Relative nonlinearity and permanence

Yun Kang [a,*], Peter Chesson [b]

[a] *Applied Sciences and Mathematics, Arizona State University, Mesa, AZ 85212, USA*
[b] *Department of Ecology and Evolutionary Biology, University of Arizona, P.O. Box 210088, Tucson, AZ 85721, USA*

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ABSTRACT

We modify the commonly used invasibility concept for coexistence of species to the stronger concept of uniform invasibility. For two-species discrete-time competition and predator–prey models, we use this concept to find broad easily checked sufficient conditions for the rigorous concept of permanent coexistence. With these results, permanent coexistence becomes a tractable concept for many discrete-time population models. To understand how these conditions apply to nonpoint attractors, we generalize the concept of relative nonlinearity and use it to show how population fluctuations affect the long-term low-density growth rate ("the invasion rate") of a species when it is invading the system consisting of the other species ("the resident") at a single-species attractor. The concept of relative nonlinearity defines circumstances when this invasion rate is increased or decreased by resident population fluctuations arising from a nonpoint attractor. The presence and sign of relative nonlinearity is easily checked in models of interacting species. When relative nonlinearity is zero or positive, fluctuations cannot decrease the invasion rate. It follows that permanence is then determined by invasibility of the resident's fixed points. However, when relative nonlinearity is negative, invasibility, and hence permanent coexistence, can be undermined by resident population fluctuations. These results are illustrated with specific two-species competition and predator–prey models of generic forms.

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1. Introduction

Determining when competing species coexist in ecological models is a key issue in theoretical ecology. A classical focus on equilibrium led to much emphasis on conditions for global and local stability of equilibria that allow coexistence of interacting species (May, 1974). A more recent appreciation of the presence and importance of population fluctuations, both in natural systems and in dynamical models, has led to a need to understand species coexistence in models that feature persistent population fluctuations. In deterministic models, this need dates from the seminal work on species coexistence by Armstrong and McGehee (1980), and in stochastic models from the preliminary studies of May (1974) and more rigorous approaches of Turelli (1981) and Chesson and Warner (1981).

Most early studies defined coexistence in terms of the invasibility criterion, which requires each species to be able to increase from low density in the presence of the rest of the community (Armstrong and McGehee, 1980; Turelli, 1981). To apply this criterion, each species is set in turn at zero density, where it is called an

invader, while the other species are unconstrained and are called residents. The long-term growth rate of each species as an invader is evaluated, and the invasibility criterion is satisfied if these growth rates are positive. Commonly, the invasibility criterion has been defined for systems of competing species. There has been no comparable approach for predator–prey models, limiting studies of these systems. Here we fill this gap by generalizing the invasibility criterion to predator–prey models. For both systems of competing species and predator–prey systems, a critical question is whether this invasibility criterion is a satisfactory condition for long-term coexistence (Chesson and Ellner, 1989; Hofbauer and Sigmund, 1998). For deterministic models, the idea of permanent coexistence, which guarantees convergence on an interior attractor from any strictly positive initial conditions, is regarded as a strong form of coexistence. However, permanence has not been widely used in population models due to the perception that it is difficult to check. To ameliorate this problem, we develop criteria for invasibility to imply permanence in two-species competition and predator–prey models.

Permanence of dynamical systems has been studied by many researchers using Lyapunov exponents (Schreiber, 2000; Garay and Hofbauer, 2003; Salceanu and Smith, 2009a,b) and average Lyapunov functions (Garay and Hofbauer, 2003; Kon, 2004). Garay and Hofbauer (2003) and Schreiber (2000) have used Lyapunov exponents and the notions of unsaturated invariant sets (compact invariant repelling sets) and measures for Kolmogorov-type

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* Corresponding author.
 E-mail addresses: yun.kang@asu.edu (Y. Kang), pchesson@u.arizona.edu (P. Chesson).

systems. Salceanu and Smith (2009a,b) use Lyapunov exponents to give sufficient conditions for uniform persistence for a large class of dissipative discrete-time dynamical systems on the positive orthant of R^n with the property that a nontrivial compact invariant set exists on a boundary hyperplane. Kon (2004) uses an average Liapunov function to study permanence of discrete-time two-species systems. He showed that the ability of an invader to increase when the resident is at an equilibrium point is sufficient for permanence under certain convexity and concavity conditions on the growth rates of the species. In this paper, we define an average Lyapunov function in terms of the time average of the invader growth rate (the long-term low-density growth rate, or invasion rate), thus connecting invasibility concepts to permanence. We are then able to give a sufficient condition for permanence in discrete-time two-species systems in terms of the *uniform invasibility criterion*, a strengthening of the standard invasibility criterion, which we define in Section 2. We make use of the concept of relative nonlinearity (Chesson, 1994) for discrete-time two-species models. This concept allows us to fully characterize the effects of nonlinearities in population growth functions, which are of major significance in the presence of nonpoint attractors, as discussed below. We are then able to extend Kon's (2004) results beyond convexity and concavity conditions to arbitrary nonlinearities. Moreover, our sufficient condition for permanence is very easy to test for a discrete-time two-species system.

The growth rates of two species are relatively nonlinear if the growth rate of one species is a nonlinear function of the growth rate of the other (Chesson, 1994). Jensen's inequality applied to average population growth rates then means that the two species will be differentially affected by fluctuating dynamics (Armstrong and McGehee, 1980; Alder, 1990; Chesson, 1994; Abrams and Holt, 2002), modifying their ability to coexist. In the present application, we use relative nonlinearity to define when long-term invader growth rates are greater when the resident is on a nonpoint attractor rather than a point attractor. To do this, we generalize the usual concept of relative nonlinearity. Originally, one nonlinear relationship between two species growth rates was used for all densities of the species. Here, we apply the concept between an invader and a resident, which means that there is a different nonlinear relationship for each invader–resident scenario. We further generalize the concept of relative nonlinearity to consider not just competitive interactions but also predator–prey interactions.

The structure of the rest paper is organized as follows: we first introduce the system and the fundamental persistence concepts (Section 2). We then demonstrate a sufficient condition for permanence for a general discrete-time two-species system in terms of the uniform invasibility criterion (Section 3). Relative nonlinearity is defined and used to derive a sufficient condition for invasibility. These results are then combined with those in Section 3 to obtain a simple sufficient condition for permanence showing when conditions at equilibrium are sufficient to define permanence, and when resident population fluctuations lead to modifications of these conditions (Section 4). We then generalize the idea of relative nonlinearity to predator–prey relationships and show how this allows permanence to be proved from invasion conditions in predator–prey systems (Section 5). Finally (Section 6), we apply our results to specific competition and prey–predator models. These applications include an example showing how fluctuations in the resident species can prevent invasion and hence permanent coexistence. We conclude with a discussion of the broader implications and prospectus for future work in this area (Section 7).

2. Model and definitions

Let x_t and y_t denote the population sizes of the two species, called species x and y respectively, in generation t. Their dynamics

over time are specified by the difference equations

$$x_{t+1} = x_t f(x_t, y_t) \tag{1}$$

$$y_{t+1} = y_t g(x_t, y_t) \tag{2}$$

where f and g, the finite rates of increase, are positive twice continuously differentiable functions of x and y. Throughout, our interest is when x and y coexist with each other in some reasonable sense. Permanence, which is a strong sense of coexistence, is our main focus. To proceed, we need to define coexistence in the language of permanence theory of nonlinear dynamic systems, which provides a mathematical framework for investigating long-term species survival where species densities may vary in any way (e.g. equilibrium, cycles, chaos), with the persistence requirement being that the species densities do not remain too close to the boundary (zero density) of the state space.

For species x and y interacting with each other in an ecological community, we say that they coexist in the sense of permanence if and only if there exist positive constants $b < B$, such that for any initial condition $x_0 > 0, y_0 > 0$,

$$b \leq \liminf_{t \to \infty} \min\{x_t, y_t\} \leq \limsup_{t \to \infty} \max\{x_t, y_t\} \leq B. \tag{3}$$

This is equivalent to saying that the system (1)–(2) is permanent in dynamical systems theory. In the rest of this paper, when we say the system (1) and (2) is "permanent" we mean that the two species coexist in this sense of permanence, i.e. the populations of the two species are uniformly bounded both from above and below eventually. One half of this condition is boundedness from above, which is generally much easier to prove than boundedness from below. As a consequence, it is often proved separately, or simply assumed, in discussions of permanence. For this reason, it is given a name in its own right, viz dissipativity. This concept also deserves a formal defintion as we shall use it much. Thus, we say that the system (1) and (2) is dissipative if there exists a positive constant B, such that for any initial state, $x_0, y_0 \geq 0$,

$$\limsup_{t \to \infty} \max\{x_t, y_t\} \leq B.$$

Note that dissipativity is stronger than the boundedness from above in (3) because the initial conditions for dissipativity allow one (or trivially both) species to be zero.

To define the *uniform invasibility criterion*, we need to consider the dynamics of each species alone. In the language of invasibility analysis, these are the single-species resident states. If species y is absent, then we have

$$x_{t+1} = x_t f(x_t, 0). \tag{4}$$

Similarly, when species y is a resident and x is absent, we have

$$y_{t+1} = y_t g(0, y_t). \tag{5}$$

We use the notation x^*, y^* for the equilibrium population sizes of the two species considered separately, as in (4) and (5). The quantity $\ln(x_{t+1}/x_t)$, which we denote as $r_x(x_t, y_t)$, is a suitable definition of the per capita growth rate of species x from time t to time $t + 1$ for the discrete-time case. It is given as

$$r_x(x_t, y_t) = F(x_t, y_t) = \ln f(x_t, y_t). \tag{6}$$

Note that this definition implies that F has the same monotonicity as f. The average growth rate of species x from time 0 to time t, with the initial state (x_0, y_0), is

$$r_x^t(x_0, y_0) = \frac{\sum_{i=0}^{t-1} r_x(x_i, y_i)}{t} = \frac{\ln\left(\prod_{i=0}^{t-1} f(x_i, y_i)\right)}{t}. \tag{7}$$

Since the lim sup of the sequence $\{r_x^t(x_0, y_0)\}_{t=0}^{\infty}$ always exists, we can define the long-term growth rate as this superior limit with the notation

$$\check{r}_x(x_0, y_0) = \limsup_{t \to \infty} r_x^t(x_0, y_0). \qquad (8)$$

If the ordinary limit of $r_x^t(x_0, y_0)$ exists, then we can define the long-term growth rate as

$$\bar{r}_x(x_0, y_0) = \lim_{t \to \infty} r_x^t(x_0, y_0). \qquad (9)$$

Similarly, we can define $r_y(x_t, y_t)$ as the per capita growth rate of species y at (x_t, y_t) with corresponding definitions of the quantities defined above in terms of species x. The quantities $\check{r}_x(0, y_0)$ and $\check{r}_y(x_0, 0)$ (or, $\bar{r}_x(0, y_0)$ and $\bar{r}_y(x_0, 0)$ if the limits exist) give the average invasion speed of the invader (Rand et al., 1994). We use these invasion rates to define the invasibility criterion. We use here a stronger sense of invasibility (uniform invasibility) than is commonly used in the ecological literature, as discussed below. This stronger sense of invasibility is needed to prove permanence.

Using the notation above, we define that the system (1)–(2) is uniformly mutually invasible if

A1: $\bar{r}_x(x_0, 0) = 0$ for all $x_0 > 0$ and $\check{r}_y(x_0, 0) > 0$ for all $x_0 \geq 0$.
A2: $\bar{r}_y(0, y_0) = 0$ for all $y_0 > 0$ and $\check{r}_x(0, y_0) > 0$ for all $y_0 \geq 0$.

Condition **A1** implies that when species x is a resident and species y is an invader, the long term growth rate of species x should be zero, i.e., for all $x_0 > 0, \bar{r}_x(x_0, 0) = 0$. If species y can successfully invade, then the supremum growth rate $\check{r}_y$ (shorthand for $\check{r}_y(x_0, y_0)$) should be positive when y is rare, i.e. $\check{r}_y > 0$ for all $x_0 \geq 0$ and $y_0 = 0$. Here, $\check{r}_y$ is the external Lyapunov exponent (Ferriere and Gatto, 1995), which gives the invasion speed of species y. Condition **A2** implies the same situation when species y is a resident and species x is an invader.

The requirements $\check{r}_y(x_0, 0) > 0, \check{r}_x(0, y_0) > 0$ for all $x_0, y_0 \geq 0$, are critical for proving permanence of the system (1)–(2), i.e., all the attractors on the x- and y-axes must have positive external Lyapunov exponents. Positive invasion rates for only some resident initial values, x_0 and y_0, are not sufficient for permanence (Ferriere and Gatto, 1995). When the limits of the sequences $\{r_i^t\}_{t=0}^{\infty}, i = x, y$ exist, the uniform invasibility criterion can be restated as

HOA1: $\bar{r}_x(x_0, 0) = 0$ for all $x_0 > 0$ and $\bar{r}_y(x_0, 0) > 0$ for all $x_0 \geq 0$.
HOA2: $\bar{r}_y(0, y_0) = 0$ for all $y_0 > 0$ and $\bar{r}_x(0, y_0) > 0$ for all $y_0 \geq 0$.

In general, it cannot be guaranteed that the system (1)–(2) will have the requirements for **HOA1** and **HOA2** for all resident initial conditions. Even if the system (1)–(2) satisfies other conditions for ergodicity such as requiring the resident dynamics to be given by *S-unimodal* maps (Thunberg, 2001), e.g., Ricker's models and Hassell's models (de Melo and van Strien, 1993; Thunberg, 2001; Avila et al., 2003), all that is assured is that the average growth rate $\bar{r}_i(x_0, y_0), i = x, y$ exists for *almost every* initial state (i.e. excepting a set of Lebsgue measure zero). In this paper, we are able to find a simple sufficient condition for permanence of the system (1)–(2) that does not require a check for each initial state, which makes the concept of permanence tractable in practice.

When the invasibility criterion is applied in ecological models for fluctuating populations, it is in a weaker form than is given here. Rather than insisting that $\bar{r}_y(x_0, 0) > 0$ for all $x_0 \geq 0$ and $\bar{r}_x(0, y_0) > 0$ for all $y_0 \geq 0$, initial x_0 and y_0 values from unstable invariant sets are ignored. Commonly it is assumed that an ergodic attractor exists that is the ω limit set of almost all initial values for each species as a resident. These invasion rates are evaluated by simulation for the resident on this attractor to the extent that can be determined by simulation methods. As we shall see later, quite apart of any inaccuracy of simulation, this definition of invasibility may hold in many important cases where the permanence criterion is not satisfied. Thus, we refer to the definition of invasibility used here as "uniform invasibility" to distinguish it from the definition more commonly used in ecological literature. For simplicity, however, we use "invasibility" below when in fact we mean "uniform invasibility".

3. Invasibility criterion and permanence

The uniform invasibility criterion **A1** and **A2** for two species coexistence requires each species to be able to increase from low density in the presence of the other species. The quantities $\bar{r}_i(x_0, y_0), i = x, y$, when they exist, or more generally, $\check{r}_i(x_0, y_0)$, $i = x, y$ when they do not, are the long-term per capita growth rates of species x and y, which can be used to quantify species coexistence (Chesson, 1994). In this section, we show that if the long-term per capita growth rates of both species x and y in the dissipative system (1)–(2) satisfy the uniform invasibility criterion then these two species coexist.

Theorem 3.1. *Assume that the system* (1)–(2) *is dissipative. Then if the invasibility criterion* **A1** *and* **A2** *holds, it is permanent.*

Note that the uniform invasibility criterion **A1** and **A2** implies that the invader y (or x) can invade the resident species x (or y) with the positive invasion rates $\check{r}_y$ (or $\check{r}_x$), which are positive external (normal) Lyapunov exponents. Since the system is dissipative, the theorem follows from Theorem 2.2 of Hutson (1984) by defining a Lynaponov function $P(x, y) = xy$. The connection with invasibility is appreciated when it is noted that the log of the ratio $P(x_t, y_t)/P(x_0, y_0)$ equals $r_x^t(x_0, y_0) + r_y^t(x_0, y_0)$, which is evaluated in the limit as $x_0 y_0$ goes to zero, corresponding to each invasion scenario. The supremum over t of the result needs to be positive for permanence, which is guaranteed by uniform invasibility. Our Theorem 3.1 shows that the uniform invasibility criterion is a sufficient condition for the permanence of the system (1)–(2) when it is dissipative. This result is similar to Theorem 3.1 of Kon (2004), but defines the invasion growth rate explicitly for connection with uniform invasibility. Note, that for this theorem, differentiability conditions on f and g are not necessary. It is sufficient for these functions to be continuous.

Theorem 3.1 ensures that invasibility implies permanence of dissipative systems. Beyond the requirement that invaders have positive invasion rates, the use of this theorem requires two other issues to be resolved. First resident long-term growth rates must be zero, and second the system must be dissipative. We now demonstrate easily established circumstances in which these two issues are satisfied, leaving only invasion rates to be checked in application of the theorem. We first state the full set of conditions defining these circumstances.

Assume that the system (1)–(2) satisfies the following conditions

C1: $f(0, 0) > 1, g(0, 0) > 1$ and $f(x, y) > 0, g(x, y) > 0$ for any $x > 0, y > 0$.
C2: $\lim_{x \to \infty} f(x, 0) = a_1 < 1$ and $\lim_{y \to \infty} g(0, y) = a_2 < 1$.
C3: For boundary equilibria $(x^*, 0)$ and $(0, y^*)$ with $x^* > 0, y^* > 0, f(0, y^*) > 1$ and $g(x^*, 0) > 1$.
C4: All $\frac{\partial f(x, 0)}{\partial x}, \frac{\partial f(x, y)}{\partial y}, \frac{\partial g(x, y)}{\partial x}$ and $\frac{\partial g(0, y)}{\partial y}$ are negative for all $(x, y) \in [0, \infty) \times [0, \infty)$.

Condition **C1** guarantees that the populations of species x and y will move away from the origin $(0, 0)$. Condition **C2** implies that both species x and y have sufficient intraspecific competition to drive their finite rates of increase below 1 at high abundances, which keeps their populations bounded in the single-species state. Condition **C3** ensures that both species x and y have positive growth rates as invaders at the resident equilibrium. The last condition **C4** implies that both species x and y suffer intraspecific and interspecific competition, and also that the resident equilibria of **C3** are unique. Condition **C4**, together with **C2**, ensures dissipativity. In addition, this last condition implies that both functions $f(x, 0)$ and $g(0, y)$ have inverses. We do not need all of these conditions for the individual results, but in general it is obvious which conditions are needed for which results, and we do not remark on this further.

The formal results below are proved in Appendix B. Here we merely provide a sketch of the argument.

To prove that the resident long-term growth rates $\bar{r}_x(x, 0)$ and $\bar{r}_y(0, y)$ are zero, we introduce the single-species model

$$x_{t+1} = x_t f(x_t),$$

corresponding to the resident condition for each species. Then we have the following result.

Lemma 3.1 (*Permanence in the Single-species Case*). *Let $x_{t+1} = x_t f(x_t)$ where the map $f : [0, \infty) \to [0, \infty)$ is differentiable. If*

(a) $f(x) > 0$ *for all $x > 0$ with $f(0) > 1$ and*
(b) $\lim_{x \to \infty} f(x) \leq a_1 < 1$.

Then x_t is bounded from both infinity and zero by fixed constants, for t large enough. Hence, it is permanent in $\{x : x > 0\}$. Moreover,

$$\bar{r}_x(x_0) = 0 \quad \text{for all } x_0 > 0.$$

The proof of this lemma is given in Appendix B. Briefly, it involves noting that with $f(0) > 1$, x_t must grow from low density, and continuity of the map prevents it from falling below a certain minimum positive value from high density. Hence, it bounded from below by a fixed constant for t large enough, for each x_0. Boundedness from above follows similarly. Together, these results give permanence. This boundedness guarantees that $(\ln x_t - \ln x_0)/t$ converges to 0 as t converges to infinity. Because this quantity is simply the time average of $r_x(x_t)$, we see that

$$\bar{r}_x(x_0) = 0 \quad \text{for all } x_0 > 0.$$

Corollary 3.1 (*Average growth rates of competition models*). *If the system (1)–(2) satisfies Conditions **C1–C4**, then*

$$\bar{r}_x(x_0, 0) = 0 \quad \text{and} \quad \bar{r}_y(0, y_0) = 0 \quad \text{for all } x_0 \geq 0, y_0 \geq 0.$$

Proof. Since the system (1)–(2) satisfies Condition **C1–C4**, each species in its resident state satisfies the conditions for Lemma 3.1. Hence the statement holds. □

Now we are able to show the system is dissipative if it satisfies Conditions **C1–C4** by applying results in Lemma 3.1 and its corollary.

Lemma 3.2 (*Dissipative*). *If the system (1)–(2) satisfies Conditions **C1–C4**, then it is dissipative.*

The proof is given in Appendix B by using the fact that the population of species x cannot be greater than the population when its competitor y is absent, due to interspecific competition, i.e. $\partial f(x, y)/\partial y < 0$. Therefore, if the population of a resident species is bounded without its competitor present in the community, then its population must be bounded when the competitor is in the community. Applying the same reasoning for y in the presence of x, the system is shown to be dissipative.

4. Relative nonlinearity

In the previous section, we showed that the uniform invasibilty criterion **A1** and **A2** is a sufficient condition for the permanence of the dissipative system (1)–(2). In this section, we introduce the concept of the relative nonlinearity, which allows us to answer the question of when fluctuations have a critical role in species coexistence. Moreover, using this concept we show how permanence can be demonstrated quite easily in a broad range of situations. However, we are not able cover all cases that arise commonly in practice, but we are able to remove the concept of permanence from a mere theoretical possibility when populations fluctuate to a concept that does have serious practical application.

The term "relative nonlinearity" is normally used to refer to a species coexistence mechanism that results from different species having different nonlinear responses to competition together with fluctuations in time or space in the intensity of competition (Chesson, 1994, 2000). However, these factors need not always have a positive effect on coexistence, i.e., depending on the circumstances, they might undermine coexistence (Chesson, 2000). Here we consider both positive and negative effects of relative nonlinearity on species coexistence.

Assume that $F(x, 0)$ and $G(0, y)$ of the system (1)–(2) have inverse functions for the domains $x > 0, y > 0$. These functions are denoted by $F^{-1}(r_x, 0)$ and $G^{-1}(0, r_y)$. Denote by F_x and F_{xx}, and G_y and G_{yy}, the first and second derivatives respectively of F and G with respect to x and y. In addition, assume that $F_x(x, 0)$ and $G_y(0, y)$ are not equal to 0 for any nonnegative x or y. We measure the nonlinearity of $F(x, y)$ with respect to x and y as

$$\tau_x^F = \frac{F_{xx}(x, 0)}{F_x(x, 0)} \quad \text{and} \quad \tau_y^F = \frac{F_{yy}(0, y)}{F_y(0, y)},$$

with corresponding definitions of τ_x^G and τ_y^G for $G(x, y)$. The relative nonlinearities of these two functions are now defined as

$$\tau_y^F - \tau_y^G, \tag{10}$$

$$\tau_x^G - \tau_x^F. \tag{11}$$

These τ differences define how much the two functions differ from being related linearly. For example $\tau_x^G - \tau_x^F = 0$ if and only if $F(x, 0)$ and $G(x, 0)$ are linearly related to each other. Hence, $\tau_x^G - \tau_x^F$ measures their relative nonlinearity. These definitions of relative nonlinearity differ from the original definition of Chesson (1994, 2000) by defining it specifically for the cases where one species is an invader (at zero density), whereas Chesson (1994, 2000) restricts it to situations where it can be defined in the same way at all densities. The definition here in terms of two different quantities, one for each species as the invader, allows more general situations to be considered.

Assuming now that species x is in the invader state, and species y is in the resident state, if their population dynamics (1)–(2) satisfy the uniform invasibility criterion **A1** and **A2**, then $\bar{r}_y(0, y_0)$ is necessarily zero. In addition, by doing the exact second Taylor expansions of the growth functions r_x in x and r_y in y (Chesson and Mathias, 2010), the long-term low-density growth rate of species x with an initial condition $x_0 = 0, y_0 > 0$ can be represented as given in Box I, with $\{(0, y_i)\}_{i=0}^{\infty}$ being the positive orbit with initial condition with $y_0 > 0$ and

$$y_v^i = G^{-1}(0, vG(0, y_i)).$$

[See Appendix A for the detailed derivation.] The first term of (12) can be considered as *the invasion rate of species x from the fixed point $(0, y^*)$*, i.e., the invasion rate in the absence of fluctuations. Inspection of (13) shows how relative nonlinearity affects the invasion rate. Relative nonlinearity is only nonzero when the resident has persistent fluctuations, as otherwise $\Delta_x(y_0)$ converges on 0. It is also only nonzero when the relative nonlinearity measure (10) is nonzero and so represents the interaction between these two quantities. Thus, we see that the total effect of relative nonlinearity on the invasion rate is a combination of the fluctuations of the resident species, caused by a nonpoint attractor, and the relative nonlinearity measure. If this quantity (13) is positive, it indicates that the resident population fluctuations increase the invasion rate, while if it is negative, the resident population fluctuations decrease the invasion rate.

From expression (13), we can see that the sign of $\Delta_x(y_0)$ is determined by the sign of the quantity

$$\Theta_x(y) = F_y(0, y) \left(\tau_x^G(0, y) - \tau_x^F(0, y) \right), \tag{14}$$

provided that the sign of $\Theta_x(y)$ does not change with y. Similarly, the long-term low-density growth rate (the invasion rate) species y can be represented as

$$\check{r}_y(x_0, 0) = G(x^*, 0) + \Delta_y(x_0) \tag{15}$$

$$\check{r}_x(0, y_0) = F(0, y^*) + \Delta_x(y_0) \tag{12}$$

where

$$\Delta_x(y_0) = \limsup_{t \to \infty} \frac{\sum_{t=0}^{t-1} G^2(0, y_i) \int_0^1 \frac{F_y(0, y_v^i)}{G_y(0, y_v^i)^2} (\tau_y^F(0, y_v^i) - \tau_y^G(0, y_v^i))[1-v]dv}{t} \tag{13}$$

Box I.

with $\Delta_y(x_0)$ defined analogously to $\Delta_x(y_0)$ by swapping x and y, F and G. The sign of $\Delta_y(x_0)$ is determined by the quantity

$$\Theta_y(x) = G_x(x, 0)\left(\tau_y^F(x, 0) - \tau_y^G(x, 0)\right). \tag{16}$$

For convenience of nomenclature, we say the system has *positive relative nonlinearities* if both (14) and (16) are uniformly nonnegative. Note that permanence requires the lim inf and lim sup to be bounded away from zero and infinity for all positive initial conditions. Similarly, in our definition of invasibility, we require positive invasion rates $\check{r}_x$ (or $\check{r}_y$) from all $y_0 > 0$ (or $x_0 > 0$). These both require that $G(x^*, 0) > 0$ and $F(0, y^*) > 0$, i.e. each species must be able to invade when the other species is at the fixed point of its resident state. Assuming these conditions are satisfied, we now see that positive relative nonlinearity implies invasibility and hence permanence. Focusing on y invading x, there are three scenarios:

1. $\Delta_y(x_0) > 0$, therefore, $\check{r}_y(x_0, 0) = G(x^*, 0) + \Delta_y(x_0) > 0$.
2. $\Delta_y(x_0) < 0$, but, $\check{r}_y(x_0, 0) = G(x^*, 0) + \Delta_y(x_0) > 0$.
3. $\Delta_y(x_0) < 0$, and $\check{r}_y(x_0, 0) = G(x^*, 0) + \Delta_y(x_0) < 0$.

The first case represents the case when the invasion rate $\check{r}_y$ is always greater for the non-point attractor than for the fixed point. The second case represents the case when the invasion rate $\check{r}_y$ is smaller for the non-point attractor than for the point attractor but still keeps the positive sign. The first and second cases have the potential to satisfy the sufficient conditions of the permanence for the system. The last case represents the case when fluctuations associated with the non-point attractor undermine permanence because then the invasion rate is lower than that predicted by the point attractor. In this case, the system has no permanence due to existing attractors on the x-axis. There are many models (Kon, 2006; Kang et al., 2008; Kuang and Chesson, 2008) presenting this scenario under some proper parameter ranges. The uniform invasibility criterion **A1** and **A2** requires both (12) and (15) to be positive for all initial positive initial states of the resident. A system with positive relative nonlinearity then satisfies the uniform invasibility criterion, and hence is permanent. For competition models, the derivatives $F_y(0, y)$ and $G_x(x, 0)$ are negative, and so positive relative nonlinearity means nonpositive values of the relative nonlinearity measures, (10) and (11). Thus, we have the following theorem.

Theorem 4.1 (*Positive relative nonlinearity and invasion criterion*). *Assume that the system* (1)–(2) *satisfies* **C1–C4**. *Then, if the system has positive relative nonlinearity, i.e.*

$$\tau_x^G - \tau_x^F = \frac{G_{xx}}{G_x} - \frac{F_{xx}}{F_x} \le 0 \tag{17}$$

and

$$\tau_y^F - \tau_y^G = \frac{F_{yy}}{F_y} - \frac{G_{yy}}{G_y} \le 0. \tag{18}$$

Then, it satisfies the uniform invasibility criterion **A1** *and* **A2**. *Therefore, it is permanent.*

Proof. Condition **C1–C4** implies that the system is dissipative according to Lemma 3.2. In addition, Condition **C4** gives $G_x < 0$

and $F_y < 0$, which indicates that the system has positive relative nonlinearity when combined with the inequalities (17)–(18). Therefore, positive relative nonlinearity coupled with positive invader growth at the resident point equilibrium guarantees positive invader growth from all positive resident initial densities. To complete the demonstration that the uniform invasibility criterion holds here, we just need to show that resident long-term growth rates $\bar{r}_x(x_0, 0)$ and $\bar{r}_y(0, y_0)$ are zero from all positive resident initial states. This directly follows from Corollary 3.1. Then, applying Theorem 3.1, we see that the system is permanent. □

Note that when the residents have globally stable fixed points, the second term of the expressions (12) and (15) is zero, i.e., $\Delta_x = \Delta_y = 0$. This implies that positivity of $\check{r}_x(0, y)$ and $\check{r}_y(x, 0)$ is determined by the quantities $F(0, y^*)$ and $G(x^*, 0)$. It follows that Theorem 4.1 has the simple corollary.

Corollary 4.1 (*Fixed Point and Permanence*). *If the system* (1)–(2) *satisfies Condition* **C1–C4**, *in addition, both* $(x^*, 0)$ *and* $(0, y*)$ *are globally attractive in the resident states of* x *and* y, *then the system* (1)–(2) *is permanent.*

These results on relative nonlinearity and permanence generalize the results of Kon (2004) for the case of twice differentiable f and g. We now derive special cases in the following corollary.

Corollary 4.2 (*Convexity and concavity*). *Assume that the system* (1)–(2) *satisfies* **C1–C4**. *Then, the system is permanent if both* $F(0, y)$ *and* $G(x, 0)$ *are convex, and, both* $F(x, 0)$ *and* $G(0, y)$ *are concave.*

Note that if $F(x, y)$ and $G(x, y)$ are both linear functions of x, y, which makes the model a discrete-time version of the Lotka–Volterra model, then the second terms of (12) and (15) are zero too. In this case, the coexistence of species x and y is determined by the positivity of $F(0, y^*)$ and $G(x^*, 0)$, as demonstrated previously by Hofbauer et al. (1987).

5. Relative nonlinearity and permanence of prey–predator models

In a prey–predator model, the prey growth rate is a decreasing function of predator density, but the predator growth rate is an increasing function of prey abundance. Most important, the predator growth rate is commonly negative at zero prey abundance. Thus, the predator cannot survive without the prey. This fact means that the uniform invasibility criterion, as presented above for competition models, does not apply. However, we are able to obtain a suitable invasibility condition for a predator–prey model by focusing on predator invasion of a resident prey under conditions that ensure that when the predator is absent, the prey are permanent. Assume that the system (1)–(2) is a dissipative prey–predator system where species x is the prey and species y is the predator with $g(0, y) < 1$. The uniform invasibility criterion for a predator–prey system is then

PA $\bar{r}_x(x_0, 0) = 0$ and $\check{r}_y(x_0, 0) > 0$ for all $x_0 > 0$.

A sufficient condition for the system to be permanent can be stated as follows.

Theorem 5.1. *Assume that the system* (1)–(2) *is a continuous and dissipative prey–predator model with*

$$f(0,0) > 1 \quad and \quad g(0,y) < 1 \quad for\ all\ y \geq 0.$$

If the system satisfies Condition **PA**, *then it is permanent.*

Note that the difference between Condition **PA** and Condition **A1** is that $\check{r}_y(x_0, 0) > 0, x_0 > 0$ instead of $\check{r}_y(x_0, 0) > 0$, $x_0 \geq 0$, which is due to the fact that $\check{r}_y(0, 0)$ is not positive. In order to avoid the fixed point $(0, 0)$, this involves separately demonstrating permanence of x and y in their joint system. First, we can show that prey x is persistent in the joint system (1)–(2) by applying Hutson's (1984) Theorem 2.2 and its Corollary 2.3 with the average Lyapunov function $P(x, y) = x$. Then, we can restrict the system in the space $[b, B] \times [0, B]$. This allows us to apply Hutson's (1984) Theorem 2.2 to obtain permanence of y in the joint system by using the average Lyapunov function $P(x, y) = y$. Note that differentiability conditions are not required for this theorem. Continuity of f and g is sufficient.

In competition models, we have seen that positive relative non-linearity $\Theta_y(x) \geq 0, x \geq 0$ is a sufficient condition for $\check{r}_y(x_0, 0) > 0, x_0 > 0$, when invasion from the resident equilibrium is possible. Now we define conditions that under which a prey–predator system (1)–(2) is permanent as follows:

P1: $f(x, y) > 0$, for any $x > 0, y > 0, f(0, 0) > 1$ and $\lim_{x\to\infty} f(x, 0) \leq a_1 < 1$ for any $x > 0$.
P2: $g(x, y) > 0, 0 \leq g(0, y) < 1$ for all $x > 0, y > 0$ and

$$\lim_{y\to\infty} g(x, y) = a_2(x) < 1 \quad for\ any\ given\ x > 0.$$

P3: If $f(x^*, 0) = 1$ with $x^* > 0$, then $g(x^*, 0) > 1$.
P4: $\frac{\partial f(x,0)}{\partial x} < 0, \frac{\partial f(x,y)}{\partial y} \leq 0, \frac{\partial g(x,y)}{\partial x} > 0$ for all $x \geq 0, y \geq 0$.

Condition **P1** guarantees that the prey x is permanent without the predator y. In **P2**, the condition $0 < g(0, y) < 1$ implies that the predator goes extinct without the prey; the condition $\lim_{y\to\infty} g(x, y) = a_2 < 1$ for any given $x > 0$ implies that for any given prey population size, x, the finite rate of increase of the predator drops below 1. Such behavior is normally described as predator interference, i.e. predator individuals interact negatively with one another limiting their ability to hunt prey. Alternatively, this condition might represent intraspecific competition for some other resource, such as nesting sites, rather than for prey. Condition **P3** ensures that the predator y has a positive growth rate at the prey's equilibrium x^*. The last condition **P4** says that the prey species suffers intraspecific competition in the absence of the predator, and suffers from the presence of the predator, while the predator benefits from the presence of the prey. Note **P4** also implies that $f(x, 0)$ has an inverse, which additionally implies uniqueness of the prey equilibrium x^* in the absence of the predator.

Lemma 5.1 (*Dissipativity*). *If the system* (1)–(2) *satisfies condition* **P1–P4**, *then it is dissipative.*

That the prey population is bounded is a consequence of Lemma 3.1. The key difference between competition models and prey–predator models resides in the fact that the predator population growth rate increases as a function of the prey population, and the predator would go extinct without the prey. Since the prey population size x is bounded by some positive number B, the finite rate of increase of the predator y is less than $g(B, y_t)$. This allows us to apply similar arguments to the proof of Lemma 3.2 to show using Condition **P2** that the predator y is bounded. The detailed proof is given in Appendix B.

The concept of relative nonlinearity applies also to predator–prey systems, but in this case all we have to consider is

relative nonlinearity with a resident prey species because the predator cannot be resident without the prey, and the prey population is permanent regardless of the presence of the predator. The system has positive relative nonlinearity when

$$\Theta_y = G_x(\tau_x^G - \tau_x^F) = G_x \left(\frac{G_{xx}}{G_x} - \frac{F_{xx}}{F_x} \right) = G_{xx} - \frac{G_x F_{xx}}{F_x} \geq 0.$$

Note that here Θ_y and $\tau_x^G - \tau_x^F$ have the same sign because G_x is positive in predator–prey models. Thus, we have the following theorem.

Theorem 5.2. *Assume that the system* (1)–(2) *satisfies* **P1–P4**. *If it has positive relative nonlinearity, i.e.*

$$\tau_x^G - \tau_x^F \geq 0 \quad for\ all\ x > 0,$$

then the system is permanent.

Proof. According to Lemma 5.1, Condition **P1–P4** guarantees that the system (1)–(2) is dissipative. Condition **P1** implies that prey x is permanent in the absence of the predator. Applying Lemma 3.1, gives $\bar{r}_x(x_0, 0) = 0$ for all $x_0 > 0$. Positive relative nonlinearity implies Condition **PA**. Hence from Theorem 5.1, the system is permanent. $\square$

Kon (2004) used convexity and concavity conditions for predator–prey systems. If both $G(x, 0)$ and $F(0, y)$ are convex (or linear), then $G_{xx} \geq 0$ and $F_{xx} \geq 0$. Moreover, Condition **P4** implies that $\frac{G_x}{F_x} \leq 0$. Thus, from the equation above for Θ_y we see that the system has positive relative nonlinearity. Hence, a direct corollary of Theorem 5.2 is

Corollary 5.1. *Assume that the system* (1)–(2) *satisfies* **P1–P4**. *If both $G(x, 0)$ and $F(x, 0)$ are convex, then the system is permanent.*

Like the situation with competition models, it is possible for fluctuating dynamics to undermine coexistence because the quantity $\Delta_y(x) < 0$ for almost every $x_0 > 0$, due to prey population fluctuations. A sufficiently large negative $\Delta_y(x)$ can then make the predator invasion rate negative even though the predator can invade the prey equilibrium. Permanence fails, and this can lead phenomena such as bistability. For instance, a plant-herbivore model in Kang et al. (2008) shows bistability between interior attractors and boundary attractors as a consequence of fluctuating dynamics of the plant population. Also, Kon (2006) shows that there are multiple attractors between interior attractors and boundary attractors caused by the fluctuating dynamics of the host in a host-parasitoid model.

6. Applications

In this section, we apply the results to particular competition and prey–predator models. In addition, we give an example showing that $\Delta_y(x) < 0$ for almost every $x > 0$ caused by the fluctuating prey population.

6.1. A competition model

We present a simple competition model that conveniently illustrates the concept of relative nonlinearity. This model is studied by Kon (2004) to illustrate results on permanence from convexity and concavity conditions. Here we use the model to illustrate relative nonlinearity, but we use a different parameterization than Kon (2004) that makes the results simpler and more ecologically meaningful. Here the dynamics of x and y are given as follows:

$$x_{t+1} = x_t e^{r_1 \left[1 - (\alpha_{11}x_t)^{v_{11}} - (\alpha_{12}y_t)^{v_{12}} \right]} \tag{19}$$

$$y_{t+1} = y_t e^{r_2 \left[1 - (\alpha_{21}x_t)^{v_{21}} - (\alpha_{22}y_t)^{v_{22}} \right]} \tag{20}$$

where $r_i > 0, \alpha_{ij} > 0, v_{ij} > 0, i, j = 1, 2$. This model satisfies Conditions **C1**, **C2** and **C4** for a competition model. The boundary

equilibria are easily seen to be $(1/\alpha_{11}, 0), (0, 1/\alpha_{22})$. These correspond to the carrying capacities in the standard Lotka–Volterra competition models as paramaterized by Chesson (2000). Moreover, the conditions for invasion of resident equilibria (Condition **C3**) are the same as in the standard Lotka–Volterra model, viz, $\alpha_{11} > \alpha_{21}$ and $\alpha_{22} > \alpha_{12}$. However, this is not the standard Lotka–Volterra model, but a variation on it similar to the sorts of models suggested by Ayala et al. (1973), Hassell and Comins (1976). Of most significance here we can use the concept of relative nonlinearity to see when the system is permanent. The nonlinearity measures, τ, take simple forms, for example

$$\tau_x^F = \frac{v_{11} - 1}{x}, \qquad \tau_x^G = \frac{v_{21} - 1}{x}$$

and the relative nonlinearities are

$$\tau_y^F - \tau_y^G = \frac{v_{12} - v_{22}}{y}, \qquad \tau_x^G - \tau_x^F = \frac{v_{21} - v_{11}}{x}.$$

It follows that the condition for positive relative nonlinearity (nonpositive τ differences) is $v_{jj} \geq v_{ij} > 0, i \neq j, i, j = 1, 2$. The following corollary gives us the parameter ranges of $r_i, v_{ij}, \alpha_{ij}, i, j = 1, 2$ so that the system is permanent.

Corollary 6.1. *Assume that* (19)–(20) *satisfies* $v_{jj} \geq v_{ij} > 0, i \neq j, i, j = 1, 2$ *and* $\alpha_{ij} > 0, i, j = 1, 2$. *Then, the system is permanent, if*

$$\alpha_{jj} > \alpha_{ij}, \quad i \neq j, \ i, j = 1, 2.$$

Our competition model is essentially the same as Kon's (2004), but we substantially broaden the parameter range for which permanence is known.

6.2. A prey–predator model

Let x_t and y_t represent the population densities of prey x and predator y respectively at generation t. Then, a prey–predator model can be defined as

$$x_{t+1} = x_t \left(s_1 + b_1 e^{-a_{11}x_t^{v_{11}} - a_{12}y_t^{v_{12}}} \right) \tag{21}$$

$$y_{n+1} = y_t \left(s_2 + b_2 e^{a_{21}x_t^{v_{21}} - a_{22}y_t^{v_{22}}} \right) \tag{22}$$

where $s_1 + b_1 > 1, 0 < s_1 < 1, 0 < s_2 + b_2 < 1, a_{ij} > 0, v_{ij} > 0, i, j = 1, 2$. With these parameter constraints, this system satisfies Condition **P1, P2, P4**. For the prey boundary equilibrium, we solve

$$s_1 + b_1 e^{-a_{11}x_n^{v_{11}}} = 1$$

for x. This yields exactly one nontrivial boundary equilibrium equal to

$$\left(\left(\frac{\ln\left(\frac{b_1}{1-s_1}\right)}{a_{11}} \right)^{\frac{1}{v_{11}}}, 0 \right).$$

Substituting this boundary equilibrium into the finite rate of increase of the predator, we find that Condition **P3** holds when

$$\left(\frac{\ln\left(\frac{b_1}{1-s_1}\right)}{a_{11}} \right)^{\frac{1}{v_{11}}} > \left(\frac{\ln\left(\frac{1-s_2}{b_2}\right)}{a_{21}} \right)^{\frac{1}{v_{21}}}. \tag{23}$$

Relative nonlinearity here becomes

$$\tau_x^G - \tau_x^F = \frac{1}{x} \left(v_{21} - v_{11} + \frac{s_2 a_{21} v_{21} x^{v_{21}}}{s_2 + b_2 e^{a_{12}x^{v_{12}}}} + \frac{s_1 a_{11} v_{11} x^{v_{11}}}{s_1 + b_1 e^{-a_{11}x^{v_{11}}}} \right).$$

This expression converges on $(v_{21} - v_{11})/x$ for small x, from which it is clear that the whole expression is positive for all positive x if

and only if $v_{21} > v_{11}$. As G_x is always positive, this means that the condition for positive relative nonlinearity is $v_{21} > v_{11}$. Thus, the following corollary gives a sufficient condition for permanence of the predator–prey system.

Corollary 6.2. *Assume that* $s_1 + b_1 > 1, 0 < s_1 < 1, 0 < s_2 + b_2 < 1, \alpha_{ij} > 0, v_{ij} > 0, i, j = 1, 2$. *If* $v_{21} \geq v_{11}$ *and inequality* (23) *holds, then the system* (21)–(22) *is permanent.*

6.3. Resident population fluctuations leading to a negative invasion rate

The concept of relative nonlinearity allows us to understand when population fluctuations have critical roles in species coexistence. In this subsection, we give an example of when fluctuating dynamics associated with a nonpoint attractor undermine permanence because they make the invasion rate negative while the invasion rate from the resident fixed point is positive. Both models studied in Kon (2006) and Kang et al. (2008) provide examples. Here we use following host-parasitoid interaction model studied by Kon (2006):

$$x_{t+1} = x_t e^{r - x_t - y_t} \tag{24}$$

$$y_{t+1} = \theta x_t \left[1 - e^{-y_t} \right] \tag{25}$$

where $r > 0$ is the maximum growth rate of the host and $\theta > 0$ is the number of parasitoids emerging on average from each parasitized host. This system is dissipative and the host x is permanent. To derive the nonlinearity measures, we note that

$$F_x(x, 0) = -1, \qquad F_{xx}(x, 0) = 0$$
$$G_x(x, 0) = \frac{1}{x}, \qquad G_{xx}(x, 0) = -\frac{1}{x^2}.$$

The predator invasion rate at the host fixed point is $G(x^*, 0) = G(r, 0) = \ln(r\theta)$. Using the notation $\{(x_i, 0)\}_{i=0}^\infty$ for a positive orbit for the host as a resident, with initial value $x_0 > 0$, formula (15) for $\Delta_y(x_0)$ gives

$$\check{r}_y(x_0, 0) = \ln(r\theta) - \limsup_{t \to \infty} \frac{\sum_{i=0}^{t-1} \int_0^1 \frac{1}{(r - vx_i)^2} [1 - v] \, dv}{t}. \tag{26}$$

As $\Delta_y(x_0)$ is negative here, relative nonlinearity reduces the invasion rate $\check{r}_y$. When $r\theta > 1$, the fixed point $(r, 0)$ gives a positive parasitoid invasion rate, i.e., $G(r, 0) = \ln(r\theta) > 0$. For certain values of r, host population fluctuations can cause the parasitoid invasion to fail. For instance, in the case $r = 3.25, \theta = 1/1.05$, $\check{r}_y = -0.105$ (Figure 6, Kon, 2006), which implies that the invading parasitoid y has a negative invasion rate due to a sufficiently large negative value of $\Delta_y(x_0)$. This means there are boundary attractors on the x-axis.

7. Discussion

Many authors (e.g., Fonda, 1988; Freedman and So, 1989; Schreiber, 2000; Salceanu and Smith, 2009a,b) have studied sufficient conditions for permanence of dynamical systems. However, these conditions in general are difficult to check. Thus, in applications, the invasibility criterion is often used to study the coexistence of two species (Ferriere and Gatto, 1995; Chesson, 1994; Kuang and Chesson, 2008). In this paper, we connect these two concepts by introducing the idea of uniform invasibility for discrete-time two-species population models and finding sufficient conditions for uniform invasibility and permanent coexistence. Most important, we show that uniform invasibility implies permanence under mild conditions. Although Kon (2004) derived similar results based on the seminal work of Hutson (1984), he did not make explicit connection with invasibility ideas.

The concept of permanence is of most value in the presence of nonpoint attractors because then asymptotic sfbility of an equilibrium is too limited a concept for species coexistence. However, population fluctuations arising from nonpoint attractors can have major effects on coexistence itself (Armstrong and McGehee, 1980; Alder, 1990; Chesson, 1994; Kuang and Chesson, 2008). Here, we study that connection using the concept of relative nonlinearity, which precisely identifies when the invasion rate depends on the fluctuating dynamics of the resident species. When relative nonlinearity is zero, fluctuations have no effect on this invasion rate, and the invasion rate can be found simply by substituting the resident equilibrium into the growth rate of the invader. Our results here lead to simple, easy to check sufficient conditions for uniform invasibility and permanence applicable to a broad range of situations. We use these results also to show when fluctuations can undermine invasibility and permanent coexistence. These situations occur when relative nonlinearity makes a sufficiently negative contribution to invader growth. These results are illustrated with a two-species competition model and a predator–prey model, both of which are readily analyzed by these techniques and have a generic quality. Our results generalize those of Kon (2004) who used convexity and concavity assumptions on population growth rates to understand situations when invasion of resident point equilibria would be sufficient for permanence.

The notion of relative nonlinearity has most commonly been used in the past for the situation where the per capita growth rates of each species can be written as a function of a common dynamical variable, called a competitive factor, which might be a common resource exploited by each species, or a common predator. The relative nonlinearity measure, $\tau_F - \tau_G$, then defines the extent to which the growth rate of each species is a different nonlinear function of that competitive factor. In the simplest circumstances, the competitive factor is written as a function of the densities of the two species (Alder, 1990). However, the idea that relative nonlinearity might be defined in terms of multiple competitive factors was discussed by Chesson (1994), which is in fact what is done here. The two factors here are the densities of each of the species. We only need to consider them in the resident–invader situation, which simplifies their presentation. Study of models with a single-competitive factor has focused on the case where $\tau_F - \tau_G$ is of fixed sign, as has been the case in the applications of interest. In this case, fluctuating dynamics decrease the invasion rate of one species and increase the invasion rate of the other species. Under certain circumstances (Chesson, 1994) this allows both species to increase as invaders. However, this is not sufficient for uniform invasibility because it normally does not apply for all initial conditions, as discussed below. Moreover, positive relative nonlinearity, as defined here is not possible, and so Theorem 4.1 demonstrating permanence does not apply.

Although our results substantially broaden the range of situations in which permanent coexistence can be demonstrated in applications, there remain important situations in which there is no practical technique for demonstrating permanence. These are the situations where relative nonlinearity is negative or indeterminate. Then, relative nonlinearity might reduce an invasion rate to negative values for some initial values of the resident despite a positive invasion rate at the resident fixed point, destroying permanence. Checking that this does not occur is difficult in general because, in discrete-time models, resident dynamics might have an infinite number of disjoint invariant sets, for example as occurs in the commonly used Ricker model and many other models based on unimodal maps (May and Oster, 1976). In such cases, determining whether the invasion rate is positive for all positive initial resident states will often be impractical in the absence of positive relative

nonlinearity. Although uniform invasibility continues to imply permanence, establishing uniform invasibility is not always a practical proposition.

The difficulty of establishing uniform invasibility in some cases highlights a deficiency with permanence as a general notion of species coexistence. The requirement that both populations be bounded away from 0 and infinity for all positive initial conditions is a very strong condition. A weaker condition that exempts a set of initial conditions of Lebesgue measure zero would be more useful in important applications involving nonpoint attractors. For instance, the original concept of relative nonlinearity (Armstrong and McGehee, 1980; Chesson, 1994, 2009; Kuang and Chesson, 2008) for a single competitive factor, as discussed above, was of interest because it identified situations in which population fluctuations are essential for coexistence. These cases are characterized by the feature that invasion from the resident fixed point is impossible for at least one species. Relative nonlinearity, however, when combined with fluctuating dynamics may allow invasion from initial values other than the resident fixed point. However, permanence, and also the uniform invasibility concept used here to prove permanence, fail. This means that permanence and uniform invasibility are inadequate for the study of the kind of coexistence applying in these situations. In general, these situations have been studied using an invasibility concept that ignores exceptional points and assumes a unique attractor of almost all initial values of the resident. For models of the real world, a concept that would fail due exceptional behavior on sets of measure zero is unlikely to be broadly useful unless those sets of measure zero have the status of attractors, because the noise in nature means that the system would not stay in such sets. For this reason, the concept of permanence needs to be generalized to exclude sets of measure zero. Most important, theory allowing practical application of the more general concept is needed. Especially useful would be a permanence concept and methodology for applications that demonstrate how population fluctuations can promote species coexistence (Armstrong and McGehee, 1980; Chesson, 1994, 2009; Kuang and Chesson, 2008). Nevertheless, even with a weaker more useful concept, it would still of value to know when a stronger concept is applicable. The work described here substantially broadens the range of situations in which the strong coexistence condition, permanence as defined here, can be established, and highlights important situations when it must fail.

Acknowledgments

Appendix A. Derivation of relative nonlinearity (12) and (15)

Here we derive the relative nonlinearity measure based on Chesson and Mathias (2010).

Assuming now that species x is in the invader state, and species y is in the resident state, if their population dynamics (1)–(2) satisfy the uniform invasibility criterion **A1** and **A2**, then the $\bar{r}_y(0, y_0)$ is necessarily zero, i.e.,

$$\bar{r}_y(0, y_0) = \lim_{t \to \infty} \frac{\sum\limits_{t=0}^{t-1} G(0, y_i)}{t} \tag{A.1}$$

where $\{(0, y_t)\}_{t=0}^{\infty}$ is a positive orbit of the system (1)–(2) with initial condition $y_0 > 0$.

$$\check{r}_y(x_0, 0) = G(x^*, 0) + \Delta_y(x_0)$$

where

$$\Delta_y(x_0) = \limsup_{t \to \infty} \frac{\sum_{i=0}^{t-1} F(x_i, 0)^2 \int_0^1 [1-v] \frac{G_x(x_v^i,0) \left[\frac{G_{xx}(x_v^i,0)}{G_x(x_v^i,0)} - \frac{F_{xx}(x_v^i,0)}{F_x(x_v^i,0)} \right]}{F_x^2(x_v^i,0)} dv}{t}$$

where $x_v^i = F^{-1}(vF(x_i, 0), 0)$.

Box II.

Suppose that $F(x, 0)$ and $G(0, y)$ of the system (1)–(2) have inverse functions for all $x > 0, y > 0$, which are denoted by $F^{-1}(r_x, 0)$ and $G^{-1}(0, r_y)$. In particular, we have the following equalities hold:

$$r_y(0, y) = G(0, y) \Rightarrow y = G^{-1}(0, r_y). \tag{A.2}$$

Then applying (A.2) to $r_x(0, y) = F(0, y)$, we have the following:

$$r_x(0, y) = F(0, y) = F(0, G^{-1}(0, r_y)). \tag{A.3}$$

For convenience, define $r_g = G(0, y) = G(y)$, $r_f = F(0, y) = F(y)$. Then, according to (A.3), we have

$$r_f = F \circ G^{-1}(r_g). \tag{A.4}$$

In particular, for each $(0, y_i) \in \{(0, y_t)\}_{t=0}^{\infty}$, we denote

$$r_g^i = G(y_i) \tag{A.5}$$

$$r_f^i = F(0, y_i) = F \circ G^{-1}(r_g^i) = F \circ G^{-1} \circ G(y_i). \tag{A.6}$$

Then by doing the exact second Taylor expansion on r_f with respect to r_g around $r_g = 0$ according to (A.4), we have

$$r_f = F \circ G^{-1}(0) + \left(\left. \frac{dF \circ G^{-1}(r_g)}{dr_g} \right|_{r_g=0} \right) r_g$$

$$+ (r_g)^2 \int_0^1 [1-v] \frac{d^2(F \circ G^{-1}(r_g))}{d(r_g)^2} (vr_g) dv. \tag{A.7}$$

Since $G(0, y^*) = 0$, then by (A.3), (A.6), (A.5) and (A.7), we have

$$\frac{\sum_{i=0}^{t-1} r_f^i}{t} = F(0, y^*) + \left. \frac{dF \circ G^{-1}(r_g)}{dr_g} \right|_{r_g=0} \frac{\sum_{i=0}^{t-1} r_g^i}{t}$$

$$+ \frac{\sum_{i=0}^{t-1} (r_g^i)^2 \int_0^1 [1-v] \frac{d^2 F \circ G^{-1}}{d(r_g)^2} (vr_g^i) dv}{t}. \tag{A.8}$$

Since $r_f^i = F(0, y_i)$ and $r_g^i = G(0, y_i)$, the equality (A.8) can be rewritten as

$$\frac{\sum_{i=0}^{t-1} F(0, y_i)}{t} = F(0, y^*) + \left. \frac{d(F \circ G^{-1})(r_g)}{dr_g} \right|_{r_g=0} \frac{\sum_{i=0}^{t-1} G(0, y_i)}{t} \tag{A.9}$$

$$+ \frac{\sum_{i=0}^{t-1} G(0, y_i)^2 \int_0^1 [1-v] \frac{d^2(F \circ G^{-1})}{d(r_g)^2} (vG(0, y_i)) dv}{t}. \tag{A.10}$$

Then according to (A.1), the second term of (A.9) goes to 0 as $t \to \infty$; therefore, we have

$$\check{r}_x(0, y_0) = F(0, y^*) + \Delta_x(y_0) \tag{A.11}$$

where

$$\Delta_x(y_0) = \limsup_{t \to \infty} \frac{\sum_{i=0}^{t-1} G(0, y_i)^2 \int_0^1 [1-v] \frac{d^2(F \circ G^{-1})}{d(r_g)^2} (vG(0, y_i)) dv}{t}.$$

Since

$$\frac{d(F \circ G^{-1})(r_g)}{d(r_g)} = \frac{F_y(G^{-1}(r_g))}{G_y(G^{-1}(r_g))},$$

we have

$$\frac{d^2(F \circ G^{-1})(r_g)}{d(r_g)^2} = \frac{F_{yy}(G^{-1}(r_g)) - \frac{G_{yy}(G^{-1}(r_g))F_y(G^{-1}(r_g))}{G_y(G^{-1}(r_g))}}{G_y^2(G^{-1}(r_g))}$$

$$= \frac{F_y(G^{-1}(r_g)) \left[\frac{F_{yy}(G^{-1}(r_g))}{F_y(G^{-1}(r_g))} - \frac{G_{yy}(G^{-1}(r_g))}{G_y(G^{-1}(r_g))} \right]}{G_y^2(G^{-1}(r_g))}.$$

Therefore, we can rewrite $\Delta_x(y_0)$ as

$$\Delta_x(y_0) = \limsup_{t \to \infty} \frac{\sum_{i=0}^{t-1} G(0, y_i)^2 \int_0^1 [1-v] \frac{F_y(y_v^i) \left[\frac{F_{yy}(y_v^i)}{F_y(y_v^i)} - \frac{G_{yy}(y_v^i)}{G_y(y_v^i)} \right]}{G_y^2(y_v^i)} dv}{t}$$

where $y_v^i = G^{-1}(vG(0, y_i))$. Similarly, let $\{(x_i, 0)\}_{i=0}^{\infty}$ be the positive orbit with the initial condition $x_0 > 0$, then we can derive the long-term low-density growth rate (the invasion rate) of the invading species y, in the presence of its competitor, species x, as given in Box II.

Appendix B. Useful lemmas

Lemma B.1. *Let $x_{t+1} = x_t f(x_t)$ where the map $f : [0, \infty) \to [0, \infty)$ is differentiable. If*

(a) *$f(x) > 0$ for all $x > 0$ and $f(0) > 1$ and*
(b) *there exists a $B > 0$ such that for any initial condition $x_0 > 0$, we have*

$$\limsup_{t \to \infty} x_t < B.$$

Then the system is permanent in $\{x : x > 0\}$, i.e., there exists a $b > 0$, such that for any initial condition $x_0 > 0$, we have

$$\liminf_{t \to \infty} x_t > b.$$

Moreover, this implies that

$$\bar{r}_x(x_0) = 0 \quad \text{for all } x_0 > 0.$$

Proof. Define $z_t = \ln(x_t)$. Since we know that eventually $x_t < B$, $r_{min} = \inf_{0 \le x \le B} \ln(f(x)) < 0$ is finite because $f(x)$ is continuous and strictly positive for all $x > 0$. Since the growth rate $\ln(f(x))$ is continuous, it is positive at low values of x. Thus, defining $\epsilon = \min\{x : f(x) = 1\}$ and $b = \epsilon e^{r_{min}}$, we have $0 < b < \epsilon < B$. Beginning with x below ϵ, each step z_t must increase until it hits

or exceeds $\ln(\epsilon)$. However, by Condition (b) z_t can never exceed $\ln(B)$. Thus, z_t can never decrease by more than r_{min} in one step. This means that after z_t has exceeded $\ln(\epsilon)$ it can never fall below $r_{min} + \ln(\epsilon)$ before its growth rate is positive again. It follows that z_t cannot fall below $r_{min} + \ln(\epsilon)$. Hence, $x_t \geq \epsilon e^{r_{min}}$ if t is large enough and $x_0 > 0$.

Let $(x_i)_{i=0}^{\infty}$ to be the positive orbit of the map starting at $x_0 > 0$, then we have

$$\liminf_{t \to \infty} \frac{\ln \frac{b}{x_0}}{t} \leq \liminf_{t \to \infty} \frac{\ln \frac{x_t}{x_0}}{t} \leq \limsup_{t \to \infty} \frac{\ln \frac{x_t}{x_0}}{t} \leq \limsup_{t \to \infty} \frac{\ln \frac{B}{x_0}}{t}.$$

As both ends of this string of inequalities are zero, and $r_x^t(x_0) = (\ln x_t / x_0)/t$, we see that $\bar{r}_x(x_0)$ exists and equals 0 for all $x_0 > 0$. $\square$

Proof of Lemma 3.1. Define $r_{max} = \sup_{x \geq 0} \ln(f(x))$. This is finite because f is continuous and converges on a finite constant at infinity. Let $z_n = \ln(x_n)$. Since $f(x)$ converges to $a_1 < 1$ as x goes to infinity, there is a K and an ϵ such that $\ln(a_1) < -\epsilon < 0$ and

$$\ln(f(x)) < -\epsilon \text{ for } x > K.$$

Thus,

$$z_{n+1} < z_n - \epsilon, \text{ for } z_n > \ln(K),$$

and

$$z_{n+1} \leq r_{max} + \ln(K) = \ln(B), \text{ for } z_n \leq \ln(K).$$

Now let us consider the following two cases:

1. If $z_0 \leq \ln(K)$, then $z_n \leq \ln(B)$ for all n because $z_1 \leq \ln(B)$ and if $z_n \leq \ln(B)$ either $z_n < \ln(K)$ or $z_{n+1} < z_n$. Hence $z_{n+1} \leq \ln(B)$. Thus by induction, z_n remains below $\ln(B)$ if $z_0 \leq \ln(K)$.
2. If $z_0 > \ln(K)$, then there is a k such that $z_k < \ln(K)$. Here k can be calculated explicitly as less than $\frac{z_0 - \ln(K)}{\epsilon}$. Using k in place of 0 in case 1, we see that $z_n < \ln(B)$ for $n > k$.

Combining this result with Lemma B.1 completes the proof. $\square$

Proof of Lemma 3.2. We want to show that for any nonnegative initial condition (x_0, y_0), x_t is bounded for t large enough. From Condition **C4** $\frac{\partial f(x,y)}{\partial y} < 0$, we have

$$x_{t+1} = x_t f(x_t, y_t) \leq x_t f(x_t, 0).$$

Define $r_m = \sup_{(x \geq 0, y \geq 0)} \ln(f(x, y)) = \sup_{x \geq 0} \ln(f(x, 0))$. This is finite because f is continuous and converges on a finite constant at infinity. Let $z_n = \ln(x_n)$. Since $f(x, y) \leq f(x, 0)$ and $\lim_{x \to \infty} f(x, 0) = a_1 < 1$, there is a K and an ϵ such that

$$\ln(f(x, y)) < -\epsilon < 0 \quad \text{for any } x > K, y \geq 0.$$

Thus,

$$z_{n+1} < z_n - \epsilon, \quad \text{for } z_n > \ln(K),$$

and

$$z_{n+1} \leq r_m + \ln(K) = \ln(B), \quad \text{for } z_n \leq \ln(K).$$

Then applying a similar argument to the proof of Lemma 3.1, we can conclude that x_t is bounded for t large enough. Reciprocally, y_t is bounded for t large enough. Therefore, the system is dissipative. $\square$

Proof of Lemma 5.1. Since the system satisfies Condition **P1-P4**, the same proof as Lemma 3.2 proves the boundness of prey x, i.e., there exists $B > 0$ such that for any nonnegative initial condition (x_0, y_0), we have

$$\limsup_{t \to \infty} x_t < B.$$

Due to the condition $\frac{\partial g(x,0)}{\partial x} > 0$, we gain the following inequality:

$$y_{t+1} = y_t g(x_t, y_t) \leq y_t g(B, y_t).$$

If $g(B, 0) \geq 1$, then the argument used to prove Lemma 3.2, applies to show the boundedness of the predator y. In the case that $g(B, 0) < 1$, the predator population cannot grow once the prey has fallen below B, after which it in fact decreases monotonically to zero. Therefore, the population of species y is also bounded for large t, which implies that the system is dissipative. $\square$

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