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

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Short title: Movement and population competition

Key words: Competitive exclusion principle, Lotka-Volterra competition model, Movement ecology, Population dynamics, Taxis

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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 an *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 & 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 & 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 behavioural or environmental factors affect the survival of competing populations? This questions 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 & Yin, 2009), predation (Morozov et al., 2008), control efforts (Chen, 2006), and spatial stochasticity (Neuhauser & 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 & 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 & 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 & 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). 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 & Murray, 1993; Potts & Lewis, 2014) with the reaction-diffusion equations of spatial population dynamics (Namba, 1989; Durrett & Levin, 1994; Tilman & 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 & 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 competitions (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 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

135   negative effect on the population growth of the other population. In the absence of such

136   competition, we assume that each population exhibits logistic growth.

137   Our model is based on the Lotka-Volterra competition model (Lotka, 1932; Volterra, 1926),

138   but also incorporates movement in two different ways. First, movement is assumed to have a

139   diffusive aspect, modelling the spread of each population over time, a property that has been

140   considered in several previous works [e.g. Kan-On (1997); Dancer et al. (1999); Murray (2001);

141   Girardin & Nadin (2015)]. Second, each population exhibits taxis in response to the presence of

142   the other population. As far as we are aware, this second aspect is a novel addition to Lotka's

143   competition model. However, competition models where taxis is mediated by a chemical have

144   been considered (Painter & Sherratt, 2003; Horstmann, 2011; Stinner et al., 2014), usually in

145   the context of cell biology, and have some resemblance to our model.

146   The equations describing our model are as follows

147
$$\frac{\partial u}{\partial t} = \underbrace{D\nabla^2 u}_{\text{Diffusive movement}} - \underbrace{c_1 \nabla \cdot [u\nabla v]}_{\text{Taxis towards } v} + \underbrace{ru(K-u) - a_1 uv}_{\text{competition dynamics}} , \qquad (1)$$

148
$$\frac{\partial v}{\partial t} = \underbrace{D\nabla^2 v}_{\text{Diffusive movement}} - \underbrace{c_2 \nabla \cdot [v\nabla u]}_{\text{Taxis towards } u} + \underbrace{rv(K-v) - a_2 uv}_{\text{competition dynamics}} . \qquad (2)$$
149

150   Here, c_1 and c_2 represent the strength of taxis response by u and v, respectively. Parameters

151   a_1 and a_2 denote the deleterious effect of competition on the population sizes of u and v,

152   respectively, r is the infinitesimal growth rate of each population, and K is the carrying capacity

153   of the environment.

154   Equations (1-2) bear some similarity to cross-diffusion. The difference is that, in cross-

155   diffusion models, the taxis terms $\nabla \cdot [u\nabla v]$ and $\nabla \cdot [v\nabla u]$ are replaced with cross-diffusion terms

156   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).

157   (Here, $\alpha_{uu}, \alpha_{uv}, \alpha_{vu}, \alpha_{vv}$ are constants.) Confusingly, the term 'cross-diffusion' has occasionally

158   been used instead of 'taxis' in some works, for example the predator-prey model of (Tsyganov

159   et al., 2004). However, we are not aware of any studies prior to this one 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 Equations (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 Equations (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 & 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

187 responses to knowledge of the past positions of animals are increasingly being detected in animal

188 populations, between populations of both different species (Seppänen et al., 2007; Latombe

189 et al., 2014; Vanak et al., 2013) and the same species (Potts et al., 2014).

190   Mathematically, when indirect movement responses to foreign populations are modelled,

191 they lead to advection by each population in response to the distribution of the other population

192 [see Potts & Lewis (2016a) in the case of extrinsic signals and Potts & Lewis (2016b) for intrinsic

193 signals]. This often turns out to be very similar to the taxis response that appears in Equations

194 (1-2). To illustrate this, an example of how these taxis terms arise from indirect interaction

195 processes is given in Supplementary Appendix A, in the case of scent-marking. Here, the key

196 assumption is that the distribution of scent marks tend towards an equilibrium state at a much

197 faster rate than the population distributions. In scenarios where such assumptions are valid,

198 Equations (1-2) are appropriate for modelling movement responses to foreign populations due

199 to indirect extrinsic or intrinsic signals, as well as direct inter-animal sensing.

200   In this paper, we consider the case of *strong competition*, where $a_1, a_2 > r$ in Equations (1-

201 2). For the spatially implicit model, given by setting $c_1 = c_2 = D = 0$ in Equations (1-2), it is

202 well-known that there are two stable steady-states for strong competition, given by $u = (K, 0)$

203 and $(u, v) = (0, K)$. The final state of the dynamical system is then determined purely by its

204 initial condition (Lotka, 1932; Murray, 2011). By explicitly incorporating space, our aim is to

205 investigate whether taxis may reverse the predictions of spatially implicit models.

206   We use the 1D version of the model in Equations (1-2) to enable faster numerical in-

207 vestigation, noting that the analogous 2D model gives almost identical results in test cases

208 (Supplementary Appendix B). Our system is defined on an interval $0 \leq x \leq L$ with zero-flux

209 boundary conditions, meaning that the net migration at each end of the interval is zero, i.e. as

210 many animals leave the interval as arrive. To reduce the number of parameters in our model,

211 for easier analysis, we introduce the following dimensionless parameters

212
213
$$\tilde{x} = \frac{x}{L}, \; \tilde{t} = \frac{tD}{L^2}, \; \tilde{u}(\tilde{x}, \tilde{t}) = \frac{u(x,t)}{K}, \; \tilde{v}(\tilde{x}, \tilde{t}) = \frac{v(x,t)}{K}, \; \tilde{r} = \frac{rKL^2}{D}, \; \tilde{a}_i = \frac{a_iKL^2}{D}, \; \gamma_i = \frac{c_iK}{D}, \quad (3)$$

214 for $i = 1, 2$. Then, dropping the tildes over the letters to ease notation, we arrive at the

215 following system of dimensionless equations, defined on the interval $0 \leq x \leq 1$,

216
$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} - \gamma_1 \frac{\partial}{\partial x} \left[u \frac{\partial v}{\partial x} \right] + ru(1 - u) - a_1 uv, \tag{4}$$

217
218
$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} - \gamma_2 \frac{\partial}{\partial x} \left[v \frac{\partial u}{\partial x} \right] + rv(1 - v) - a_2 uv, \tag{5}$$

219 which are subject to the following zero-flux boundary conditions

220
$$\left\{ \frac{\partial u}{\partial x} - \gamma_1 \left[u \frac{\partial v}{\partial x} \right] \right\} \bigg|_{x=0,1} = 0, \tag{6}$$

221
222
$$\left\{ \frac{\partial v}{\partial x} - \gamma_2 \left[v \frac{\partial u}{\partial x} \right] \right\} \bigg|_{x=0,1} = 0. \tag{7}$$

223 We solve Equations (4-7) numerically for a variety of parameter values, given as follows. We

224 set $\gamma_1 = 0$ and $a_2 = 2000$ and have initial conditions such that u starts on the left and v on the

225 right, with equal population densities. Specifically, $u(x, 0)$ and $v(x, 0)$ are smooth monotonic

226 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

227 $x < 0.5 - \epsilon$, and $v(x, 0) = 1$ for $x > 0.5 + \epsilon$, and ϵ is arbitrarily small (see Figure 1a; see

228 also Supplementary Appendix C for details of the choice of ϵ). We let the parameters r, γ_2,

229 and a_1 vary. However, we insist that $a_1 < a_2 = 2000$, so that u is the stronger population.

230 We also insist that $r < a_1$ so that we are in the parameter regime corresponding to strong

231 competition. Finally, we set $\gamma_2 \geq 0$, so that v employs an aggressive movement strategy in an

232 attempt to out-compete u. The particular parameter values we investigate fall into the regions

233 $0.02 \leq r/a_2 \leq 0.75$ and $0.85 \leq a_1/a_2 < 1$. Supplementary Appendix C gives details of the

234 numerical methods used to study this system.

235 ## 2.2   Results

236 In our simulations, one of two constant steady-state solutions is always reached, which corre-

237 spond 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'. Figure 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, Equations (4) and (5) must be solved on an infinite line. However, due to the complexity of the 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 Equations (4-7). Supplementary Appendix C details the numerical method used.

In the case $\gamma_1 = \gamma_2 = 0$, Girardin & 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 Figures 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

265 exactly with the points at which the fate of u switches from extinction to dominance (Figure

266 1b). Therefore the travelling wave velocity provides a convenient way to measure the ultimate

267 fate of u and v.

268   Two interesting non-monotonic relationships arise from this analysis. The first is shown in

269 Figure 2. As the infinitesimal reproduction rate, r, is increased from 0, the critical aggression

270 speed, γ_2^*, decreases initially. This is due to the increased ability of population v to reproduce

271 and grow having made aggressive moves into u's area. However, as r is increased towards

272 a_1, we are moving closer and closer towards the region where $a_1 < r < a_2$, which is a region

273 where u always wins, no matter what the advection strength or initial conditions. As such, γ_2^*

274 increases as $r \to a_1$.

275   The second non-monotonic relationship is the subject of Figure 3. Here, we see that aggres-

276 sive movement strategies are only advantageous up to a point. Although, for certain values of

277 a_1/a_2, increasing γ_2 can cause the travelling wave to reverse direction, further increases in γ_2

278 can cause the travelling wave to switch once more, meaning that v eventually dies out if it is

279 overly aggressive. The reason for this reversal in fortunes can be understood by examining the

280 transient state of the travelling wave solutions (Figure 4; Supplementary Videos SV1, SV2).

281 Just after time $t = 0$, a group from population v pushes into the range of population u, creating

282 a non-monotonic population profile. This then dies out leaving the front of v less steep than

283 for lower γ_2. Consequently, the size of v at the population overlap is too small to push v into

284 u, even with the help of a strong advective effect.

2.3   Incorporating environmental heterogeneity

286 In heterogeneous environments, the reproduction rate, r, will vary over space if certain parts

287 of the landscape are more conducive to survival and reproduction than others. Because the

288 sign of the travelling wave speed depends on r (Figures 2 and 3), we sometimes observe species

289 co-existence in such landscapes. This will happen if the parameters on the left-hand side of

290 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 Figure 5. Interestingly, the spatial pattern of the population distributions are 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 Equations (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 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 Equations (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 popu-

316 lation is intruding into its range, it will increase its aggression towards the foreign population.

317 Therefore, if $u(x, t)$ is increasing at some point x, $\gamma_2(x, t)$ will increase. Likewise, an increase

318 in $v(x, t)$ leads to an increase in $\gamma_1(x, t)$. A simple model of this is given as follows

319
320
$$\frac{\partial \gamma_1}{\partial t} = \beta \frac{\partial v}{\partial t}, \qquad \frac{\partial \gamma_2}{\partial t} = \beta \frac{\partial u}{\partial t}, \tag{8}$$

321 where β is a constant. By integrating with respect to t, we see that Equations (8) have the

322 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

323 convenience, we assume that there is no advection at time $t = 0$, so that $\gamma_1(x, 0) = \gamma_2(x, 0) = 0$.

324   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 Equations

325 (4-7), we arrive at the following equations, which give the study system for this section

326
$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} - \beta \frac{\partial}{\partial x}\left[(v - v_0)u\frac{\partial v}{\partial x}\right] + ru(1 - u) - a_1 uv, \tag{9}$$

327
$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} - \beta \frac{\partial}{\partial x}\left[(u - u_0)v\frac{\partial u}{\partial x}\right] + rv(1 - v) - a_2 uv, \tag{10}$$

328
$$\left\{\frac{\partial u}{\partial x} - \beta(v - v_0)\left[u\frac{\partial v}{\partial x}\right]\right\}\bigg|_{x=0,1} = 0, \tag{11}$$

329
330
$$\left\{\frac{\partial v}{\partial x} - \beta(u - u_0)\left[v\frac{\partial u}{\partial x}\right]\right\}\bigg|_{x=0,1} = 0, \tag{12}$$

331 where $u_0(x) = u(x, 0)$ and $v_0(x) = v(x, 0)$. We solve Equations (9-12) numerically for the same

332 parameter values and initial conditions as for the static model in Section 2 (see Supplementary

333 Appendix C for details of the numerical methods).

334   The appearance of $u_0(x)$ and $v_0(x)$ in Equations (9-12) means that the system depends for

335 all time on its initial conditions. Hence they are crucial to the long-term behaviour and must

336 be chosen carefully. From a mathematical point of view, any number of initial conditions could

337 be considered. However, we have chosen biologically-relevant initial conditions that mimic a

338 likely 'first contact' scenario between two competing populations, whereby one population is

339 predominantly on the left-hand side of the interval and the other on the right (see Figure 1a).

340 These conditions are especially pertinent if either (a) one population has arrived as an invasion

341 event, or (b) the populations were originally non-contiguous (so not competing), but then the

342 range of one expanded over time towards the range of the other.

3.2 Results

344 For a large range of parameter values, the system in Equations (9-12) reaches a co-existence

345 steady state, with population u mainly concentrated on the left-hand side of the terrain and v

346 on the right (Figure 6, bottom panels). In particular, for given values of a_1, a_2, and r, within

347 the range we examined, there is a critical value of β above which co-existence is observed

348 in Equations (9-12), and below which the steady-state solution is $u_*(x) = 1$ and $v_*(x) = 0$.

349 We denote this critical value by β^* and plot it for various a_1 and r in Figure 6 (top panels),

350 with $a_2 = 2000$ kept constant (as in Section 2.1). To our knowledge, this is the first time

351 that co-existence has been observed in a model of strong competition inside an homogeneous

352 landscape.

353   Two clear trends emerge. First, β^* decreases as a_1 increases towards a_2. The reason for

354 this is that the competitive advantage of u becomes more marginal the closer a_1 is to a_2, so

355 the rate of change of γ_i (the strength of aggressive movement) does not need to be as high for

356 co-existence to emerge. Second β^* depends in a non-monotonic fashion on r. For each value

357 of a_1, the curve attains a minimum at some critical value of r between 0 and a_1. This mirrors

358 the trend seen in Figure 2 and can be explained in an identical fashion (see Section 2.2).

4 Discussion

360 Movement is often cited as key to spatial population dynamics (Nathan et al., 2008; Morales

361 et al., 2010). In particular, it is well-known that animals often adjust their movement in

362 response to the presence of competitors. Here, we have shown that such responses can dramat-

363 ically effect the ability of populations to survive. By employing a tactical movement strategy

364 up the density gradient of a competing population, an otherwise weaker population can survive

365 and even dominate, causing its competitors to be eliminated from the landscape. When ani-

mals are able to modify these movement strategies over time, co-existence of strongly competing populations is possible, even in an 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 (Figure 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 & Odell, 1987; Petrovskii & 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 & 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 (Figure 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's more, if they push too fast, movement can have a deleterious effect (Figure 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 (Figure 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 & 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 & Odell, 1987) and indirect (Potts & Lewis, 2016a,b) interactions can be made.

Despite this, there are limitations of reaction-advection-diffusion 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 a good representation of the presence of actual animals (Durrett & 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 equilibriates 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 inter-actions 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 under-standing biological invasions (Gatenby & 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 verious taxis resposes 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 & 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). However, 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

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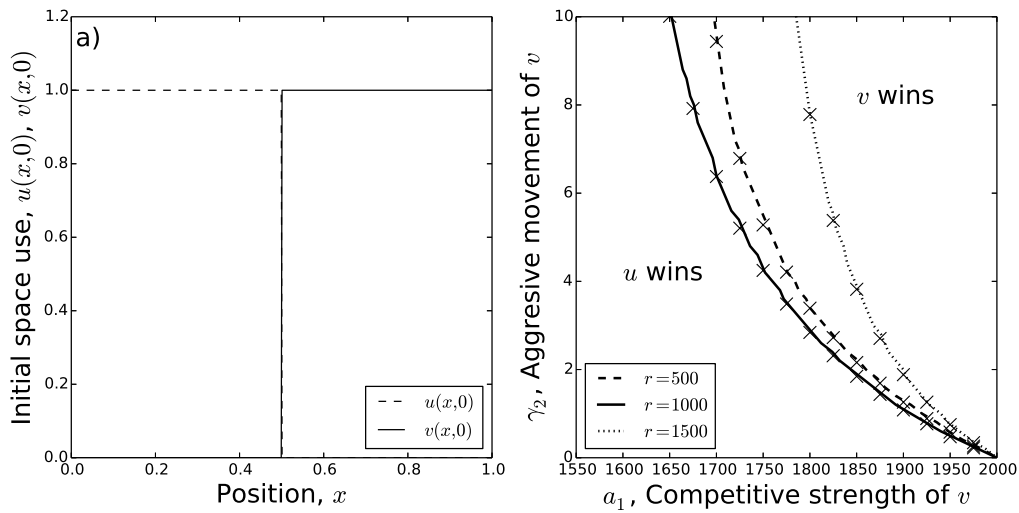
Fig. 1. Switch in fate due to movement strategies. Panel (a) shows the initial conditions of two populations, u and v, in our numerical analysis. Fixing $\gamma_1 = 0$, and $a_2 = 2000$, panel (b) shows which of u and v end up winning for different values of r, a_1, and γ_2 (see Equations 4 and 5). For 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.
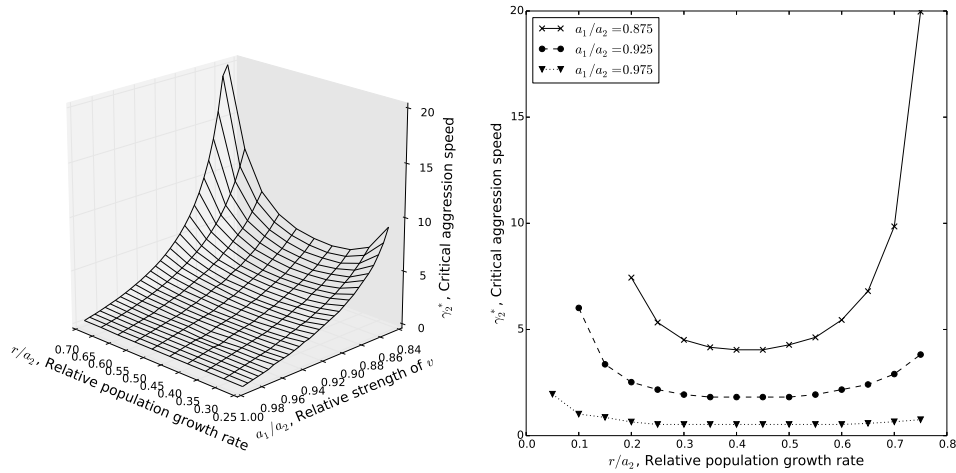
Fig. 2. Critical aggression speed, where the travelling-wave changes from right-to left-wards movement. The left-hand panel shows the dependence of the critical aggression speed, γ_2^*, on a_1/a_2 (the relative strength of v) and r/a_2 (the populations' growth rate relative to the constant $a_2 = 2000$). 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).
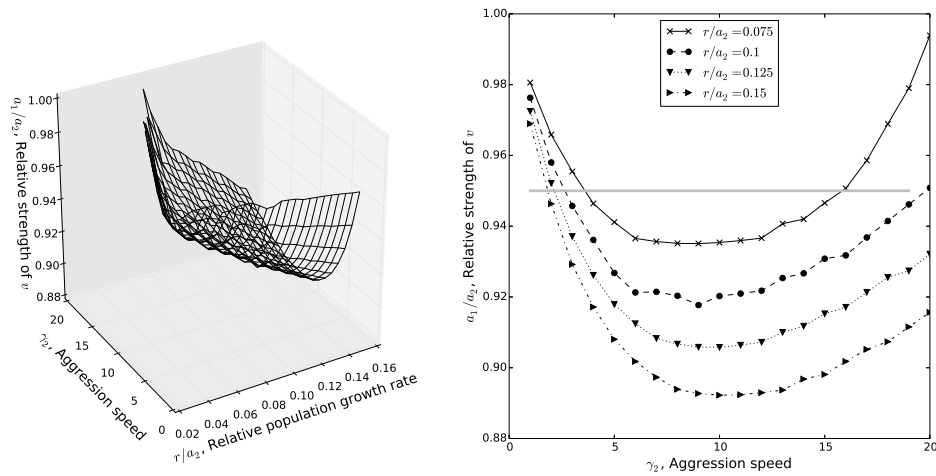
Fig. 3. Non-monotonic dependence of the travelling wave direction on the aggression speed. The surface in the left-hand panel shows places where the travelling wave speed is zero. For certain fixed values of r, a_1, and a_2, there are two values of the aggression speed, γ_2, where the travelling wave 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 Figure 4, where $r/a_2 = 0.075$.
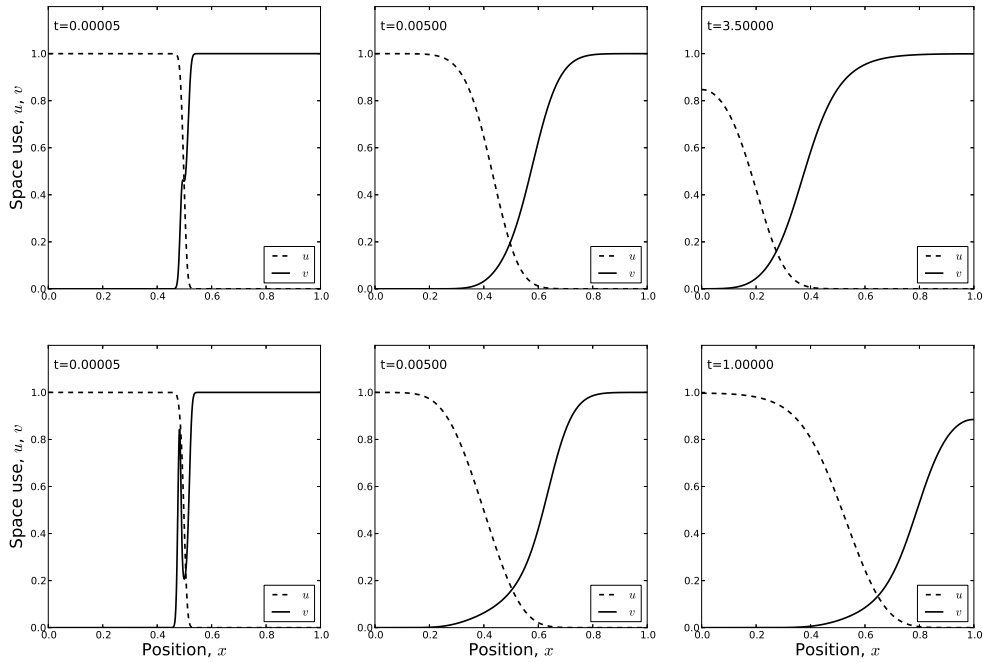
Fig. 4. Transient dynamics of different aggression levels. The top row shows the space use at three points in time when the aggression speed of v is enough to push back the travelling wave. Parameters are $a_1 = 1900$, $a_2 = 2000$, $\gamma_1 = 0$, $\gamma_2 = 5$, $r = 150$, and times t are shown in 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 artifact: 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.
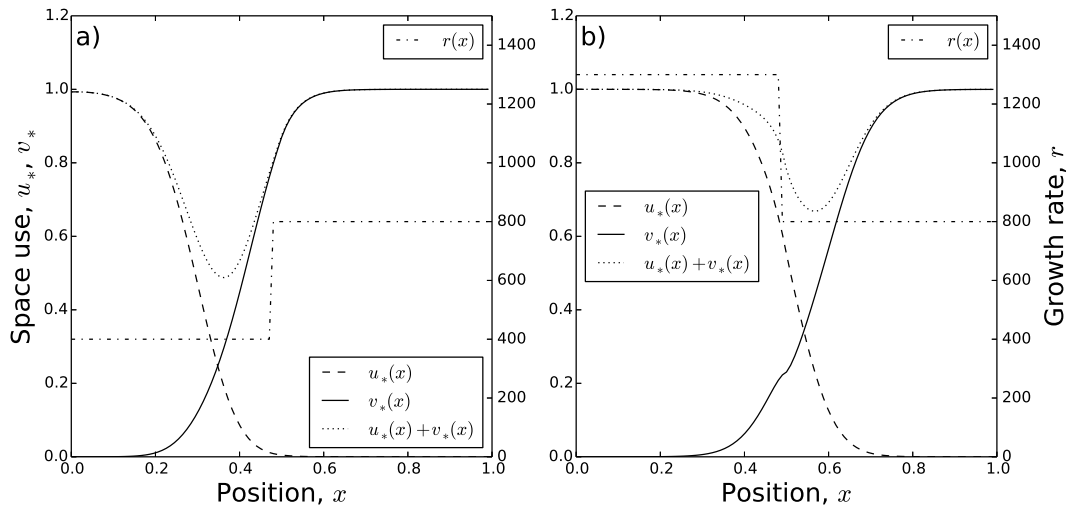
Fig. 5. Co-existence of strongly competing populations in heterogenous environments. When the environmental conditions cause the reproductive rate, r, to vary over space, it is possible to observe co-existence of populations. Space use is plotted when $u(x,t)$ and $v(x,t)$ are at steady-state, denoted 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.
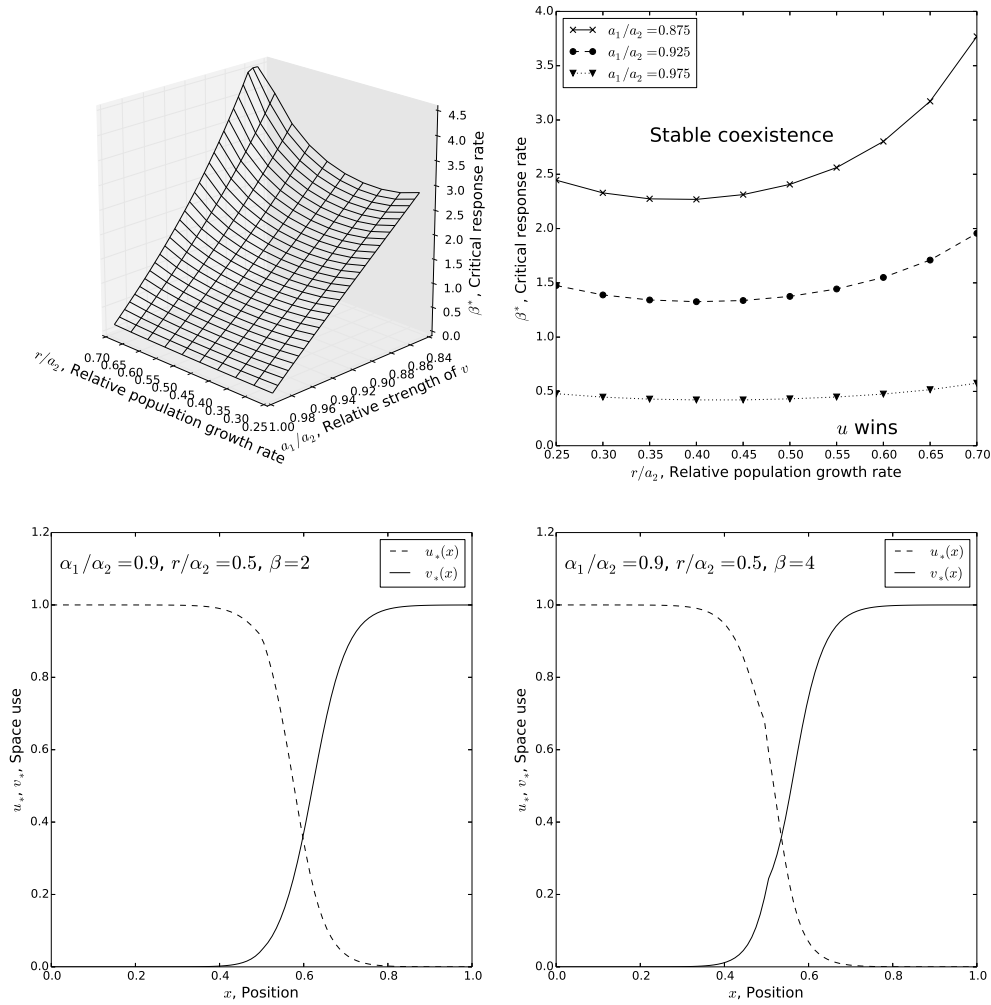
Fig. 6. Co-existence of strongly competing populations in homogeneous environments. Here, we analyse the model from Equations (9-12), where the advection is density dependent. The top-left panel shows the values of β^*, above which the system converges to a co-existence steady-state, and below which 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.