

# Diffusion-driven instabilities and emerging spatial patterns in patchy landscapes

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1 **Abstract**

2 Spatial variation in population densities across a landscape is a feature of many ecological  
3 systems, from self-organised patterns on mussel beds to spatially restricted insect outbreaks. It  
4 occurs as a result of environmental variation in abiotic factors and / or biotic factors structuring  
5 the spatial distribution of populations. However the ways in which abiotic and biotic factors  
6 interact to determine the existence and nature of spatial patterns in population density remain  
7 poorly understood. Here we present a new approach to studying this question by analysing  
8 a predator-prey patch-model in a heterogenous landscape. We use analytical and numerical  
9 methods originally developed for studying nearest-neighbour (juxtacrine) signalling in epithelia  
10 to explore whether and under which conditions patterns emerge. We find that abiotic and  
11 biotic factors interact to promote pattern formation. In fact, we find a rich and highly complex  
12 array of coexisting stable patterns, located within an enormous number of unstable patterns.  
13 Our simulation results indicate that many of the stable patterns have appreciable basins of  
14 attraction, making them significant in applications. We are able to identify mechanisms for these  
15 patterns based on the classical ideas of long-range inhibition and short-range activation, whereby  
16 landscape heterogeneity can modulate the spatial scales at which these processes operate to  
17 structure the populations.

18 **Key words**

19 Diffusion-driven instability, heterogeneous landscape, patch model, pattern formation,  
20 predator-prey.

# 1 Introduction

One of the great challenges in ecology is to uncover and explain the mechanisms that lead to observed spatial patterns of species distributions. For many species, abundance varies spatially as individuals track environmental variation, such as abiotic factors or resources, across a landscape (Leroux et al., 2013; Ergon et al., 2001). Alternatively, spatial distribution patterns can arise in the absence of external forces, due to the pattern-formation mechanism of short-range activation and long-range inhibition (Zelnik et al., in press; Rietkerk et al., 2002; Wang et al., 2010b), or due to density-dependent dispersal leading to phase separation (Liu et al., 2013). These two mechanisms typically create stationary patterns, although moving patterns occur in the presence of advection (Siero et al., 2015; Perumpanani et al., 1995; Sato and Iwasa, 1993). Temporally varying patterns may also arise from asynchronous cycling caused by invasions or obstacles (Sherratt et al., 1995; Petrovskii and Malchow, 2001; Sherratt et al., 2002). The best-studied of these processes is the Turing mechanism, and ecologists have recently identified appropriate long-range inhibition in a number of natural ecosystems and documented corresponding patterns (Rietkerk and van de Koppel, 2008; Deblauwe et al., 2008; Meron, 2012). Our work is concerned with the interplay between extrinsic and intrinsic generation of temporally constant spatial patterns. We develop a theoretical framework and illustrate it with some examples of how environmental variation and intrinsic interaction can combine to create patterns at various spatial scales.

Spatial variation in environmental conditions occurs at various (landscape) scales both naturally, e.g. altitude variation within mountainous regions, and through human intervention, e.g. networks of marine reserves, managed forests, or agricultural systems. Spatial scales of population patterns arising from species interactions (Turing scale) depend on the range of activation and inhibition, i.e. the strength of these interactions and the relative movement of individuals. On one extreme, if the landscape scale is much smaller than the Turing scale, then one can expect to observe intrinsically generated patterns that extend over large regions in space, potentially with small variations to reflect local conditions. Conversely if the landscape scale is large compared to the Turing scale of species interaction, one expects intrinsically generated patterns that change on the long spatial scale of environmental variation (Voroney et al., 1996).

Several authors have studied Turing pattern formation in heterogeneous landscapes. Benson et al. (1993b) investigated pattern formation with constant kinetic parameters and spatially varying diffusion coefficients, see also (Benson et al., 1993a, 1998). Voroney et al. (1996) studied the interplay of Turing patterns and cyclic dynamics that result from a chemical reaction with an additional immobile but spatially heterogeneous complexing agent. Page et al. (2003) considered the generation of patterns near an interface where kinetic parameters change their values abruptly. Subsequent work included smoothly varying monotone and periodic changes in kinetic parameters (Page et al., 2005), see also Garzón-Alvarado et al. (2012) for more intensive numerical simulations in patchy, 2-dimensional domains. Recently Sheffer et al. (2013) and Yizhaq et al. (2014) investigated the interplay between environmental templates and self-organisation in the formation of patterned vegetation in semi-arid regions. Using both theoretical and empirical approaches, they showed that both mechanisms play significant roles in the pattern formation process, with their relative contributions depending on rainfall levels.

In this work, we take a landscape ecology perspective and subdivide the environment into distinct patches. A patch is defined as an environmentally homogeneous geographic region whose spatial extent is comparable to the species' dispersal scale so that a population can be assumed relatively homogeneous within a patch. Population dynamics on each patch are then coupled

67 via migration between patches. Such multi-patch models have a long and distinguished history  
 68 in spatial and community ecology (see for example (Cantrell et al., 2012) for a discussion).  
 69 In this framework, we study conditions for spatial patterns to evolve in the interesting range  
 70 where the landscape scale is comparable to the Turing scale (see above). We implement habitat  
 71 heterogeneity through patch attributes and movement bias.

72 A series of papers explores pattern formation in epithelia where cell-cell interaction is domi-  
 73 nated by nearest-neighbour (juxtacrine) signalling (Owen and Sherratt, 1998; Owen et al., 2000;  
 74 Webb and Owen, 2004a; O’Dea and King, 2011, 2013; Wearing et al., 2000; Wearing and Sher-  
 75 ratt, 2001). In these works, all cells have equal properties (i.e. there is no spatial variation),  
 76 and interaction between neighbouring cells is non-linear. We will adapt some of the analytical  
 77 methods used there for our model. A closely related model for a linear inhomogeneous array of  
 78 coupled chemical reactors was studied in Horsthemke and Moore (2004) as a discretised version  
 79 of the work in Voroney et al. (1996).

80 We begin by deriving the predator-prey patch model that forms the basis of our study. We  
 81 explore emergent patterns with a numerical bifurcation analysis when the number of patches is  
 82 small. We find a large number of patterns, often stably coexisting, and complex bifurcation dia-  
 83 grams. In the second part, we perform a linear stability analysis when the number of patches is  
 84 large. For reference and comparison, we identify the stability conditions for the spatially homo-  
 85 geneous model. We compare and contrast these results and discuss the ecological implications  
 86 of our findings.

## 87 2 The Model

88 In a linear landscape of patches of two types (type 1 and type 2), arranged to be periodically  
 89 alternating, we denote by  $u_{1,2}, v_{1,2}$  the respective densities of two interacting species. In our  
 90 explicit calculations, we focus on predator-prey interaction where a type-1 patch is suitable for  
 91 the prey and a type-2 patch is not. Viewing landscapes as mosaics of patches of different quality  
 92 is common in landscape ecology and also arises in managed ecosystems, for example, a series of  
 93 marine reserves along a coastline (Botsford et al., 2001; Gouhier et al., 2010) or intercropping  
 94 in agriculture (Jones and Sieving, 2006).

95 On a patch of type  $i$ , the dynamics of these species evolve according to the equations

$$\dot{u}_i = f_i(u_i, v_i), \quad \dot{v}_i = g_i(u_i, v_i). \quad (1)$$

96 Throughout, we assume that functions  $f_i, g_i$  are sufficiently smooth and that the system preserves  
 97 non-negativity of solutions.

98 We denote by  $L_i$  the length of patch type  $i$ , and by  $L = L_1 + L_2$  and  $l = L_1/L_2$  the landscape  
 99 period and patch size ratio, respectively. We say that a *tile* consists of a patch of type 1 and  
 100 its adjacent patch of type 2 on the right. Hence, a tile represents one period of the landscape  
 101 (see Figure 1(a)). We denote species’ densities on tile  $j$  by  $u_{1,2}^j, v_{1,2}^j$ . We note here that “tile” is  
 102 introduced only as a convenient way to describe the system, not as an ecological unit.

103 We model movement by a discrete diffusion process, so that moving from one good patch  
 104 to the next requires moving through a bad patch. Individuals of species  $u$  ( $v$ ) leave a patch  
 105 of type 1 with migration rate  $\mu_u$  ( $\mu_v$ ) and move to one of the adjacent patches of type 2 with  
 106 equal probability. The leaving rate for patch type 2 is multiplied by  $\kappa_u$  ( $\kappa_v$ ) to account for  
 107 patch-dependent dispersal behavior. If  $\kappa_{u,v} > 1$  ( $\kappa_{u,v} < 1$ ) then the average time spent in a

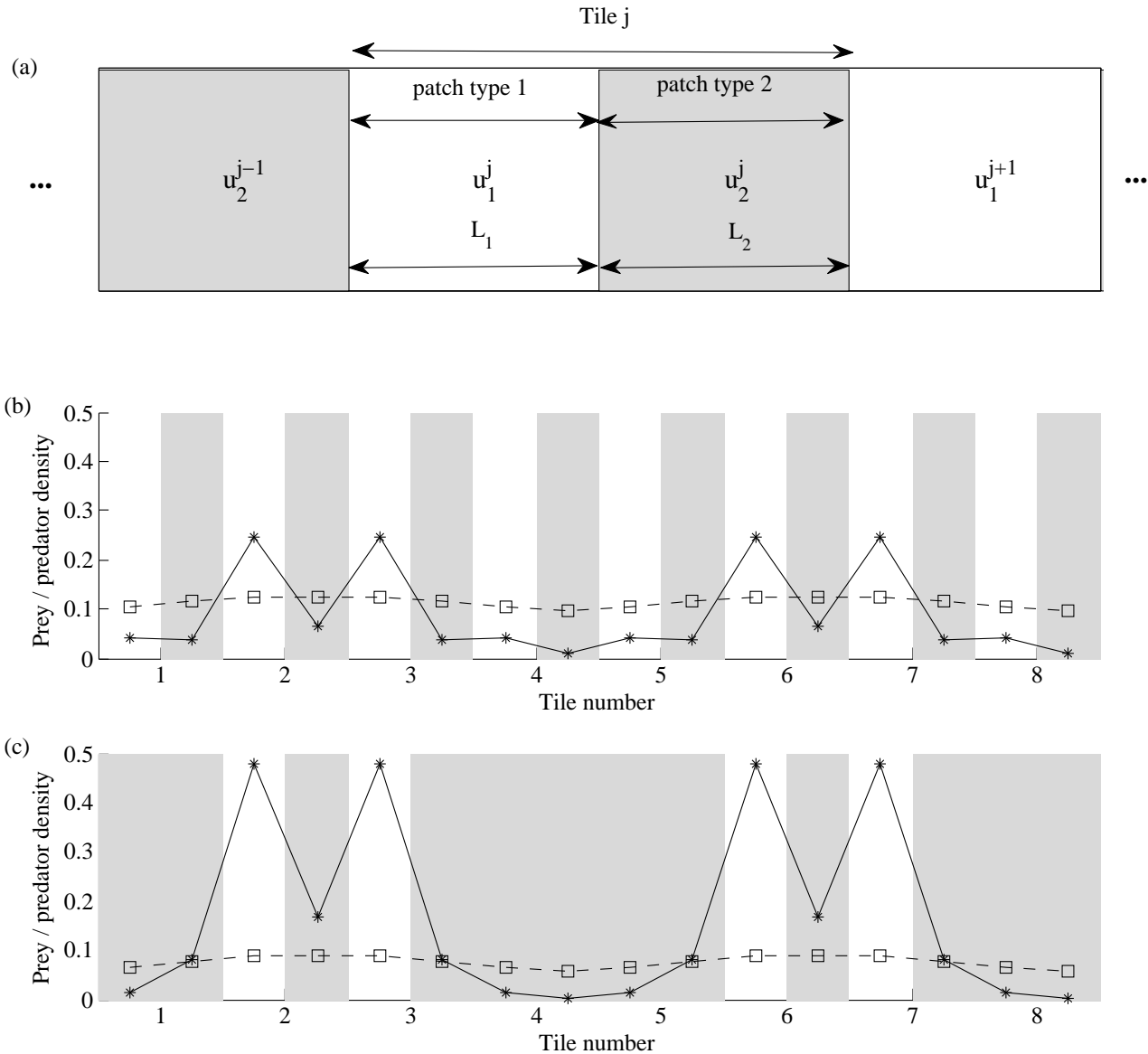


Figure 1: Diagram of patch and tile structure (a) and example pattern solutions (b), (c). (a) illustrates the landscape made up of a series of tiles, with each tile made up of two patches, one of type 1 and one of type 2 with patch sizes  $L_1$  and  $L_2$  respectively. (b) illustrates a stationary solution of the model (2,3) for the parameter values  $\mu_u = 0.5$ ,  $\mu_v = 5$ ,  $l = 1$ ,  $b = 0.1$ ,  $s = 0.2$ ,  $m = 0.6$ ,  $\kappa_{u,v} = 1$ ,  $q = 2.8$ . Prey density is denoted by stars and solid lines and predator density by squares and dashed lines. The pattern in prey density  $u_i^j$  is of period 4 on a periodic landscape consisting of 8 tiles. The white regions correspond to the type 1 ('good') patches and the light grey regions correspond to the type 2 ('bad') patches. The prey density in the 'good' patches on tiles 1, 4, 5, and 8 is low, in particular it is lower than the prey density in the 'bad' patch on tiles 2 and 6. (c) illustrates the result of converting the patches 1, 4, 5 and 8 from (b) to bad patches. The result is that the prey density on the remaining good patches is increased while the predator density is decreased on all patches.

108 patch of type 2 is shorter (longer), so that overall movement is biased towards patch type 1  
 109 (type 2). The spatially coupled model system reads

$$\begin{aligned}
 \dot{u}_1^j(t) &= \mu_u \left[ \kappa_u \frac{u_2^j + u_2^{j-1}}{2} - u_1^j \right] + f_1(u_1^j, v_1^j), \\
 \dot{u}_2^j(t) &= \mu_u l \left[ \frac{u_1^j + u_1^{j+1}}{2} - \kappa_u u_2^j \right] + f_2(u_2^j, v_2^j), \\
 \dot{v}_1^j(t) &= \mu_v \left[ \kappa_v \frac{v_2^j + v_2^{j-1}}{2} - v_1^j \right] + g_1(u_1^j, v_1^j), \\
 \dot{v}_2^j(t) &= \mu_v l \left[ \frac{v_1^j + v_1^{j+1}}{2} - \kappa_v v_2^j \right] + g_2(u_2^j, v_2^j),
 \end{aligned} \tag{2}$$

110 where the multiplication of  $\mu_u, \mu_v$  by  $l$  in the equations on type-2-patches is the scaling factor  
 111 that accounts for conservation of individuals. In the case of a finite number of tiles ( $N$ ) we close  
 112 the system by assuming periodic boundary conditions such that  $u_i^1 = u_i^N$  and  $v_i^1 = v_i^N$ . Periodic  
 113 boundary conditions allow for easy comparison to dynamics on an infinite domain, moreover  
 114 they are equivalent to Neumann boundary conditions on a domain of length  $N/2$ .

## 115 Dynamics on a patch

116 On patches of type 1 ('good') we choose the non-dimensional Leslie or May model (May, 1974;  
 117 Strohm and Tyson, 2009; Mukhopadhyay and Bhattacharyya, 2006) for predator species  $v$  and  
 118 prey species  $u$ , given by

$$f_1(u, v) = u(1 - u) - \frac{uv}{b + u}, \quad g_1(u, v) = sv \left( 1 - \frac{v}{qu} \right). \tag{3}$$

119 In this scaling,  $b$  denotes the half-saturation constant of the Holling type II functional response.  
 120 The predator grows logistically with intrinsic rate  $s$  and carrying capacity  $qu$ . This formulation  
 121 arises from the assumption of variable predator-territory size (Turchin, 2001).

122 Patches of type 2 ('bad') are unsuitable for the prey so that we replace the logistic growth  
 123 term by a linear death term. Predator dynamics depend only on prey abundance and not on  
 124 patch type. Hence, model equations on patches of type 2 are given by

$$f_2(u, v) = -mu - \frac{uv}{b + u}, \quad g_2 = g_1. \tag{4}$$

125 On an isolated good patch, there is a unique positive steady state, given by

$$u_* = \frac{1}{2} \left( 1 - b - q + \sqrt{(1 - b - q)^2 + 4b} \right), \quad v_* = qu_*. \tag{5}$$

126 Parameter  $q$  is the ratio of predator-to-prey steady-state densities and will be used as a bifur-  
 127 cation parameter later. The community matrix at this state,

$$J = \begin{bmatrix} 1 - 2u_* - \frac{b(1-u_*)}{b+u_*} & -\frac{u_*}{b+u_*} \\ sq & -s \end{bmatrix}, \tag{6}$$

128 has positive determinant. The stability therefore depends on the sign of the trace. The trace is  
 129 zero when

$$1 - 2u_* - b \frac{1 - u_*}{b + u_*} = s. \tag{7}$$

130 If  $s$  is large, then this equation has no solution and the steady state is stable. If  $s$  is small enough,  
 131 there are two critical values  $q_{H,1} < q_{H,2}$  where a Hopf bifurcation occurs. The steady state is  
 132 unstable for  $q_{H,1} < q < q_{H,2}$  and a stable limit cycle exists. Depending on parameter values, the  
 133 bifurcation at  $q_{H,2}$  may be subcritical so that a limit cycle may exist for values  $q > q_{H,2}$  (Gasull  
 134 et al., 1997). For the parameter values we use in the next section ( $b = 0.1, s = 0.2$ ), these  
 135 critical points are  $q_{H,1} \approx 0.895$ , and  $q_{H,2} \approx 4.05$ , and the latter bifurcation is subcritical.

### 136 Dynamics on a tile

137 When we couple the dynamics on a good patch with those on a bad patch, migration has a  
 138 stabilising effect on the dynamics. For all parameters sets that we have studied, numerical  
 139 investigation suggests that there is a unique positive stable coexistence steady state. We do not  
 140 attempt to find exact conditions for when this happens since our focus is on the question of  
 141 spatial pattern formation at a landscape level.

142 Qualitatively, this stabilisation occurs when the bad patch is large enough, movement rates  
 143 are large enough, and movement preference for the good patch is not too strong. The periodic  
 144 orbits for intermediate values of  $q$  on a single good patch can also be present on a tile if the  
 145 influence of the bad patch is weak enough. The latter scenario arises, for example, when the  
 146 size of the good patch is much larger than that of the bad patch, when migration rates are very  
 147 small so that the patches are only weakly coupled, or when migration preference for the good  
 148 patch is particularly strong.

149 For our base-line parameters, we fix patch sizes to be equal ( $l = 1$ ) and choose migration  
 150 without patch preference ( $\kappa_{u,v} = 1$ ). We also fix migration rates so that the prey moves much  
 151 less ( $\mu_u = 0.5$ ) than the predator ( $\mu_v = 5$ ). The population dynamics parameters are fixed at  
 152  $b = 0.1, s = 0.2$ , and  $m = 0.6$ . Then, numerically, the dynamics on an entire tile show a unique,  
 153 globally stable positive steady state for all  $q \in (0, 10]$  even though the dynamics on a single good  
 154 patch can have oscillations for intermediate values of  $q$ . We will return to some aspects of cyclic  
 155 dynamics in section 3.2.

## 156 3 Methods and Results

157 We structure our analysis of pattern formation in the heterogeneous landscape into two parts.  
 158 First we use a numerical bifurcation method to study patterns when the number of tiles is  
 159 relatively small. Depending on our bifurcation parameter  $q$ , we document a large number of  
 160 complex, stable, steady spatial patterns. Secondly, we use linear analysis to derive the disper-  
 161 sion relation of the ‘spatially homogeneous steady state’ on an infinite patchy landscape. This  
 162 approach allows us to identify stability boundaries and the onset of spatial patterns with re-  
 163 spect to all other parameters, in particular those parameters governing movement and landscape  
 164 attributes. Finally, we discuss the similarities and differences between the two approaches.

165 The term ‘homogeneous steady state’ warrants some explanation. Our system does not  
 166 support a homogeneous steady state in the classical sense where prey and predator densities are  
 167 constant in space, i.e. independent of patch type. However, if we consider the tile as the basic  
 168 spatial unit, we do obtain a steady state solution where each of the four densities  $u_1^j, u_2^j, v_1^j$  and  
 169  $v_2^j$  is independent of tile-number  $j$ . We refer to this solution as our homogeneous solution or  
 170 *tile-independent solution*.

171 Unless otherwise stated explicitly, parameter values in this section are  $\mu_u = 0.5, \mu_v = 5$ ,  
 172  $l = 1, b = 0.1, s = 0.2, m = 0.6, \kappa_{u,v} = 1$  and  $q = 1.8$ .

### 3.1 Numerical bifurcation results for small systems

The simplest solution of our model is the homogeneous steady state. Our extensive program of numerical simulations suggests that when parameter  $q$  is either sufficiently small or sufficiently large, there is a unique solution of this type, which is globally stable.

For intermediate values of  $q$ , simulations reveal “patterns” by which we mean locally stable time-independent solutions in which the predator and prey densities are not the same in all tiles. We undertook a numerical investigation of such patterns via numerical bifurcation analysis, for which we used the software package AUTO (Doedel, 1981; Doedel et al., 1991, 2006). For a relatively small value of  $q$  (e.g.  $q = 1$ ) we calculated numerically the  $j$ -independent solution. We then continued this solution numerically, looking for bifurcations to patterned solutions and then continuing these pattern solution branches. AUTO is able to detect not only the existence of patterns, but also to determine their stability as model solutions. This approach to investigating periodic solutions of spatially discrete systems has been used previously in developmental biology, for epithelia in which there is direct cell–cell contact via juxtacrine signalling (Wearing and Sherratt, 2001; Webb and Owen, 2004b; O’Dea and King, 2013). Although it is simple in concept, the approach raises many technical difficulties in the present context, and we discuss these in detail in Appendix A, focussing here on the results of our analysis.

Figure 2 shows the bifurcation diagrams for  $N = 2, 4, 6, 8$  tiles, plotting the values of  $u_1^j$  against  $q$ ; (examples of bifurcation diagrams for odd number tiles can be found in the supplementary material). The thin black lines denote unstable patterns (spatially non-constant steady states), and the thin yellow-black dashed lines denote unstable tile-independent solutions. The thick bright yellow lines are stable tile-independent (“period 1”) solutions, and the other thick coloured lines denote stable patterns; representative patterns are shown in the same colours above the main plot. The black stars denote results from a series of 1000 simulations for each of  $q = 1.0, 1.25, 1.5, \dots$ . Here we solved the equations with initial conditions in which each variable was chosen randomly from a uniform distribution between 20% and 200% of its value in the tile-independent solution. In these simulations, we solved for a long time and then plotted the values of  $u_1^j$  for each  $j$ .

For  $N = 2$ , the bifurcation diagram is relatively simple. The tile-independent solution is stable for  $q < 1.89$  and  $q > 4.03$ . At these two critical values it changes stability, giving rise to a looped branch of period-2 solutions. For  $N = 4$ , the tile-independent solution loses stability a little earlier, at  $q = 1.59$ , with a patterned solution branch emanating subcritically. There are three different stable portions of patterned solution branches, with small overlaps. These overlaps imply two coexisting stable patterns, and this is confirmed by simulation results for  $q = 3.75$ , with 607/1000 of the initial conditions generating the purple pattern, and the remaining 393/1000 giving the bright green pattern. Note that a doubled version of the pattern solution branch for  $N = 2$  is necessarily also a solution for  $N = 4$ , but it is unstable on the larger domain. For  $N = 6$  the number of solution branches is significantly greater, forming a complicated network, and there are eight separate stable sections of solution branches: one of period 2, two of period 3, and five of period 6. The brown solution branch is a tripled version of the pattern solution branch for  $N = 2$ : the whole of this branch is necessarily a solution for  $N = 6$ , but only a small part of it is stable. For some values of  $q$  there are three coexisting stable patterns, all of which are observed in our simulations. For  $N = 8$  the bifurcation is slightly simpler, but again there are multiple coexisting stable patterns for significant ranges of  $q$ .

To illustrate the rapidly increasing complexity of emergent patterns, Figure 3 shows the

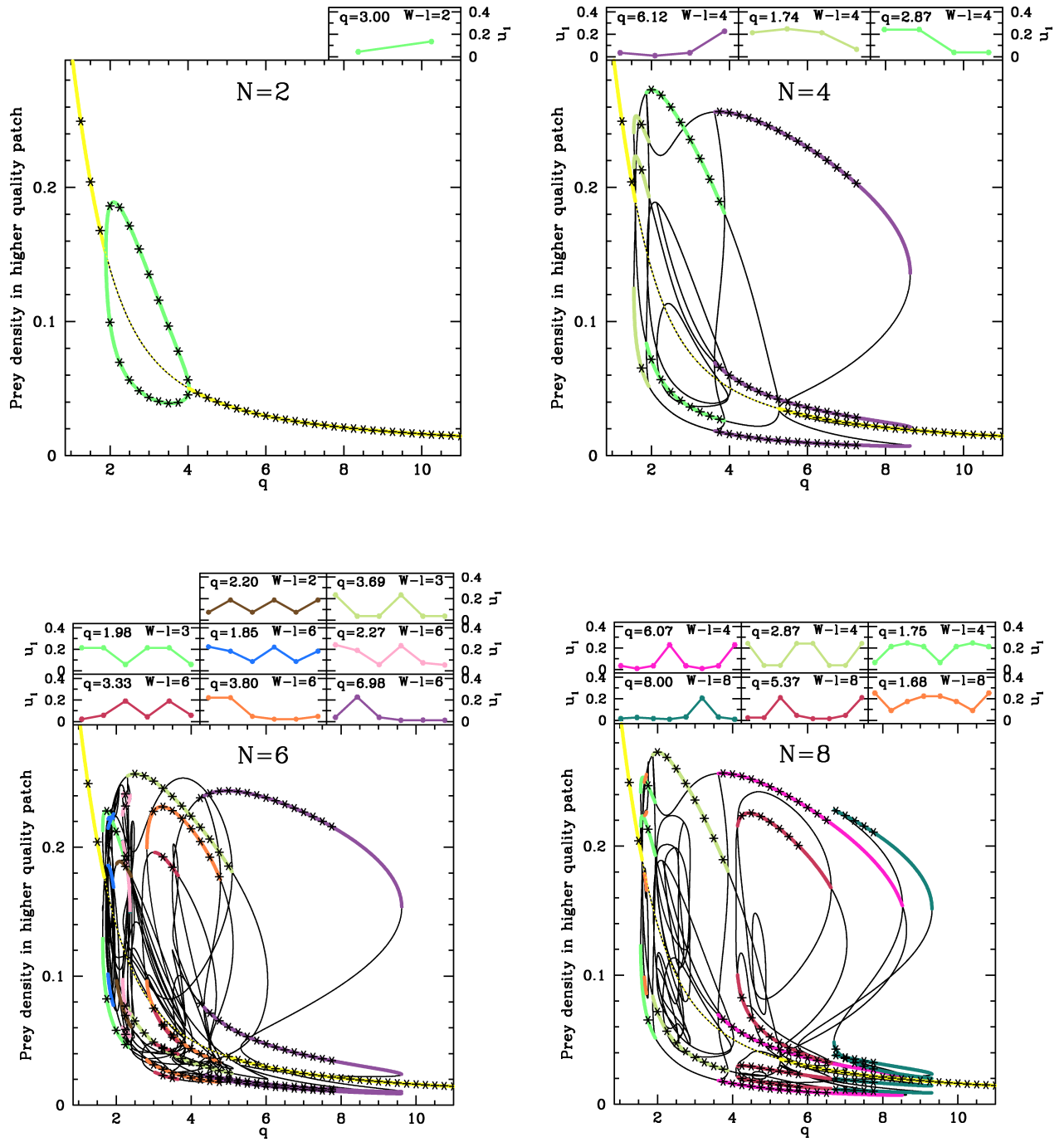


Figure 2: Bifurcation diagrams showing the values of  $u_1^j$  in stationary solutions of the model (2,3) as a function of  $q$ , for  $N = 2, 4, 6, 8$  tiles. Thin black lines denote unstable solutions, thick bright yellow lines denote stable tile-independent (period-1) solutions, and thick coloured lines denote patterns. Each stable part of a solution branch is plotted in a different colour, and representative examples of the corresponding patterns are shown above the main figure panels. Black stars denote results from a series of 1000 simulations for each of  $q = 1.0, 1.25, 1.5, \dots$ . Here we solved the equations with the value of each variable at  $t = 0$  chosen randomly from a uniform distribution between 20% and 200% of its value in the tile-independent solution. We plot the values of  $u_1^j$  for each  $j$  at  $t = 10^8$ : this large solution time is necessary because there can be long transients near unstable solutions. To avoid numerical solutions getting trapped near solutions that are only just unstable, we used a small absolute tolerance of  $10^{-8}$ .

219 results for  $N = 12$  and  $N = 16$ . The network of solution branches is so complicated that in  
 220 many places no space is visible between them, and there are many stable pattern branches:  
 221 19 for  $N = 12$  and 54 for  $N = 16$ . Moreover the wide variety of coexisting stable patterns  
 222 is reflected in the results of our simulations: for most values of  $q$  in our range, many different  
 223 patterns develop, depending on initial conditions. Note that to improve clarity, we do not show  
 224 simulation results in Figure 3 but they are included in the online supplementary material, where  
 225 we show bifurcation diagrams for  $N = 2, 3, \dots, 10, 12$  and 16, plus representative patterns from  
 226 each stable portion of a solution branch.

227 The overall message of our results is that unless the number of tiles  $N$  is very small, there  
 228 is a rich and highly complex array of stable patterns, located within an enormous number of  
 229 unstable patterns. Moreover our many of the stable solution branches arise in our simulations  
 230 using random initial conditions, which indicates that they have appreciable basins of attraction,  
 231 and should therefore be observable in real systems. Since the numerical bifurcation methods  
 232 applied in this section require intensive computations, we present an alternative approach to  
 233 study pattern formation in the next section.

### 234 3.2 Dispersion relation, stability and patterns

235 An analytic approach for studying pattern-formation conditions is to linearise at a spatially  
 236 constant steady state and to derive the dispersion relation that gives the temporal growth  
 237 rate of perturbations of a certain wave number. This technique is well established in reaction-  
 238 diffusion equations (Murray, 2001) and coupled lattices (Webb and Owen, 2004a; Wearing et al.,  
 239 2000; Lubensky et al., 2011) and networks (Wolfrum, 2012). As discussed previously, we obtain  
 240 a homogeneous solution only on the level of tiles. We denote this tile-independent state as  
 241  $(u_1^*, u_2^*, v_1^*, v_2^*)$ . The spatial relation of  $u_1^*, v_1^*$  and  $u_2^*, v_2^*$  within a tile needs to be reflected in the  
 242 perturbation ansatz. Hence, after we linearise the equations in (2), we look for solutions of the  
 243 form

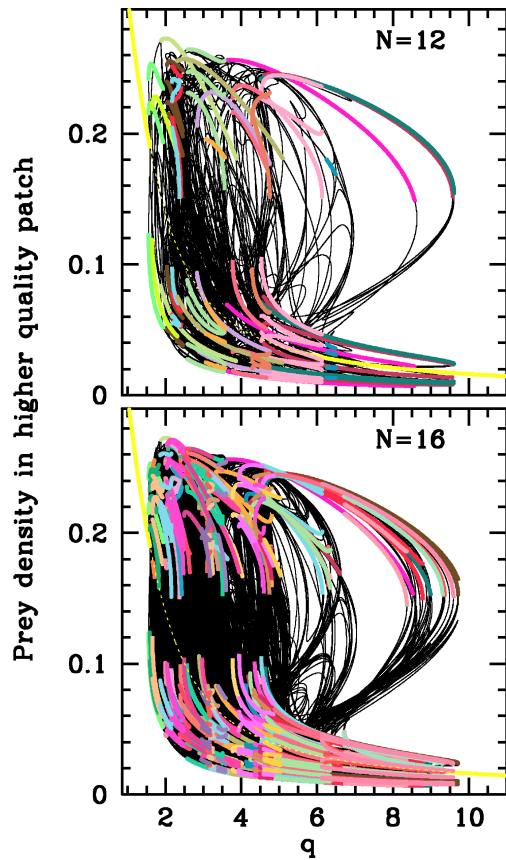
$$\tilde{u}_1^j(t) = \bar{u}_1 \exp(\sigma t + jki), \quad \tilde{u}_2^j(t) = \bar{u}_2 \exp\left(\sigma t + \left(j + \frac{1}{2}\right) ki\right), \quad (8)$$

244 and similarly for  $v_n$ , where  $\bar{u}_n$  is a constant, and  $i^2 = -1$ . The temporal growth rate of the  
 245 solution is given by  $\sigma$ , the wave number is  $k$ , and  $j$  is the discrete (integer) distance corresponding  
 246 to tile number. To interpret  $k$  as a wave number corresponding to wavelength  $N$  on the lattice,  
 247 it needs to be of the form  $k = N/2\pi$ ; however, for analytical purposes, it is helpful to consider  
 248 it as a continuous variable. Here,  $N$  is shortest number of tiles needed to see a pattern of that  
 249 wave length, this is not the same as the  $N$  defined in section 3.1, but it is closely related and so  
 250 we use the same letter. Since the centre of a type-2-patch is halfway between two consecutive  
 251 type-1-patches (see Figure 1(a)) we need to evaluate the linearisation on bad patches at  $j + 1/2$ ,  
 252 as it appears in (8).

253 The desired solutions exist if the constants  $\bar{\mathbf{x}}^T = (\bar{u}_1, \bar{u}_2, \bar{v}_1, \bar{v}_2)$  satisfy the linear system  
 254  $(M - \sigma I)\bar{\mathbf{x}} = \mathbf{0}$ , where

$$M = \begin{pmatrix} -\mu_u + f_{1u} & \kappa_u \mu_u \cos(\pi/N) & f_{1v} & 0 \\ l\mu_u \cos(\pi/N) & -\kappa_u l\mu_u + f_{2u} & 0 & f_{2v} \\ g_{1u} & 0 & -\mu_v + g_{1v} & \kappa_v \mu_v \cos(\pi/N) \\ 0 & g_{2u} & l\mu_v \cos(\pi/N) & -\kappa_v l\mu_v + g_{2v} \end{pmatrix}, \quad (9)$$

255 and  $N = 2\pi/k$  is the wavelength as above. Partial derivatives of the interaction terms are




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Figure 3: Bifurcation diagrams as in Figure 2 for  $N = 12$  and 16 tiles. For improved visual clarity we omit simulation results, but otherwise all details are as in Figure 2. In view of the large number of stable portions of solution branches, we do not show examples here, but a representative pattern from each stable portion is plotted in the online supplementary material.

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256 denoted by subscripts, for example

$$f_{1u} = \frac{\partial f_1}{\partial u} \Big|_{(u_1^*, v_1^*)}, \quad g_{2v} = \frac{\partial g_2}{\partial v} \Big|_{(u_2^*, v_2^*)},$$

257 and the other terms analogously. From the condition that the solution to this linear system be  
258 non-trivial, we obtain the dispersion relation

$$F(k, \sigma) = \det(M - \sigma I) = 0. \quad (10)$$

259 For spatial pattern formation we require the steady state to be (i) stable to homogeneous per-  
260 turbations (i.e.  $\Re(\sigma) < 0$  when  $k = 0$ ), and (ii) unstable to inhomogeneous perturbations  
261 (i.e.  $\Re(\sigma) > 0$  for some  $k \neq 0$ ). We illustrate and discuss the stability boundary of the  $j$ -  
262 independent solution in several figures below. In each figure, we indicate whether a perturbation  
263 of wavelength  $N$  can grow with a positive real eigenvalue ( $\sigma > 0$ , white region) or will decay  
264 with a real negative eigenvalue ( $\sigma < 0$ , black region) or non-real eigenvalue with negative real  
265 part ( $\Re(\sigma) < 0$ , grey region). We expect patterns to form in the white region. To generate these  
266 figures, we calculated the stable tile-independent steady state by numerically solving Equations  
267 (2) on a single tile with periodic boundary conditions. For each wavelength, we then found the  
268 characteristic polynomial of  $M$  and evaluated its roots numerically (using the `root` command  
269 in MATLAB). We focus our results on the effects of movement-related parameters.

## 270 Relative dispersal ability

271 A key requirement for classical diffusion-driven pattern formation is a difference in dispersal  
272 ability, to achieve short-range activation and long-range inhibition (Murray, 2001). Since the  
273 prey corresponds to the activator in our model and the predator to the inhibitor, we expect  
274 that patterns form when the relative dispersal ability  $\mu_v/\mu_u$  is large enough. Figure 4 (a)  
275 shows essentially this behaviour, but the situation is slightly more complex than in the case of  
276 a homogeneous landscape. In Figure 4 (a) we fixed  $\mu_u = 0.5$  and varied  $\mu_v$ . When  $\mu_v = \mu_u$ ,  
277 no patterns form. As  $\mu_v$  increases, patterns of wavelength 3 and 4 emerge, and the range of  
278 unstable wavelengths increases as  $\mu_v$  increases. Note that the white region between  $N = 1$  and  
279  $N = 2$  corresponds to non-integer wavelengths and is not observable on our lattice. We note  
280 that a different class of spatio-temporal dynamics arises when predator dispersal is very small.  
281 The dispersion relation then predicts periodic traveling waves, i.e. instabilities with non-real  $\sigma$   
282 and  $\Re\sigma > 0$ . This scenario is present in panel (a) for values of  $\mu_v$  below 0.1004 (thin white strip  
283 at the bottom of the figure). The dynamics on an isolated good patch are oscillatory, and prey  
284 dispersal propagates these oscillations in space to generate periodic traveling waves.

285 In Figure 4 (b) we instead fixed  $\mu_v = 5$  and varied  $\mu_u$ . When  $\mu_u \geq 1$ , no patterns form. As  $\mu_u$   
286 decreases, patterns with small wavelengths ( $3 \leq N \leq 6$ ) emerge as expected from the previous  
287 scenario. The choice of  $\mu_v$  seems to constrain the range of unstable wavelengths that can be  
288 obtained by varying  $\mu_u$ , but not vice versa (compare panel (a)). Rietkerk and van de Koppel  
289 (2008) also observed the key role of long distance negative feedback in determining the existence  
290 and regularity of patterns. As  $\mu_u$  decreases even further, the homogeneous state becomes stable  
291 again, even though the ratio  $\mu_v/\mu_u$  is large. In this case, the range of activation becomes too  
292 small to spread across the neighbouring bad patch since the residency time in the good patch  
293 ( $\frac{1}{\mu_u}$ ) is high. For the chosen parameter values, the dynamics on an isolated good patch are  
294 oscillatory (as discussed in section 2), but the relatively large predator movement stabilises the  
295 dynamics. The analysis suggests mobile predators and prey are both needed to observe patterns,  
296 however a low predator residency time in good patches appears to be an important ingredient  
297 for determining the wavelength of resulting patterns.

298 **Movement bias  $\kappa_u$  and  $\kappa_v$**

299 The dispersion relation predicts that no patterns form when prey movement is heavily biased  
 300 towards good patches (e.g.  $\kappa_u > 1.4$  in Figure 4 (c)). As  $\kappa_u$  decreases, perturbations of relatively  
 301 small wavelengths ( $2 \leq N \leq 6$  for the chosen parameters) become unstable and patterns arise.  
 302 Even though the movement rates are constant in this figure, the emergence and disappearance of  
 303 patterns can be explained in terms of the relative scales of activation and inhibition as follows. By  
 304 decreasing  $\kappa_u$ , the residence time in bad patches ( $\frac{1}{\mu_u \kappa_u}$ ) is increased, which effectively increases  
 305 travel time between two consecutive good patches. Thereby the activation range decreases. Vice  
 306 versa, increasing  $\kappa_u$  decreases the residence time in bad patches. Effectively, prey move faster  
 307 through the landscape, thereby increasing the activation range and destroying any potential  
 308 patterns.

309 With movement bias of the predator, the same mechanisms are in effect. Since long-range  
 310 inhibition aides pattern formation, these mechanisms produce contrasting results (not shown).  
 311 As  $\kappa_v$  increases, predators bias their movement towards good patches by decreasing their resi-  
 312 dence time in the bad patches. This behaviour effectively increases their overall movement rate,  
 313 and with increased inhibition range, patterns may form.

314 **Patch size**

315 Pattern formation can occur for intermediate size of good patches relative to bad patches.  
 316 Figure 4 (d) shows the case of fixed  $L_2$  and varying  $L_1$ , but the reverse case is qualitatively the  
 317 same. When the ratio  $l = L_1/L_2$  is small, prey growth on good patches cannot compensate for  
 318 prey death in bad patches to produce enough activation for patterns to form. At intermediate  
 319 ranges, good patches are large enough to enhance prey growth and bad patches are large enough  
 320 to stabilise the oscillatory dynamics on good patches. When  $l$  is large, then the oscillatory  
 321 dynamics on a good patch cannot be stabilised by the (relatively) small bad patches, and the  
 322 dynamics on each tile are oscillatory. Due to movement, these local oscillations then form  
 323 periodic traveling waves. Webb and Owen (2004b) also found periodic travelling waves in their  
 324 lattice model of intracellular signalling. As the focus of the current work is the study of stable  
 325 patterns we leave the study of the periodic travelling waves for future work.

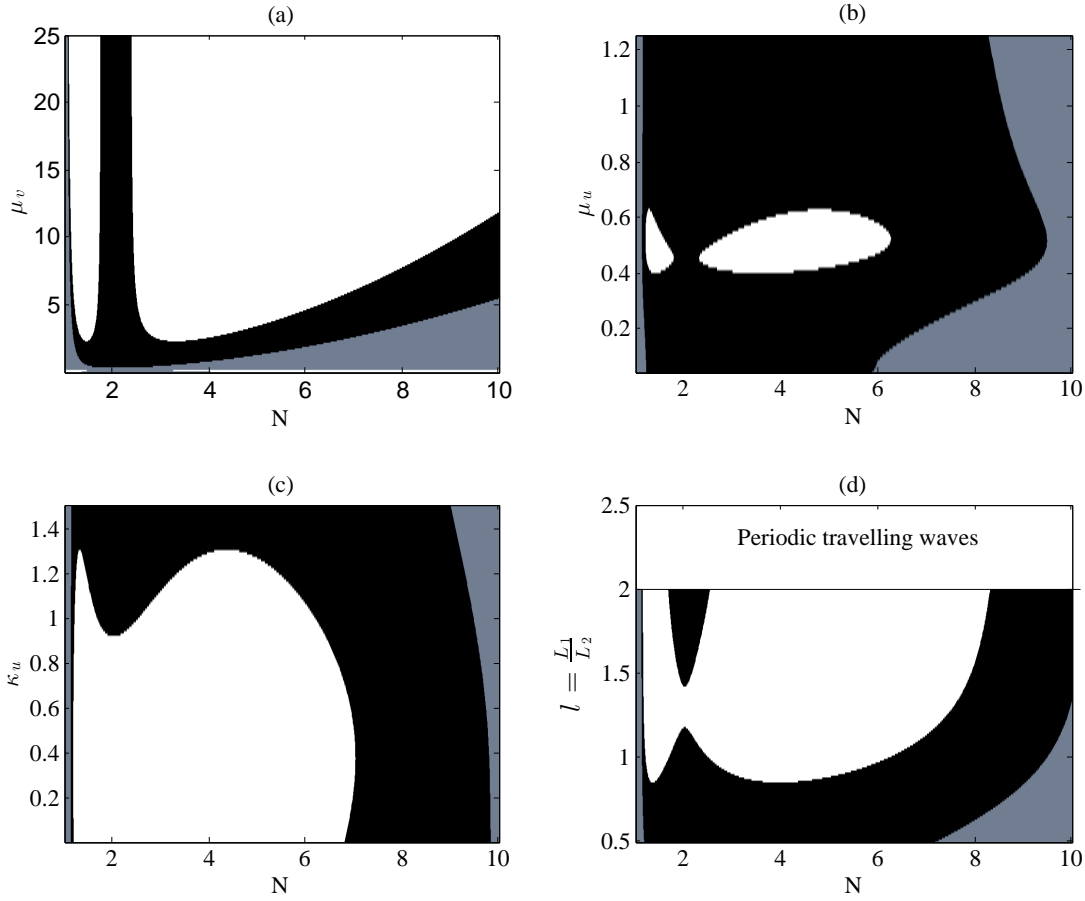
326 **Homogeneous versus heterogeneous landscapes**

327 To complete this section, we ask what effect the bad patches have on the occurrence of patterns  
 328 compared to a homogeneous landscape. When all patches are good patches (i.e.  $f_1 = f_2, g_1 = g_2$ ),  
 329 then we have a homogeneous landscape, consequently there is no patch preference (i.e.  $\kappa_{u,v} = 1$ ).  
 330 In this case, the four-dimensional system (9) reduces to two equations, and the dispersion relation  
 331 can be written explicitly as

$$K^2(\mu_u \mu_v)(1+l)^2 + K[\sigma(\mu_u + \mu_v)(1+l) - a_{11}\mu_v(1+l) - a_{22}\mu_u(1+l)] + [\sigma^2 - \sigma(a_{11} + a_{22}) + a_{11}a_{22} - a_{12}a_{21}] = 0 \quad (11)$$

where  $K = \sin^2(k/4)$  and  $a_{ij}$  are the entries in the community matrix  $J$  given in Equation (6), i.e.  $a_{11} = f_{1u}$ ,  $a_{22} = g_{1v}$  and so on. The conditions for diffusion-driven instabilities in this dispersion relation are

$$a_{11} + a_{22} < 0, \quad a_{11}a_{22} - a_{12}a_{21} > 0, \quad a_{11}\mu_v + a_{22}\mu_u > 0, \\ 4(a_{11}a_{22} - a_{12}a_{21})\mu_u\mu_v < a_{11}\mu_v + a_{22}\mu_u.$$




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Figure 4: Stability boundaries illustrating the outcome of the linear stability analysis of the patch-independent (period 1) solution on an infinite, one-dimensional spatial domain. The white regions indicate values of the parameter ( $y$ -axis) for which we expect to obtain a pattern of wavelength  $N$  ( $x$ -axis). In the white region the patch-independent solution is stable to spatially homogeneous perturbations, and unstable to spatially varying perturbations of wavelength  $N$ . In the black and grey regions the period 1 solution is stable to spatially varying perturbations of wavelength  $N$ . In the black regions, the dominant eigenvalue associated with spatially varying perturbations of wavelength  $N$  is real, in the grey regions, it is not. We illustrate in (a) the effect of predator migration rate, (b) the effect of prey migration rate, (c) the effect of prey patch preference, and (d) the effect of relative patch size, on pattern formation. In both (a) and (d) periodic travelling wave solutions are predicted; this occurs in the small white region at the bottom of figure (a) ( $\mu_v \approx 0.1004$ ) and in the top region of figure (d) ( $l \geq 2.0276$ ).

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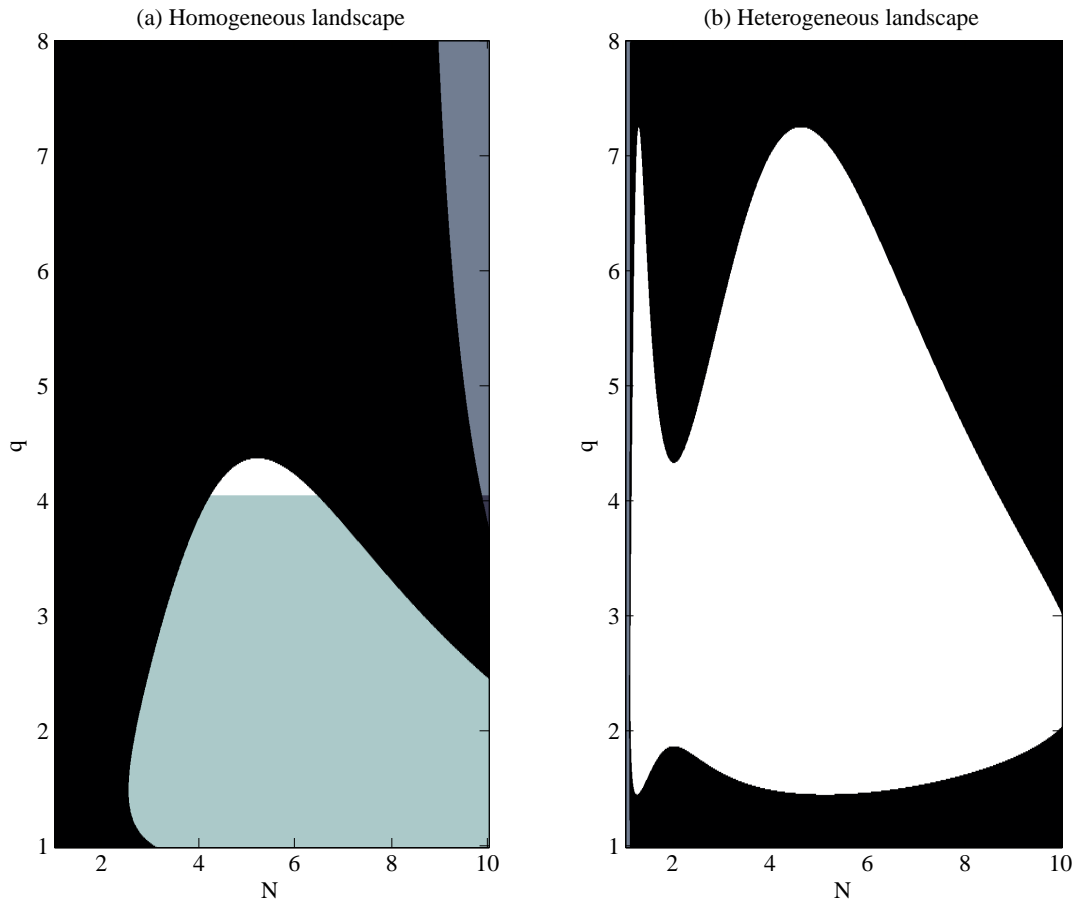
332 These conditions are the familiar ones for reaction-diffusion equations with movement rates  $\mu_{u,v}$   
 333 replacing diffusion constants (cf. Murray (2001)). This similarity is understandable since in a  
 334 homogeneous landscape, our model is essentially a midpoint discretisation of a continuous-space  
 335 model. Note that relative patch size  $l = L_1/L_2$  drops out from the relation, as it should in a  
 336 homogeneous landscape.

337 The two plots in Figure 5 illustrate the difference in the stability behaviour of the tile-  
 338 independent solution for a homogeneous (two good patches per tile, left plot) and heterogeneous  
 339 (a good and a bad patch per tile, right plot) landscape. (We use two good patches per tile so that  
 340 we can compare the length scales of the emergent patterns between the two types of landscapes.)  
 341 In the homogeneous landscape, only a very narrow range of  $q$  leads to pattern formation for a  
 342 limited range of wavelengths  $N$  (white region). There is a large region of oscillatory solutions  
 343 when  $q < 4$  (see Section 2), but the entire region  $q > 5$  has a stable homogeneous solution. In  
 344 the heterogeneous landscape, the region of pattern formation is much larger (white region, right  
 345 plot). The presence of bad patches stabilises all the oscillations for  $q < 4$  so that spatial patterns  
 346 can emerge there. In addition, patterns can arise for values of  $q$  up to at least 7; much larger  
 347 than in the homogeneous case. We hypothesise that the small-scale variation in the steady-state  
 348 densities that is generated by the presence of bad patches can act as a catalyst that favours  
 349 pattern formation.

### 350 3.3 Comparison of the different approaches

351 The numerical continuation method in Section 3.1 revealed a great number of coexistent spatial  
 352 patterns, but was limited to a single bifurcation parameter and required intensive computations.  
 353 The analytical dispersion-relation method in Section 3.2 captures the stability behaviour of the  
 354 tile-independent state in an infinite landscape relatively easily, but cannot detect other patterns  
 355 and is based only on linear stability. We compare the two methods in Figure 6. For each  
 356 wavelength ( $N$ ), the hashed bars in (a) indicate the range of  $q$  for which the tile- independent  
 357 solution is unstable according to the numerical method applied to the nonlinear model. The  
 358 white bars in (a) indicate the values of  $q$  for which (locally stable) non-trivial spatial patterns  
 359 exist. The white region in (b) corresponds to linear instability of the tile-independent state  
 360 according to the dispersion relation.

361 We see that the instability region for finitely many tiles (hashed bars, panel (a)) correspond  
 362 reasonably well to the instability region on the infinite landscape (white region, panel (b)), but  
 363 that the pattern formation region (white bars, panel (a)) is much larger than the instability  
 364 region of the tile-independent solution. Specifically, we saw in Figure 2 that all primary bifur-  
 365 cations from the period-1 pattern are sub-critical. Despite this, the linear analysis still predicts  
 366 the patterns for small wavelengths with reasonable success. For example, in the case  $N = 4$ ,  
 367 a period-4 pattern branches sub-critically from the period-1 pattern, and only becomes stable  
 368 once it folds back. Secondary bifurcations lead to additional patterns that are stable and fold  
 369 back to the period-1 pattern long after this period-1 pattern is stable again. As the propen-  
 370 sity for secondary bifurcations increases, the ability of the linear analysis to predict patterns  
 371 decreases. Diffusion-driven instabilities arising in reaction-diffusion models typically result from  
 372 supercritical solutions so that the linear stability analysis predicts patterns well, at least close to  
 373 the bifurcation point. In discrete-space systems, however, sub-critical bifurcations are common  
 374 (O’Dea and King, 2013). And even continuous-space systems can exhibit numerous sub-critical  
 375 bifurcations in the presence of an advection term (Sherratt, 2013; van der Stelt et al., 2013;  
 376 Siteur et al., 2014). Hence, the linear stability analysis can serve as an entry point into study-  
 377 ing pattern formation, but to obtain the full picture, one has to consider the nonlinear model




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Figure 5: Comparison of stability conditions, according to the dispersion relation, between the homogeneous (panel a) and heterogeneous (panel b) landscape. The homogeneous landscape consists of only good patches whereas the heterogeneous landscape has good and bad patches alternating. White, black and dark grey colours indicate Turing instability and stability, respectively, as in previous figures. The light grey shaded region in (a) indicates that the patch-independent (period 1) solution is unstable to spatially homogeneous perturbations giving rise to population cycles and preventing Turing pattern formation. We use the baseline parameters with the exception of  $\mu_v = 10$ .

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378 entirely.

## 379 4 Discussion

380 One of the great challenges in ecology is to explain the mechanisms behind the observed spatio-  
381 temporal variation in species densities. Such spatial variation could be (i) *externally imposed* in a  
382 heterogeneous landscape by variations in habitat quality, or (ii) arise on homogeneous landscapes  
383 from species interaction and dispersal through diffusion-driven instabilities or other feedback  
384 mechanisms that lead to *self-organised* population patterns. The former view is reflected in  
385 habitat suitability models where population abundance is correlated with local habitat features  
386 and resource availability (Ergon et al., 2001). Documenting the latter has been a highly active  
387 area of ecological research in recent years (Rietkerk et al., 2004). Examples can be found in  
388 arid ecosystems (Rietkerk and van de Koppel, 2008), marine systems (Wang et al., 2010a),  
389 and also in other areas of the biophysical sciences such as developmental biology and coupled  
390 chemical reactors (Gilbert, 1994; Horsthemke and Moore, 2004). In reality, both aspects are  
391 likely to interact (Schmitz, 2010). The strength of this interaction and the expected resulting  
392 patterns depend on the relative length scales of the different mechanisms (Sheffer et al., 2013;  
393 Benson et al., 1993b). If the spatial extent of landscape features is much larger than the length  
394 scale on which biological feedbacks (through dispersal and species dynamics) operate, then any  
395 patterns in species abundance are likely to be self-organised. If the two scales are comparable  
396 then we expect the two mechanisms to interact such that spatial patterns are more difficult to  
397 predict. Sheffer et al. (2013) propose a conceptual framework and empirical setting to explore  
398 this influence of spatial scales.

399 We developed a theoretical framework to understand the spatial patterns that arise in a  
400 predator-prey system where external factors and self-organisation interact. We represented  
401 the heterogeneous landscape generated by abiotic factors as a series of periodically alternating  
402 patches, and the population dynamics on each patch as a system of differential equations. While  
403 pattern formation has been studied in other contexts on homogeneous lattices and networks of  
404 patches (Wearing et al., 2000; Lubensky et al., 2011; Formosa-Jordan et al., 2012), to the best  
405 of our knowledge, our model is the first application of these ideas to spatial ecology and the first  
406 attempt to deal with strong heterogeneity (but see Webb and Owen (2004a) for a related idea).  
407 Due to the spatial heterogeneity, this system does not have a spatially constant steady state on  
408 the level of patches. Instead, there is a steady state that is spatially constant on the level of  
409 tiles. Within each tile, species densities vary between the good and bad patch, reflecting the  
410 populations tracking externally imposed landscape heterogeneity. We employed linear dispersion  
411 relation and numerical bifurcation analysis to study the stability of this steady state to spatially  
412 non-uniform perturbations as well as the occurrence of stable, spatially non-uniform (on the  
413 level of tiles) states.

414 We found that (i) the homogeneous (tile-level) state can be destabilised by non-constant  
415 spatial perturbations (e.g. Figure 1); that (ii) there are potentially many stable, coexisting,  
416 spatially-structured states with reasonably large basins of attraction (e.g. Figure 2). Similar  
417 results are known on homogeneous networks (Wolfrum, 2012). In addition, we find that (iii)  
418 externally imposed spatial heterogeneity seems to have the potential to promote self-organised  
419 spatial patterns (e.g. Figure 5). Sheffer et al. (2013) had reached a similar conclusion from their  
420 conceptual model of vegetation patterning. The patterns we find can be explained with the clas-  
421 sical mechanisms (Segel and Jackson, 1972; Gierer and Meinhardt, 1972) of long-range inhibition

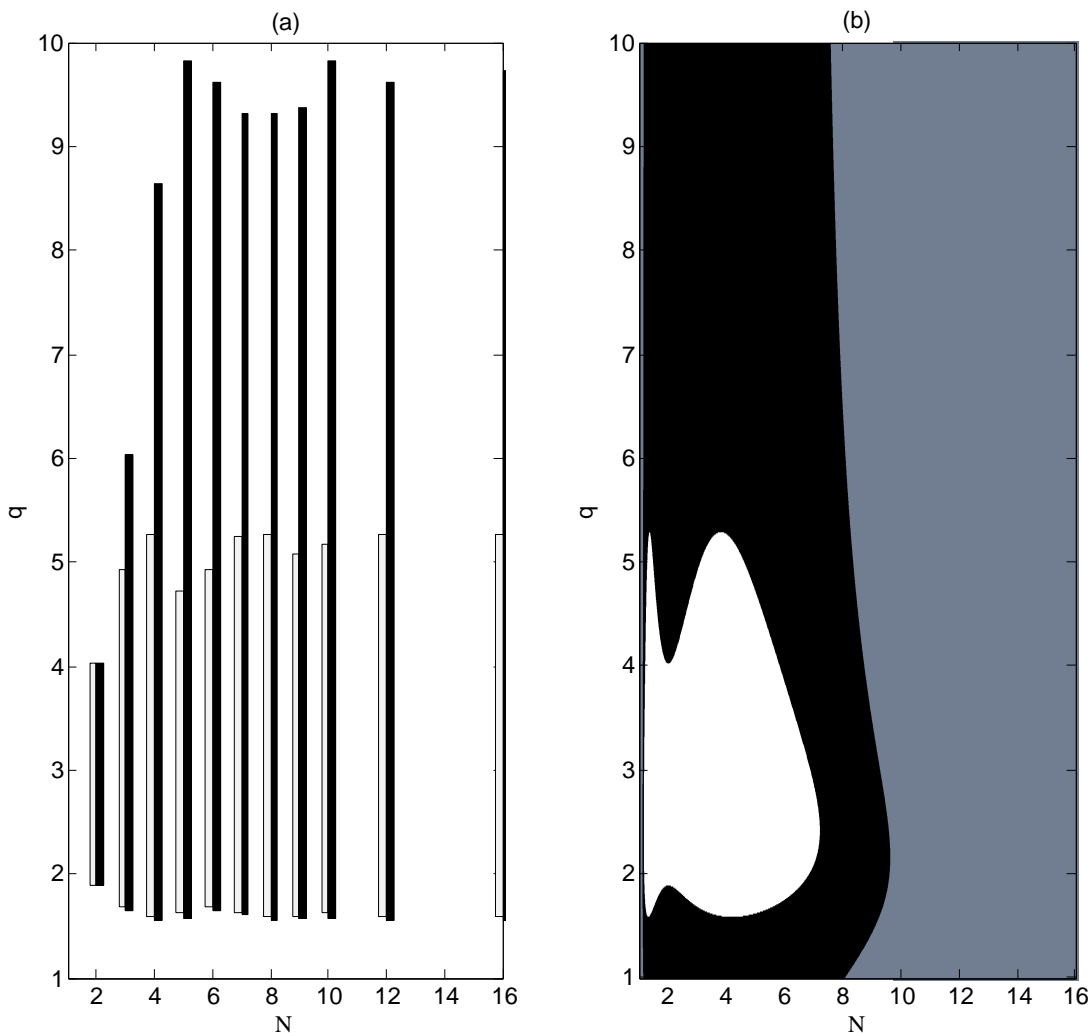


Figure 6: Stability boundary plots comparing the results from the full non-linear bifurcation analysis (a) to the results of the linear stability analysis of the patch-independent (period 1) solutions on an infinite one dimensional spatial domain (b). In (a) the hashed bars indicate the range of  $q$  which give unstable patch-independent (period 1) solutions found from the numerical bifurcation analysis of the full non-linear model. The white bars indicate the full range of  $q$  where patterns arise in the full non-linear model. The white region in (b) indicates values of the parameter  $q$  for which we expect to obtain a pattern of wavelength  $N$ . In the white region the patch-independent (period 1) solution is stable to spatially homogeneous perturbations, but is unstable to spatially varying perturbations of wavelength  $N$ . In the black and grey regions the period 1 solution is stable to spatially varying perturbations of wavelength  $N$  and patterns are not possible according to the linear analysis. The difference between the black and grey regions is that dominant eigenvalues are real and complex respectively.

422 (predator) and short-range activation (prey), when properly taking into account how dispersal  
423 rates, patch residence times and landscape configuration interact to create the length scale of  
424 biological feedbacks. The difference in predator-prey dispersal ability required for long-range  
425 inhibition and short range activation is often observed in marine systems. Marine piscivores reg-  
426 ularly migrate across spatial scales much larger than the habitat occupied by their prey (Spencer  
427 and Collie, 1995) , and so marine environment may provide a good setting for potential appli-  
428 cations of our findings.

429 Our results have particular implications for the management of biological systems, for exam-  
430 ple the alteration of existing habitats and the design of reserves. For example, optimal design  
431 and spacing of systems of marine reserves is usually based on maximising the likelihood of pop-  
432 ulation persistence, but once persistence is guaranteed, interaction with other populations is  
433 often not considered (but see Gouhier et al. (2010)). Between two consecutive marine reserves  
434 (good patches) lies a region of unprotected habitat (bad patch) where prey death is high due  
435 to harvesting. Our results show that long-range spatial patterns may arise in such a situation.  
436 Figure 1(b), for example, shows a period-4 pattern on a system of eight tiles where the prey  
437 density in the good patches on tiles 1, 4, 5, and 8 is low, even lower than the prey density in the  
438 bad patches in tiles 2 and 6. It might be tempting to conclude that the good patches in tiles  
439 1, 4, 5, and 8 are not successful reserves that could be removed. We simulated the system with  
440 those four patches converted to bad patches (Figure 1(c)), and we found that this local change  
441 caused by patch conversion has a global effect, elevating the prey density on all of the remaining  
442 good patches. The original pattern wavelength is typically preserved and the predator densities  
443 (not shown) are also globally affected, often showing a decrease in density. These observations  
444 apply equally well to naturally heterogeneous habitats. When patterns arise in heterogeneous  
445 landscapes, the steady-state population density need not be uniformly high on good patches;  
446 it may, in fact, be lower on some good patches than on some bad patches (Figure 1). Hence,  
447 neither are low population densities in good patches a sign of impending collapse, nor is low  
448 population density a sign for low habitat quality. Both can merely be a consequence of species  
449 interaction and spatial coupling.

450 There are many examples of spatially periodic habitats of the type considered in our model.  
451 One particularly rich example is semi-arid vegetation, which tends to self-organise into patterns  
452 because of the positive feedback between vegetation density and water infiltration (Rietkerk  
453 et al., 2004; Meron, 2012; Sherratt, 2015). Bonachela et al. (2015) have shown that the spatial  
454 heterogeneity created by periodic patterns of termite mounds plays an important regulatory  
455 role for the vegetation patterns that develop in this heterogeneous landscape. Most notably,  
456 they predicted that the heterogeneity increases resilience to reductions in rainfall, a result in  
457 keeping with the work of Yizhaq et al. (2014) on spatial heterogeneity in soil water diffusion.  
458 Moreover the vegetation itself provides a spatially patterned habitat for other fauna, although  
459 this is an aspect of semi-arid ecosystems that has received little attention in the literature.  
460 Other examples of spatial patterns at the whole ecosystem scale include mussel beds (Wang  
461 et al., 2010a), intertidal mudflats (Weerman et al., 2012), ribbon forests (Bekker et al., 2009)  
462 and peat bogs (Eppinga et al., 2009). In each case these systems provide patterned habitats  
463 for other components of the ecosystem, although again this has been little studied, with the  
464 research focus being on the landscape patterning itself.

465 We have demonstrated that unless the number of tiles is small, there can be a large number of  
466 coexisting stable spatial patterns, many of which have an appreciable basin of attraction. Many  
467 of these solutions are very similar to one another, implying that populations can be in any of a  
468 range of stable patterns, which differ only slightly. For example, a variety of different patterns

469 could become established on similar landscapes, depending on initial conditions or environmental  
470 perturbations. Empirical evidence for this statement comes from Sheffer et al. (2013). In the  
471 same vein, landscape alterations may have a number of unexpected consequences for population  
472 densities. Species abundances could change far beyond the range of the actual alteration if  
473 the system is moved between basins of attraction for two distinct patterns. Based on our  
474 observation that landscape heterogeneity can promote spatial patterns, landscape alterations  
475 that increase heterogeneity could lead to emergent patterns where there were none to begin  
476 with. The mechanisms that we uncovered complement those found by Page et al. (2003) in a  
477 developmental context. In Page *et al.*'s work, a spatial discontinuity in the population dynamic  
478 parameters drove the pattern formation, and the resulting patterns were centred around this  
479 discontinuity. In our case, the patterns are not originating from such parameter discontinuities,  
480 instead they occur across the entire domain driven by spatial coupling as well as the short-range  
481 destabilising effect of the prey and the long-range stabilising effect of the predators.

482 It is well known that standard Lotka-Volterra or Rosenzweig-MacArthur predator-prey mod-  
483 els do not support diffusion-driven instabilities on homogeneous landscapes (Okubo and S.A.,  
484 2001), while the model by Leslie and May that we considered does (Mukhopadhyay and Bhat-  
485 tacharyya, 2006). Fasani and Rinaldi (2011) showed that the Rosenzweig-MacArthur model can  
486 readily show the required activator-inhibitor structure by including one of at least nine potential  
487 demographic factors for the predator. While not all factors enhanced the propensity for pattern  
488 formation, their result suggests that the ideas presented here may have wide applicability. Fur-  
489 thermore, since we observed pattern formation in the heterogeneous landscape for a much wider  
490 range of parameters than for a homogeneous landscape, and especially for parameter values  
491 where the model on an isolated good patch has oscillatory dynamics, we conjecture that most  
492 of our results are fairly robust and apply to more general predator-prey models. Some support  
493 for this conjecture comes from work by Strohm and Tyson (2009) who compared the dynamics  
494 of several predator-prey models on a simple fragmented landscape and found that results were  
495 largely insensitive to model type. Future work will have to explore how robust our results are  
496 with respect to other modelling assumptions, for example, the arrangement and sizes of patches.

497 Managed ecological settings are not the only context within which our work is applicable.  
498 Heterogeneous environments are also present in developmental biology. As an embryo grows,  
499 patterns are laid down in a hierarchical fashion with new patterns forming on top of earlier  
500 patterns. Spatially discrete models have been used to describe developmental pattern formation  
501 before, but not in the context of a heterogeneous domain. Instead, coupled ODEs have been  
502 used to describe juxtacrine signalling (a means of nearest neighbour communication that occurs  
503 in closely packed cells), but the assumption has been one of a homogenous spatial environment  
504 on which fine-grained patterns form in developing tissue. Our approach offers a new way to  
505 study pattern formation on a heterogenous domain. Previous studies of pattern formation had  
506 largely been limited to simple cases of spatially-dependent step-functions in diffusion or kinetic  
507 parameters (Benson et al., 1993b; Page et al., 2003).

## 508 **Acknowledgments**

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## 516 Appendix A

517 In section 3.1 we presented the results of a numerical bifurcation analysis of our model equa-  
518 tions. In this Appendix we discuss the details of this method, highlighting the various technical  
519 difficulties that we encountered and how we overcame them. Readers considering reproducing  
520 the figures should be aware that they require large amounts of computer time. Taken together,  
521 all of the numerical continuations for  $N = 16$  took about 2 weeks on a Linux PC with a 2.83GHz  
522 Intel Core 2 Quad Q9500 processor.

523 Our basic approach is to calculate numerically the patch-independent solution for a relatively  
524 small value of  $q$ , and then numerically continue the solution in  $q$  from this starting point,  
525 detecting bifurcations and following bifurcating branches. We performed our calculations using  
526 the software package AUTO97 (Doedel, 1981; Doedel et al., 1991, 2006). The values of key AUTO  
527 parameters are: `ips=1` (stationary solutions of ODEs); `isp=1` (enable detection of bifurcation  
528 points); `isw=1` (enable branch switching); `iid=0` (minimal diagnostics; otherwise the file `fort.9`  
529 becomes extremely big). With these settings, AUTO attempts to calculate not only the primary  
530 solution branch, but also the bifurcating branches from the first `|mxbf|` bifurcation points. In  
531 principle therefore, AUTO should automatically calculate the entire bifurcation diagram in a  
532 single run. However a major difficulty arises in practice when solution branches are loops.  
533 Then the numerical continuation will typically trace round the loop several times before ending  
534 when the number of continuation steps reaches its pre-assigned maximum `nmx`. Therefore each  
535 bifurcation point on the loop is recorded several times, and each occurrence acts as a starting  
536 point for a new branch calculation, causing bifurcation points along the branch to be located  
537 several times. These bifurcating branches may themselves be loops, in which case there will  
538 be multiple recording of bifurcation points for each replicate of the branch. Repetition of this  
539 process gives the potential for an exponential increase in the number of times a solution branch  
540 is calculated as a function of the number of bifurcations separating it from the primary solution  
541 branch. It turns out that looped solution branches are quite common for our equations. Moreover  
542 the same problem can occur when the numerical continuation turns around at the end of a  
543 solution branch and recomputes it in the opposite direction; in theory this should be prevented  
544 by setting `mxbf < 0`, but in practice it sometimes happens anyway.

545 This multiple calculation of bifurcation points and solution branches is a feature of all our  
546 computations. It means that however large `|mxbf|` is, the calculation will always continue until  
547 this upper limit on the number of solution branches is attained, and one can never be certain  
548 whether or not the resulting bifurcation diagram is complete. We took `mxbf = -4000`, which  
549 compares with the value `|mxbf| = 10` used in most examples in the AUTO manual. The vast  
550 majority of the 4000 solution branches that are then calculated are repeats: nevertheless there  
551 may be omissions. Therefore we augmented the basic calculation with an additional step. For  
552 each value of  $q$  in the set  $1.0, 1.25, 1.5, 1.75, \dots$  we ran 1000 simulations of the model equations  
553 with initial conditions in which each variable was chosen randomly from a uniform distribution  
554 between 20% and 200% of its value in the patch-independent solution. Many of the patterns  
555 generated by these simulations lie on solution branches that have already been calculated, but  
556 typically some do not, due to the incompleteness of the preliminary bifurcation diagram. In  
557 such cases, we performed separate runs of AUTO starting from the pattern found via simulation,  
558 with `mxbf` reset to 10; we deliberately set `mxbf > 0` in this case. During such a run, one wants to  
559 record  $w_1^j$  for all values of  $j$  since these should all be plotted on the bifurcation diagram; however  
560 AUTO only records up to 6 variable values (in the `fort.7` output file), which presents a problem  
561 for  $N > 6$ . One possible remedy would be to edit the AUTO source code to output more variable  
562 values. However we adopted the alternative strategy of doing  $N$  separate runs of AUTO, starting

563 from  $(u_1^j, u_2^j, v_1^j, v_2^j) = (\tilde{u}_1^{j+k \pmod{N}}, \tilde{u}_2^{j+k \pmod{N}}, \tilde{v}_1^{j+k \pmod{N}}, \tilde{v}_2^{j+k \pmod{N}})$  where  $(\tilde{u}_1^j, \tilde{u}_2^j, \tilde{v}_1^j, \tilde{v}_2^j)$  is  
564 the pattern found via simulation, and  $k = 0, 1, \dots, N - 1$ .

565 It is important to note one consequence of our two-step method for calculating the bifurcation  
566 diagrams, which is that we cannot guarantee that we have calculated all of the solution branches.  
567 Indeed, for the very complicated diagrams for  $N = 12$  and  $N = 16$ , we think that it is very  
568 likely that our results omit some unstable solution branches, although given the dense network of  
569 such branches it would probably be difficult to distinguish the results visually if some additional  
570 branches were included. Because we use the results from a large volume of simulations to  
571 give starting points for numerical continuation, we think it likely that we have calculated the  
572 vast majority of the branches with stable parts. However we cannot rule out the possibility of  
573 additional stable portions of solution branches that have either very small extent in  $q$ , or a very  
574 small basin of attraction.

575 We also mention two other more minor technical difficulties, for the benefit of readers con-  
576 sidering using our approach themselves. Firstly, in some cases AUTO erroneously detects some  
577 Hopf bifurcation points. These occur when two real eigenvalues change sign simultaneously: nu-  
578 merical discretisation introduces very small imaginary parts to these eigenvalues, causing AUTO  
579 to detect a Hopf bifurcation. These do not cause any difficulties in practice, and so can safely be  
580 ignored – in particular AUTO does not automatically attempt to trace limit cycle branches em-  
581 anating from Hopf bifurcation points. Alternatively the “Hopf bifurcations” can be eliminated  
582 by reducing the error tolerances and step sizes. We have not found any genuine Hopf bifurca-  
583 tions in any of the bifurcation diagrams we calculated. Secondly, the fact that most solution  
584 branches are calculated many times causes very long rendering times for plots. To avoid this,  
585 we processed the data files before plotting, removing repeated solution branches. Specifically,  
586 we removed branches whose first 20 points were within a small tolerance of the first 20 points  
587 of a previous branch.

588 We end this Appendix with a full listing of the various AUTO parameters that we used  
589 in our calculations. NDIM=4N, IPS=1, IRS=0, ILP=0, NICP=1, ICP=1, NTST=50, NCOL=4,  
590 IAD=3, ISP=1, ISW=1, IPLT=0, NBC=0, NINT=0, NMX=4000, RLO=0.6, RL1=15.0, A0=0, A1=100,  
591 NPR=4000, MXBF=-4000, IID=2, ITMX=8, ITNW=5, NWTN=3, JAC=0, EPSL=10<sup>-7</sup>, EPS=10<sup>-7</sup>,  
592 EPSS=10<sup>-5</sup>, DS=0.0005, DSMIN=0.0001, DSMAX=0.005, IADS=1, NTHL=1, I=11, THL=0, NTHU=0,  
593 NUZR=0. The only variation in these values was to MXBF, which was set to 10 or 1 in some runs,  
594 as discussed above.

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