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

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4 **Short title:** Movement and population competition

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.

29 1 Introduction

30 Predicting the survival of populations in competitive environments is a key question in ecology,
31 with applications to conservation decisions (Lande et al., 2003), biological invasions (Lewis
32 et al., 2016), and management of changing ecosystems (Tylianakis et al., 2008). Indeed, the
33 question is not restricted to ecology, with studies existing in fields as diverse as criminology
34 (Brantingham et al., 2012) and cancer studies (Gatenby & Gawlinski, 1996). However, predic-
35 tion is impossible without an understanding of the mechanisms of species competition, together
36 with tools to quantify mathematically their effects on demographic patterns (Murray, 2001;
37 Lewis et al., 2016). Animal movement is emerging as an important mechanism underlying
38 inter- and intra-species interactions, as the movement decisions that animals make in response
39 to these interactions play an important role in shaping the ‘life-path’ of the animal (Nathan
40 et al., 2008; Börger, 2016). Although it is reasonable to expect that movement responses to
41 competitors could have a big effect on the ability of animals to survive, population dynamics
42 models incorporating these factors are rare (Armsworth & Roughgarden, 2005; Morales et al.,
43 2010).

44 Despite this, inter-population competition is one of the oldest phenomena in ecology to be
45 given rigorous mathematical treatment, with the first model dating back to Lotka (1932) and
46 Volterra (1926), so popularly termed the Lotka-Volterra competition (LVC) model. Although
47 the original LVC model is spatially implicit, and so does not explicitly incorporate animal
48 movement, various foundational predictions have been made from its analysis. One is that
49 stable co-existence of two competing populations is only possible if intra-population competition
50 is stronger than inter-population competition. This situation is called *weak competition*. In
51 contrast, for *strong competition*, where inter-population competition is more deleterious than
52 intra-population competition, the LVC model predicts bi-stability: only one of the populations
53 will survive in the long run and the other will die out, with stable co-existence impossible.
54 This predicted inability for strongly competing populations to co-exist is sometimes called
55 *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 a
67 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
69 analysis, so remains popular [see e.g. Lewis et al. (2016, Chapter 4) and references therein].
70 Indeed, a spatial version of the SLVC model incorporating diffusive movement has been studied
71 mathematically by several authors (Dancer et al., 1999; Crooks et al., 2004; Nakashima &
72 Wakasa, 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 the
80 fine-tuned situation where competition is essentially equal between the two populations (Brant-
81 ingham et al., 2012; Dancer et al., 1999)]. In other words, stable co-existence is essentially never
82 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 incorporate
93 movement responses between the two populations. This is in part inspired by recent empirical
94 studies showing that top-predators change their movement when close to competing predators
95 (Vanak et al., 2013). Our aim is to understand the effect of such movements on the spatial
96 population dynamics. The key idea is that movement responses may be used by an otherwise
97 ‘weaker’ population to ‘push back’ the travelling wave, causing a reversal in the eventual fate
98 of the populations. Mathematically, these movement responses are encoded in an *advection*
99 term, leading to a system of reaction-advection-diffusion equations. These naturally combine
100 the advection-diffusion equations of taxis models (Lewis & Murray, 1993; Potts & Lewis, 2014)
101 with the reaction-diffusion equations of spatial population dynamics (Namba, 1989; Durrett
102 & Levin, 1994; Tilman & Kareiva, 1997). Roughly, the ‘advection’ term means that we are
103 including directed motion (sometimes called ‘taxis’), the ‘reaction’ term refers to birth and
104 death processes, and the ‘diffusion’ term to the unknown drivers of movement, modelled as a
105 random process.

106 Despite these three aspects being clearly important to demographic dynamics, the com-
107 bination of all three is rare in mathematical ecology, with most studies focussing on either
108 ‘advection’ or ‘reaction’. Although a few exceptions exist – such as prey-taxis studies (Kareiva
109 & Odell, 1987; Lee et al., 2009) and stratified diffusion (Shigesada et al., 1995) – these represent

110 just the tip of the iceberg regarding taxis properties in response to external or internal cues:
111 e.g. competing predators moving in response to the presence of the other population (Vanak
112 et al., 2013; Potts et al., 2013), prey avoiding places where predators live (Latombe et al., 2014;
113 Bastille-Rousseau et al., 2015), and so forth. Since statistical and data-collection techniques
114 are beginning to uncover such movement responses (Vanak et al., 2013; Potts et al., 2014;
115 Hays et al., 2016), it is important for theoretical studies to catch-up with the data analysis by
116 examining the effect of taxis on population dynamics.

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

126 **2 Static movement response**

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

129 **2.1 The Model**

130 In this section, our model considers two competing populations of animals, whose distribution
131 functions are given by $u(x, t)$ and $v(x, t)$, where x denotes position (in one- or two-dimensions)
132 and t is time. These populations could be thought of either as two different species, or two
133 groups (e.g. packs, flocks or tribes) from the same species. They are both assumed to be
134 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

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

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

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 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

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

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

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

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

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

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 $0 \leq x \leq 1$,

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

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

218
 219 which are subject to the following zero-flux boundary conditions

$$220 \quad \left. \left\{ \frac{\partial u}{\partial x} - \gamma_1 \left[u \frac{\partial v}{\partial x} \right] \right\} \right|_{x=0,1} = 0, \quad (6)$$

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

222
 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

238 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
 239 either $u_*(x) = 1$ and $v_*(x) = 0$, so we say ‘ u wins’, or $u_*(x) = 0$ and $v_*(x) = 1$, so we say
 240 ‘ v wins’. Figure 1b displays the regions of parameter space where there is a switch from u
 241 winning to v winning. Notice that increasing γ_2 (the strength of aggressive movement by v)
 242 enables v to win even when it is weaker than u : i.e. when a_1 is smaller than a_2 . Thus we see
 243 movement triggering a switch in the predictions of the spatially implicit analysis.

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

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

262 In Figures 2 and 3, we plot the critical value of γ_2 at which the wave-velocity switches
 263 direction from positive (right) to negative (left) for various values of r and a_1 such that $r <$
 264 $a_1 < a_2 = 2000$. 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 $r \rightarrow a_1$.

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.

285 **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

291 the right-hand side are such that travelling waves move leftwards. Some example situations
 292 where this happens are given in Figure 5. Interestingly, the spatial pattern of the population
 293 distributions are slightly out-of-phase with the spatial pattern of the environment. Indeed,
 294 in the area of poorer resources, and close to the edge between the two habitats, the total
 295 population density is slightly lower than the carrying capacity. Notice that this co-existence
 296 phenomenon only occurs when there is *both* taxis in response to foreign populations *and* spatial
 297 variation in r . Without the former, the travelling wave direction will always be to the right if
 298 $a_1 < a_2$ (left if $a_1 > a_2$), regardless of the value of r .

299 **3 Dynamic movement response**

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

313 **3.1 The Model**

314 We begin with the model given by Equations (4-7) but replace the constants γ_1 and γ_2 with
 315 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

$$319 \quad \frac{\partial \gamma_1}{\partial t} = \beta \frac{\partial v}{\partial t}, \quad \frac{\partial \gamma_2}{\partial t} = \beta \frac{\partial u}{\partial t}, \quad (8)$$

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

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

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

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

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

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.

343 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).

359 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 dramati-
 363 cally 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-

366 mals are able to modify these movement strategies over time, co-existence of strongly competing
367 populations is possible, even in an homogeneous environment. This calls into question assump-
368 tions about the conditions under which one population will exclude competing populations
369 from space (Barabás et al., 2016).

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

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

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

391 Although taxis mechanisms can be helpful for population survival, our numerical experi-
392 ments demonstrate that the usefulness is limited. It will not always be possible for populations

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

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

411 Despite this, there are limitations of reaction-advection-diffusion equations for modelling
412 animal interactions. If the interactions are direct then coupling them through a density function
413 requires there to be a suitably large number of animals so that the continuum description a
414 good representation of the presence of actual animals (Durrett & Levin, 1994). Otherwise, it is
415 necessary to use a stochastic individual-based model [e.g. Giuggioli et al. (2011)]. If interactions
416 are indirect via marks on the environment, then the population density function will only
417 accurately mirror the presence of marks if the distribution of the marks equilibrates quickly
418 compared to the probability distribution of the animals (see Supplementary Appendix A).
419 Finally, if some individuals exhibit long-range movements then an integro-difference formulation

420 may be more realistic than reaction-advection-diffusion equations and can lead to different
421 dynamics (Lewis et al., 2016; Kawasaki et al., 2017).

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

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

438 As well as these applied challenges, we highlight the need for greater analytic understanding
439 of the model studied here, as well as its variants (e.g. incorporating various taxis responses into
440 predator-prey models, or models of more than two interacting species etc.). At present, the
441 best understanding of travelling-wave solutions to spatial SLVC models are given in Girardin
442 & Nadin (2015). There, quite advanced analytic techniques were required to give exact bounds
443 on the travelling-wave speed in a simplified version of our system. In particular, no advective
444 term was present, so movement is simply diffusive, and inter-species competition is arbitrarily
445 stronger than intra-species competition. To extend these results to gain analytic insight into the
446 models studied here would require significant mathematical effort. One possible way forward

447 might come by leveraging the techniques from the genetics literature that lead to ‘Bartonian
448 waves’ (Barton, 1979; Jansen et al., 2008). However, our results suggest that this effort is much
449 needed, both for theoretical and applied ecology.

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

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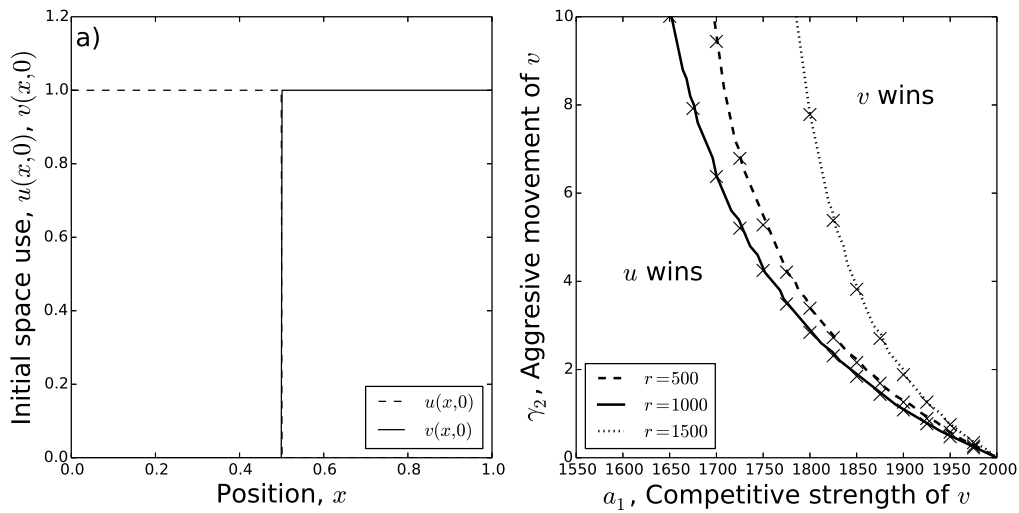


Fig. 1. Switch in fate due to movement strategies. Panel (a) shows the initial conditions of two populations, u and v , in our numerical analysis. Fixing $\gamma_1 = 0$, and $a_2 = 2000$, panel (b) shows which of u and v end up winning for different values of r , a_1 , and γ_2 (see Equations 4 and 5).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

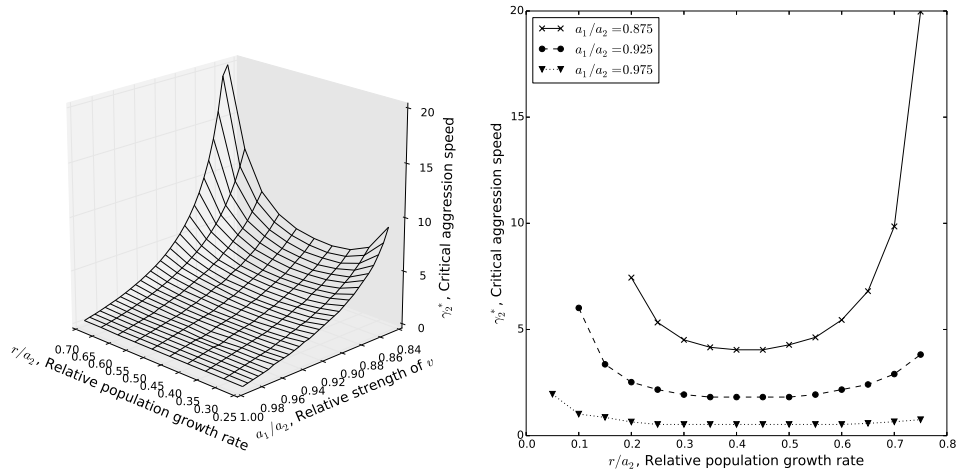


Fig. 2. Critical aggression speed, where the travelling-wave changes from right- to left-wards movement. The left-hand panel shows the dependence of the critical aggression speed, γ_2^* , on a_1/a_2 (the relative strength of v) and r/a_2 (the populations' growth rate relative to the constant $a_2 = 2000$).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

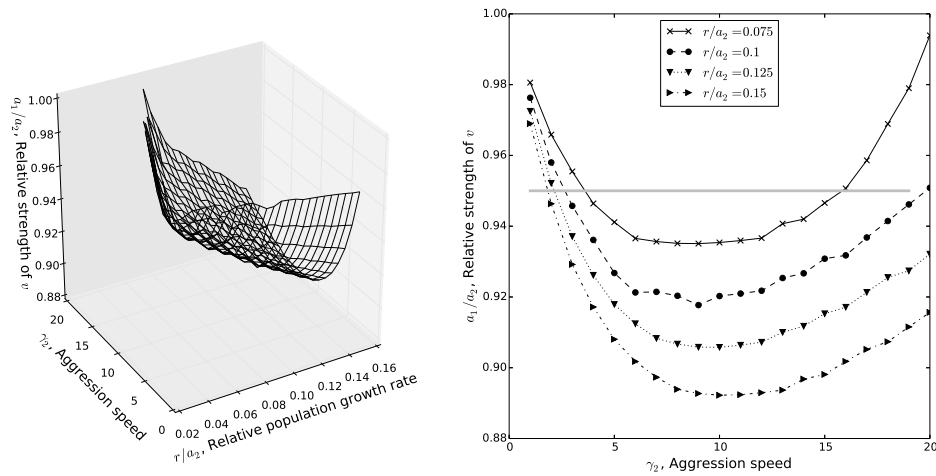


Fig. 3. Non-monotonic dependence of the travelling wave direction on the aggression speed. The surface in the left-hand panel shows places where the travelling wave speed is zero. For certain fixed values of r , a_1 , and a_2 , there are two values of the aggression speed, γ_2 , where the travelling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

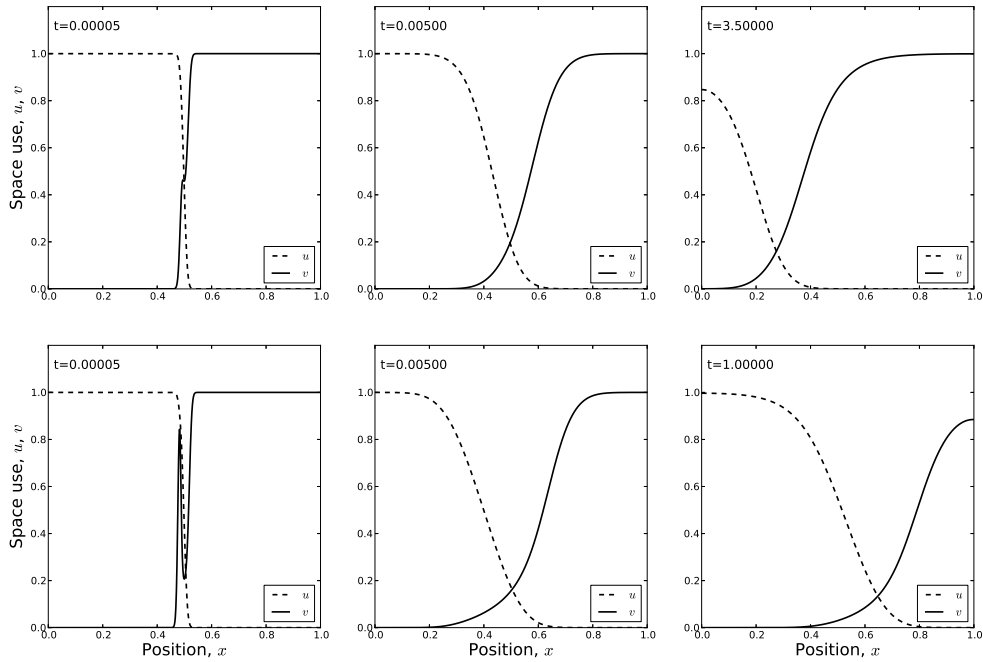


Fig. 4. Transient dynamics of different aggression levels. The top row shows the space use at three points in time when the aggression speed of v is enough to push back the travelling wave. Parameters are $a_1 = 1900$, $a_2 = 2000$, $\gamma_1 = 0$, $\gamma_2 = 5$, $r = 150$, and times t are shown in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

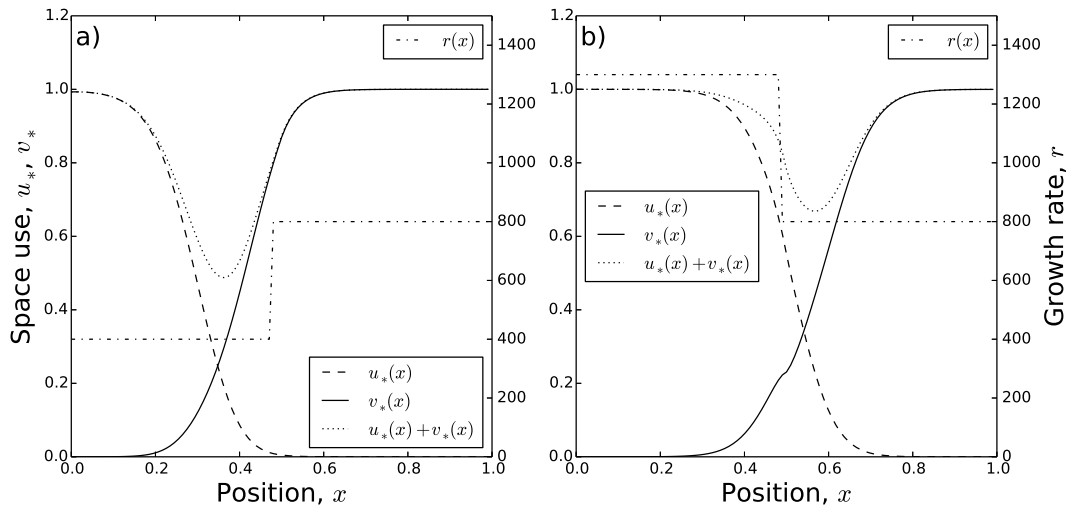


Fig. 5. Co-existence of strongly competing populations in heterogeneous environments. When the environmental conditions cause the reproductive rate, r , to vary over space, it is possible to observe co-existence of populations. Space use is plotted when $u(x, t)$ and $v(x, t)$ are at steady-state, denoted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

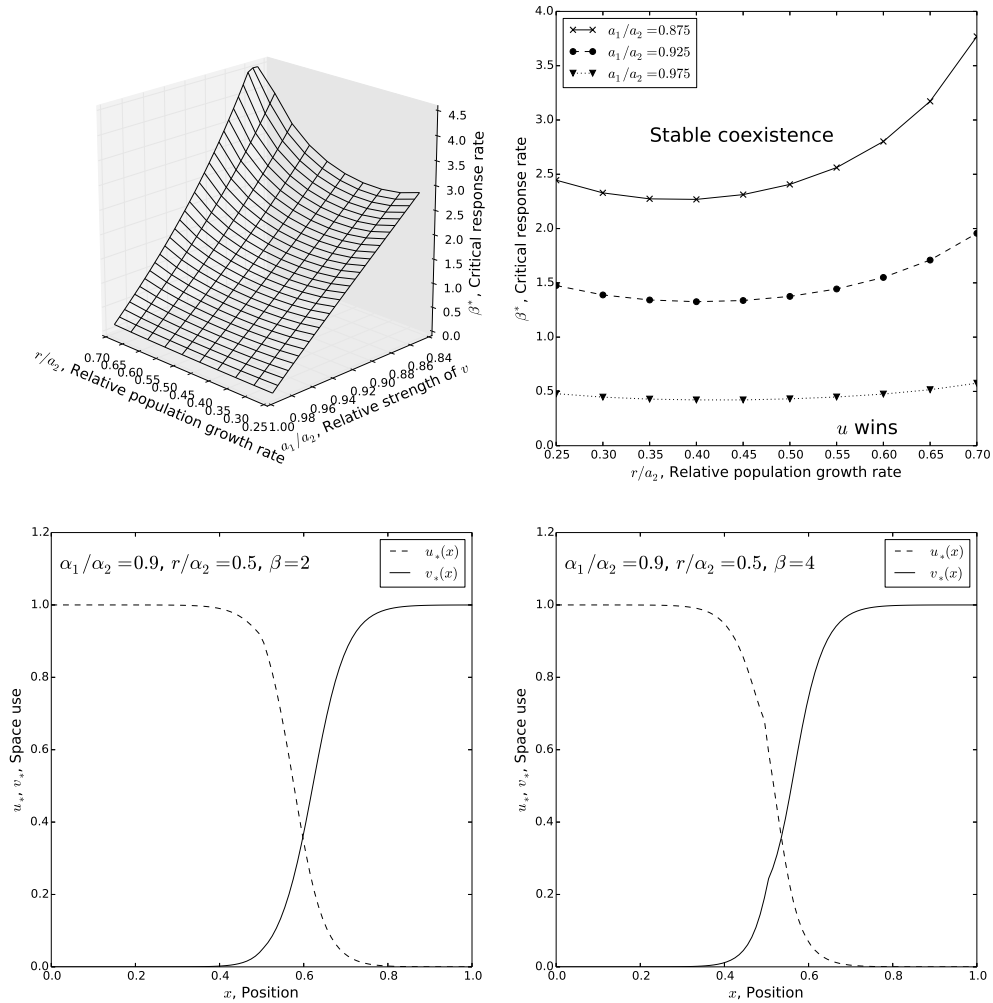


Fig. 6. Co-existence of strongly competing populations in homogeneous environments. Here, we analyse the model from Equations (9-12), where the advection is density dependent. The top-left panel shows the values of β^* , above which the system converges to a co-existence steady-state, and below which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