. 2010).  Given appropriate data, IDE models solved over stylized landscapes are a useful way

417 to integrate these different features of the life cycle and landscape, and calculate their net effects.

418 Although this kind of approach is currently rare in spatial ecology, it is similar to use of matrix

419 projection models (Caswell 2001) in nonspatial population ecology.  In particular, the similarity

420 is use of a simple model as a first step for calculating net effects of environmental conditions

421 throughout the life cycle (Crone et al. 2011).  The existence of such a framework may act as a

422 motivation for more empirical studies, as evidenced by thousands of empirically-based matrix

423 population models (e.g., Salguero-Gomez et al. 2014, 2016).

424 In recent years, increasing attention has been paid to managing landscapes for range

425 shifts, in the context of climate change.  In spite of this broad literature, few quantitative models

426 explore the rate of range expansion in the context of current landscapes, and those that do tend to

427 assume movement is most likely through the highest quality habitat (Thomas et al. 2001, Wilson

428 et al. 2009; but see Hui et al. 2012). We have shown how working from simple mechanisms of

429 spatial population dynamics fundamentally shifts current thinking about creating landscapes that

430 are permeable to wildlife. Specifically, the quality and quantity of inter-habitat matrix is a

431 fundamental determinant of landscape permeability. Of course, there are also cases where

432 increased landscape permeability is not desirable. We may want to restrict the ability of pest

433 species to invade or expand their ranges (Lutscher and Musgrave 2017). Similarly, permeability

434 may be undesirable if movement synchronizes local population fluctuations, possibly leading to

435 increased extinction risk (cf. Himes-Boor et al. 2018, but see Haddad et al. 2014). Our approach

436 could be a starting point to assess the consequences of landscape structure for species of

437 management concern, regardless of whether the goal is to enhance or restrict the potential for

438 range expansion. We hope that this study will provide motivation for measuring habitat-quality /

439 movement tradeoffs across a range of taxa, and that our example will encourage use of a

440 theoretical framework for integrating their effects.

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606 **Table 1.** Movement parameter values estimated for high-quality habitat and the three land cover

607 types classified as matrix.

| Land cover type | Population Growth rate[1] | Diffusion ($m^2/sec$) | Edge preference[2] | Mortality (flight-*sec*) |
|---|---|---|---|---|
| High quality habitat | 7.96 | 0.055 | NA | $1.18 \times 10^{-5}$ |
| Matrix types | | | | |
| Sink (low-quality habitat) | 0.80 | 0.169 | 0.50 | $1.18 \times 10^{-5}$ |
| Open | 0.00 | 0.831 | 0.50 | $1.18 \times 10^{-5}$ |
| Forest | 0.00 | 0.134 | 0.85 | $1.18 \times 10^{-5}$ |

608 [1]Adult female butterflies in the next generation per adult female in this generation, if the landscape consisted only of

609 this habitat type.

610 [2]Proportion entering high-quality habitat when released at matrix-habitat patch edges; $z$ = two times this proportion

611 minus 1

612

**Figures**

**Figure 1.** Empirical patterns of movement in higher- (HQ) vs. lower- (LQ) quality land cover types, compiled from 78 cases in which researchers measured diffusion or related metrics in relation to an independent measure of habitat quality (e.g., food resource availability, habitat structure). All = all taxonomic groups combined, compared to studies divided into taxonomic groups with similar sample size in our database: Leps = Lepidoptera (butterflies and moths), Vert = Chordata (vertebrates), Arth = other arthropods (insects and related taxa such as spiders and crustaceans, excluding Lepidoptera), and Other = all taxa that did not fit one of the first groups.

**Figure 2**. Stylized periodic landscape used to calculate rates of range expansion in a heterogeneous landscape. The landscape consists of parallel stripes of high-quality habitat and inter-habitat matrix, and is defined by the respective lengths of habitat ($l_1$) and matrix ($l_2$). Landscape period is the sum of the two distances; 2.5 periods are shown in this figure.

**Figure 3.** Range expansion in homogeneous versus heterogeneous landscapes. Predicted rates of range expansion are solved for landscapes with a 1-km period. "None" for the matrix type refers to landscapes composed of 100% high-quality habitat, and other matrix types are as defined by parameters shown in Table 1. (A) patterns across landscapes with 0-50% high-quality habitat. (B) expanded view of very degraded environments (0-5% high-quality habitat, the area defined by the blue box in panel (A)).

**Figure 4.** Effects of lower matrix survival on range expansion, solved for a 1-km period landscape, with 15% high-quality habitat. These results are for cases with no preference at patch

636    edges (i.e., equal probabilities of entering high- and low-quality habitat), and diffusion, D, =

637    0.055 m$^2$/sec and daily survival, s, = 0.83 (equal to mortality of $1.18 \times 10^{-5}$/sec of active time;

638    Table 1) in high quality habitat (similar to the open matrix/high-quality habitat landscape that

639    maximizes the rate of range expansion). The solid line identifies the rate of range expansion in

640    landscapes composed of 100% high quality habitat. Symbols identify empirically-estimated

641    parameters for Baltimore checkerspots in open matrix (●) and high-quality habitat (+).
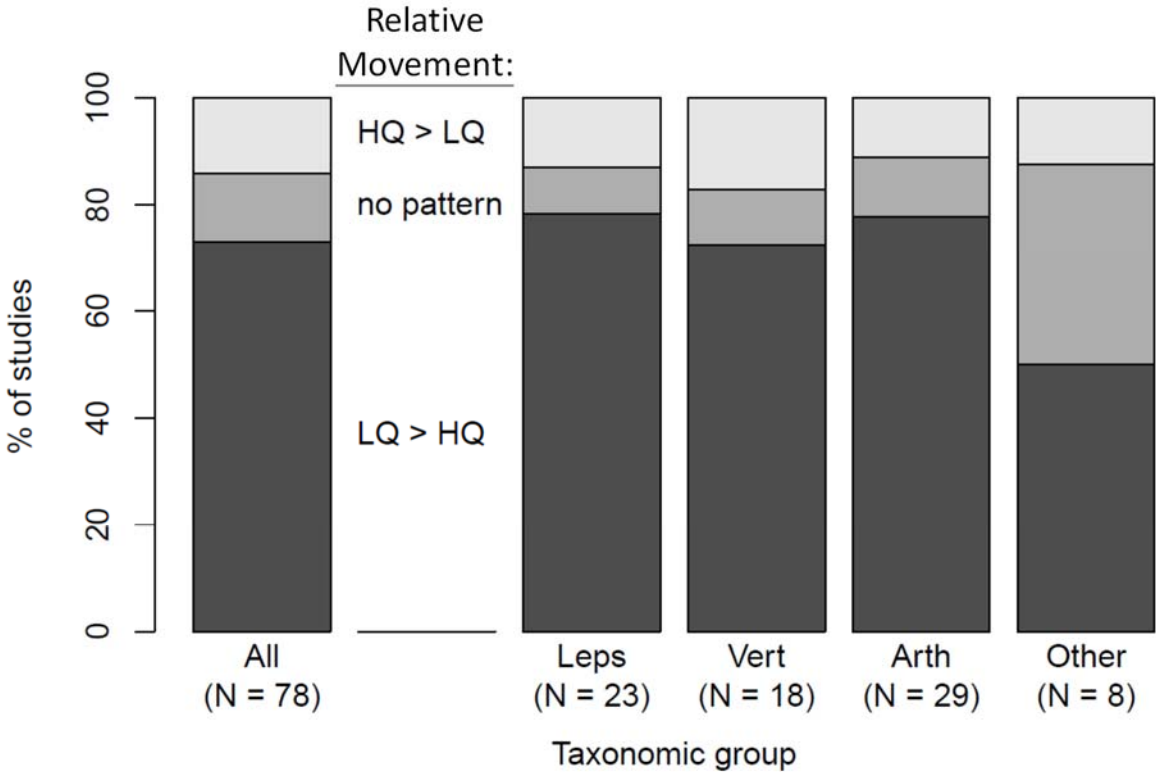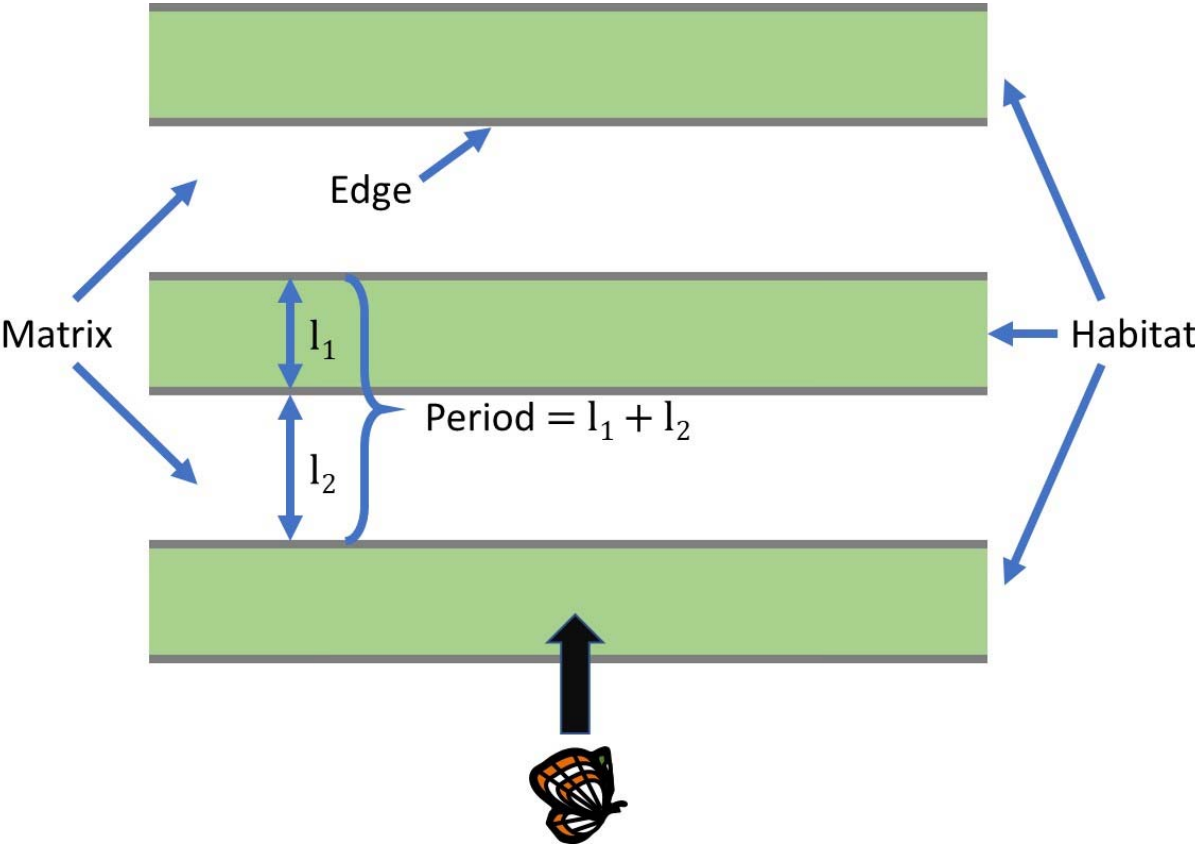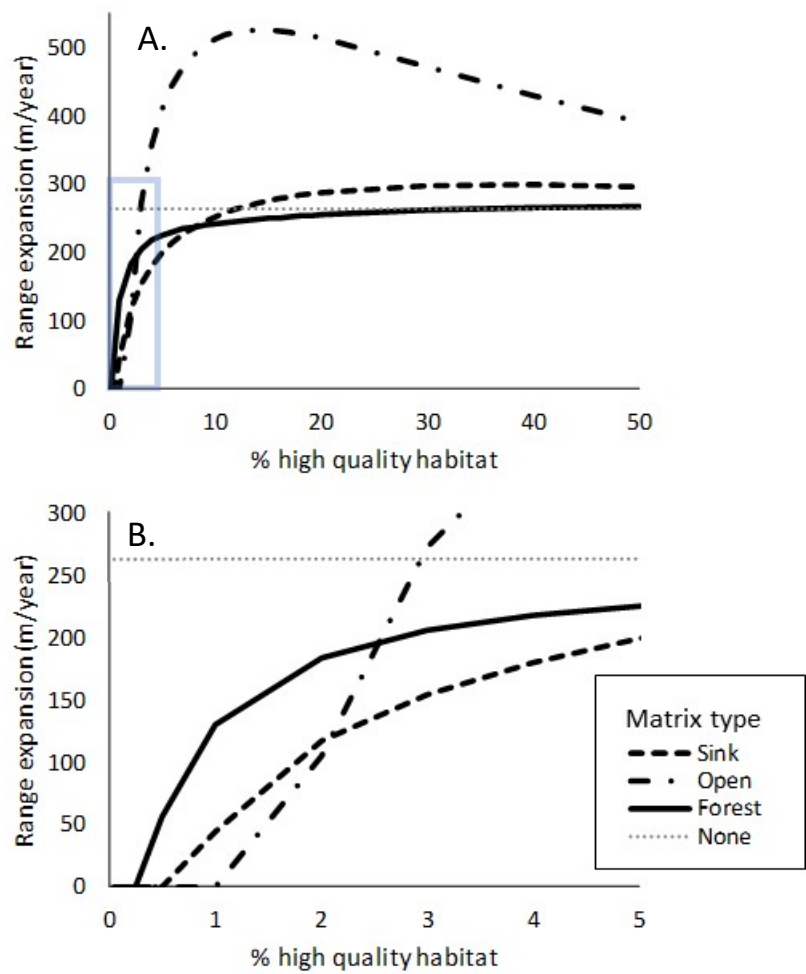
642

643    Figure 1.

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648    Figure 2.

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Figure showing horizontal green habitat bands separated by white matrix gaps, with labels "Edge", "Matrix", "Habitat", measurements $l_1$ and $l_2$, and $\text{Period} = l_1 + l_2$, with a butterfly below.

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Figure 3.

Figure 4.



Rate of Range Expansion (m/year)