



HAL
open science

Spatial heterogeneity alters the trade-off between growth and dispersal during a range expansion

Patrizia Zamberletti, Lionel Roques, Florian Lavigne, Julien Papaïx

► **To cite this version:**

Patrizia Zamberletti, Lionel Roques, Florian Lavigne, Julien Papaïx. Spatial heterogeneity alters the trade-off between growth and dispersal during a range expansion. 2022. hal-03770639

HAL Id: hal-03770639

<https://hal.science/hal-03770639v1>

Preprint submitted on 6 Sep 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Spatial heterogeneity alters the trade-off between growth and dispersal during a range expansion

Patrizia Zamberletti^{1,*}

Lionel Roques¹

Florian Lavigne²

Julien Papaix¹

1. INRAE, BioSP, 84914, Avignon, France;

2. Université de Rouen Normandie, CNRS, Laboratoire de Mathématiques Raphaël Salem, France;

* Corresponding author; e-mail:patrizia.zamberletti@inrae.fr.

Keywords: Eco-evo model, Reaction-diffusion system, Evolutionary R-D trade-off, fragmented space, nonlocal competition.

Abstract

2 Individuals who invest more in the development of their dispersal-related traits often
reduce their investment in reproduction. Thus, there are two possible eco-evolutionary
4 strategies: grow faster or disperse faster ($R - D$ arbitrage). Here we explore, through
a reaction-diffusion model, how spatial heterogeneity can shape the $R - D$ trade-off by
6 studying the spreading dynamics of a consumer species exploiting a resource in a spa-
tially fragmented environment. Based on numerical simulations and analytical solutions
8 derived from simpler models, we show that the classical mathematical symmetry be-
tween the effects of growth and dispersal on the spatial spreading speed is broken in the
10 presence of competition between phenotypes. At the back of the forefront, the dynamics
is almost always driven by the R specialists. On the forefront, R -strategies are favored
12 in spatially homogeneous environments, but the introduction of heterogeneity leads to a
shift towards D -strategies. This effect is even stronger when spatial heterogeneity affects
14 the diffusion term and when spatial fragmentation is lower. Introducing mutations be-
tween phenotypes produces an advantage towards the R -strategy and homogenizes the
16 distribution of phenotypes, also leading to more polymorphism on the forefront.

1 Introduction

18 Rapid evolution in species traits can affect their ecological dynamics which in turn feed-
back on the evolutionary potential (Bonte and Bafort, 2019; Burton et al., 2010). Such
20 interaction between ecological and evolutionary dynamics is crucial to understand the
demography when species shift their range as in the case of evolutionary rescue (Anci-
22 aux et al., 2019), migrational meltdown (Ronce and Kirkpatrick, 2001), biological invasion
(Szűcs et al., 2019). Population expansion is an ecological process mainly driven by traits
24 related to reproduction and dispersal (Deforet et al., 2019; Turchin, 1998). Dispersal af-
fects capabilities to exchange individuals and genes among different habitats (Legrand
26 et al., 2017). Dispersal traits have been proven to be related to body dimension and
condition (Duthie et al., 2015; Helms and Kaspari, 2015; Steenman et al., 2015), affecting
28 competitive abilities, food web interactions (Bonte and de la Pena, 2009) or metabolic
processes (Hirt et al., 2017). As a consequence, there are many examples where individ-
30 uals who invest more in the development of their traits related to the dispersal strategy
reduce the effort in foraging and reproduction (*e.g.*, reducing their mating period or with
32 lower egg mass) (Baguette and Schtickzelle, 2006; Bonte and Bafort, 2019; Hanski et al.,
2006). In such cases, two possible evolutionary strategies exist: dispersing faster or grow-
34 ing stronger (Deforet et al., 2019). This results in a species' trait trade-off that shapes the
ecological and evolutionary dynamics of populations.

36 During invasion process, there is evidence that trait evolution can be very rapid alter-
ing demographic processes (Griette et al., 2015; Perkins et al., 2013). At the forefront, *i.e.*,
38 in the frontmost part of the population range, studies highlight that spread rate jointly
depends on population growth and dispersal, and that the evolution of these traits can

40 results in an accelerating spread (Fisher, 1937; Perkins et al., 2013). For example, Perkins
et al. (2013) focused on how life-history or dispersal traits impact spread rates of the cane
42 toad, *Rhinella marina*, in Australia by combining a stage-structured population dynamics
model and an evolutionary quantitative genetic model. They pointed out that rapid evo-
44 lution of life-history and dispersal traits at the forefront could have led to a more than
twofold increase in the distance spread by cane toads across northern Australia. Indeed,
46 spatial sorting of high-dispersal individuals drove dispersal evolution at the forefront
and may have resulted in the accumulation of individuals with extreme dispersal abili-
48 ties at its edge, accelerating invasion (Bouin et al., 2012; Perkins et al., 2013; Shine et al.,
2011). However, the individuals leading the forefront should also face novel evolutionary
50 pressures on reproduction, due to low population densities (Kelehear and Shine, 2020).
An example of the interactions between dispersal and other key life history traits, such
52 as reproduction, is wing polymorphism of various species of insects (Zera and Denno,
1997). The flight capability (defined by developed wings and flight muscles) is negatively
54 correlated with age at first reproduction and fecundity (Denno, 1994). Thus, the energy
efforts for flight and reproduction lead to a trade-off for internal resources (Zera and
56 Denno, 1997).

Reaction-diffusion models are particularly well suited to the study of biological in-
58 vasions and range expansions in general (Shigesada and Kawasaki, 1997; Turchin, 1998),
and to mathematically formalize the relationship between species life-history traits and
60 expansion speed. The first spatio-temporal models of this type considered a homoge-
neous environment and neglected adaptation (Skellam, 1951). In this case, if the popu-
62 lation is initially concentrated in a bounded region, the organisms spread with a speed
equal to $2\sqrt{RD}$ (Fisher, 1937; Kolmogorov et al., 1937), where R is the intrinsic growth

64 rate of the population and D is the diffusion coefficient which measures the dispersal
capacities of the individuals. The population density tends to keep a constant profile: it
66 converges to a traveling wave. The reaction-diffusion framework can be easily adapted
to take into account spatial and/or temporal heterogeneities (Shigesada and Kawasaki,
68 1997). Several theoretical studies considered such models, and proposed a generaliza-
tion of the notion of traveling wave to spatially-fragmented environments (Berestycki and
70 Hamel, 2002, 2005; Berestycki et al., 2005; Weinberger, 2002). These studies, and other
references that we mention in the following sections, have provided a detailed under-
72 standing of the dependence of the spreading speed on spatial fragmentation, according
to the particular traits they affect (R , D or both), in the absence of adaptation. In partic-
74 ular, very different effects of fragmentation have been observed, depending on whether
they affect R or D (Hamel et al., 2011).

76 Some recent works have proposed to take into account genetic adaptation in these
spatio-temporal models, thanks to an additional variable, say y (interpreted as a pheno-
78 typic trait), a mutation term modeled with a Laplace diffusion operator, and a nonlocal
selection term (Alfaro et al., 2017, 2013; Alfaro and Peltier, 2021; Peltier, 2020). These
80 models describe adaptation along an environmental gradient, that is, a gradual change
in various factors in space that determine the phenotypic traits that are favored by their
82 growth rate $R(x, y)$. Here, each spatial position x is associated with a different optimal
trait, *i.e.*, a trait which leads to a maximal growth rate. The value of this optimal trait
84 may be proportional to the position (Alfaro et al., 2013; Peltier, 2020), may depend pe-
riodically on x (Alfaro and Peltier, 2021), or may change with time (Alfaro et al., 2017).
86 Another important part of this literature has been interested in the case where the trait is
the diffusion coefficient D (Benichou et al., 2012; Berestycki et al., 2015; Bouin and Calvez,

88 2014; Bouin et al., 2012), and mostly focused on the acceleration of the range expansion
in this case, due to the selection of the individuals with enhanced dispersal abilities. The
90 objective of these works was mainly to explain the acceleration of the range expansion of
can toads since their introduction in Australia, and the corresponding model is often re-
92 ferred to as the “cane toad equation”. Recently, this framework has been applied to other
traits such as the Allee threshold (Alfaro et al., 2021). In all of these reaction-diffusion
94 based models, the additional phenotypic variable only affects a single biological param-
eter, either directly when this variable is the trait itself such as the diffusion term D or
96 the Allee threshold, or indirectly when the growth rate $R(x, y)$ depends on an abstract
trait y . This means that trade-off between traits are not considered. Recently, Bouin et al.
98 (2018) considered such a trade-off between dispersal and growth in the cane toad equa-
tion. They mainly focused on theoretical mathematical results and on the occurrence of
100 acceleration, in a homogeneous environment, depending on the rate of increase of the
mortality term when the diffusion term is increased.

102 In this work, we develop a reaction-diffusion model to describe the phenotype-space-
time dynamics of a consumer species in a fragmented space during a range expansion.
104 We focus on the trade-off between the growth rate $R(x, y)$ and dispersal rate $D(x, y)$,
which are both defined as functions of the space variable x and the phenotype variable
106 y . In a spatially homogeneous environment and in the absence of mutations and Allee
effects, the standard formula $V = 2\sqrt{RD}$ clearly shows that growth and dispersal play a
108 similar role on the spreading speed (Kolmogorov et al., 1937). We analyze here how this
symmetry in the effects of R and D may be broken when facing spatial fragmentation, in
110 the presence of competition between phenotypic traits or in the presence of mutations.

2 Model and methods

2.1 Eco-evolutionary dynamics

112

At time t and location x , the density of the consumer phenotype y is defined by $c(t, x, y)$.

{model}

114

We describe the spatial dispersion in a one-dimensional environment with a Laplace diffusion operator, corresponding to random walk movements of the individuals, with a

116

mobility parameter (also called diffusion coefficient) $D(x, y)$ (Shigesada and Kawasaki, 1997; Turchin, 1998). We assume a one-dimensional phenotype $y \in (y_{\min}, y_{\max})$. The mu-

118

tations between phenotypes are also described with a Laplace diffusion approximation (Hamel et al., 2020; Tsimring et al., 1996) with constant mutation coefficient $\mu \geq 0$. The

120

mutation coefficient μ is proportional to the mutation rate (per individual per generation) and to the average mutation effect on phenotype (Hamel et al., 2020). Finally, the

122

population grows logistically with a spatially variable growth rate $R(x, y)$. Competition occurs locally on the geographical space but globally over phenotypes through a nonlocal

124

term, and is modulated by a parameter γ . This leads to the following reaction-diffusion model for the phenotype-space-time dynamics of the consumer population:

126

$$\begin{aligned} \partial_t c(t, x, y) = & \partial_{xx}(D(x, y) c(t, x, y)) + \mu \partial_{yy} c(t, x, y) \\ & + c(t, x, y) \left(R(x, y) - \gamma \int_{y_{\min}}^{y_{\max}} c(t, x, s) ds \right), \end{aligned} \quad (1)$$

128

130

with $t > 0$, $x \in \mathbb{R}$ and $y \in (y_{\min}, y_{\max}) \subset \mathbb{R}$. In all cases, we assume an initial condition $c(0, x, y) = \mathbb{1}_{x < 0}$, the characteristic function of the domain $(x, y) \in (-\infty, 0) \times$

132

(y_{\min}, y_{\max}) , and we focus on the spreading of the solution to the right, that is in the direction of positive x . In addition, we assume no-flux boundary conditions at the bound-

134 aries $y = y_{\min}$ and $y = y_{\max}$:

$$\partial_y c(t, x, y_{\min}) = \partial_y c(t, x, y_{\max}) = 0,$$

136 so that in the absence of demography (*i.e.*, if $R = \gamma = 0$), and with an integrable initial
condition $c(0, x, y)$, the global population size $\mathbf{C}(t) = \int_{\mathbb{R} \times (y_{\min}, y_{\max})} c(t, x, y) dx dy$ would
138 remain constant.

2.2 *Modeling genetic and spatial fragmentation in dispersal and growth*

140 Spatial fragmentation in environmental conditions are assumed to impact the consumer
growth rate R and its mobility D . Genetic and environmental effects on R and D are
142 assumed to be additive. The parameters

$R_0 > 0$ and $D_0 > 0$ are the basal values for growth and diffusion. These basal values
144 are modified according to a genetic effect, R_g , respectively D_g , and a environmental
effect, R_s , respectively D_s . The parameter L controls the spatial fragmentation: $R_s(x/L)$
146 and $D_s(x/L)$ are L -periodic. A small value of L corresponds to a highly fragmented
(or rapidly varying) environment, and a large value corresponds to a low fragmented
148 (or slowly varying) environment. Moreover, we also test the effect of introducing an
amplitude effect to scale the fragmentation with respect to the scenario presented (see
150 Appendix A).

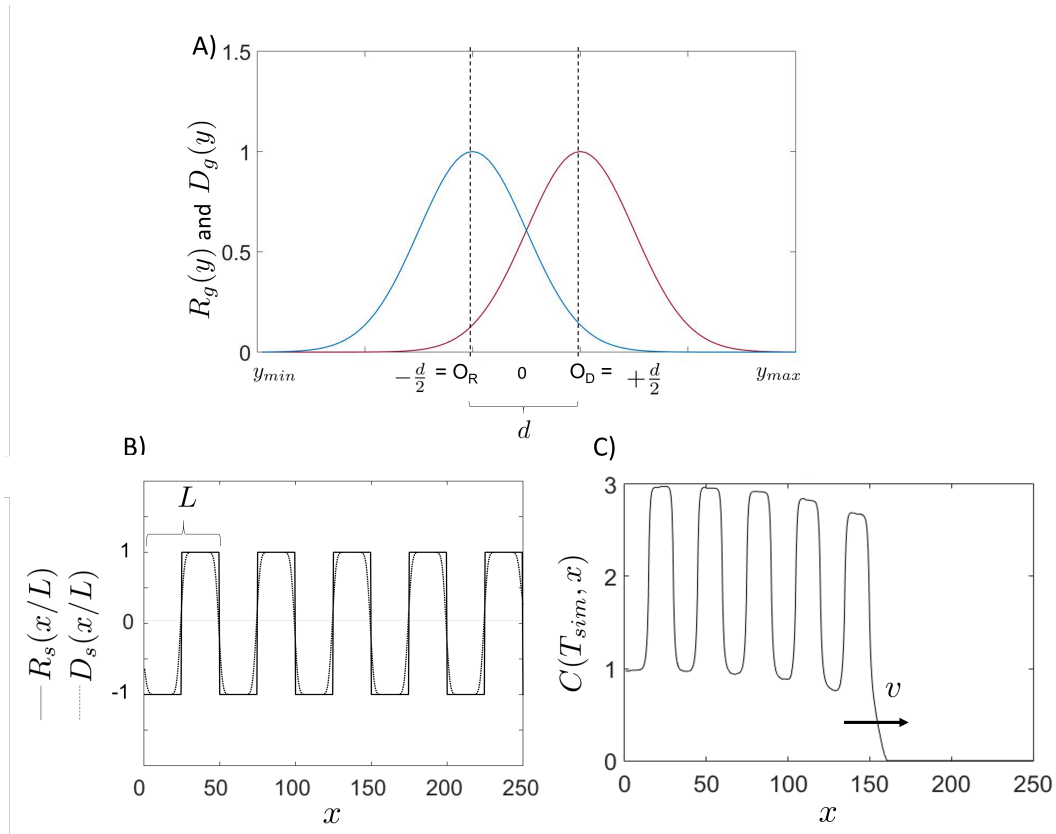


Figure 1: **Genetic and environmental effects on growth (R) and dispersal (D).** The panel A displays the curves representing the genetic effect for the dispersal rate $D_g(y)$ (red) and growth rate $R_g(y)$ (blue) expressed as a function of phenotypic traits $y \in (y_{min}, y_{max})$. The coefficient d is the distance between the optima for dispersal and growth rate. The panel B shows the environmental effect for the dispersal ($D_s(x/L)$) (dotted line) and ($R_s(x/L)$) (solid line). The panel C shows an example of resulting total population density $C(T_{sim}, x)$ (see Equation (5)) obtained from the solution of the Equation (1) at time $T_{sim} = 60$ along with the position x , with the parameter values: $\mu = 0$, $d = 2$, $R_0 = 1$, $D_0 = 1$, $\sigma = 1$ for in the Scenario R_{het} .

{fig:0d0r}

152 *Genetic effect.* Given its trait value y the genetic effect on the growth rate R and the diffusion coefficient D is assumed to be Gaussian (Figure 1):

$$R_g(y) = \exp(-(y + d/2)^2 / (2\sigma^2)), \quad (2)$$

$$154 \quad D_g(y) = \exp(-(y - d/2)^2 / (2\sigma^2)) \quad (3)$$

156 where $d > 0$ corresponds to the distance between the two optima. The optimum trait for diffusion represents the consumer optimal dispersal strategy, and the optimum trait for
 158 the growth rate represents the consumer optimal resource exploitation strategy. Here, we assume that the optimum traits are symmetric with respect to 0, $O_R = -d/2$ and
 160 $O_D = +d/2$ for the growth rate and dispersal, respectively. The coefficient σ , fixed to 1 in the following, is the standard deviation of the Gaussian function and indicates the
 162 intensity of selection around the optimal trait value (smaller σ means higher intensity of selection).

164 *Environmental effect.* The terms $R_s(x/L)$ and $D_s(x/L)$ describe the periodic variations over the space x (Figure 1B). Here, R_s is a 1-periodic piecewise constant function of mean
 166 0, with $R_s(x) = R_0$ on $[0, 1/2)$ and $R_s(x) = -R_0$ on $[1/2, 1)$. Equivalently, D_s is a smooth 1-periodic function, with mean value 0, and bounded from below by $-D_0$ (so that D
 168 is always positive). More precisely, we define the 1-periodic function $\delta_1(x)$ such that $\delta_1(x) = D_0$ in $[0, 1/2)$ and $\delta_1(x) = -D_0$ in $[1/2, 1)$.

170 Then, D_s is obtained by regularizing δ_1 with a convolution by a smooth function:

$$172 \quad D_s(x) = \int_{\mathbb{R}} \delta_1(x - z) \phi(z) dz,$$

with ϕ a Gaussian function with small variance.

2.3 Simulation scenario

We define three scenarios, depending on the presence of spatial fragmentation, and on
 176 its effects on growth or dispersal:

- Scenario H : spatially homogeneous coefficients. In this case,

$$R(x, y) = R_h(y) := R_0 + R_g(y) \text{ and } D(x, y) = D_h(y) := D_0 + D_g(y).$$

- Scenario R_{het} : fragmented growth and homogeneous dispersal. In this case,

$$R(x, y) = R_0 + R_g(y) + R_s(x/L) \text{ and } D(x, y) = D_h(y) = D_0 + D_g(y).$$

- Scenario D_{het} : homogeneous growth and fragmented dispersal. In this case,

$$R(x, y) = R_h(y) = R_0 + R_g(y) \text{ and } D(x, y) = D_0 + D_g(y) + D_s(x/L).$$

Under these scenarios, we numerically simulated the model of Equation (1), to ex-
 178 plore the phenotypic trait composition in the population with different parameter value
 combinations. Specifically, we focused on: i) the period of fragmentation L , considering
 180 rapidly (small period $L = 2$) and slowly (large period $L = 10$) varying environments; ii)
 the distance d between the two optima, where we considered a short distance for weak
 182 trade-off ($d = 2$) and a large distance for strong trade-off ($d = 4$); iii) and, the mutation
 parameter $\mu = 0$ (no mutations) or $\mu = 0.1$. The equations are solved numerically by
 184 transforming them into lattice dynamical systems (continuous time, discrete space with
 small space step), and using a Runge-Kutta method over a fixed spatial domain (defined
 186 as $x \in [0; 250]$ by step 0.5). The phenotype space is defined between $y_{min} = -5$ and
 $y_{max} = 5$ by step $\delta_x = 0.1$. The implementation is performed by using the software
 188 Matlab[®] (code repository: DOI 10.17605/OSF.IO/V6N4M).

2.4 The spreading speed

{Speed}

190 The consumer species $R - D$ trade-off is investigated by focusing on the spreading prop-
 192 erties and analyzing the population forefront under the defined scenarios. The spreading
 speed (to the right) V is the asymptotic rate at which a population, initially concentrated
 to the left of some point, expands its spatial range. It can be defined here as the smallest
 194 speed such that, if an observer travels to the right (*i.e.*, towards increasing x values) with
 this speed, he will observe that the population density vanishes. In mathematical terms,
 196 V is the only speed such that:

$$\begin{aligned} \sup_{x \geq z} C(t, x + wt) &\xrightarrow[t \rightarrow +\infty]{} 0 && \text{for all } w > V \text{ and } z \in \mathbb{R}, \\ \inf_{x \leq z} C(t, x + wt) &\not\xrightarrow[t \rightarrow +\infty]{} 0 && \text{for all } w < V \text{ and } z \in \mathbb{R}, \end{aligned} \quad (4)$$

with $C(t, x)$ the population density at spatial position x :

$$C(t, x) = \int_{y_{\min}}^{y_{\max}} c(t, x, y) dy. \quad (5)$$

198 For each phenotype y , the spreading speed $v(y)$ of the phenotype y can be defined as
 well by replacing $C(t, x + wt)$ with $c(t, x + wt, y)$ in the above expressions.

200 The existence of a spreading speed and analytical characterizations have been ob-
 tained for standard equations with spatially homogeneous coefficients and local compe-
 202 tition terms (Aronson and Weinberger, 1975, 1978; Fife and McLeod, 1977; Kolmogorov
 et al., 1937). Comparable results have been obtained with a periodically varying coeffi-
 204 cient as in Equation (1) and a local competition term (Berestycki and Hamel, 2002, 2005),
 namely for equations of the form:

$$\begin{aligned} \partial_t c(t, x, y) = \partial_{xx}(D(x, y) c(t, x, y)) + \mu \partial_{yy} c(t, x, y) \\ + c(t, x, y) (R(x, y) - \gamma c(t, x, y)). \end{aligned} \quad (6)$$

210 Here, the difference with Equation (1) is that the individuals with phenotype y only
interact with individuals with the same phenotype. As we did not assume an Allee
212 effect in Equation (1), the solutions should be pulled by the individuals in the leading
edge of the colonization (Roques et al., 2012; Stokes, 1976). Their speed should therefore
214 only depend on the growth term through its linearization around 0, here $R(x, y)c(t, x, y)$.
We therefore conjecture that the spreading speeds V of the solutions of the nonlocal
216 Equation (1) and the local equation (6) are equal. This conjecture is supported by the
results of Alfaro et al. (2013), which deal with a nonlocal equation of the form (1), with a
218 constant diffusion term D and with a growth term of the form $R(x, y) = r(y - Bx)$, with
 $r(y) = r_{\max} - by^2$ (to each position x is attached an optimal phenotype Bx). This would
220 imply that the fastest phenotype,

$$y^* = \operatorname{argmax}_{y \in (y_{\min}, y_{\max})} v(y),$$

222 has the same speed for the two Equations (1) and (6) with and without nonlocal in-
teractions. As the fastest phenotype, y^* does not compete with other phenotypes, its
224 speed should indeed not be influenced by the competition term, and therefore be the
same for the two equations. This conjecture is also supported by the results of Girardin
226 (2017) (Theorems 1.6 and 1.7), who studied an analogue of (1), but with a discrete phe-
notype space and a spatially homogeneous environment, leading to a system of reaction-
228 diffusion equations coupled by discrete Laplace mutation term.

For Equation (6), under our three scenarios (H, R_{het}, D_{het}) , more or less explicit for-
230 mulas for the spreading speed are available. Thus, we compare these approximations
of the spreading speeds with numerical results, using approached models and limiting
232 cases of rapidly and slowly varying environments and we compare these approximations
with numerical results.

234 First, when the environment is spatially homogeneous (scenario H), *i.e.*, when $R(x, y) =$
 $R_h(y)$ and $D(x, y) = D_h(y)$, and in the absence of mutations ($\mu = 0$), the spreading speed
 236 associated with a phenotype y is $v(y) = 2\sqrt{R_h(y) D_h(y)}$ (Kolmogorov et al., 1937). In
 that case, and according to the values of d and σ (see Equations (2) and (3)), the fastest
 238 phenotypes can be the generalist, $y^* = 0$ or the two specialists, $y^* = O_R = -d/2$ and
 $y^* = O_D = d/2$, see Appendix B. The overall spreading speed defined by Equation (4) is
 240 $V = 2\sqrt{R_h(y^*) D_h(y^*)}$. When the environmental fragmentation only impacts the growth
 rate $R(x, y)$ keeping the diffusion coefficient spatially homogeneous $D(x, y) = D_h(y)$
 242 (scenario R_{het}), a general formula for the spreading speed has been obtained by Beresty-
 cki and Hamel (2005). Their results also encompass the case of a fragmented diffusion co-
 244 efficient $D(x, y)$ but spatially homogeneous growth rate $R(x, y) = R_h(y)$ (scenario D_{het}).
 However, in this case, their result holds true for equations with "Fickian" spatial diffu-
 246 sion term, *i.e.*, $\partial_x(D(x, y) \partial_x c)$ instead of the Fokker-Planck diffusion $\partial_{xx}(D(x, y) c)$ in (6)
 (Roques, 2013; Turchin, 1998).

248 In the spatially fragmented cases (scenarios R_{het} and D_{het}) the formulas rely on vari-
 ational characterizations which make them hardly tractable, even numerically (see Ap-
 250 pendix B). More tractable formulas for the phenotype spreading speeds can be obtained
 for rapidly varying (*i.e.*, when the period is small, $L \rightarrow 0$) and slowly varying (*i.e.*, when
 252 the period is large, $L \rightarrow \infty$) environments in the absence of mutations (*i.e.*, $\mu = 0$)
 (Hamel et al., 2010, 2011; Smaly et al., 2009). These formulas are summarized in Table
 254 1, see also Appendix B for more mathematical details. We check the accuracy of the
 analytical approximations in Table 1 and we compare them with numerical simulations
 256 for the considered scenarios.

Table 1: Theoretical phenotype spreading speeds for Equation (6) with $\mu = 0$ (no mutation) for rapidly varying environments $L \rightarrow 0$ and slowly varying environments $L \rightarrow \infty$.

Spatial fragmentation		$L \rightarrow 0$	$L \rightarrow \infty$
Scenario H	$R_h(y), D_h(y)$	$v(y) = 2\sqrt{R_h(y) D_h(y)}$	$v(y) = 2\sqrt{R_h(y) D_h(y)}$.
Scenario R_{het}	$R(x, y), D_h(y)$	$v_{R_{het},0}(y) = 2\sqrt{R_h(y) D_h(y)}^*$	$v_{R_{het},\infty}(y) = 4\sqrt{D_h(y)} \times \frac{(R^+(y))^2 + (R^-(y))^2 + (R^+(y) + R^-(y)) \sqrt{\Delta(y)}}{(R^+(y) + R^-(y) + 2\sqrt{\Delta(y)})^2}^{**}$
Scenario D_{het} (Fickian diffusion)	$R_h(y), D(x, y)$	$v_{D_{het},0}(y) = 2\sqrt{R_h(y) \langle D_1 \rangle_H(y)}^{***}$	$v_{D_{het},\infty}(y) = 2\sqrt{R_h(y) \langle \sqrt{D_1} \rangle_H(y)}^{***}$

Where:

* $v_{R_{het},0}(y) = 2\sqrt{\bar{R}_x(y) D_h(y)}$ with $\bar{R}_x(y) = R_0 + R_g(y) + \int_0^1 R_s(x) dx = R_h(y)$.

** $R^+(y) = R_h(y) + R_0, R^-(y) = R_h(y) - R_0, \Delta(y) = (R^+(y))^2 + (R^-(y))^2 - R^+(y) R^-(y)$.

*** $\langle F \rangle_H(y) = \left(\int_0^1 \frac{dx}{F(x,y)} \right)^{-1}$ the harmonic mean of F , and $D_1(x, y) = D_0 + D_g(y) + D_s(x)$.

{tab:speed}

3 Results

{Res}

258 The forefront profiles highlight the role of the $R - D$ trade-off, the environmental hetero-
 geneity and the mutation in influencing the spreading speed of the different phenotypes
 260 (Figures 2-5). In Section 3.1 we analyze these figures, then, in Section 3.2 we use the
 theoretical formulations to better understand the numerical simulations.

262 Hereafter, we identify the strategies favoring the selection of phenotypes with a be-
 havior that increases dispersal capacities as D-strategy (namely, when $y^* > 0$), with a
 264 generalist behavior as G-strategy (namely, when $y^* = 0$) and with a behavior that in-
 creases growth rate as R-strategy (namely, when $y^* < 0$). As at the back of the front the
 266 R-strategy is always selected, our focus is entirely dedicated to the trade-off among R
 and D on the forefront, see Appendix C.

268 3.1 The $R - D$ trade-off selecting the fastest strategy on the forefront

{sec:num2D}

In the absence of mutation ($\mu = 0$), when $d = 2$, the forefront is composed mostly by
270 one phenotype with a low degree of specialization on R and D (Figure 2A, C and E;
Figure 4A, C and E). For scenarios H and R_{het} , when fragmentation is high, numerical
272 simulations show a small shift towards the R -strategy (Figure 2A and C, Table 2). In-
stead, when there is a slowly varying environment, the shift occurs towards D -strategy
274 (Figure 2E, Table 2). Under scenario D_{het} , whatever environment fragmentation, there is
a clear shift towards the D -strategy (Figure 4 C and E, Table 2).

276 When $d = 4$, the colonization is mostly driven by the D -strategy (Figures 2 and 4
B, D and F). A less fragmented habitat ($L = 10$), under the scenario R_{het} , increases the
278 advantage of the D -specialist on the forefront, shifting the trade-off in favour of the D -
strategy (see Figure 2 D *vs.* F). For the scenario D_{het} , the difference between weak and
280 strong trade-off is even more remarkable as the advantage is completely shifted in favor
of the strategy $y^* = O_D$ (see Figure 4D), defining also a different forefront profile.

282 These outcomes are completely blurred when introducing a positive value for the
mutation coefficient. In fact, the presence of mutations leads to a homogenization of
284 the phenotypic distribution and therefore to a wider phenotype ensemble that leads the
forefront: all of the phenotypes should theoretically spread with the same asymptotic
286 speed (see Girardin, 2017, in a homogeneous case with discrete phenotype space). Yet,
the population densities (Figures 3 and 5) indicate that the R -strategy becomes the pre-
288 ferred one almost in all cases when $d < d_{cr}$, except for the scenario D_{het} with a slowly
varying environment (Figure 5 E). The D -specialist is still the fastest phenotype under
290 the scenario D_{het} in case of strong trade-off ($d = 4$) (Figure 5D and F). However, we notice

that the shape of the solution at the leading part of the expansion is quite unusual. In all
292 cases, we observe a "bump" corresponding to a fraction of the population which adopts
the D -strategy. Thus, the expansion may take advantage of the larger diffusion coefficient
294 of the D -specialists and of the larger growth rate of the R -specialist by allowing more
polymorphism at the leading edge of the propagation.

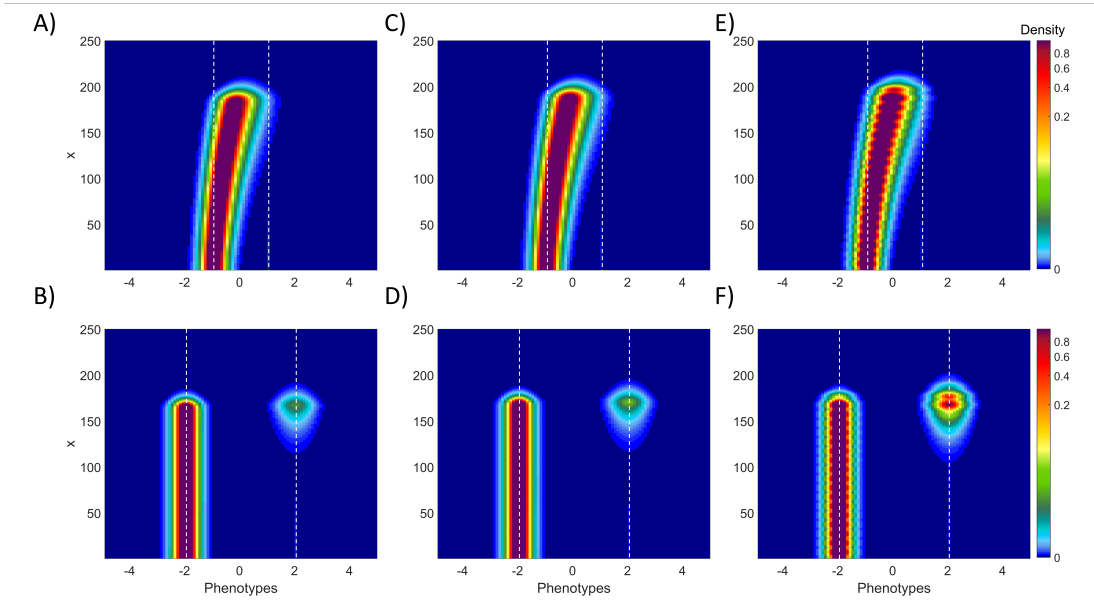


Figure 2: **Population density contrasting scenario R_{het} (Panels C, D, E, F) with scenario H (Panels A and B) without mutation.** The forefront profiles show the population density with respect to the phenotypes and the space variables. Over lines the trade-off strength is showed: weak trade-off ($d = 2$) (Panel A, C, E) and strong trade-off ($d = 4$) (Panel B, D, F). Over columns the effect of the period L is showed: rapidly varying environment ($L = 2$) (Panel C and D) and slowly varying environment (Panel E and F). Solutions are obtained by numerically simulating the Equation (1) and results are reported at time $T_{sim} = 60$. White dashed lines highlight the optimum values (*i.e.*, $O_D = d/2$ and $O_R = -d/2$).

{fig:FrontRh}

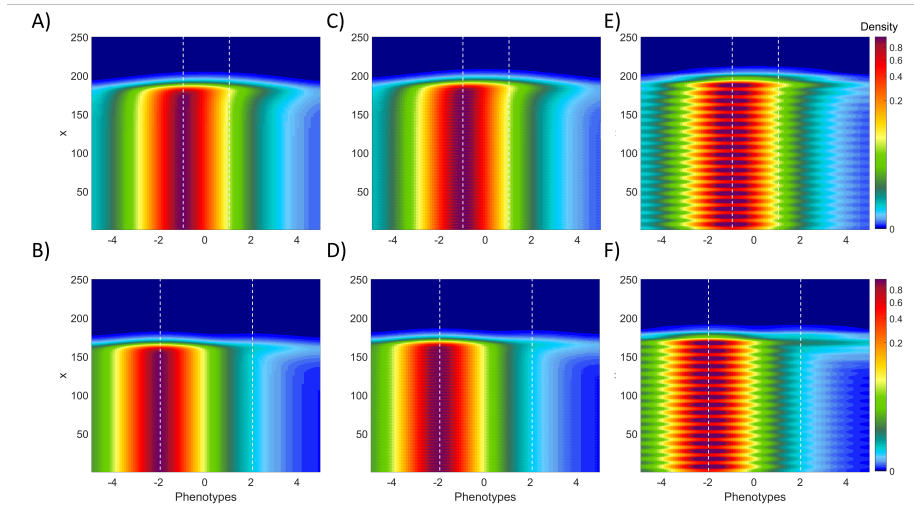


Figure 3: Population density contrasting scenario R_{het} with scenario H with mutation. Caption description is the same of Figure 2, but considering a positive value for mutation ($\mu > 0$).

{fig:FrontRhm μ }

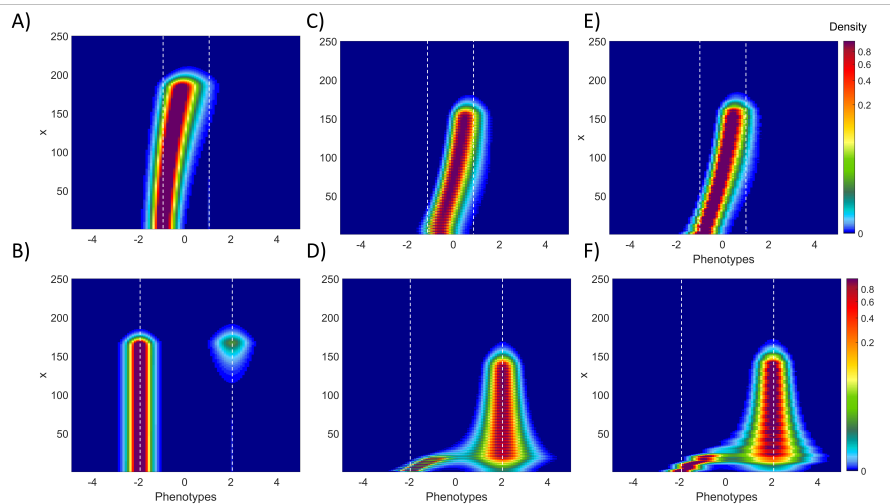


Figure 4: Population density contrasting scenario D_{het} with scenario H without mutation. Caption description is the same of Figure 2, but for scenario D_{het} .

{fig:FrontDh}

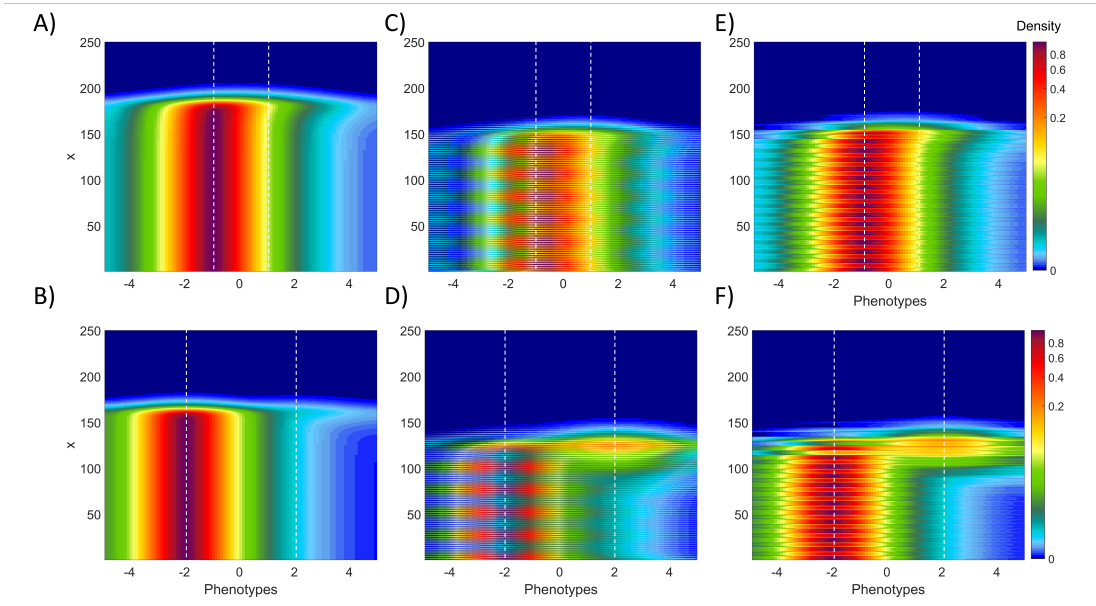


Figure 5: **Population density contrasting scenario D_{het} with scenario H with mutation.** Caption description is the same of Figure 2, but for scenario D_{het} with a positive value for mutation $\mu > 0$.

{fig:FrontDhmu}

3.2 *Insight from the theoretical speeds*

{sec:theor_speed}

296

In this section, we compare the numerical simulations of Equation (1) presented in Figures 2-5 with the analytical formulations presented in Figure 6 and Table 1. We first check if the outcomes that can be obtained from the theoretical speeds match with the numerical results. These outcomes are summarised in Table 2. Second, when there is a good match, we use the explicit formulas to explain the observed trends. We recall that the theoretical speeds of Table 1 were derived with the simpler local model (6) with $\mu = 0$ and therefore do not take the nonlocal competition and mutation effects into account.

298

300

302

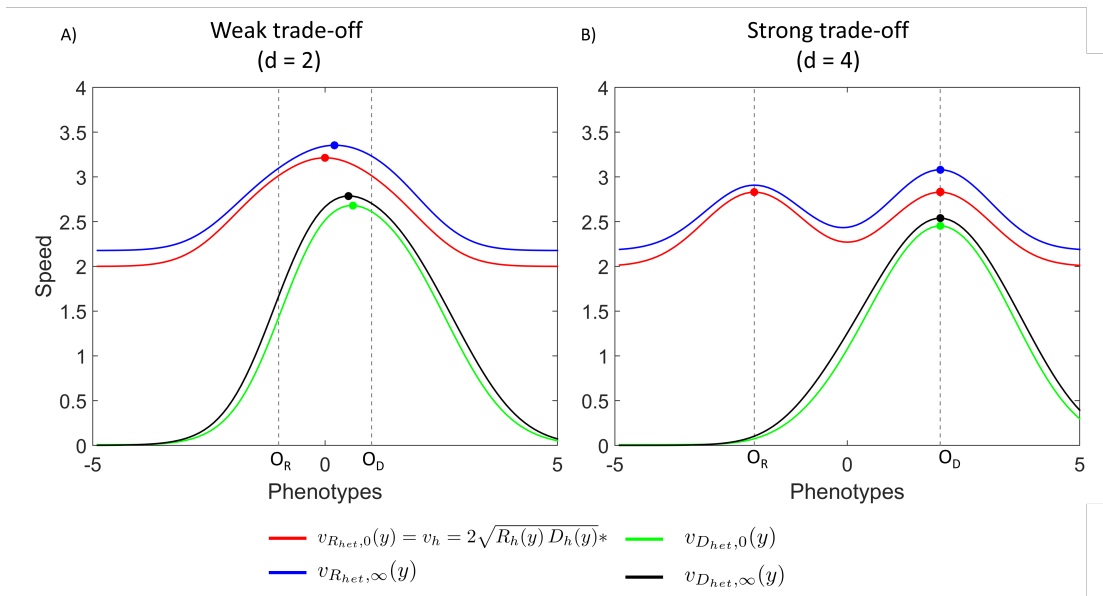


Figure 6: **Theoretical phenotype spreading speeds.** The theoretical phenotype spreading speeds presented in Table 1 are showed in function of phenotypes $y \in [-5, 5]$ considering a weak trade-off ($d = 2$) (Panel A) and a strong trade-off ($d = 4$) (Panel B). Different colors refers to the formulations of the spreading speed highlighted in Table 1, the dots represent the fastest phenotype leading the forefront. Dashed lines highlight the positions of the optimum traits O_R and O_D .

{fig:v_th}

304 In absence of mutation ($\mu = 0$), there is a critical threshold d_{cr} on the distance d
between the optima ($d_{cr} \approx 2.4$ with our parameter values, see Appendix B), such that the
306 function $v(y) = 2\sqrt{R_h(y)D_h(y)}$, corresponding to the spreading speed, either admits
one ($d < d_{cr}$) or two ($d > d_{cr}$) maxima. When $d < d_{cr}$ (i.e., $d = 2$) and with a rapidly
308 varying environment, the generalist behavior is expected to be selected as the fastest trait
following the theoretical formulations under scenarios H and R_{het} . However, numerical
310 simulations show a small shift towards the R-strategy (Table 2). Instead, when there is a

slowly varying environment, or when heterogeneity impacts D , theoretical formulations
 312 consistently predict a shift towards the D-strategy (Table 2, Figure 6).

In the scenario D_{het} , the theoretical speed $v_{D_{het},0}(y) = 2\sqrt{R_h(y) \langle D_1 \rangle_H(y)}$ in rapidly
 314 varying environments (small period $L = 2$ in the numerical results, $L \rightarrow 0$ in Table 1)
 involves the harmonic mean of the diffusion term. Contrarily to the arithmetic mean, the
 316 harmonic mean gives a higher weight to small values. Thus, small values of $D(x, y)$, even
 on a very small spatial interval, should lead to small speeds $v_{D_{het},0}(y)$, based on the results
 318 of Table 1. This leads to an imbalance in favor of the D-strategies (compare $v_{D_{het},0}(y)$ and
 $v(y)$ in Figure 6; Figure 4A and B *vs.* Figure 4C and D), which avoid very small values of
 320 $D(x, y)$. In the case of slowly varying environments (large period $L = 10$ in the numerical
 results, $L \rightarrow +\infty$ in Table 1), the theoretical speed $v_{D_{het},\infty}(y) = 2\sqrt{R_h(y) \langle \sqrt{D_1} \rangle_H(y)}$
 322 again involves an harmonic mean of the diffusion term (here, its square root) which
 explains the advantage of the D-strategy, as in the case of rapidly varying environments.

When heterogeneity is introduced on R (scenario R_{het}), in rapidly varying environ-
 324 nments, the theoretical formulas predict that the strategy remains unchanged (G when
 $d < d_{cr}$ or R+D when $d > d_{cr}$) compared to the homogeneous scenario (H). The theoret-
 326 ical spreading speed of each phenotype in the scenario R_{het} , $v_{R_{het},0}(y) = 2\sqrt{R_h(y) D_h(y)}$,
 328 is indeed the same as the speed $v(y)$ obtained in the homogeneous scenario H (both
 curves are superimposed in Figure 6): as the spatial arithmetic mean of the growth rate
 330 (noted $\bar{R}_x(y)$ in the legend of Table 1) is precisely equal to R_h , the homogenization results
 of Smailly et al. (2009) imply that the two speeds are equal. In the numerical simulations
 332 (see Table 2, lines A for numerical and C for theoretical), there are some discrepancies,
 as with a rapidly varying environment ($L = 2$), the homogenization limit is not reached.
 334 Hence, we observe a slight shift of the G-strategy towards the R-strategy when $d < d_{cr}$.

When $d > d_{cr}$, the two strategies are present on the forefront, with a slight advantage for
 336 the D-strategy (Figure 2A and B *vs.* Figure 2C and D). In slowly varying environments,
 the theoretical formulas and the numerical simulations consistently predict a shift to-
 338 wards the D-strategy. In this last case, the formula for $v_{R_{het},\infty}(y)$ can be written in the
 form $2\sqrt{F(y)D_h(y)}$, for some function F which satisfies $F(O_D) \approx (32/27)R_0$ (to be
 340 compared with $R_h(O_D) \approx R_0$) and $F(O_R) \sim R_0 + 1$ for small R_0 (to be compared with
 $R_h(O_R) = R_0 + 1$). Thus, compared to the homogeneous case ($v(y) = 2\sqrt{R_h(y)D_h(y)}$),
 342 the heterogeneity on R creates an asymmetry in favor of the D-strategy which manages
 to keep a growth rate larger than R_0 .

344 When $\mu > 0$ (see Table 2 line B), as expected, there are some discrepancies between
 the numerical results and the theoretical predictions. However, the arguments above may
 346 explain some of the observations. First, in the scenario D_{het} in most cases (except when
 $d < d_{cr}$ in rapidly varying environments) we again observe a shift towards D-strategies
 348 which is most probably due to the "harmonic mean" effect described above. We note
 that this shift is stronger in slowly varying environments. In the scenario R_{het} , although
 350 the R-strategy is always selected when $\mu > 0$, the positive effect of the heterogeneity on
 the maintenance of the D-strategy which we noted above in the theoretical formulas is
 352 still visible on Figure 3F, which shows more polymorphism compared to the scenario H.

We note the positive effect of increasing the period L (equivalently, reducing the
 354 environmental fragmentation) on the spreading speeds: this effect, which is obvious
 in Figure 6 can also be observed in Figures 2-5.

		H	R_{het}		D_{het}	
			Rapidly varying	Slowly varying	Rapidly varying	Slowly varying
$d < d_{cr}$	A	-0.1	-0.1	0.1	0.5	0.3
	B	-0.7	-0.7	-0.7	-0.7	0.1
	C	0	0	0.2	0.6	0.5
$d > d_{cr}$	A	R+D	0.95	1	0.95	0.95
	B	-1.2	-1.3	-1.35	0.5	0.8
	C	R+D	R+D	1	1	1

Table 2: **Fastest phenotypes leading the forefront.** The table reports the values of the fastest phenotype leading the forefront with respect to the optimum value ($2y^*/d$). Results of numerical simulations of the Equation 1 are compared over the lines considering the presence and absence of mutation and the theoretical formulas: A) $y^* = \operatorname{argmax}(v_{sim}(y))$, with $\mu = 0$; B) $y^* = \operatorname{argmax}(v_{sim}(y))$, with $\mu > 0$; C) $y^* = \operatorname{argmax}(v_{th}(y))$, corresponding to the spreading speed v_{th} reported in Table 1. The corresponding strategy is highlighted: Blue cells correspond to R-strategies ($2y^*/d < 0$) and red cells to D-strategies ($2y^*/d > 0$). White cells correspond to generalists ($2y^*/d = 0$) or when both strategies lead to the same speed (noted R+D). $d < d_{cr}$ correspond to a weak trade-off ($d = 2$), $d > d_{cr}$ correspond to a strong trade-off ($d = 4$). Rapidly varying correspond to a period of heterogeneity $L = 2$ and slowly varying correspond to a period of heterogeneity $L = 10$.

{table:strategie}

4 Discussion

356

Dispersing faster or growing stronger? In this work, we studied which of these strategies
358 is selected in populations invading a heterogeneous environment. We gathered analytical
solutions from the literature and performed numerical simulations of a reaction-
360 diffusion model describing the demo-genetic dynamics of a population invading a one-
dimensional environment. Results show that the symmetrical effects of growth and dis-
362 persal on the spreading speed is broken in the presence of competition between phe-
notypes, shrinking the population density around the optimum values. From here we
364 observe that, at the back of the forefront, the dynamics is almost always carried out
by the *R*-specialists, while, on the forefront, the selection of the fastest strategy is less
366 obvious.

In this study, we identify the main following results: i) *R*-strategies are favored in spa-
368 tially homogeneous environments, but the introduction of heterogeneity leads to a shift
towards *D*-strategies, with at least more polymorphism at the forefront; ii) due to a "har-
370 monic mean effect" that we have highlighted through analytical expressions obtained
with a simpler model, this phenomenon is even stronger when spatial heterogeneity af-
372 fects the diffusion term. In this case, the introduction of spatial heterogeneity can lead to
a complete switch from an *R*-strategy to a *D*-strategy; iii) the spatial fragmentation does
374 not affect a lot the *R* – *D* trade-off, but tends to modulate the polymorphism: in situa-
tions where only *R*-strategists are present at the forefront when the level of fragmentation
376 is high (small *L*), both *R*-strategists and *D*-strategists tend to be present at the forefront
in low fragmented environments made of large patches (large *L*); iv) mutations produce
378 an advantage towards the *R*-strategy, and homogenize the phenotype distribution, also

leading to more polymorphism on the forefront; v) these effects can be observed with a
380 weak trade-off (such that the generalist $y^* = 0$ leads the population in a homogeneous
model without interactions), but become even stronger with a strong trade-off (such that
382 R -strategists and D -strategists have the same speed in a homogeneous model with-
out interactions) and vi) the comparison among theoretical and numerical simulations
384 allows checking when formulas obtained with a simpler model lead to results which are
consistent with of a more complex one.

386 Some of these results (points i,ii,iii) are in accordance with the ones of Burton et al.
(2010), who used an individual-based spatial model to study the evolution of three traits
388 in a population undergoing range expansion. When resources are highly fragmented, the
trade-off favors to the selection of an R -strategy on the forefront as high resource avail-
390 ability and fecundity facilitate expansion by increasing population growth. By contrast,
in a low fragmented environment, the faster dispersers take advantage of their mobility
392 to reach the most favorable habitats and lead the forefront. Evolution thus leads to the
selection of a greater capacity for dispersion. Conversely, when heterogeneity impacts
394 dispersal, only the D -specialists confer the maximal speed and persist on the forefront,
whatever the level of spatial fragmentation. Recently, given two species having growth
396 and dispersal coefficients R_1, D_1 and R_2, D_2 (for species 1 and 2 respectively), Deforet
et al. (2019) found that the evolutionary outcome mainly depends on the simple condi-
398 tion $v_1 = 2\sqrt{R_1 D_1} > v_2 = 2\sqrt{R_2 D_2}$, with success of the fastest (here, species 1). In our
work, the use of the theoretical formulas of Table 1 mainly relies on the same assumption,
400 that the fastest trait drives the expansion. In most cases, our results show that the obser-
vations of Deforet et al. (2019) remain true in a more general context with a continuum of
402 traits and possibly mutations between traits. However, we also observed some discrepan-

cies in the presence of mutations, which tend to advantage the R-strategy. Additionally,
404 as recently observed by Keenan and Cornell (2021) in a homogeneous environment, in
the presence of mutations, the furthest forward phenotypes are not necessarily those
406 associated with the largest value of the product RD (see below).

Duputié and Massol (2013) argues that natural selection tends to favor dispersal to
408 face spatio-temporal variation in local conditions. Consequently, more dispersive pheno-
types are expected to predominate in unstable habitats, while less dispersive phenotypes
410 are common in stable habitats and populations. Here, we found that in the bulk of the
population, which corresponds to a saturated population, the R-strategy is always pre-
412 ferred, which is not always the case at the forefront. By definition, the expanding part
of the population encounters a more variable environment, especially when the envi-
414 ronment is itself highly heterogeneous. In such cases, we observed a shift towards the
D-strategy. These findings are also consistent with the “Spatial sorting theory” which
416 predicts that, at the forefront, dispersal may be strongly favored because of the accumu-
lation of the best dispersers (Phillips et al., 2008; Shine et al., 2011; Travis and Dytham,
418 2002).

The presence of mutations homogenizes the spreading speed between morphs, even
420 in presence of nonlocal competition. We also establish that polymorphism, caused by
mutation, is maintained in the presence of spatial fragmentation impacting the R and D
422 coefficients. Another possible effect of mutation is an increased spreading speed. Taking
again a system with only two morphs (as in Deforet et al. (2019), but with a mutation
424 term), typically an R -specialist and a D -specialist, Elliott and Cornell (2012) and Morris
et al. (2019) investigated the effect of varying R and D on the spreading speed. They
426 found that the system would spread faster in the presence of both phenotypes than

just one phenotype would spread in the absence of mutation for certain combination
428 of R and D values. In a similar way, using the results of Girardin (2017), Keenan and
Cornell (2021) considered the $R - D$ trades-off in the case of N phenotypes in a homo-
430 geneous environment, and obtained some conditions on the curvature of the trade-off
curve $(D, R(D))$ such that this “anomalous” faster speed emerges. Here, although the
432 trade-off curve $(D, R(D))$ has positive curvature, we did not observe this phenomenon:
in all of our simulations of Figures 3-5, the speed is reduced when $\mu > 0$, compared to
434 the speed of the fastest trait when $\mu = 0$. The theoretical results of Keenan and Cornell
(2021) require a vanishing small mutation rate, and their numerical results use a muta-
436 tion coefficient 10^{-6} (to be compared with $\mu/(\delta_x)^2 = (0.1)/(0.1)^2 = 10$ in our continuous
framework), which may explain these differences.

438 Future works could consider a more detailed analysis of the lineages that pull the
forefront, to determine for instance if the D -specialists in Figures 3 and 5 are produced by
440 mutation from R -specialists or correspond to a self-sustaining fraction of the population.
In that respect, one could reconstruct the genealogies of the fractions composing the
442 population using the methods in (Roques et al., 2012). We recall that our results depend
on the assumptions about the form of the dispersal and growth rate functions and the
444 fragmentation definition. For instance, we do not take an Allee effect into account. It is
demonstrated to have important consequences on the invasions dynamics and especially
446 on the lineages that compose the forefront (Andrade-Restrepo et al., 2019; Chuang and
Peterson, 2016; Roques et al., 2012).

Literature Cited

- Alfaro, M., H. Berestycki, and G. Raoul (2017). The effect of climate shift on a species
450 submitted to dispersion, evolution, growth, and nonlocal competition. SIAM Journal
on Mathematical Analysis 49(1), 562–596.
- 452 Alfaro, M., J. Coville, and G. Raoul (2013). Travelling waves in a nonlocal reaction-
diffusion equation as a model for a population structured by a space variable and a
454 phenotypic trait. Communications in Partial Differential Equations 38(12), 2126–2154.
- Alfaro, M., L. Girardin, F. Hamel, and L. Roques (2021). When the Allee threshold is
456 an evolutionary trait: persistence vs. extinction. Journal de Mathématiques Pures et
Appliquées 155, 155–191.
- 458 Alfaro, M. and G. Peltier (2021). Populations facing a nonlinear environmental gradient:
steady states and pulsating fronts. arXiv preprint arXiv:2101.08078 32(02), 209–290.
- 460 Anciaux, Y., A. Lambert, O. Ronce, L. Roques, and G. Martin (2019). Population per-
sistence under high mutation rate: from evolutionary rescue to lethal mutagenesis.
462 Evolution 73(8), 1517–1532.
- Andrade-Restrepo, M., N. Champagnat, and R. Ferrière (2019). Local adaptation, dis-
464 persal evolution, and the spatial eco-evolutionary dynamics of invasion. Ecology
letters 22(5), 767–777.
- 466 Aronson, D. G. and H. F. Weinberger (1975). Nonlinear diffusion in population genetics,
combustion, and nerve pulse propagation. In J. A. Goldstein (Ed.), Partial Differential

- 468 Equations and Related Topics, Berlin, Heidelberg, pp. 5–49. Springer Berlin Heidelberg.
- 470 Aronson, D. G. and H. G. Weinberger (1978). Multidimensional nonlinear diffusion arising in population genetics. Adv Math 30(1), 33–76.
- 472 Baguette, M. and N. Schtickzelle (2006). Negative relationship between dispersal distance and demography in butterfly metapopulations. Ecology 87(3), 648–654.
- 474 Benichou, O., V. Calvez, N. Meunier, and R. Voituriez (2012). Front acceleration by dynamic selection in fisher population waves. Physical Review E 86(4), 041908.
- 476 Berestycki, H. and F. Hamel (2002). Front propagation in periodic excitable media. Comm Pure Appl Math 55(8), 949–1032.
- 478 Berestycki, H. and F. Hamel (2005). Gradient estimates for elliptic regularizations of semilinear parabolic and degenerate elliptic equations. Communications in Partial
480 Differential Equations 30(1-3), 139–156.
- Berestycki, H., F. Hamel, and L. Roques (2005). Analysis of the periodically fragmented
482 environment model: II - Biological invasions and pulsating travelling fronts. J Math Pures Appl 84(8), 1101–1146.
- 484 Berestycki, N., C. Mouhot, and G. Raoul (2015). Existence of self-accelerating fronts for a non-local reaction-diffusion equations. arXiv preprint arXiv:1512.00903.
- 486 Bonte, D. and Q. Bafort (2019). The importance and adaptive value of life-history evolution for metapopulation dynamics. Journal of Animal Ecology 88(1), 24–34.

- 488 Bonte, D. and E. de la Pena (2009). Evolution of body condition-dependent dispersal in
metapopulations. Journal of Evolutionary Biology 22(6), 1242–1251.
- 490 Bouin, E. and V. Calvez (2014). Travelling waves for the cane toads equation with
bounded traits. Nonlinearity 27(9), 2233.
- 492 Bouin, E., V. Calvez, N. Meunier, S. Mirrahimi, B. Perthame, G. Raoul, and R. Voituriez
(2012). Invasion fronts with variable motility: phenotype selection, spatial sorting and
494 wave acceleration. Comptes Rendus Mathematique 350(15-16), 761–766.
- Bouin, E., M. H. Chan, C. Henderson, and P. S. Kim (2018). Influence of a mortality trade-
496 off on the spreading rate of cane toads fronts. Communications in Partial Differential
Equations 43(11), 1627–1671.
- 498 Burton, O. J., B. L. Phillips, and J. M. Travis (2010). Trade-offs and the evolution of
life-histories during range expansion. Ecology letters 13(10), 1210–1220.
- 500 Chuang, A. and C. R. Peterson (2016). Expanding population edges: theories, traits, and
trade-offs. Global change biology 22(2), 494–512.
- 502 Deforet, M., C. Carmona-Fontaine, K. S. Korolev, and J. B. Xavier (2019). Evolution at the
edge of expanding populations. The American Naturalist 194(3), 291–305.
- 504 Denno, R. F. (1994). Life history variation in planthoppers. In Planthoppers, pp. 163–215.
Springer.
- 506 Duputié, A. and F. Massol (2013). An empiricist’s guide to theoretical predictions on the
evolution of dispersal. Interface focus 3(6), 20130028.

- 508 Duthie, A. B., K. C. Abbott, and J. D. Nason (2015). Trade-offs and coexistence in fluctuating environments: evidence for a key dispersal-fecundity trade-off in five nonpollinating fig wasps. The American Naturalist 186(1), 151–158.
- 510
- Elliott, E. C. and S. J. Cornell (2012). Dispersal polymorphism and the speed of biological invasions. PloS one 7(7), e40496.
- 512
- Fife, P. C. and J. McLeod (1977). The approach of solutions of nonlinear diffusion equations to traveling front solutions. Arch Ration Mech Anal 65(1), 335–361.
- 514
- Fisher, R. A. (1937). The wave of advance of advantageous genes. Ann Eugen 7, 335–369.
- 516
- Girardin, L. (2017). Non-cooperative Fisher–KPP systems: traveling waves and long-time behavior. Nonlinearity 31(1), 108.
- 518
- Griette, Q., G. Raoul, and S. Gandon (2015). Virulence evolution at the front line of spreading epidemics. Evolution 69(11), 2810–2819.
- 520
- Hamel, F., J. Fayard, and L. Roques (2010). Spreading speeds in slowly oscillating environments. Bull Math Biol 72(5), 1166–1191.
- 522
- Hamel, F., F. Lavigne, G. Martin, and L. Roques (2020). Dynamics of adaptation in an anisotropic phenotype-fitness landscape. Nonlinear Analysis: Real World Applications 54, 103107.
- 524
- Hamel, F., G. Nadin, and L. Roques (2011). A viscosity solution method for the spreading speed formula in slowly varying media. Indiana Univ Math J 60, 1229–1247.
- 526
- Hanski, I., M. Saastamoinen, and O. Ovaskainen (2006). Dispersal-related life-history trade-offs in a butterfly metapopulation. Journal of animal Ecology 75(1), 91–100.
- 528

- Helms, J. and M. Kaspari (2015). Reproduction-dispersal tradeoffs in ant queens. Insectes sociaux 62(2), 171–181.
530
- Hirt, M. R., T. Lauermann, U. Brose, L. P. Noldus, and A. I. Dell (2017). The little things that run: a general scaling of invertebrate exploratory speed with body mass. Ecology 98(11), 2751–2757.
532
- Keenan, V. A. and S. J. Cornell (2021). Anomalous invasion dynamics due to dispersal polymorphism and dispersal–reproduction trade-offs. Proceedings of the Royal Society B 288(1942), 20202825.
534
536
- Kelehear, C. and R. Shine (2020). Tradeoffs between dispersal and reproduction at an invasion front of cane toads in tropical australia. Scientific Reports 10(1), 1–7.
538
- Kolmogorov, A. N., I. G. Petrovsky, and N. S. Piskunov (1937). Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique. Bull Univ État Moscou, Sér. Int. A 1, 1–26.
540
- Legrand, D., J. Cote, E. A. Fronhofer, R. D. Holt, O. Ronce, N. Schtickzelle, J. M. Travis, and J. Clobert (2017). Eco-evolutionary dynamics in fragmented landscapes. Ecography 40(1), 9–25.
542
544
- Morris, A., L. Börger, and E. Crooks (2019). Individual variability in dispersal and invasion speed. Mathematics 7(9), 795.
546
- Peltier, G. (2020). Accelerating invasions along an environmental gradient. Journal of Differential Equations 268(7), 3299–3331.
548
- Perkins, T., B. L. Phillips, M. L. Baskett, and A. Hastings (2013). Evolution of dispersal

- 550 and life history interact to drive accelerating spread of an invasive species. Ecology
letters 16(8), 1079–1087.
- 552 Phillips, B. L., G. P. Brown, J. M. Travis, and R. Shine (2008). Reid’s paradox revisited: the
evolution of dispersal kernels during range expansion. the american naturalist 172(S1),
554 S34–S48.
- Ronce, O. and M. Kirkpatrick (2001). When sources become sinks: migrational meltdown
556 in heterogeneous habitats. Evolution 55(8), 1520–1531.
- Roques, L. (2013). Modèles de réaction-diffusion pour l’écologie spatiale. Editions Quae.
- 558 Roques, L., J. Garnier, F. Hamel, and E. K. Klein (2012). Allee effect promotes diversity
in traveling waves of colonization. Proc Natl Acad Sci USA 109(23), 8828–8833.
- 560 Shigesada, N. and K. Kawasaki (1997). Biological Invasions: Theory and Practice. Oxford
Series in Ecology and Evolution, Oxford: Oxford University Press.
- 562 Shine, R., G. P. Brown, and B. L. Phillips (2011). An evolutionary process that assembles
phenotypes through space rather than through time. Proceedings of the National
564 Academy of Sciences 108(14), 5708–5711.
- Skellam, J. G. (1951). Random dispersal in theoretical populations. Biometrika 38, 196–
566 218.
- Smailly, M. E., F. Hamel, and L. Roques (2009). Homogenization and influence of frag-
568 mentation in a biological invasion model. arXiv preprint arXiv:0907.4951.
- Steenman, A., A. Lehmann, and G. Lehmann (2015). Life-history trade-off between

- 570 macroptery and reproduction in the wing-dimorphic pygmy grasshopper *Tetrix subu-*
lata (Orthoptera Tetrigidae). Ethology Ecology & Evolution 27(1), 93–100.
- 572 Stokes, A. N. (1976). On two types of moving front in quasilinear diffusion. Math
Biosci 31, 307–315.
- 574 Szűcs, M., E. Vercken, E. V. Bitume, and R. A. Hufbauer (2019). The implications
of rapid eco-evolutionary processes for biological control—a review. Entomologia
576 Experimentalis et Applicata 167(7), 598–615.
- Travis, J. M. and C. Dytham (2002). Dispersal evolution during invasions. Evolutionary
578 Ecology Research 4(8), 1119–1129.
- Tsimring, L. S., H. Levine, and D. A. Kessler (1996). RNA virus evolution via a fitness-
580 space model. Physical review letters 76(23), 4440–4443.
- Turchin, P. (1998). Quantitative Analysis of Movement: Measuring and Modeling
582 Population Redistribution in Animals and Plants. Sinauer, Sunderland, MA.
- Weinberger, H. F. (2002). On spreading speeds and traveling waves for growth and
584 migration in periodic habitat. J Math Biol 45, 511–548.
- Zera, A. J. and R. F. Denno (1997). Physiology and ecology of dispersal polymorphism
586 in insects. Annual review of entomology 42(1), 207–230.