

Faster movement in habitat matrix
promotes range shifts in heterogeneous landscapes

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Abstract: Ecologists often assume that range expansion will be fastest in landscapes composed entirely of the highest quality habitat. Theoretical models, however, show that range expansion depends on both habitat quality and habitat-specific movement rates. Using data from 78 species in 70 studies, we find that animals typically have faster movement through lower-quality environments (73% of published cases). Therefore, if we want to manage landscapes for range expansion, there is a tradeoff between promoting movement with non-hostile matrix, and promoting population growth with high-quality habitat. We illustrate how this tradeoff plays out using an exemplar species, the Baltimore checkerspot butterfly. For this species, we calculate that the expected rate of range expansion is fastest in landscapes with ~15% high-quality habitat. Behavioral responses to non-habitat matrix have often been documented in animal populations, but rarely included in empirical predictions of range expansion. Considering movement behavior could change land planning priorities from focus on high-quality habitat only to integrating high- and low-quality land cover types, and evaluating the costs and benefits of different matrix land covers for range expansion.

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 a species will invade a landscape at rate $c^* = \sqrt{rD}$ (Skellam 1951), i.e., range expansion

increases with both the population growth rate, r , and movement (diffusion rate), D . The intuitively appealing principle that both higher growth rates and faster movement increase range expansion applies under a variety of more complicated models and assumptions (e.g., Shigesada et al. 1986, Maciel & Lutscher 2013), possibly also moderated by a species' preference for different habitat types at patch edges (Musgrave & Lutscher 2014). Common starting assumptions for predicting range expansion in heterogeneous landscapes are that movement occurs primarily through high-quality habitat, and that the habitat type that confers the highest growth rate (e.g., high-quality habitat from a demographic perspective) is also best for movement (e.g., Johnson 1992, Hill et al. 2001, Opdam 2004). If this were the case, then range expansion would be fastest through homogeneous landscapes composed of 100% high-quality habitat.

However, two empirical patterns suggest that the relationship between movement and habitat quality, and, therefore, the relationship between landscape composition and range expansion, is more complicated. First, although many animals show preference for higher quality habitat at patch interfaces, this preference is rarely perfect. In many animal populations, a substantial minority of individuals leave high-quality habitat at patch edges, e.g., 10% of bush crickets released at edges between grassland habitat and forest matrix entered the forest (compared to a null expectation of 50%; Kindvall 1999) and 20% of scarce large blue butterflies released at edges between meadow habitat and forest matrix left into the forest (Skorka et al. 2013). Therefore, the nature of the matrix, and of movement through the matrix, may contribute significantly to rates of range expansion (cf. Ricketts 2001).

Second, at least some animal species move more quickly through lower quality land cover types. For example, Schultz (1998) quantified Fender's blue butterfly movement using diffusion coefficients; Fender's blues moved $0.6 \text{ m}^2/\text{sec}$ in host plant habitat patches, and 8.6

m²/sec in prairie matrix with no host plants. Similarly, Kuefler et al. (2010) measured squared displacement of a wetland butterfly, the Appalachian brown, across multiple habitat types; these butterflies moved 467 m²/5-sec interval in upland fields (matrix), compared to 105 m²/5-sec interval in wetlands (habitat). More generally, area-restricted search, in which animals move more slowly in areas where they encounter more resources, is a common movement syndrome in foraging predators (Kareiva and Odell 1988). All else being equal, slower movement causes animals to spend more time in a particular land cover type (Turchin 1991, Schultz et al. 2017), which suggests a general fitness advantage of slower movement in higher-quality habitat.

If some proportion of animals leave high-quality habitat and move more quickly through the matrix than through high-quality habitat, this creates a tradeoff for land managers between increasing population growth by increasing the proportion of high-quality habitat and increasing movement by increasing the proportion of non-hostile matrix on the landscape. Two past modeling studies have shown that the presence of matrix on the landscape can sometimes enhance range expansion: Lutscher and Musgrave (2017) calculated range expansion using an integrodifference equation model; they found that, for a range of realistic parameter values for emerald ash borer, ash-free “barrier zones” could increase rates of ash borer invasion. Bocedi et al. (2014) explored general simulation models (not tuned to any particular organism) that assumed animals had a dispersal phase in which they searched for habitat patches until they either found suitable habitat for settling or died. They found that landscapes with relatively small proportions of high-quality habitat could lead to the most rapid rates of range expansion, as long as mortality in the matrix was not too high. However, it is not clear from these two modeling studies whether there is generally an empirical tradeoff between faster movement and higher demographic quality among land cover types, and whether this tradeoff translates into

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

Here, we evaluate this tradeoff empirically in two ways: First, we test whether animals generally tend to move more quickly or more slowly through lower-quality or matrix land cover types than through high-quality habitat, by compiling data from past studies that independently estimated habitat quality and movement. A negative relationship between movement and habitat quality is necessary (although not sufficient) for a habitat-quality / movement tradeoff to exist in relation to range expansion. Second, we calculate the expected rate of range expansion, i.e., the net effect of the habitat-quality / movement tradeoff, for a focal species, the Baltimore checkerspot butterfly (*Euphydryas phaeton*), across a range of landscape scenarios. (Notably, recent theoretical advances (Musgrave and Lutscher 2014) allow us to calculate expected rates of range expansion in heterogeneous environments, rather than building simulation models.) This case study allows us to evaluate conditions under which an increase in the percentage of low-quality habitat leads to an increased rate of range expansion, despite reduced population growth, because of faster movement in the matrix habitat, using parameters measured, using parameters measured across four land cover types in natural populations (Brown and Crone 2016, Brown et al. 2017a&b). Together, the two parts of this paper (1) show that a habitat-quality / movement tradeoff is common in natural populations, (2) illustrate a straightforward method for calculating the balance of this tradeoff from field data, and (3) demonstrate that, for real populations, landscape heterogeneity is likely to promote range expansion.

Empirical patterns of movement

Methods:

We compiled an initial list of 267 movement studies conducted in heterogeneous environments by searching for papers that cited classic studies of movement in heterogeneous environments and papers cited within. In addition, we searched Web of Science for all papers that used the terms “Area Restricted Search”, “Residence Index”, and papers within ecology and biology journals that used the term “diffusion.” We screened these papers for studies that included estimates of movement measured as net distance moved per time (or a response variable that related monotonically to the rate of net displacement) in at least two habitat types, as well as independent estimates of habitat quality for these habitat types, as indicated by demographic rates such birth or death rates, food density, and/or population growth rates. We excluded studies in which habitat quality was assumed but not measured (e.g., assuming suburban versus natural areas represent “low” and “high” quality, respectively), in which habitat quality was inferred from movement behavior (e.g., foraging behavior of pelagic birds as an indicator of prey density), or if the measured movement metric confounded net displacement with other aspects of behavior such as preference at patch boundaries (e.g., studies of residence time in patches could reflect slower movement *or* higher preference at patch boundaries). Based on these criteria, we retained 70 of the original 267 studies (listed in Table S1). We divided cases into categories for which (1) movement was faster in higher-quality habitat, (2) no preference or unclear pattern, and (3) movement was faster in lower-quality habitat. We compiled taxonomic data (Phylum, Class, Order, Family, Genus, Species) for these 78 species (<https://www.itis.gov/>; accessed November 2017).

We evaluated the potential effects of phylogeny on the relationship between habitat quality and movement using binomial family, logit link, generalized linear mixed models (GLMMs) with various metrics of taxonomy (combinations of Phylum, Order, Class and/or

Family) as random effects. Because binomial models require yes/no responses, these analyses included only the studies that could be classified as faster movement in higher vs. lower quality habitat; ten species with unclear patterns were not included in GLMMs. We used intercept-only models (with taxonomic random effects) to compare the proportion of studies with faster versus slower movement in lower quality environments, and tested whether the proportion of “faster” studies differed significantly from 0.5, i.e., whether the value of the intercept on a logit scale differed significantly from 0. Models were implemented using the lme4 package (Bates et al. 2015) in R (R Core Team 2016). We evaluated taxonomic effects by comparing model AICs. We did not pursue further phylogenetic analyses because of the complete lack of taxonomic effects (see *Results* below), and the large breadth of phylogenetic distance included in our set of studies, e.g., the single representative of Division Myxomycota (Kingdom Fungi) would have especially high leverage.

We found no evidence for taxonomic patterns (see *Results*). Therefore, we estimated the proportion of studies in each category (faster in higher-quality, no pattern, faster in lower-quality) using ordinal multinomial logistical regression (‘polr’ function in the MASS package (Venables & Ripley 2002) in R). Confidence limits were obtained by parametric bootstrapping, i.e., 95% quantiles of 1000 simulated data sets obtained by applying the ‘sim’ function to the original model, re-analyzed with the ‘polr’ function.

Results

We found 70 studies comparing movement in high- and low-quality habitat types for 78 species from seven Phyla and one Division. Studies were heavily biased toward arthropods and vertebrates, especially in the Lepidoptera (butterflies and moths) and Coleoptera (beetles) insect

orders, and in the Aves (birds) and Mammalia (mammals) vertebrate classes (Supplementary Table 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). 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 (Supplementary Table S3). 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

had faster movement in low- than high-quality environments, and only 14% (95% CI = 7.7-28.1%) had faster movement in high-quality environments (Fig. 1).

Predicting range expansion in heterogeneous landscapes

General approach:

Our literature review demonstrates that animals tend to move faster through lower-quality land cover types. However, heterogeneous landscapes facilitate movement only when the benefits of faster movement outweigh the demographic costs of lower-quality habitat, and when animals enter the matrix frequently enough to experience these benefits. To explore how this tradeoff plays out, we calculate the balance of habitat-quality / movement tradeoffs, using field data from an exemplar species, the Baltimore checkerspot, across four land cover types.

Specifically, we used a spatially heterogeneous integrodifference equation (IDE) model to calculate the expected rate of range expansion in landscapes consisting of high-quality habitat in combination with one of three matrix types. In addition to including key aspects of spatial heterogeneity, IDEs separate the time scales of different demographic processes, unlike traditional differential or difference equation models (Powell and Zimmerman 2004).

Specifically, we used the model presented by Musgrave and Lutscher (2014), adjusted for butterfly life history (see Supplemental Material S4: Dispersion relation), and solved over a 1-dimensional, periodic landscape (Fig. 2) to calculate range expansion of the Baltimore checkerspot butterfly under a range of landscape scenarios. This IDE model captures key aspects of butterfly biology, including preference at patch interfaces.

We chose a periodic landscape as a general approach for modeling heterogeneous environments for several reasons. First, this simplified landscape leads to a tractable model; the

solution is an analytical calculation, not a numerical simulation. Second, the rate of range expansion starting from a point in a 1-dimensional landscape is the same as the rate of expansion starting from a line in a 2-dimensional landscape composed of parallel stripes of habitat (Shigesada et al. 1986) (Fig. 2). A line is a reasonable first approximation of an altitudinal or poleward range limit, so the approximation is particularly appropriate in the context of species' range expansions with climate change. Third, periodic landscapes are characterized by only two, ecologically meaningful, parameters: the length of the period and the proportion of high-quality habitat (or, equivalently, the widths of parallel stripes of habitat of types 1 and 2). Exploration of alternative landscape configurations may be a fruitful area of research, but, to date, these have not led to general mathematical solutions (Kinezaki et al. 2010). Hence, rates of range expansion would need to be solved numerically over specific landscape configurations. Given their analytical tractability, periodic landscapes are a useful starting configuration for assessing rates of range expansion when the specific landscape context is unknown, or might be variable.

The calculation of spread rates in this model is based on habitat-specific, density-independent growth. Negative density dependence does not affect rates of range expansion under most conditions (van den Bosch et al. 1990, Sullivan et al. 2017). Positive density dependence (Allee effects) generally leads to more restrictive conditions for invasion (Dewhurst & Lutscher 2009, Musgrave et al. 2015). Density dependent movement can also affect rates of range expansion (Altwegg et al. 2013, Bocedi et al. 2014). Further study of both could be a productive area for future research, although density dependence, especially Allee effects, can also be very difficult to quantify in natural populations (Liermann & Hilborn 1997). Parameters for our case study (described in *Model parameterization & implementation*, below) were estimated during a

period of rapid and monotonic population growth (2013-2015, see Crone 2018), so are likely to represent conditions at the front of an invading population.

Study system

The Baltimore checkerspot is a univoltine meadow species that has in recent decades been decreasing in abundance in southern portions of its range (Frye et al. 2013) and increasing in more northern locations (Breed et al. 2013). In addition to simply having available data, the Baltimore checkerspot is interesting as a case study because different matrix land cover types show different features that might promote range expansion. Specifically, we (Brown et al. 2017b) divided the landscape into four land-cover types in which we measured demography and movement. These were high-quality habitat (open meadow areas with a high density of host plants and nectar resources) and three land cover types we here refer to as matrix: sink habitat that could not support a population in isolation (i.e., low-quality habitat with lower densities of host plants and nectar sources), open matrix (structurally similar meadows with very few resources, e.g., hayfields), and forests (structurally dissimilar areas without host plants and with few nectar sources) (Brown et al. 2017b). Relative to high-quality habitat, butterflies moved faster through all matrix types, but movement was fastest through open matrix (Table 1). Reproduction was possible (though not sufficient to balance mortality) in sink habitat but not in other matrix land cover types. Finally, butterflies showed preference for high-quality habitat and other open land cover types at forest boundaries, but no preference at habitat/sink or habitat/open interfaces.

Model parameterization & implementation

We use the “case S” for interface conditions from Musgrave & Lutscher (2014), in which rates of diffusion while moving differ between two patch types, but the proportion of time flying does not (based on empirical differences in parameter values for Baltimore checkerspot; Brown et al. 2017b). Therefore, range expansion is described by the following dispersion relation, which relates the asymptotic rate of range expansion, c , to an unknown shape parameter, s , as a function of species-specific vital rates (survival, reproduction, and movement, defined below):

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

In this equation l_1 is the width of stripes of land cover type 1, l_2 is the width of stripes of land 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 $q_i = \mu_i \sqrt{(1 - e^{-s c \hat{r}_i})}$.

To calculate rates of population expansion in heterogeneous environments, we minimized eq(1) as a function of s with respect to c (see, e.g., Shigesada et al. 1986, Musgrave and Lutscher 2014). We used field-estimated values of the parameters for habitat-specific diffusion (D_i), reproductive rate (\hat{r}_i), edge preference, (\bar{z}), and mortality, (m_i). [μ_i is the inverse of average dispersal distance, calculated from mortality and diffusion as described in (4) below.] Values of these parameters (see Table 1) were measured in field studies (Brown and Crone 2016, Brown et al. 2017a&b) as described briefly here:

(1) Habitat-specific diffusion coefficients, D_1 and D_2 , were measured by following individual flight paths, and using Kareiva and Shigesada’s equation for approximating correlated random walks with diffusion (Brown & Crone 2016, Brown et al. 2017b).

(2) Realized population growth rates, \hat{r}_1 and \hat{r}_2 , were measured by calculating the habitat-specific ratio of eggs per adult, multiplied by the probability that eggs survive to eclose as mature females. In this system, females mate soon after eclosion (E. Crone & L. Brown, *pers obs.*), and we see no evidence of mate limitation. For models presented here, we use the

conservative lower estimate of fecundity presented by Brown and Crone (2016), not their higher estimate corrected for finite patch size in our (large) study site.

(3) Preference at patch edges, \bar{z} , is calculated from the proportion of butterflies that choose habitat type 2 when exactly at patch boundaries; $(1+z)/2$ is the proportion choosing habitat type 2, and $\bar{z} = \frac{1-z}{1+z}$. We estimated this preference by releasing butterflies at habitat boundaries, and recording their location after fixed distances. Fixed-diameter edge circles are a common metric of preference at patch edges in butterfly field studies (Schultz 1998, Kuefler et al. 2010). However, they are an approximation of the exact edge preference as assumed by Musgrave and Lutscher (2014) and earlier mathematical models (Ovaskainen & Cornell 2013) because field observations over discrete intervals of time or space may be influenced by rates of movement in each habitat type, as well as preference when exactly at the edge. This bias appeared to be small in our system (E. Crone, *pers. obs.*), e.g., we did not observe animals crossing back and forth over the edge while waiting for them to leave the circles.

(4) Average lifetime dispersal distances, $\frac{1}{\mu_1}$ and $\frac{1}{\mu_2}$, were calculated from habitat-specific movement and loss rates, where loss occurs due to mortality and, possibly, settling of dispersing individuals. We assume that butterflies move and lay eggs at a constant (though possibly habitat-specific) rate throughout their life cycle (McIntire et al. 2007, Brown & Crone 2016), an assumption based largely on field observations, but also on the fact that the nutrients in butterfly eggs come from resources consumed as an adult, as well as resources consumed as a larva (O'Brien et al. 2004). Therefore, the rate of loss is due only to mortality 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

habitat-specific diffusion and mortality rates, respectively. To obtain appropriate units for this ratio, daily survival from capture-recapture data were converted to survival per seconds of time during daily activity (Brown & Crone 2016). Our estimate of loss during dispersal includes only loss due to mortality, in contrast to Musgrave and Lutscher (2014), who included loss due to settling of dispersing propagules as well as to mortality. However, the same dispersion relation holds when parameterized in terms of average dispersal distance (as derived in Supplemental Material S4: Dispersion Relation), emphasizing the generality of the original result.

Using these parameters, we calculated spread rates through heterogeneous landscapes consisting of high-quality habitat combined with each of the different matrix land cover types. We varied the proportion of high quality habitat from 0-50%, and solved the equation for landscape periods of 0.5, 1, 5, and 10 km. Our baseline projections assumed that adult survival was the same in all land cover types, based on Baltimore checkerspot field observations. For comparison, we explored this possibility by calculating rates of range expansion in scenarios where survival, as well as fecundity, was reduced in the matrix.

Model predictions

Patterns of range expansion were generally similar across different spatial scales of environmental heterogeneity (Suppl. Fig. S5). As expected from general analyses of this model (Musgrave and Lutscher 2014), the rate of invasion increased with increasing landscape period (Suppl. Fig. S5). However, this effect was modest and did not change the qualitative effects of landscape heterogeneity or matrix composition. Therefore, we focus comparison of matrix types on the model solved for a 1-km period landscape (Fig. 3).

Baltimore checkerspot range expansion was fastest in landscapes composed of only high-quality habitat and open matrix. As long as the landscape consisted of at least 3% high-quality habitat, range expansion was faster in a heterogeneous habitat-open matrix landscape than homogeneous high-quality habitat alone (Fig. 3). The optimal combination for range expansion was ~15% high-quality habitat; adding more high-quality habitat beyond this point gradually reduced the rate of range expansion (Fig. 3A). In very degraded landscapes with 1-3% high-quality habitat, the amount of high-quality habitat was the main factor limiting range expansion and the type of matrix made little difference (Fig. 3B). However, in the most degraded landscapes (< 1% high-quality habitat), rates of range expansion were dominated by edge behavior; range expansion was faster when the landscape included forest matrix than sink or open matrix because edge preference at forest edges prevented individuals from leaving habitat and spending too much time in the matrix. Low-quality sink habitat increased range expansion only in landscapes with >10% high-quality habitat, and was never the matrix type with the fastest rate of invasion. However, in the most degraded landscapes (< 1% high-quality habitat), populations were able to persist (rates of range expansion > 0) in more highly degraded landscapes if the matrix was sink habitat than if it was open matrix (thresholds of 0.5% and 1%, respectively).

Over a wide range of lower survival values in matrix, Baltimore checkerspot range expansion was faster in heterogeneous landscapes composed of 15% high-quality habitat and 85% open matrix landscapes than in 100% high-quality habitat (Fig. 4). For the observed rate of diffusion in open matrix, range expansion was faster in heterogeneous landscapes over all realistic survival values.

Discussion

In an era of unprecedented pressures on land, both the empirical pattern of faster movement in lower quality habitat and the checkerspot case study suggest the positive message that range expansion can occur through landscapes with a low proportion of high-quality habitat. For example, in the past, urban/suburban areas have often been written off as impermeable to wildlife. Nonetheless, European cities have, on average, 19% green space (range 2-46%) (Fuller & Gaston 2009), and major US cities range from 19-69% green space (Richardson et al. 2012). At the present time, this greenspace is probably mostly wildlife-unfriendly, e.g., traditional lawns and non-native ornamentals. Replacing some of this green space with native plants has high conservation potential for insects and other human-friendly wildlife species, especially if the goal is to make landscapes permeable for range shifts. More generally, in urban/suburban and agricultural areas, focusing on providing strategic “stepping stones” of very high-quality habitat (at 1-5% land cover) could be a much more feasible way to make landscapes permeable to wildlife than attempting to create continuous areas of high-quality habitat.

Although 1-5% high-quality habitat sounds achievable in many contexts, this calculation assumes that high-quality habitat is well-understood and restored and/or maintained to remain high quality (which is not always the case in protected areas, cf. Jones et al. 2018). In addition, narrow specialist species such as Baltimore checkerspots perceive only a fraction (wet meadows with host and nectar plants) of their biotope (prairie) as highly suitable. Overall, only about 5-10% of historic habitat remains for many of the most threatened habitat types such as upland prairies and wetlands (Hoekstra et al. 2010), and habitat loss is widely cited as a leading cause of species endangerment and extinction (e.g., Mazar et al. 2018). Therefore, in many cases, habitat restoration may be needed to achieve the >1% high-quality habitat needed for range expansion

by species like the Baltimore checkerspot. Furthermore, effects of partial habitat restoration could be unpredictable. For example, many agri-environment restoration schemes include only some of the resources required for species persistence, e.g., food resources but not breeding habitat for pollinators and birds (Kleijn et al. 2011). There is a risk that these, like Baltimore checkerspot sink habitat, would trigger slower movement without sufficiently boosting population growth, leading to a reduced net impact on range expansion.

For a given amount of high-quality habitat, the Baltimore checkerspot case study also illustrates that rates of range expansion can vary widely with different matrix land cover types. This conclusion contrasts with past studies of species range shifts that typically focus on the spatial distribution of suitable habitat (Hill et al. 2001), but rarely on the nature of the matrix land cover types or vital rates (e.g., survival and movement) in the matrix. Our results emphasize the importance of understanding how movement differs among land cover types. For example, “resistance” estimated by the number of animals moving through a particular habitat type (Ricketts 2001) reflects both the tendency for animals to enter a land cover type at edges and their rate of movement through that land cover type (Kuefler et al. 2010). These two attributes have different effects on range expansion (see eq (1), Musgrave and Lutscher 2014, Lutscher and Musgrave 2017, and contrast “forest” and “sink” habitat types in this study, which have very similar movement rates, but differ in demography and edge behavior, in Fig 3).

Together, the potential benefits and costs of landscape heterogeneity point to the need to assess the habitat-quality / movement tradeoff using demographic and movement data for target species, in relation to existing land cover and/or proposed restoration schemes. The Baltimore checkerspot may be an unusual species, in that it has a very high population growth potential (8-fold increase per year) and highly habitat-dependent movement (15-fold difference between open

matrix and high-quality habitat). It would be useful to compare this case study to others, but, at the present time, there are few other species for which habitat-specific movement and vital rates have been measured throughout the life cycle. Ecologists often assume that spatial population models are prohibitively data intensive (see, e.g., Saura et al. 2014). However, all of the relevant parameters have been measured individually for a variety of taxa and land cover types: movement (1000's of taxa; Kays et al. 2015), survival and reproduction (1000's of taxa; Salguero-Gomez et al. 2014, 2016), and, to a lesser extent, preferences at edges (e.g., Kuefler et al. 2010). Given appropriate data, IDE models solved over stylized landscapes are a useful way to integrate these different features of the life cycle and landscape, and calculate their net effects. Although this kind of approach is currently rare in spatial ecology, it is similar to use of matrix projection models (Caswell 2001) in nonspatial population ecology. In particular, the similarity is use of a simple model as a first step for calculating net effects of environmental conditions throughout the life cycle (Crone et al. 2011). The existence of such a framework may act as a motivation for more empirical studies, as evidenced by thousands of empirically-based matrix population models (e.g., Salguero-Gomez et al. 2014, 2016).

Despite the large literature on climate-driven range shifts, few quantitative models explore the rate of range expansion in the context of current landscapes, and those that do tend to assume movement is most likely through the highest quality habitat (Thomas et al. 2001, Wilson et al. 2009; but see Hui et al. 2012). We present a contrasting perspective. We have shown how working from simple mechanisms of spatial population dynamics fundamentally shifts current thinking about creating landscapes that are permeable to wildlife. Specifically, the quality and quantity of inter-habitat matrix is a fundamental determinant of range expansion. For some, possibly many, species, formerly under-appreciated mixed-use landscapes, including urban and

suburban areas, could be a vital component of climate change resilience. For most species, range expansion is likely to be facilitated by movement through non-hostile matrix land cover types in landscapes with a moderate amount of the highest quality habitat. We hope that these possibilities will provide motivation for measuring habitat-quality / movement tradeoffs across a range of taxa, and that our example will encourage use of a theoretical framework for integrating their effects.

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

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

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

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: Lep = 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

edges (i.e., equal probabilities of entering high- and low-quality habitat), and diffusion, D , = $0.055 \text{ m}^2/\text{sec}$ and daily survival, s , = 0.83 (equal to mortality of $1.18 \times 10^{-5}/\text{sec}$ of active time; Table 1) in high quality habitat (similar to the open matrix/high-quality habitat landscape that maximizes the rate of range expansion). The solid line identifies the rate of range expansion in landscapes composed of 100% high quality habitat. Symbols identify empirically-estimated parameters for Baltimore checkerspot in open matrix (●) and high-quality habitat (+).

Figure 1.

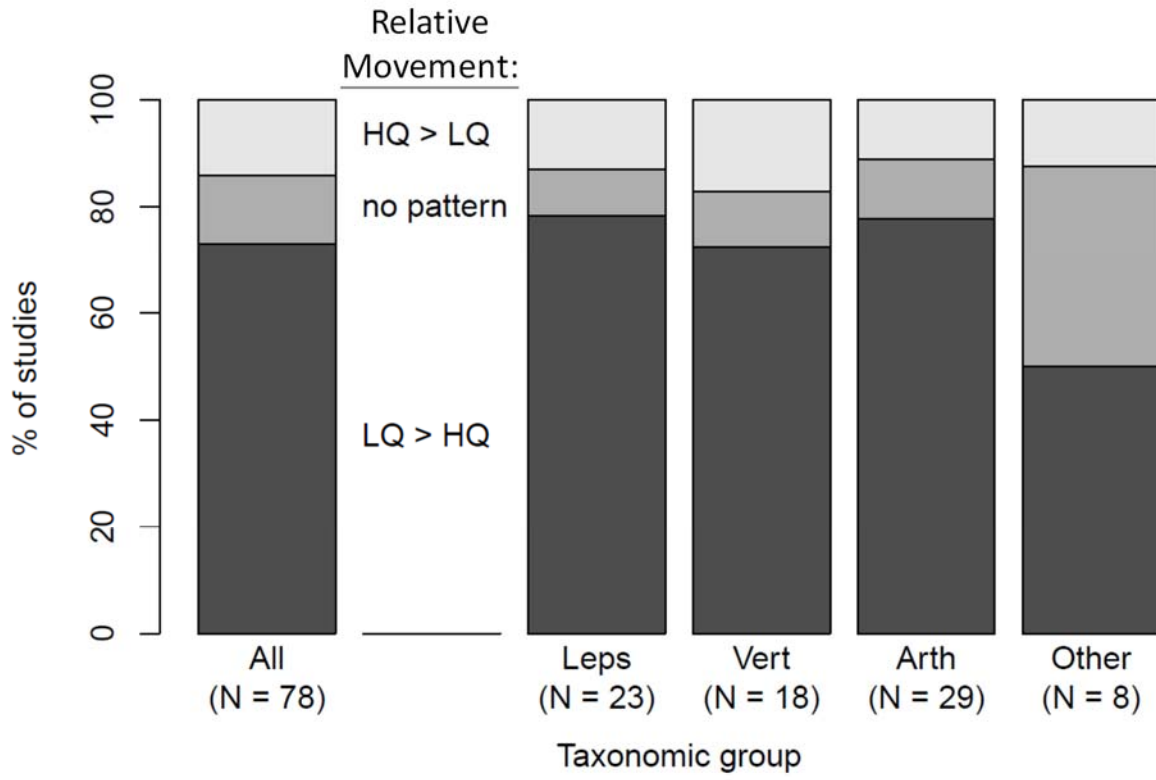


Figure 2.

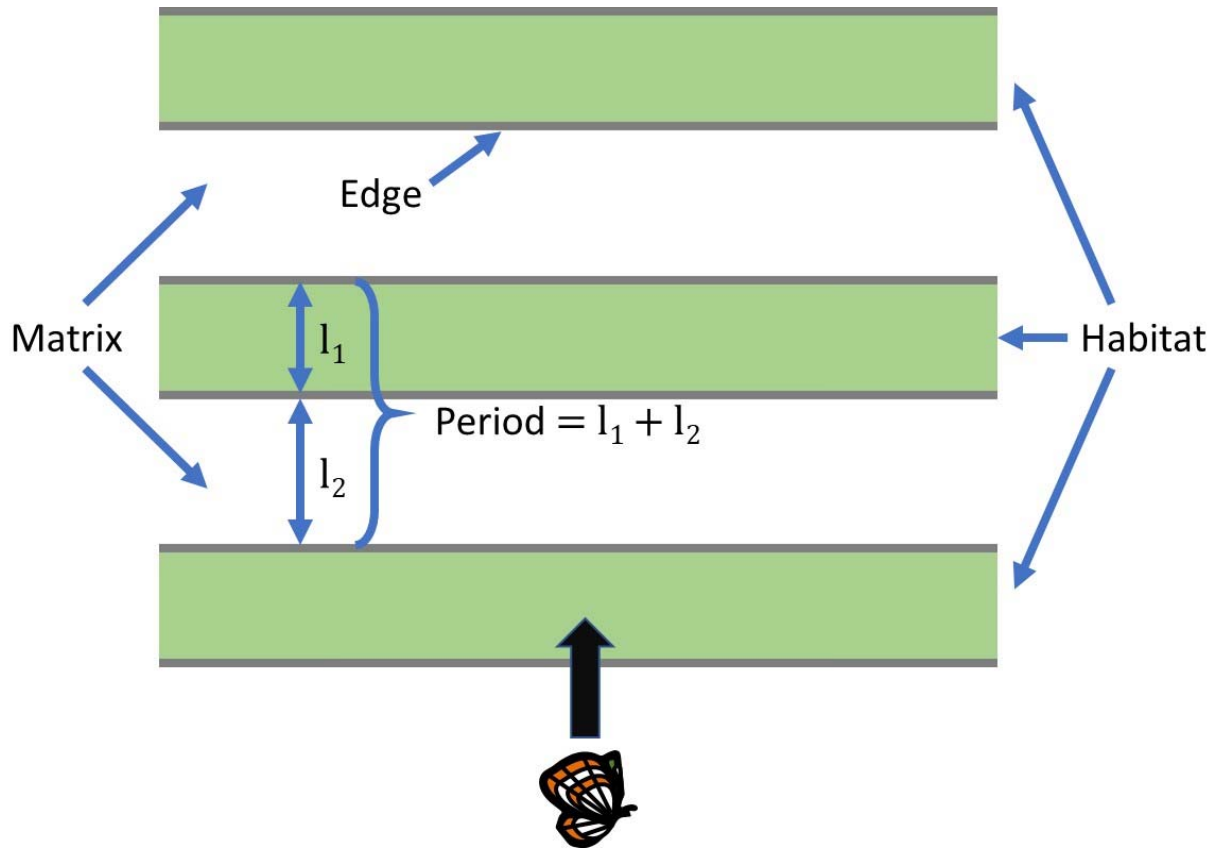


Figure 3.

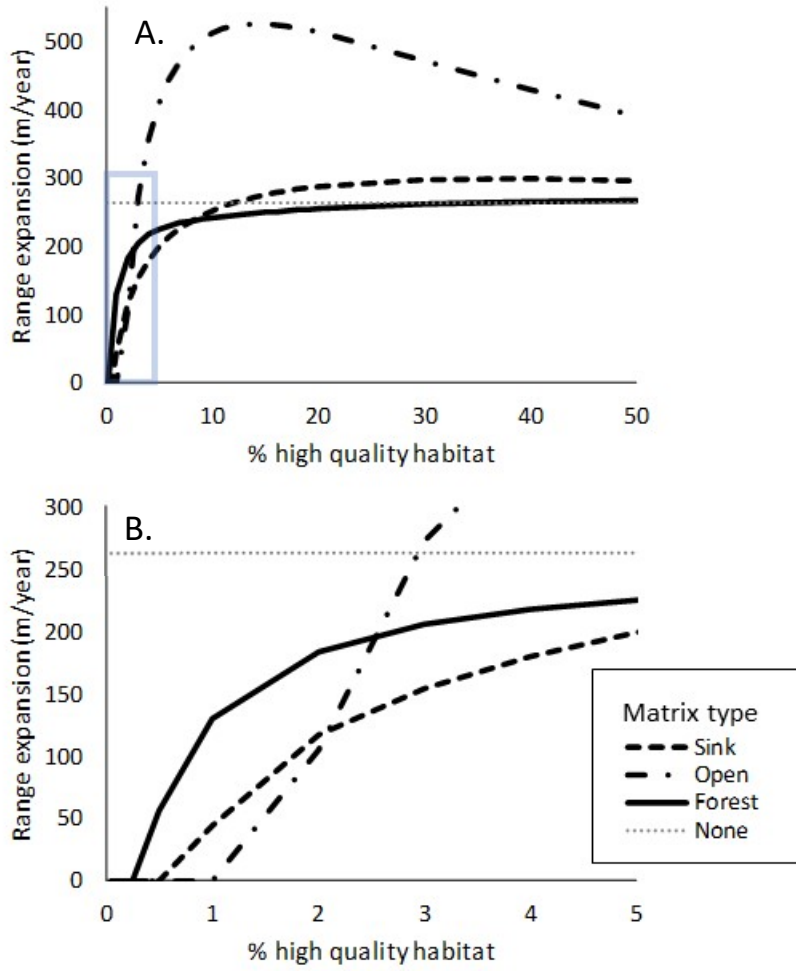


Figure 4.

