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Highlights

- A spatially explicit, stage-structured Lotka-Volterra competition model is proposed
- Using heuristic arguments, we obtain approximate asymptotic spread speed solutions
- Adding stage structure alone is insufficient to alter predicted spread speeds
- Accompanied by specific heterogeneities, stage structure does alter spread speeds

Invasion dynamics of competing species with stage-structure

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ABSTRACT: The spread of an invasive species often results in a decline and subsequent disappearance of native competitors. Several models, primarily based on spatially explicit Lotka-Volterra competition dynamics, have been developed to understand this phenomenon. In general, the goal of these models is to relate fundamental life history traits, for example dispersal ability and competition strength, to the rate of spread of the invasive species, which is also the rate at which the invasive species displaces its native competitor. Stage-structure is often an important determinant of population dynamics, but it has received little attention in the context of Lotka-Volterra invasion models. For many species, behaviors like dispersal and competition depend on life-stage. To describe the processes of invasion in these species, it is important to understand how behaviors that vary as a function of life-stage can impact spread rate. In this paper, we develop a spatially explicit, stage-structured Lotka-Volterra competition model. By comparing spread speed predictions from this model to spread speed predictions from an analogous single-stage model, we are able to determine when stage-structure is important and how stage-dependent behavior can alter the characteristics of an invasion.

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Introduction

Rising levels of globalization are facilitating the introduction and spread of an increasing number of alien invasive species (Meyerson and Mooney 2007). While this has health, economic and environmental consequences, some of the most devastating effects are reductions to native species populations and losses in biodiversity (Vitousek et al. 1997). In the United States, about 42% of all species listed as threatened or endangered under the Endangered Species Act are at risk because of competition with or predation by a non-native species (Pimentel et al. 2005; Stohlgren and Schnase 2006; Wilcove et al. 1998); in other parts of the world, this fraction can be even higher (Armstrong 1995; Pimentel et al. 2005).

Although there are many possible biotic interactions that could result in an invasive species displacing a native population, one common mechanism is competitive exclusion (Mooney and Cleland 2001). Argentine ants (*Linepithema humile*), for example, displace native ants by locating food patches more rapidly and recruiting to them more heavily, thereby usurping a disproportionate fraction of food resources (Holway 1999). Superior competition for food is also cited as a contributing factor behind the displacement of the native gecko, *Lepidodactylus lugubris*, by the invasive gecko *Hemidactylus frenatus* across the Pacific basin (Petren and Case 1996) and the displacement of the native red squirrel (*Scuirus vulgaris*) by the North American grey squirrel (*Scuirus carolinensis*) in Britain (Kenward and Holm 1993). Beyond competition for food, other limiting resources may be important as well. In both California and South Africa, competition for space is likely responsible for displacement of a variety of native mussels by the Southern European mussel *Mytilus galloprovincialis* (Carlton et al. 1999). Likewise, in Europe, competition for shelter appears to be an important factor governing displacement of native crayfish by the invasive North American species, *Pacifasticus leniusculus* (Vorburger and Ribi 1999).

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In general, the faster an invasive species spreads, the more rapidly it will displace its native competitors. Thus, the rate of spread of an invasive species is an important metric for evaluating the risks that the invader poses to native biodiversity (Neubert and Parker 2004). For this reason, a number of models have been developed to predict the spread speed of an invasive species as a function of basic life-history parameters, for example dispersal ability and reproductive rate. Although the majority of these models consider only the invasive species, several incorporate biotic interactions, including competition with other species populations. Okubo et al. (1989), for example, developed a reaction-diffusion model based on Lotka-Volterra competition to describe the encroachment of grey squirrels into red squirrel habitat in Britain. Using a linear approximation, Okubo et al. (1989) estimated the spread speed of the grey squirrel population as a function of grey squirrel dispersal, grey squirrel reproduction, and red and grey squirrel competition coefficients. More recently, Weinberger et al. (2002) have generalized the results in Okubo et al. (1989). These studies, as well as similar discrete-time models (Hart and Gardner 1997), have shown that resident competitors can slow or even stop the invasion of an introduced species.

In addition to competition, another factor that might influence the spread rate of an invasive species is the age-structure of its population. This is because many species-level traits governing spread rate are stage-dependent. In birds, for example, juveniles tend to disperse farther than adults; in mammals, this trend is reversed (Neubert and Caswell 2000). Likewise, in almost all species, reproduction only occurs after a period of development, meaning that juveniles either do not breed or else breed at a much lower rate than older individuals. Stage-dependence can also be important in governing some of the interspecific interactions that influence the spread of an invasive species. In the case of the invasive North American crayfish (*Pacifasticus leniusculus*), for example, the outcome of competition for shelter is largely determined by crayfish size which, in turn, depends on crayfish age. Because the North American crayfish grows faster than native European species, the North American invader is often at an advantage (Vorburger and Ribi 1999).

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Although stage-structure has been considered in single-population models of invasion (Neubert and Parker 2004; Thieme 1979), the importance of stage-structure to invasion in competitive models remains unknown (but see (Al-Omari and Gourley 2003) for a partial answer to this question). Previous studies of non-spatial competition models suggest that single-stage and multi-stage models often differ with respect to predicted dynamics and coexistence outcomes (Hassell and Comins 1976; Liu et al. 2002; Mougi and Nishimura 2005). Thus, it is likely that the inclusion of stage-dependence in competition models could also affect spread speed predictions. In order to explore the importance of stage-structure to the characteristics of an invasion, we develop an extended version of the spatially explicit Lotka-Volterra model from Okubo et al. (1989). Specifically, we consider a 2-species competition model where both species have a juvenile and an adult phase and where dispersal, reproduction, and competition depend not only on the species involved, but also on their respective life-stages. Using our model, we predict spread speed as a function of the life-history parameters of both the invasive species and its native competitor. In particular, we focus on the effects of parameter variation across life-stages. Ultimately, this allows us to examine the role of stage-structure in the invasion-competition process, and to identify those stage-dependent variables that are most important in determining invasion characteristics in competitive contexts.

Method

Similar to Okubo et al. (1989), our basic model consists of a set of coupled reaction-diffusion equations. We model competition by assuming Lotka-Volterra type interactions, and we model dispersal using isotropic diffusion. Specifically, the system is defined as

$$\frac{\partial s_i}{\partial t} = d_i \frac{\partial^2 s_i}{\partial x^2} + f_I s_I - m_i s_i - a_{ii} s_i^2 - a_{iI} s_i s_I - a_{ir} s_i s_r - a_{iR} s_i s_R \qquad (1.a)$$

$$\frac{\partial s_I}{\partial t} = d_I \frac{\partial^2 s_I}{\partial x^2} + p_i s_i - m_I s_I - a_{II} s_I^2 - a_{Ii} s_I s_i - a_{Ir} s_I s_r - a_{IR} s_I s_R \qquad (1.b)$$

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$$\frac{\partial s_r}{\partial t} = d_r \frac{\partial^2 s_r}{\partial x^2} + f_R s_R - m_r s_r - a_{rr} s_r^2 - a_{ri} s_r s_i - a_{rI} s_r s_I - a_{rR} s_r s_R \tag{1.c}$$

$$\frac{\partial s_R}{\partial t} = d_R \frac{\partial^2 s_R}{\partial x^2} + p_r s_r - m_R s_R - a_{RR} s_R^2 - a_{Ri} s_R s_i - a_{RI} s_R s_I - a_{Rr} s_R s_r \tag{1.d}$$

where t is time, s_j is the abundance of species 'j', f_j is its birth rate , p_j is its rate of maturation, d_j is its

rate of dispersal/diffusion, m_j is its rate of loss (which may be due to death or, in the case of juveniles,

both death and maturation) and a_{jk} is the competition coefficient for the effect of species k on species j.

Species are defined as follows: $'i'$ and $'I'$ denote juveniles and adults of the invading species,

respectively, while $'r'$ and $'R'$ denote juveniles and adults of the resident species. For the sake of

simplicity, we have assumed that only juveniles mature, and that only adults are capable of breeding.

Notice, however, that the latter assumption is not necessary, since m_i for juveniles can be reinterpreted to

include death, maturation, and birth. In Appendix A, we present a non-dimensionalized version of the

model in (1). Although we will focus on dimensional parameters in the main text, our explorations of

specific parameter combinations are motivated by our non-dimensionalization scheme.

To estimate the spread speed of an invasion as a function of species life-history parameters, we use both

an approximate solution, based on the work in Weinberger et al. (2002), and a numerical solution of the

full model (Eq. 1), as described below. In general, our goal is to compare results from the two-stage

model in equation (1) to results from an analogous single-stage model. The single-stage model that we

use for comparison is given by

$$\frac{\partial s_I}{\partial t} = D_I \frac{\partial^2 s_I}{\partial x^2} + F_I S_I - A_{II} S_I S_I - A_{IR} S_I S_R \tag{2.a}$$

$$\frac{\partial s_R}{\partial t} = D_R \frac{\partial^2 s_R}{\partial x^2} + F_R S_R - A_{RR} S_R S_R - A_{RI} S_R S_I \tag{2.b}$$

where we have used capitalized parameters and state variables to distinguish the single-stage model from

the two-stage model.

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Approximate Solution

Weinberger et al. (2002) developed the mathematical theory of spread speeds for multi-species cooperative systems. In that paper, conditions were given which insure that all species spread at the same spread speed, and that this speed agrees with the more easily calculated speed of a linearized problem. In order to apply methods from Weinberger et al. (2002) to equation (1), we must first convert (1) into a cooperative system. Unfortunately, the standard change of variables for converting a competitive Lotka-Volterra model into a cooperative Lotka-Volterra model does not work for our stage-structured system. The change of variables approach does not work because the model includes both intraspecific and interspecific competition between juveniles and adults in the invading species and resident species. However, because our model is approximately linear near the resident equilibrium, a heuristic argument motivates us to assume the following change of variables: $s_i = s_i$, $s_I = s_I$, $u_r = r^* - s_r$, $u_R = R^* - s_R$, where r^* and R^* are, respectively, the equilibrium values of resident juveniles and adults when they are the only species present (i.e., prior to introduction of the invasive species). Applying our change of variables and dropping all higher order terms gives the linear system

$$\frac{\partial s_i}{\partial t} = d_g \frac{\partial^2 s_i}{\partial x^2} - (m_i + a_{ir}r^* + a_{iR}R^*)s_i + f_I s_I \tag{3.a}$$

$$\frac{\partial s_I}{\partial t} = d_G \frac{\partial^2 s_I}{\partial x^2} - (m_I + a_{Ir}r^* + a_{IR}R^*)s_I + p_i s_i \tag{3.b}$$

$$\frac{\partial u_r}{\partial t} = d_r \frac{\partial^2 u_r}{\partial x^2} - (m_r + 2a_{rr}r^* + a_{rR}R^*)u_r + (f_R - a_{rR}r^*)u_R + (a_{ri}s_i + a_{rI}s_I)r^* \tag{3.c}$$

$$\frac{\partial u_R}{\partial t} = d_R \frac{\partial^2 u_R}{\partial x^2} - (m_R + 2a_{RR}R^* + a_{Rr}r^*)u_R + (p_r - a_{Rr}R^*)u_r + (a_{Ri}s_i + a_{RI}s_I)R^* \tag{3.d}$$

which is now a cooperative system under the conditions $f_R - a_{rR}r^* > 0$ and $p_r - a_{Rr}R^* > 0$. Using this approximation and spread speed formulas for linear cooperative systems established in Weinberger et al. (2002) , and under certain parameter restrictions, it is possible to obtain an expression for the spread speed (see Appendix B), which is shown (below) to match predictions from the full system in equation

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(1) for a wide range of parameters. The spread speed is the asymptotic rate at which the invader with positive initial distribution on a bounded interval expands its spatial range.

There is one special case where the approximate spread speed solution is particularly simple and insightful. Specifically, when adults and juveniles of the invading species disperse at equal rates, $d_i = d_I \equiv D_I$, but have potentially different competition coefficients and loss rates, the approximate expression for the spread speed of the invasion, $\bar{c}$, is (see Appendix B)

$$\bar{c} = \sqrt{2D_I} \sqrt{\sqrt{(R^*\Delta_a^R + r^*\Delta_a^r + \Delta_m)^2 + 4f_Ip_i} - (R^*\Sigma_a^R + r^*\Sigma_a^r + \Sigma_m)} \; . \quad (4)$$

In (4), $\Delta_a^R = a_{IR} - a_{iR}$ is the difference between the effect of resident adults on adult invaders and the effect of resident adults on juvenile invaders. $\Delta_a^r = a_{Ir} - a_{ir}$ is the same, but for the effect of resident juveniles rather than resident adults. Likewise, $\Sigma_a^R = a_{IR} + a_{iR}$ is the sum of the effect of resident adults on both juvenile and adult invaders, while $\Sigma_a^r = a_{Ir} + a_{ir}$ is the sum of the effect of resident juveniles. Finally, $\Delta_m = m_{ai} - m_{ji}$ is the difference between the loss rate of adult invaders and the loss rate of juvenile invaders, while $\Sigma_m = m_{ai} + m_{ji}$ is the sum of the two loss rates. Equation (4) provides an asymptotic spread speed at which the invader spreads for large time, t. In the next section, we demonstrate how formula (4) works to predict the spreading speed of the full nonlinear system (1) for several biologically meaningful cases. Additional interpretation of Eq. (4) and results from the approximate solution appear in the Discussion.

Numerical Solution: To find numerical estimates of spread speed, we begin by assuming that resident adults and juveniles are established at their (well-mixed, monoculture) equilibrium abundances across a finite domain $-L \leq x \leq L$, where L is the domain size, and is selected large enough to ensure that $s_I(|L|, t) + s_i(|L|, t) < \delta_1$, with $\delta_1 = 10^{-6}$ (i.e., the total invader population reaching the boundary is less than some small threshold). We then introduce a narrow pulse of invaders at the center of the

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domain. Specifically we choose $s_i(x, 0) = i^* e^{-x^2}$, and $s_I(x, 0) = I^* e^{-x^2}$ where i^* and I^* are the equilibrium densities of the juvenile and adult invaders respectively in an invader monoculture. Using the *pdepe* package in Matlab, we then numerically integrate Eq. (1), assuming Dirchlet boundary conditions (we also tested Neumann boundary conditions, and found boundary conditions to have no effect, which is to be expected based on our select of L sufficiently large to ensure that the invader does not reach the boundary at high densities over the course of the simulation). As the invaders spread out toward the domain edges, we perform a numerical search for the approximate location of the invasion wave-front as a function of time − that is, beginning from the center of the domain and moving to the right, we searched for the first x value in the solution vector obtained from *pdepe* that gives $s_I(t) + s_i(t)$ above some small threshold, δ_2. We take this to be the wavefront. Specifically, we find ϕ_t such that

$$\begin{cases} s_I(t) + s_i(t) > \delta_2 & 0 < x < \phi_t \\ s_I(t) + s_i(t) < \delta_2 & \phi_t < x < L \end{cases} \tag{5}$$

where $\delta_1 \ll \delta_2 = 10^{-4}$ is the small threshold used to track the progress of the invasion wave. ϕ_t describes the location of the wave front at time t based on the location of density level $\delta 2$. In practice, simulations are not sensitive to the value of $\delta 2$, provided that it is sufficiently small. Consider the time-points $t_1, t_2, ..., t_m$ and the corresponding values $\phi_{t1}, \phi_{t2}, ..., \phi_{tm}$. The average wave front propagation speed, $\tilde{c}$, which provides an estimate for the spreading speed, is then given by

$$\tilde{c} = \frac{\sum_{i=1}^{m} t_i \phi_{t_i}}{\sum_{i=1}^{m} t_i^2}$$

This can be written in the more compact form

$$\tilde{c} = (\boldsymbol{t}^T \boldsymbol{t})^{-1} \boldsymbol{t}^T \boldsymbol{\phi} \tag{6}$$

where t is a vector of time-points and ϕ is a corresponding vector of wave-front locations. We obtain $\tilde{c}$ by fitting a straight line to the $\phi \times t$ curve using a least-squares calculation; however, to avoid fitting transient dynamics, we only apply equation (6) to the linear region of the $\phi \times t$ curve, after all transient behavior has disappeared. To ensure that we are only fitting the linear regime, we insist that our least-squares fit gives $R^2 > 0.999$, which will not be true if we attempt to fit time-points during the transient phase.

Parameters: Except when stated otherwise, we focus on comparing results from our stage-structured model to results from the fully parameterized, single-stage competition model in Okubo et al. (1989). To achieve comparable parameterization schemes across the two models, we assume birth, maturation, and death rates for the two-stage model that reproduce the low-density population growth rates from the single-stage model. In addition, we require that our choices for these parameters yield the same age-structures as the Leslie matrices used to parameterize the original model (Okubo et al. 1989). Competition and diffusion coefficients are also selected to match those used in Okubo et al. (1989). Appendix C provides a detailed summary of our parameterization scheme.

While maturation rates, death rates, and fecundity must vary across stages to satisfy our constraints on population growth rate and stage structure, this is not true for diffusion or competition coefficients. For these parameters, we consider scenarios in which juvenile and adult coefficients are identical, as well as scenarios in which the coefficients differ between stages. To ensure that all comparisons are fair (i.e., not determined by an overall increase/decrease in diffusion or competition), we select stage-dependent diffusion and competition coefficients such that the population averages of these parameters would remain constant in a well-mixed system at equilibrium. If, for example, juvenile diffusion increases, then adult diffusion must decrease by a corresponding amount to ensure that the average diffusion coefficient across the entire population remains the same.

Results

Single-Stage vs. Stage-Structured Models

We begin by considering the effect of stage-structure itself. Starting from equation (4), which assumes that $d_i = d_I \equiv D_I$, we set $a_{ir} = a_{iR} = a_{Ir} = a_{IR} \equiv A_{IR}$. This gives

$$\bar{c} = 2\sqrt{D_I F_I}\sqrt{1 - A_{IR}\left(\frac{\mathcal{R}^*}{F_I}\right)} \tag{7}$$

where $F_I = \frac{1}{2}\sqrt{\Delta_m^2 + 4f_I p_i} - \frac{\Sigma_m}{2}$ corresponds to the population growth rate of the invader in the single-stage model (see Appendix D) and $\mathcal{R}^* = R^* + r^*$ is the size of the entire resident population. By applying a similar linear approximation to the single-stage model in equation (2) (see Appendix D), we can show that the predicted spread speed for the simpler, single-stage model is identical to the spread speed for the stage structured model (see Appendix D), suggesting that stage structure, in and of itself, does not impact spread speed. This is because separating individuals into different stages that share the same parameters is equivalent to not separating them at all. For the remainder of the paper, we will not distinguish between the single-stage model and the two-stage model with identical parameters across stages, but will use a single curve to represent both.

Stage-Structured Interspecific Competition

Next, we consider the effects of stage-structured interspecific competition. Based on our linear approximation (see Appendix B), we expect that the invasion spread speed will only depend on interspecific competition exerted by the residents on the invaders, and not on interspecific competition exerted by the invaders on the residents. If adult and juvenile invaders experience the same per-capita level of interspecific competition, then $a_{ir}r^* + a_{iR}R^* = a_{Ir}r^* + a_{IR}R^*$. However, we also require that the average competition experienced by the entire invading population (at equilibrium) be comparable to the competition experienced by the invading population in the single-stage model. For this reason, it

must also be true that $\frac{(a_{ir}r^* + a_{iR}R^*)i^* + (a_{Ir}r^* + a_{IR}R^*)I^*}{i^* + I^*} \equiv A_{IR}(r^* + R^*)$, where i^* and I^* are the equilibrium

abundances of the two invader stages in an invader monoculture (i.e., when only invaders are present). In

this case, equation (4) again reduces to equation (7). Thus, stage-structured interspecific competition does

not alter the spread speeds of the invasion provided that both juvenile and adult invaders face similar

levels of competitive pressure.

Results change, however, when juvenile invaders experience either more or less interspecific competition

than their adult counterparts. Figure 1a shows both numerical and analytical (see equation (4)) spread

speed predictions for the invader population as a function of interspecific competition from the resident

population. In this figure, we assume that $a_{ir} = a_{iR} \equiv A_{IR}\left(\frac{i^* + I^*}{i^* + \rho I^*}\right)$ and that $a_{Ir} = a_{iR} \equiv \rho A_{IR}\left(\frac{i^* + I^*}{i^* + \rho I^*}\right)$,

where ρ is a measure of how much more intense interspecific competition is in the adult stage as

compared to the juvenile stage. These two relationships ensure that the average competition faced by the

invader population remains constant (at equilibrium) and equal to the competition faced by invaders in the

single-stage model, $\frac{(a_{ir}r^* + a_{iR}R^*)i^* + (a_{Ir}r^* + a_{IR}R^*)I^*}{i^* + I^*} \equiv A_{IR}(r^* + R^*)$. $\rho = 1$ indicates that both stages

experience equal competition; $\rho < 1$ indicates that adult invaders face less competition than juvenile

invaders; $\rho > 1$ indicates that adult invaders face more competition than juvenile invaders. Figure 1b

expands on the results from Figure 1a by showing the invasion spread speed as a function of interspecific

competition coefficients for both adult and juvenile invaders.

From Figure 1, we see that the invader population advances at a faster rate when interspecific competition

is relatively more intense in the juvenile stage, and at a slower rate when competition is relatively more

intense in the adult stage. To understand this result more fully, we again rely on our assumed

relationships from above and substitute $a_{ir} = a_{iR} \equiv A_{IR}\left(\frac{i^* + I^*}{i^* + \rho I^*}\right)$ and $a_{Ir} = a_{iR} \equiv$

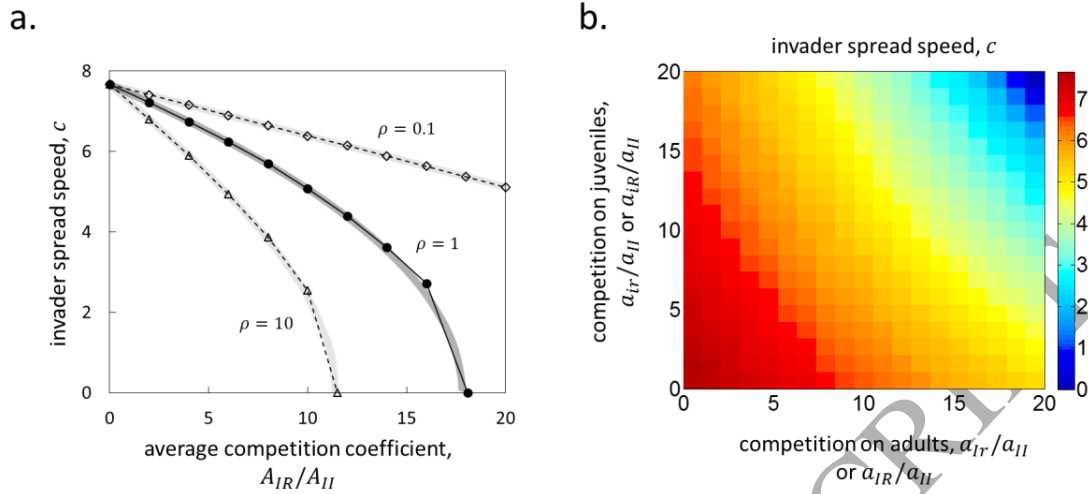$\rho A_{IR}\left(\frac{i^* + I^*}{i^* + \rho I^*}\right)$ into equation (4). We then take the following derivative

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Figure 1 (a) Spread speed of the invasion as a function of average interspecific competition across adult and juvenile invaders, A_{IR}. The linear approximation, equation (4), is shown as thick solid lines while the numerical solution of the full model is shown as thin lines. Stage-structured interspecific competition coefficients are defined as: $a_{ir} = a_{iR} \equiv A_{IR}\left(\frac{i^*+I^*}{i^*+\rho I^*}\right)$ and $a_{Ir} = a_{lR} \equiv \rho A_{IR}\left(\frac{i^*+I^*}{i^*+\rho I^*}\right)$. $\rho = 10$ (dotted line, open triangles) indicates that adult invaders experience 10 times as much interspecific competition as juvenile invaders, $\rho = 1$ (solid line, closed circles) indicates that adult and juvenile invaders experience equal interspecific competition and $\rho = 0.1$ (dotted line, open diamonds) indicates that adult invaders experience $1/10^{\text{th}}$ as much interspecific competition as juvenile invaders. (b) Spread speed of the invasion as a function of interspecific competition on adult and juvenile invader populations, a_{iR}, a_{ir}, a_{IR}, and a_{Ir}. Stage-structured interspecific competition coefficients are defined as $a_{ir} = a_{iR}$ and $a_{Ir} = a_{IR}$. Invader spread speeds are shown as a heat-map, with red indicating faster spread speeds and blue indicating slower spread speeds. In both figures, invader intraspecific competition coefficients are defined as: $a_{ii} = a_{II} = a_{Ii} = a_{iI} = A_{II}$, and figure axes are non-dimensionalized by dividing invader interspecific competition coefficients by the invader intraspecific competition coefficient. All other parameters are as defined in Appendix C.

$$\frac{dc^*}{d\rho}\bigg|_{\rho=1} = \frac{1}{2} A_{IR}(R^* + r^*) \sqrt{\frac{D_I}{F_I - A_{IR}(R^* + r^*)}} \left(\frac{\Delta_m}{\sqrt{4f_I p_i + \Delta_m^2}} - \left(\frac{i^* - I^*}{i^* + I^*} \right) \right) \qquad (8)$$

where, as before, $F_I = \frac{1}{2}\sqrt{\Delta_m^2 + 4f_I p_i} - \frac{\Sigma_m}{2}$ is the overall population growth rate of the invader. Equation

(8) suggests that the invasion spread speed will decrease with increasing interspecific adult competition

provided that $\frac{i^*}{I^*} > \frac{F_I + m_{ai}}{F_I + m_{ji}}$, but will increase with increasing interspecific adult competition otherwise.

(Note that because of the equivalences necessary to hold population growth rate and adult mortality

constant, an increase in interspecific adult competition necessarily implies a decrease in interspecific

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juvenile competition). Thus, comparing systems with the same overall population growth rate, and the same juvenile and adult mortality (but variable fecundity and maturation rates), we see that spread speed will become an increasing function of interspecific adult competition when the relative abundance of juveniles at equilibrium drops below a critical value. For the simplest scenario, with equivalent juvenile and adult loss rates, the critical value turns out to be $\frac{i^*}{I^*} = 1$. Thus, spread speed increases with decreased interspecific competition on the less abundant stage. Numerical simulations again support this conclusion (see Appendix G).

Stage-Structured Intraspecific Competition

Next, we consider stage-structured intraspecific competition. In this case, the spread speed of the invasion is given by equation (7), suggesting that intraspecific competition in the invader population does not affect invasion rates, and that intraspecific competition in the resident population only affects invasion rates if it alters the total abundance of the resident species at the resident species equilibrium. If adult and juvenile residents experience the same per-capita level of intraspecific competition, then $a_{rr}r^* + a_{rR}R^* = a_{Rr}r^* + a_{RR}R^*$. However, we also require that the average competition experienced by the entire resident population (at equilibrium) be comparable to the competition experienced by the resident population in the single-stage model. For this reason, it must also be true that $\frac{(a_{rr}r^* + a_{rR}R^*)r^* + (a_{Rr}r^* + a_{RR}R^*)R^*}{r^* + R^*} \equiv A_{RR}(r^* + R^*)$. In this case, the total abundance of resident species, $\mathcal{R}^*$, only depends on the average competition coefficient, A_{RR}, and not on how this is partitioned among stages (see Appendix F). Consequently, stage-structured intraspecific competition does not impact the spread speed of the invader, provided that both adult residents and juvenile residents experience the same level of intraspecific competition.

The situation is different when adult residents experience either more or less intraspecific competition than juvenile residents. If, for example, $a_{rr} = a_{rR} \equiv A_{RR}\left(\frac{r^* + R^*}{r^* + \lambda R^*}\right)$ and $a_{Rr} = a_{RR} = \lambda A_{RR}\left(\frac{r^* + R^*}{r^* + \lambda R^*}\right)$,

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where λ is a measure of how much more intense intraspecific competition is in the adult stage, then $\mathcal{R}^*$ is a function of λ; thus from equation (7), the spread speed of the invader will depend on λ as well. Figure 2a shows spread speed predictions for both the linear approximation (equation (7)) and the numerical solution as a function of the average intraspecific competition coefficient for the resident population for scenarios where adult invaders experience less ($\lambda = 0.1$), equivalent ($\lambda = 1$), and more ($\lambda = 10$) intraspecific competition than their juvenile counterparts. Figure 2b expands on the results from Figure
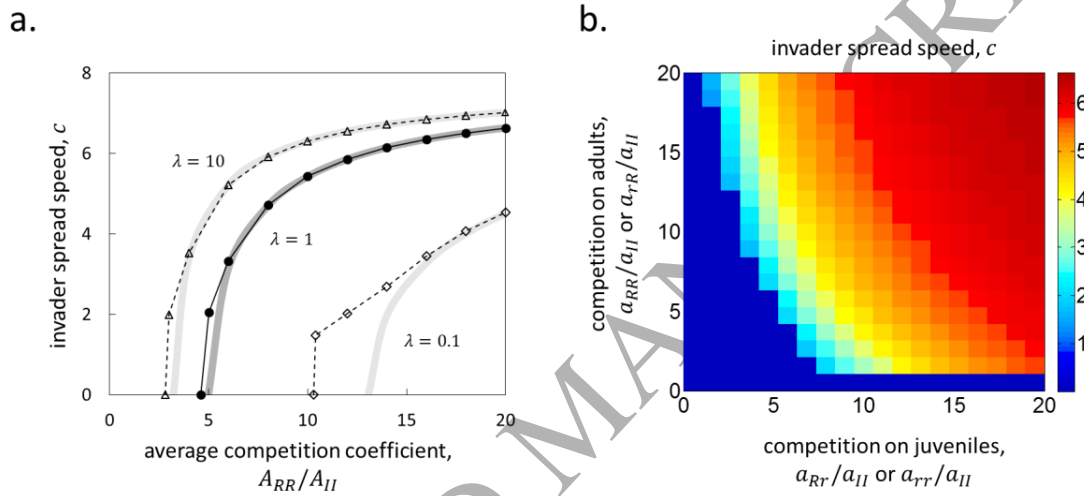

Figure 2 (a) Spread speed of the invasion as a function of average intraspecific competition across adults and juveniles of the resident population, A_{RR}. The linear approximation, equation (4), is shown as thick solid lines while the numerical solution of the full model is shown as thin lines. Stage-structured intraspecific competition coefficients are defined as: $a_{rr} = a_{rR} \equiv A_{RR}\left(\frac{r^*+R^*}{r^*+\lambda R^*}\right)$ and $a_{Rr} = a_{RR} = \lambda A_{RR}\left(\frac{r^*+R^*}{r^*+\lambda R^*}\right)$. $\lambda = 10$ (dotted line, open triangles) indicates that adults in the resident population experience 10 times as much intraspecific competition as juveniles, $\lambda = 1$ (solid line, closed circles) indicates that adults and juveniles in the resident population experience equal intraspecific competition and $\lambda = 0.1$ (dotted line, open diamonds) indicates that adults in the resident population experience $1/10^{th}$ as much intraspecific competition as juveniles. (b) Spread speed of the invasion as a function of intraspecific competition on adults and juveniles in the resident population, a_{rR}, a_{rr}, a_{RR}, and a_{Rr}. Stage-structured intraspecific competition coefficients are defined as $a_{rr} = a_{rR}$ and $a_{Rr} = a_{RR}$. Spread speeds of the invader are shown as a heat-map, with red indicating faster spread speeds and blue indicating slower spread speeds. In both figures, intraspecific competition coefficients for the invading population are defined as: $a_{ii} = a_{II} = a_{Ii} = a_{iI} = A_{II}$, and figure axes are non-dimensionalized by dividing intraspecific competition coefficients for the resident population by intraspecific competition coefficients for the invading population. All other parameters are as defined in Appendix C.

2a by showing spread speed of the invasion as a function of both juvenile and adult intraspecific competition among residents.

Not unexpectedly, higher rates of intraspecific competition among residents (and thus overall lower resident abundances) result in faster spread speeds of the invasion. Less obviously, invaders spread more quickly when intraspecific competition is more intense on the adult residents than on the juvenile residents. Similar to interspecific competition, this trend appears to depend on the relative abundance of adult to juvenile residents. Thus, when adult residents strongly outnumber juveniles, invader spread speeds are faster with increased intraspecific competition on the less abundant juvenile resident stage (and thus decreased intraspecific competition on the more abundant adult resident stage; numerical results not shown).

Stage-Structured Dispersal

Next, we consider the effects of stage-structured dispersal. In this case, our linear approximation does not give a simple expression for spread speed. However, it is still possible to use this approximation to obtain an estimate of spread speed (see Appendix B). In addition, we can use our numerical scheme (see Methods) to determine spread speed based on a full solution of the PDE in system (1). Figure 3a shows spread speed predictions for both the linear approximation and the numerical solution as a function of the average diffusion coefficient of the invader. In Figure 3a, we assume that $d_i = D_I \left(\frac{i^* + I^*}{i^* + \sigma I^*} \right)$ and that $d_I \equiv \sigma D_I \left(\frac{i^* + I^*}{i^* + \sigma I^*} \right)$, such that the average diffusion coefficient across the entire invading population remains constant and equal to the diffusion coefficient of invaders in the single-stage model, $\frac{d_i i^* + d_I I^*}{i^* + I^*} \equiv D_I$. σ, like ρ and λ, is a measure summarizing differences between adult and juvenile invaders. Specifically, σ captures how readily and how much adults invaders disperse relative to juveniles. Figure 3b extends the results in Figure 3a by considering spread speed as a function of both adult and juvenile dispersal. From Figure 3, we see that increasing adult dispersal increases the overall rate of spread of the population, whereas increasing juvenile dispersal does the opposite. Again, this relationship is reversed

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when adults outnumber juveniles, thus the invaders spread faster when the less abundant stage has a

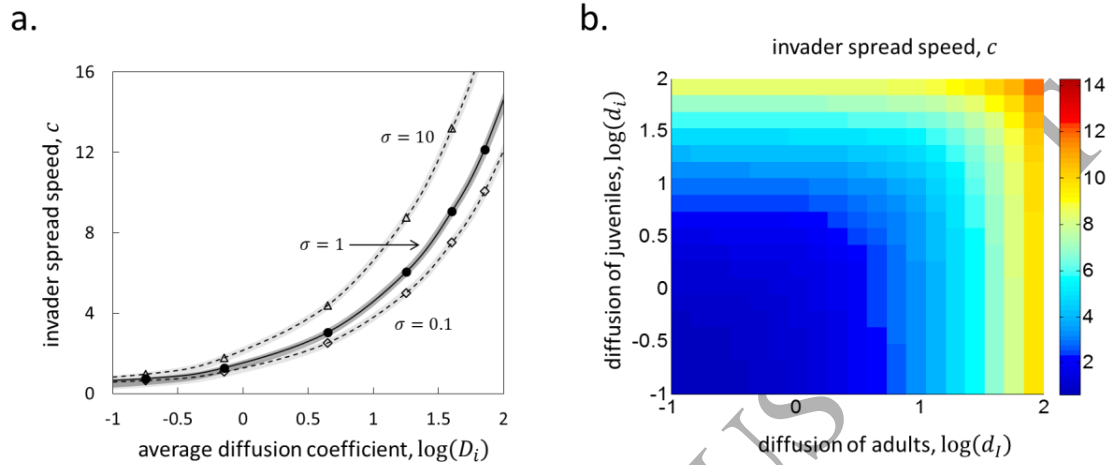higher dispersal rate (numerical results not shown).

Figure 3 (a) Spread speed of the invasion, as a function of average invader diffusion, for both the linear approximation (thick solid lines) and the numerical solution of the full model (thin lines). Stage-structured diffusion coefficients are defined as follows: $d_i \equiv D_I \left(\frac{i^*+I^*}{i^*+\sigma I^*} \right)$ and $d_I = \sigma D_I \left(\frac{i^*+I^*}{i^*+\sigma I^*} \right)$. $\sigma = 10$ (dotted line, open triangles) indicates that invading adults disperse 10 times as much as invading juveniles, $\sigma = 1$ (solid line, closed circles) indicates that invading adults and juveniles disperse at equal rates and $\sigma = 0.1$ (dotted line, open diamonds) indicates that invading adults disperse $1/10^{th}$ as much as juveniles. (b) Spread speed of the invasion as a function of adult and juvenile diffusion, d_i and d_I. Spread speeds are shown as a heat-map, with red indicating faster spread speeds and blue indicating slower spread speeds. All other parameters are as defined in Appendix C.

Discussion

In the context of competition models, spread speed conveys the rate at which a native species will be

displaced by an alien introduction. This provides important guidance regarding which invasive species

should receive the most immediate and most aggressive attention – critical information, given the limited

funds that are typically available for managing invasions. Efforts to predict the spread speed of different

invasive species vary widely. The simplest approach is to build differential or integro-difference equation

models based on one or two fundamental life-history traits (for example population growth rate and

dispersal) and then to use these models to derive simple expressions for spread rate as a function of

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species characteristics (Fisher 1937; Li et al. 2005; Okubo et al. 1989). At the other extreme are computationally intensive stochastic simulation models (Pitt et al. 2009; Rushton et al. 1997; Sebert-Cuvillier et al. 2008). These models incorporate extremely detailed life-histories, and account for realistic spatial and environmental variables through integration with geographic information systems (GIS). Intermediate between the highly abstract differential equation or integro-difference models and the large-scale simulations are efforts to extend simple models to more complicated scenarios. The goal is two-fold. First, because simple models can help to elucidate the qualitative roles of specific life-history traits or environmental variables, these models can often explain results from more detailed simulations. This helps to pin-point the particular factors in the simulation models that are important determinants of spread speed outcomes. Second, because predictions from simple models are relatively robust (or, at the very least, it is easier to identify the conditions under which they will fail), qualitative models can yield broadly applicable guiding principles for management decisions. This is beneficial, because it circumvents the need for time-consuming and costly model building for every different invasive species scenario.

In this paper, we extend a spatially explicit Lokta-Volterra competition model (Okubo et al. 1989) by including stage structure. Interestingly, just as the single-stage model suggested that competition modifies the spread speed of an invasion by adding a negative term corresponding to 'competitive drag', our model shows that, even when stage-structure is added, spread speed has a similar functional form (Eqs. 4 and 7). In our model, however, the 'competitive drag' term becomes much more complicated. Despite this, we find that the existence of stage structure, in and of itself, does not alter spread speed predictions (Eq. 7 and Appendix D). Rather, to alter spread speed predictions, stage structure must be accompanied by specific forms of heterogeneity among stages (see below). For example, we find that spread speeds are not affected when different stages of the invasive species face different levels of intraspecific competition, when different stages of the resident species disperse at different rates, or when different stages of the resident population either face or exert different levels of interspecific competition

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(Eq. 4). Meanwhile, spread speeds are affected when different stages of the resident population face different levels of intraspecific competition, when different stages of the invasive population disperse at different rates, or when different stages of the invasive population face different levels of interspecific competition (Eq. 4).

The fact that neither stage-structured intraspecific competition in the invasive species nor stage-structured dispersal of the resident species matter to the invasion speed should not be surprising: even in the original model, these parameters have a limited effect (Okubo et al. 1989). For a similar reason, it is also not surprising that stage-structured interspecific competition on the resident species has no impact on the spread speed of the invasive species. It is, however, surprising that inter-stage differences in the levels of interspecific competition exerted by the resident species have a minimal effect on the spread speed of the invasive species. This is surprising because overall competitiveness of the resident species is expected to impact spread of the invasive species (Okubo et al. 1989). Our findings, however, show that, although the overall competition from the resident population can affect spread of the invader, it does not matter how resident competitiveness is partitioned – entirely as a result of juveniles, entirely as a result of adults, or as a result of both. Whereas stage-structured interspecific competition does not matter when stage differences are restricted to the competitiveness of the resident species, stage-structure does matter when the different stages of the invasive species experience different competitive pressures (see Figure 1). Under this scenario, the two invasive stages would travel at different rates, if they were not linked by birth (Fagan et al. 2002) and maturation processes. However, because the stages are, in fact, linked demographically, the spread of the invasion depends on the competition faced by both stages (Eq. 7) and how it is partitioned. Overall, we find that the invasion tends to be faster when the competitive pressure is weaker on the less abundant stage. A similar result emerges for diffusion. The spread speed depends on both juvenile and adult dispersal (Eq. 7), and the invasion occurs more rapidly when the less abundant stage disperses most. The final parameter where stage-structure matters is intraspecific competition in the resident population. Similar to interspecific competition in the invading population, stage-structured

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intraspecific competition does not matter when both adults and juveniles of the resident species are equally restricted by intraspecific competition. However, concentrating intraspecific competition on the less abundant stage of the resident species causes the invasive species to progress faster.

Previous models have considered the issue of stage-dependent dispersal on rates of spread of invasive species (Neubert and Caswell 2000; Thieme 1979). Neubert and Caswell (2000), for example, suggest that unstructured models will generally overestimate spread speeds because they ignore stages where dispersal does not occur. This is a common feature of many invasive species. In plants, for example, dispersal is almost always concentrated in the juvenile/seed stage; alternatively, in holometabolous insects, larvae are often relatively sessile while adults are winged. Many successful invaders have some non-dispersing life-stages and, as a result, some models of invasive spread based on integro-difference equations have accounted for periods without movement and demonstrated how such non-dispersing stages can lead to an overall decrease in spread rate (Lewis 1997; Miller and Tenhumberg 2010). In contrast, our modeling approach addresses the impacts of population structure while holding constant the average dispersal rate across the entire invasive population. Such a comparison is facilitated in the current study because we focus on reaction-diffusion models, where diffusion coefficients can be averaged across the population. Standardization in integro-difference models would require more subtle equalization schemes.

Whereas differences in stage-dependent dispersal have been previously examined as a factor governing invasion processes, differences in competitive interactions have received less emphasis. Indeed, the few studies that do consider stage-structured competition in the context of an alien invasion focus on the sensitivity of particular life-stages of the resident species. In contrast, our work demonstrates that the level of competitive pressure on different stages of the invasive species can be equally important in governing invasion dynamics. In particular, we find that, all else being equal, spread speed increases with decreasing interspecific competition on the less abundant stage (i.e., increasing interspecific competition on the more abundant stage). Given that stage-structured competition is well documented across a range

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of different taxa (Hill et al. 1993; Peterson et al. 2004; Sakai et al. 2001), it seems likely that future studies in invasion biology should consider this key life-history trait.

More generally, our investigation of stage-structured spread in competitive contexts indicates that there are a range of native and invasive traits that can lead to particularly fast invasion processes that rapidly displace resident populations. These include 1) dispersal concentrated in the less abundant stage of the invasive population, 2) stronger intraspecific competition on the less abundant stage of the resident population, and 3) weaker interspecific competition on the less abundant stage of the invasive population. These findings point to key life-history traits of native and invasive species that should be monitored to assess the threat posed by the arrival of any invasive species.

Appendix A - Nondimensionalization

To non-dimensionalize equation (1) in the main text, we set

$$\hat{s}_q = \frac{s_q \alpha_{rr} L^2}{d_r} \tag{A.1.a}$$

$$\hat{x} = \frac{x}{L} \tag{A.1.b}$$

$$\hat{t} = \frac{t d_r}{L^2} \tag{A.1.c}$$

This gives

$$\frac{\partial \hat{s}_i}{\partial \hat{t}} = \kappa_i \frac{\partial^2 \hat{s}_i}{\partial \hat{x}^2} + \zeta_I \hat{s}_I - \lambda_i \hat{s}_i - \alpha_{ii} \hat{s}_i^2 - \alpha_{iI} \hat{s}_i \hat{s}_I - \alpha_{ir} \hat{s}_i \hat{s}_r - \alpha_{iR} \hat{s}_i \hat{s}_R \tag{A.2.a}$$

$$\frac{\partial \hat{s}_I}{\partial \hat{t}} = \kappa_I \frac{\partial^2 \hat{s}_I}{\partial \hat{x}^2} + \sigma_i \hat{s}_i - \lambda_I \hat{s}_I - \alpha_{II} \hat{s}_I^2 - \alpha_{Ii} \hat{s}_I \hat{s}_i - \alpha_{Ir} \hat{s}_I \hat{s}_r - \alpha_{IR} \hat{s}_I \hat{s}_R \tag{A.2.b}$$

$$\frac{\partial \hat{s}_r}{\partial \hat{t}} = \frac{\partial^2 \hat{s}_r}{\partial \hat{x}^2} + \zeta_R \hat{s}_R - \lambda_r \hat{s}_r - \hat{s}_r^2 - \alpha_{ri} \hat{s}_r \hat{s}_i - \alpha_{rI} \hat{s}_r \hat{s}_I - \alpha_{rR} \hat{s}_r \hat{s}_R \qquad \text{(A.2.c)}$$

$$\frac{\partial \hat{s}_R}{\partial \hat{t}} = \kappa_R \frac{\partial^2 \hat{s}_R}{\partial \hat{x}^2} + \sigma_r \hat{s}_r - \lambda_R \hat{s}_R - \alpha_{RR} \hat{s}_R^2 - \alpha_{Ri} \hat{s}_R \hat{s}_i - \alpha_{RI} \hat{s}_R \hat{s}_I - \alpha_{Rr} \hat{s}_R \hat{s}_r \qquad \text{(A.2.d)}$$

where $\kappa_q = \frac{d_q}{d_r}$, $\zeta_q = \frac{f_q L^2}{d_r}$, $\sigma_q = \frac{p_q L^2}{d_r}$, $\lambda_q = \frac{m_q L^2}{d_r}$, and $\alpha_{qj} = \frac{a_{qj}}{a_{rr}}$.

Appendix B - Spread Speed of the Linear System

To compute the spread speed for the linearized system in (3) we need

$$f_R - a_{rR} r^* > 0 \text{ and } p_r - a_{Rr} R^* > 0 \qquad . \qquad \text{(B.1)}$$

From Weinberger et al. (2002), the matrix used to find the spreading speed is given by

$$C_\mu = \begin{pmatrix} d_i \mu^2 - n_{11} & f_I & 0 & 0 \\ p_i & d_I \mu^2 - n_{22} & 0 & 0 \\ r^* a_{ri} & r^* a_{rI} & d_r \mu^2 - n_{33} & f_R - r^* a_{rR} \\ R^* a_{Ri} & R^* a_{RI} & p_r - R^* a_{Rr} & d_R \mu^2 - n_{44} \end{pmatrix} \qquad \text{(B.2)}$$

where $n_{11} = m_i + r^* a_{ir} + R^* a_{iR}$, $n_{22} = m_I + r^* a_{Ir} + R^* a_{IR}$, $n_{33} = m_r + 2r^* a_{rr} + R^* a_{rR}$ and $n_{44} = m_R + 2R^* a_{RR} + r^* a_{Rr}$. Rewriting equation (B.2) as

$$C_\mu = \begin{pmatrix} C_{11}(\mu) & 0 \\ C_{21} & C_{22}(\mu) \end{pmatrix} \qquad \text{(B.3)}$$

where each C_{ij} is a 2×2 matrix, we use $\lambda_1(\mu)$ to denote the principal eigenvalue of $C_{11}(\mu)$ and $\lambda_2(\mu)$ to denote the principal eigenvalue of $C_{22}(\mu)$. The stability criterion of the resident species monoculture in the two-dimensional resident species only system is $\lambda_2(0) < 0$, and instability of the resident species monoculture in the full four-dimensional system implies $\lambda_1(0) > 0$. The spreading speed of the linear system (3) is given by

$$c^* = \inf_{\mu > 0} \frac{\lambda_1(\mu)}{\mu}, \qquad \text{(B.4)}$$

provided that $\lambda_1(\mu^*) > \lambda_2(\mu^*)$, where μ^* is the number at which the infimum in c^* is attained.

Appendix C - Parameterization

Parameters

<u>Intrinsic net growth rates</u>: In order to preserve both the intrinsic net growth rate and the age-structure suggested in Okubo et al. (1989), we consider the following well-mixed system

$$\frac{ds_a}{dt} = f_A s_A - m_a s_a \tag{C.1.a}$$

$$\frac{ds_A}{dt} = p_a s_a - m_A s_A \qquad A, a = R, r \text{ or } I, i \tag{C.1.b}$$

and require that

$$\lim_{t \to \infty} \frac{s_i(t) + s_I(t)}{s_i(t-1) + s_I(t-1)} = 2.27 \tag{C.2.a}$$

$$\lim_{t \to \infty} \frac{s_r(t) + s_R(t)}{s_r(t-1) + s_R(t-1)} = 1.84 \tag{C.2.b}$$

$$\lim_{t \to \infty} \frac{s_i(t)}{s_I(t)} = 2.94 \tag{C.2.c}$$

$$\lim_{t \to \infty} \frac{s_r(t)}{s_R(t)} = 2.07 \tag{C.2.d}$$

Equations (C.2.a-b) ensure that the stage-structured model has the same overall rate of population increase as the Leslie matrices in Okubo et al. (1989). Similarly, equations (C.2.c-d) ensure that the stage-structured model has the same age-structure as the Leslie matrices in Okubo et al. (1989). This, however, leaves us with two free parameters. For adult fecundity, we assume the quoted rates of reproduction; thus considering only females, $f_I = 4.5$ and $f_R = 3$. For maturation, we assume $p_i = p_r = 0.35$, which is slightly less than the quoted rate of 0.5 for survival from juveniles to adults. We select this lower value in order to compensate for the continuous nature of our model, which enables a fraction of

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the juvenile population to mature without suffering through a full period of juvenile death. In general, we find that results are not particularly sensitive to the p values that are chosen. Table 1 outlines the parameters governing net population growth rate, taking into account the conditions in equation (C.2)

	Symbol	Invading Species	Resident Species
fecundity (y^{-1})	f	4.5	3
maturation rate (y^{-1})	p	0.35	0.35
juvenile death (y^{-1})	m_j	0.71	0.84
adult death (y^{-1})	m_a	0.21	0.11

Carrying capacities: We take carrying capacities directly from Okubo et al. (1989) and assume that stages compete equally with one another. This gives

$$a_{ii} = a_{iI} = a_{Ii} = a_{II} = 0.1 \text{ ha} = 0.1\text{ha}\frac{0.01\text{km}^2}{\text{ha}} = 0.001 \text{ km}^2$$

$$a_{rr} = a_{rR} = a_{Rr} = a_{RR} = 1.33 \text{ ha} = 1.33 \text{ ha}\frac{0.01\text{km}^2}{\text{ha}} = 0.0133 \text{ km}^2$$

Competition coefficients: We consider competition coefficients taken from Figure 1 in Okubo et al. (1989). Again, we ignore stage structure, at least for the initial analysis. This gives

$$a_{ir} = a_{iR} = a_{Ir} = a_{IR} = \gamma_1 a_{rr} = 0.5 * 0.0133 \text{ km}^2 = 0.00667 \text{ km}^2$$

$$a_{ri} = a_{rI} = a_{Ri} = a_{RI} = \gamma_2 a_{ii} = 1.5 * 0.001 \text{ km}^2 = 0.0015 \text{ km}^2$$

where $\gamma_1 = 0.5$ and $\gamma_2 = 1.5$ are relative competition coefficients in Figure 1 of Okubo et al. (1989).

Diffusion rates: We explore a range of diffusion rates for each of the stages and species considered. Specifically, we study spread speed as a function of the non-dimensionalized parameters κ_i, κ_r, and κ_R.

Appendix D – Comparison to Single-Stage Model

We begin by solving the set of equations in (C.1) for the invading species. This gives

$$s_i(t) = \frac{e^{\gamma t}(\gamma s_I(0) + m_i s_I(0) + p_i s_i(0))(\theta - m_i) + e^{-\theta t}(-\theta s_I(0) + m_i s_I(0) + p_i s_i(0))(\gamma + m_i)}{p_i\sqrt{4f_I p_i + \Delta_m^2}} \quad \text{(D.1.a)}$$

$$s_I(t) = \frac{e^{\gamma t}\big(\gamma s_I(0)+m_i s_I(0)+p_i s_i(0)\big)-e^{-\theta t}\big(-\theta s_I(0)+m_i s_I(0)+p_i s_i(0)\big)}{\sqrt{4f_I p_i+\Delta_m^2}} \tag{D.1.b}$$

where $\gamma = \frac{1}{2}\sqrt{\Delta_m^2 + 4f_I p_i} - \frac{\Sigma_m}{2}$ and $\theta = \frac{1}{2}\sqrt{\Delta_m^2 + 4f_I p_i} + \frac{\Sigma_m}{2}$. Substituting both parts of equation (D.1)

into the equation (C.2.a) gives

$$\lim_{t\to\infty} \frac{s_i(t)+s_I(t)}{s_i(t-1)+s_I(t-1)} = 2.27 = e^\gamma \tag{D.2}$$

From equation (2) in the main text, the single-stage model that is comparable to equation (C.1) is

$$\frac{dS_I}{dt} = F_I S_I \tag{D.3}$$

Integrating equation (D.3) gives

$$S_I(t) = S_I(0)e^{F_I t} \tag{D.4}$$

Substituting equation (D.4) into the single-stage equivalent of equation (C.2.a) gives

$$\lim_{t\to\infty} \frac{S_I(t)}{S_I(t-1)} = 2.27 = e^{F_I} \tag{D.5}$$

Comparing equations (D.2) and (D.5), we conclude that a suitably parameterized two-stage model will

have $\gamma = \frac{1}{2}\sqrt{\Delta_m^2 + 4f_I p_i} - \frac{\Sigma_m}{2} = F_I$, where F_I is the population growth rate in the single-stage model.

Next, we consider the spread speed prediction for the single-stage system under the same linear

approximation that we used for the two-stage model. In this case, we substitute $U_R = \mathcal{R}^* - S_R$ into

equation (2) from the main text, where $\mathcal{R}^*$ is the equilibrium number of residents in the absence of

competition from the invaders. This gives

$$\frac{\partial s_I}{\partial t} = D_I \frac{\partial^2 s_I}{\partial x^2} - A_{IR}\mathcal{R}^* S_I + F_I S_I + \text{higher order terms} \tag{D.6.a}$$

$$\frac{\partial u_R}{\partial t} = D_R \frac{\partial^2 u_R}{\partial x^2} + (F_R - 2A_{RR}\mathcal{R}^*)U_R + A_{RI}S_I\mathcal{R}^* + \text{higher order terms} \tag{D.6.b}$$

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From equation (D.6), the matrix used to find the spread speed is

$$B_\mu = \begin{pmatrix} D_I\mu^2 - A_{IR}\mathcal{R}^* + F_I & 0 \\ A_{RI}\mathcal{R}^* & D_R\mu^2 - A_{RI}\mathcal{R}^* \end{pmatrix} \qquad (D.7)$$

Denoting $\lambda_0(\mu)$ the eigenvalue of the matrix in equation (D.7), the spread speed is given by

$$\bar{C} = \inf_{\mu>0} \frac{\lambda_0(\mu)}{\mu} = 2\sqrt{D_I F_I}\sqrt{1 - A_{IR}\left(\frac{\mathcal{R}^*}{F_I}\right)} \quad , \qquad (D.8)$$

which is identical to the spread speed of the two-stage model when competition and diffusion coefficients do not depend on stage.

Appendix E – Comparison to Okubo Model

We begin by finding an approximate expression for $\mathcal{R}^*$, the abundance of residents in a resident monoculture. Specifically, we consider the following differential equation

$$\frac{dS_R}{dt} = F_R S_R - A_{RR} S_R S_R \qquad (E.1)$$

which is the well-mixed/non-spatial analog to equation (2.b) in the main text, and where we have set $S_I = 0$ because there are no members of the invading species in the resident monoculture. $\mathcal{R}^*$, is then given by finding the equilibrium solution to equation (E.1)

$$F_R/A_{RR} = \mathcal{R}^* \qquad (E.2)$$

Substituting equation (E.2) into equation (7) gives

$$\bar{c} = 2\sqrt{D_I F_I}\sqrt{1 - \left(\frac{F_R A_{IR}}{F_I A_{RR}}\right)} \qquad (E.3)$$

A key assumption necessary for obtaining the approximation in Okubo et al. (1989) is that both resident and invading species breed at equivalent rates, thus $F_R = F_I$. In this case, equation (E.3) reduces to

$$\bar{c} = 2\sqrt{D_I F_I}\sqrt{1 - \frac{A_{IR}}{A_{RR}}} \qquad\qquad (E.4)$$

which is identical to the approximation obtained in the original study.

Appendix F – Resident Species Abundance

The abundances of juveniles and adults of the resident species in a well-mixed resident monoculture are given by

$$0 = f_R R^* - m_r r^* - a_{rr}(r^*)^2 - a_{rR} r^* R^* \qquad\qquad (F.1.a)$$

$$0 = p_r r^* - m_R R^* - a_{RR}(R^*)^2 - a_{Rr} R^* r^* \qquad\qquad (F.1.b)$$

Under the assumption $a_{rr} r^* + a_{rR} R^* = a_{Rr} r^* + a_{RR} R^*$, equation (F.1) can be rewritten

$$0 = f_R R^* - m_r r^* - r^*(a_{rr} r^* + a_{rR} R^*) \qquad\qquad (F.2.a)$$

$$0 = p_r r^* - m_R R^* - R^*(a_{RR} R^* + a_{Rr} r^*) \qquad\qquad (F.2.b)$$

Adding Eqs (F.2.a) and (F.2.b) together and assuming that $\frac{(a_{rr} r^* + a_{rR} R^*) r^* + (a_{Rr} r^* + a_{RR} R^*) R^*}{r^* + R^*} \equiv A_{RR} \mathcal{R}^*$

gives

$$0 = f_R R^* - m_r r^* + p_r r^* - m_R R^* - A_{RR}(\mathcal{R}^*)^2 \qquad\qquad (F.3)$$

Equation (F.3) implicitly defines the total abundance of residents, $\mathcal{R}^*$. Because this depends only on A_{RR}, we conclude that stage-structure does not matter, provided that adults and juveniles experience equal intraspecific competition.

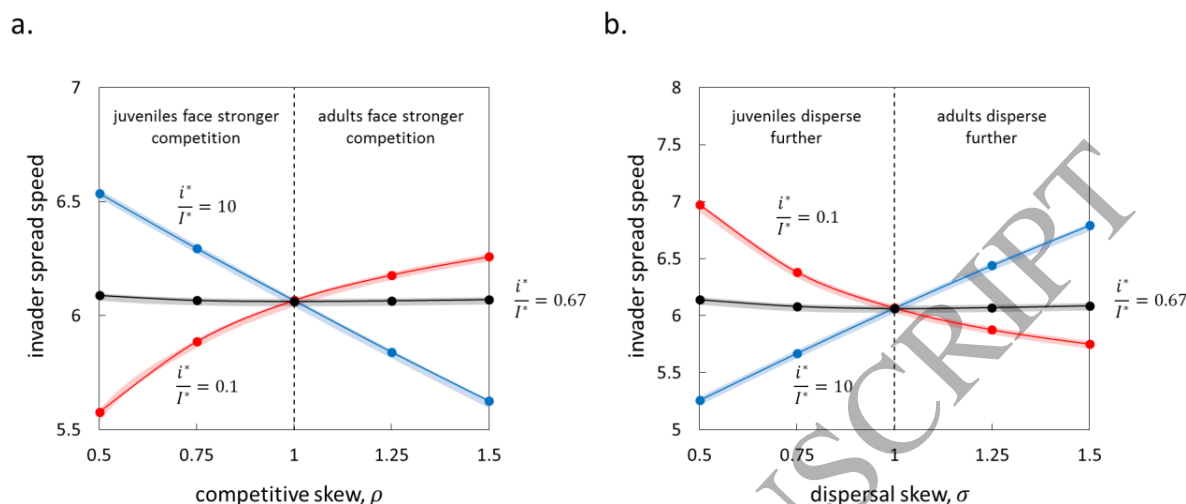# Appendix G – Spread Speed as a Function of Competitive or Dispersal Skew

Figure G.1 Invader spread speeds as a function of competitive skew (a) and dispersal skew (b). Blue lines indicate systems in which juveniles greatly outnumber adults, red lines indicate systems in which adults greatly outnumber juveniles and black lines indicate systems where the juvenile:adult ratio is such that spread speeds are relatively independent of competitive or dispersal skew. Thick solid lines show results from the linear approximation. Thin lines with closed circles represent results from the simulation model. Notice that the thick and thin lines are effectively superimposed because the match is so good.

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