Bridging the scale gap: predicting large-scale population dynamics from small-scale variation in strongly heterogeneous landscapes

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Running Headline Bridging the scale gap

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Abstract

1. Often, ecologists are challenged with a mismatch of scales: how do we upscale from local variation and available data to landscape-level models and predictions?
2. We present a general recipe for coarse-graining from local to landscape-scale reaction-diffusion equations when spatial heterogeneity is small in extent compared to dispersal of organisms. Our homogenization approach uses the fundamental ecological concepts of Turchin's *residence index* and Skellam's *dynamic level*.
3. Our approach opens avenues to new ecological theory that connects different scales, which we illustrate using predator-prey interactions. It also presents opportunities for using the increasingly available small-scale data for landscape-level predictions, such as range expansion rates.
4. We find several unexpected nonlinear relationships between the movement behavior on the local level and the spatially implicit and explicit outcomes at the landscape-level, e.g., predator spread rate may increase *or* decrease when predators move faster locally. Our method provides a mechanistic link for population dynamics and data integration across spatial and temporal scales, addressing a fundamental goal of landscape ecology.

1 Introduction

Ecologists are often challenged by complex scale relationships: we want to understand and predict population dynamics on large spatial and temporal scales, but we can typically only measure and observe processes on small scales. Methods exist to obtain local population growth and movement models from observational data (e.g., Turchin (1998)). Theory exists to calculate, say, spread rates and persistence conditions from homogeneous

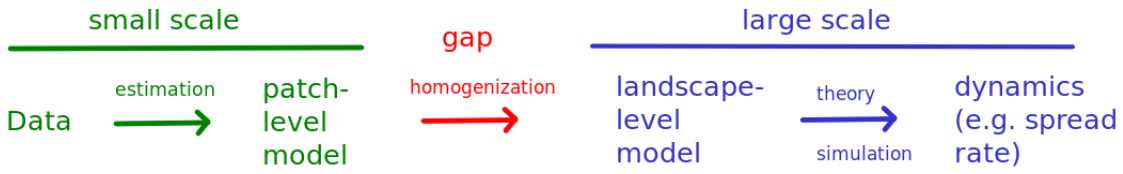


Figure 1: The gap between available small-scale observation (green, left) and desired large-scale prediction (blue, right). Data are available on the small scale and methods exist for estimating parameters for patch-level models (Turchin, 1998). Theory is in place and simulation is feasible to obtain desired outcomes from landscape-level models (Fagan *et al.*, 2002). We show here that homogenization theory helps bridge the gap; see also Garlick *et al.* (2011, 2014).

landscape-level models (e.g., Fagan *et al.* (2002)). How to obtain landscape-level models from habitat-level information is the gap that we bridge here (Figure 1). Our approach is based on homogenization, a mathematical theory of coarse-graining or weighted averaging, with weights that emerge from the theory. It applies when individuals, over their lifetimes, experience several different habitat types that affect their movement behaviors and vital rates. Our formulas give precise relationships for how to include small-scale variation into landscape-scale models. Our method can be used to develop new understanding of mechanisms that drive large-scale population outcomes, and also to connect increasingly available small-scale experimental and observational data to large-scale predictions (e.g., range expansion speed) that can inform landscape management.

In a review of multi-scale empirical studies, Wheatley and Johnson (2009) find little consistency in the choice of observational scales in experiments, which makes cross-scale results difficult to compare and generalize. Whenever empirical data of ecological interactions are collected, movement and habitat heterogeneity must be taken into account through appropriate scaling. How to do this, is the general question of upscaling or coarse-graining. It is an old tenet, following for example from Jensen's inequality, that one should "not average the data, but average the model." Researchers have developed mean field, pair approximation and moment methods (Metz, 2000), scale transition theory (Chesson, 1998; Melbourne and Chesson, 2006; Chesson, 2012), used dimensional analysis (Englund

and Cooper, 2003) and statistical approaches (Inouye, 2005), or considered experimental design (Hewitt *et al.*, 2007) to address this. Such methods were reviewed in a dedicated journal issue (Morozov and Poggiale, 2012). All these approaches make several somewhat similar assumptions of scale separation, for example that interactions are local or that individuals experience the full range of landscape variation during their lifetime (Getz *et al.*, 2018; Morozov and Poggiale, 2012). They obtain results on an aggregate level, such as overall population growth rate, that contains space only implicitly. Our method makes similar assumptions (see box in Figure 2) but retains a spatially explicit dynamic model, from which one can then derive quantities such as overall population growth rate (as in previous models) or spatial spread rate (that cannot be obtained from previous approaches).

Recent models of individual movement and population growth in strongly heterogeneous ("patchy") landscapes and their applications to invasion and conservation ecology show certain surprising effects, which could easily have been missed with aggregate models that do not incorporate the same level of small-scale detail. Maciel and Lutscher (2013) studied population dynamics in patchy landscapes with reaction–diffusion equations that included individual movement behavior at patch boundaries and patch preferences. This information is available from field studies for many species (Crone and Schultz, 2008; Reeve *et al.*, 2008). Applying this modeling framework, Lutscher and Musgrave (2017) showed that reducing host availability could have the unintended consequence of speeding up the range expansion of a forest insect pest. Similarly, Crone *et al.* (2019) demonstrated the importance of relatively small fractions of high-quality habitat for conservation and range expansion of species at risk.

Including large amounts of small-scale data into population models increases model complexity and inhibits explicit analysis. Even numerical simulations often require advanced techniques such as adaptive mesh refinement (Gilbert *et al.*, 2017). Our method is based on homogenization analysis of multiscale models (Pavliotis and Stuart, 2008). The

underlying idea is that if individuals encounter many habitat types during their lifetime, then their lifetime dynamics should be approximated reasonably well by an appropriately weighted average of the conditions encountered in these habitats. The goal is to obtain the correct averages that lead to a homogeneous landscape-level model with (approximately) the same properties as the model that includes all the detailed small-scale information.

Some applications of homogenization to spatial spread models exist, e.g., Reid's paradox (Powell and Zimmermann, 2004), or chronic wasting disease (Garlick *et al.*, 2014). For sessile organisms (e.g., plants), the requirement that an individual experiences different habitat types can be replaced by its offspring (e.g., seeds) covering many different habitat types; see Neupane and Powell (2015) for tree migration mitigated by birds, or Duncan *et al.* (2017) for invasive plants. In all these cases, the scale of landscape variation (y) was small compared to the extent (x) of the phenomenon, so that individuals encounter many different habitat types during their life time. In fact, different scales, expressed as the ratio $\varepsilon = y/x$, arise in many ecological systems (Table 1). If they do, homogenization theory helps reduce complex, spatially heterogeneous equations to simpler, spatially homogeneous equations that nonetheless approximate the behavior of the complex equations very well (Pavliotis and Stuart, 2008). The parameters of the homogenized model encode the patch-scale variation as appropriate multiscale averages.

In patchy landscapes, the abrupt change in environmental conditions across patch edges prohibits us from applying classical homogenization theory directly. Previous applications were somewhat case specific, but Yurk and Cobbold (2018) presented the first rigorous treatment for a single-species model. Applications of their theory to competition systems (Maciel and Lutscher, 2018) and stage-structured populations (Alqawasmeh and Lutscher, 2019) demonstrated the usefulness of homogenization theory and reiterated the importance of including small-scale processes in large-scale models. The approach in Yurk and Cobbold (2018) is highly technical, but the mathematical theory has now matured so that it connects to long-standing concepts from ecological theory and can be consistently

used and applied to multi-species systems.

We present our general homogenization method for transforming a multi-patch reaction-diffusion model with spatial variation on the small scale into a landscape model with appropriately averaged coefficients. The method enables the development of ecological theory that explains landscape-level population outcomes in terms of habitat-level quantities, and it allows the use of local data in landscape models to predict large-scale outcomes such as spatial spread rates. We focus on the case of two interacting species and two habitat types, though it is straightforward to extend the method to additional species and habitats. We illustrate the utility of the method by applying it to predator-prey interactions. We uncover new connections between the large-scale properties of the system, e.g., an effective landscape-scale functional response, and the movement behavior at the habitat level. We present our method for simplified one-dimensional habitats where two patch types alternate periodically in space. This setting may seem somewhat limiting for applications, but it provides a first important step towards including fine-scale information into large-scale prediction. Moreover, the interpretation of our formulas does not require the periodicity assumption, and we speculate that they apply more generally, although the mathematical theory on this matter is still being developed. The extension to two spatial dimensions seems more challenging; we return to this question in the discussion. The one-dimensional theory is best suited for applications to spatial spread, which is our focus here. We summarize the key assumptions of our method in the box in Figure 2.

2 Methods

Our method takes a multi-patch reaction-diffusion model with spatial variation on the small-scale into a landscape model with appropriately averaged coefficients on the large-scale. The mathematical aspects of homogenization theory are quite technical (Pavliotis and Stuart, 2008); see Supplementary Material. The underlying ideas, however, are quite intuitive: If the environment of an organism changes rapidly in time, the growth of

Example	Landscape scale (x)	Habitat scale (y)	Slow time scale (t)	Fast time scale (τ)	ε
Spread of chronic wasting disease in deer[1]	3km (daily deer movement)	30 meters (landscape classification)	years (time scale of infection)	days	0.01
Seed dispersal by animals[2]	100's meters (plant migration)	~ 2 meters (seed caching)	100's years	year	0.01
Spread of Mountain Pine beetle[3]	kilometers (dispersal distance)	hectare (forest composition)	year (generation time)	hours/day (beetle dispersal)	0.1
Marine green turtle homing navigation[4]	20 kilometers (daily movement)	1 kilometer (flow field changes)	1 month (navigation time)	day	0.1

Table 1: Example study systems where habitat averaging is applicable: ε is the ratio of habitat (y) to landscape-scale (x). [1] Garlick *et al.* (2011). [2] Powell and Zimmermann (2004). [3] Powell and Bentz (2014). [4] Painter and Hillen (2015).

the organism is well described by some appropriately weighted temporal average of the environmental conditions (Hastings, 2012). If, instead, an organism moves through a temporally constant but spatially varying landscape of many patches, it will encounter the conditions on the different patches as temporal variation. As in the temporal case, the organisms' growth should then be determined by a suitable average of this spatial variation with weights that indicate how much time the organism spends in the different patches.

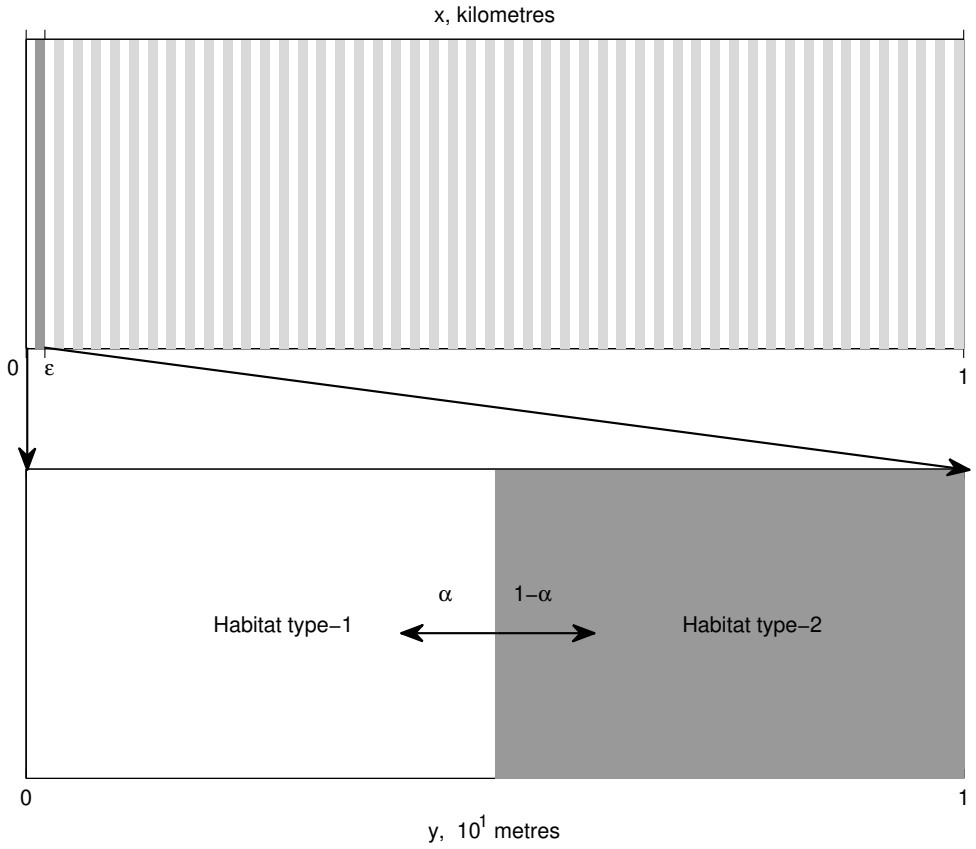
Bridging the scale gap consists of three steps. First, one identifies the appropriate spatial and temporal scales and formulates a reaction-diffusion model for demography and movement within and between small-scale patches. Second, one applies our method of homogenization to derive the large-scale model. Because of scale separation, habitat-level demography is slow compared to movement within and between adjacent patches, so that appropriately averaged population growth acts on locally equilibrated movement dynamics. The resulting model and formulas for the averaged coefficients are given in Table 2. Third, one analyzes the landscape-scale model according to the question at hand, e.g., to derive population persistence conditions or spread rates.

2.1 Step 1: Defining spatial and temporal scales

We choose the spatial and temporal scales according to the scientific questions considered. For example, to study the spread of an organism on a scale of kilometres in a landscape consisting of several habitat types, each of which extends on the order of 100 metres, we naturally have (i) the landscape-scale measured in kilometres and (ii) the habitat-scale measured in 100s of metres. Central to our approach is the assumption that the habitat-scale is (much) smaller than the landscape-scale. We denote by ε the ratio of the two scales ($\varepsilon = 0.1$ in the example). The density of the organism scales accordingly: if there are U organisms per kilometre on the landscape-scale then there are $u = \varepsilon U$ organisms per 100 metres on the habitat-scale.

Our next central assumption is that organisms, through dispersal, encounter several habitat types over their lifetime, and that the time they spend in any one habitat is relatively short. Hence, we also have two temporal scales. We expect that the phenomenon on the landscape-scale over large times is sufficiently well described by an appropriate average of the processes on the habitat-scale over short times. We also expect that the times spent in each habitat appear as weights in this average.

To define the two temporal scales, we consider the analogy of a movie. Suppose we watch a movie of a biological invasion, where the width of the screen corresponds to several kilometers (landscape) and time corresponds to years. To observe the same invasion on the habitat-scale, we would "zoom in" so that the screen corresponds to several hundred metres (habitat). We specify a magnification factor, such that y 100s of metres on the habitat-scale is $x = \varepsilon y$ kilometres on the landscape-scale (Figure 2). Simultaneously, we would need to slow down the movie or else the invasion would pass through the screen too quickly. Accordingly, we define a scaling factor ($\hat{\varepsilon}$) that relates τ units of the short time to $t = \hat{\varepsilon}\tau$ time units on the long time scale, which is given by the phenomenon that we study (e.g., in years). The scaling factor for time is determined by the movement model that we use. For a diffusion process, we choose the shorter time scale such that



Key assumptions in our work

1. Habitat varies on a much smaller scale than the landscape-scale.
2. Organisms encounter several habitat types over the course of their lifetime and spend relatively little time in any one habitat.
3. On the habitat-scale, the effects of intra- and interspecific interactions on demography are small compared to movement.
4. Movement can be described by a diffusion process (can be generalized).
5. The landscape is periodic (can be generalized).
6. The landscapes is one-dimensional (can be generalized).

Figure 2: Illustration of spatial scales: landscape (top panel) and habitat (lower panel). Individuals at a patch interface move to habitat 1 with probability α and to habitat 2 with probability $1 - \alpha$. The first three key assumptions are essential for applying homogenization theory. Assumptions 4–6 are used here to obtain explicit formulas but can be generalized. All assumptions and their implied limitations are examined in more detail in the discussion.

the magnitude of the mean squared displacement per unit time (MSD) of the organism is the same when viewed on the landscape- or the habitat-scale:

$$\text{MSD} = \frac{\text{distance}^2}{\text{time}} = \frac{\overbrace{\langle y^2 \rangle}^{\substack{\text{Magnitude of} \\ \text{habitat-scale MSD}}}}{\tau} = \frac{\overbrace{\langle x^2 \rangle}^{\substack{\text{Magnitude of} \\ \text{landscape-scale MSD}}}}{t} . \tag{1}$$

Substituting $x = \varepsilon y$ and $t = \hat{\varepsilon}\tau$ to find $\hat{\varepsilon}$, the scaling factor for time is $\hat{\varepsilon} = \varepsilon^2$. For the example where the landscape is measured in kilometres and the invasion is observed over years, a habitat-scale of 100 metres gives $\varepsilon = 0.1$ and $\hat{\varepsilon} = 0.01$. Thus, our short time scale is 0.01×1 year, roughly half a week. If we choose transport instead of diffusion models for movement, we obtain a different temporal scaling (Lutscher and Hillen, 2021).

The examples in Table 1 satisfy our key assumptions (see Figure 2). In practice, the method works surprisingly well even when the difference in spatial scales is not as large and/or if organisms encounter only few habitat types over their lifetime. Simulations show a very good approximation of the full model by the homogenization (Garlick *et al.*, 2011; Duncan *et al.*, 2017; Yurk and Cobbold, 2018).

2.2 Step 2: Patch-level reaction-diffusion equations and landscape equations

Our idealized landscape consists of periodically alternating patches of two different habitat types (Shigesada *et al.*, 1986), whose spatial extent is much smaller than the scale of the study question (Figure 2). We formulate reaction-diffusion equations for two interacting populations on each habitat patch and connect these via interface conditions that describe individual movement behavior at patch boundaries. We denote by y (x) the spatial coordinate on a habitat patch (landscape) and by τ (t) the fast (slow) time-scale. These quantities are related by $x = \varepsilon y$ and $\tau = \varepsilon^2 t$ (see above). The length of a habitat patch of type i, measured on the habitat-scale is ℓ_i, such that the period is $\ell_1 + \ell_2 = 1$. On

the landscape-scale, the period is ε. We let $u(y,\tau)$ and $v(y,\tau)$ denote the density of the two populations on the habitat-scale. The reaction-diffusion equations governing their dynamics are

$$\text{Habitat level dynamics} \begin{cases} \dfrac{\partial u}{\partial \tau} &= D_i^u \dfrac{\partial^2 u}{\partial y^2} + \varepsilon^2 f_i(u,v), \\ \\ \dfrac{\partial v}{\partial \tau} &= D_i^v \dfrac{\partial^2 v}{\partial y^2} + \varepsilon^2 g_i(u,v), \end{cases} \tag{2}$$

where D_i^u (D_i^v) denote the diffusion coefficients of population u (v) on type-i habitat. Functions f_i and g_i denote the net growth of u and v on habitat type i, respectively. The factor ε^2 indicates that demography on the habitat-scale is slow compared to the landscape-scale. At a boundary between two habitat types, individuals of population u (v) choose to move to habitat type 1 with probability α^u (α^v) and to habitat type 2 with probability $1-\alpha^u$ ($1-\alpha^v$); see Supplementary Material S.1 for details.

We define $U(x,t)$ and $V(x,t)$ as the respective population densities at the landscape-scale, averaged over habitat types. Strictly speaking, U and V are approximations to this spatial average. Yurk and Cobbold (2018) showed, by numerical simulation, that they are highly accurate under the assumptions in Figure 2. The equations that these variables satisfy are given in Table 2 and discussed in the next section. Their derivation can be found in Supplementary Material S.1.

3 Results

The population densities on the landscape-scale, averaged over one period at the habitat-scale, satisfy the habitat-averaged landscape equations (HALE), Table 2, equations (3). At this level, the equations are homogeneous, but the diffusion coefficients and the growth functions are appropriate averages, indicated by $\widehat{\ }$, of the small-scale heterogeneity (also in Table 2). We give a detailed discussion novel interpretations in terms of the classic

Habitat-averaged landscape equations (HALE)

$$\text{Landscape level dynamics} \begin{cases} \dfrac{\partial U}{\partial t} = \hat{D}^u \dfrac{\partial U}{\partial x^2} + \hat{f}(U,V), \\ \dfrac{\partial V}{\partial t} = \hat{D}^v \dfrac{\partial V}{\partial x^2} + \hat{g}(U,V), \end{cases} \tag{3}$$

Here $\hat{f}(U,V)$ is the landscape-scale growth rate for population U,

$$\hat{f}(U,V) = \frac{\varepsilon^{-1} f_1\left(\dfrac{\rho_1^u}{\langle\rho^u\rangle}\varepsilon U, \dfrac{\rho_1^v}{\langle\rho^v\rangle}\varepsilon V\right)\ell_1 + \varepsilon^{-1} f_2\left(\dfrac{\rho_2^u}{\langle\rho^u\rangle}\varepsilon U, \dfrac{\rho_2^v}{\langle\rho^v\rangle}\varepsilon V\right)\ell_2}{\ell_1+\ell_2}. \tag{4}$$

The formula for $\hat{g}$ is analogous. The landscape-level diffusion coefficient for U is

$$\hat{D}^u = \langle\alpha^u\rangle^{-1}\langle\rho^u\rangle^{-1} = \left(\frac{(1-\alpha^u)\ell_1 + \alpha^u\ell_2}{\ell_1+\ell_2}\right)^{-1}\left(\frac{\rho_1^u\ell_1 + \rho_2^u\ell_2}{\ell_1+\ell_2}\right)^{-1}, \tag{5}$$

and similar for $\hat{D}^v$, where ρ_i^u are the habitat residence indices for U:

$$\rho_1^u = \frac{1}{D_1^u(1-\alpha^u)} \quad \text{and} \quad \rho_2^u = \frac{1}{D_2^u\alpha^u}. \tag{6}$$

We denote by $\langle\cdot\rangle$ the average of a function over one spatial period. The average residence index is then

$$\langle\rho^u\rangle = \frac{\rho_1^u\ell_1 + \rho_2^u\ell_2}{\ell_1+\ell_2}, \tag{7}$$

and similar for $\langle\rho^v\rangle$.

Table 2: Landscape-scale equations that arise from the homogenization process. The formulas show how the landscape-level parameters and functions are obtained from their habitat-level counterparts.

ecological concepts of residence index (Turchin, 1998) and dynamic level (Skellam, 1973). The averaged demography generally differs quantitatively and qualitatively from the local demography (section 3.3).

3.1 Connecting movement to residence indices

Residence indices naturally appears as weights in the averages in Table 2 because of their relation to the time an individual spends in each patch. Turchin (1998) defines the *residence index* at any point in space as a quantity proportional to the steady-state population density in a pure movement model (i.e. without growth). It can be measured empirically (Turchin, 1998). When organisms move via ecological diffusion, the residence index is the inverse of motility (diffusion), so that organism density at steady state is high where motility is low and vice versa. The residence index is therefore a relative measure of the time spent at each location in the absence of births and deaths. Here, residence index is modified by the probability of choosing a certain habitat type, see eq. (6). If, say, an individual preferentially chooses type-1 habitat when it reaches a habitat boundary ($\alpha^u > 1/2$), then the effective leaving rate of type-1 habitat is decreased, and the time spent in type-1 habitat is increased. The reverse is true when preference is for type-2 habitat ($\alpha^u < 1/2$).

Following Powell and Zimmermann (2004), we use residence index to heuristically derive and explain the expressions for the landscape-level diffusion coefficients (5). We consider a patch of length Δy (with unit length in the perpendicular direction). The residence time in this patch is proportional to (residence index) $\times\, \Delta y \times 1$, (where the '1' stands for the perpendicular direction and carries the units of length). As residence index is defined only up to a constant of proportionality, we scale the residence index by $\langle \alpha^u \rangle$ and consider $\rho_i^u \langle \alpha^u \rangle$. This has two useful properties: (i) when there is no patch preference ($\alpha^u = 1/2$), the scaled residence index of habitat i is the inverse of the habitat diffusion coefficient, consistent with Powell and Zimmermann (2004); (ii) the scaled residence index

in type-1 (type-2) habitat is an increasing (decreasing) function of α^u, so preference for habitat 1 increases residence time in habitat 1. Using the scaled residence indices, residence time in type-1 habitat is proportional to

$$\rho_1^u \langle \alpha^u \rangle \Delta y \times 1 = \frac{1}{D_1^u \frac{1-\alpha^u}{\langle \alpha^u \rangle}} \Delta y, \tag{8}$$

and analogously in type-2 habitat. The average residence index in a small region of landscape is proportional to

$$\frac{\frac{1}{D_1^u \frac{1-\alpha^u}{\langle \alpha^u \rangle}} \ell_1 + \frac{1}{D_2^u \frac{\alpha^u}{\langle \alpha^u \rangle}} \ell_2}{\ell_1 + \ell_2}. \tag{9}$$

The inverse of this average (proportional) residence index is exactly the landscape-level diffusion coefficient in eq. (5), analogous to Powell and Zimmermann (2004), and as it was for simpler models at the patch level described above (Turchin, 1998).

3.2 Connecting population growth to dynamic level

Dynamic level is related to residence index and appears in the arguments of the growth functions in eq. (4). In the absence of population growth, Skellam (1973) defines the *dynamic level* such that individuals diffuse from high to low dynamic level. He uses the analogy that heat (population) moves in response to differences in temperature (dynamic level). This is true in materials with jumps in thermal properties, e.g., a hand placed on a wall. Heat flows if there is a temperature difference between the hand and the wall. At equilibrium, heat will be discontinuous but temperature will not. Animal populations flow in response to gradients in dynamic level (from high to low). At equilibrium, the dynamic level is spatially constant even if the population density is not. In our model, population density is not spatially constant because of patch preferences and variation in motility between habitats. We take advantage of the property that dynamic level is spatially constant at steady state in our derivation of the landscape-level equations, and consequently

dynamic level appears in the expressions for population growth (Supplementary Material S.1).

Demography is so slow that our model on the habitat-scale can be thought of as a pure movement model without population growth, allowing us to define the dynamic level. Turchin (1998) showed that equilibrium population density (u^*) is the dynamic level multiplied by residence index (ρ), provided movement is not density-dependent. This allowed him to partition population density into the product of two separate processes, density-dependence and spatial-dependence (Turchin, 1998):

$$u^*(y) = \overbrace{\rho(y)}^{\text{residence index}} \times \text{const.} = \overbrace{\rho(y)}^{\text{residence index}} \times \overbrace{\frac{\int u^*(y)dy}{\int \rho(y)dy}}^{\text{dynamic level at equilibrium}} . \tag{10}$$

The expression for the dynamic level at equilibrium is simply the average density divided by the average residence index.

In our case, the residence index is constant on each habitat patch with values ρ_i^u, and the average density in a habitat is εU. Hence, the corresponding expression for $u^*(y)$ in our notation is

$$\overbrace{\rho_i^u}^{\text{residence index}} \times \overbrace{\frac{\varepsilon U}{\langle \rho^u \rangle}}^{\text{dynamic level at equilibrium}} . \tag{11}$$

This is exactly the first argument of f_i in eq. (4). Hence, the habitat-level densities that we consider are precisely the steady-state values of the small-scale movement equations, expressed in terms of dynamic level and residence index. This could have been expected since the population changes slowly on the habitat-scale. The landscape-level population growth functions are then the averages of these habitat-level functions over one spatial period, converted to density at the landscape-level by dividing by ε.

3.3 Step 3: Analyzing the landscape-scale model, application to predator-prey interactions

Our HALE method gives many insights into how small-scale variation affects large-scale outcomes, e.g., how functional responses scale from the habitat- to the landscape-level and how small-scale heterogeneity affects large-scale population persistence and invasion speed. We illustrate this utility and step 3 of our method by studying the dynamics of a predator-prey community in a fragmented landscape. We choose a Rosenzweig–MacArthur model, where the prey grows logistically with growth rate λ and intraspecific competition strength μ, and is consumed according to functional response ϕ. Prey biomass is converted into predator biomass linearly with parameter γ. Predators die at rate m. On the habitat-scale (see (2)), u and v denote the densities of prey and predator, respectively, with habitat-type dependent functions

$$f_i(u,v) = u(\lambda_i - \mu u) - \phi_i(u)v \quad \text{and} \quad g_i(u,v) = \gamma\phi_i(u)v - mv. \tag{12}$$

For simplicity, we assume that γ, μ, and m are independent of habitat type and type-2 habitat always has the lower prey growth rate ($\lambda_2 < \lambda_1$). The non-spatial dynamics are well known: if λ_i is positive, the prey can grow from low density to carrying capacity $u^* = \lambda_i/\mu$. If the predator is sufficiently efficient (if $\gamma\phi_i(u^*) - m > 0$), then it can grow from low density, and there is a positive coexistence state of predator and prey (Supplementary Material S.4).

Applying the HALE framework (Table 2) gives the landscape-scale model

$$\frac{\partial U}{\partial t} = \hat{D}^u \frac{\partial U}{\partial x^2} + (\hat{\lambda} - \hat{\mu}U)U - \widehat{\phi}(U)V, \quad \frac{\partial V}{\partial t} = \hat{D}^v \frac{\partial V}{\partial x^2} + \gamma\widehat{\phi}(U)V - mV, \tag{13}$$

where

$$\hat{\lambda} = \lambda_1 \frac{\rho_1^u}{\langle \rho^u \rangle} \frac{\ell_1}{(\ell_1 + \ell_2)} + \lambda_2 \frac{\rho_2^u}{\langle \rho^u \rangle} \frac{\ell_2}{(\ell_1 + \ell_2)} = \frac{\lambda_1 \rho_1^u \ell_1 + \lambda_2 \rho_2^u \ell_2}{\rho_1^u \ell_1 + \rho_2^u \ell_2} \tag{14}$$

and

$$\hat{\mu} = \varepsilon\mu \left[\left(\frac{\rho_1^u}{\langle \rho^u \rangle} \right)^2 \frac{\ell_1}{(\ell_1 + \ell_2)} + \left(\frac{\rho_2^u}{\langle \rho^u \rangle} \right)^2 \frac{\ell_2}{(\ell_1 + \ell_2)} \right] \tag{15}$$

are the appropriately averaged low-density growth rate and strength of intraspecific competition. The averaged diffusion coefficients from (5). Clearly, $\hat{\lambda}$ is a weighted average of the habitat-level growth rates with weights $\rho_i^u \ell_i$, representing the time spent in habitat type i. If the two growth rates are identical ($\lambda_1 = \lambda_2$), then landscape and habitat growth rate are the same ($\hat{\lambda} = \lambda_1$). Similarly, m does not change between the habitat and landscape-scale. In contrast, even though μ is constant between the two habitat types, the effective $\hat{\mu}$ depends on residence times and patch lengths because intraspecific competition requires interaction between individuals, and therefore depends on how pairs of individuals spend their time in the different habitats. In particular, $\hat{\mu}$ is the weighted average of the habitat-level strengths of intraspecific competition, where the weights are the proportion of time spent in type-i habitat ($\frac{\rho_i^u}{\langle \rho^u \rangle} \cdot \frac{\ell_i}{\ell_1 + \ell_2}$) and the relative density of prey in type-i habitat ($\frac{\rho_i^u}{\langle \rho^u \rangle}$). The factor of ε in (15) indicates that interactions are rare on the habitat-scale.

We can simplify the expressions by introducing the ratios of the residence indices, $R^u = \rho_1^u / \rho_2^u$, and patch lengths, $R^\ell = \ell_1 / \ell_2$. We find

$$\hat{\lambda} = \frac{\lambda_1 R^u R^\ell + \lambda_2}{R^u R^\ell + 1} \quad \text{and} \quad \hat{\mu} = \varepsilon\mu \frac{((R^u)^2 R^\ell + 1)(R^\ell + 1)}{(R^u R^\ell + 1)^2}. \tag{16}$$

These expressions are particularly useful when relating our models to data since they require only relative and no absolute measurements.

How prey-only dynamics depend on habitat heterogeneity has been studied in detail by Yurk and Cobbold (2018) and Maciel and Lutscher (2013). Here, we concentrate on the predator dynamics.

3.3.1 Individual behavior: Functional response

The functional response is a crucial ingredient in modeling the interaction of a predator and its prey. Scale transition theory shows that the functional response at the landscape scale can differ in structure from the functional response at the habitat scale (Bergström *et al.*, 2006; Englund and Leonardsson, 2008; Melbourne and Chesson, 2006). This difference arises from interaction between spatial variation in population densities and the nonlinear functional response at the habitat scale (Chesson *et al.*, 2005). We demonstrate how the landscape-level functional response arises in our homogenization approach and how that may affect model predictions later. At the habitat level, we choose Holling's type II functional response

$$\phi_i(u) = \frac{a_i u}{1 + a_i h_i u} \,. \tag{17}$$

Here, a_i and h_i are the attack rate and the handling time at the habitat level. These two quantities relate to the graph of $\phi_i(u)$. The slope at zero is $\phi_i'(0) = a_i$ and the asymptote is $\phi_i(\infty) = 1/h_i$. When prey density is low, predation is limited by the predator's attack rate; when prey density is high, it is limited by the handling time.

According to formula (4), the functional response on the landscape-level is

$$\widehat{\phi}(U) = \frac{A_1 U}{1 + A_1 H_1 U} + \frac{A_2 U}{1 + A_2 H_2 U} \,, \tag{18}$$

with appropriately scaled A_i and H_i, namely

$$A_i = \varepsilon\, a_i \, \frac{\rho_i^v}{\langle \rho^v \rangle} \, \frac{\rho_i^u}{\langle \rho^u \rangle} \, \frac{\ell_i}{\ell_1 + \ell_2} \quad \text{and} \quad H_i = h_i \left(\frac{\rho_i^v}{\langle \rho^v \rangle} \right)^{-1} \left(\frac{\ell_i}{\ell_1 + \ell_2} \right)^{-1} .$$

The landscape-level functional response, $\widehat{\phi}$, has exactly the same qualitative properties as ϕ: it grows monotonically and approaches an asymptote (Figure 3). Thus, the effective

attack rate and handling time on the landscape-level are

$$A_{\text{eff}} = \widehat{\phi}'(0) = A_1 + A_2 \quad \text{and} \quad H_{\text{eff}} = \frac{1}{\widehat{\phi}(\infty)} = \left(\frac{1}{H_1} + \frac{1}{H_2}\right)^{-1}. \tag{19}$$

We can express these two quantities in terms of their habitat-level parameters and only three ratios, namely, R^u, R^ℓ, and $R^v = \rho_1^v/\rho_2^v$ as

$$A_{\text{eff}} = \varepsilon(R^\ell + 1)\frac{a_1 R^u R^v R^\ell + a_2}{(R^u R^\ell + 1)(R^v R^\ell + 1)} \quad \text{and} \quad H_{\text{eff}} = \frac{R^v R^\ell + 1}{\frac{R^v R^\ell}{h_1} + \frac{1}{h_2}}. \tag{20}$$

Since the landscape-level handling time, H_{eff}, is a harmonic mean with weights $R^v R^\ell$, it is monotone in R^v and R^ℓ (Figure 4(a)). The effective attack rate, however, depends strongly on how predator and prey use space relative to one another. If both spend more of their time in the same (different) habitat type, the effective attack rate increases (decreases) (Figure 4(b)).

The effective attack rate and handling time (19) are both averages of the scaled habitat-level attack rates and handling times. Specifically, a_i is scaled by the proportion of time the prey spend in type-i habitat ($\frac{\rho_i^u}{\langle \rho^u \rangle} \cdot \frac{\ell_i}{\ell_1+\ell_2}$) and relative predator density in type-i habitat ($\frac{\rho_i^v}{\langle \rho^v \rangle}$). Handling time h_i is scaled by the reciprocal of relative time the predator spends in type-i habitat ($\frac{\rho_i^v}{\langle \rho^v \rangle} \cdot \frac{\ell_i}{\ell_1+\ell_2}$).

Given the effective attack rate and handling time, as well as the shape of the function, it is tempting to write the landscape-level functional response as

$$\widetilde{\phi}(U) = \frac{A_{\text{eff}} U}{1 + A_{\text{eff}} H_{\text{eff}} U}. \tag{21}$$

However, we show that $\widetilde{\phi}(U) > \widehat{\phi}(U)$ for all $U > 0$ (Supplementary Material S.4). Therefore, while the effective landscape-level attack rate and handling time can be obtained from the habitat-level quantities through appropriate averaging, the actual functional response is always below the simple Holling type II functional response one could obtain

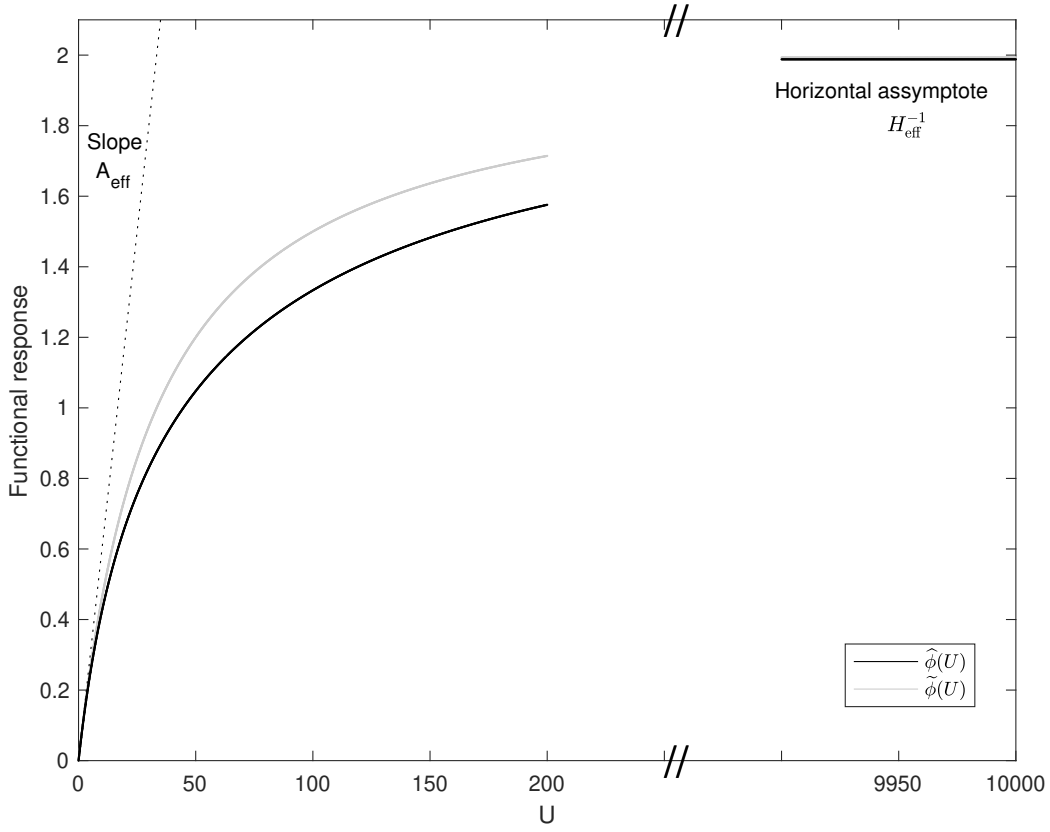


Figure 3: Landscape-level functional response ((18), black curve) and corresponding "best guess" Holling type II functional response ((21), grey curve). Both functions have slope A_{eff} at the origin (dotted line) and approach the same asymptote as U approaches infinity. The landscape-level functional response always lies below the Holling type II functional response. Parameters: $A_1 = 0.01$, $A_2 = 0.05$, $H_i = 1$.

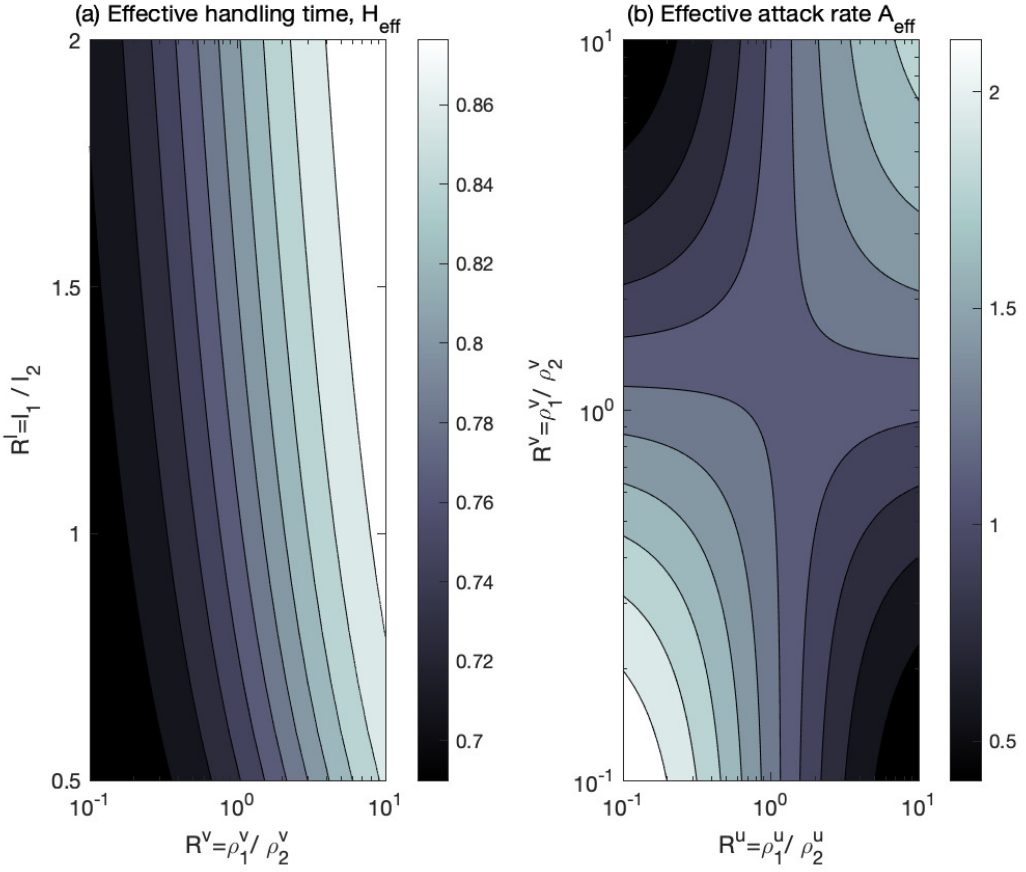


Figure 4: Effective handling time (a) and attack rate (b) as functions of the ratios of the residence indices and the patch lengths. Parameters: $a_1 = 1$, $a_2 = 1.25a_1$, $h_1 = 1$, $h_2 = 0.75h_1$, $R^\ell = 1$.

through assuming that (21) applies at the landscape-level. This means that one cannot get the correct landscape-level functional response by fitting (21) to aggregated data. Instead, one has to go through the bottom-up approach described in the previous section. Using $\widetilde{\phi}$ instead of $\widehat{\phi}$ will overestimate the predator's likelihood of persistence and speed of spread, as we shall see in the subsequent two sections.

3.3.2 Implicit spatial dynamics: predator persistence

The predator persists at the landscape-scale when the prey-only state, $(U^*, 0)$, is unstable, i.e., when

$$\gamma\widehat{\phi}(U^*) > m. \tag{22}$$

This condition depends on the effects of movement behavior as expressed through the ratios of the residence indices ($R^u = \rho_1^u/\rho_2^u$ and $R^v = \rho_1^v/\rho_2^v$). The predator can persist unconditionally when the prey spends roughly equal time in both habitat types (Figure 5). When the prey spends much more time in one of the two habitats, then the predator must match that relative residence time in order to persist. However, if prey spend most of their time in habitat where prey growth rate is low (R^u small in Figure 5(a)) or negative (R^u small in 5(b)), the predator will go extinct, independent of its movement behavior. Obviously, the predator will go extinct if the prey itself cannot persist (shaded region in Figure 5(b)), but the relationship between movement behavior and predator persistence in the other cases warrants closer consideration.

Two mechanisms underlie our observations: the attack rate increases when the movement behaviors are aligned (Figure 4(b)), and there are nonlinear relationships between U^*, $\widehat{\phi}(U^*)$ and R^u. Prey density at the prey-only steady state (U^*) is lowest when prey spend most of their time in poorer quality habitat and intermediate when they spend most of their time in higher quality habitat (Figure 6(a)). The maximum occurs when the time spent in the two habitats is roughly equal, so that the benefits of high growth rates balance with the cost of high intraspecific competition (Yurk and Cobbold, 2018).

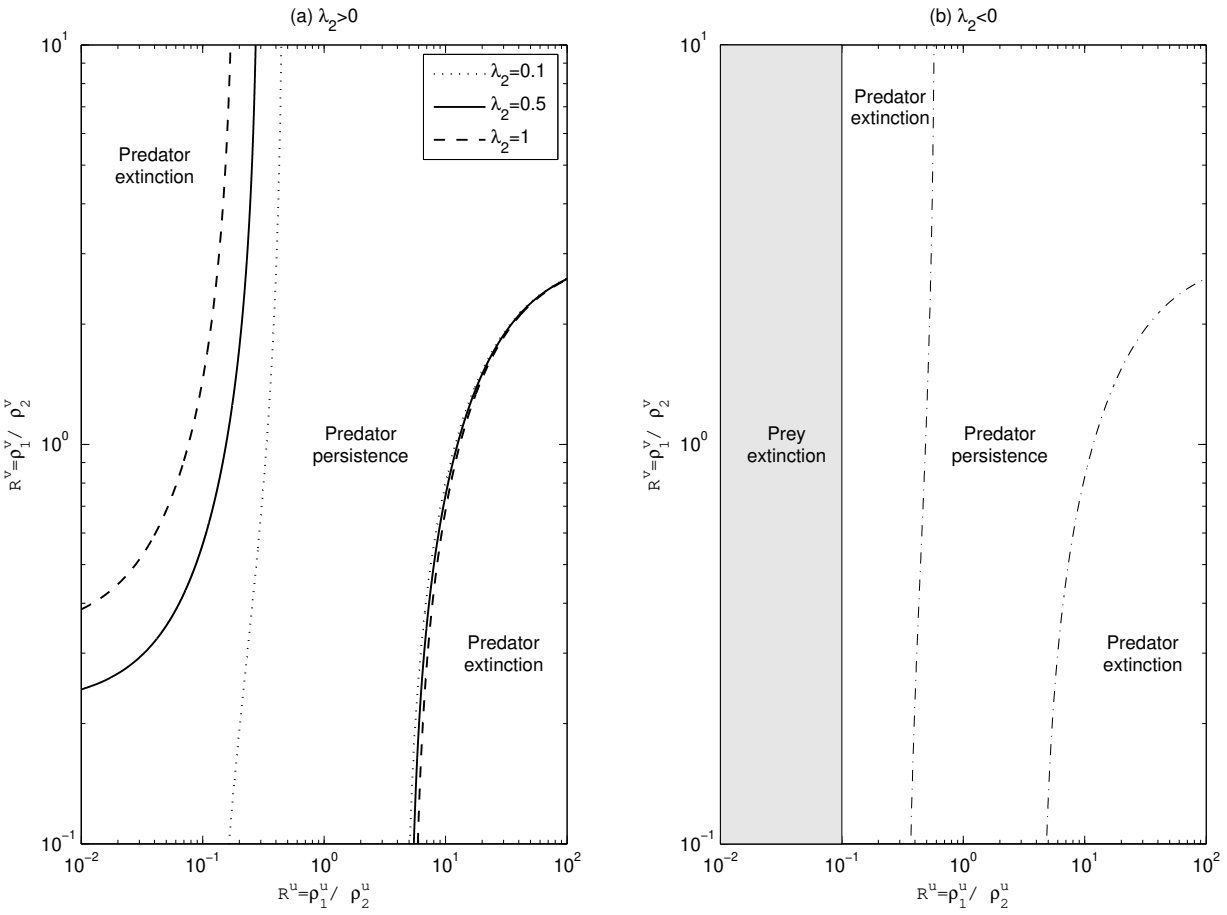


Figure 5: Predator persistence condition (22) as a function of the relative residence indices of predator and prey ($R^u = \rho_1^u/\rho_2^u$ and $R^v = \rho_1^v/\rho_2^v$). Predators persist between the pair of corresponding curves and become extinct outside this region, where predator movement behavior does not align with prey movement behavior. (a) both habitats are source habitats ($\lambda_1 \geq \lambda_2 > 0$); (b) type 2 is a sink habitat ($\lambda_1 > 0 > \lambda_2$). Parameters: $\lambda_1 = \mu_i = a_i = h_i = R^\ell = 1$, $\gamma = 5$, $m = 3.75$.

The relationship between R^u and $\widehat{\phi}(U^*)$ that determines predator persistence does not necessarily reflect the relationship between R^u and U^* since $\widehat{\phi}$ also depends on R^u explicitly. When prey use habitats roughly equally ($R^u \approx 1$), predator growth rate is fairly insensitive to predator space use (Figure 6(b)). When prey spend more time in good habitat ($R^u \gg 1$), predator growth rate is high when predators also spend most of their time in good habitat (dotted curve). Analogously, when prey spend more time in bad habitat ($R^u \ll 1$), prey density is low but predators can still have a high growth rate by also spending most of their time in bad (for the prey) habitat (dash-dot curve). Hence, when prey use the habitat roughly equally, prey density is maximized and determines predator growth rate. When prey use the habitat unevenly, prey density decreases, and predators have to follow this uneven habitat use to increase the attack rate.

3.3.3 Explicit spatial dynamics: predator spread rate

When predators can persist, they will spread in the landscape when introduced locally. We study how their spread rate depends on movement behavior and space use, always assuming that predator and prey can stably coexist (detailed conditions in Supplementary Material S.4). The spread rate of the predator (c^v) can be obtained from the linearization of system (13) at the prey-only state $(U^*, 0)$ (Fagan *et al.*, 2002) as

$$c^v = 2\sqrt{\widehat{D^v}(\gamma\widehat{\phi}(U^*) - m)}. \tag{23}$$

When we fix the movement behavior of the predator, the spread rate depends on prey movement in the same way as $\widehat{\phi}(U^*)$ and can therefore be inferred from Figure 6. For example, it is a hump-shaped function of R^u and increases with λ_2 (Figure 7(a)). Since predators spend equal time in the two habitat types ($R^v = 1$, $\widehat{D^v} = 1$), the maximum spread rate for intermediate values of R^u reflects the same two mechanisms as above: (i) prey density is highest when prey use both patch types roughly equally, and (ii) the landscape-scale attack rates are highest when prey and predator have roughly the same

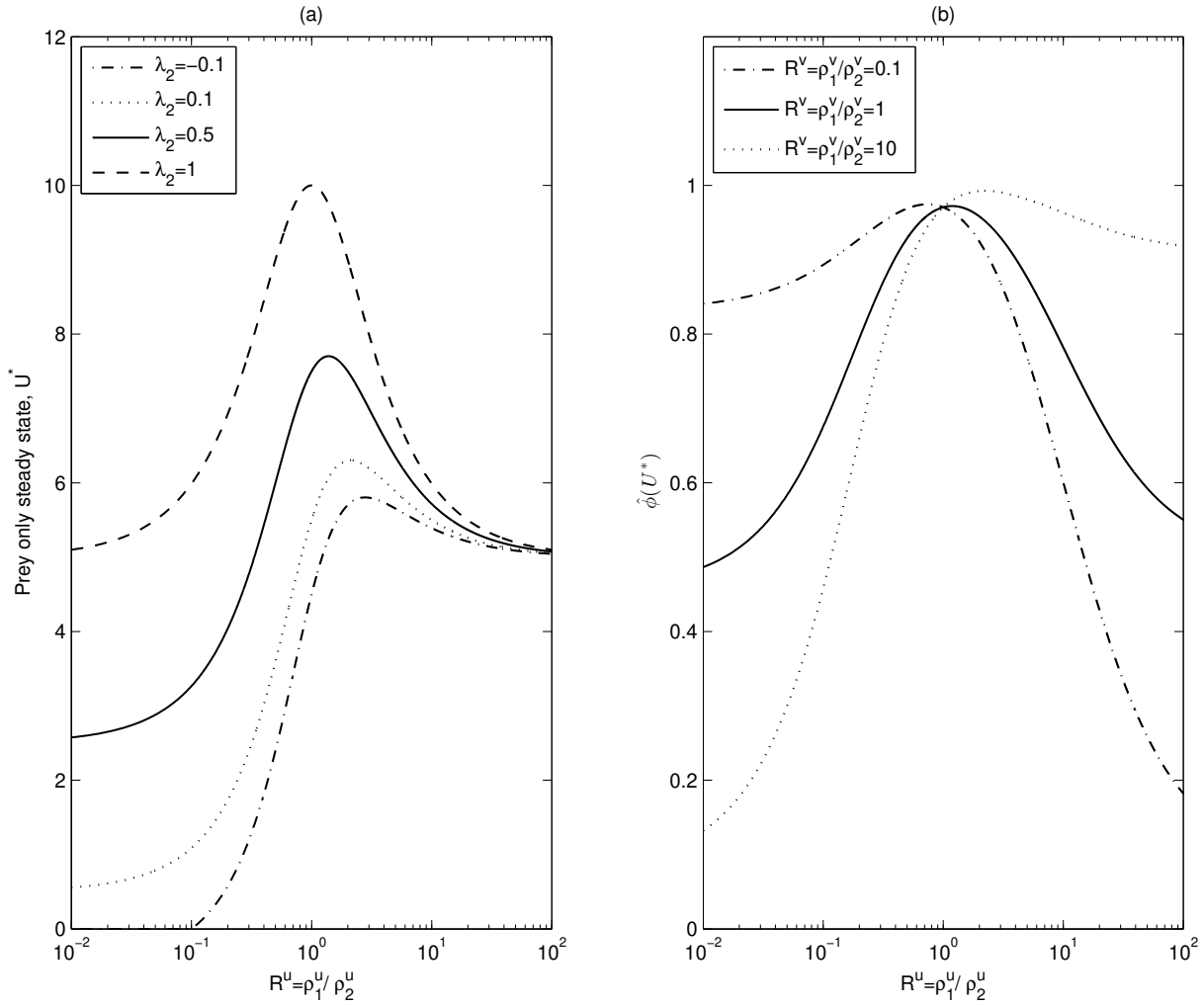


Figure 6: (a) Prey-only steady state (U^*) and (b) functional response at the prey-only steady state ($\hat{\phi}(U^*)$) as a function of the ratio of the prey residence indices $R^u = \rho_1^u/\rho_2^u$. All three scenarios in (b) correspond to the solid curve in (a). Parameters: $\lambda_1 = 1$, $\mu_i = 1$, $a_i = h_i = R^\ell = R^v = 1$ and in (b) $\lambda_2 = 0.5$.

ratio of residence times.

When predator movement behavior varies, more surprising results arise. For example, increasing the predator diffusion coefficient in type-2 habitat (with all other parameters fixed), does not necessarily increase predator spread rate, as we would expect. While the landscape-level diffusion coefficient (5) increases with both habitat-level diffusion coefficients, the effective attack rate can increase *or* decrease in ρ_2^v (Figure 4) and therefore also in D_2^v. Hence, while $\widehat{D}^v$ increases with D_2^v, $\widehat{\phi}$ may increase or decrease with D_2^v. The predator spread rate depends on their product (23), which can increase or decrease with D_2^v. When prey spend much of their time in type-1 habitat, increasing predator movement in type-2 habitat increases predator spread rate (Figure 7(b)). When prey spend very little time in type-1 habitat, increasing predator movement in type-2 habitat decreases predator spread rate. In the former case, prey and predator space use are increasingly aligned, whereas in the latter case, they are increasingly opposed.

4 Discussion

Dispersing organisms can encounter many habitat types over the course of their lifetime. Local habitat conditions and individual movement shape a population's distribution and flow through the landscape. Dynamics at the landscape-scale can therefore differ significantly from those at the habitat-scale (Melbourne and Chesson, 2006; Thogmartin and Knutson, 2007). Thus, a formal framework to systematically relate small-scale habitat-level variations in conditions and behaviour to large-scale landscape-level dynamics and distributions is a vital tool for deepening our understanding of the mechanisms driving landscape-scale dynamics. Our HALE framework provides the desired landscape-level equations, using homogenization, a technique of spatial averaging. From these landscape-level equations, ecological theory can be developed that offers novel insight into how environmental variation shapes landscape-scale population dynamics in patchy landscapes.

In light of Jensen's inequality, it is not surprising that our HALE framework involves

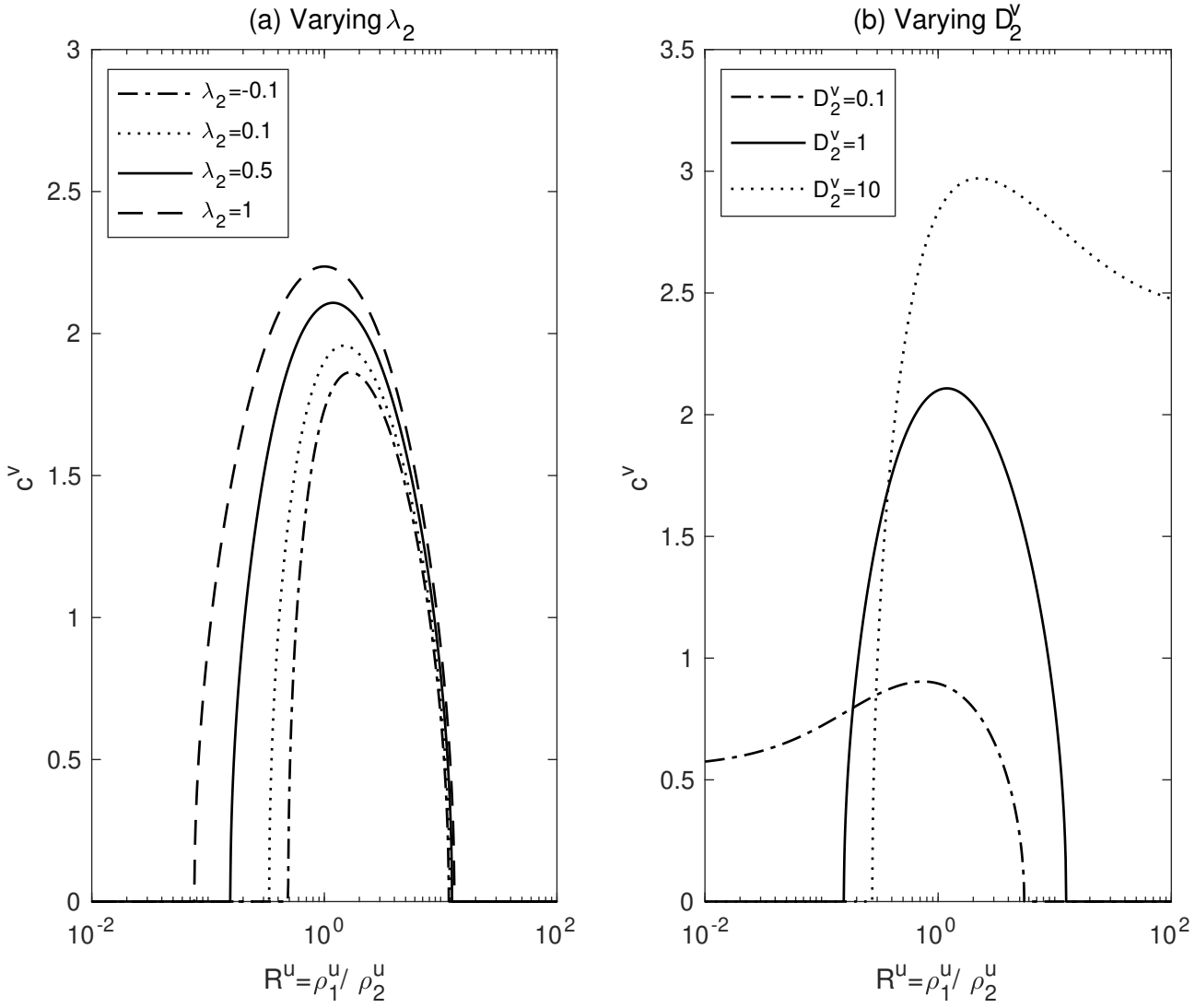


Figure 7: Predator spread rates as a function of the ratio of the prey residence indices $R^u = \rho_1^u/\rho_2^u$. We vary (a) prey low-density growth rate, and (b) predator diffusion, in habitat 2. The solid line corresponds to the same parameter set across both plots. Parameters: $\lambda_1 = 1$, $\lambda_2 = 0.5$, $\gamma = 5$, $m = 3.75$ $\mu_i = a_i = h_i = R^\ell = R^v = 1, \widehat{D^v} = 1$ and in (b) $D_1^v = 1$, $\alpha^v = 0.5$, giving $R^v = D_2^v$ and $\widehat{D^v} = 2R^v/(R^v + 1)$.

averaging the model (habitat-level growth and interaction functions) rather than the data (habitat-level parameters). It has been widely recognized that one cannot simply average environmental conditions to infer dynamics (Ruel and Ayres, 1999). Non-linear response functions together with environmental variance can shift the dynamical behavior away from what linearly averaged conditions would predict. This observation is also at the heart of *scale transition theory* (Melbourne and Chesson, 2006; Chesson, 2012), an alternative framework for scaling from habitat to landscape-level models.

As with our approach, scale transition theory may also begin with a high-resolution patch model (e.g., equations (2)) that explicitly incorporates individual movement, organisms' habitat choices, and heterogeneity. The high-resolution patch model can be solved to predict spatial covariances between the densities of interacting species or between population densities and local landscape characteristics that affect fitness (Chesson, 2012). Scale transition theory accounts for these covariances in approximating landscape-level quantities that emerge as parameters in dynamical models of spatially averaged population densities. At the heart of both approaches is the assumption that dispersal processes occur at a faster rate than demographic processes so that local variation in relative population densities is determined largely by habitat-level movement rates.

Our work differs from scale transition theory and other existing up-scaling methods (Metz, 2000; Morozov and Poggiale, 2012) in that the result is a landscape-level model that remains spatially explicit. While other methods average out spatial variation across the entire landscape, including for the state variables, the HALE framework averages out habitat-level but not landscape-level variation. Spatial resolution is reduced, simplifying the model, but not lost altogether. Our approach retains the influence of local variation in habitat type, habitat quantity, and species movement rules, and reveals how these rules change as we move from habitat to landscape-scale. Most notably, we retain the ability to predict their effects on large-scale spatio-temporal dynamics, e.g., invasion speeds.

The importance and insights of a bottom-up approach are illustrated by our predator–

prey example in section 3.3. Predator attack rate at the landscape-scale is maximized when prey and predator align their space use so that their ratios of the habitat residence times are similar ($R^u \approx R^v$). Aligning space use might seem a surprising strategy when it requires a predator to have a high residence time where habitat-level attack rates are low (Figure 5(b), top right). The landscape-level attack rate is high because predators spend most of their time in the same locations as the prey. Even though attacks may be less successful in these locations, the number of encounters keeps the landscape-level attack rate high. Essentially, there is little benefit to being efficient at catching prey in locations where prey rarely go (Figure 5(b), bottom right). When habitats are "spatial anchors" for both prey and predator then their space use has been shown to align (Smith *et al.*, 2019). In the puma-vincuñas system in Argentina, predators preferred meadow habitat as it provided cover when stalking prey, while prey relied on meadow habitat for foraging, despite the increased predation risk. Aligning space use ultimately favored the predators, as they successfully found and killed their prey, a result predicted by our landscape-scale attack rates.

Since our HALE framework is based on residence indices, it easily accommodates recent advances in inference and statistical modeling of spatial movement. For example, Hooten *et al.* (2019) provide a method for estimating residence times using resource selection functions and partial differential equations. They capitalize on the growing availability of spatial movement data from telemetry tracking and aerial surveys. Telemetry data can be used to estimate residence times at the habitat scale even when this scale is small (e.g. meters). For example, Johnson *et al.* (2008) developed methods to extrapolate paths between GPS measurements, which Garlick *et al.* (2011) successfully used to calculate residence times for mule dear on 30m $\times$ 30m grid squares, the typical scale of land cover maps.

Our approach also provides a mathematically sound method for dealing with issue of biases that are introduced when scaling up landscape maps for use in dynamic modeling.

Bocedi *et al.* (2012) assessed how range expansion is affected by the resolution of the landscape, dispersal and demography in dynamic simulation models. Such models are increasingly used to make predictions about potential impacts of climate change and land management. Often, grid cells from raster maps are aggregated to facilitate computation over large geographical areas, but this aggregation is typically done in a naïve way, without considering, for example, that the upscaled mean dispersal distance or prey handling time on a larger grid cell may not be spatial averages of those on the finer resolution grid. Bocedi *et al.* (2012) found that the extent of range expansion was overestimated when landscape maps and ecological processes were upscaled using simple spatial averages. We make the same prediction for predator invasion speeds (see section 3.3.1), but are also able to attribute mechanism to this behaviour. Overestimation can arise if one assumes that the ecological process (here predator functional response) in the upscaled model has the same functional form as in the fine-scale model. This assumption is invalid because of the interaction between nonlinearity in the functional response and spatial variation (Chesson, 2012). We provide a method for correctly scaling up these ecological processes and removing the systematic biases that can occur when upscaling is done in a naïve way. Homogenization, the foundation of our method, accurately predicts upscaled dispersal kernels and rates of range expansion (Garlick *et al.*, 2011; Yurk and Cobbold, 2018; Duncan *et al.*, 2017).

Our idealized landscape consists of two periodically alternating habitat types. Our method generalizes to multiple habitat types by replacing the averages in equation (4) with their multi-type equivalences (Supplementary Material S.1). Individuals still need to encounter these habitats many times over their lifetime, i.e., patches must be small. Such a requirement is reasonable. For example, mule deer explore up to 38 habitat (land cover) types during a season in southern Utah (Garlick *et al.*, 2014), so that the requirements of the theory are easily satisfied. Our approach also generalizes to more than two species (Garlick *et al.*, 2014).

It is more challenging to generalize the method to non-periodic landscapes. In fact, if landscape composition changes fundamentally over the scale of interest, one cannot expect a landscape-scale equation with spatially constant coefficients to accurately represent the dynamics of populations. Homogenization theory, however, does not require periodicity. If habitat types vary on a small *and* on a larger scale, homogenization theory can be used to derive large-scale equations that contain spatially changing small-scale averages (Pavliotis and Stuart, 2008). The resulting equations are still difficult to analyze, but there is a highly relevant intermediate case. Landscapes are often quasi-periodic, i.e., there is a spatial scale, larger than the habitat-scale, at which the habitat-level averages are relatively constant. For example, landscapes in southern Utah are reasonably close to quasi-periodic (Garlick *et al.*, 2011). In that case, one can apply homogenization for periodic landscapes, but the mathematical derivation of this result is more cumbersome.

Our method is formulated for one-dimensional landscapes. While such a simplification is reasonable when studying spatial spread, other applications require two-dimensional models. The formulation of reaction-diffusion equations in two-dimensional homogeneous landscapes is straight forward (Turchin, 1998), and corresponding matching conditions at interfaces between habitat types have also been derived (Ovaskainen and Cornell, 2003). Applying homogenization theory is much harder in two dimensions. Garlick *et al.* (2014) gave mathematical formulas for the case of an ecological diffusion operator even in an aperiodic landscape, but without preference for certain habitat types. Habitat preference can induce directionality in overall movement behavior that makes homogenization difficult. In the one-dimensional case that we presented, it is relatively easy to ensure that this directionality averages to zero at the landscape scale, i.e., even though individuals prefer one patch type over another locally, their movement shows no preferred direction on the landscape scale. Our results are expressed not only in mathematical formulas but in certain averages of ecologically relevant and measurable quantities, which are in some sense "coordinate free". In fact, quantities such as the average residence time can be

measured for two-dimensional landscapes and then be used in our formulas even if some local information is not available separately.

HALE provides a comprehensive framework for scaling up spatially explicit models for diffusive movement of organisms in small-scale patchy environments to give landscape-scale descriptions of population dynamics. Various aspects of the theory underlying our approach have previously been used to successfully study the spread of wildlife diseases (Garlick *et al.*, 2014), insects (Powell and Bentz, 2014) and plants (Powell and Zimmermann, 2004). These studies focused on the movement processes only and in the absence of edge-related behavior. Our approach encompasses those applications and illustrates how we can scale up ecological processes in a systematic and informative way that connects to classical concepts in ecology, namely residence index and dynamic level. From the HALE framework we can develop ecological theory to explain the contrasting dynamics that can sometimes be observed between habitat- and landscape-scale studies. At the heart of our findings is the insight that fine-scale movement and behavior can have marked effects on landscape-level outcomes through the interaction of nonlinear response functions and environmental variation.

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Statement of contributions

BY, CAC, FL conceived the ideas and BY designed method; CAC conducted the numerical work; CAC and FL led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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