

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.

37

38

39 **Introduction**

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

56 In this paper, we evaluate how landscape composition affects range expansion, using
57 recent extensions of longstanding theories of invasion dynamics to heterogeneous landscapes
58 (Musgrave & Lutscher 2014, Lutscher & Musgrave 2017). Our work is motivated by theoretical
59 results and empirical patterns that point to an underappreciated role of matrix land cover types
60 for range expansion. In homogeneous landscapes, simple reaction-diffusion models predict that
61 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 m²/sec in host plant habitat patches, and 8.6

85 m²/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 m²/5-sec interval in upland fields (matrix), compared to 105 m²/5-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 movement 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

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

188 There was no apparent effect of taxonomy on the proportion of studies with faster
189 movement in low-quality habitat (Appendix S3: Table S1). GLMMs with random effects of
190 Phylum, Class, Order and/or Family never improved model AICs relative to a simple GLM with
191 no taxonomic structure. Because of their limited replication within units, Genus and Species
192 were not included as taxonomic levels in GLMMs. Preliminary evaluation of these models
193 indicated overparameterization. Furthermore, estimates of variance among Phyla and Classes
194 were 0. In the GLMM with all four taxonomic levels included, the variance estimates for
195 Phylum, Class, and Family were 0, and the model was identical to the Order-only model. Of the
196 68 cases with a clear directional response, 83.8% showed faster net movement (diffusion or
197 related metrics) in lower-quality environments (binomial family, logit link GLM; 95% CI: 73.9-
198 91.3%, test for difference from 50%: $Z = 5.00$, $P < 0.001$). Analysis of all studies (including
199 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

203 **Predicting range expansion in heterogeneous landscapes**

204 *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 (Dewhurst & 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):

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

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 $q_i = \mu_i \sqrt{(1 - e^{-s c \hat{r}_i})}$.

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). [μ_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 occurs 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.

441

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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	1.18×10^{-5}
Matrix types				
Sink (low-quality habitat)	0.80	0.169	0.50	1.18×10^{-5}
Open	0.00	0.831	0.50	1.18×10^{-5}
Forest	0.00	0.134	0.85	1.18×10^{-5}

608 ¹Adult female butterflies in the next generation per adult female in this generation, if the landscape consisted only of
 609 this habitat type.

610 ²Proportion entering high-quality habitat when released at matrix-habitat patch edges; $z =$ two times this proportion
 611 minus 1

612

613 **Figures**

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

621

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

626

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

633

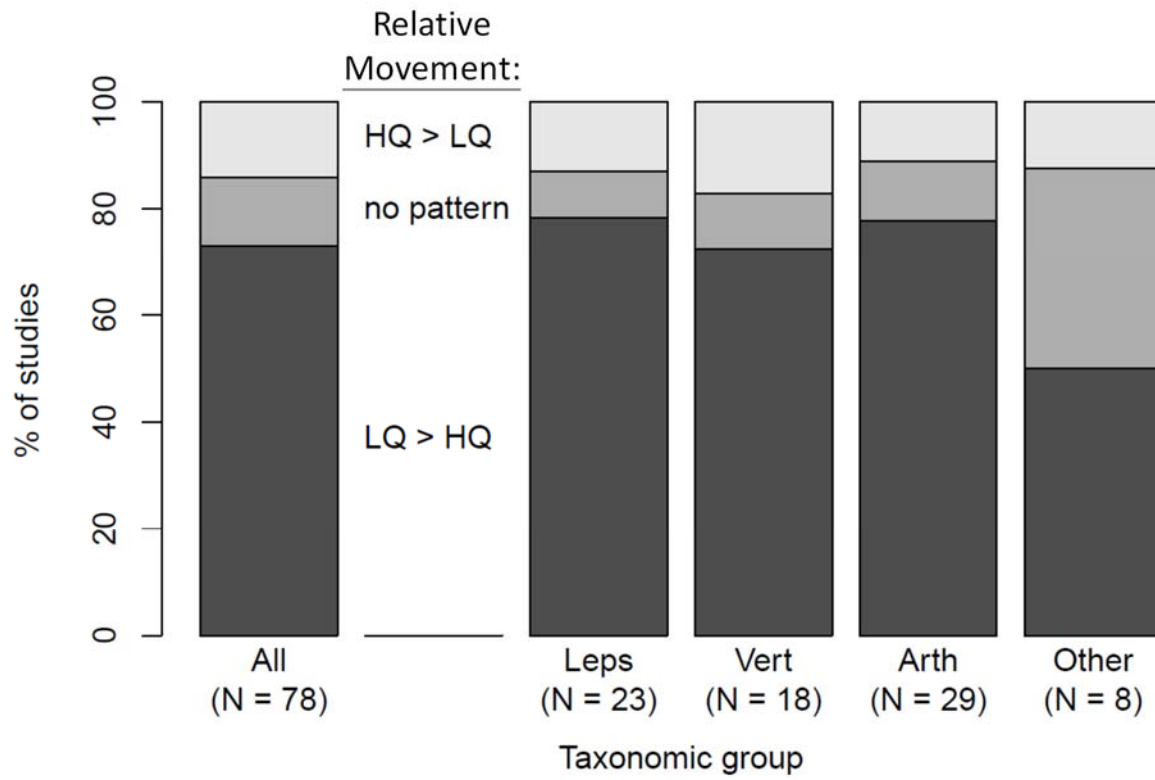
634 **Figure 4.** Effects of lower matrix survival on range expansion, solved for a 1-km period
635 landscape, with 15% high-quality habitat. These results are for cases with no preference at patch

636 edges (i.e., equal probabilities of entering high- and low-quality habitat), and diffusion, D , =
637 $0.055 \text{ m}^2/\text{sec}$ and daily survival, s , = 0.83 (equal to mortality of $1.18 \times 10^{-5}/\text{sec}$ 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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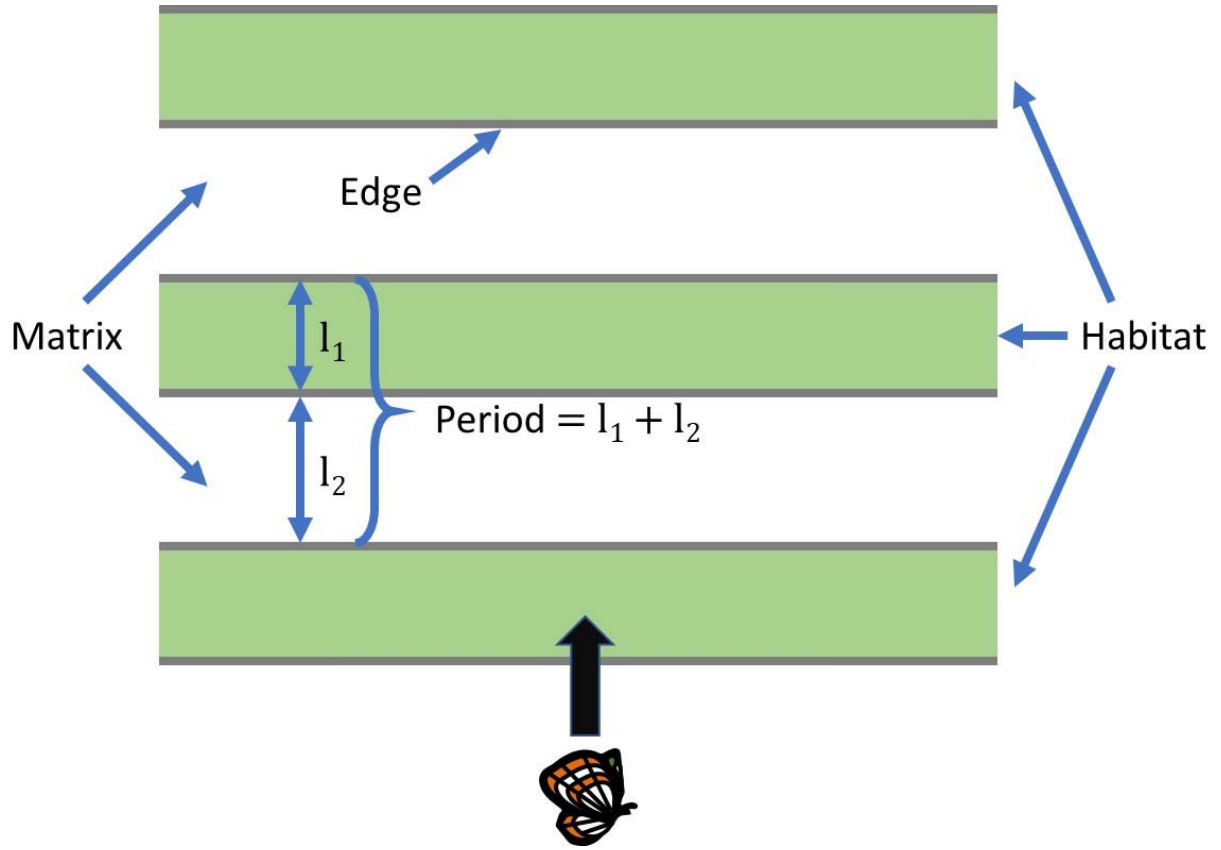
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648 Figure 2.

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Figure 3.

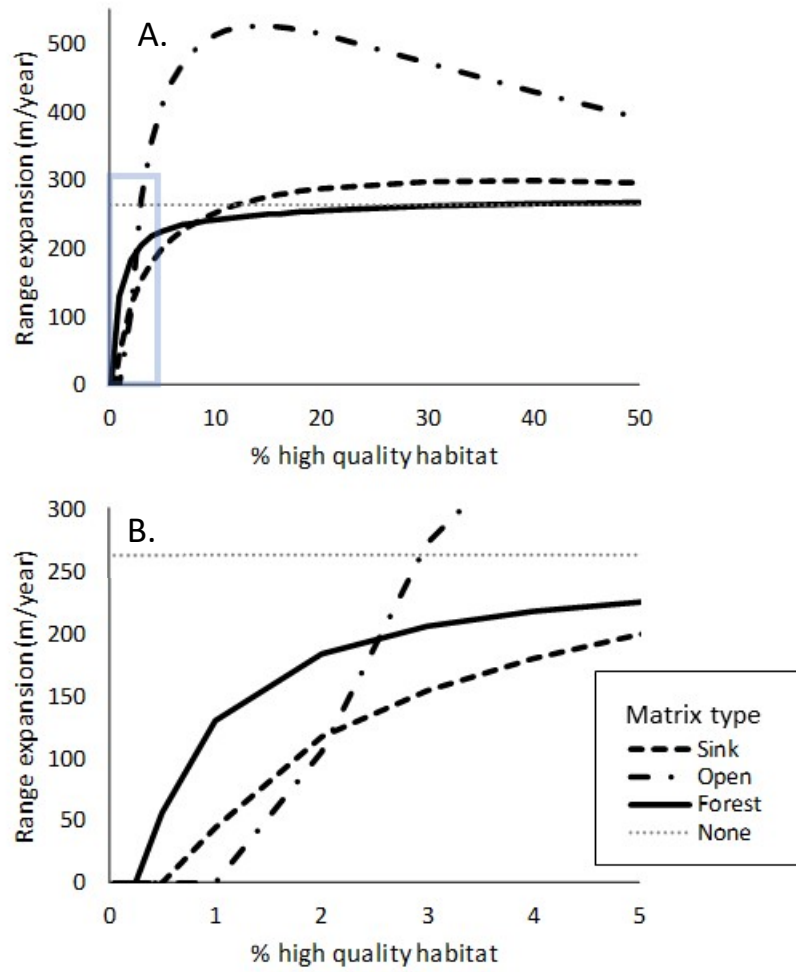


Figure 4.

