

Title:

2 Behavioral responses to resource heterogeneity can accelerate biological invasions

4 Running head:

Resource heterogeneity increases spread

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16 **Abstract**

18 The abundance and spatial distribution of resources in a landscape and the behavioral re-  
sponse of individuals determines whether and how fast an invasive species spreads in an en-  
20 vironment. Whether and how landscape manipulations can be used to slow invasive species  
is of great interest, in particular in forest ecosystems, where tree removal, thinning, and  
22 increasing tree diversity are discussed as management options. Classically, the focus is on  
availability and accessibility of resources; more recent considerations include individual-level  
24 behavioral movement responses to a spatially heterogeneous resource distribution. We derive  
a novel model for insect-host dynamics that includes three common behavioral aspects of  
foraging: higher movement rate in resource-poor areas, lower ovipositioning rate in resource-  
26 poor areas, and movement preference for resource-rich areas. We show that each of these  
basic mechanisms can increase the speed of invasion in a source-sink landscape above that  
28 in a homogeneous landscape with larger overall resource availability. We parameterize our  
model and illustrate our results with data for Emerald ash borer, a recent highly destructive  
30 forest pest in North America. Our results highlight the importance of empirical work on  
movement behavior in different landscape types and near the interface between types.

32

**Keywords:** Biological invasion, landscape heterogeneity, dispersal behavior, Spatial  
34 spread, forest insect pest

## 36 Introduction

38 The question of how landscape characteristics affect the spread of invasive species continues  
and global change, and incurred economic and ecological costs are high (Aukema et al., 2011),  
40 yet large-scale attempts to actively remove or destroy an invading population have yielded  
limited success, are expensive and may carry harmful side effects (Liebhold and Tobin, 2008).  
42 Increasingly, management goals focus on local detection and control (Sharov et al., 2002).  
Specifically, based on the idea of ‘fire-breaks’ (With, 2002) and its epidemiological analogue  
44 of ‘ring vaccination’, the question is whether, how, and to what extent manipulation of  
landscape structure, i.e. resource availability and distribution, could help control biological  
46 invasions.

Overall availability of resources clearly is a determining factor of spread and abundance of  
48 an invading species (Barbosa and Schaefer, 1997; Dewhurst and Lutscher, 2009; Rigot et al.,  
2014; Shigesada et al., 1986), and removal of resources has been suggested as control mea-  
50 sure, at least when the invading species is highly host specific (Brockerhoff et al., 2010). In  
Ontario, a 10×30km large ash-free ‘barrier zone’ was established to halt the spread of Emer-  
52 ald Ash borer (*Agrilus planipennis* Fairmaire) but was unsuccessful. Large-scale removal of  
resources is often expensive, infeasible, and met with local resistance (CBC, 2002). The-  
54 oretical investigations (Marsula and Wissel, 1994; With, 2004) and empirical observations  
(Rigot et al., 2014) suggest that landscape fragmentation, e.g. the localized distribution of  
56 available resources, affects invasion processes and may offer opportunities to control spatial  
spread. For example, buffer zones around uncleared windthrow have been recommended as  
58 management practice to avoid forest insect pest outbreaks after disturbance (Nikolov et al.,  
2014).

60 However, empirical and simulation studies point to the possibility that low-resource areas  
(‘matrix habitat’) interspersed with high-resource habitat patches can increase individual  
62 dispersal distance due to individual adaptation of movement behavior (Kuefler et al., 2010).  
In particular, if basic dispersal behaviors such as attraction to high-resource patches and  
64 avoidance of low-resource areas are implemented in individual-based simulation models,  
the population spread rate may be higher in a heterogeneous landscape as compared to a  
66 homogeneous landscape, even when controlling for the total amount of available resource  
(Mercader et al., 2011a,b).

68 Instead of simply removing resources, more recent considerations and recommendations  
center on the idea that diversity might be a means to slow invasions (Brockerhoff et al.,  
70 2006; Jactel et al., 2005), specifically with regards to invasive forest insects. According to  
the ‘resource concentration hypothesis’ a high plant diversity would reduce the availability  
72 and accessibility of a specific host plant. According to the ‘enemy release hypothesis’ the  
absence of natural predators in a newly colonized area allows for faster spread. Therefore,  
74 Jactel et al. (2006) argue that increased plant diversity could sustain a larger natural enemy  
diversity and thereby slow invasions. It is evident that the interplay between landscape  
76 characteristics, life cycle and dispersal behavior of the pest species is crucial in determining  
the speed of spatial spread.

78 Increasing amounts of data on individual dispersal behavior are available, and in partic-  
ular edge behavior has received much attention in past years (Ries et al., 2004; Schultz

80 and Crone, 2001). Until recently, however, these complex individual-level behaviors could  
82 only be included in individual-based simulation models but not in analytical models, even  
84 though the latter offer ‘significant advantages’ (Mercader et al., 2011a), such as paramete-  
86 ter estimation or availability of explicit solutions. Now, theoretical advances (Maciel and  
88 Lutscher, 2013) allow us to include this level of detail into analytical dispersal models that  
90 have traditionally played an important role in studying species range expansions in homo-  
geneous habitats (Hastings et al., 2005). Based on these advances, we develop a strategic  
model for the spread of a pest species in a heterogeneous landscape and test how several  
individual-level movement behaviors affect population-level spread speeds. Our model is  
inspired by the invasion of the Emerald Ash borer (*Agribus planipennis* Fairmaire) and its  
interaction with its host tree (*Fraxinus*).

The Emerald Ash borer (EAB) is a fairly recent and extremely devastating arrival to  
92 North America, that could decimate 85% of all ash trees in Canada and the US (Kovacs  
94 et al., 2010). It was discovered near Detroit in 2002 and has since spread to many US states  
96 and Canadian provinces (Cappaert et al., 2005). Gravid females lay eggs on the bark of the  
98 tree, preferentially high in the crown of the tree. Larvae bore into the bark and feed on  
the phloem. Insects emerge in the summer, mate and fly for oviposition. As phloem gets  
destroyed, trees become girdled and eventually die. Since bore holes are very small and high  
in the tree, detection of the beetle is extremely difficult. Most attempts of containment to  
date have failed.

100 Our model tracks the density of insects and the density of the resource (phloem) in space  
and time. The dynamics of growth and consumption are given by discrete maps; movement  
102 of insects for oviposition is described by a ‘dispersal kernel’. This kernel includes individual  
movement behavior in response to spatial resource distribution; it differs significantly from  
104 well-known dispersal kernels such as the Gaussian or the Laplace kernel. Specifically, we  
consider that individuals (i) adjust movement rates to habitat quality; (ii) adjust oviposition  
106 rates to habitat quality; and (iii) adjust movement preference based on habitat quality. By  
exploring each of the three mechanisms independently, we can show that increased mobility  
108 in resource-poor regions can speed up an invasion; that decreased ovipositioning in resource-  
poor regions can speed up an invasion; and that increased attraction to resource-rich areas  
110 can have either effect, depending on the landscape configuration. Using all three mechanisms  
in conjunction, we demonstrate that attraction to resource-rich areas interacts nonlinearly  
112 with the other two mechanisms to create a somewhat surprising effect where the population  
spread rate is virtually constant even as overall resource availability and accessibility de-  
114 creases greatly. To the extent possible, we parameterize our model and illustrate our results  
using data from published studies on EAB.

## 116 Model and Methods

We picture an idealized landscape consisting of two types of patches of lengths  $l_1$  and  $l_2$ ,  
118 respectively, periodically alternating with period  $l = l_1 + l_2$ , see panel A in Fig. 1 and  
Shigesada et al. (1986). We refer to the two patch types as ‘good’ or ‘bad’, according to the  
120 growth conditions for the invading species. A good patch represents high availability and  
accessibility of resources, low presence of natural enemies and low or no control measures. A

122 bad patch can result from the application of insecticide that increases mortality, it can result  
 123 from thinning, which reduces phloem availability and enhances the vigour of remaining host  
 124 trees, and it can result from higher diversity where host phloem availability and accessibility  
 125 is reduced and generalist predation may be enhanced. If  $l_2 = 0$  then the landscape is  
 126 homogeneously ‘good’.

### Individual dispersal in a patchy landscape

128 We begin by describing the ovipositioning process of a female insect as a random walk in a  
 heterogeneous landscape, where local attributes affect ovipositioning behavior.

130 A gravid female performs a random walk with diffusion coefficients  $D_1$  and  $D_2$  depending  
 on patch type, and oviposits with rates  $\alpha_1$  and  $\alpha_2$ , respectively. At an interface between  
 132 a good and a bad patch, the insect chooses to move into the good patch with probability  
 $(1+z)/2$  and into a bad patch with probability  $(1-z)/2$ , so that  $z \in [-1, 1]$  is a measure of  
 134 patch preference with  $z > 0$  indicating a preference for the good patches. From this process,  
 Musgrave and Lutscher (2014a) derived the ‘kernel’  $K(x, y)$ , i.e. the probability density  
 136 function (with respect to space  $x$ ) of eggs deposited by a female that began the oviposition  
 process at location  $y$ . When the landscape is homogeneous (i.e.  $l_2 = 0$  or  $D_1 = D_2$  and  
 138  $\alpha_1 = \alpha_2$  and  $z = 0$ ), then this kernel is simply the double exponential or Laplace distribution  
 (Neubert et al., 1995)

$$K_L(x, y) = \frac{a}{2} \exp(-a|x - y|), \quad a = \sqrt{\alpha_1/D_1}, \quad (1)$$

140 with mean dispersal distance  $1/a$ . When the landscape is not homogeneous, there is no simple  
 expression for the kernel. We give a brief summary of our previous work in Appendix S1.  
 142 Instead, we illustrate the kind of kernel that can arise from the process in a heterogeneous  
 landscape in panel A in Fig. 1. The kernel looks like a ‘ragged’ Laplace kernel where lower  
 144 oviposition rates in bad patches ( $\alpha_2 < \alpha_1$ ) and/or higher diffusion rates in bad patches  
 ( $D_2 > D_1$ ) lead to lower egg density in bad patches but higher egg density in good patches.  
 146 For illustrations of the effect of patch preference, i.e.  $z \neq 0$ , please see Musgrave and Lutscher  
 (2014a).

### 148 Population dynamics between years

Our population model tracks the density of (female) eggs ( $E_t$ ) deposited in year  $t$  and the  
 150 corresponding density of remaining phloem ( $P_t$ ). From one year to the next, eggs survive  
 and hatch with probability  $s$ , and larvae survive and mature to emergence with a probability  
 152  $(1 - e^{-P_t/\bar{P}})$  that increases with phloem levels. Higher values of parameter  $\bar{P}$  indicate higher  
 phloem requirements for successful larval development. The average number of eggs per  
 154 emergent adult female is denoted by  $r$ , and the sex-ratio of offspring is 1:1 (Cappaert et al.,  
 2005). We assume that mating is not a limitation for the insect. We model the fraction of  
 156 phloem that remains from one year to the next as a decreasing function of larvae, given by  
 $e^{-wsE_t}$ . Higher values of parameter  $w$  indicate stronger negative impact of larvae on phloem.  
 158 Since the time in which EAB can kill a tree (4-5 years) is much faster than the re-growth  
 of trees to provide a significant source of phloem, we neglect re-growth in this model. The

160 dynamics of eggs and phloem from year to year are described by the equations

$$\begin{aligned}
 E_{t+1} &= \frac{r}{2} (1 - e^{-P_t/\bar{P}}) s E_t, \\
 P_{t+1} &= P_t e^{-wsE_t}.
 \end{aligned}
 \tag{2}$$

162 The dynamics of this model are simple. Phloem density declines to zero whereas egg density may initially increase if phloem levels are high enough but will eventually decrease to zero.

### Combined spatial spread model

164 To combine the dynamics of eggs and phloem with the spatial redistribution represented by the kernel  $K$ , we denote by  $x$  the location in a one-dimensional landscape and write  $E_t(x)$  and  $P_t(x)$  for the respective densities of eggs and phloem. Since only eggs and not phloem are redistributed spatially, the densities satisfy the equations

$$\begin{aligned}
 E_{t+1}(x) &= \int_{\Omega} K(x, y) \frac{r}{2} (1 - e^{-P_t(y)/\bar{P}}) s E_t(y) dy, \\
 P_{t+1}(x) &= P_t(x) e^{-wsE_t(x)}.
 \end{aligned}
 \tag{3}$$

168 When the landscape is homogeneous and  $K$  is the Laplace kernel, we numerically observe solutions where the egg density forms a constant-speed traveling pulse, moving into high-  
170 phloem areas and leaving behind a landscape devoid of phloem (Fig. 1, panel B). The pulse changes shape somewhat from one generation to the next but remains relatively narrow for  
172 all times.

When the landscape is not homogeneous, we observe a ‘ragged’ pulse, whose profile  
174 reflects the quality of the landscape. This ‘pulse’ advances at constant speed into the high-phloem area and leaves behind a region without phloem. Panel C in Fig. 1 depicts such a  
176 solution, where initial phloem levels are set to zero in bad patches. Accordingly, egg levels peak in good patches. Eggs could be deposited in bad patches but will not survive nor  
178 mature there.

In the simulation in Panel C in Fig. 1, individuals move faster in bad patches ( $D_2 > D_1$ )  
180 and deposit eggs at a lower rate there ( $\alpha_2 < \alpha_1$ ). There is no patch preference ( $z = 0$ ). We observe that the pulse moves faster in the heterogeneous landscape and is spread over a  
182 wider area. In the ‘Results’ section, we study in detail how the speed of advancement of the ragged pulse depends on the movement-related parameters ( $D_i, \alpha_i, z$ ).

### 184 Parameter estimation

Before we explore the dependence of the spread rate on movement parameters, we present  
186 the base-line values of parameters for all simulations (unless otherwise noted). We are able to get point estimates for all parameters from recently published literature on EAB (Anulewicz  
188 et al., 2008; Rutledge and Keena, 2012; Crosthwaite et al., 2011; McCullough and Siegert, 2007; Mercader et al., 2011b). We measure  $E_t$  in # eggs/km and  $P_t$  in  $\text{m}^2/\text{km}$ . For all  
190 simulations reported below, we use  $r = 70$  (eggs per female) and  $s = 0.55$  (probability of winter survival). The scaling parameter for phloem requirement of larvae is  $\bar{P} = 5000\text{m}^2/\text{km}$ ,

192 whereas the impact of larvae on phloem gives  $w = 0.000005\text{km}/\text{larvae}$ . Parameters for  
the Laplace kernel in (1) come from an estimation of a mean dispersal distance of 0.22km  
194 (Mercader et al., 2009; Siegert et al., 2010). When 70 eggs are deposited in a 6-week dispersal  
period, we find an ovipositioning rate of  $\alpha \approx 2/\text{day}$ , and a diffusion constant of  $D \approx$   
196  $0.1\text{km}^2/\text{day}$ . For details of the estimation process, please see Section 6.2 in Musgrave (2013).

## Methods

198 We used extensive numerical simulations of model (3) to determine the speed at which  
the ragged pulse of insects advances and phloem levels decline in space. We initialized  
200 phloem levels at  $P_0(x) = 2200\text{m}^2/\text{km}$ . In the heterogeneous case, we used this value in good  
patches but reduced initial phloem levels in bad patches (see ‘Results’). We placed a density  
202 corresponding to 35 eggs (i.e. the average number of female eggs produced by a single female)  
within a single good patch. Then we tracked the furthest forward location at which the egg  
204 density exceeds a certain threshold over time and calculated the long-term average speed.  
The result is independent of the threshold value chosen.

206 Since equations (3) do not form a monotone system, there is currently no theory to  
determine the spreading speed analytically, in particular, it is an open question whether  
208 the “linear conjecture” (van den Bosch et al., 1992) holds for this system. According to  
this conjecture, the spreading speed could be determined by linearizing the equations at the  
210 leading edge where  $E \approx 0$  and  $P \approx P_0$ . We compared the results of our simulations with the  
analytic speed formula obtained from linearizing the equations (Musgrave, 2013) and found  
212 that the numerical result and the analytical prediction agreed very well. We therefore suggest  
that the linear conjecture holds for this system. Some support for this suggestion comes from  
214 a related model in continuous time (Britton, 1986). We used the analytic formulas to explore  
how movement behavior of gravid females in patchy landscapes of varying resource quality  
216 affects the speed of spread. We give the relevant formulas in Appendix S1.

## Results

218 In a homogeneously good landscape with the Laplace kernel to describe egg distribution, the  
population pulse travels at a speed of  $c_h = 0.82\text{km}/\text{year}$  and the phloem density retreats at  
220 the same rate. This speed is within the range of observed speeds between 0.4-0.7km/year  
in small infestations and 1.2-1.7km/year in larger infestations (Mercader et al., 2016). Over  
222 large scales, EAB has spread much faster, but this spread was almost certainly vectored by  
human transportation, which is not the focus of our work.

224 We use this value of  $c_h = 0.82\text{km}/\text{year}$  (with index  $h$  for ‘homogeneous’) as a benchmark  
to compare the effects of landscape structure and movement mechanisms with regards to  
226 spreading speed. Speed  $c_h$  is an increasing function of survival probability ( $s$ ), initial phloem  
availability ( $P_0$ ), reproductive output ( $r$ ) and dispersal distance ( $1/a$ ), but decreases with  
228 phloem requirement ( $\bar{P}$ ). It is independent of the effect on phloem ( $w$ ), see Appendix S1.

230 We begin with a scenario where dispersal behavior is unaffected by landscape hetero-  
geneity. For example, an insecticide is available against EAB (Thompson, 2013) and there  
is no evidence that EAB could sense and avoid trees that were inoculated. Other forest

232 pests have wind-dispersed larvae who cannot control dispersal behavior and therefore cannot  
233 adapt movement to localized removal of their host plant, for example the pine bark scale  
234 *Matsucoccus feytaudi* (Rigot et al., 2014). We simulated three scenarios in which we (i)  
235 reduced survival probability ( $s$ ) by 75% in bad patches to model inoculation; (ii) reduced  
236 phloem levels ( $P_0$ ) by 90% in bad patches to model thinning; and (iii) reduced phloem levels  
237 to zero in bad patches to model complete resource removal. In all cases, we used the Laplace  
238 kernel. As expected, we found that the actual spread rate ( $c$ ) decreases as the area where  
239 these measures are implemented (i.e. the length of bad patches) increases (Fig. 2). We note,  
240 however, that the plotted curves are concave down, so that the sensitivity of speed to inter-  
241 vention measures increases with (relative) size of intervention area. A significant proportion  
242 of the area needs to be treated or managed before a substantial effect on the spreading speed  
243 is visible. Even a 75% reduction in winter survival in the entire landscape (i.e.  $l_1 = 0, l_2 = l$ )  
244 does not stop the invasion.

In the following, we investigate in detail what happens if landscape heterogeneity does  
245 affect dispersal rates, oviposition behavior and patch preference. We fix the quality of bad  
246 patches as characterized by a 90% reduction in the initial phloem levels. This implementation  
247 can represent actual removal of host trees or more generally the combined effect of decreased  
248 availability and accessibility of hosts and increased mortality from, say, generalist predation  
249 in a highly diverse patch of landscape. We first consider each of the movement parameters  
250 separately. We do not consider in detail the effects of population dynamics parameters in  
251 heterogeneous landscapes since they are the same as in the homogeneous landscape. We give  
252 a quick illustration at the end of Appendix S1.

## 254 **Movement and oviposition rates**

An insect could reduce its dispersal rate in bad patches ( $D_2 < D_1$ ), for example if bad  
255 patches pose physical obstructions or if individuals engage in thorough searching behavior.  
256 More likely, individuals will move faster in bad patches ( $D_2 > D_1$ ) to find better habitat.  
257 Even when dispersal is passive landscape characteristics can still influence dispersal patterns.  
258 For example, the wind-dispersed larvae of the pine bark scale move further in clearings than  
259 in forest (Rigot et al., 2014). When individuals move slower in bad patches, the spread rate  
260 is reduced, but when they move faster in bad patches the spread rate is increased (Fig. 3). In  
261 fact, the spread rate in the heterogeneous landscape can be higher than in the homogeneously  
262 good landscape, even though the heterogeneous landscape provides significantly lower overall  
263 resource (phloem) availability.

Since EAB larvae can only survive in ash trees, one can expect that the egg deposition  
264 rate in a bad patch would be lower than in a good patch ( $\alpha_2 < \alpha_1$ ). Numerical simulations  
265 show that lower oviposition rates in bad patches give higher spread speeds, all else being  
266 equal. The implicit expression for the linearized speed (see Appendix S1) depends only on  
267 the ratios  $\alpha_i/D_i$  as does the Laplace kernel (1). Therefore, if the egg deposition rate in a  
268 bad patch is half that in a good patch, the result on the spread rate is the same as if the  
269 diffusion rate in a bad patch is twice that in a good patch. Hence, Fig. 3 also captures the  
270 results of varying oviposition rates. The mechanisms between the two effects, are closely  
271 related. Whether individuals move faster in bad patches or deposit fewer eggs per unit time,  
272 in either case, an egg has a higher chance to be carried further and to be deposited in a good  
273 landscape.

patch, so that the invasion can proceed faster than without behavioral adjustments.

## 276 **Preference for good patches**

278 Preference for good patches has two antagonistic effects on spread speed (Musgrave and  
280 Lutscher, 2014b). Increased patch preference increases residence time in good patches and  
282 thereby egg deposition in good patches. Overall population growth rate is increased, and  
284 therefore also spread rate. On the other hand, high preference for good patches decreases  
286 the number of dispersal events between adjacent good patches and thereby decreases the  
population spread rate. The numerical results in Fig. 4, panel A, show that for the parameter  
values chosen here, the former mechanism is stronger for low and intermediate preferences  
and the latter only shows at very strong preference levels. The highest spread rate occurs at  
intermediate preference for good patches, and the optimal preference level increases as the  
fraction of bad patches decreases.

Accordingly, when there is a weak preference for (or against) good patches, the spread  
288 speed is slightly higher (or lower) than in the absence of any preference (solid versus dashed  
curves in Fig. 4, panel B). When the preference for good patches is stronger, then the effect  
290 on spread rate depends on the relative size of bad patches (dash-dot curve, same figure).  
When only a small fraction of the landscape is bad, strong preference substantially slows the  
292 invasion, but when a large fraction of the landscape is bad, it speeds up the invasion.

## **Combined behavior**

294 When all three components of movement behavior interact, we observe that weak preference  
for good patches hardly affects the invasion speed determined by movement and oviposition-  
296 ing rate (solid versus dashed curves in Fig. 5). In particular, the spread rate in a heteroge-  
neous landscape of good and bad patches can be higher than in a homogeneous landscape  
298 of only good patches. A strong preference for good patches can decrease the spread rate  
below the speed in a homogeneous landscape (dash-dot curve, same figure). However, this  
300 curve has a ‘plateau’ where population spread rate is largely insensitive to the fraction of bad  
patches in the landscape. The strong preference for good patches ensures that the population  
302 can reproduce sufficiently to persist, and the effectively faster transport of eggs through bad  
patches ensures relatively fast overall population spread.

## 304 **Discussion**

Interventions against biological invasions and their concomitant, often devastating effects on  
306 local fauna and flora continue to pose great challenges for ecosystem management (Brocker-  
hoff et al., 2006). Since the application of direct control measures (e.g. insecticides) can be  
308 controversial (e.g. side effects, cost), indirect measures, such as mating disruption, biological  
control or removal of resources species, are increasingly explored (Brockerhoff et al., 2010).  
310 In the case of forest insect pests, several silvicultural measures have been discussed, ranging  
from increasing tree vigor through thinning to resource removal or increasing tree diversity  
312 (Muzika and Liebhold, 2000; Jactel et al., 2006; Liebhold, 2012; Nikolov et al., 2014). How-  
ever, species-specific simulation models demonstrated that individual dispersal behavior in

314 response to localized resource distributions could increase spatial spread rates as compared to  
a homogeneous landscape with an equal amount of total resources (Mercader et al., 2011b,a).  
316 Our work is the first analytically tractable model that explores how mechanistic movement  
behavior in response to heterogeneous resource distribution affects population spread rates.

318 We identified three individual-level mechanisms that can lead to increased population  
spread rates in heterogeneous landscapes, even when the total resource availability is substan-  
320 tially reduced compared to the homogeneous case. These mechanisms are (i) increased move-  
ment rate in low-resource patches; (ii) decreased oviposition rates in low-resource patches;  
322 and (iii) preference for high-resource patches. These mechanisms are not limited to ovipo-  
sitioning forest insects but apply generally when individuals of an invasive species engage  
324 in exploitative behavior (low  $D$  and high  $\alpha$ ) in high-resource patches and in explorative  
behavior (high  $D$  and low  $\alpha$ ) in low-resource patches. Patch preference (attraction to high-  
326 resource regions) in isolation exerts two antagonistic effects on population spread rate and  
interacts nonlinearly with the other behavioral effects. We therefore caution that if the in-  
328 vading organisms adjust their movement behavior to the occurrence of less favorable habitat,  
then well-intentioned management measures could inadvertently speed up population spread  
330 rates.

Our strategic analytical model complements the tactical simulation model by Mercader  
332 et al. (2011b), who considered similar mechanisms and a much more detailed life-history  
model for EAB. They used a phenomenological approach to model patch avoidance and  
334 attraction by adjusting the ‘functional distance’ between patches. We include explicitly  
movement behavior in intervening habitat and at habitat boundaries. Our model significantly  
336 extends earlier analytical models for biological invasions in homogeneous and heterogeneous  
landscapes (Shigesada et al., 1986; Hastings et al., 2005), incorporates recent developments  
338 on movement at interfaces (Maciel and Lutscher, 2013) and has the advantage of providing  
analytical formulas; see Appendix S1. It is one step forward toward integrating (optimal)  
340 foraging theory with spatial spread models. However, including additional life-history details,  
such as the switch from a two to one year development time of larvae in stressed trees (Siegert  
342 et al., 2006) and the attraction of gravid females to stressed trees (Siegert et al., 2010),  
remains an analytical challenge.

344 Our model offers challenges and opportunities for empirical work. Data on edge behavior  
exist for several insect species (Schultz and Crone, 2001; Ries et al., 2004), and sophisticated  
346 numerical methods for theoretical models are being developed concurrently (Ovaskainen and  
Crone, 2009). Sometimes edge behavior or, more generally, attraction to resources (e.g. host  
348 trees) can be inferred from dispersal observations. For example, Asian longhorned beetle  
(*Anoplophora glabripennis*) is capable of flying over 2km in a season, yet typically disperses  
350 only on the order of 10-20 meters within areas of host trees (Hu et al., 2009). In fact,  
eradication efforts have been fairly successful, presumably since initial infestations remain  
352 spatially confined (Hu et al., 2009). With regards to our model, we speculate that the  
preference for good patches ( $z$ ) is very high for this beetle so that spread rates are low. In  
354 the future, we could implement various eradication measures into our model and determine  
optimal strategies. At the other end of the spectrum, beech scale (*Cryptococcus fagisuga*) is  
356 a flightless insect that, together with the induced beech bark disease has spread at rates of  
6-8km/year (Wainhouse, 1980) and up to 14km/year (Morin et al., 2007) in eastern North  
358 America. First instars of beech scale disperse passively by wind, and their relatively high

spread rates have been attributed to higher windspeeds above forests (Wainhouse, 1980).  
360 In this case of passive dispersal, forest composition might not affect movement behavior  
but gaps in forest cover could induce differential movement and “patch preference” from air  
362 flow patterns around forest edges. Whether and how management of such passively dispersed  
invasive species could use landscape alterations is an open question. Going forward, collecting  
364 sufficient individual-level data for newly established invasive species remains a challenge.  
As these potential invaders are identified, more intense efforts are necessary to determine  
366 not only their life cycle characteristics but also their movement behavior in heterogeneous  
landscapes.

368 We focused our work on the speed of spatial spread, but the simulations in Fig. 1 show at  
least two other significant effects: the ragged pulse of invading insects in the heterogeneous  
370 landscape (panel C) has a larger spatial extent and a greater total amount of invading  
individuals than in the homogeneous case (panel B), even though the landscape contains only  
372 half the amount of resource. A detailed investigation of these effects and some analytical  
expressions are the subject of ongoing work.

374 A technical limitation that our model shares with all diffusion-based species spread mod-  
els is that of ‘infinitely long tails’ or ‘infinitely fast propagation’. Clearly, when the spatial  
376 extent of an area that is completely devoid of resources is greater than the maximum disper-  
sal distance of any invading individuals, the population front should not spread (Marsula and  
378 Wissel, 1994). Including a maximum dispersal distance in the underlying movement model  
to generate dispersal kernels would allow us to study these relative scales in the future.

380 Another question of spatial scale relates to so-called stratified dispersal, where long-  
distance dispersal events create satellite populations that spread locally (Shigesada et al.,  
382 1995). In such a scenario, our work applies only to the local spread of satellite populations.  
This localized aspect of species’ invasions has received great attention recently since most  
384 intervention measures are local in nature and some have reported success in slowing invasions  
(Moody and Mack, 1988; Sharov and Liebhold, 1998; Taylor and Hastings, 2004; Liebhold  
386 and Tobin, 2008). Long-distance dispersal is often facilitated by dispersal vectors (e.g. human  
transportation) and requires different consideration and modeling approaches.

388 Our model did not include an Allee effect, yet Allee effects play a role in many invasion  
processes. Even in a homogeneous landscape, there is no simple speed formula when an  
390 Allee effect is present, but two recent numerical and semi-analytical studies explored the  
impacts of landscape heterogeneity and Allee effect on invasion speeds (Musgrave et al.,  
392 2015; Maciel and Lutscher, 2015). Equally important, our model did not include an increased  
mortality risk in bad patches for the dispersing individuals (e.g. due to energy requirements or  
394 predation). The theory to include patch-specific dispersal mortality is developed (Musgrave  
and Lutscher, 2014a). While a complete investigation of this effect is beyond the scope of  
396 our work here, we include a short exploration in Appendix S1. The most important insight  
is that if dispersal mortality occurs only in bad patches then it has a very small effect when  
398 the fraction of bad patches is small. In particular, the increase in spreading speed due to  
movement behavior in bad patches still occurs, even for relatively large dispersal mortality  
400 (see Appendix S1: Fig. S2).

In our work, we viewed disturbances as negative for the invading species, for example  
402 through the localized application of insecticide or the reduction of availability and accessi-  
bility of resources. Another view of biological invasions is that an invading species benefits

404 from disturbances (With, 2002), for example, when contiguous forest is interrupted and edges  
create opportunities for species with higher light requirement. Our work indicates that rel-  
406 atively small, localized disturbances, combined with appropriate dispersal behavior, could  
lead to reasonably high population spread rates of these disturbance-loving species.

408 Our work also applies to intentional facilitation of spread for example as mitigation  
measures for climate-change effects. As temperature isoclines move poleward, there is great  
410 concern that certain species will not be able to keep pace with their ecological niches (Leroux  
et al., 2013). Suggestions to mitigate negative effects on population persistence include the  
412 creation of ‘stepping stones’, high quality habitat patches that enable a species to move  
with their climatic requirements (Saura et al., 2013). Our results show that spatial spread  
414 rates in heterogeneous environments can be higher than in homogeneous environments, even  
when the overall resource abundance is lower. Accordingly, species endangered by climate  
416 change might be able to spread pole-ward faster than their spread rates in homogeneous  
environments predict. Such an increased speed might help those species to keep up with the  
418 speed of climate change.

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## Figure legends

### 570 **Figure 1**

**Panel a:** Dispersal kernel in a patchy landscape (solid line) compared to the Laplace kernel (dash-dot). Periodically spaced good patches are indicated by thick black lines on the  $x$ -axis. Parameters are  $D_1 = 0.1$ ,  $D_2 = 0.3$ ,  $\alpha_1 = 2$ ,  $\alpha_2 = 1$ , and  $z = 0$ . Parameters for the Laplace kernel are  $D_1 = 0.1$  and  $\alpha_1 = 2$ . **Panel b:** Egg (solid) and phloem (dashed) density at time  $t = 15$  in a homogeneous landscape with Laplace dispersal kernel. The insect population moves in the direction of the arrow, leaving phloem-depleted landscape in its wake. Population dynamics parameter values are as in ‘Parameter estimation’ and the mean dispersal distance is  $\frac{1}{a} = 0.22\text{km} = \sqrt{\alpha_1/D_1}$ . At  $t = 0$ , an initial density of 70 eggs is uniformly distributed over the range  $\pm 0.1\text{km}$ . **Panel c:** Egg (solid) and phloem (dashed) density at time  $t = 15$  in a heterogeneous landscape with kernel and parameters as in panel A. The initial distribution is the same as in B.

582

### **Figure 2**

584 Reduction of spread speed ( $c/c_h$ ) as a function of the relative area treated ( $l_2/l$ ) with three different measures in bad patches: (i) 75% reduction in winter survival (dash-dot), (ii) 90% reduction of initial phloem (dashed), and (iii) complete removal of resources (solid), see text for more explanation.

588

### **Figure 3**

590 Spread speed ( $c/c_h$ ) as a function of the relative area treated ( $l_2/l$ ) is slower when individuals move slower in bad patches (dotted:  $D_2 = 0.5D_1$ ), or faster when individuals move faster (solid:  $D_2 = 2D_1$ , dash-dot:  $D_2 = 3D_1$ ). The dashed curve with equal movement rates ( $D_2 = D_1$ ) is the same as in Fig. 2 for comparison. Other parameters are held fixed at their baseline values. Equivalently, the speed is faster when egg deposition rates are smaller in bad patches (solid:  $\alpha_2 = 1/2\alpha_1$ , dash-dot:  $\alpha_2 = 1/3\alpha_1$ ) and slower if deposition rates are higher (dotted:  $\alpha_2 = 2\alpha_1$ ) with other parameters fixed at baseline values.

### 598 **Figure 4**

**Panel a:** Spread speed is a hump-shaped function of preference for good patches. The location of the maximum depends on the fraction of remaining good habitat (dashed: 75%, solid: 50%, dash-dot: 25%). Initial phloem levels in bad patches are only 10% of those in good patches; all other parameters, including movement parameters, are the same between the two patch types. **Panel b:** Weak positive preference slightly increases spread rate (top solid curve,  $z = 0.1$ ), weak negative preference decreases it (bottom solid curve,  $z = -0.1$ ), compared to no preference (dashed curve,  $z = 0$ , same as in Fig. 2). Strong preference (dash-dot curve,  $z = 0.5$ ) can slow spread for small bad patches but increases spread for large bad patches. Other movement parameters are the same between the two patch types.

608

### **Figure 5**

610 Spread speed with weak preference (solid,  $z = 0.1$ ) differs only little from speed without preference (dashed,  $z = 0$ ) as egg deposition rate changes in bad patches (different values of  $\alpha_2$ ). Strong preference (dash-dot,  $z = 0.5$ ,  $\alpha_2 = 1$ ) decreases spread speed below  $c_h$  but also

612

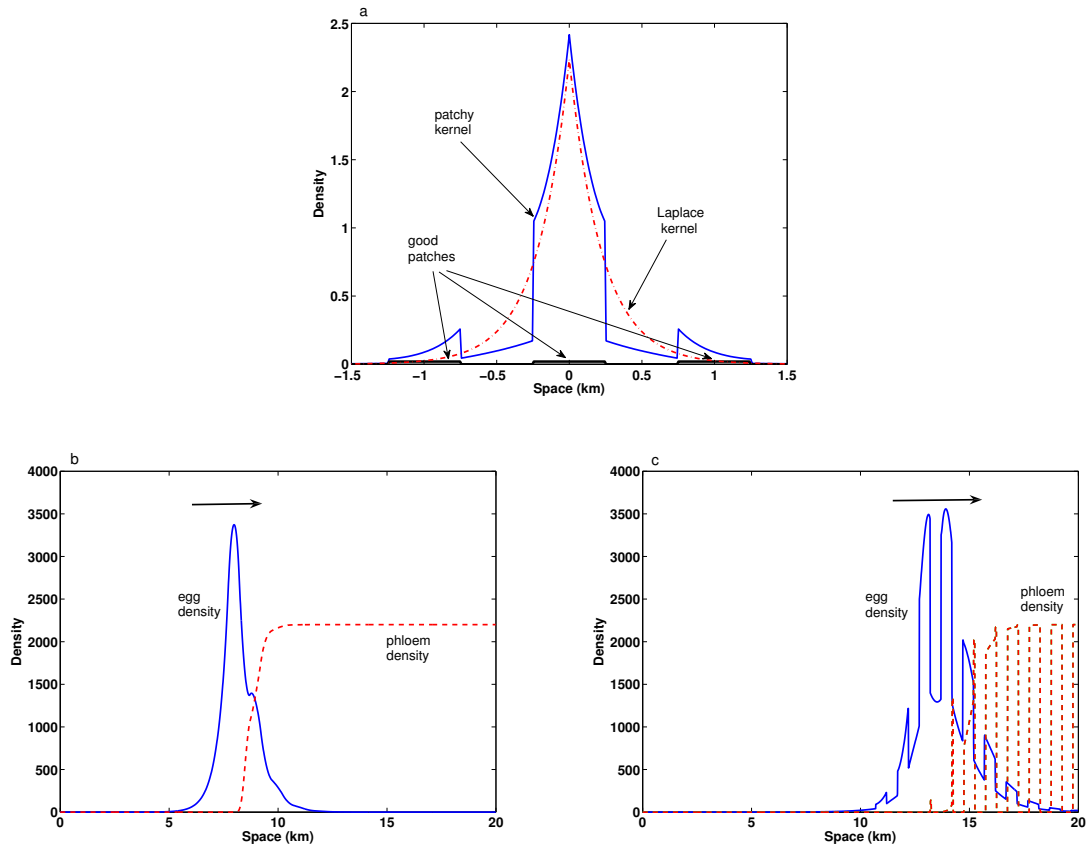


Figure 1:

makes it insensitive to changes in the fraction of bad area.

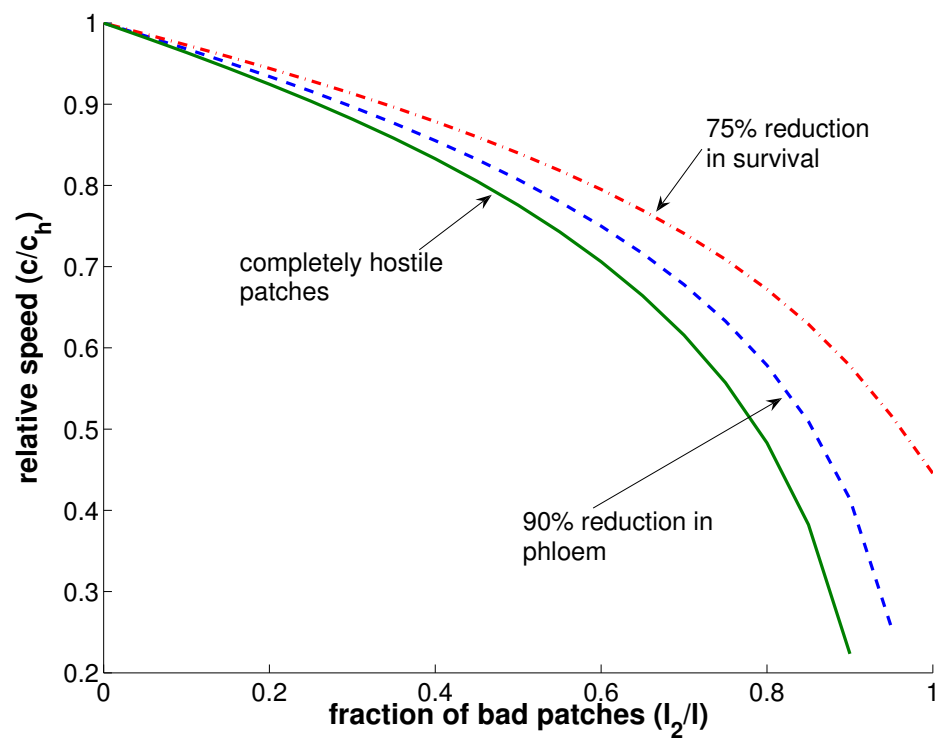


Figure 2:

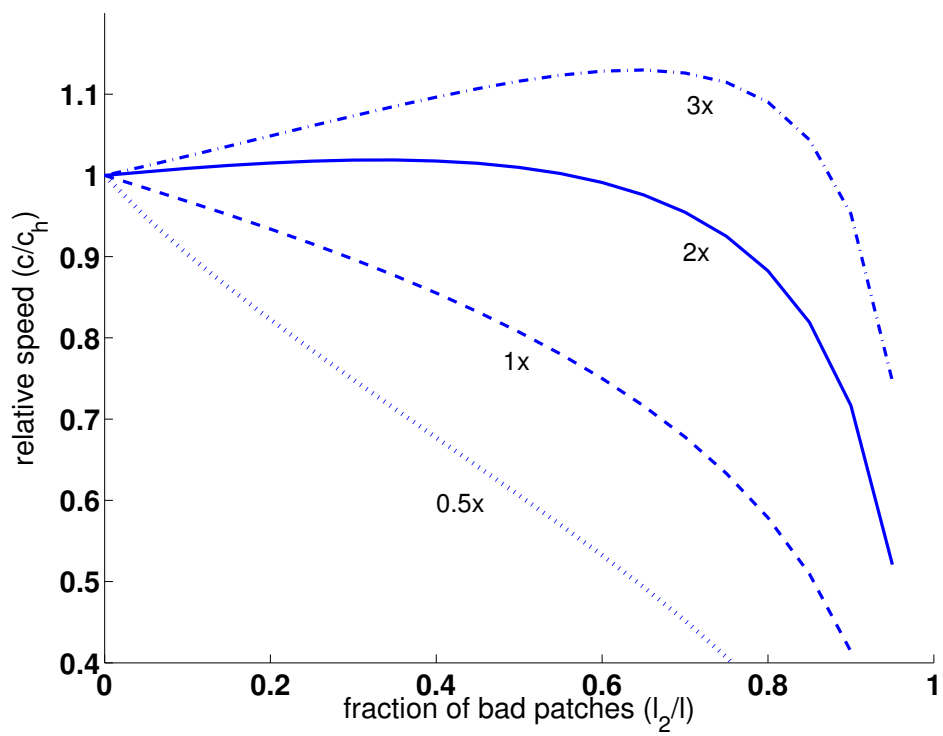


Figure 3:

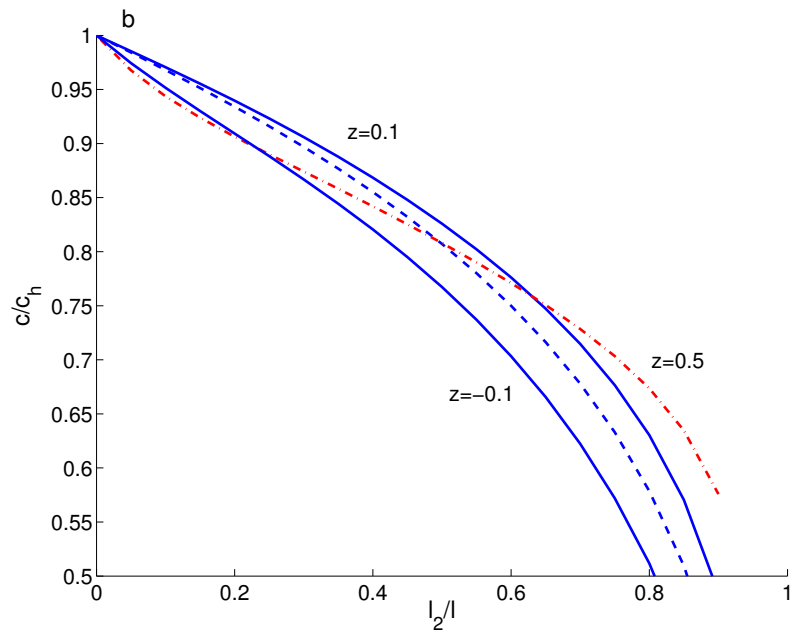
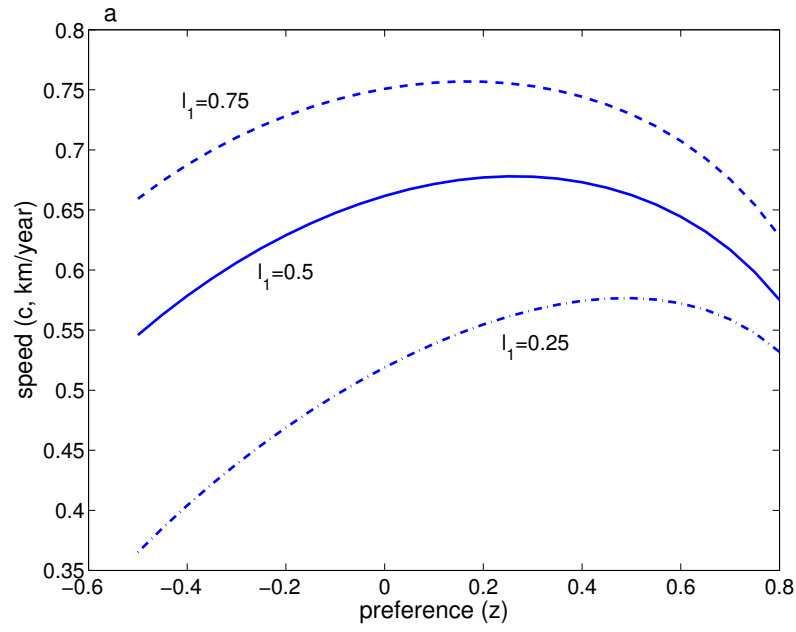


Figure 4:

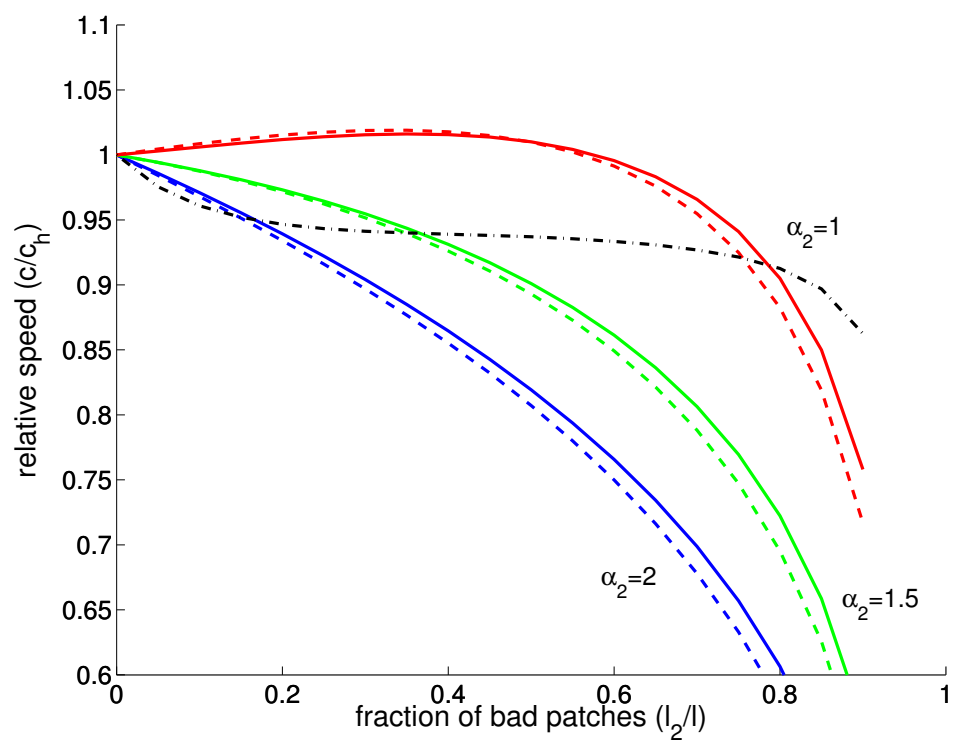


Figure 5:

**Appendix S1** – Lutscher and Musgrave, Behavioral responses to resource heterogeneity can accelerate biological invasions

We present a very brief mathematical background on random walks, diffusion equations, and spreading speeds for the mathematically inclined reader. We refer to Neubert et al. (1995); Maciel and Lutscher (2013); Musgrave and Lutscher (2014a,b); Ovaskainen and Cornell (2003); Turchin (1998) for more details.

**From random walks to diffusion equations**

We describe the location of an individual that performs an unbiased random walk with settling on a regular one-dimensional grid. Within a fixed time step  $\Delta t$  the individual moves with probability  $p\Delta t$  from its current location with a fixed step length  $\Delta x$  either to the left or right with equal probability  $1/2$ . The probability that the individual stops its walk and settles at the current location is  $\alpha\Delta t$ . All parameters are assumed positive.

We let  $u(x, T; y)$  denote the probability density of the location  $x$  at time  $T$  of an individual that was at location  $y$  at  $T = 0$ . In the parabolic limit, when space and time steps are small (i.e.  $\Delta t, \Delta x \rightarrow 0$ ) and the limit

$$\lim_{\Delta t, \Delta x \rightarrow 0} \frac{(\Delta x)^2}{2\Delta t} = D \tag{S1}$$

is finite, then density  $u(x, T; y)$  satisfies the reaction diffusion equation

$$\frac{\partial u}{\partial T} = pD \frac{\partial^2 u}{\partial x^2} - \alpha u, \quad u(x, 0; y) = \delta(x - y), \tag{S2}$$

where  $\delta(x)$  is the Dirac mass concentrated at  $x$ . Eventually, the individual will settle with probability 1. The distribution of locations where the individual settles is given by the ‘kernel’

$$K(x, y) = \int_0^\infty \alpha u(x, T; y) dT. \tag{S3}$$

This expression can be calculated explicitly to be the Laplace kernel from Eq. (1) (for  $p = 1$ ).

**From patch preference to matching conditions**

When the landscape is not homogeneous, parameters  $p$  and  $\alpha$  can vary in space. When the landscape consists of patches that are homogeneous within but differ between, a random walk within a patch is still described by a diffusion equation as above. We denote by  $D_i = p_i D$  and  $\alpha_i$  the parameters in a patch of type  $i$ . At an interface ( $x_I$ ) between two patch types, the individual can choose to enter the ‘good’ patch with probability  $(1 + z)/2$  and the ‘bad’ patch with probability  $(1 - z)/2$ . Then one can derive so-called matching conditions for the density  $u$  and its derivative at this interface. When the good patch is located to the right of  $x_I$  and the bad patch to the left, then these matching conditions read

$$\lim_{x \nearrow x_I} u(x, T; y) = \frac{D_1(1 - z)}{D_2(1 + z)} \lim_{x \searrow x_I} u(x, T; y), \tag{S4}$$

and

$$D_2 \lim_{x \nearrow x_I} \frac{\partial}{\partial x} u(x, T; y) = D_1 \lim_{x \searrow x_I} \frac{\partial}{\partial x} u(x, T; y), \quad (\text{S5})$$

The definition of the kernel for the location where the individual settles changes only slightly, namely,

$$K(x, y) = \int_0^\infty \alpha(x) u(x, T; y) dT, \quad (\text{S6})$$

where  $\alpha(x) = \alpha_1$  in good patches and  $\alpha(x) = \alpha_2$  in bad patches. An explicit expression for  $K$  cannot be derived. A comprehensive study of the resulting kernel was given by Musgrave and Lutscher (2014a).

### Linearizing the integrodifference equation

The spreading speed for a linear integrodifference equation in a homogeneous environment can be calculated according to a well-known formula (below). Whether the spreading speed of a nonlinear equation is equal to that of its linearization is often difficult to prove. When we linearize the system of equations in (3) at the state where  $E = 0$  and  $P = P_0$ , we find that the second equation gives  $P_{t+1} = P_t$ , which means that  $P_t = P_0$  remains constant in the linearization. Substituting this constant makes the equation for  $E$  into a linear equation, namely

$$E_{t+1}(x) = \int_{\Omega} K(x, y) \underbrace{\frac{r}{2} (1 - e^{-P_0/\bar{P}})}_{\rho} s E_t(y) dy = \int_{\Omega} K(x, y) \rho E_t(y) dy. \quad (\text{S7})$$

When  $K(x, y) = \tilde{K}(x - y)$ , then the spreading speed for this linear equation is given by the formula

$$c^* = \min_{s>0} c(s) := \min_{s>0} \frac{1}{s} \ln[\rho M(s)], \quad (\text{S8})$$

where  $M(s) = \int \tilde{K}(x) e^{sx} ds$ . In particular, the spreading speed for this linearized equation is independent of parameter  $w$ . The speed is an increasing function of  $r, s, P_0$  and a decreasing function of  $\bar{P}$  since  $\rho$  has the same properties.

### Speeds in patchy landscapes

If parameters in the linear equation (S7) vary with patch type, then so does  $\rho$ , and we write  $\rho_i$  for the overall linearized growth rate on patch type  $i$ . With the kernel given by the random walk process described above, we can still write the spreading speed as  $c^* = \min_{s>0} c(s)$ , but there is no explicit expression for  $c(s)$ . Instead, function  $c(s)$ , also called the dispersion relation, is defined implicitly by the relation

$$\frac{q_1^2 + (q_2 \bar{z})^2}{2\bar{z}q_1q_2} \sinh(q_1 l_1) \sinh(q_2 l_2) + \cosh(q_1 l_1) \cosh(q_2 l_2) = \cosh(sl), \quad (\text{S9})$$

where  $q_i = \sqrt{\sqrt{D_i/\alpha_i} [1 - \exp(-sc(s))\rho_i]}$  and  $\bar{z} = (1 - z)/(1 + z)$ . We note that the diffusion coefficients and settling rates only appear as quotients in this expression. The relation can be used to evaluate  $c(s)$  numerically, and then find the minimum over all positive values  $s$ . This procedure was used to produce the plots for the speeds in this work.

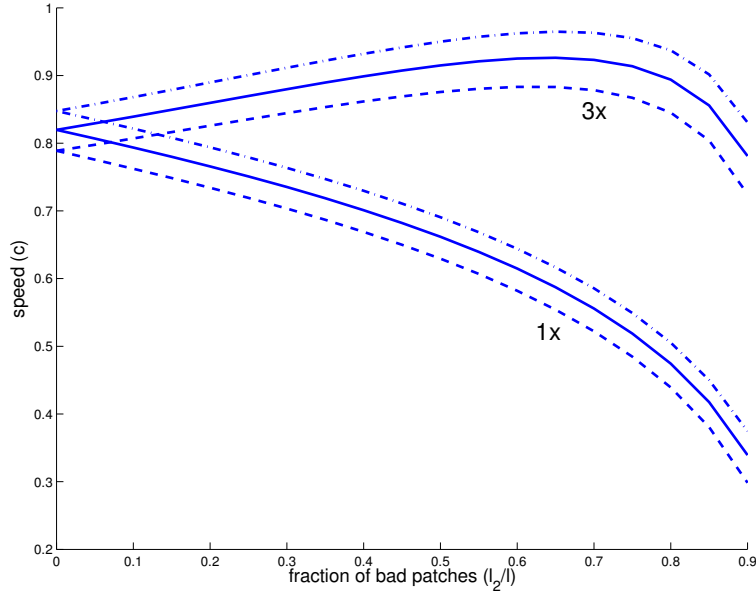


Figure S1: Actual spread speed increases as the combined population-dynamics parameter  $\rho = r(1 - e^{-P_0/\bar{P}})s/2$  increases. The solid lines are the same as in Fig. 3. Dashed curves indicate a 10% reduction in  $\rho$ , whereas dash-dot curves indicate a 10% increase. All other parameters are as in Fig. 3. The upper three curves ( $3\times$ ) depict the case where diffusion in bad patches is three times that in good patches; the lower curves ( $1\times$ ) have equal diffusion in good and bad patches.

### Sensitivity with respect to population dynamics parameters

In the main text, the focus is to find how the speed of spread depends on movement-related parameters. Here, we briefly mention how the speed depends on the population dynamics parameters of the model. From the linearized equation in (S7), it is clear that we only need to check the dependence on the composite parameter  $\rho$ , or  $\rho_i$ . The speed increases as this parameter increases while all other parameters are held constant. Fig. S1 illustrates this effect in parallel with Fig. 3 from the main text. It shows the absolute speed as a function of the fraction of bad patches when the diffusivity in bad patches equals that in good patches ( $1\times$ ) or is three times as large ( $3\times$ ). In each case, the solid line corresponds to the default parameters. The dashed curve corresponds to reducing  $\rho$  by 10% and the dash-dot curve illustrates an increase of  $\rho$  by 10%.

### Mortality during dispersal

Habitat patches of ‘bad’ quality can induce mortality of the dispersing organisms. This mortality should reduce the spread rate and could potentially counterbalance the increase in spread rate that can arise from movement behavior in bad patches. The theory presented by Musgrave and Lutscher (2014a,b) and summarized above allows for mortality during dispersal. The changes to the theory are relatively small.

We denote the mortality rate per unit time with  $\beta$ . Then the movement equation in (S2) turns into

$$\frac{\partial u}{\partial T} = pD \frac{\partial^2 u}{\partial x^2} - (\alpha + \beta)u, \quad u(x, 0; y) = \delta(x - y), \quad (\text{S10})$$

but the definition of  $K$  in (S3) remains unchanged. The formula for the dispersion relation in (S9) is also unchanged, but the  $q_i$  now contain the ‘effective’ growth rate

$$\hat{\rho}_i = \rho_i \frac{\alpha_i}{\alpha_i + \beta_i}, \quad (\text{S11})$$

where  $\rho_i$  is as in (S7), and  $\alpha_i, \beta_i$  are the oviposition rate and mortality rate in patch type  $i$ .

If dispersal mortality is independent of patch type, then it acts as if reproductive output were reduced. If dispersal mortality is larger in bad than in good patches, then its effect is small when the fraction of bad patches is small and increases as that fraction increases. In particular, even when bad patches incur dispersal mortality, an increase in spread rate due to movement behavior is still possible.

We illustrate this effect in Fig. S2, where we compare the scenario without mortality (solid lines, same as in Fig. 3 and Fig. S1) to two kinds of mortality. The dash-dot curve corresponds to patch-independent dispersal mortality at rate 1 per day. The dashed curve was generated with zero dispersal mortality in good patches and mortality rate of 10 per day in bad patches.

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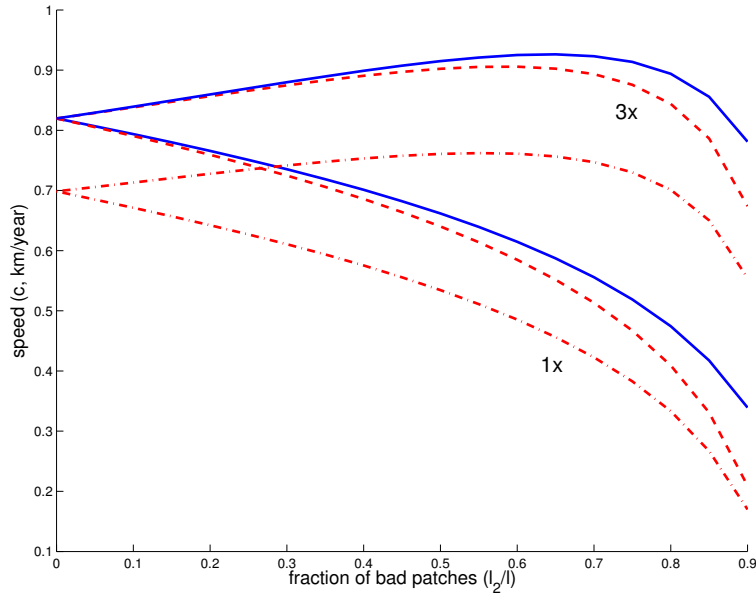


Figure S2: Actual spread speed decreases with dispersal mortality. The solid lines indicate no dispersal mortality; they are the same as in Fig. 3. Dash-dot lines have patch independent dispersal mortality ( $\beta_1 = \beta_2 = 1$ ). Dashed lines have no dispersal mortality in good patches ( $\beta_1 = 0$ ) and high dispersal mortality in bad patches ( $\beta_2 = 10$ ). The upper three curves ( $3\times$ ) depict the case where diffusion in bad patches is three times that in good patches; the lower curves ( $1\times$ ) have equal diffusion in good and bad patches. All other parameters are as in Fig. 3.