On the importance of dimensionality of space in models of space-mediated population persistence

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Abstract

Spatially explicit models have become widely used in today’s mathematical ecology to study persistence of populations. For the sake of simplicity, population dynamics is often analyzed with 1-D models. An important question is: how adequate is such 1-D simplification of 2-D (or 3-D) dynamics for predicting species persistence. Here we show that dimensionality of the environment can play a critical role in the persistence of predator–prey interactions. We consider 1-D and 2-D dynamics of a predator–prey model with the prey growth damped by the Allee effect. We show that adding a second space coordinate into the 1-D model results in a pronounced increase of size of the domain in the parametric space where predator–prey coexistence becomes possible. This result is due to the possibility of formation of a number of 2-D patterns, which is impossible in the 1-D model. The 1-D and the 2-D models exhibit different qualitative responses to variations of system parameters. We show that in ecosystems having a narrow width (e.g. mountain valleys, vegetation patterns along canals in dry areas, etc.), extinction of species is more probable compared to ecosystems having a pronounced second dimension. In particular, the width of a long narrow natural reserve should be large enough to guarantee nonextinction of species via interaction of 2-D population patches.

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1. Introduction

There is growing evidence to support the idea that space is among the most important factors facilitating persistence of populations in nature (Comins et al., 1992; Solé et al., 1992; Rand and Wilson, 1995; Comins and Hassell, 1996; Rohani et al., 1997; Petrovskii et al., 2004). It was shown in different models that a pronounced heterogeneity of the environment often results in species survival, impossible otherwise (Chesson and Warner, 1981; Pacala and Roughgarden, 1982; Holmes et al., 1994; White et al., 1996; Chesson, 2000). Analysis of many spatially explicit models indicates that persistence of species dispersing in space increases essentially (compared to the same models without space), even when the interactions take place in a uniform environment. In models of host–pathogen interactions (Hassell et al., 1994; Comins and Hassell, 1996; Wood and Thomas, 1996; Wilson et al., 1999), in predator–prey systems (Savill and Hogeweg, 1997; Gurney et al., 1998; Petrovskii et al., 2002, 2005a, b; Morozov et al., 2006) and in plant–pollinator–exploiter systems (Bronstein et al., 2003; Wilson et al., 2003), the addition of a spatial dimension into a given model (both for discrete and continuous approaches) often provides coexistence of species, preventing the extinction that would take place in the non-spatial case.

For many ecosystems, the vertical space dimension can be neglected, and the species interactions in the two-dimensional horizontal environment can be considered. Moreover, for the sake of simplicity, in many spatially explicit models population persistence is analyzed in 1-D
space. From a methodological point of view, an important issue is to compare how such 1-D simplifications of 2-D dynamics affects the results and predictions regarding the persistence of populations.

Comparison of dynamics in 1-D and 2-D space contributes to a general theory of population dynamics by showing how an increase of complexity, caused by adding a second space coordinate, will affect mechanisms of species persistence (Matano, 1979; Whitehead and Walde, 1992; Wilson et al., 1995). Another particular interest is whether the size of the domain in parametric space (corresponding to species persistence) changes significantly with changing spatial dimensionality of a model. Such an analysis is necessary for choosing the right dimensionality for a given model to analyze a particular ecological problem (e.g., designing of natural reserves). In the case when formation of 2-D spatial structures becomes vital for species survival, one should consider 2-D species interactions.

In this paper, we compare 1-D and 2-D spatial dynamics of a conceptual predator–prey system where the prey growth is damped by the strong Allee effect (the growth becomes negative at low density, see Allee, 1938; Dennis, 1989). A great significance of the strong Allee effect for the ecosystems’ invisibility, persistence, and extinction of species is widely acknowledged in ecology (Berryman, 1981; Lande, 1987; Stephens et al., 1999; Keitt et al., 2001; Taylor and Hastings, 2005). We use the continuous modeling approach based upon reaction–diffusion models and consider the environment to be homogeneous in space and time.

We obtained that apart from a pronounced increase in system complexity, adding a second space coordinate into 1-D model essentially affects system persistence. For a wide range of parameters, the 2-D model shows a coexistence of a prey and its predator; whereas the corresponding 1-D model exhibits extinction of both species regardless the choice of initial conditions. We analyze mechanisms of species persistence in the 2-D case and show that the enhancement of persistence is due to a number of different patterns of 2-D dynamics, most of them being impossible in the 1-D space. This demonstrates that 1-D simplification of a 2-D model could seriously mislead us when analyzing the persistence of populations. We discuss the generality of our results for other spatial models and possible applications for the design of natural reserves.

2. The model

We consider 1-D and 2-D dynamics of the following predator–prey system with prey growth damped by the Allee effect (see Owen and Lewis, 2001; Petrovskii et al., 2005a):

\[
\frac{\partial U}{\partial T} = D_1 \nabla^2 U + r U (U - K_0)(K - U) - \frac{UV}{1 + UA},
\]

(1)

\[
\frac{\partial V}{\partial T} = D_2 \nabla^2 V + k \frac{UV}{1 + UA} - mV,
\]

(2)

where \( U, V \) are the densities of prey and predator, respectively; \( D_1, D_2 \) are diffusion coefficients. Influence of the Allee effect on prey growth is parameterized by a polynomial cubic function (Lewis and Kareiva, 1993; Owen and Lewis, 2001), where \( K \) is the carrying capacity and \( K_0 \) is the critical threshold of survival (here we consider the strong Allee effect, \( K_0 < K \)). The trophic response of the predator is assumed to be of Holling type II; \( m \) is the predator mortality, \( k \) is the food utilization coefficient. In both the 1-D and the 2-D cases, we consider species interactions in a fully homogeneous environment.

To reduce the number of parameters we pass to a dimensionless form of equations by introducing \( u = U/K, v = V/(Kk), t = T(Kk\mu), x = X(Kk\mu D_1)^{1/2}, y = Y(Kk\mu D_1)^{1/2} \)

\[
\frac{\partial u}{\partial t} = \nabla^2 u + gu(1 - u) - \frac{uv}{1 + ux},
\]

(3)

\[
\frac{\partial v}{\partial t} = v\nabla^2 v + \frac{uv}{1 + ux} - \delta v,
\]

(4)

where \( u, v \) are dimensionless densities of prey and predator, \( \varepsilon = D_2/D_1 \) is the ratio of diffusion coefficients, for the other parameters we have: \( \alpha = K\mu, \beta = K_0/K, \gamma = rK/(k\mu), \) and \( \delta = m/(Kk\mu) \).

Note that in ecological literature, the term ‘persistence’ has different definitions and meanings. A comprehensive discussion of the topic can be found in Cantrell and Cosner (2003). In particular, the strictest definition is 'the uniform persistence' which implies that any population density (for all non-zero initial conditions) may not decrease below a certain positive number (which depends on the initial condition) for all \( t > 0 \) (Freedman and Moson, 1990). However, this definition cannot be applied to an important category of real populations showing extinction at low densities (e.g. populations subject to a strong Allee effect). In this case, the persistence depends on the initial densities (which should exceed a certain threshold) and is often referred as a 'conditional persistence' (Cantrell and Cosner, 2003).

In this paper, we deal with the conditional persistence of populations, since for any parameter set, the homogeneous state with \( u = v = 0 \) (the extinction state) in the model is always stable. Note that the coexistence of prey and predator without extinction for \( t > 0 \) is possible only when the maximum of the prey density at some points of space is larger than the critical threshold \( \beta \). Thus, in the case that there exist some initial distributions for which the prey density exceeds \( \beta \) for \( t > 0 \), this parameter set will be attributed to the domain of conditional persistence. In the paper, for the sake of brevity, we shall use further the term ‘persistence’ instead of ‘conditional persistence’, by keeping in mind the above-mentioned difference between the conditional and uniform persistence.

A detailed investigation of (3) and (4) in 2-D space becomes prominently more complicated compared to the 1-D case, since even for relatively ‘simple’ (but ecologically meaningful) initial conditions the number of parameters...
characterizing distributions becomes essentially larger. This makes a complete analysis of the parameter space impossible. On the other hand, even a comprehensive analysis of dynamics, engendered by initial distributions of a particular form, is of limited use since utilization of distributions with more complex geometrical shape can reveal new patterns of dynamics. We show below some examples of such a situation. This phenomenon is related to the existence of multiple attractors.

We try to detour the mentioned obstacle regarding the choice of initial conditions. Here, we are more interested in variation of sizes of the domain of persistence in parametric space while increasing space dimension, rather than in a detailed description of all patterns of dynamics. Having this purpose in mind, we have developed an algorithm for estimating the borders for the domain of persistence, applicable both in the 1-D and the 2-D cases (see Appendix A).

3. Results

We performed numerical simulations of (3) and (4) by using the finite-difference method; in most cases, we applied the explicit scheme. The space and time steps were chosen as follows: $\Delta x = 0.25$; $\Delta t = 0.001$ for the 1-D case and $\Delta x = 0.5$; $\Delta t = 0.01$ for the 2-D case. To avoid possible numerical artifacts, we checked modifications in the results while decreasing mesh steps. Moreover, in the 2-D case, a portion of the results was reproduced by using the alternative directions scheme. The size $L$ of the habitat was chosen sufficiently large: $L = 200$ to reduce the influence of the boundaries (in the 2-D case we consider a square habitat $L \times L$). For both dimensionalities, we considered the ‘no-flux’ boundary conditions.

We set the half-saturation density $z$ equal to a certain hypothetical value (here we choose $z = 0.2$) and construct a number of $\beta - \delta$ diagrams showing domains of persistence for different fixed values of $\gamma$ and $\varepsilon$ in both the 1-D and the 2-D cases. First, we assume diffusion coefficients to be equal ($\epsilon = 1$). The case of different diffusion coefficients will be addressed in Section 4. We assume that $\beta < 0.5$ (otherwise invasion is impossible, see Owen and Lewis, 2001) and $\Theta = 1/(1 + z) < \delta$ (otherwise the predator always goes extinct, Petrovskii et al., 2005a). To reveal domains of persistence we applied the algorithm from Appendix A. Technical aspects of construction of domains of persistence both in the 1-D and the 2-D cases are described in detail in Appendix B. We remind the reader that we study the conditional persistence of species.

Fig. 1 shows the persistence domains in the 1-D and 2-D cases built for $\gamma = 3$. The nature of the regions in the diagram is as follows: For domain I, extinction of species always takes place for the non-spatial, 1-D and 2-D spatial cases, regardless the choice of initial conditions. In domain II, persistence becomes possible in the 2-D case, but is impossible in both the 1-D and the non-spatial cases. In domain III, persistence is possible only for the 1-D case and impossible neither for the non-spatial model nor for the 2-D model (here we do not take into account the degenerated 2-D dynamics dependent only on one space coordinate). Domain IV corresponds to coexistence of species for both spatial dimensionalities and extinction in the non-spatial model. Domain V is characterized by possibility of species persistence in the non-spatial case.

Thus, the diagram shows that by adding a second spatial coordinate into the 1-D model (3–4) the total size of the domain of persistence increases, especially for lower values of the critical threshold $\beta$. An important question, however, concerns the robustness of this result to variation of the other model parameters, in particular, to variation of $\gamma$ characterizing the rate of prey growth. By using the same method as for Fig. 1, we built domains of persistence for smaller and larger values of $\gamma$.

Figs. 2a and b show the domains of species persistence for $\gamma = 1$ and 6, respectively. The meaning of domains is the same as in Fig. 1. For small $\gamma$ (Fig. 2a) the difference between the 1-D and the 2-D cases, regarding sizes of domains of persistence, is rather small (i.e. the area of IV is prominently larger than that of II or III). However, for large values of $\gamma$ (Fig. 2b), an increase in 2-D persistence becomes apparent. Fig. 2b demonstrates that adding a second space dimension can lead to a four-fold increase in the total area of domain of space-mediated persistence.

Analysis of Figs. 1 and 2 also demonstrates the tendency that an increase in the rate of prey growth facilitates species extinction in the 1-D case. The total area of domains III and IV decreases when $\gamma$ increases. On the contrary, for the 2-D model, the size of domain of persistence increases when $\gamma$ increases, due to a prominent increase in size of domain II. We discuss an important ecological interpretation of this property in Section 4.

The central question arising when comparing the dynamics of the 1-D and 2-D models is: what are the
mechanisms providing persistence in 2-D space and no persistence in the 1-D space? Our numerical study shows that this phenomenon includes different qualitative and quantitative aspects and suggests that it cannot be reduced to a manifestation of only one pattern of dynamics.

We found that for parameters from domain II (situated near its right-hand border) persistence becomes possible via formation of interacting spiral waves for small values of the critical threshold $\beta$. An example of such dynamics is given in Figs. 3b and c for $\delta = 0.37$, $\beta = 0.1$, $\alpha = 1$, $\gamma = 3$, $\epsilon = 0.2$. Snapshots of prey density are shown (predator density exhibits similar behavior). To obtain the pattern shown in Figs. 3b and c we applied the algorithm from Appendix A (with parameters $\delta_0 = 0.45$; $\delta_1 = 0.37$; $t_0 = 500$; $\tau = 300$ and $a = 10$; $q = 0.2$; $A_1 = 20$; $A_2 = 10$ in (A3, A4)). The snapshot of the prey density at $t = t_0 = 500$ (i.e. the ‘starting’ distribution for decreasing $\delta$) is shown in Fig. 3a. For the sake of convenience, we describe the process after transition to $\delta_1$ in terms of new time unit: $t' = t - (t + t_0)$.

For somewhat smaller $\delta$, formation of spiral waves is hampered. Instead, irregular patches with spiral tips are formed. This situation is shown in Figs. 3d and e for $\delta = 0.23$ (other parameters are the same as in Figs. 3b and c). This figure is obtained by using the same method as in Figs. 3b and c, with the same starting distribution (Fig. 3a). Note that for the parameters from Figs. 3b–e, the corresponding 1-D model exhibits only traveling pulses spreading over space, which does not lead to species establishment (Petrovskii et al., 2005a).

By considering invasion processes with some other initial conditions, one can obtain periodically circular waves for a wide range of parameters from domain II. This pattern can be realized, for example, for the following initial distributions:

\[
u(x, y) = p \text{ if } |x - L/2| \leq \Delta_{11} \text{ and } |y - L/2| \leq \Delta_{12},\]
\[\text{otherwise } u(x, y) = 0,
\]

\[
v(x, y) = q \text{ if } |x - L/2 - a| \leq \Delta_{21} \text{ and } |y - L/2 - b| \leq \Delta_{22} \text{ otherwise } v(x, y) = 0,
\]

where $p$, $q$, $\Delta_{11}$, $\Delta_{12}$, $\Delta_{21}$, $\Delta_{22}$, $a$, $b$ are positive parameters.

Figs. 4a and b show snapshots of prey density obtained from (5) and (6) with $p = 1$, $q = 0.5$, $\Delta_{11} = 20$, $\Delta_{12} = 20$, $\Delta_{21} = 20$, $\Delta_{22} = 20$, $a = 5$, $b = 30$ for $\delta = 0.37$, $\beta = 0.1$, $\epsilon = 1$, $\gamma = 3$, $\alpha = 0.2$. A concentric wave train (target waves) arises from two spiral tips. This example demonstrates the existence of multiple attractors exhibiting persistence in (3) and (4).

With a further decrease in $\delta$ near the left-hand border of domain II ($0 < \beta < 0.3$, Fig. 1), species persistence is possible via interaction of separated patches with irregular shapes of high species density; patches move, merge, disappear, produce new patches, and so on (see Figs. 4c and d for $\delta = 0.205$, other parameters being same as in Fig. 3). This figure is obtained from the distribution in Fig. 3a and applying the same algorithm.

For larger values of $\beta$ (approximately for $0.3 < \beta < 0.35$ for Fig. 1) 2-D species distributions become an ensemble of quasi-stationary patches with immobile centers (patch profiles can oscillate). An example of such a pattern is shown in Figs. 4e and f obtained for $\delta = 0.49$, $\beta = 0.3$. This pattern is obtained like those from Fig. 3 (with $\delta_0 = 0.55$; $\delta_1 = 0.49$, other parameters being the same). Note that similar behavior can also be observed by starting directly from (5–6). In the latter case, smaller number of patches are formed. Here, formation of quasi-stationary patches does not require different diffusion coefficients, i.e. the patterns arise due to a mechanism different from the classical Turing mechanism (cf. Murray, 1989).

Finally, we studied the dynamics corresponding to domain III (Figs. 1 and 2) where 2-D species persistence
Fig. 3. Patterns of 2-D persistence corresponding to extinction in the 1-D system ($\beta = 0.1; \gamma = 3; \varepsilon = 1; \alpha = 0.2$). Only snapshots of prey density are shown. Black and white colors correspond to high and very low species densities, respectively. (a) Spatial distribution which is used as 'starting' distribution to provide the other patterns of the figure. (b), (c) Interacting spiral waves obtained for $\delta = 0.37$. (d), (e) Irregular structures with spiral tips obtained for $\delta = 0.23$. For the sake of convenience, we use the shifted time unit: $t' = t - (\tau + t_0)$ with $t_0 = 500; \tau = 300$. For details, see the text.
Fig. 4. Patterns of 2-D persistence corresponding to extinction in the 1-D system ($\gamma = 3; \varepsilon = 1; \alpha = 0.2$). Only snapshots of prey density are shown. Black and white colors correspond to high and very low species densities, respectively. (a), (b) Periodical generation of concentric rings from interacting spiral ends obtained for $\beta = 0.1, \delta = 0.37$ and initial distributions (5–6) with $p = 1, q = 0.5, A_{11} = 20, A_{12} = 20, A_{21} = 20, A_{22} = 20, a = 5, b = 30$. (c), (d) Interacting patches of irregular form obtained for $\beta = 0.1, \delta = 0.205$ by using a similar method as in Fig. 3. (e), (f) Quasi-stationary patches obtained for $\delta = 0.49, \beta = 0.3$ by using a similar method as in Fig. 3. For the sake of convenience, we use a shifted time unit for (c)–(f): $t' = t - (t + t_0)$ with $t_0 = 500; \tau = 300$. For details see text.
becomes impossible, whereas it is possible for the 1-D case. Numerical simulations show that for this domain, 1-D persistence takes place via formation of quasi-stationary patches (1-D analog of the regime shown in Figs. 4e and f). Thus, for larger values of the threshold \( \beta \), an increase of out-flux of prey through a patch border due to space curvature does not allow persistence of patches, which is possible for 1-D patches.

4. Discussion

In this paper, we show a critical role of dimensionality of space in models of space-mediated persistence of populations. We study the persistence of species subject to the strong Allee effect and consider conditional persistence of those species. We demonstrate that the use of a spatially explicit population models in 1-D and 2-D spaces predicts essentially different results regarding species survival. To the best of our knowledge, this issue has not been addressed yet comprehensively in the current ecological literature.

We show that in the 2-D case, the size of the domain in parametric space, corresponding to space-mediated persistence in the considered model, becomes essentially larger. The population of prey in 2-D space becomes prominently more resistant to extinction than in 1-D space. This is especially true for larger rates of prey growth and when the threshold of survival of prey is not too high. We show that this phenomenon is to be attributed to a number of mechanisms and patterns of 2-D dynamics (see Figs. 3 and 4). Most of these patterns do not suggest 1-D analogs.

Passing from the 1-D to the 2-D space helps us to understand the somewhat paradoxical behavior of the considered predator–prey system (see Petrovskii et al., 2005a). An increase in prey growth rate results in a pronounced decrease in persistence in the 1-D case (cf. Figs. 1 and 2). This phenomenon is somewhat similar to the well known ‘paradox of enrichment’ when an increase in the rate of prey multiplication (via increasing supply of nutrients) leads to destabilization of the system and to a further species extinction (Rosenzweig, 1971; Abrams and Roth, 1994; Petrovskii et al., 2004). In models (3) and (4), this paradox becomes solved when considering the 2-D dynamics. For large \( \gamma \), species survival becomes possible via formation of 2-D patterns (spiral waves and irregular 2-D patches similar to those in Figs. 3d, e, 4c and d), impossible in the 1-D case and the domain of species survival essentially increases in size. This example demonstrates that using the 1-D simplification of a 2-D population model sometimes leads to a wrong conclusion in terms of qualitative behavior of the model.

Although being relatively rare in nature, some ecosystems can be approximately considered as one-dimensional. Among important examples are: patterns of vegetation growing along canals or rivers in dry areas; narrow valleys in long mountains chains. The 1-D model (3–4) can be applied also to plankton in rivers and small steams, after adding the appropriate advection terms and considering processes in a reference frame moving with a constant speed of the current (see Lewis and Kareiva, 1993). Our model predicts an increase in the probability of extinction of species in those systems (for other conditions being equal) compared to ecosystems having a pronounced second dimension.

Our analysis shows that in a 2-D habitat with rectangular borders \( L_1 \times L_2 \) with a large length \( L_1 \) but a narrow width \( L_2 \), the system behavior becomes similar to that of a 1-D model and often leads to species extinction even for parameters belonging to the constructed domain of 2-D persistence. Fig. 5 illustrates such a situation. The snapshots are obtained by using the same method as in Figs. 3d and e (with the same parameter values). The upper row shows snapshots in case of a subcritical width (\( L_2 = 40 \)) of the habitat. Species distribution becomes one-dimensional (see snapshot for \( t = 240 \)) and the species will go extinct. On the contrary, for a supercritical width (\( L_2 = 80 \), the lower row), coexistence of species becomes possible for all time. Note that an exact value of critical width (we found \( L_{2cr} = 50 \) for the given example) slightly depends on initial conditions. Our simulations show, however, that for small values of \( L_2 \), extinction takes place regardless of the choice of initial conditions and persistence will always take place for large \( L_2 \). Note that similar results regarding poor conditions for species survival in long narrow areas was obtained analytically earlier, but only for some single species models (Cantrell and Cosner, 2003) where the species density had a shape of single population patch. Here a supercritical width of the area is necessary to guarantee nonextinction of populations via interactions of moving patches. Note that the existence of a critical size of the 2-D habitat has been found in multi-species models (e.g., Hassell et al., 1991; Comins et al., 1992).

An important ecological application of the above result concerns the design of natural reserves. In particular, it confirms the empirical rule standing that for a reserve having a lengthy shape and small width, species coexistence is more menaced compared to reserves with a more pronounced second dimension (see Diamond, 1975 and references therein). This also shows the importance of spatially explicit models for designing natural reserves. Although these models were severely criticized because of lack of data for their validation (Ruckelshaus et al., 1997; Beissinger and Westphal, 1998; Mooij and DeAngelis, 1999), application of such models becomes useful when considering species interactions in a habitat of a particular geometrical shape (e.g. Matano and Mimura, 1983) which is not always doable with implicit metapopulation models.

All previous results were obtained in the case of equal diffusivities, i.e. for \( \varepsilon = 1 \). We have examined whether this factor is crucial. We studied the following range of \( \varepsilon : 0.2 \leq \varepsilon \leq 3 \). Numerical analysis in the indicated parameter range shows that variation of \( \varepsilon \) does not change the results obtained with \( \varepsilon = 1 \). It confirms that adding a second space direction into the 1-D model leads to a
considerable increase of total size of domain of persistence in the $\beta$-$\delta$ plane (for the sake of brevity we do not demonstrate the corresponding diagrams). As before, enhancing of persistence becomes more pronounced for small $\beta$ and for large $\gamma$. It is to be mentioned that for other parameters being constant, a decrease in $\epsilon$ leads to an increase in size of domain of space-mediated persistence (and a vice versa).
The system we considered here is widely used in ecological modeling (e.g., Lewis and Kareiva, 1993; Bazykin, 1998; Fagan and Bishop, 2000; Fagan et al., 2002; Petrovskii et al., 2002), making our results quite relevant for different ecological applications. An important question, however, is: Can the results form this paper be extended more generally to other special explicit models? Our preliminary analysis of a number of models confirms our expectation regarding essential changing in persistence properties while passing from the 1-D to the 2-D space.

In particular, we found that the obtained results remain valid when the half-saturation constant $x$ is equal to zero and the predation is described by the bilinear Lotka-Volterra term. This fact allows another important interpretation of models (3) and (4), since for $x = 0$ it gives the well known SI model of infectious diseases (Murray, 1989; Petrovskii and Venturino, 2004; Petrovskii et al., 2005b). Moreover, analysis of the more complex SIR model with the susceptible subpopulation subject to the strong Allee effect demonstrates an increase in species persistence to an infectious disease in 2-D space (Petrovskii and Venturino, 2004; Petrovskii et al., 2005b). We should mention, as well, the important results of Matano (1979), where it was shown that for bi-stable reaction-diffusion systems of two and more dimensions there exist stable nonconstant solutions impossible in one-dimensional case. Another example comes from the investigation of competition models in 2-D domains with a nonconvex border. It was shown that for such an environment a coexistence of antagonistic species becomes possible (Matano and Mimura, 1983; Mimura et al., 1991). The 1-D analog of those models would always predict an extinction of antagonistic species becomes possible (Matano and Thomas, 1996).

An interesting issue in the context of the current work would be to investigate how a further transition to the 3-D spatially explicit population models will influence space mediated population’s persistence predicted by the 1-D and the 2-D models. We should note, however, that adding a third (vertical) space coordinate for most ecosystems could not be done in a simple way (i.e., one cannot simply add the corresponding diffusion term). In real ecosystems, the properties of the physical environment become essentially heterogeneous along the vertical direction (e.g., attenuation of light with depth in the ocean), which hampers a simple comparison of models with different space dimensionalities.

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**Appendix A**

Here, we describe an algorithm which we have developed to estimate the borders of domains providing species persistence in model (3–4) both for the 1-D and the 2-D cases. We study the case of conditional persistence of species (see Section 2).

First, we assume that the species establish themselves in the habitat via an invasion process (a joint invasion of both species) and consider the following distributions for $t = 0$:

$$u(x) = 1 \text{ if } |x - L/2| \leq A_1 \text{ otherwise } u(x, 0) = 0, \quad (A1)$$

$$v(x) = v_0 \text{ if } |x - L/2 - x_0| \leq A_2 \text{ otherwise } v(x, 0) = 0,$$  

$$u(x, y) = 1 \text{ if } (x - L/2)^2 + (y - L/2)^2 \leq A_1^2$$

$$\text{otherwise } u(x, y) = 0,$$  

$$v(x, y) = q \text{ if } (x - L/2 - a)^2 + (y - L/2)^2 \leq A_2^2$$

$$\text{otherwise } v(x, y) = 0$$  

in the 1-D case and the 2-D case, respectively.

Here, $v_0, q, A_1, A_2, a, x_0$ are positive parameters; $L$ is the size of the habitat (in 2-D case we consider a square habitat $L \times L$).

For fixed values of $\alpha, \gamma, \epsilon$, we build $\beta$–$\delta$ parametric diagrams showing domains of persistence when starting from (A1–A4). However, this gives us auxiliary diagrams, providing only preliminary information, especially in the 2-D case.

During the second step, we study a further dynamics in a post-invasion period when species have already established themselves (and transient regimes died out). We use the obtained asymptotic dynamics as new initial conditions and vary a model parameter, by trying to enter domains where a direct establishment of species from (A1–A4) was impossible. This has an obvious ecological meaning since it models changes in environmental conditions or evolutionary changes in species fitness. For the sake of simplicity, here we vary only $\delta$

$$\delta(t) = \delta_0 + (\delta_1 - \delta_0)(t - t_0)/\tau \quad \text{if } \quad t_0 < t < \tau + t_0,$$

$$\delta = \delta_1 \quad \text{for } \quad t > \tau + t_0,$$  

where $\delta_1$ and $\delta_0$ are the final and initial values of $\delta$; $\tau$ is the time of transition, $t_0$ is the starting moment for variation of $\delta$ (we take $t_0$ sufficiently large to let the transients die out).

In case when after transition to $\delta_1$, predator–prey coexistence takes place for $t > \tau + t_0$, we consider that this parameter set also belongs to the domain of persistence. We vary $\delta_0$ and $\delta_1$ and add ‘new’ domains where persistence of species becomes possible to the diagrams obtained with (A1)–(A4). A final diagram is obtained by re-unifying all parameter sets exhibiting species persistence no matter how these regimes are obtained. The details
concerning choice of $\delta_0$ can be found in Appendix B when we carry out the described procedure after construction of preliminary diagrams with (A1)–(A4).

Appendix B

Here we apply the algorithm from Appendix A for construction of persistence domains of model (3–4) for the 1-D and the 2-D cases. We consider $\gamma = 3; \epsilon = 1; \alpha = 0.2$.

Fig. 6a shows domains of persistence (the hatched regions) in the 1-D case after invasion of the habitat starting from (A1–A2). All regimes of persistence in the post-invasion period can be divided into 3 main groups (see Petrovskii et al., 2005a for details): irregular (and period-
ical) spatiotemporal oscillations (domain 2); establishment

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Fig. 6. Construction of the domains of persistence in parametric space for predator–prey interactions in (3–4) for the 1-D and the 2-D models ($\gamma = 3; \epsilon = 1; \alpha = 0.2$) by applying the algorithm from Appendix A. For details, see Appendix B.
of homogeneous distributions (domain 3); formation of quasi-stationary patches with immobile centers separated by areas with densities close to zero (domain 4). For domain 1, extinction of both species takes place regardless of the choice of parameters in (A1) and (A2). In Fig. 6a, we also show the borders of the persistence domain in non-spacial (0-D) case. These are: (1) the curve $l$ on the left (the dashed curve, corresponding to disappearance of a stable limit cycle via homoclinic bifurcation, Bazykin, 1998) and the vertical line $\delta = \Theta = 1/(1 + \alpha)$ on the right side.

Our numerical simulations show that neither domains 2 nor 4 increases essentially in size (less than 0.1%) while varying model parameters in a post-invasion period (as described in Appendix A). On the other hand, domain 3, corresponding to homogeneous species distributions, can be enlarged until the whole region of persistence in the 0-D case, by considering homogeneous distributions as initial conditions. We should note, however, that for parameters close to $l$, possibility of persistence via homogeneous distributions is of little ecological use since for heterogeneous perturbations with relatively small (but finite) magnitudes, the distributions become heterogeneous, which, finally, leads to species extinction. The final diagram of persistence in the 1-D case is represented in Fig. 6b (hatched region).

Figs. 6c–f show construction of the diagram of species persistence in the 2-D case. Possibility of a 'direct' establishment of species via invasion from (A3–A4) is shown in Fig. 6c; hatched regions correspond to species establishment in the habitat. The meaning of the numbers characterizing domains is the same as in Fig. 6a. Note, however, that we found that for a fixed set of parameters in domain 4 (near its left border, $0.3 < \beta < 0.4$), two different regimes of quasi-stationary patches with different sizes and exhibiting different temporal dynamics can be obtained, the actual outcome being dependent on initial conditions. Moreover, for domain 4, in a narrow region near its right border, different initial conditions can lead either to quasi-stationary patches or to spatiotemporal oscillations in the whole habitat. In this sense, there is no strict border between domains 4 and 2, since for a small stripe in parameter space there is coexistence between both types of dynamics. Here, however, we do not consider these multi-attractors in detail, since each of them exhibits persistence of both species.

Domain 1 of extinction consists of two regions (1 and $1^*$): one of them (region $1^*$) is situated inside domain 2 and corresponds to propagation of concentric rings of species densities, which finally leads to extinction. Note that the narrow stripe-like band of domain 2, separating domains $1^*$ and 1, corresponds to realization of a patchy spread (see Petrovskii et al., 2002; Morozov et al., 2006 for details).

We test a possibility of species persistence in domain 1 by using asymptotic post-invasion dynamics as new initial conditions. After transients die out, we change the parameter $\delta$ according to (A5). Fig. 6d illustrates schematically the choice of $\delta_0$ and transitions to $\delta_1$ by arrows. The performed numerical experiments show, surprisingly, that for domain $1^*$ species persistence becomes possible when starting from post-invasion distributions of domain 2. Moreover, the choice of the initial value of $\delta_0$ in (A5) is not of that importance for a fixed value of $\beta$. Numerical simulations show that the left hand border of the domain of persistence can be also extended when diminishing $\delta$ (this is shown schematically by small arrows), albeit this expansion is rather small. The result of the fulfilled procedure is shown in Fig. 6e, with $\tau = 300$, $t_0 = 500$ in (A5). The curve $l$ is the border of persistence in non-spacial case. The final diagram of the persistence domain in 2-D model (taking into account possibility of persistence via homogeneous distributions) is represented in Fig. 2f. A use of different values of time of transition $\tau$ (we considered $\tau = 500$ and 0, i.e. instantaneous transition) does not show a further visible increase in size of persistence domain.

References