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

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

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

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12 Abstract

13 Animal movement is a key mechanism for shaping population dynamics. The effect of interac-
14 tions between competing animals on a population's survival has been studied for many decades.
15 However, interactions also affect an animal's subsequent movement decisions. Despite this, the
16 indirect effect of these decisions on animal survival is much less well-understood. Here, we in-
17 corporate movement responses to foreign animals into a model of two competing populations,
18 where inter-specific competition is greater than intra-specific competition. When movement is
19 diffusive, the travelling wave moves from the stronger population to the weaker. However, by
20 incorporating behaviourally-induced directed movement towards the stronger population, the
21 weaker one can slow the travelling wave down, even reversing its direction. Hence movement
22 responses can switch the predictions of traditional mechanistic models. Furthermore, when
23 environmental heterogeneity is combined with aggressive movement strategies, it is possible
24 for spatially segregated co-existence to emerge. In this situation, the spatial patterns of the
25 competing populations have the unusual feature that they are slightly out-of-phase with the
26 environmental patterns. Finally, incorporating dynamic movement responses can also enable
27 stable co-existence in an *homogeneous* environment, giving a new mechanism for spatially-
28 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).

56 The existence of bi-stability in the Strongly competitive LVC model (henceforth SLVC
57 model) naturally leads to the question of which additional ecological processes may affect
58 convergence to one or other of the stable states. Or, to put it in more biological terms,
59 which behavioural or environmental factors affect the survival of competing populations? This
60 questions leads to a wealth of possibilities for study, which have been the subject of numerous
61 works. Examples include those on the effects of environmental heterogeneity (Zhu & Yin,
62 2009), predation (Morozov et al., 2008), control efforts (Chen, 2006), and spatial stochasticity
63 (Neuhauser & Pacala, 1999). In this paper, we will focus on one specific behavioural factor:
64 movement responses to competing populations.

65 Incorporating movement of any kind requires that we construct spatially explicit models
66 of population dynamics. The simplest way to do this is by adding diffusive movement to
67 a spatially implicit model. Although more technical procedures exist for incorporating space
68 (Durrett & Levin, 1994), this method provides a base-line starting point for mathematical anal-
69 ysis, so remains popular [see e.g. Lewis et al. (2016, Chapter 4) and references therein]. Indeed,
70 a spatial version of the SLVC model incorporating diffusive movement has been studied math-
71 ematically by several authors (Dancer et al., 1999; Crooks et al., 2004; Nakashima & Wakasa,
72 2007).

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

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

92 In this paper, we extend this reaction-diffusion model of strong competition to incorpo-
93 rate movement responses between the two populations. This is in part inspired by recent
94 empirical studies showing that top-predators change their movement when close to compet-
95 ing predators (Vanak et al., 2013). Our aim is to understand the effect of such movements
96 on the spatial population dynamics. The key idea is that movement responses may be used
97 by an otherwise ‘weaker’ population to ‘push back’ the travelling wave, causing a reversal
98 in the eventual fate of the populations. Mathematically, these movement responses are en-
99 coded in an *advection* term, leading to a system of reaction-advection-diffusion equations.
100 These naturally combine the advection-diffusion equations of taxis models (Lewis & Murray,
101 1993; Potts & Lewis, 2014) with the reaction-diffusion equations of spatial population dynam-
102 ics (Namba, 1989; Durrett & Levin, 1994; Tilman & Kareiva, 1997). Roughly, the ‘advection’
103 term means that we are including directed motion (sometimes called ‘taxis’), the ‘reaction’
104 term refers to birth and death processes, and the ‘diffusion’ term to the unknown drivers of
105 movement, modelled as a random process.

106 Despite these three aspects being clearly important to demographic dynamics, the combina-
107 tion of all three is rare in mathematical ecology, with most studies focussing on either ‘advection’
108 or ‘reaction’. Although a few exceptions exist – such as prey-taxis studies (Kareiva & Odell,
109 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
 142 of 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

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

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

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
 156 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.,
 157 1979). (Here, $\alpha_{uu}, \alpha_{uv}, \alpha_{vu}, \alpha_{vv}$ are constants.) Confusingly, the term 'cross-diffusion' has
 158 occasionally been used instead of 'taxis' in some works, for example the predator-prey model
 159 of (Tsyganov et al., 2004). However, we are not aware of any studies prior to this one that

160 combine taxis terms of the form $\nabla \cdot [u\nabla v]$ and $\nabla \cdot [v\nabla u]$ with Lotka-Volterra-type competition
161 models.

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

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

183 Biologically, examples of responses to extrinsic signals abound in both intra-species (King,
184 1973; Stamps, 1977; Kimsey, 1980; Smith et al., 2012; Potts et al., 2013) and inter-species
185 (Nieh et al., 2004; Seppänen et al., 2007; Hughes et al., 2010) spatial competition. Intrinsic
186 signals – i.e. using memory – are harder to detect directly, but have been posited as a key

187 mechanism behind animal movement and spatial distribution (Fagan et al., 2013). Further-
188 more, movement responses to knowledge of the past positions of animals are increasingly being
189 detected in animal populations, between populations of both different species (Seppänen et al.,
190 2007; Latombe et al., 2014; Vanak et al., 2013) and the same species (Potts et al., 2014).

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

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

207 We use the 1D version of the model in Equations (1-2) to enable faster numerical in-
208 vestigation, noting that the analogous 2D model gives almost identical results in test cases
209 (Supplementary Appendix B). Our system is defined on an interval $0 \leq x \leq L$ with zero-flux
210 boundary conditions, meaning that the net migration at each end of the interval is zero, i.e. as
211 many animals leave the interval as arrive. To reduce the number of parameters in our model,

212 for easier analysis, we introduce the following dimensionless parameters

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

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

$$217 \quad \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} - \gamma_1 \frac{\partial}{\partial x} \left[u \frac{\partial v}{\partial x} \right] + ru(1-u) - a_1 uv, \quad (4)$$

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

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

$$221 \quad \left\{ \frac{\partial u}{\partial x} - \gamma_1 \left[u \frac{\partial v}{\partial x} \right] \right\} \Big|_{x=0,1} = 0, \quad (6)$$

$$222 \quad \left\{ \frac{\partial v}{\partial x} - \gamma_2 \left[v \frac{\partial u}{\partial x} \right] \right\} \Big|_{x=0,1} = 0. \quad (7)$$

224 We solve Equations (4-7) numerically for a variety of parameter values, given as follows. We
225 set $\gamma_1 = 0$ and $a_2 = 2000$ and have initial conditions such that u starts on the left and v on the
226 right, with equal population densities. Specifically, $u(x, 0)$ and $v(x, 0)$ are smooth monotonic
227 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
228 $x < 0.5 - \epsilon$, and $v(x, 0) = 1$ for $x > 0.5 + \epsilon$, and ϵ is arbitrarily small (see Figure 1a; see
229 also Supplementary Appendix C for details of the choice of ϵ). We let the parameters r , γ_2 ,
230 and a_1 vary. However, we insist that $a_1 < a_2 = 2000$, so that u is the stronger population.
231 We also insist that $r < a_1$ so that we are in the parameter regime corresponding to strong
232 competition. Finally, we set $\gamma_2 \geq 0$, so that v employs an aggressive movement strategy in an
233 attempt to out-compete u . The particular parameter values we investigate fall into the regions
234 $0.02 \leq r/a_2 \leq 0.75$ and $0.85 \leq a_1/a_2 < 1$. Supplementary Appendix C gives details of the
235 numerical methods used to study this system.

236 2.2 Results

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

245 The explanation for this switch in fortunes of u and v can be understood by leveraging the
 246 idea of a travelling wave solution. Technically, for such a solution to exist, Equations (4) and (5)
 247 must be solved on an infinite line. However, due to the complexity of the system, we are unable
 248 to calculate this analytically (in fact, exact travelling wave speeds are not known even where
 249 $\gamma_1 = \gamma_2 = 0$), and numerics require using a bounded line-segment. Moreover, the numerical
 250 solution of a diffusion-reaction system in a finite domain is known to approximate the stable
 251 travelling wave solution with high precision over the time when the front is sufficiently far
 252 away from the domain boundary, and hence the perturbation induced by the boundary is small
 253 (Murray, 2001; Fife, 2013; Lewis et al., 2016). As such, we numerically measure an approximate
 254 travelling wave speed using the system defined on $[0, 1]$ in Equations (4-7). Supplementary
 255 Appendix C details the numerical method used.

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

263 In Figures 2 and 3, we plot the critical value of γ_2 at which the wave-velocity switches
 264 direction from positive (right) to negative (left) for various values of r and a_1 such that $r <$
 265 $a_1 < a_2 = 2000$. This critical aggression speed is denoted by γ_2^* . Values of γ_2^* correspond
 266 exactly with the points at which the fate of u switches from extinction to dominance (Figure
 267 1b). Therefore the travelling wave velocity provides a convenient way to measure the ultimate
 268 fate of u and v .

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

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

286 2.3 Incorporating environmental heterogeneity

287 In heterogeneous environments, the reproduction rate, r , will vary over space if certain parts
 288 of the landscape are more conducive to survival and reproduction than others. Because the

289 sign of the travelling wave speed depends on r (Figures 2 and 3), we sometimes observe species
290 co-existence in such landscapes. This will happen if the parameters on the left-hand side of
291 the terrain are in the correct regime for a rightward travelling wave, and the parameters on
292 the right-hand side are such that travelling waves move leftwards. Some example situations
293 where this happens are given in Figure 5. Interestingly, the spatial pattern of the population
294 distributions are slightly out-of-phase with the spatial pattern of the environment. Indeed,
295 in the area of poorer resources, and close to the edge between the two habitats, the total
296 population density is slightly lower than the carrying capacity. Notice that this co-existence
297 phenomenon only occurs when there is *both* taxis in response to foreign populations *and* spatial
298 variation in r . Without the former, the travelling wave direction will always be to the right if
299 $a_1 < a_2$ (left if $a_1 > a_2$), regardless of the value of r .

300 **3 Dynamic movement response**

301 In the model given by Equations (4-7), we assume that the movement responses of each popu-
302 lation, given by γ_1 and γ_2 , are constant. In reality, animals may be able to alter their response
303 mechanism, depending on the current situation. As shown in Section 2, if a population is
304 being pushed back by a travelling wave of advancing foreign population, it may benefit the
305 former population to move aggressively towards the latter. However, if the former population
306 is not being pushed back then there is no benefit in such aggressive movement. Indeed, from
307 the individual's perspective, there is a negative effect of moving aggressively towards the other
308 population, as interactions with the other population are more likely to have a negative effect
309 than interactions with its native population. Therefore there is a trade-off between making
310 aggressive movements for the social benefit of a declining population, and retreating from ag-
311 gressive encounters for individual benefit. In this section, we explore the demographic patterns
312 that arise from this trade-off, by allowing the aggression parameters, γ_1 and γ_2 , to vary over
313 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 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

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

where β is a constant. By integrating with respect to t , we see that Equations (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 Equations (4-7), we arrive at the following equations, which give the study system for this section

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

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

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

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

where $u_0(x) = u(x, 0)$ and $v_0(x) = v(x, 0)$. We solve Equations (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 Equations (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

338 be considered. However, we have chosen biologically-relevant initial conditions that mimic a
339 likely ‘first contact’ scenario between two competing populations, whereby one population is
340 predominantly on the left-hand side of the interval and the other on the right (see Figure 1a).
341 These conditions are especially pertinent if either (a) one population has arrived as an invasion
342 event, or (b) the populations were originally non-contiguous (so not competing), but then the
343 range of one expanded over time towards the range of the other.

344 3.2 Results

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

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

360 4 Discussion

361 Movement is often cited as key to spatial population dynamics (Nathan et al., 2008; Morales et al.,
362 2010). In particular, it is well-known that animals often adjust their movement in response

363 to the presence of competitors. Here, we have shown that such responses can dramatically
364 effect the ability of populations to survive. By employing a tactical movement strategy up the
365 density gradient of a competing population, an otherwise weaker population can survive and
366 even dominate, causing its competitors to be eliminated from the landscape. When animals
367 are able to modify these movement strategies over time, co-existence of strongly competing
368 populations is possible, even in an homogeneous environment. This calls into question assump-
369 tions about the conditions under which one population will exclude competing populations
370 from space (Barabás et al., 2016).

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

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

384 Without density-dependence, incorporating resource heterogeneity into the model can en-
385 able co-existence of both populations (within certain parameter ranges). Co-existence due
386 to the interplay of movement and resource heterogeneity has also been observed by previous
387 studies [e.g. Amarasekare (2003), Débarre & Lenormand (2011)]. However, these models of-
388 ten assume that each set of environmental conditions differentially affects the growth rate of
389 different populations. A key outcome of our model is that the two populations can have the

390 same intrinsic growth rate at each point in space, but spatially segregated co-existence may
391 yet occur (Figure 5).

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

401 Our mathematical model of taxis 'up the density gradient' can be viewed as modelling any
402 one of a number of biological mechanisms. For small, high-density organisms, it may be possible
403 to sense directly the change in population density gradient, for example by sight or touch.
404 However, for other organisms, the density gradient might be inferred from traces left in the
405 environment by competitors (Nieh et al., 2004; Seppänen et al., 2007; Hughes et al., 2010), for
406 example by scent-marking. Alternatively, some species might determine the possible presence
407 of competitors by remembering places where competitors were recently observed (Vanak et al.,
408 2013; Potts & Lewis, 2016a). All three interpretations can be modelled by the sort of reaction-
409 advection-diffusion equations we have studied here. Indeed precise mathematical links between
410 reaction-advection-diffusion equations and both direct (Kareiva & Odell, 1987) and indirect
411 (Potts & Lewis, 2016a,b) interactions can be made.

412 Despite this, there are limitations of reaction-advection-diffusion equations for modelling
413 animal interactions. If the interactions are direct then coupling them through a density func-
414 tion requires there to be a suitably large number of animals so that the continuum description
415 a good representation of the presence of actual animals (Durrett & Levin, 1994). Otherwise,
416 it is necessary to use a stochastic individual-based model [e.g. Giuggioli et al. (2011)]. If in-

417 teractions are indirect via marks on the environment, then the population density function
418 will only accurately mirror the presence of marks if the distribution of the marks equilibrates
419 quickly compared to the probability distribution of the animals (see Supplementary Appendix
420 A). Finally, if some individuals exhibit long-range movements then an integro-difference for-
421 mulation may be more realistic than reaction-advection-diffusion equations and can lead to
422 different dynamics (Lewis et al., 2016; Kawasaki et al., 2017).

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

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

439 As well as these applied challenges, we highlight the need for greater analytic understand-
440 ing of the model studied here, as well as its variants (e.g. incorporating various taxis re-
441 sponses into predator-prey models, or models of more than two interacting species etc.). At
442 present, the best understanding of travelling-wave solutions to spatial SLVC models are given
443 in Girardin & Nadin (2015). There, quite advanced analytic techniques were required to give

444 exact bounds on the travelling-wave speed in a simplified version of our system. In particular,
445 no advective term was present, so movement is simply diffusive, and inter-species competition
446 is arbitrarily stronger than intra-species competition. To extend these results to gain analytic
447 insight into the models studied here would require significant mathematical effort. One possible
448 way forward might come by leveraging the techniques from the genetics literature that lead to
449 ‘Bartonian waves’ (Barton, 1979; Jansen et al., 2008). However, our results suggest that this
450 effort is much needed, both for theoretical and applied ecology.

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

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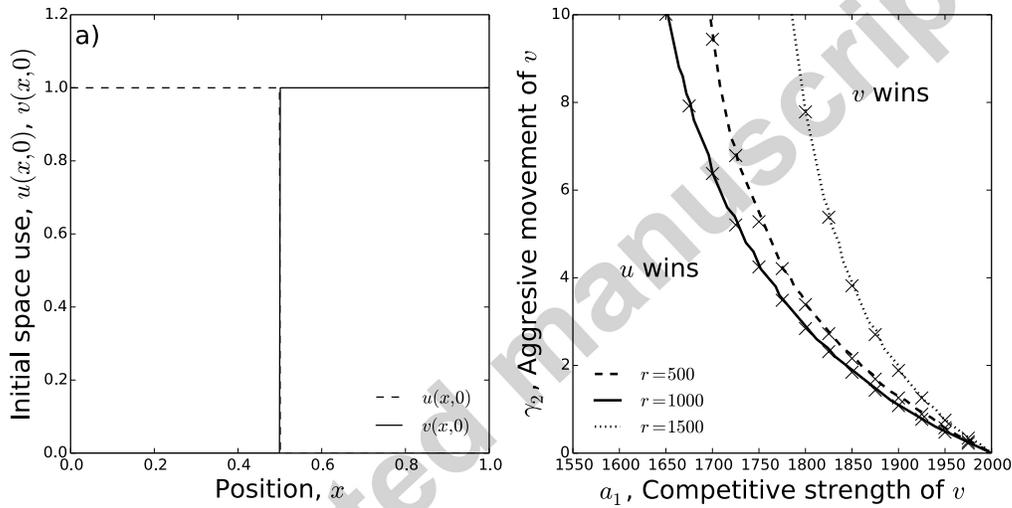


Fig. 1. Switch in fate due to movement strategies. Panel (a) shows the initial conditions of two populations, u and v , in our numerical analysis. Fixing $\gamma_1 = 0$, and $a_2 = 2000$, panel (b) shows which of u and v end up winning for different values of r , a_1 , and γ_2 (see Equations 4 and 5). 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.

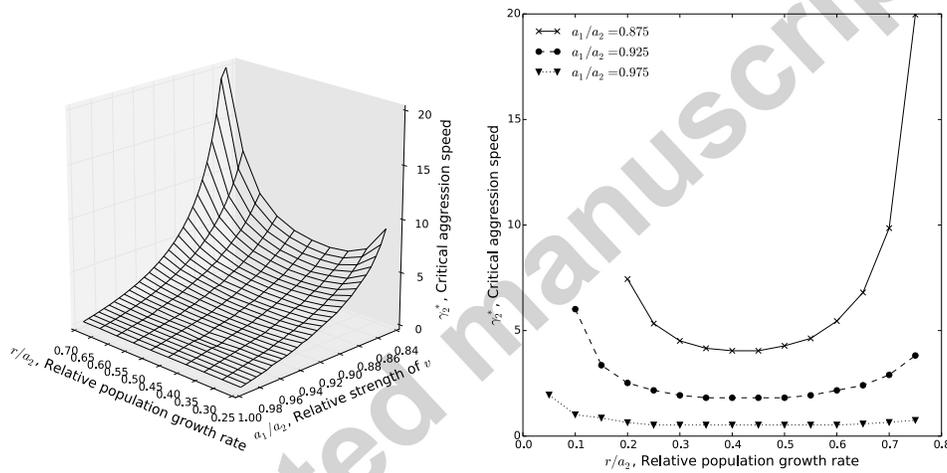


Fig. 2. Critical aggression speed, where the travelling-wave changes from right- to left-wards movement. The left-hand panel shows the dependence of the critical aggression speed, γ_2^* , on a_1/a_2 (the relative strength of v) and r/a_2 (the populations' growth rate relative to the constant $a_2 = 2000$). 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).

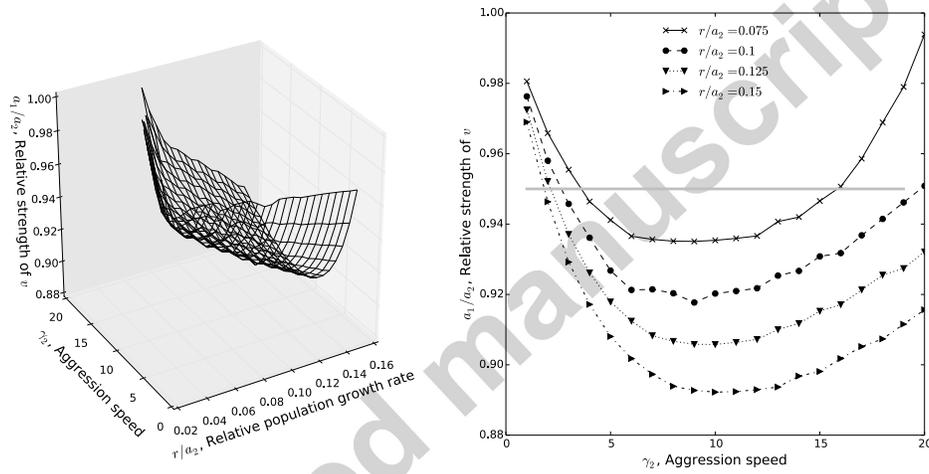


Fig. 3. Non-monotonic dependence of the travelling wave direction on the aggression speed. The surface in the left-hand panel shows places where the travelling wave speed is zero. For certain fixed values of r , a_1 , and a_2 , there are two values of the aggression speed, γ_2 , where the travelling 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 $r/a_2 = 0.075$.

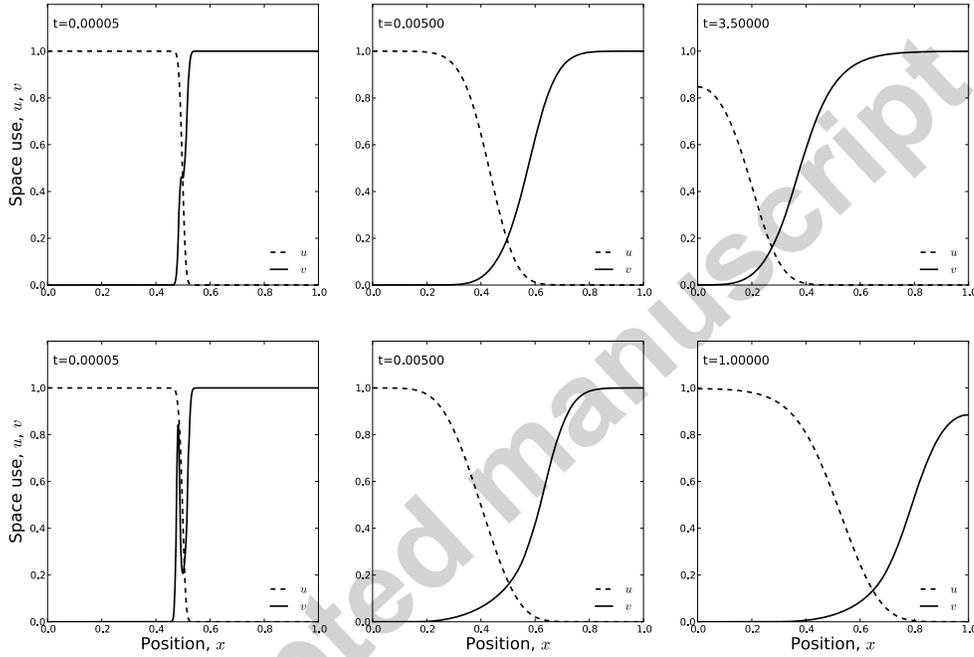


Fig. 4. Transient dynamics of different aggression levels. The top row shows the space use at three points in time when the aggression speed of v is enough to push back the travelling wave. Parameters are $a_1 = 1900$, $a_2 = 2000$, $\gamma_1 = 0$, $\gamma_2 = 5$, $r = 150$, and times t are shown in 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.

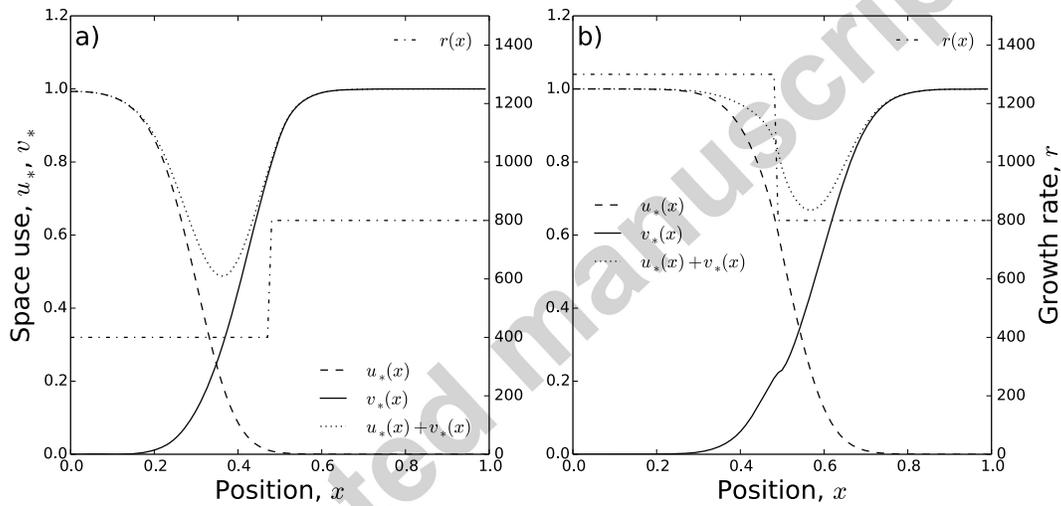


Fig. 5. Co-existence of strongly competing populations in heterogeneous environments. When the environmental conditions cause the reproductive rate, r , to vary over space, it is possible to observe co-existence of populations. Space use is plotted when $u(x, t)$ and $v(x, t)$ are at steady-state, denoted 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.

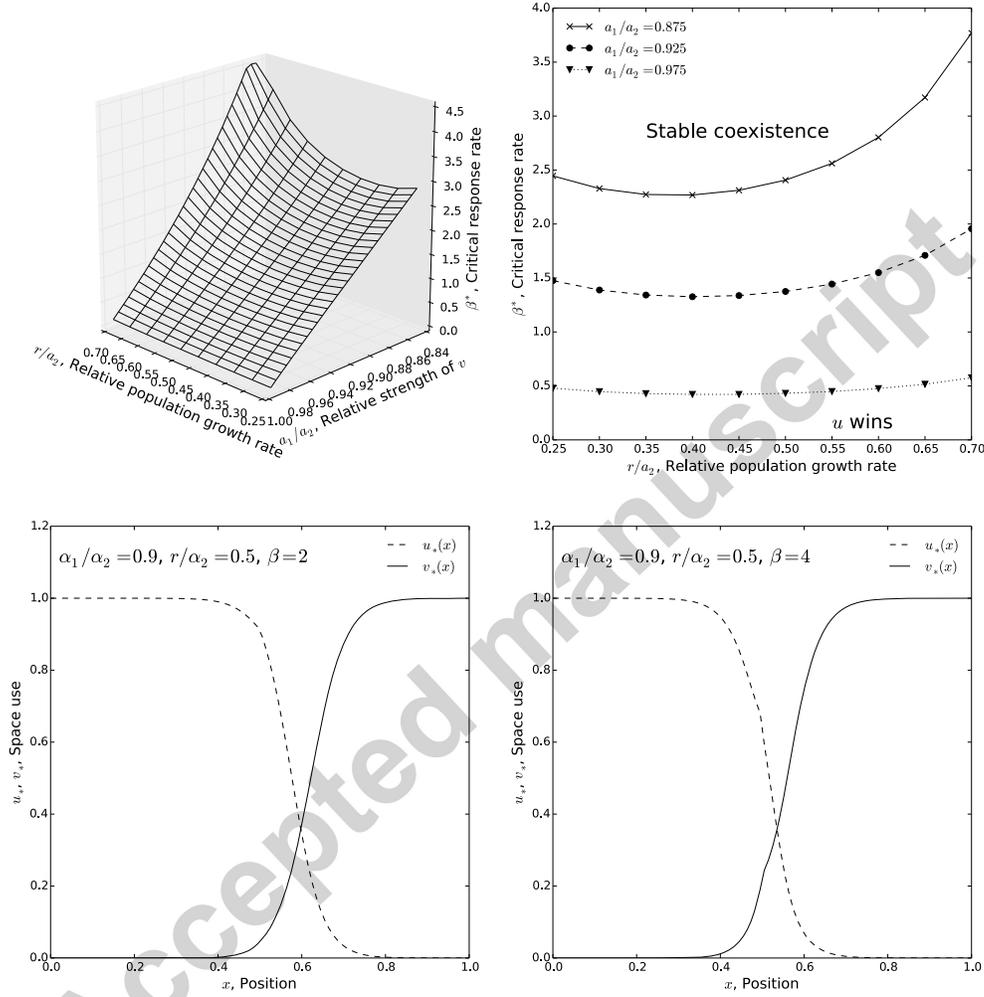


Fig. 6. Co-existence of strongly competing populations in homogeneous environments. Here, we analyse the model from Equations (9-12), where the advection is density dependent. The top-left panel shows the values of β^* , above which the system converges to a co-existence steady-state, and below which 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 .