The role of population inertia in predicting the outcome of stage-structured biological invasions

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ABSTRACT

Deterministic dynamic models for coupled resident and invader populations are considered with the purpose of finding quantities that are effective at predicting when the invasive population will become established asymptotically. A key feature of the models considered is the stage-structure, meaning that the populations are described by vectors of discrete developmental stage- or age-classes. The vector structure permits exotic transient behaviour—phenomena not encountered in scalar models. Analysis using a linear Lyapunov function demonstrates that for the class of population models considered, a large so-called population inertia is indicative of successful invasion. Population inertia is an indicator of transient growth or decline. Furthermore, for the class of models considered, we find that the so-called invasion exponent, an existing index used in models for invasion, is not always a reliable comparative indicator of successful invasion. We highlight these findings through numerical examples and a biological interpretation of why this might be the case is discussed.

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1. Introduction

Invasion is a key biological process that plays a crucial role in structuring ecological systems. However, invasive species also threaten native biodiversity worldwide [1]. Biological invasions are influenced by environmental stresses, exploitation, habitat fragmentation, human travel, transportation, pollution and, increasingly, climate change [2]. Writing in [3], Lodge comments "*The difficulty of testing for patterns from real case studies has led to a potentially fruitful increase in mathematical ... models of invasion*". Why invaders invade, and what characterises a successful invader, are hugely important questions that have been the focus of much research by biologists, ecologists and mathematicians for at least the last 60 years, arguably since the monograph of Elton [4]. Needless to say, the study of biological invasion and its prediction is mature and the resulting academic literature is vast, although biological invasion is not even a universally agreed term [5].

We refer the reader to, for example, [6–12] and the references therein for further background.

From a mathematical modelling perspective, the potential for asymptotic (that is, long term) biological invasion may be inferred by computing the invasion exponent, introduced in [13]. We recall that the invasion exponent is the linearised exponential growth rate of the invader from zero with the resident at a nonzero equilibrium, say at carrying capacity. If the invasion exponent is negative, then invasion is predicted to fail asymptotically. More precisely, linear stability theory guarantees that any invasion attempt fails when the initial abundance of invader is small enough and the resident does not deviate too far away from its starting equilibrium. However, to use these tools to predict invasion relies on overcoming the caveats concerning "small enough" and "not too far away". To properly understand the asymptotic outcome of an invasion attempt requires a deeper understanding of the underlying dynamics. The pivotal object is the basin of attraction [14, Section 8.2] (also known as the stability region [15]) of the resident-only equilibrium which is the set of initial states, that is, initial resident–invader distributions, from which the combined populations converge to the resident-only equilibrium.

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Determining analytically the basin of attraction of a given equilibrium of a non-linear model is non-trivial, often intractable, and instead subsets of basins of attractions are estimated using Lyapunov functions [14, Chapter 2].

We consider deterministic, discrete-time (difference equation) dynamic models for two interacting populations—termed a resident and an invader. The models seek to capture an *in situ* initial point of invasion, and the focus is therefore on establishment of the invader (see, for example, [16]), rather than spatial spread. As such the models do not contain an explicit spatial component. The resident and invader are modelled in density-dependent competition with one another through, for example, competition for the same resources. Our rationale is that the resident and invader are phenologically similar and thus have similar life-histories but, at some abundances, the invader is fitter (in a sense we make precise later) than the resident. Such a situation admits the possibility of successful invasion which, presently, we take to mean that from its initially "small" abundance the invader persists asymptotically. The enhanced fitness of the invader is a consequence of a density-dependent vital rate, denoted α, that is assumed to appear only in the invader dynamics. To (deliberately) complicate matters, we assume that α acts as an Allee effect [17] as well, so that invader fitness is penalised at lower abundance. The inclusion of the Allee effect results in a negative invasion exponent which indicates that invasion should fail when the initial abundance of invader is low. We refer the reader to [18] for more background on the use and role of Allee effects in modelling biological invasions. Given the above setup we seek indicators of when an invasion attempt is likely to be successful. In other words, we seek proxies for the "size" of the basin of attraction of the resident-only equilibrium.

A crucial phenomenon of stage-structured (that is, vector valued) dynamical systems is transient behaviour or transients—short term behaviour, particularly dynamics that deviate away from equilibrium. Engineers and numerical analysts have recognised for many years the importance of transient dynamics. Dahlquist and Lozinskii independently introduced the logarithmic norm in [19] and [20], respectively, to capture transients in numerical schemes. The logarithmic norm has more recently been termed the initial growth rate by some authors; see, for example, [21, p. 653]. Ecologists are increasingly recognising transients as a source of important, yet less predictable, dynamics [22–26]. Transient dynamics of even seemingly simple linear models (specified by (2.1)) can be exotic and depend on both the projection matrix and the initial state. Furthermore, no one scalar index entirely captures transient behaviour. This is in marked contrast to asymptotic dynamics which, for linear systems with nonzero initial state, is often wholly determined by a single scalar quantity—the spectral radius of the projection matrix. We comment that neither linear stability theory, which is based on eigenvalues, or knowledge of the basin of attraction, describe transient behaviour.

Appealing to a linear Lyapunov functional demonstrates that the quantity known as population inertia [27] in the context of matrix population modelling of the linearised invader dynamics is indicative of the outcome of an invasion attempt. Inertia is the ratio of asymptotic population size of linearised matrix projection models relative to linearised projections from steady-state. It is a function of both the life-history parameters of a population and its initial distribution. Our main result, Theorem 1, contains a sufficient condition for an invasion attempt to fail. It states in words that population inertia acts as a proxy for the "size" of the basin of attraction in that, all else equal, the basin shrinks with increasing inertia. Then for a given invader abundance, the model with lower inertia will have a larger basin of attraction and therefore a lesser risk of being invaded. As a Lyapunov-type argument, the theorem is conservative in its estimates and does not state that large population inertia implies that an invasion attempt will succeed. However, numerical examples suggest that this converse statement is also true: the larger the inertia, the higher the risk of an invasion succeeding. An informal explanation of this phenomenon is that inertia is also indicative of transient growth of the invader—itself a requirement for invasion. That inertia depends on the initial population distribution helps to capture its role in invasion. Furthermore, the linear Lyapunov analysis highlights a relationship between initial invader abundance, population inertia and the Allee effect/boost to fitness function α in determining the outcome of an invasion. Consequently, the estimates obtained in deriving Theorem 1 yield an inverse relationship between the boost to invader fitness from α required for a successful invasion and population inertia. The numerical examples also demonstrate that the same inverse relationship is not observed between the boost to invader fitness from α required for a successful invasion and invasion exponent. In other words, a more negative invasion exponent does not always imply that a larger boost to invader fitness is required for a successful invasion. Our observations suggest a rule of thumb: large population inertia of an invasion attempt indicates that the invasion attempt is likely to be successful, even when the invasion exponent is negative. In addition, when population inertia is large then the exact functional form or contribution from density-dependences and Allee effects is less important. This foreknowledge is useful owing to the difficulty of accurately modelling the "correct" density-dependences noted in, for example, [28].

The present work draws on the PhD thesis [29, Chapter 6] of the second author and the masters thesis[1] of the third, and is organised as follows. Section 2 describes structured population models and culminates in presenting the class of coupled resident–invader models we consider. Section 3 revisits population inertia and contains our main result. Section 4 contains numerical examples and Section 5 is the discussion. Mathematical proofs of our assertions are recorded in the appendices.

Notation: In order to appeal to as broad an audience as possible, we have tried to limit the use of technical mathematical notation. Here we introduce some notation. The symbol $\mathbb{N}_0$ denotes the set of nonnegative integers. For positive integer n, $\mathbb{R}^n$ denotes usual real n-dimensional Euclidean space and $\mathbb{R}^n_+$ denotes the nonnegative orthant. A vector z in $\mathbb{R}^n$ belongs to $\mathbb{R}^n_+$, denoted $z \in \mathbb{R}^n_+$ if $z_k \geq 0$ for every k, where z_k denotes the kth component of z. We call vectors $z \in \mathbb{R}^n_+$ nonnegative and say that $z \in \mathbb{R}^n_+$ is positive if $z_k > 0$ for every k. As usual, we let $\mathbb{R} = \mathbb{R}^1$ and $\mathbb{R}_+ = \mathbb{R}^1_+$. For vector $z \in \mathbb{R}^n$, the term $\|z\|_1$ denotes the vector one-norm of z

$$\|z\|_1 := \sum_{k=1}^n |z_k| = \sum_{k=1}^n z_k, \quad \text{if } z \text{ nonnegative.}$$

Throughout the manuscript the superscript ^{T} denotes matrix or vector transposition, so that if $z \in \mathbb{R}^n$ then z^T is a row vector. Finally, recall that a square nonnegative matrix A is primitive if there exists an integer k such that every component of A^k is positive.

2. Coupled resident–invader population models

2.1. Matrix population projection models for single populations

Matrix population projection models (PPMs) are simple, yet popular, tools for modelling the change of abundance or density of a population over time. The monograph [30] by Caswell is dedicated to their study, and we refer the reader as well to the textbook [31] as an alternative reference. PPMs are structured population models, meaning that the modelled population is partitioned into discrete age-, size- or stage- (such as larval, pupal, adult, etc.) classes. A linear, time-invariant matrix PPM is given by

$$y(t+1) = Ay(t), \quad y(0) = y^0, \quad t = 0, 1, 2, \ldots, \tag{2.1}$$

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[1] Available on request from Stuart Townley.

where $y(t) \in \mathbb{R}_+^n$ denotes the structured population, in integer n stage-classes, with initial population distribution y^0 and A is an $n \times n$ componentwise nonnegative matrix. The time-steps t in (2.1) are assumed fixed: a week, month, or breeding cycle, for instance.

The matrix A in (2.1) is often called the projection matrix, and contains life-history parameters of the population, such as recruitment, survival and transitions between stage-classes. When A is primitive (a reasonable assumption for meaningful ecological models [32]) and $y^0 \neq 0$ then the asymptotic behaviour of the model (2.1) is determined entirely by the spectral radius of A, denoted $r(A)$. We recall that the spectral radius of a square matrix M is defined as

$$r(M) := \max\{|\lambda| \,:\, \lambda \in \sigma(M)\}, \tag{2.2}$$

where $\sigma(M)$ denotes the spectrum of M, that is, its set of eigenvalues. If M is nonnegative and primitive then the celebrated Perron–Frobenius Theorem [33,34] (for a more recent treatment see [35, pp. 26–27]) implies that $r(M)$ is an eigenvalue of M and that every other eigenvalue of M has modulus strictly less than $r(M)$. Consequently, the spectral radius in this case is sometimes called the *dominant eigenvalue* or *asymptotic growth rate*. When $r(A) < 1$ or $r(A) = 1$ then the population $y(t)$ modelled by (2.1) is predicted to decline to zero or reach a nonzero, constant population distribution over time, respectively.

A downside with matrix PPMs (2.1) is that when $r(A) > 1$ they predict asymptotically unbounded, exponential growth—a situation that is impossible physically. A refinement of the model (2.1) is to include density-dependence, so that the population at the next time-step is not linearly proportional to the current population. Models of the form

$$x(t+1) = (A_R + e\phi(\|x(t)\|_1)f^T)x(t), \quad x(0) = x^0, \quad t = 0, 1, 2, \ldots, \tag{2.3}$$

have been used to model both fish species in [36, pp. 316–323] or monocarpic plants, such as Platte Thistle, in [37]. The model (2.3) is still a structured population model, with n stages, say, and contains both density-independent and -dependent components. Here the $n \times n$ matrix A_R models vital rates that are assumed to be density-independent. We assume that

$$r(A_R) < 1, \tag{2.4a}$$

which is certainly always the case if A_R only contains survival and growth rates (to subsequent stage-classes). The term $e\phi(\|x(t)\|_1)f^T$ in (2.3) models recruitment into the population which are the vital rates that are assumed to be density-dependent. The nonnegative vector e describes the distribution of new population members and f^T is a nonnegative vector weighting the recruitment contribution of each stage-class. The function ϕ models density-dependence, owing to competition for resources in the population at higher abundances and is assumed to satisfy

$\phi : \mathbb{R}_+ \to \mathbb{R}_+$ is a nonzero, differentiable and strictly

decreasing function. (2.4b)

The dynamics of models of the form (2.3) have been studied by many authors across numerous scientific and engineering contexts, such as in [38] for population modelling. Depending on the interplay between the components A_R, e, f and ϕ and under certain mathematical conditions it is known, for example, that (2.3) may exhibit asymptotic extinction, blowup or global asymptotic stability of a unique equilibrium. As ϕ is assumed strictly decreasing, in Appendix A we demonstrate that the scaling condition

$$1 = \phi(1)f^T(I - A_R)^{-1}e, \tag{2.4c}$$

and assumption

$A_R + ef^T$ is primitive, (2.4d)

together imply that

$$x^* := \gamma(I - A_R)^{-1}e, \tag{2.5}$$

is a unique nonzero equilibrium of (2.3) satisfying

$$x^* = (A_R + \phi(\|x^*\|_1)ef^T)x^*, \tag{2.6}$$

where $\gamma > 0$ is a normalisation constant ensuring that $\|x^*\|_1 = 1$. The primitivity assumption (2.4d) in fact implies that $A_R + ef^Tp$ is primitive for every $p > 0$ and, as already mentioned, is a reasonable assumption for ecological models.

We have not yet imposed assumptions that determine the dynamic behaviour of (2.3) away from the equilibrium x^*. Since we are primarily interested in behaviour near x^* and want to include as large a range of models as possible, we only prescribe the local assumption that

$$r(A_R + \phi(1)ef^T + \phi'(1)ef^Tx^*\mathbb{1}^T) < 1, \tag{2.4e}$$

where ϕ' denotes the derivative of ϕ and $\mathbb{1} \in \mathbb{R}_+^n$ is given by

$$\mathbb{1}^T := \begin{bmatrix} 1 & 1 & \ldots & 1 \end{bmatrix}.$$

Assumption (2.4e) implies that the equilibrium x^* of (2.3) is asymptotically stable, as explained in more detail in Section 2.3.

Remark 2.1. Deterministic models typically admit rescaling of their state-variables and parameters to give dimensionless quantities. The choice that x^* has $\|x^*\|_1 = 1$ is an essentially arbitrary scaling choice (made for ease of comparison) and may be replaced by $\|x^*\|_1 = \kappa$ for any $\kappa > 0$ by replacing $\phi(1)$ by $\phi(\kappa)$ in (2.4c) and throughout the manuscript. In the present context of modelling biological invasion the quantity $\|x^*\|_1 = 1$ is assumed to be "large" in absolute terms.

2.2. Coupled resident–invader population models

To model potential biological invasion into a resident population, denoted x, an invasive population is included and denoted z. The resident and invader are in competition, implying that their dynamics are coupled. The invader is assumed to be phenologically similar to the resident, and so its dynamics are also prescribed by a model of the form (2.3) with several terms in common. However, in order to possess some fitness advantage over the resident, the invader is assumed to have a density-dependent vital rate that differs from that of the resident. An invasion attempt means that the invader is introduced into the resident–invader model in a small proportion to the resident which is initially at its unique positive equilibrium x^*, given by (2.5). Therefore, the initial population distribution posits the resident at x^* and the invader at a "small" initial abundance. The stage-classes that are invaded into are not yet fixed. The source of an invasion attempt could include immigration, random mutation, planned reintroduction or unintentional transportation by humans [39].

The above considerations motivate a coupled resident–invader model of the form

$$\left.\begin{aligned}
x(t+1) &= (A_R + \phi(\|x(t)\|_1 + \|z(t)\|_1)ef^T)x(t), & x(0) &= x^*, \\
z(t+1) &= (A_I + \phi(\|x(t)\|_1 + \|z(t)\|_1)ef^T \\
&\quad + \alpha(\|z(t)\|_1)bc^T)z(t), & z(0) &= z^0,
\end{aligned}\right\} \; t = 0, 1, 2, \ldots \tag{2.4f}$$

where A_R, A_I are $n \times n$ nonnegative matrices, b, c, e and f are nonnegative, nonzero vectors with n components and $\alpha, \phi : \mathbb{R}_+ \to \mathbb{R}_+$ are nonnegative valued, continuous functions. The interpretation of the components in (2.4f) is similar to that of (2.3). Here the vectors b and c determine the entry (or entries) where the density-dependence α acts, which note appears only in the invader dynamics. The initial invader population distribution z^0 is assumed to be "small", representing a group of invaders at the point of invasion. Analogously to A_R, we impose two structural assumptions on A_I, namely,

$$r(A_I) < 1, \quad \text{and} \tag{2.4g}$$

$A_I + bc^T + ef^T$ is primitive, (2.4h)

the latter implying that $A_I + bc^T q + ef^T p$ is primitive for all $p, q > 0$.

One aspect to describing the fate of an invasion attempt is an understanding of the potential equilibria of (2.4f). We let the pair $(\bar{x}, \bar{z})$ with $\bar{x}, \bar{z} \in \mathbb{R}^n_+$ denote an equilibrium of (2.4f), meaning that $\bar{x}$ and $\bar{z}$ together satisfy

$$\bar{x} = (A_R + \phi(\|\bar{x}\|_1 + \|\bar{z}\|_1)ef^T)\bar{x},$$
$$\bar{z} = (A_I + \phi(\|\bar{x}\|_1 + \|\bar{z}\|_1)ef^T + \alpha(\|\bar{z}\|_1)bc^T)\bar{z}.$$

More details are given in Appendix A but, in summary, $(0, 0)$ and $(x^*, 0)$ are equilibria of (2.4f) by construction, independently of α. As mentioned in the Introduction, a premise of the current contribution is to test the reliability of the invasion exponent (described in detail in Section 2.3) in predicting the outcome of an invasion attempt, which we achieve through the inclusion of α. To ensure that the invasion exponent is negative we assume that α acts as an Allee effect: penalising invader fitness at low abundances of invader, which we capture as

$$A_I + \alpha(0)bc^T < A_R. \tag{2.4i}$$

The matrix inequality (2.4i) is understood componentwise, and means that every entry of $A_I + \alpha(0)bc^T$ is no bigger than that of A_R, and at least one entry is smaller. If the stronger condition

$$A_I + \alpha(q)bc^T < A_R, \quad \forall q \geq 0, \tag{2.7}$$

holds for α, then the only stable equilibrium[2] of (2.4)–(2.4i) is $(x^*, 0)$. Intuitively, the condition (2.7) implies that when the resident is initially present (that is, $\|x(0)\|_1 > 0$) the invader is too unfit to reach a nonzero equilibrium. Note that (2.7) *does not* rule out a perhaps significant transient presence of invader or other dynamic behaviour, such as a transition to periodic trajectories. In light of the Allee effect condition (2.4i), to permit the possibility of asymptotic establishment of the invader, the function α must boost invader fitness at some abundances. The assumption

there exists q with $0 < q < 1$ such that
$$\phi(1)f^T(I - (A_I + bc^T\alpha(q)))^{-1}e = 1, \tag{2.4j}$$

ensures the existence of (at least one, nonzero) co-existent equilibrium $(\hat{x}, \hat{z})$ of (2.4f). Certainly, for (2.4j) to hold, the condition (2.7) must fail, which means that there exists a q^* between zero and one such that a component of $A_I + \alpha(q^*)bc^T$ is bigger than or equal to the corresponding component of A_R. At these abundances the function α is increasing invader fitness. In the terminology of [18], the conjunction of (2.4i) and (2.4j) implies that α is a *strong* or *critical* Allee effect. Under assumption (2.4j) then there exist equilibria with nonzero invader part, depending on α. A sufficient condition for (2.4j) is that

there exists q with $0 < q < 1$ such that $A_I + \alpha(q)bc^T = A_R$.

We let (2.4) denote the resident–invader model and associated assumptions (2.4)–(2.4j) and seek to describe the resulting dynamic behaviour of (2.4). What constitutes a successful invasion is, of course, a matter of definition, that may largely depend on the specific context. Arguably, an invasion attempt *fails* if the solution x, z of (2.4) returns to the resident-only equilibrium $(x^*, 0)$ over time. For the purposes of the present contribution, we shall say that an invasion attempt *succeeds* if the invader abundance grows and persists asymptotically. For given model data $A_R, A_I, b, c, e, f, \phi$ and α, determining the outcome of an invasion attempt described by (2.4) amounts to whether (x^*, z^0) belongs to the basin of attraction of the resident-only equilibrium $(x^*, 0)$ or not. In the next section we recall the invasion exponent [13] of the model (2.4) and describe its role in estimating the basin of attraction.

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[2] Indeed, under assumption (2.7) there may be other equilibria of (2.4f), but they are all unattractive as $\|x(0)\|_1 = \|x^*\|_1 = 1 > 0$.

2.3. Linearisations and the invasion exponent

Let $\mathscr{B}$ denote the basin of attraction of the equilibrium $(x^*, 0)$ of (2.4), which recall is defined as

$$\mathscr{B} := \{(x^0, z^0) \in \mathbb{R}^n \times \mathbb{R}^n : \text{ the solution } x, z \text{ of (2.4) with } x(0)$$
$$= x^0 \text{ and } z(0) = z^0 \text{ satisfies } x(t) \to x^* \text{ and } z(t) \to 0 \text{ as } t \to \infty\}.$$

By definition of being an equilibrium, the set $\mathscr{B}$ always contains $(x^*, 0)$, and so $\mathscr{B}$ is never empty. A biological interpretation is that the larger $\mathscr{B}$ is, the "harder" it is for an invasion attempt to succeed.

Linear stability theory guarantees certain qualitative properties of $\mathscr{B}$ are described by the invasion exponent, which we discuss next. Linearising the resident–invader model (2.4) around $(x^*, 0)$ yields the approximation:

$$\begin{bmatrix} \tilde{x}(t+1) - x^* \\ \tilde{z}(t+1) \end{bmatrix}$$
$$= \underbrace{\begin{bmatrix} A_R + \phi(1)ef^T + \phi'(1)ef^Tx^*\mathbb{1}^T & \phi'(1)ef^Tx^*\mathbb{1}^T \\ 0 & A_I + \alpha(0)bc^T + \phi(1)ef^T \end{bmatrix}}_{=:\mathcal{A}}$$
$$\times \begin{bmatrix} \tilde{x}(t) - x^* \\ \tilde{z}(t) \end{bmatrix}, \ t = 0, 1, 2, \ldots, \tag{2.8}$$

where $\mathcal{A}$ is the Jacobian at $(x^*, 0)$ of (2.4f) and $\tilde{x}$ and $\tilde{z}$ denote the approximate resident and invader populations, respectively. The eigenvalues of $\mathcal{A}$ determine the asymptotic stability of the equilibrium $(x^*, 0)$ of (2.4f). Specifically, the equilibrium $(x^*, 0)$ is asymptotically stable if $r(\mathcal{A}) < 1$ which implies that $\mathscr{B}$ contains (at least) an open ball centred at $(x^*, 0)$, that is, there exists some $\eta > 0$ such that

$$\mathscr{N} := \{(x^0, z^0) \in \mathbb{R}^n \times \mathbb{R}^n : \|(x^0, z^0) - (x^*, 0)\| < \eta\} \subseteq \mathscr{B},$$

where $\|\cdot\|$ denotes a norm on the product space $\mathbb{R}^n \times \mathbb{R}^n$. Of course, $\mathscr{B}$ may be much larger than $\mathscr{N}$: the condition $r(\mathcal{A}) < 1$ itself does not say. In any case, if $r(\mathcal{A}) < 1$ then invasion attempts by sufficiently low initial abundances of invaders should fail. Owing to the upper-triangular block structure of $\mathcal{A}$, it follows that

$$r(\mathcal{A}) = \max\{r(A_R + \phi(1)ef^T + \phi'(1)ef^Tx^*\mathbb{1}^T), r(A_{\text{inv}})\}, \tag{2.9}$$

where $A_{\text{inv}} := A_I + \alpha(0)bc^T + \phi(1)ef^T$ and

$$\theta := \ln(r(A_{\text{inv}})), \tag{2.10}$$

is the invasion exponent. Since the resident equilibrium x^* is assumed to be asymptotically stable (2.4e), in light of (2.9), $r(\mathcal{A}) < 1$ occurs precisely when $r(A_{\text{inv}}) < 1$; equivalently when $\theta < 0$, that is, when the invasion exponent is negative. However, the conjunction of the scaling condition (2.4c), the Allee effect condition (2.4i) and the primitivity assumption (2.4h) implies that the model (2.4) always possesses $r(A_{\text{inv}}) < 1$ and so $\theta < 0$.

3. Population inertia and linear Lyapunov functions

The matrix PPM (2.1) with state variable y, the density-dependent single population model (2.3) with state variable x and the coupled resident–invader model (2.4) with state variables x (for resident) and z (for invader) are examples of *positive dynamical systems* because, naturally, their state-variables are componentwise nonnegative. Positive dynamical systems, and related monotone dynamical systems, are well-studied. We refer the reader to, for example, [40–42] for more background. As well as enabling the modelling of physically or biologically motivated systems, the positivity imparts rich additional mathematical structure (such as the already used Perron–Frobenius Theorem) which we shall exploit in seeking to predict biological invasion. We shall make use of the fact that the left eigenvector of a primitive matrix corresponding to the spectral radius induces a linear functional which, novelly in this context, acts as a Lyapunov function

for the invader dynamics of the resident–invader model (2.4). Consequently, we derive a sufficient condition for an invasion attempt to fail. As we explain, the functional also arises in matrix projection modelling where it is called population inertia [27].

By way of motivation, consider first the matrix PPM (2.1), and assume from hereon in that A in (2.1) is primitive. Associated with A is the spectral radius $r(A)$ (see (2.2)), its stable stage-structure w and reproductive vector v^T which are the unique (up to scaling) positive right and left eigenvectors of A corresponding to $r(A)$, respectively. Under these assumptions, the solution y of (2.1) satisfies

$$\lim_{t \to \infty} r(A)^{-t} y(t) = \frac{v^T y^0}{v^T w} w. \tag{3.1}$$

The vector w is called the stable-stage structure because, by construction, $Aw = r(A)w$. Therefore, populations distributed according to w do not change their proportional distribution over time (though their abundance changes via multiplication by the spectral radius $r(A)$). The vector v^T is called the reproductive vector as it contains the reproductive values (as in [43]) of each stage-class [44]. The product $v^T y^0$ that appears in the numerator of (3.1) contains the contributions to the asymptotic population from the initial population distribution y^0. The nonnegative constant

$$\frac{v^T y^0}{v^T w}, \tag{3.2}$$

is defined as the population inertia of A from y^0 and note is the scalar multiplier on the right-hand side of (3.1). Noting that the population inertia from $y^0 = w$ is one; the population inertia of A from arbitrary y^0 is a long term multiplicative ratio of the size of the population projected from y^0 compared to that projected from stable stage-structure w. Since inertia obviously increases with increasing $\|y^0\|_1$, to compare the inertia of y_1^0 and y_2^0, say, both are scaled so that, for instance, $\|y_1^0\|_1 = \|y_2^0\|_1 = 1$. Although inertia describes an asymptotic quantity of a matrix PPM, it has a link to transient behaviour as well. To see this define the functional

$$\mathbb{R}_+^n \ni y \mapsto V(y) := \frac{v^T y}{v^T w}, \tag{3.3}$$

which induces a norm on $\mathbb{R}_+^n$, equivalent to the one-norm, as v^T a positive vector implies that

$$\min_{1 \le j \le n} \frac{v_j}{v^T w} \|y\|_1 \le V(y) \le \max_{1 \le j \le n} \frac{v_j}{v^T w} \|y\|_1, \quad \forall y \in \mathbb{R}_+^n.$$

Since v^T is the left eigenvector of A corresponding to the eigenvalue $r(A)$ it follows that V is a Lyapunov function for (2.1) because

$$V(y(t+1)) = \frac{v^T y(t+1)}{v^T w} = \frac{v^T A y(t)}{v^T w}$$
$$= r(A) \frac{v^T y(t)}{v^T w} = r(A) V(y(t)), \quad t = 0, 1, 2, \dots. \tag{3.4}$$

The scalar difference equation (3.4) has solution

$$V(y(t)) = r(A)^t V(y^0), \quad t = 0, 1, 2, \dots. \tag{3.5}$$

In particular, if $r(A) < 1$ then $V(y(t)) \to 0$ as $t \to \infty$ and as v^T is positive it follows that

$$y(t) \to 0 \quad \text{as } t \to \infty. \tag{3.6}$$

However, by inspection of the right-hand side of (3.5) the short term growth (or decline) of $V(y(t))$, and thus that of $y(t)$, is proportional to $V(0)$—the population inertia of A from y^0. Of course, when $r(A) < 1$ then (3.6) is straightforward to see without using V as the solution y of the linear PPM (2.1) may be written down explicitly. We proceed to demonstrate that V defined analogously to (3.3) but in terms of the linearised invader dynamics, induces a Lyapunov function for the *nonlinear* invader specified in (2.4). We formulate our main mathematical result as the following theorem, a proof of which is given in Appendix B.

Theorem 1. *Given the coupled resident–invader model (2.4), let ξ^T and ζ denote the positive left and right eigenvectors of $A_{inv} = A_I + \alpha(0)bc^T + \phi(1)ef^T$ corresponding to $r(A_{inv}) =: r < 1$, respectively, and define $V : \mathbb{R}_+^n \to \mathbb{R}_+$ by*

$$\mathbb{R}_+^n \ni y \mapsto V(y) := \frac{\xi^T y}{\xi^T \zeta}.$$

Writing $z^0 = \delta \bar{z}$ where $\delta > 0$ and $\bar{z} \in \mathbb{R}_+^n$ has $\|\bar{z}\|_1 = 1$, let x and z denote the solution of (2.4) and additionally assume that there exists $a > 0$ such that

$$|\alpha(y) - \alpha(0)| \le a|y|, \quad \forall y \ge 0. \tag{3.7}$$

There exists $\delta_0 > 0$ such that if $0 < \delta < \delta_0$, then

$$\varepsilon := (v^T e) \max_i \left(\frac{f_i}{\xi_i} \right) \max_{t \in \mathbb{N}_0} |\phi(\|x(t)\|_1 + \|z(t)\|_1) - \phi(1)| < \frac{1-r}{2}. \tag{3.8}$$

If $\delta \in (0, \delta_0)$ satisfies

$$a\delta \Delta V(\bar{z}) < 1 - (r + \varepsilon) < 1, \tag{3.9}$$

where

$$\Delta := (\xi^T b)(\xi^T \zeta) \max_j \left(\frac{1}{\xi_j} \right) \max_i \left(\frac{c_i}{\xi_i} \right), \tag{3.10}$$

then

$$z(t) \to 0, \quad \text{as } t \to \infty.$$

Theorem 1 provides a sufficient condition, namely the estimate (3.9), for an invasion attempt to fail. The next section, Section 4, contains numerical examples highlighting the conclusions of Theorem 1. Before that we provide some remarks.

Remark 3.1. The estimate (3.9) relates the roles of the Allee effect/boost to fitness function α, captured through a, the population inertia of the linearised invader dynamics $V(\bar{z})$ and the initial invader abundance or density δ. Particularly we see that their product must be small to ensure that invasion fails, which suggests that when one is fixed, there is an inverse relationship between the other two. The quantity Δ in (3.9) is a constant, that depends on the model in question. Note that Δ is independent of the scaling of ξ chosen, and the product $\Delta V(\bar{z})$ is independent of the scaling of ζ chosen.

4. Examples

For our numerical examples we consider an age-structured resident–invader model (2.4) with three age-classes, so that $n = 3$. We choose

$$A_R = \begin{bmatrix} 0 & 0 & 0 \\ g_1 & 0 & 0 \\ 0 & g_2 & 0 \end{bmatrix}, \quad A_I = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & g_2 & 0 \end{bmatrix},$$

$$e = \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix}, \quad b = \begin{bmatrix} 0 \\ g_1 \\ 0 \end{bmatrix}, \quad \begin{array}{l} f^T = [f_1 \ f_2 \ f_3], \\ c^T = [1 \ 0 \ 0], \end{array} \tag{4.1}$$

for $0 < g_1, g_2 < 1$ and $f_1, f_2, f_3 > 0$. The g_i denote transition rates from stage-class i to $i+1$ and, as survival rates, are no greater than one. Each f_i denotes the recruitment rate (fecundity combined with survival) of stage-class i. We separately consider invasion into each stage class, yielding $z^0 = \delta \bar{z}$ with $\delta > 0$ and

$$\bar{z} \in \left\{ \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} 0 \\ 1 \\ 0 \end{bmatrix}, \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix} \right\}.$$

The parameter $\delta > 0$ denotes the initial abundance of invader. We assume that the density-dependence ϕ is given by

$$\mathbb{R}_+ \ni q \mapsto \phi(q) := \exp\left(-\frac{q}{10} \right), \tag{4.2}$$
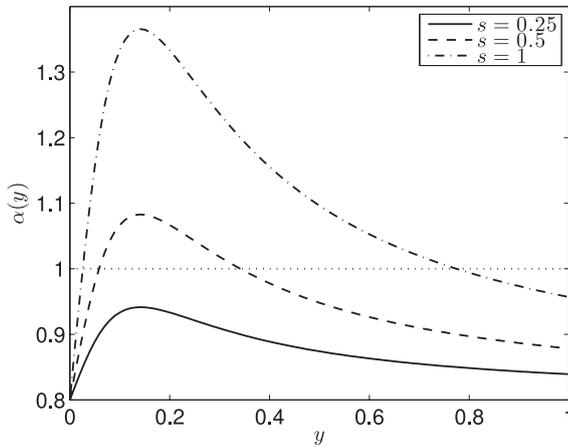
Fig. 1. Graphs of the function α in (4.3) for three values of strength parameter, s.

which satisfies (2.4b). The vital rates g_1, g_2, f_1, f_2 and f_3 are still to-be-determined, but recall are chosen to satisfy the scaling condition (2.4c)

$$1 = \phi(1)f^T(I - A_R)^{-1}e = \phi(1)[f_1 + f_2 g_1 + f_3 g_1 g_2].$$

To parameterise a family of Allee effects α, we choose

$$\mathbb{R}_+ \ni q \mapsto \alpha(q) := \frac{4}{5}\left(1 + s\frac{10q}{1 + 50q^2}\right), \quad s > 0, \tag{4.3}$$

where $s > 0$ is a strength parameter. As s increases the function $\alpha(q)$ takes larger values for positive q, denoting increasing invader fitness, but $\alpha(0) = 0.8 < 1$ is independent of s. Consequently, for every positive s, α satisfies (2.7). Fig. 1 contains the graphs of α for several values of s: regions where $\alpha(y) > 1$ denote invader abundances at which the invader is fitter than the resident. In Appendix C we demonstrate that the condition (2.4j) holds for the data specified by (4.1)–(4.3) (when the parameter $s > 0$ is larger than a critical value denoted s_m).

By way of explanation of (4.1), we note that for $g_1, g_2, f_1, f_2, f_3 > 0$ the density-*independent* resident matrix $A_R + ef^T$ equals the Leslie matrix [45]:

$$\begin{bmatrix} f_1 & f_2 & f_3 \\ g_1 & 0 & 0 \\ 0 & g_2 & 0 \end{bmatrix}. \tag{4.4}$$

The inclusion of ϕ in (2.4f) ensures that the recruitment component ef^T (the top row of the matrix in (4.4)) is density-dependent. Similarly, the density-*independent* invader matrix is $A_I + ef^T + bc^T$ and equals that in (4.4). In the full model (2.4f), α multiplies the growth rate g_1 of the invader projection matrix which, at low invader abundances, is smaller than that of the resident. Here α is acting as an Allee effect; penalising invader survival. However, at larger abundances, α takes values greater than one, boosting invader survival compared to that of the resident.

To explore the roles of s and population inertia in determining the outcome of an invasion attempt we perform the following numerical study. We fix

$$g_1 = g_2 = 0.1, \tag{4.5}$$

in (4.1) and generate models (2.4) by varying the initial abundance δ, the age-class which is invaded into, the recruitment terms f_1, f_2, f_3 and the strength parameter s in α. First, four δ values are used, varying between

$$6.25 \times 10^{-4} \leq \delta \leq 4 \times 10^{-3}, \tag{4.6}$$

corresponding to 0.0625%–0.4% of initial resident abundance, dependent on which age-class is invaded into. As we explained in Remark 2.1, the dimensionless scaling assumption $\|x^*\|_1 = 1$ denotes

a "large" resident abundance. Therefore, although δ in (4.6) is a small proportion of $\|x^*\|_1 = 1$, we assume that it is still reasonably large in absolute terms.

With ϕ and g_1, g_2 chosen in (4.2) and (4.5), respectively, the equation (2.4c) determines a plane in the remaining three unknowns f_1, f_2 and f_3. The section of this plane in the positive orthant, that is,

$$f_1, f_2, f_3 > 0.01 \quad \text{such that} \quad \exp\left(-\frac{1}{10}\right)\left[f_1 + \frac{f_2}{10} + \frac{f_3}{100}\right] = 1, \tag{4.7}$$

is partitioned into 400 points (equally spaced in the (f_1, f_2)–plane), generating 400 models (2.4). The Leslie matrix $A_R + ef^T$ in (4.4) is *not* primitive if $f_2 = f_3 = 0$ and so the lower bound for the f_i in (4.7) simply prevents that possibility. For each choice of δ and f^T satisfying (4.6) and (4.7), respectively, the strength parameter s in (4.3) is increased from $\sqrt{2}/4$ to 16 in increments of 0.01 and the minimum s recorded that resulted in successful invasion. An invasion is considered successful if for 10 successive time steps t_i

$$\|x(t_i)\|_1 < 1 - \frac{\sqrt{2}}{10} \approx 0.8586 \quad \text{or} \quad \|x(400)\|_1 < 1 - \frac{\sqrt{2}}{10}, \tag{4.8}$$

and unsuccessful otherwise. The minimum s required for a successful invasion when invasion occurred, or $s = 0$ when no invasion occurred, is plotted against the population inertia and the invasion exponent of the linearised invader in Figs. 2–4. The specific choices for the successful invasion threshold in (4.8) and strength parameter interval $[\sqrt{2}/4, 16]$ are justified in Appendix C. Briefly, they are consequences of the choice of model data (4.1)–(4.3) and (4.5) and the resulting equilibrium analysis. The number $1 - \sqrt{2}/10$ in (4.8) is the largest possible resident equilibrium abundance for which the invader is also at a nonzero equilibrium.

From Figs. 2(a)–4(a) the following trends are observed:

(i) the largest value of population inertia is achieved in the third stage class, which also has a larger range of inertias than stage classes one and two (compare the x-axes of Figs. 2(a)–4(a));

(ii) at very low values of inertia, invasion did not succeed for any s or δ value, marked by crosses (see bottom left of Figs. 3(a) and 4(a));

(iii) for fixed population inertia, the minimal s required for successful invasion decreases as δ increases (the increase in δ is depicted in different line styles from dotted through to solid);

(iv) for fixed s, invasion is successful if the combination of δ and inertia together are sufficiently large (for each horizontal line in the figures, as δ decreases, the population inertia required for successful invasion increases);

(v) for fixed δ, the minimal s required for successful invasion decreases as inertia increases (for each line style, there is a broadly inverse relationship between minimal s required for successful invasion and population inertia);

(vi) invasion attempts into the third stage class succeed at lower initial abundances δ than invasion into the first stage class (the δ values used to generate Fig. 4(a) are smaller than those used in Figs. 2(a) and 3(a)—see the figure legends).

The trends observed in (ii)–(v) are suggested by (the admittedly conservative) Theorem 1. For the choice of model (4.1)–(4.3), the estimate (3.9) for an invasion attempt to fail becomes

$$a\delta \Delta V(\bar{z}) = 8s\delta\left[\frac{\xi_2}{\xi_1}(\xi^T\zeta)\max_{1 \leq j \leq 3}\left(\frac{1}{\xi_j}\right)\right]V(\bar{z}) < 1 - (r + \varepsilon) < 1,$$

where we have substituted the choice of b and c into the expression (3.10) for Δ and have obtained $a = 8s$ in (3.7) via

$$|\alpha(y) - \alpha(0)| \leq \alpha'(0)y = 8sy, \quad \forall y \geq 0.$$

As the quantities Δ and r depend on f^T, they vary as f^T varies. Despite this variation, Figs. 2(a)–4(a) demonstrate that there is still a (broadly)
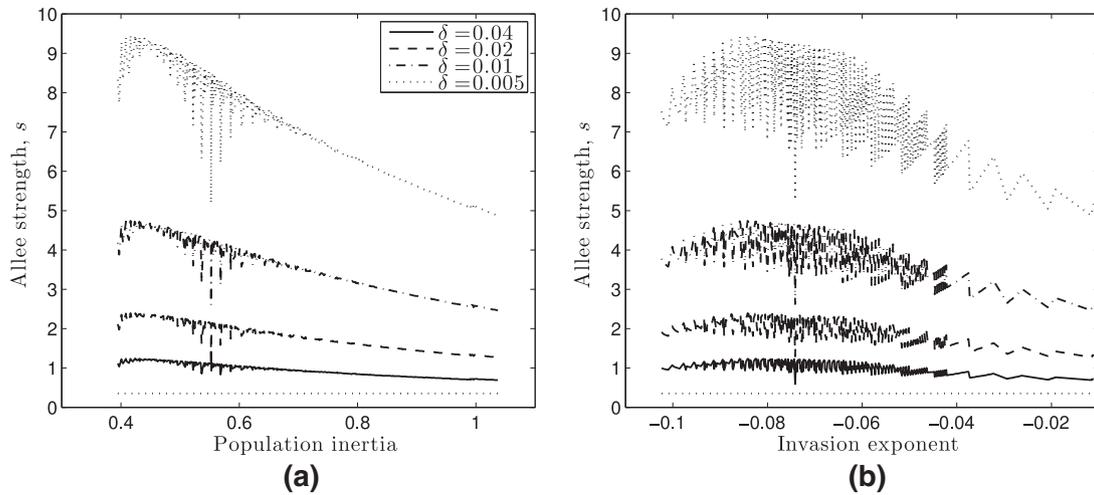
Fig. 2. Invasion into the first stage class: Minimal *s* required for successful invasion plotted against inertia (a) and invasion exponent (b) of the coupled-resident–invader model (2.4) specified in Section 4. Different line styles correspond to different initial invader abundance δ. The horizontal dotted line denotes $s = s_m$, the smallest *s* value considered.
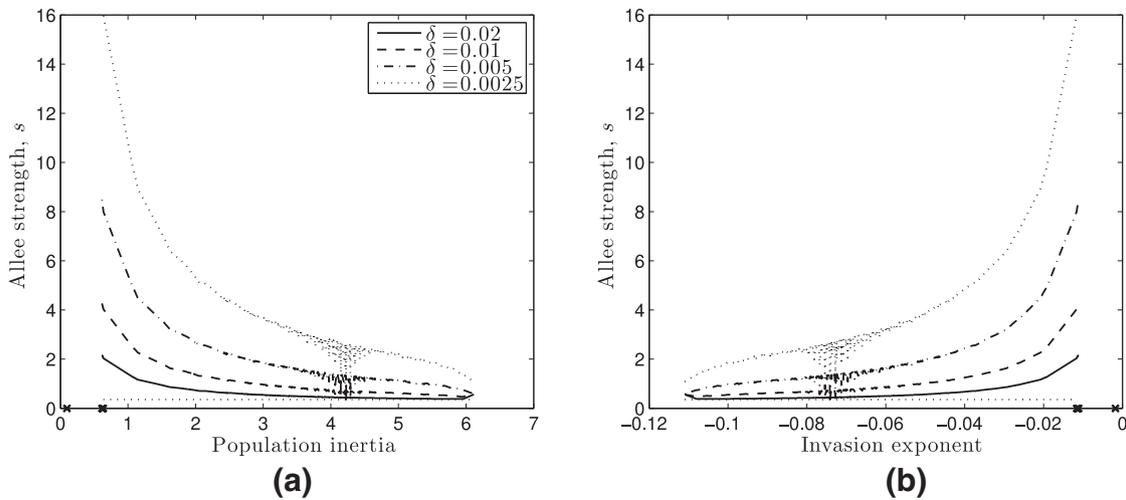
Fig. 3. Invasion into the second stage class: Minimal *s* required for successful invasion plotted against inertia (a) and invasion exponent (b) of the coupled-resident–invader model (2.4) specified in Section 4. Different line styles correspond to different initial invader abundance δ. The horizontal dotted line denotes $s = s_m$, the smallest *s* value considered.
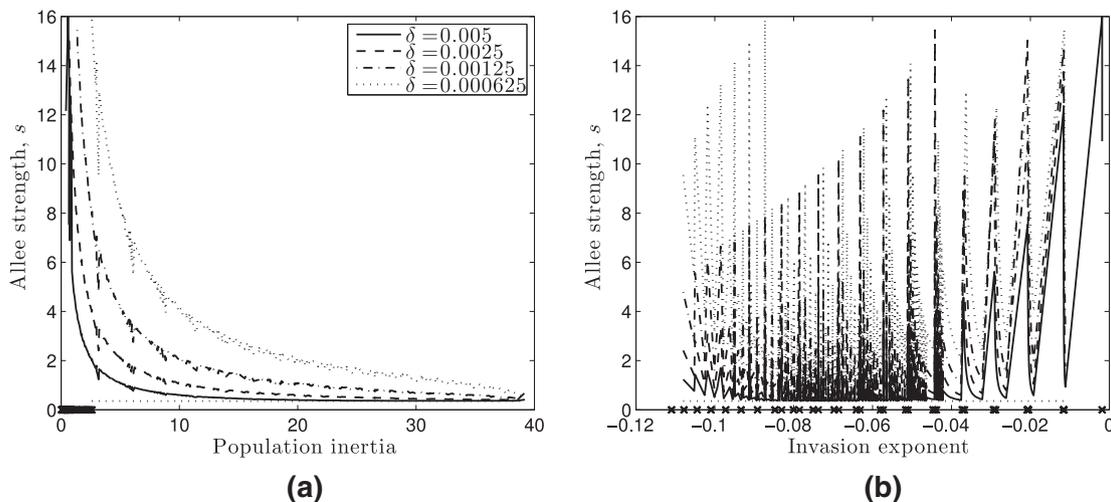
Fig. 4. Invasion into the third stage class: Minimal *s* required for successful invasion plotted against inertia (a) and invasion exponent (b) of the coupled-resident–invader model (2.4) specified in Section 4. Different line styles correspond to different initial invader abundance δ. The horizontal dotted line denotes $s = s_m$, the smallest *s* value considered..

inverse relationship between population inertia and the minimal s required for a successful invasion. Property (vi) may be attributed to the fact that stage-class three admits much larger values of inertia than stage-class one, and thus a smaller δ is required for a successful invasion attempt.

From Figs. 2(b)–4(b) we see that the corresponding relationships in (iv) and (v) between the minimal s required for invasion and invasion exponent *do not* always hold. Indeed, compared to (v), in Figs. 2(b)–4(b) there is a (roughly) decreasing, increasing and then no obvious monotone relationship between invasion exponent and minimal s required for successful invasion, respectively.

5. Discussion

A mathematical investigation into a class of structured models for coupled resident–invader populations has been conducted. The aim of the investigation has been to help answer the question "what quantifiers are indicative in predicting the outcome of an invasion attempt?" We consider mean-field models with an additional Allee effect which ensures that at infinitesimally small abundance of an invasion attempt, invasion will fail. Therefore, it is reasonable to expect that in order to reach a critical threshold abundance, fitter invaders will have to find a fitness advantage elsewhere. What we find from our study is that a proxy for this fitness advantage is the (linearised) invader's population inertia—invasive populations with high population inertia are better adapted to invade than those with lower inertia. More precisely, our main result, Theorem 1, states that for the class of models (2.4) considered, when the combination of inertia, the initial invader abundance and boost to invader fitness from density-dependent terms is small, then invasion cannot succeed. Furthermore, there is an inverse relationship between these three quantities, so for a fixed initial abundance of invader, as inertia increases, the boost to invader fitness required so that an invasion attempt *does not* fail is smaller. The dependence on the three parameters was estimated by appealing to the fact that, as an example of a positive system, underpinned by the Perron–Frobenius Theorem, the model admits a linear Lyapunov functional. In the special case of linear matrix PPMs used in ecological modelling, the Lyapunov functional used goes by the name of population inertia. A heuristic explanation of why large population inertia is indicative of successful invasion is that inertia is an index of transient growth or decline. Loosely speaking, initial invader population distributions with large inertia amplify rapidly in the short term meaning that after just a few time-steps the linearisation (2.8) is not a reliable approximation of (2.4). Conversely, initial invader population distributions that have low inertia tend to attenuate in the short term, from which the linearisation (2.8), now justifiably usable, predicts asymptotic extinction of the invader.

Parallel to the role of population inertia in predicting the outcome of an invasion attempt, we also considered the role of the invasion exponent. Our numerical examples demonstrated that the invasion exponent was not always a reliable indicator of the outcome of an invasion attempt. Particularly we noted that an increasing exponent (which might suggest invasion becoming more likely) did not always result in a smaller boost to invader fitness required for successful invasion. In Fig. 3(b) the opposite relationship was observed: invasion exponents close to zero required a large boost to fitness for successful invasion, and in Fig. 4(b) no obvious monotone relationship was observed. Why should the invasion exponent provide a less reliable comparative index in predicting invasion than an index of transient growth or decline? To fully answer that question is beyond the scope of the present contribution, and instead we provide some suggestions. The transition from non-invasion to invasion in the model is a qualitative shift of dynamical behaviour. That such a transition might not be well predicted by changes in an eigenvalue (the invasion exponent) was highlighted in the seminal work [50] related to the transition from laminar to turbulent flow in hydrodynamic stability theory and

was itself motivated by the apparent mismatch between predictions based on models and real observations. The subsequent research on the so-called pseudospectrum and pseudospectral techniques [51] seeks, amongst other things, to describe the dynamics of *non-normal* dynamical systems. A matrix A is normal if $A^T A = A A^T$, and non-normal otherwise. Non-normal matrices are pervasive in that almost every square matrix is non-normal in the same manner that almost every square matrix is invertible. A dynamical system is non-normal if its Jacobian is a non-normal matrix (assuming of course that the Jacobian is well-defined). Broadly speaking, a main result is that the qualitative behaviour of non-normal dynamical systems and qualitative changes of dynamical behaviour, such as the transition from laminar to turbulent flow, are not well-described by eigenvalues, but rather by the pseudospectrum. The pseudospectrum of a matrix A is the set of complex numbers that are "nearly" eigenvalues (informally, they are the eigenvalues of a perturbation of A, $A + E$, say, where the norm of E is small). Normal matrices have benign pseudospectra, and non-normal matrices may have very complicated pseudospectra. The *departure from normality*, that is, exactly how "non-normal" is a non-normal matrix is not captured entirely by any one scalar index [51, Section 48], much like transient dynamics. However, through the study of pseudospectra, a connection is made between non-normal matrices and marked transient growth or decline—as has been documented in a biological context in, for example, [25]. When recruitment is large compared to survival rates, population projection matrices are typically non-normal. In projection matrix models, if the recruitment vector f^T is highly skewed, so that some stage-classes are much more fecund than others, then the left eigenvector v^T (the so-called reproductive vector in ecological models) usually is as well. Wide variation in the components of v^T gives rise to stage-classes with very large inertia, and stages with very small inertia. It is these former stage-classes that are much more likely to succeed in an invasion attempt, as observed across Figs. 2(a)–4(a).

The models we consider are mean-field, averaged or population level, and as deterministic models do not contain stochastic components. Stochasticity in ecological modelling is typically divided into demographic and environmental stochasticity [46], and is a powerful language for describing ecological processes. Indeed, Liebhold & Bascompte write in [47]: "Random processes affect the dynamics of virtually all populations." Our justification for using deterministic models is that they often appear as the limit (as population size tends to infinity) of finite-size population models; an example being the Lotka predator-prey differential equations, see [48]. Deterministic models for invasion, such as those considered here, are then most appropriate and efficacious when the number of resident individuals is large in absolute terms (which, of course, in practice is species specific). Our assertions are relevant when an invasion attempt is by a large number of individuals (but a small proportion of the resident population). We refer the reader to the work of McKane and collaborators, such as the review [49] and the references therein, for more information on stochastic and deterministic models in biology and ecology and particularly how the latter provide approximation of the former in the limit as population size tends to infinity. In summary, the outcome of many biological processes (such as the success or failure of an invasion attempt) involving just a few individuals is essentially random and thus will be only crudely approximated by population level models.

In closing, we reiterate our central thesis that one should critique carefully the reliance on infinitesimals (overcoming the caveat "how small is small enough") tied to using the invasion exponent to predict the outcome of invasion in stage-structured models. An obvious retort to our findings is, well, "how large is large population inertia?" In light of Theorem 1 our response is that population inertia *is* a comparative measure—if one modelled population has a larger inertia than another then, all else equal, it is more likely to be a successful invader.

Appendix A. Equilibria analysis

Here we describe equilibria of the single population model (2.3), the coupled resident–invader model (2.4f) and the role of the extra assumptions in (2.4). That zero and (0,0) are equilibria of (2.3) and (2.4f), respectively, is clear. We note that if $z(0) = 0$ then (2.4f) collapses to (2.3). We proceed to derive the equilibrium x^* of (2.3) which, in light of the previous sentence, implies that $(x^*, 0)$ is an equilibrium of (2.4). An equilibrium x^* of (2.3) satisfies (2.6) and occurs if, and only if, x^* is an eigenvector of $A_R + \phi(\|x^*\|_1)ef^T$ corresponding to the eigenvalue one. For $y \geq 0$, one is an eigenvalue of $A_R + \phi(y)ef^T$ if, and only if, there exists $v \in \mathbb{R}^n$, $v \neq 0$ such that

$$(A_R + \phi(y)ef^T)v = v. \tag{A.1}$$

Since $r(A_R) < 1$ and thus $1 \notin \sigma(A_R)$, $I - A_R$ is invertible and we may rearrange (A.1) to give

$$\phi(y)ef^Tv = (I - A_R)v \quad \Rightarrow \quad (I - A_R)^{-1}\phi(y)ef^Tv = v,$$

and multiplying by f^T on the left yields

$$\phi(y)f^T(I - A_R)^{-1}ef^Tv = f^Tv. \tag{A.2}$$

Since $1 \notin \sigma(A_R)$ it follows from (A.1) that $f^Tv \neq 0$ which we invoke in (A.2) to deduce that

$$\phi(y)f^T(I - A_R)^{-1}e = 1. \tag{A.3}$$

According to (2.4c), f^T is chosen so that (A.3) holds when $y = 1$. Furthermore, as ϕ is strictly decreasing, (A.3) *only* holds for $y = 1$. A straightforward calculation using x^* defined by (2.5) shows that (A.3) is sufficient for x^* to satisfy (2.6). Therefore, (2.4c) is necessary and sufficient for x^* defined by (2.5) with $\|x^*\|_1 = 1$ to be an equilibrium of (2.3). Since $A_R + \phi(1)ef^T$ is assumed primitive in (2.4d), it follows from the Perron–Frobenius Theorem that x^* is unique up to multiplication by a positive scalar. The scaling γ of x^* has been fixed, however, by the constraint that $\|x^*\|_1 = 1$. We note further that the above arguments demonstrate that the conditions (A.3) and (A.1) imply one another and are thus equivalent.

A general equilibrium $(\hat{x}, \hat{z})$ of (2.4f) satisfies

$$\hat{x} = (A_R + \phi(\|\hat{x}\|_1 + \|\hat{z}\|_1)ef^T)\hat{x}, \tag{A.4a}$$

and

$$\hat{z} = (A_I + \alpha(\|\hat{z}\|_1)bc^T + \phi(\|\hat{x}\|_1 + \|\hat{z}\|_1)ef^T)\hat{z}, \tag{A.4b}$$

where note that we only seek nonnegative solutions, so that $\hat{x}, \hat{z} \in \mathbb{R}^n_+$. If $\hat{x} \neq 0$, then from (A.4a) and the derivation of $(x^*, 0)$ above, it follows that

$$\|\hat{x}\|_1 + \|\hat{z}\|_1 = 1, \tag{A.5}$$

as $A_R + \phi(\|\hat{x}\|_1 + \|\hat{z}\|_1)ef^T$ only has spectral radius one when the argument of ϕ is equal to one. If $\hat{z} = 0$, then we recover $(\hat{x}, \hat{z}) = (x^*, 0)$, so assume that $\hat{z} \neq 0$. The condition (A.5) now implies that both

$\|\hat{x}\|_1, \|\hat{z}\|_1 < 1$. Clearly, (A.4b) holds if, and only if,

$$1 \in \sigma(B) \quad \text{where} \quad B := A_I + \alpha(\|\hat{z}\|_1)bc^T + \phi(1)ef^T. \tag{A.6}$$

In words, (A.4b) is equivalent to one being an eigenvalue of the matrix B given in (A.6). Recalling that (A.1) and (A.3) are equivalent (derived above), it follows that (A.6) is equivalent to

$$\phi(1)f^T(I - (A_I + bc^T\alpha(\|\hat{z}\|_1))^{-1}e = 1. \tag{A.7}$$

To see this argue from (A.1) with A_R replaced by $A_I + bc^T\alpha(\|\hat{z}\|_1)$ and y replaced by 1. The equation (A.7) has at least one solution with $\|\hat{z}\|_1 \in (0, 1)$ by assumption (2.4j). Moreover, every solution $q \in (0, 1)$ of (2.4j) gives rise to an equilibrium $(\hat{x}, \hat{z})$ with $\hat{x} = (1 - q)x^*$ and $\hat{z}$ an eigenvector of B in (A.6) corresponding to the eigenvalue one with $\|\hat{z}\|_1 = q$. The eigenvector $\hat{z}$ is uniquely determined by the Perron–Frobenius Theorem (as here $r(B) = 1$).

Note that an invader only equilibrium $(0, z^*)$ occurs if, and only if, there exists $q > 0$ such that

$$\phi(q)f^T(I - (A_I + \alpha(q)bc^T))^{-1}e = 1. \tag{A.8}$$

Each solution $q > 0$ of (A.8) gives rise to the unique equilibrium $(0, z^*)$ where z^* is the positive eigenvector of $A_I + \alpha(q)bc^T + \phi(q)ef^T$ corresponding to the eigenvalue one, with $\|z^*\|_1 = q$. Again, unicity of z^* is ensured by the Perron–Frobenius Theorem.

To see that both the zero equilibrium and any invader-only equilibrium $(0, z^*)$ with $\|z^*\|_1 < 1$ are not attractive, and hence not asymptotically stable, let v_*^T denote the simple, positive left eigenvector of $A_R + \phi(1)ef^T$, corresponding to the eigenvalue one, and consider the functional $y \mapsto V(y) = v_*^Ty$ (see (3.3)), which is positive definite on $\mathbb{R}^3_+$. For $t = 0, 1, 2, \ldots$, the resident population $x(t)$ satisfies

$$W(x(t + 1)) = v_*^Tx(t + 1) = W(x(t)) + v_*^Tef^Tx(t)[\phi(N(t)) - \phi(1)],$$
$$\geq (1 + \varepsilon)W(x(t)), \quad \text{whenever } 0 \leq N(t) < \rho \leq 1, \tag{A.9}$$

for some fixed $\rho \in (0, 1)$ and $\varepsilon > 0$.

Appendix B. Proof of Theorem 1

The existence of (a sufficiently small) $\delta_0 > 0$ such that $\varepsilon > 0$ defined by (3.8) which satisfies

$$0 < \varepsilon < \frac{1 - r}{2},$$

for all $\delta \in (0, \delta_0)$ is ensured by the asymptotic stability of (2.4) and the continuity of ϕ. For $\delta \in (0, \delta_0)$ we now compute for $t \in \mathbb{N}_0$

$$0 \leq V(z(t + 1)) = \frac{\xi^Tz(t + 1)}{\xi^T\zeta} = \frac{\xi^T}{\xi^T\zeta}(A_I + \alpha(\|z(t)\|_1)bc^T$$
$$+ \phi(\|x(t)\|_1 + \|z(t)\|_1)ef^T)z(t)$$
$$= rV(z(t)) + (\xi^Tb)[\alpha(\|z(t)\|_1) - \alpha(0)]\frac{c^Tz(t)}{\xi^T\zeta}$$
$$+ (\xi^Te)[\phi(\|x(t)\|_1 + \|z(t)\|_1) - \phi(1)]\frac{f^Tz(t)}{\xi^T\zeta},$$
$$\leq rV(z(t)) + a(\xi^Tb)\|z(t)\|_1\frac{c^Tz(t)}{\xi^T\zeta}$$
$$+ (\xi^Te)[\phi(\|x(t)\|_1 + \|z(t)\|_1) - \phi(1)]\frac{f^Tz(t)}{\xi^T\zeta}, \tag{B.1}$$

where we have used the bound (3.7) for α to obtain (B.1). Invoking (3.8) to estimate the final term on the right-hand side of (B.1) yields the inequality

$$V(z(t + 1)) \leq (r + \varepsilon)V(z(t)) + a(\xi^Tb)\|z(t)\|_1 \max_i \left(\frac{c_i}{\xi_i}\right)V(z(t)). \tag{B.2}$$

We seek to bound $\|z(t)\|_1$ on the right-hand side of (B.2) by a term involving $V(z(t))$. To that end, noting that

$$\|z(t)\|_1 = \sum_{k=1}^{n} z_k(t) = \sum_{k=1}^{n} \frac{\xi_k z_k(t)}{\xi_k} \leq \max_k \left(\frac{1}{\xi_k}\right) \xi^T z(t)$$

$$= \max_k \left(\frac{1}{\xi_k}\right) (\xi^T \zeta) V(z(t)), \tag{B.3}$$

since each $\xi_k > 0$, we insert (B.3) into (B.2) to obtain

$$V(z(t+1))$$
$$\leq \left(r + \varepsilon + a(\xi^T b)(\xi^T \zeta) \max_j \left(\frac{1}{\xi_j}\right) \max_i \left(\frac{c_i}{\xi_i}\right) V(z(t))\right) V(z(t)). \tag{B.4}$$

The claim in the theorem follows once the bracketed term on the right-hand side of (B.4) is less than one for all $t \in \mathbb{N}_0$. However, by induction, this follows from (B.4) once it holds for $t = 0$, as then the quantity $V(z(t))$ is decreasing with increasing t. In other words, if

$$r + \varepsilon + a(\xi^T b)(\xi^T \zeta) \max_j \left(\frac{1}{\xi_j}\right) \max_i \left(\frac{c_i}{\xi_i}\right) V(z(0)) < 1,$$

then the theorem holds, which is precisely (3.9), as required.

Appendix C. Supplementary analysis for numerical examples

Here we apply the results of Appendix A to the model (4.1)–(4.3) considered in Section 4. These calculations are also used to help determine suitable parameter ranges for our numerical projections.

For A_R, A_I, b and c given by (4.1) a shared equilibrium $(\hat{x}, \hat{z})$ with $\hat{z} \neq 0$ occurs if, and only if, the invader abundance at equilibria $\|\hat{z}\|_1$ satisfies

$$\alpha(\|\hat{z}\|_1) = 1, \tag{C.1}$$

as here $A_I + \alpha(\|\hat{z}\|_1)bc^T = A_R$. With α given by (4.3), the condition (C.1) is the s-dependent quadratic equation in $\|\hat{z}\|_1$

$$\frac{4}{5}\left(1 + s\frac{10\|\hat{z}\|_1}{1 + 50\|\hat{z}\|_1^2}\right) = 1. \tag{C.2}$$

Solving (C.1) or, equivalently, (C.2), yields two candidate invader abundances at co-existent equilibrium:

$$\|\hat{z}_1\|_1 = \frac{4s - \sqrt{16s^2 - 2}}{10}, \tag{C.3a}$$

and

$$\|\hat{z}_2\|_1 = \frac{4s + \sqrt{16s^2 - 2}}{10}, \tag{C.3b}$$

where note that $\|\hat{z}_1\|_1 \leq \|\hat{z}_2\|_1$. For $\|\hat{z}_1\|_1$ and $\|\hat{z}_2\|_1$ in (C.3) to be real-valued requires that

$$s \geq s_m := \frac{\sqrt{2}}{4}. \tag{C.4}$$

Elementary analysis demonstrates that $\|\hat{z}_1\|_1 = \|\hat{z}_1(s)\|_1 \leq 1$ for all $s \geq s_m$, and so for these values of s, (2.4) admits the co-existent equilibrium $(\hat{x}_1, \hat{z}_1)$, given by

$$\hat{x}_1 = (1 - \|\hat{z}_1\|_1)x^* \quad \text{and} \quad \hat{z}_1 = \|\hat{z}_1\|_1 x^*, \tag{C.5}$$

where x^* and $\|\hat{z}_1\|_1$ are given by (2.5) and (C.3a), respectively. The function $s \mapsto \|\hat{z}_2(s)\|_1$ is an increasing, unbounded function of s, and takes the value one at $s = 51/40$. The constraints

$$0 \leq \|\hat{x}_2\|_1 \quad \text{and} \quad 0 \leq \|\hat{z}_2\|_1 \leq \|\hat{x}_2\|_1 + \|\hat{z}_2\| = 1,$$

for a co-existent equilibrium imply that (2.4) admits a second co-existent equilibrium $(\hat{x}_2, \hat{z}_2)$, given by

$$\hat{x}_2 = (1 - \|\hat{z}_2\|)x^* \quad \text{and}$$

$$\hat{z}_2 = \|\hat{z}_2\|x^*, \quad \text{for all } s \text{ such that} \quad s_m \leq s \leq \frac{51}{40}. \tag{C.6}$$

In summary, for $0 \leq s < s_m$ there are no (nonzero) co-existent equilibria. For $s_m < s < 51/40$ there are two, distinct co-existent equilibria, given by (C.5) and (C.6). For $s > 51/40$ there is one co-existent equilibrium, given by (C.5).

When $s \in (0, s_m)$, then $\alpha(y) < 1$ for all $y \geq 0$ and the only possible equilibrium with nonzero invader component is $(0, z^*)$, which is not attractive for any nonzero initial resident population, by (A.9). Since s_m is the minimal Allee strength such that $\alpha(y) = 1$ for some y, at which point we expect the invader to (possibly) reach a nonzero equilibrium, the search over $s > 0$ in Section 4 was started at s_m. Since the vital rate $g_1\alpha(\|z(t)\|_1)$ denotes the growth rate from age-class one to two, it must take values between zero and one. To ensure that

$$g_1 \max_{y \geq 0} \alpha(y) = 0.1 \max_{y \geq 0} \alpha(y) < 1,$$

places an upper bound on the strength parameter $s > 0$. Elementary calculus shows that

$$0.1 \max_{y \geq 0} \alpha(y) \leq 1 \quad \Rightarrow \quad s \leq s_M := \frac{23}{\sqrt{2}} \approx 16.2.$$

Therefore, to explore the s parameter space where invasion might be expected, it is varied between $\sqrt{2}/4$ and $16 < 23/\sqrt{2}$.

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