Journal of Theoretical Biology 420 (2017) 190–199

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Fortune favours the brave: Movement responses shape demographic dynamics in strongly competing populations

Jonathan R. Potts[a,*], Sergei V. Petrovskii[b]

[a] School of Mathematics and Statistics, University of Sheffield, Hicks Building, Hounsfield Road, Sheffield S3 7RH, UK
[b] Department of Mathematics, University of Leicester, Leicester LE1 7RH, UK

ARTICLE INFO

Keywords:
Competitive exclusion principle
Lotka–Volterra competition model
Movement ecology
Population dynamics
Taxis

ABSTRACT

Animal movement is a key mechanism for shaping population dynamics. The effect of interactions between competing animals on a population's survival has been studied for many decades. However, interactions also affect an animal's subsequent movement decisions. Despite this, the indirect effect of these decisions on animal survival is much less well-understood. Here, we incorporate movement responses to foreign animals into a model of two competing populations, where inter-specific competition is greater than intra-specific competition. When movement is diffusive, the travelling wave moves from the stronger population to the weaker. However, by incorporating behaviourally induced directed movement towards the stronger population, the weaker one can slow the travelling wave down, even reversing its direction. Hence movement responses can switch the predictions of traditional mechanistic models. Furthermore, when environmental heterogeneity is combined with aggressive movement strategies, it is possible for spatially segregated co-existence to emerge. In this situation, the spatial patterns of the competing populations have the unusual feature that they are slightly out-of-phase with the environmental patterns. Finally, incorporating dynamic movement responses can also enable stable co-existence in a *homogeneous* environment, giving a new mechanism for spatially segregated co-existence.

1. Introduction

Predicting the survival of populations in competitive environments is a key question in ecology, with applications to conservation decisions (Lande et al., 2003), biological invasions (Lewis et al., 2016), and management of changing ecosystems (Tylianakis et al., 2008). Indeed, the question is not restricted to ecology, with studies existing in fields as diverse as criminology (Brantingham et al., 2012) and cancer studies (Gatenby and Gawlinski, 1996). However, prediction is impossible without an understanding of the mechanisms of species competition, together with tools to quantify mathematically their effects on demographic patterns (Murray, 2001; Lewis et al., 2016). Animal movement is emerging as an important mechanism underlying inter- and intra-species interactions, as the movement decisions that animals make in response to these interactions play an important role in shaping the 'life-path' of the animal (Nathan et al., 2008; Börger, 2016). Although it is reasonable to expect that movement responses to competitors could have a big effect on the ability of animals to survive, population dynamics models incorporating these factors are rare (Armsworth and Roughgarden, 2005; Morales et al., 2010).

Despite this, inter-population competition is one of the oldest phenomena in ecology to be given rigorous mathematical treatment, with the first model dating back to Lotka (1932) and Volterra (1926), so popularly termed the Lotka–Volterra competition (LVC) model. Although the original LVC model is spatially implicit, and so does not explicitly incorporate animal movement, various foundational predictions have been made from its analysis. One is that stable co-existence of two competing populations is only possible if intra-population competition is stronger than inter-population competition. This situation is called *weak competition*. In contrast, for *strong competition*, where inter-population competition is more deleterious than intra-population competition, the LVC model predicts bi-stability: only one of the populations will survive in the long run and the other will die out, with stable co-existence impossible. This predicted inability for strongly competing populations to co-exist is sometimes called *competitive exclusion* (Hardin, 1960; Kishimoto, 1990).

The existence of bi-stability in the Strongly competitive LVC model (henceforth SLVC model) naturally leads to the question of which additional ecological processes may affect convergence to one or other of the stable states. Or, to put it in more biological terms, which

---

[*] Corresponding author.
E-mail address: j.potts@sheffield.ac.uk (J.R. Potts).

http://dx.doi.org/10.1016/j.jtbi.2017.03.011
Received 8 November 2016; Received in revised form 20 February 2017; Accepted 10 March 2017

behavioural or environmental factors affect the survival of competing populations* This question leads to a wealth of possibilities for study, which have been the subject of numerous works. Examples include those on the effects of environmental heterogeneity (Zhu and Yin, 2009), predation (Morozov et al., 2008), control efforts (Chen, 2006), and spatial stochasticity (Neuhauser and Pacala, 1999). In this paper, we will focus on one specific behavioural factor: movement responses to competing populations.

Incorporating movement of any kind requires that we construct spatially explicit models of population dynamics. The simplest way to do this is by adding diffusive movement to a spatially implicit model. Although more technical procedures exist for incorporating space (Durrett and Levin, 1994), this method provides a base-line starting point for mathematical analysis, so remains popular (see e.g. Lewis et al., 2016, Chapter 4 and references therein). Indeed, a spatial version of the SLVC model incorporating diffusive movement has been studied mathematically by several authors (Dancer et al., 1999; Crooks et al., 2004; Nakashima and Wakasa, 2007).

When environmental features are incorporated into this model, co-existence patterns may occur. One set of examples feature non-convex domain shapes (Mimura et al., 1991), modelling geographic features such as peninsulas or curved valleys. Another include inhomogeneous boundary conditions (Crooks et al., 2004), modelling environmental heterogeneity on the boundaries of the population range. However, when the environment is homogeneous and convex, as is typical of many ecological situations, then this diffusive SLVC model predicts that only one of the competing populations ultimately survives (Kan-On, 1997) (except in the fine-tuned situation where competition is essentially equal between the two populations, Brantingham et al., 2012; Dancer et al., 1999). In other words, stable co-existence is essentially never predicted by the diffusive SLVC model in homogeneous environments.

From the perspective of biological invasions, the diffusive SLVC model predicts that a stronger invading population will spread into a weaker native population via a travelling wave. The invading population eventually dominates, causing the native population to be wiped out. Recently, Girardin and Nadin (2015) gave analytic conditions on the direction of this travelling wave, relating the competition strength to species diffusivity, in the limiting case where the inter-specific competition is arbitrarily larger than intra-specific competition. In principle, this enables prediction of which populations may succeed in an invasion scenario, by understanding of the diffusive and competition parameters governing the movement and growth of both native and alien populations.

In this paper, we extend this reaction–diffusion model of strong competition to incorporate movement responses between the two populations. This is in part inspired by recent empirical studies showing that top-predators change their movement when close to competing predators (Vanak et al., 2013; Swanson et al., 2016). Our aim is to understand the effect of such movements on the spatial population dynamics. The key idea is that movement responses may be used by an otherwise 'weaker' population to 'push back' the travelling wave, causing a reversal in the eventual fate of the populations. Mathematically, these movement responses are encoded in an *advection* term, leading to a system of reaction–advection–diffusion equations. These naturally combine the advection–diffusion equations of taxis models (Lewis and Murray, 1993; Potts and Lewis, 2014) with the reaction–diffusion equations of spatial population dynamics (Namba, 1989; Durrett and Levin, 1994; Tilman and Kareiva, 1997). Roughly, the 'advection' term means that we are including directed motion (sometimes called 'taxis'), the 'reaction' term refers to birth and death processes, and the 'diffusion' term to the unknown drivers of movement, modelled as a random process.

Despite these three aspects being clearly important to demographic dynamics, the combination of all three is rare in mathematical ecology, with most studies focussing on either 'advection' or 'reaction'. Although a few exceptions exist – such as prey-taxis studies (Kareiva and Odell, 1987; Lee et al., 2009) and stratified diffusion (Shigesada et al., 1995) – these represent just the tip of the iceberg regarding taxis properties in response to external or internal cues: e.g. competing predators moving in response to the presence of the other population (Vanak et al., 2013; Potts et al., 2013), prey avoiding places where predators live (Latombe et al., 2014; Bastille-Rousseau et al., 2015), and so forth. Since statistical and data-collection techniques are beginning to uncover such movement responses (Vanak et al., 2013; Potts et al., 2014; Hays et al., 2016), it is important for theoretical studies to catch-up with the data analysis by examining the effect of taxis on population dynamics.

Our work represents a key step in this direction. In particular, we seek to answer two questions: (i) Can taxis responses enable a population to 'punch above its weight' in competition with another population, causing it to survive when otherwise it would die out* (ii) Under what circumstances might such movement processes lead to co-existence of multiple strongly competitive populations* It is often believed that such co-existence can only occur when relatively complex ecological processes are involved, often involving environmental heterogeneity (Amarasekare, 2003). Here, we hypothesise that movement responses can provide a new mechanism of co-existence between strongly competitive populations (Hardin, 1960; Barabás et al., 2016).

2. Static movement response

We begin by examining the case where animals have a fixed movement response to foreign populations. In the next section, we examine the effect of allowing this to vary over time.

2.1. The model

In this section, our model considers two competing populations of animals, whose distribution functions are given by $u(x, t)$ and $v(x, t)$, where x denotes position (in one- or two-dimensions) and t is the time. These populations could be thought of either as two different species, or two groups (e.g. packs, flocks or tribes) from the same species. They are both assumed to be competing for space in the same ecological niche, so animals from one population have a negative effect on the population growth of the other population. In the absence of such competition, we assume that each population exhibits logistic growth.

Our model is based on the Lotka–Volterra competition model (Lotka, 1932; Volterra, 1926), but also incorporates movement in two different ways. First, movement is assumed to have a diffusive aspect, modelling the spread of each population over time, a property that has been considered in several previous works (e.g. Kan-On, 1997; Dancer et al., 1999; Murray, 2001; Girardin and Nadin, 2015). Second, each population exhibits taxis in response to the presence of the other population. As far as we are aware, this second aspect is a novel addition to Lotka's competition model. However, competition models where taxis is mediated by a chemical have been considered (Painter and Sherratt, 2003; Horstmann, 2011; Stinner et al., 2014), usually in the context of cell biology, and have some resemblance to our model.

The equations describing our model are as follows

$$\frac{\partial u}{\partial t} = \underbrace{D\nabla^2 u}_{\text{Diffusive movement}} - \underbrace{c_1\nabla\cdot[u\nabla v]}_{\text{Taxis towards } v} + \underbrace{ru(K-u) - a_1uv}_{\text{competition dynamics}}, \tag{1}$$

$$\frac{\partial v}{\partial t} = \underbrace{D\nabla^2 v}_{\text{Diffusive movement}} - \underbrace{c_2\nabla\cdot[v\nabla u]}_{\text{Taxis towards } u} + \underbrace{rv(K-v) - a_2uv}_{\text{competition dynamics}}. \tag{2}$$

Here, c_1 and c_2 represent the strength of taxis response by u and v, respectively. Parameters a_1 and a_2 denote the deleterious effect of competition on the population sizes of u and v, respectively, r is the infinitesimal growth rate of each population, and K is the carrying capacity of the environment.

Eqs. (1)–(2) bear some similarity to cross-diffusion. The difference is that, in cross-diffusion models, the taxis terms $\nabla\cdot[u\nabla v]$ and $\nabla\cdot[v\nabla u]$ are replaced with cross-diffusion terms of the form $\nabla^2[(\alpha_{uu}u+\alpha_{vu}v)u]$ and $\nabla^2[(\alpha_{uv}u+\alpha_{vv}v)v]$, respectively (Shigesada et al., 1979). (Here, α_{uu}, α_{uv}, α_{vu}, α_{vv} are constants.) Confusingly, the term 'cross-diffusion' has occasionally been used instead of 'taxis' in some works, for example the predator–prey model of Tsyganov et al. (2004). However, we are not aware of any previous studies that combine taxis terms of the form $\nabla\cdot[u\nabla v]$ and $\nabla\cdot[v\nabla u]$ with Lotka–Volterra-type competition models.

From a biological perspective, the taxis mechanism from Eqs. (1)–(2) can be understood in a number of ways. One occurs when animals can directly observe the density of the foreign population in their immediate vicinity (e.g. by sight or touch). Then they can use these observations to choose whether to adjust their movement in response to the density gradient. If c_i is positive (i=1 or 2) then the tendency will be to move from lower to higher population densities. If $c_i<0$ then the tendency will be in the other direction: from higher to lower densities. This interpretation of the taxis term in Eqs. (1)–(2) could work well for small animals that densely populate their habitat, so that they can easily detect the local population density by sensing the animals around them. Such an interpretation could also be applied beyond the animal kingdom, for example to populations of moving cellular organisms.

However, larger creatures (e.g. ungulates, canids, big cats, etc.) are likely to be more sparsely populated on the landscape than very small ones. As such, large animals could conceivably be well within another population's range and yet not be observing *directly* any of the animals that live there. Nonetheless, there are biological mechanisms of *indirect* observation by which such animals can still detect the probability of being in the range of a foreign population, even when other animals are not physically present. Such mechanisms can be broadly split into two categories: (i) *extrinsic signals*, where one population leaves signs of its existence in the physical landscape (e.g. by marking the terrain with urine or faeces), and (ii) *intrinsic signals*, where occasional interactions between animals of the two populations leave traces in the spatial memory of the animals involved, informing them of the range of the foreign population (Potts and Lewis, 2016b).

Biologically, examples of responses to extrinsic signals abound in both intra-species (King, 1973; Stamps, 1977; Kimsey, 1980; Smith et al., 2012; Potts et al., 2013) and inter-species (Nieh et al., 2004; Seppänen et al., 2007; Hughes et al., 2010) spatial competition. Intrinsic signals – i.e. using memory – are harder to detect directly, but have been posited as a key mechanism behind animal movement and spatial distribution (Fagan et al., 2013). Furthermore, movement responses to knowledge of the past positions of animals are increasingly being detected in animal populations, between populations of both different species (Seppänen et al., 2007; Latombe et al., 2014; Vanak et al., 2013) and the same species (Potts et al., 2014).

Mathematically, when indirect movement responses to foreign populations are modelled, they lead to advection by each population in response to the distribution of the other population (see Potts and Lewis, 2016a in the case of extrinsic signals and Potts and Lewis, 2016b for intrinsic signals). This often turns out to be very similar to the taxis response that appears in Eqs. (1)–(2). To illustrate this, an example of how these taxis terms arise from indirect interaction processes is given in Supplementary Appendix A, in the case of scent-marking. Here, the key assumption is that the distribution of scent marks tend towards an equilibrium state at a much faster rate than the population distributions. In scenarios where such assumptions are valid, Eqs. (1)–(2) are appropriate for modelling movement responses to foreign populations due to indirect extrinsic or intrinsic signals, as well as direct inter-animal sensing.

In this paper, we consider the case of *strong competition*, where $a_1, a_2 > r$ in Eqs. (1)–(2). For the spatially implicit model, given by setting $c_1=c_2=D=0$ in Eqs. (1)–(2), it is well-known that there are two stable steady-states for strong competition, given by $u=(K,0)$ and $(u,v)=(0,K)$. The final state of the dynamical system is then determined purely by its initial condition (Lotka, 1932; Murray, 2011). By explicitly incorporating space, our aim is to investigate whether taxis may reverse the predictions of spatially implicit models.

We use the 1D version of the model in Eqs. (1)–(2) to enable faster numerical investigation, noting that the analogous 2D model gives almost identical results in test cases (Supplementary Appendix B). Our system is defined on an interval $0\le x\le L$ with zero-flux boundary conditions, meaning that the net migration at each end of the interval is zero, i.e. as many animals leave the interval as arrive. To reduce the number of parameters in our model, for easier analysis, we introduce the following dimensionless parameters

$$\tilde{x}=\frac{x}{L},\quad \tilde{t}=\frac{tD}{L^2},\quad \tilde{u}(\tilde{x},\tilde{t})=\frac{u(x,t)}{K},\ \tilde{v}(\tilde{x},\tilde{t})=\frac{v(x,t)}{K},$$
$$\tilde{r}=\frac{rKL^2}{D},\ \tilde{a_i}=\frac{a_iKL^2}{D},\quad \gamma_i=\frac{c_iK}{D},\tag{3}$$

for i=1,2. Then, dropping the tildes over the letters to ease notation, we arrive at the following system of dimensionless equations, defined on the interval $0\le x\le 1$,

$$\frac{\partial u}{\partial t}=\frac{\partial^2 u}{\partial x^2}-\gamma_1\frac{\partial}{\partial x}\left[u\frac{\partial v}{\partial x}\right]+ru(1-u)-a_1uv,\tag{4}$$

$$\frac{\partial v}{\partial t}=\frac{\partial^2 v}{\partial x^2}-\gamma_2\frac{\partial}{\partial x}\left[v\frac{\partial u}{\partial x}\right]+rv(1-v)-a_2uv,\tag{5}$$

which are subject to the following zero-flux boundary conditions

$$\left\{\frac{\partial u}{\partial x}-\gamma_1\left[u\frac{\partial v}{\partial x}\right]\right\}\Bigg|_{x=0,1}=0,\tag{6}$$

$$\left\{\frac{\partial v}{\partial x}-\gamma_2\left[v\frac{\partial u}{\partial x}\right]\right\}\Bigg|_{x=0,1}=0.\tag{7}$$

We solve Eqs. (4)–(7) numerically for a variety of parameter values, given as follows. We set $\gamma_1=0$ and $a_2=2000$ and have initial conditions such that u starts on the left and v on the right, with equal population densities. Specifically, $u(x,0)$ and $v(x,0)$ are smooth monotonic functions such that $u(x,0)=1$ for $x<0.5-\epsilon$, $u(x,0)=0$ for $x>0.5+\epsilon$, $v(x,0)=0$ for $x<0.5-\epsilon$, and $v(x,0)=1$ for $x>0.5+\epsilon$, and ϵ is arbitrarily small (see Fig. 1a; see also Supplementary Appendix C for details of the choice of ϵ). We let the parameters r, γ_2, and a_1 vary. However, we insist that $a_1<a_2=2000$, so that u is the stronger population. We also insist that $r<a_1$ so that we are in the parameter regime corresponding to strong competition. Finally, we set $\gamma_2\ge 0$, so that v employs an aggressive movement strategy in an attempt to outcompete u. The particular parameter values we investigate fall into the regions $0.02\le r/a_2\le 0.75$ and $0.85\le a_1/a_2<1$. Supplementary Appendix C gives details of the numerical methods used to study this system.

2.2. Results

In our simulations, one of the two constant steady-state solutions is always reached, which correspond to the predictions from spatially implicit analysis (Lotka, 1932; Murray, 2011). Denoting the steady states by $u_*(x)=\lim_{t\to\infty}u(x,t)$ and $v_*(x)=\lim_{x\to\infty}v(x,t)$, these solutions are either $u_*(x)=1$ and $v_*(x)=0$, so we say 'u wins', or $u_*(x)=0$ and $v_*(x)=1$, so we say 'v wins'. Fig. 1b displays the regions of parameter space where there is a switch from u winning to v winning. Notice that increasing γ_2 (the strength of aggressive movement by v) enables v to win even when it is weaker than u: i.e. when a_1 is smaller than a_2. Thus we see movement triggering a switch in the predictions of the spatially implicit analysis.

The explanation for this switch in fortunes of u and v can be understood by leveraging the idea of a travelling wave solution. Technically, for such a solution to exist, Eqs. (4) and (5) must be solved on an infinite line. However, due to the complexity of the

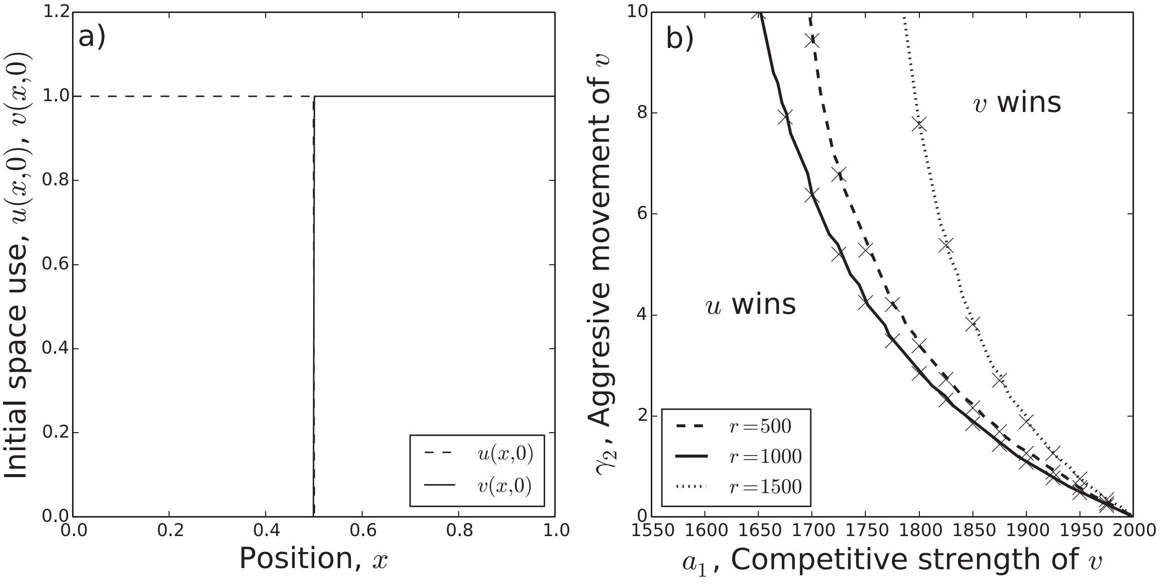

Fig. 1. Switch in fate due to movement strategies. Panel (a) shows the initial conditions of two populations, u and v, in our numerical analysis. Fixing $\gamma_1 = 0$, and $a_2 = 2000$, panel (b) shows which of u and v end up winning for different values of r, a_1, and γ_2 (see Eqs. (4) and (5)). For each value of r, below and to the left of the corresponding line, we see u winning, as predicted by non-spatial analysis. Above and to the right, we see v winning, in contradiction to the spatially implicit predictions. Crosses denote places where the travelling wave speed was measured to be zero.

system, we are unable to calculate this analytically (in fact, exact travelling wave speeds are not known even where $\gamma_1 = \gamma_2 = 0$), and numerics require using a bounded line-segment. Moreover, the numerical solution of a diffusion–reaction system in a finite domain is known to approximate the stable travelling wave solution with high precision over the time when the front is sufficiently far away from the domain boundary, and hence the perturbation induced by the boundary is small (Murray, 2001; Fife, 2013; Lewis et al., 2016). As such, we numerically measure an approximate travelling wave speed using the system defined on [0, 1] in Eqs. (4)–(7). Supplementary Appendix C details the numerical method used.

In the case $\gamma_1 = \gamma_2 = 0$, Girardin and Nadin (2015) show analytically that the asymptotic travelling wave speed (when the system is defined on an infinite line) is positive (rightward) in the limit as $a_i \to \infty$ (i=1,2) with $a_1/a_2 < 1$ kept constant. Our numerical analysis suggests that this result is also true away from this limit (Supplementary Table ST1). However, if γ_2 is increased, with $\gamma_1 = 0$ fixed, then population v advects *against* the direction of the u-travelling wave, pushing it back. This has the effect of slowing the wave down, even *reversing* its direction if the advective motion is strong enough.

In Figs. 2 and 3, we plot the critical value of γ_2 at which the wave-velocity switches direction from positive (right) to negative (left) for various values of r and a_1 such that $r < a_1 < a_2 = 2000$. This critical aggression speed is denoted by γ_2^*. Values of γ_2^* correspond exactly with the points at which the fate of u switches from extinction to dominance (Fig. 1b). Therefore the travelling wave velocity provides a convenient way to measure the ultimate fate of u and v.

Two interesting non-monotonic relationships arise from this analysis. The first is shown in Fig. 2. As the infinitesimal reproduction rate, r, is increased from 0, the critical aggression speed, γ_2^*, decreases initially. This is due to the increased ability of population v to reproduce and grow having made aggressive moves into u's area. However, as r is increased towards a_1, we are moving closer and closer towards the region where $a_1 < r < a_2$, which is a region where u always wins, no matter what the advection strength or initial conditions. As such, γ_2^* increases as $r \to a_1$.

The second non-monotonic relationship is the subject of Fig. 3. Here, we see that aggressive movement strategies are only advantageous up to a point. Although, for certain values of a_1/a_2, increasing γ_2 can cause the travelling wave to reverse direction, further increases in γ_2 can cause the travelling wave to switch once more, meaning that v eventually dies out if it is overly aggressive. The reason for this reversal in fortunes can be understood by examining the transient state of the travelling wave solutions (Fig. 4; Supplementary Videos SV1, SV2). Just after time t=0, a group from population v pushes into the range of population u, creating a non-monotonic population profile. This then dies out leaving the front of v less steep than for lower γ_2. Consequently, the size of v at the population overlap is too small to push v into u, even with the help of a strong advective effect.

2.3. Incorporating environmental heterogeneity

In heterogeneous environments, the reproduction rate, r, will vary over space if certain parts of the landscape are more conducive to survival and reproduction than others. Because the sign of the travelling wave speed depends on r (Figs. 2 and 3), we sometimes observe species co-existence in such landscapes. This will happen if the parameters on the left-hand side of the terrain are in the correct regime for a rightward travelling wave, and the parameters on the right-hand side are such that travelling waves move leftwards. Some example situations where this happens are given in Fig. 5. Interestingly, the spatial pattern of the population distributions is slightly out-of-phase with the spatial pattern of the environment. Indeed, in the area of poorer resources, and close to the edge between the two habitats, the total population density is slightly lower than the carrying capacity. Notice that this co-existence phenomenon only occurs when there is *both* taxis in response to foreign populations *and* spatial variation in r. Without the former, the travelling wave direction will always be to the right if $a_1 < a_2$ (left if $a_1 > a_2$), regardless of the value of r.

3. Dynamic movement response

In the model given by Eqs. (4)–(7), we assume that the movement responses of each population, given by γ_1 and γ_2, are constant. In reality, animals may be able to alter their response mechanism, depending on the current situation. As shown in Section 2, if a population is being pushed back by a travelling wave of advancing foreign population, it may benefit the former population to move aggressively towards the latter. However, if the former population is not being pushed back then there is no benefit in such aggressive

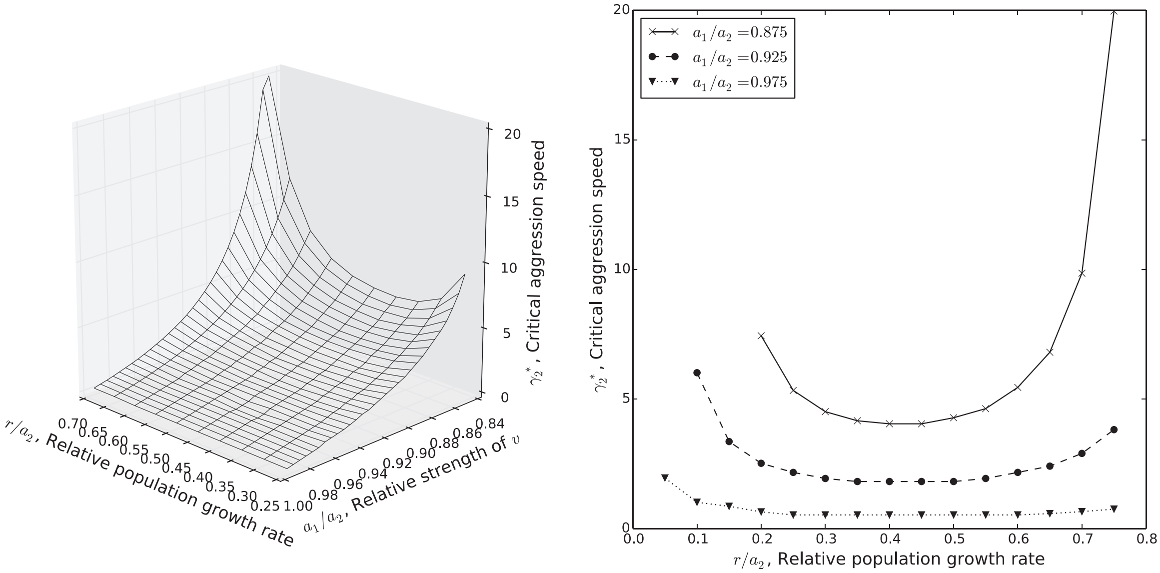

Fig. 2. Critical aggression speed, where the travelling-wave changes from right- to left-wards movement. The left-hand panel shows the dependence of the critical aggression speed, γ_2^*, on a_1/a_2 (the relative strength of v) and r/a_2 (the populations' growth rate relative to the constant $a_2 = 2000$). The right-hand panel shows cross-sections of the left-hand panel, for three values of a_1/a_2. The critical aggression speed increases as a_1/a_2 decreases. However, the dependence of γ_2^* on r is non-monotonic (explained in the main text).

movement. Indeed, from the individual's perspective, there is a negative effect of moving aggressively towards the other population, as interactions with the other population are more likely to have a negative effect than interactions with its native population. Therefore there is a trade-off between making aggressive movements for the social benefit of a declining population, and retreating from aggressive encounters for individual benefit. In this section, we explore the demographic patterns that arise from this trade-off, by allowing the aggression parameters, γ_1 and γ_2, to vary over time depending on whether animals sense a decline or increase in foreign population density.

3.1. The model

We begin with the model given by Eqs. (4)–(7) but replace the constants γ_1 and γ_2 with functions $\gamma_1(x, t)$ and $\gamma_2(x, t)$. As a population senses that a travelling wave of a foreign population is intruding into its range, it will increase its aggression towards the foreign population. Therefore, if $u(x, t)$ is increasing at some point x, $\gamma_2(x, t)$ will increase. Likewise, an increase in $v(x, t)$ leads to an increase in $\gamma_1(x, t)$. A simple model of this is given as follows

$$\frac{\partial \gamma_1}{\partial t} = \beta \frac{\partial v}{\partial t}, \quad \frac{\partial \gamma_2}{\partial t} = \beta \frac{\partial u}{\partial t}, \tag{8}$$

where β is a constant. By integrating with respect to t, we see that Eq. (8) have the solutions $\gamma_1(x, t) - \gamma_1(x, 0) = \beta[v(x, t) - v(x, 0)]$ and $\gamma_2(x, t) - \gamma_2(x, 0) = \beta[u(x, t) - u(x, 0)]$. For convenience, we assume that there is no advection at time t=0, so that $\gamma_1(x, 0) = \gamma_2(x, 0) = 0$.

By placing $\gamma_1(x, t) = \beta[v(x, t) - v(x, 0)]$ and $\gamma_2(x, t) = \beta[u(x, t) - u(x, 0)]$ into Eqs. (4)–(7), we arrive at the following equations, which give the

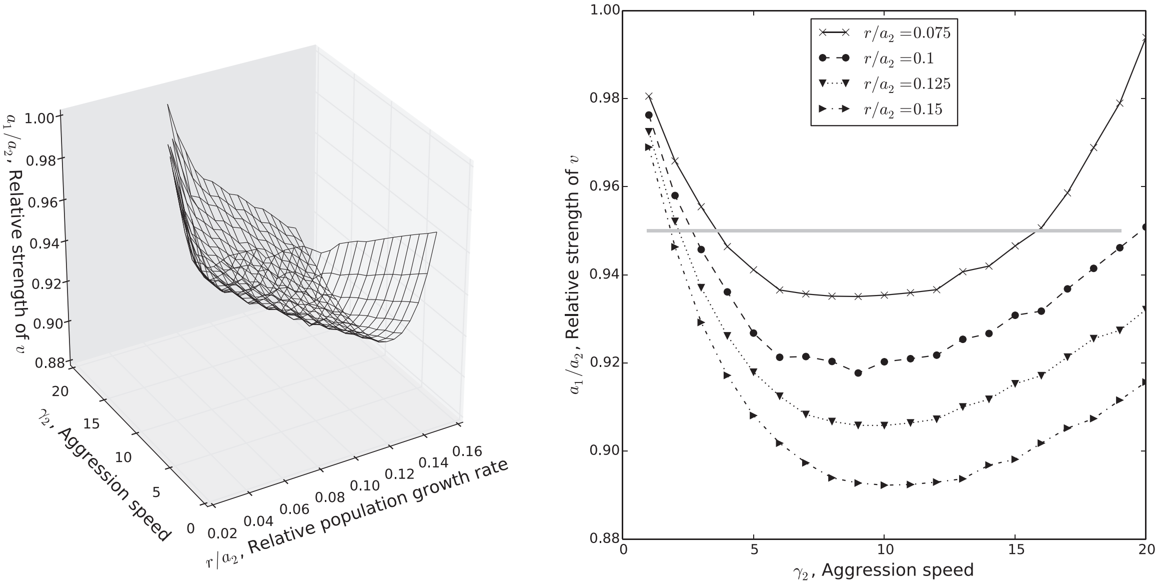

Fig. 3. Non-monotonic dependence of the travelling wave direction on the aggression speed. The surface in the left-hand panel shows places where the travelling wave speed is zero. For certain fixed values of r, a_1, and a_2, there are two values of the aggression speed, γ_2, where the travelling wave is zero. In these cases, a small amount of aggression by v can switch the travelling wave speed from positive to negative, so that v ultimately wins, but increasing γ_2 further can switch the wave speed back to positive. The right-hand panel shows this phenomenon for four fixed values of r. The thick grey line shows the parameter values used for Fig. 4, where $r/a_2 = 0.075$.

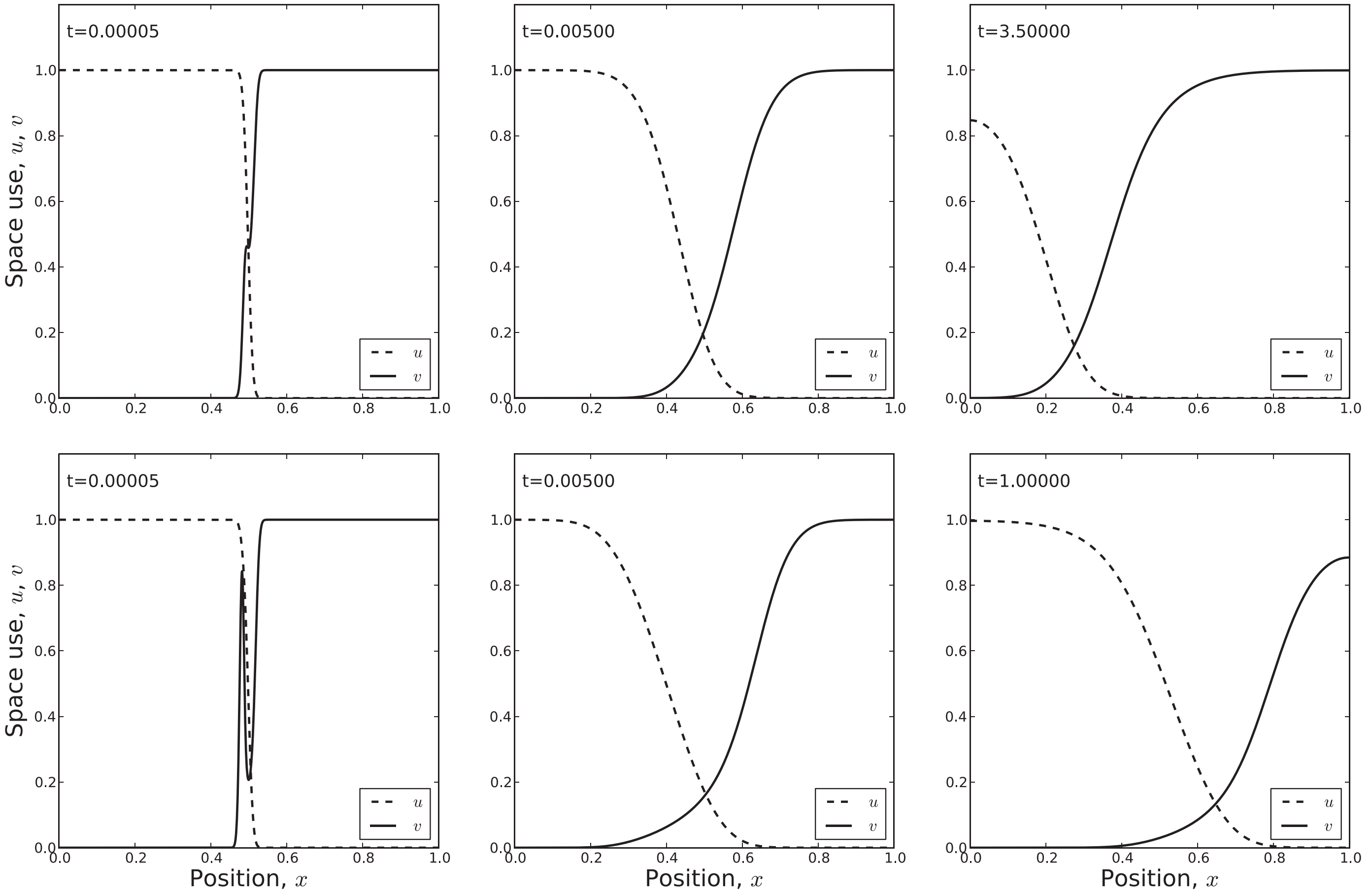

Fig. 4. Transient dynamics of different aggression levels. The top row shows the space use at three points in time when the aggression speed of v is enough to push back the travelling wave. Parameters are $a_1 = 1900$, $a_2 = 2000$, $\gamma_1 = 0$, $\gamma_2 = 5$, r=150, and times t are shown in the panels. In the bottom row, the aggression speed is excessive and the system ends with v's demise. Here, parameters are the same as in the top row, except $\gamma_2 = 20$. Animations can be found in Supplementary Videos SV1 and SV2. Note that the non-monotonic profile for t=0.00005 is not a numerical artefact: it still exists when the time-step Δt for the numerics is over 10^4 times less than the time over which the non-monotonic profile appears.

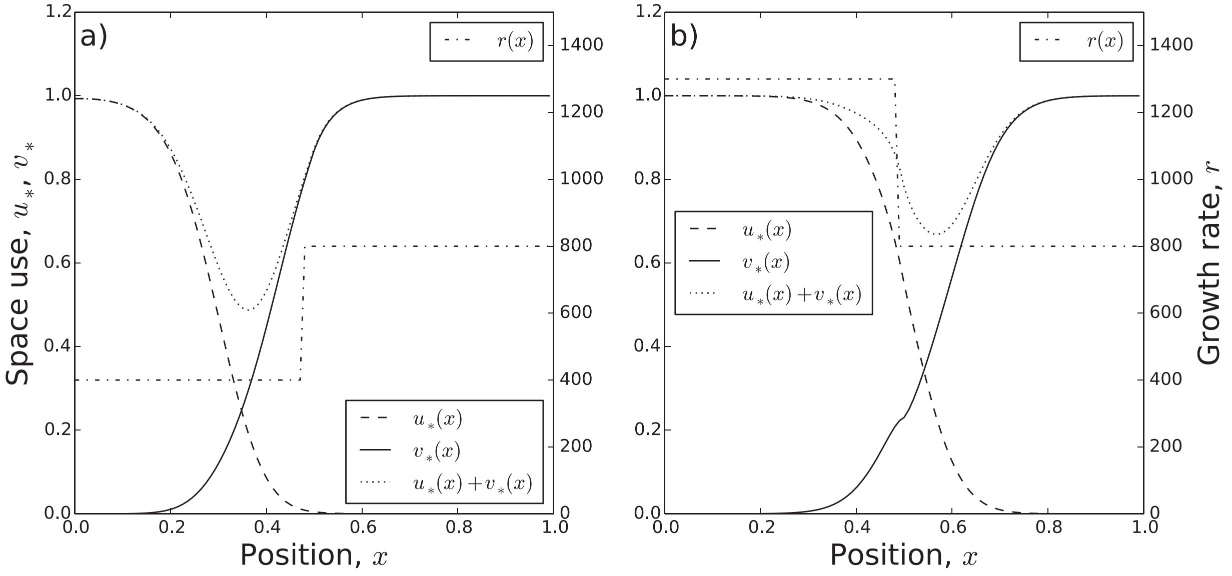

Fig. 5. Co-existence of strongly competing populations in heterogenous environments. When the environmental conditions cause the reproductive rate, r, to vary over space, it is possible to observe co-existence of populations. Space use is plotted when $u(x, t)$ and $v(x, t)$ are at steady-state, denoted by $u_*(x)$ and $v_*(x)$ respectively. Parameters (for both panels) are $a_1 = 1750$, $a_2 = 2000$, $\gamma_1 = 0$, $\gamma_2 = 5$, with $r(x)$ varying over space as shown in the panels.

study system for this section

$$\frac{\partial u}{\partial t}=\frac{\partial^2 u}{\partial x^2}-\beta\frac{\partial}{\partial x}\left[(v-v_0)u\frac{\partial v}{\partial x}\right]+ru(1-u)-a_1uv, \tag{9}$$

$$\frac{\partial v}{\partial t}=\frac{\partial^2 v}{\partial x^2}-\beta\frac{\partial}{\partial x}\left[(u-u_0)v\frac{\partial u}{\partial x}\right]+rv(1-v)-a_2uv, \tag{10}$$

$$\left.\left\{\frac{\partial u}{\partial x}-\beta(v-v_0)\left[u\frac{\partial v}{\partial x}\right]\right\}\right|_{x=0,1}=0, \tag{11}$$

$$\left.\left\{\frac{\partial v}{\partial x}-\beta(u-u_0)\left[v\frac{\partial u}{\partial x}\right]\right\}\right|_{x=0,1}=0, \tag{12}$$

where $u_0(x)=u(x,0)$ and $v_0(x)=v(x,0)$. We solve Eqs. (9)–(12) numerically for the same parameter values and initial conditions as for the static model in Section 2 (see Supplementary Appendix C for details of the numerical methods).

The appearance of $u_0(x)$ and $v_0(x)$ in Eqs. (9)–(12) means that the system depends for all time on its initial conditions. Hence they are crucial to the long-term behaviour and must be chosen carefully. From a mathematical point of view, any number of initial conditions could be considered. However, we have chosen biologically relevant initial conditions that mimic a likely ‘first contact’ scenario between two competing populations, whereby one population is predominantly on the left-hand side of the interval and the other on the right (see Fig. 1a). These conditions are especially pertinant if either (a) one population has arrived as an invasion event or (b) the populations were originally non-contiguous (so not competing), but then the range of one expanded over time towards the range of the other.

3.2. Results

For a large range of parameter values, the system in Eqs. (9)–(12) reaches a co-existence steady state, with population u mainly concentrated on the left-hand side of the terrain and v on the right (Fig. 6, bottom panels). In particular, for given values of a_1, a_2, and r, within the range we examined, there is a critical value of β above which co-existence is observed in Eqs. (9)–(12), and below which the steady-state solution is $u_*(x)=1$ and $v_*(x)=0$. We denote this critical value by β^* and plot it for various a_1 and r in Fig. 6 (top panels), with $a_2=2000$ kept constant (as in Section 2.1). To our knowledge, this is the first time that co-existence has been observed in a model of strong competition inside a homogeneous landscape.

Two clear trends emerge. First, β^* decreases as a_1 increases towards a_2. The reason for this is that the competitive advantage of u becomes more marginal the closer a_1 is to a_2, so the rate of change of γ_i (the strength of aggressive movement) does not need to be as high for co-existence to emerge. Second β^* depends in a non-monotonic fashion on r. For each value of a_1, the curve attains a minimum at some critical value of r between 0 and a_1. This mirrors the trend seen in Fig. 2 and can be explained in an identical fashion (see Section 2.2).

4. Discussion

Movement is often cited as key to spatial population dynamics (Nathan et al., 2008; Morales et al., 2010). In particular, it is well-known that animals often adjust their movement in response to the presence of competitors. Here, we have shown that such responses can dramatically affect the ability of populations to survive. By employing a tactical movement strategy up the density gradient of a competing population, an otherwise weaker population can survive and even dominate, causing its competitors to be eliminated from the landscape. When animals are able to modify these movement strategies over time, co-existence of strongly competing populations is possible, even in a homogeneous environment. This calls into question assumptions about the conditions under which one population will exclude competing populations from space (Barabás et al., 2016).

The reason for this effect of movement responses can be intuitively understood by considering what happens to a travelling wave, moving from the stronger population into the weaker. If the weaker population begins to advect up the density gradient of the stronger population then it may be able to push the travelling wave back, even reversing its direction. Thus, in the long run, the otherwise ‘weaker’ population may be able to win the competition for survival.

In reality, however, the stronger population may notice that it is being dominated and so employ a similar movement strategy in response, slowing the wave down. We have shown that, by dynamically altering their responses in such a fashion, the travelling wave will often stop moving, enabling competing populations to co-exist on the landscape (Fig. 6). Mathematically, the resulting system involves a taxis response that is both gradient- and density-dependent. Responses that involve density dependence can arise from a variety of biological mechanisms (Kareiva and Odell, 1987; Petrovskii and Li, 2003), suggesting that there may be other scenarios where co-existence may emerge as a result of taxis mechanisms.

Without density-dependence, incorporating resource heterogeneity into the model can enable co-existence of both populations (within certain parameter ranges). Co-existence due to the interplay of movement and resource heterogeneity has also been observed by previous studies (e.g. Amarasekare, 2003; Débarre and Lenormand, 2011). However, these models often assume that each set of environmental conditions differentially affects the growth rate of different populations. A key outcome of our model is that the two populations can have the same intrinsic growth rate at each point in space, but spatially segregated co-existence may yet occur (Fig. 5).

Although taxis mechanisms can be helpful for population survival, our numerical experiments demonstrate that the usefulness is limited. It will not always be possible for populations to push back a travelling wave in a strongly competitive scenario, for example if they are significantly weaker. What is more, if they push too fast, movement can have a deleterious effect (Fig. 3). Here, the aggressing population finds itself relatively isolated from the rest of the group, and cannot sustain its existence in the face of the numerous and strong competitors (Fig. 4). Thus this isolated sub-group dies out, leaving the population weakened and so unable to push the travelling wave back. As such, courage becomes fool-hardiness if too much aggressive movement is in play, and populations must seek a balanced approach to survive.

Our mathematical model of taxis ‘up the density gradient’ can be viewed as modelling any one of a number of biological mechanisms. For small, high-density organisms, it may be possible to sense directly the change in population density gradient, for example by sight or touch. However, for other organisms, the density gradient might be inferred from traces left in the environment by competitors (Nieh et al., 2004; Seppänen et al., 2007; Hughes et al., 2010), for example by scent-marking. Alternatively, some species might determine the possible presence of competitors by remembering places where competitors were recently observed (Vanak et al., 2013; Potts and Lewis, 2016a). All three interpretations can be modelled by the sort of reaction–advection–diffusion equations we have studied here. Indeed precise mathematical links between reaction–advection–diffusion equations and both direct (Kareiva and Odell, 1987) and indirect (Potts and Lewis, 2016a,b) interactions can be made.

Despite this, there are limitations of reaction–advection–diffusion

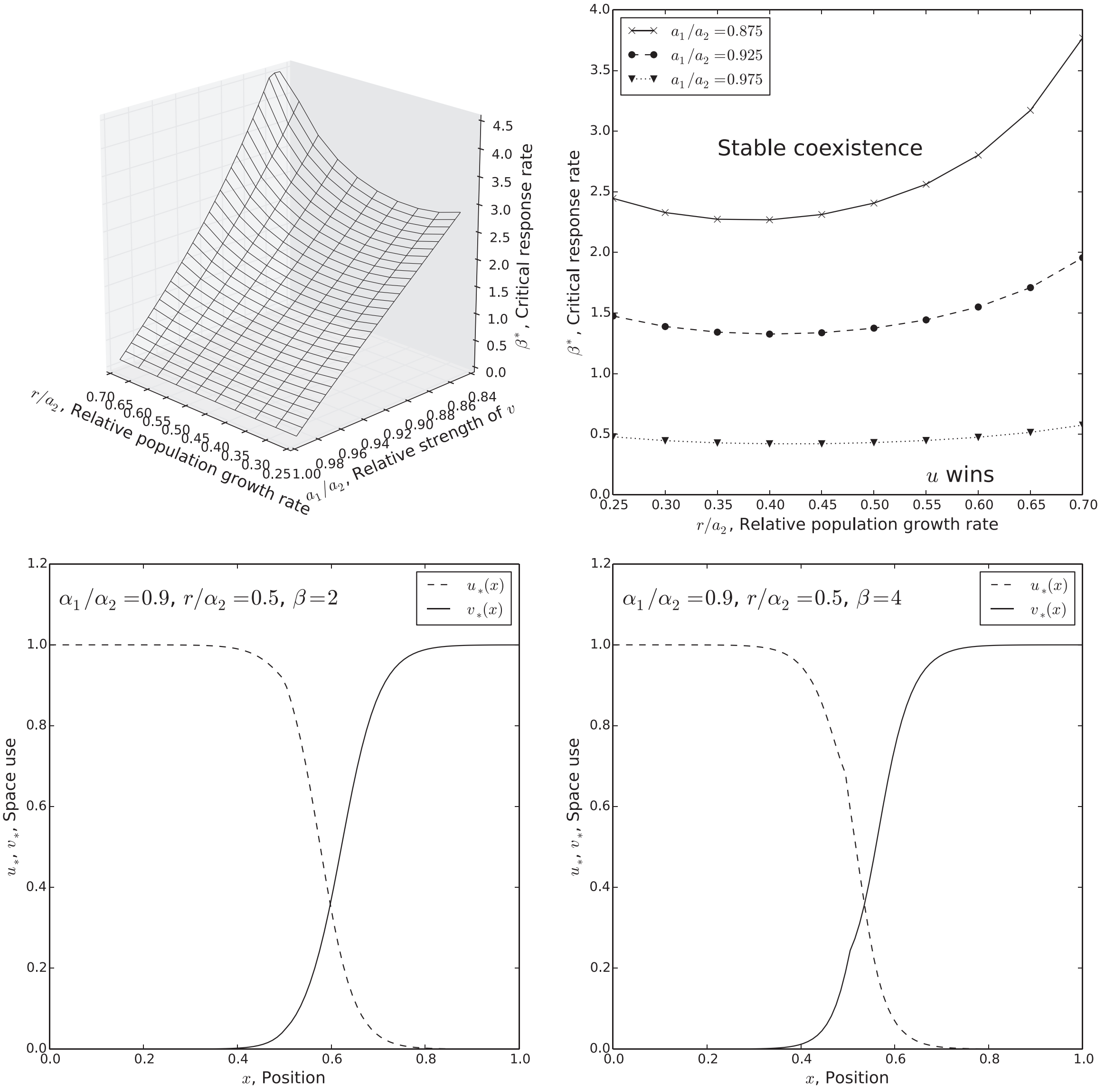

Fig. 6. Co-existence of strongly competing populations in homogeneous environments. Here, we analyse the model from Eqs. (9) to (12), where the advection is density dependent. The top-left panel shows the values of β^*, above which the system converges to a co-existence steady-state, and below which u wins and v goes extinct. The top-right panel shows cross-sections of this surface for various values of a_1/a_2. The bottom two panels show example co-existence steady-states for different parameter values. When β is just larger than β^* (bottom-left) u maintains a larger population than v, whereas for much larger β, the stable population distributions of u and v are of more similar sizes, with u only slightly larger than v (bottom-right).

equations for modelling animal interactions. If the interactions are direct then coupling them through a density function requires there to be a suitably large number of animals so that the continuum description of a good representation of the presence of actual animals (Durrett and Levin, 1994). Otherwise, it is necessary to use a stochastic individual-based model (e.g. Giuggioli et al., 2011). If interactions are indirect via marks on the environment, then the population density function will only accurately mirror the presence of marks if the distribution of the marks equilibrates quickly compared to the probability distribution of the animals (see Supplementary Appendix A). Finally, if some individuals exhibit long-range movements then an integro-difference formulation may be more realistic than reaction–advection–diffusion equations and can lead to different dynamics (Lewis et al., 2016; Kawasaki et al., 2017).

Our results highlight the importance of gathering detailed movement data on co-moving populations, as well as examining the effects on movement of direct and indirect interactions between populations and species. Simply measuring the growth and competition parameters may not be enough either to understand why competing populations might co-exist or predict future demographic dynamics. Techniques for measuring movement responses to such interactions have been increasingly developed and employed over recent years (Vanak et al., 2013; Langrock et al., 2014; Latombe et al., 2014; Potts et al., 2014). Therefore it would be a timely development to begin to factor the output of such data-inference into mechanistic models, to give more accurate predictions of demographic dynamics.

From an applied perspective, our results have potential important application for understanding biological invasions (Gatenby and Gawlinski, 1996; Lewis et al., 2016). If species are able to utilise the type of movement responses studied here, they may end up slowing down or pushing back a biological invasion of a competing species. This could ultimately lead either to species co-existence or to failure of a species to invade in a situation where current modelling might predict invasion success. As such, accurately predicting the speed and efficacy of an invasion may require an understanding of the movement responses of one species to another.

As well as these applied challenges, we highlight the need for greater analytic understanding of the model studied here, as well as its variants (e.g. incorporating various taxis responses into predator–prey models or models of more than two interacting species, etc.). At present, the best understanding of travelling-wave solutions to spatial SLVC models are given in Girardin and Nadin (2015). There, quite advanced analytic techniques were required to give exact bounds on the travelling-wave speed in a simplified version of our system. In particular, no advective term was present, so movement is simply diffusive, and inter-species competition is arbitrarily stronger than intra-species competition. To extend these results to gain analytic insight into the models studied here would require significant mathematical effort. One possible way forward might come by leveraging the techniques from the genetics literature that lead to 'Bartonian waves' (Barton, 1979; Jansen et al., 2008). Our results suggest that this effort is much needed, both for theoretical and applied ecology.

In summary, our work has brought to light the necessity for better connections between organism movement and populations dynamics. On the empirical side, we encourage greater attention to measuring movement responses to foreign populations when attempting to understand demographic dynamics. On the theoretical side, our work opens up the need for deeper examination of the effects of advective responses on population dynamics.

Acknowledgements

We thank two anonymous reviewers for constructive comments that have helped improve the paper.

Appendix A. Supplementary information

Supplementary information associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2017.03.011.

References

Amarasekare, P., 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecol. Lett. 6, 1109–1122.

Armsworth, P.R., Roughgarden, J.E., 2005. The impact of directed versus random movement on population dynamics and biodiversity patterns. Am. Nat. 165, 449–465.

Barabás, G., Michalska-Smith, M.J., Allesina, S., Leibold, M.A., Michalakis, Y., 2016. The effect of intra-and interspecific competition on coexistence in multispecies communities. Am. Nat. 188, E1–E12.

Barton, N., 1979. The dynamics of hybrid zones. Heredity 43, 341–359.

Bastille-Rousseau, G., Potts, J.R., Schaefer, J.A., Lewis, M.A., Ellington, E.H., Rayl, N.D., Mahoney, S.P., Murray, D.L., 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. Ecography 38, 1049–1059.

Börger, L., 2016. Editorial: Stuck in motion* Reconnecting questions and tools in movement ecology. J. Anim. Ecol. 85, 5–10.

Brantingham, P.J., Tita, G.E., Short, M.B., Reid, S.E., 2012. The ecology of gang territorial boundaries. Criminology 50, 851–885.

Chen, F., 2006. The permanence and global attractivity of Lotka–Volterra competition system with feedback controls. Nonlinear Anal.—Real 7, 133–143.

Crooks, E.C., Dancer, E.N., Hilhorst, D., Mimura, M., Ninomiya, H., 2004. Spatial segregation limit of a competition–diffusion system with Dirichlet boundary conditions. Nonlinear Anal.—Real 5, 645–665.

Dancer, E.N., Hilhorst, D., Mimura, M., Peletier, L.A., 1999. Spatial segregation limit of a competition–diffusion system. Eur. J. Appl. Math. 10, 97–115.

Débarre, F., Lenormand, T., 2011. Distance-limited dispersal promotes coexistence at habitat boundaries: reconsidering the competitive exclusion principle. Ecol. Lett. 14, 260–266.

Durrett, R., Levin, S., 1994. The importance of being discrete (and spatial). Theor. Popul. Biol. 46, 363–394.

Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W.w., Papastamatiou, Y.P., Forester, J., Mueller, T., 2013. Spatial memory and animal movement. Ecol. Lett. 16, 1316–1329.

Fife, P.C., 2013. Mathematical Aspects of Reacting and Diffusing Systems, vol. 28. Springer Science & Business Media, Berlin, Heidelberg, New York.

Gatenby, R.A., Gawlinski, E.T., 1996. A reaction–diffusion model of cancer invasion. Cancer Res. 56, 5745–5753.

Girardin, L., Nadin, G., 2015. Travelling waves for diffusive and strongly competitive systems: relative motility and invasion speed. Eur. J. Appl. Math. 26, 521–534.

Giuggioli, L., Potts, J.R., Harris, S., 2011. Animal interactions and the emergence of territoriality. PLoS Comput. Biol. 7, e1002008.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1297.

Hays, G.C., Ferreira, L.C., Sequeira, A.M., Meekan, M.G., Duarte, C.M., Bailey, H., Bailleul, F., Bowen, W.D., Caley, M.J., Costa, D.P., et al., 2016. Key questions in marine megafauna movement ecology. Trends Ecol. Evol. 31, 463–475.

Horstmann, D., 2011. Generalizing the Keller–Segel model: Lyapunov functionals, steady state analysis, and blow-up results for multi-species chemotaxis models in the presence of attraction and repulsion between competitive interacting species. J. Nonlinear Sci. 21, 231–270.

Hughes, N.K., Korpimäki, E., Banks, P.B., 2010. The predation risks of interspecific eavesdropping: weasel-vole interactions. Oikos 119, 1210–1216.

Jansen, V.A., Turelli, M., Godfray, H.C.J., 2008. Stochastic spread of Wolbachia. Proc, R. Soc. Lond. B: Biol. Sci. 275, 2769–2776.

Kan-On, Y., 1997. Fisher wave fronts for the Lotka–Volterra competition model with diffusion. Nonlinear Anal.—Theor. 28, 145–164.

Kareiva, P., Odell, G., 1987. Swarms of predators exhibit 'preytaxis' if individual predators use area-restricted search. Am. Nat. 130, 233–270.

Kawasaki, K., Shigesada, N., Iinuma, M., 2017. Effects of long-range taxis and population pressure on the range expansion of invasive species in heterogeneous environments. Theor. Ecol., 1–18.

Kimsey, L.S., 1980. The behaviour of male orchid bees (apidae, hymenoptera, insecta) and the question of leks. Anim. Behav. 28, 996–1004.

King, J.A., 1973. The ecology of aggressive behavior. Ann. Rev. Ecol. Syst. 4, 117–138.

Kishimoto, K., 1990. Coexistence of any number of species in the Lotka–Volterra competitive system over two-patches. Theor. Popul. Biol. 38, 149–158.

Lande, R., Engen, S., Saether, B.E., 2003. Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, U.S.A..

Langrock, R., Hopcraft, G., Blackwell, P., Goodall, V., King, R., Niu, M., Patterson, T., Pedersen, M., Skarin, A., Schick, R., 2014. Modelling group dynamic animal movement. Methods Ecol. Evol. 5, 190–199.

Latombe, G., Fortin, D., Parrott, L., 2014. Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. J. Anim. Ecol. 83, 185–198.

Lee, J., Hillen, T., Lewis, M., 2009. Pattern formation in prey-taxis systems. J. Biol. Dyn. 3, 551–573.

Lewis, M.A., Murray, J.D., 1993. Modelling territoriality and wolf–deer interactions. Nature 366, 738–740.

Lewis, M.A., Petrovskii, S.V., Potts, J.R., 2016. The Mathematics Behind Biological Invasions. Interdisciplinary Applied Mathematics, vol. 44. Springer, Switzerland.

Lotka, A.J., 1932. The growth of mixed populations: two species competing for a common food supply. J. Wash. Acad. Sci. 22, 461–469.

Mimura, M., Ei, S.I., Fang, Q., 1991. Effect of domain-shape on coexistence problems in a competition–diffusion system. J. Math. Biol. 29, 219–237.

Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill, E.H., Haydon, D.T., 2010. Building the bridge between animal movement and population dynamics. Philos. Trans. R. Soc. B 365, 2289–2301.

Morozov, A., Ruan, S., Li, B.L., 2008. Patterns of patchy spread in multi-species reaction–diffusion models. Ecol. Complex. 5, 313–328.

Murray, J., 2011. Mathematical Biology I: An Introduction. Interdisciplinary Applied Mathematics. Springer, New York.

Murray, J.D., 2001. Mathematical Biology II: Spatial Models and Biomedical Applications. Interdisciplinary Applied Mathematics. Springer, New York.

Nakashima, K., Wakasa, T., 2007. Generation of interfaces for Lotka–Volterra competition–diffusion system with large interaction rates. J. Differ. Equ. 235, 586–608.

Namba, T., 1989. Competition for space in a heterogeneous environment. J. Math. Biol. 27, 1–16.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. 105, 19052–19059.

Neuhauser, C., Pacala, S.W., 1999. An explicitly spatial version of the Lotka–Volterra model with interspecific competition. Ann. Appl. Probab. 9, 1226–1259.

Nieh, J.C., Barreto, L.S., Contrera, F.A., Imperatriz-Fonseca, V.L., 2004. Olfactory eavesdropping by a competitively foraging stingless bee, *Trigona spinipes*. Proc. R. Soc. B 271, 1633–1640.

Painter, K.J., Sherratt, J.A., 2003. Modelling the movement of interacting cell populations. J. Theor. Biol. 225, 327–339.

Petrovskii, S., Li, B.L., 2003. An exactly solvable model of population dynamics with density-dependent migrations and the allee effect. Math. Biosci. 186, 79–91.

Potts, J., Mokross, K., Lewis, M., 2014. A unifying framework for quantifying the nature of animal interactions. J. R. Soc. Interface 11, 20140333.

Potts, J.R., Harris, S., Giuggioli, L., 2013. Quantifying behavioral changes in territorial animals caused by sudden population declines. Am. Nat. 182, E73–E82.

Potts, J.R., Lewis, M.A., 2014. How do animal territories form and change* Lessons from 20 years of mechanistic modelling. Proc. R. Soc. B 281, 20140231.

Potts, J.R., Lewis, M.A., 2016a. How memory of direct animal interactions can lead to territorial pattern formation. J. R. Soc. Interface 13, 20160059.

Potts, J.R., Lewis, M.A., 2016b. Territorial pattern formation in the absence of an attractive potential. J. Math. Biol. 72, 25–46.

Seppänen, J.T., Forsman, J.T., Mönkkönen, M., Thomson, R.L., 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88, 1622–1633.

Shigesada, N., Kawasaki, K., Takeda, Y., 1995. Modeling stratified diffusion in biological invasions. Am. Nat. 146, 229–251.

Shigesada, N., Kawasaki, K., Teramoto, E., 1979. Spatial segregation of interacting species. J. Theor. Biol. 79, 83–99.

Smith, L.M., Bertozzi, A.L., Brantingham, P.J., Tita, G.E., Valasik, M., 2012. Adaptation of an ecological territorial model to street gang spatial patterns in Los Angeles. Discrete Contin. Dyn. Syst. 32, 3223–3244.

Stamps, J.A., 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58, 349–358.

Stinner, C., Tello, J., Winkler, M., 2014. Competitive exclusion in a two-species chemotaxis model. J. Math. Biol. 68, 1607–1626.

Swanson, A., Arnold, T., Kosmala, M., Forester, J., Packer, C., 2016. In the absence of a "landscape of fear": How lions, hyenas, and cheetahs coexist. Ecol. Evol. 6, 8534–8545.

Tilman, D., Kareiva, P.M., 1997. Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions, vol. 30. Princeton University Press, Princeton.

Tsyganov, M.A., Brindley, J., Holden, A.V., Biktashev, V.N., 2004. Soliton-like phenomena in one-dimensional cross-diffusion systems: a predator–prey pursuit and evasion example. Physica D 197, 18–33.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecol. Lett. 11, 1351–1363.

Vanak, A., Fortin, D., Thakera, M., Ogdene, M., Owena, C., Greatwood, S., Slotow, R., 2013. Moving to stay in place – behavioral mechanisms for coexistence of African large carnivores. Ecology 94, 2619–2631.

Volterra, V., 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. Acad. Lincei Roma 2, 31–113.

Zhu, C., Yin, G., 2009. On competitive Lotka–Volterra model in random environments. J. Math. Anal. Appl. 357, 154–170.