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Persistence, extinction, and critical patch number for island populations

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Abstract. Sufficient conditions are derived for persistence and extinction of a population inhabiting several islands. Discrete reaction-diffusion population models are analyzed which describe growth and diffusion of a population on a group of islands or a patch environment. A critical patch number is defined as the number of islands below which the population goes extinct on that group of islands. It is shown that population persistence on one island leads to population persistence for the entire archipelago. Both single-species and multi-species models are discussed.

Key words: Persistence — Extinction — Critical patch size — Reaction-diffusion equation — Island biogeography

I. Introduction

The study of island biogeography in a mathematical context began to flourish with the work of MacArthur and Wilson [15, 16]. Much work in this area has centered on the relationship between species number, island area, and distance from the mainland. In this investigation we consider species persistence and extinction behavior as related to the number of islands.

The model analyzed is a discrete version of a continuous reaction-diffusion equation. The continuous model with exponential growth was analyzed by Kierstead and Slobodkin [8] and Skellam [21]. Kierstead and Slobodkin [8] used a reaction-diffusion equation to model the formation of a plankton bloom. They found a critical patch size below which the population dies out and above which the population survives. Since their initial investigation there has been a considerable amount of research on the formation of plankton blooms. A review of many of them can be found in Okubo [19]. The investigations have concentrated on a continuous spatial environment—a model appropriate for oceanic plankton. By considering several islands or patches we extend the notion of a critical patch size to critical patch number, where critical patch number is that number of islands below which the population dies out.

Several basic assumptions are inherent in the island model due to its relationship to the continuous model. Each island provides a suitable habitat for growth and reproduction. Thus we concentrate on the relationship between the island populations and their surrounding environment. Movement between adjacent islands occurs by random diffusion, an assumption which comes from the continuous model. Other types of diffusion are discussed in Sect. IV. Surrounding the group of islands is a region unsuitable for survival. This assumption also comes from the continuous model. A final assumption is that there is no main colonization source; the only source of new members is through birth or movement from another island. This is a reasonable assumption according to DeAngelis et al. [3], since many islands are far from any mainland source and therefore may receive new colonists only from nearby islands. Generalizations of some of these assumptions are discussed in Sect. IV.

The model identification, analysis, and discussion are presented in the following sections. The next section is the model identification. Section III is a presentation of the main results. Section IV is a presentation of several examples, applications, and extensions of the basic model. The concluding section is a discussion of the results.

II. The model

The continuous reaction-diffusion model is described first. The discrete model will be subsequently obtained from the continuous model via an appropriate discretization over the spatial variable. The continuous version is given by the following initial value problem:

$$\begin{aligned} \frac{\partial u}{\partial t} &= uf(u) + D\frac{\partial^2 u}{\partial x^2}, \qquad 0 \leqslant x \leqslant L, \qquad t \geqslant 0 \\ u(x,0) &= g(x), \qquad 0 \leqslant x \leqslant L \\ u(0,t) &= 0 = u(L,t), \qquad t \geqslant 0, \end{aligned} \tag{1}$$

where the function $u(x, t)$ represents the population size at position x and time t. The constant D is positive and $g(x)$ is nonnegative on $0 \leqslant x \leqslant L$. The above model is the one analyzed by Kierstead and Slobodkin [8] and Skellam [21] with exponential growth, $f(u) = r$. In this case the solution can be explicitly determined and is given by:

$$u(x, t) = \sum_{n=1}^{\infty} C_n e^{(r-\lambda_n D)t} \sin(n\pi x/L),$$

where $\lambda_n = (n\pi/L)^2$ and

$$C_n = \frac{2}{L}\int_0^L g(x)\sin(n\pi x/L)\,dx \quad \text{for } n = 1, 2, \ldots .$$

The critical patch size is $L_c = \pi\sqrt{D/r}$. If $L < L_c$, then the population size tends to zero or species extinction, but if $L > L_c$, then there is exponential growth or species persistence.

The discrete model is obtained using a finite difference scheme of (1) over the spatial domain $0 \leqslant x \leqslant L$. For $N+1$ intervals, let $\sum_{i=l}^{N+1} l_i = L$, $x_0 = 0$, $x_1 = l_1$, $x_2 = l_1 + l_2, \ldots, x_{N+1} = \sum_{i=1}^{N+1} l_i = L$, $u(x_i, t) = v_i(t)$, and $g(x_i) = g_i$. The discrete approximation $v_i(t)$ satisfies the following system of ordinary differential equations:

$$\dot{v}_i = v_i f(v_i) + D_{i,i+1}(v_{i+1} - v_i) + D_{i,i-1}(v_{i-1} - v_i)$$
$$v_i(0) = g_i, \qquad i = 1, \ldots, N, \tag{2}$$

where $D_{i,i+1}$, $D_{i,i-1}$, and g_i are positive constants. Notice in model (2) the coefficients $D_{i,i+1}$ and $D_{i,i-1}$ can be unequal. The boundary conditions imply $v_0 = 0 = v_{N+1}$. Thus we consider a total of N islands.

Another method of obtaining the discrete model is via a random walk. Thus frequently the discrete model is taken to be of the form:

$$\dot{v}_i = v_i f(v_i) + \sum_{j=0}^{N+1} D_{ij}(v_j - v_i), \qquad i = 1, \ldots, N, \tag{3}$$

where $D_{ij} = D_{ji}$ (Allen [1, 2], Hastings [6, 7], Levin [11, 12], Namba [18], Yodzis [23]). Model (3) is a generalization of (2) to more complex spatial arrangements of islands. The following analysis considers just the linear arrangement of islands, but extensions to more complex arrangements are discussed in Sect. IV.

III. Main results

We now state the main results in regard to model (2). All of the proofs, for convenience, have been placed in the Appendix.

The following mathematical assumptions and definitions are made for model (2). The *per capita* growth rate $f(v)$ is a sufficiently smooth function such that there exists a unique solution to (2) on $[0, \infty)$. The operations on the vector $V = (v_1, \ldots, v_N)^T$ are component-wise—e.g., $V \geqslant 0$ means $v_i \geqslant 0$, $i = 1, \ldots, N$, $\lim_{t\to\infty} V(t) = 0$ means $\lim_{t\to\infty} v_i(t) = 0$, $i = 1, \ldots, N$, and $\limsup_{t\to\infty} V(t) > 0$ means $\limsup_{t\to\infty} v_i(t) > 0$, $i = 1, \ldots, N$. By species extinction we shall mean $\lim_{t\to\infty} V(t) = 0$ and by species persistence we shall mean $\limsup_{t\to\infty} v_i(t) > 0$ for some i. The proofs of the theorems rely on comparison techniques, therefore $f(v)$ is bounded.

A sufficient condition for species extinction is given in Theorem 1. In addition a critical patch number is defined as that number below which the population goes extinct.

Theorem 1. *Let* $2\underset{\sim}{D} = \min_i\{D_{i,i+1} + D_{i,i-1}\}$ *and* $\hat{D} = \max_i\{D_{i,i+1}, D_{i,i-1}\}$. *If* $\sup_{v\geqslant 0} f(v) = r$ *is positive and*

$$r < 2[\underset{\sim}{D} + \hat{D}\cos(\pi N/(N+1))], \tag{4}$$

then $\lim_{t\to\infty} V(t) = 0$. *The critical patch number is*

$$N_c = \frac{\operatorname{Arc}\cos[(r - 2\underset{\sim}{D})/2\hat{D}]}{\pi - \operatorname{Arc}\cos[(r - 2\underset{\sim}{D})/2\hat{D}]}. \tag{5}$$

Note that if r is nonpositive, inequality (4) is automatically satisfied and the population dies out.

According to Theorem 1 fewer islands than N_c implies extinction. However more islands than N_c doesn't necessarily imply persistence, since inequality (4) is a sufficient but not necessary condition for extinction. We call N_c a critical patch number because N_c is the "best" possible number for all models satisfying the hypotheses of Theorem 1. The exponential growth model with equal diffusion coefficients satisfies Theorem 1 and for this model N_c is a true critical patch number in that fewer patches than N_c implies extinction and more patches than N_c implies persistence (inequality (4) is a necessary and sufficient condition). This case illustrates the similarity between the discrete exponential model and Kierstead and Slobodkin's [8] and Skellam's [21] continuous model.

For fixed values of $\underline{D}$ and $\hat{D}$, the critical patch number is a function of r. It is a decreasing function of r (see Fig. 1); fewer islands are needed for survival as the value of r increases.

Theorem 2 states sufficient conditions for species persistence. For persistence a lower bound on the value of f near zero is needed.

Theorem 2. *Let* $2\bar{D}=\max_i\{D_{i,i+1}+D_{i,i-1}\}$. *If* $\lim_{v\to 0^+} f(v)=s$ *and*

$$s>2\bar{D}, \tag{6}$$

then $\limsup_{t\to\infty} V(t)>0$.

If f is continuous at zero, then inequality (6) can be replaced by $f(0)>2\bar{D}$. The persistence result is stronger than species persistence since the population survives on all islands. This is due to the interconnection of the islands via diffusion. The persistence of the population on one island spreads to all islands. Theorem 3 states this result formally.

Theorem 3. *If* $\lim_{t\to\infty} V(t)$ *exists and* $\lim_{t\to\infty} v_j(t)>0$ *for some* $j\in\{1,\ldots,N\}$, *then* $\lim_{t\to\infty} V(t)>0$.

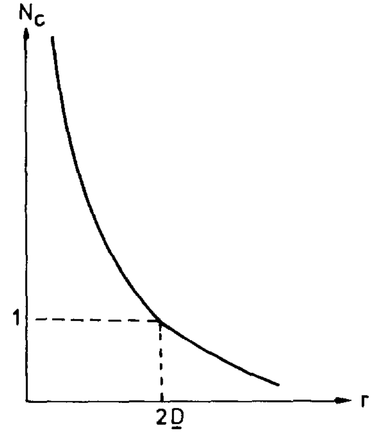

Fig. 1. The critical patch number, N_c, (Eq. (5)), is a decreasing function of r

The conclusion of Theorem 3 illustrates theoretically the importance of spatial considerations to population persistence. For example consider a system of $N-1$ islands, where the population cannot survive. If a persistent population is introduced on another island, the entire system becomes inhabited by the population. This is a case where the interplay between migration and extinction in a spatially heterogeneous environment has a stabilizing effect (May [17]).

The persistence and extinction results for multi-species communities consisting of M species and N islands are stated in Corollary 1. The function v_i^j represents the jth species on the ith island. The system of equations for v_i^j is given below:

$$\dot{v}_i^j = v_i^j f^j(v_i^1, \dots, v_i^M) + D_{i,i+1}^j(v_{i+1}^j - v_i^j) + D_{i,i-1}^j(v_{i-1}^j - v_i^j)$$

$$v_i^j(0) = g_i^j,\ i = 1, \dots, N, \qquad j = 1, \dots, M,$$

where $D_{i,i+1}^j$, $D_{i,i-1}^j$, and g_i^j are positive constants and $v_0^j = v_{N+1}^j = 0$. For notational convenience we denote the M-vector $U = (u^1, \dots, u^M)^T$ and the N-vector $V^j = (v_1^j, \dots, v_N^j)^T$. Thus U is a "species" vector and V^j is an "island" vector.

Corollary 1. *Let* $2\underline{D}^j = \min_i\{D_{i,i+1}^j + D_{i,i-1}^j\}$, $2\bar{D}^j = \max_i\{D_{i,i+1}^j + D_{i,i-1}^j\}$, *and* $\hat{D}^j = \max_i\{D_{i,i+1}^j, D_{i,i-1}^j\}$. *Assume there exist positive constants* r^j *and* s^j *such that* $\sup_{U \geqslant 0} f^j(U) = r^j$ and $\lim_{U \to 0^+} f^j(U) = s^j$. *If*

$$r^j < 2[\underline{D}^j + \hat{D}^j \cos(\pi N/(N+1))], \tag{7}$$

then $\lim_{t \to \infty} V^j(t) = 0$. *If*

$$s^j > 2\bar{D}^j, \tag{8}$$

then for every $i, i \in \{1, \dots, N\}$, *there exists* $k, k \in \{1, \dots, M\}$ *such that* $\limsup_{t \to \infty} v_i^k(t) > 0$.

In other words, if condition (7) or condition (8) is satisfied by the jth species of the multi-species community, either the jth species is eliminated over the entire group of islands or on every island at least one species survives. The extinction result is more straightforward. If inequality (7) is satisfied by all species, then the entire community of islands goes extinct. However even if inequality (8) is satisfied by all species, some species may not persist. It is interesting that we cannot predict which species will survive.

The theorems and corollary can be generalized by assuming the growth functions f and f^j are island dependent—i.e., f_i and f_i^j. Similar results hold if the functions f_i and f_i^j satisfy the assumptions for all islands, $i = 1, \dots, N$.

Theorem 3 can also be stated in terms of the multi-species community, if V is replaced by V^j.

In the next section the results are applied to several examples. Some extensions are also discussed.

IV. Applications and extensions

The results of the theorems and corollary are illustrated by some well-known ecological growth models. In the case of exponential growth, $f(v) = r$, and

$D_{i,i+1} = D_{i,i-1} = D/l^2$, condition (4) is a necessary and sufficient condition for extinction. In this case the linear system has negative eigenvalues if and only if (4) holds. For logistic growth $f(v) = r(1 - v/k)$, $\sup_{v \geq 0} f(v) = r$ and $f(0) = r$. For the spruce budworm growth equation (Ludwig et al. [13]) $f(v) = r(1 - v/k) - \gamma v/(\delta^2 + v^2)$, we also have $\sup_{v \geq 0} f(v) = r$ and $f(0) = r$. Thus if inequality (4) holds, population extinction occurs, but if $r > 2\bar{D}$, population persistence results.

For exponential, logistic, and spruce budworm growth models in the continuous model (1), it has been shown (Ludwig et al. [14]) that if $L < L_c = \pi\sqrt{D/r}$, the population goes extinct, but if $L > L_c$, the population is persistent. For model (2), if the patch number $N < N_c$, the population goes extinct, but if $N > N_c$, the population may be persistent (it is persistent for exponential growth).

Lotka-Volterra competition where $f^j(v^1, \ldots, v^M) = r^j - \sum_{k=1}^M b^{jk} v^k$ is an example where Corollary 1 is applicable. In this case $\sup_{U \geq 0} f^j(U) = r^j$ and $f^j(0) = r^j$.

In addition to these theoretical applications, an experimental study conducted by Fahrig and Merriam [4] also support our basic conclusion that more patches increase population survival. They studied white-footed mice inhabiting patches of forests and found that mouse populations in isolated woodlots (one patch) have lower growth rates and are more likely to become extinct than those in connected woodlots (more than one patch).

The results can be generalized to more complex arrangements of islands. In particular if the islands are arranged in a rectangular pattern, the finite difference scheme can be extended to these cases. Consider a rectangular pattern of size $N \times M$ where the NM-vector is given by

$$V = (v_{11}, v_{12}, \ldots, v_{1M}, v_{21}, \ldots, v_{2M}, \ldots, v_{N1}, \ldots, v_{NM})^T.$$

For the extinction result we comapre $\dot{V} \leq CV$, where C is an $NM \times NM$ symmetric block tridiagonal matrix. Matrix C can be expressed very simply using direct products, $C = I_N \otimes A + B \otimes I_M$, where A and B are tridiagonal matrices of size $M \times M$ and $N \times N$, respectively, and I_N and I_M are the $N \times N$ and $M \times M$ identity matrices. The NM eigenvalues of C are of the form $\lambda_i + u_j$, $i = 1, \ldots, M$, $j = 1, \ldots, N$, where λ_i are the eigenvalues of A and u_j are the eigenvalues of B (Lancaster [10]). The eigenvalues of A and B can be determined via the lemma given in the Appendix. Extinction results if all of the eigenvalues $\lambda_i + u_j$, are negative. For the persistence result we need s ($\lim_{v \to 0^+} f(v) = s$) to be larger than $4\bar{D}$ where $4\bar{D} = \max_{i,j}\{D_{i,i+1;j} + D_{i,i-1;j} + D_{i;j,j+1} + D_{i;j,j-1}\}$. Any island population can move between a maximum of four adjacent islands, thus the diffusion coefficients given in the expression above are representative of that diffusion.

Some other arrangements of islands are analyzed by Othmer and Scriven [20], where they consider the linear stability of a network of intercommunicating cells. However the populations and islands in their analysis correspond to chemical substances and cells. Since our results depend on comparison with a linear system, the sufficient conditions for extinction (Theorem 1 and Corollary 1) follow from their linear analysis.

Movement by random diffusion is realistic for oceanic plankton, but not for more highly developed organisms, except as a first approximation. Other types of movement such as biased diffusion (Gurney and Nisbet [5]), where movement occurs due to overcrowding, is more realistic. In the discrete model, biased diffusion can be modelled as follows: $D_{i,i+1}(v_{i+1}^2 - v_i^2) + D_{i,i-1}(v_{i-1}^2 - v_i^2)$, (Allen [2]). The persistence result of Theorem 2 is applicable if condition (6) is replaced by $\lim_{v \to 0^+} f(v)/v > 2\bar{D}$. In general persistence of the population is enhanced by biased diffusion (Allen [2]).

The zero boundary conditions are also a limiting assumption. Other types such as zero flux boundary conditions tend to increase population persistence (Allen [1]).

V. Discussion

Sufficient conditions are derived for persistence and extinction of a population inhabiting several islands. The extinction condition depends upon the critical patch number (Eq. (5)).

The relationship between the critical patch size of model (1), $L_c = \pi\sqrt{D/r}$ and the critical patch number of model (2), N_c (Eq. (5)), can be illustrated for exponential growth, $f(v) = r$ and equal diffusion coefficients, $D_{i,i+1} = D_{i,i-1} = D/l^2$. The critical patch size L_c is generally interpreted as the size at which the rate of growth within a patch is equal to the rate of loss due to diffusion into the surroundings (Okubo [19]). An analogous explanation is valid for the critical patch number. For $N_c = 1$, $r = 2\underline{D} = 2D/l^2$ (Fig. 1), the rate of growth is approximately equal to the rate of loss. If $N_c > 1$, $(r < 2\underline{D})$ and if there are fewer islands than N_c, population extinction results (Theorem 1). On the other hand, if $N_c < 1 (r > 2\underline{D})$, the population is persistent on just one island.

The connection of the islands via diffusion is important to population persistence. The presence of a persistent population on one island can lead to persistence on all of the islands (Theorem 3).

The present analysis introduces another aspect into the study of island biogeography. In addition to species number, island area, and distance from the mainland, the study of island biogeography should include the number of habitable islands, especially if the islands are relatively isolated from the mainland.

Appendix

We state a lemma and give the proofs of Theorem 1, 2, 3, and Corollary 1.

Lemma. The $N \times N$ tridiagonal matrix,

$$A = \begin{bmatrix} \alpha & \beta & & & & 0 \\ \beta & \alpha \cdot & & & & \\ & \cdot & \cdot & \cdot & & \\ & & \cdot & \cdot & \cdot & \\ & & & \cdot\,\alpha & & \beta \\ 0 & & & \beta & & \alpha \end{bmatrix} \tag{9}$$

has N distinct real eigenvalues, $\lambda_k = \alpha - 2\beta \cos(\pi k/(N+1))$, $k = 1, \ldots, N$.

For the particular matrix A the form of the eigenvalues are well known (see for example Svirezhev and Logofet [22]).

Proof of Theorem 1. Note that the assumptions on f and the fact that (2) is an autonomous system with positive initial conditions imply the solutions $v_i(t)$ exist, are unique, and positive for all $t \geq 0$.

The proof of the theorem requires a comparison principle. Since $f(v) \leq r$ the following inequalities hold for $\dot{v}_i$:

$$\dot{v}_i < \alpha v_i + \beta(v_{i-1} + v_{i+1}), \qquad i = 1, \ldots, N, \tag{10}$$

where $\alpha = r - 2\underline{D}$ and $\beta = \hat{D}$. The comparison system $\dot{W} = AW$, where $W = (w_1, \ldots, w_N)^T$ and A is given in (9) is quasi-monotone nondecreasing—i.e., the off-diagonal elements of A are nonnegative. Lakshmikantham and Leela [9] have shown that the vector solutions $V(t)$ and $W(t)$ must also satisfy the inequality given by (10), thus $V(t) < W(t)$, $t > 0$. Since all of the eigenvalues of A are negative if and only if (4) holds, $W(t)$ tends to zero, hence $V(t)$ tends to zero.

Proof of Theorem 2. We assume for purposes of contradiction that $\lim_{t\to\infty} v_i(t) = 0$ for some $i, i \in \{1, \ldots, N\}$. Recall that $v_i(t) > 0$ for $t \geq 0$. Let $\varepsilon_1 > 0$ be given such that $s - \varepsilon_1 > 2\bar{D}$, then there exists $\varepsilon_2 > 0$ such that $0 < v < \varepsilon_2$ implies $f(v) > s - \varepsilon_1$. Since $\lim_{t\to\infty} v_i(t) = 0$, there exists a $T > 0$ such that $0 < v_i(t) < \varepsilon_2$ for $t \geq T$. Thus we have $\dot{v}_i > v_i(s - \varepsilon_1 - 2\bar{D})$ which implies $v_i(t) > v_i(T)\exp(s - \varepsilon_1 - 2\bar{D})(t - T)$ for $t \geq T$, contradicting the original assumption.

Proof of Theorem 3. Consider the $(j+1)$st or $(j-1)$st island. Without loss of generality we consider the $(j+1)$st. The following differential inequality is satisfied by $\dot{v}_{j+1}$:

$$\dot{v}_{j+1} \geq v_{j+1}[f(v_{j+1}) - D_{j+1,j+2} - D_{j+1,j}] + D_{j+1,j}v_j. \tag{11}$$

For purposes of contradiction assume $\lim_{t\to\infty} v_{j+1}(t) = 0$. Choose an increasing sequence $\{t_k\}_{k=1}^{\infty}$, where $\lim_{k\to\infty} t_k = \infty$ and such that $\lim_{k\to\infty} v_{j+1}(t_k) = 0$ and $\dot{v}_{j+1}(t_k) < 0$. For t sufficiently large $(t > T)$, $v_{j+1}(T)$ is sufficiently small such that the right-hand side of (11) is positive. Hence $\dot{v}_{j+1}(t) \geq 0$, for $t > T$. This contradicts the choice of the sequence $\{t_k\}$. Thus $\lim_{t\to\infty} v_{j+1}(t) > 0$.

We have shown that any island adjacent to an island with a persistent population has a persistent population. Hence all islands have persistent populations: $\lim_{t\to\infty} V(t) > 0$.

Proof of Corollary 1. Since $f^j(v^1, \ldots, v^M) \leq r^j$ we have the differential inequality $\dot{V}^j \leq A^jV^j$, where

$$A^j = \begin{bmatrix} \alpha^j & \beta^j & & 0 \\ \beta^j & \alpha^j & \ddots & \\ & \ddots & \ddots & \ddots \\ & & \alpha^j & \beta^j \\ 0 & & \beta^j & \alpha^j \end{bmatrix}$$

is a tridiagonal matrix with $\alpha^j = r^j - 2\underline{D}^j$ and $\beta^j = \hat{D}^j$. As in the proof of Theorem 1, the solution of the comparison system $\dot{W}^j = A^jW^j$ tends to zero if and only if (7) holds. By the comparison principle, $V^j(t)$ also tends to zero.

The second part of the proof is by contradiction. Assume $\lim_{t\to\infty} v_i^k(t) = 0$ for every $k = 1, \ldots, M$. As in the proof of Theorem 2 there exist $T > 0$ and $\varepsilon_1 > 0$ such that $v_i^j(t) > v_i^j(T)\exp(s^j - \varepsilon_1 - 2\bar{D}^j)(t - T)$ for $t \geq T$, a contradiction.

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