

ECOLOGICAL AND EVOLUTIONARY DYNAMICS IN ADVECTIVE ENVIRONMENTS: CRITICAL DOMAIN SIZE AND BOUNDARY CONDITIONS

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ABSTRACT. We consider the ecological and evolutionary dynamics of a reaction-diffusion-advection model for populations residing in a one-dimensional advective homogeneous environment, with emphasis on the effects of boundary conditions and domain size. We assume that there is a net loss of individuals at the downstream end with rate $b \geq 0$, while the no-flux condition is imposed on the upstream end. For the single species model, it is shown that the critical patch size is a decreasing function of the dispersal rate when $b \leq 3/2$; whereas it first decreases and then increases when $b > 3/2$.

For the two-species competition model, we show that the infinite dispersal rate is evolutionarily stable for $b < 3/2$ and, when dispersal rates of both species are large, the population with larger dispersal rate always displaces the population with the smaller rate. For certain specific population loss rate $b < 3/2$, it is also shown that there can be up to three evolutionarily stable strategies. For $b > 3/2$, it is proved that the infinite random dispersal rate is not evolutionarily stable, and that, for some specific $b > 3/2$, a finite dispersal rate is evolutionarily stable. Furthermore, for the intermediate domain size, this dispersal rate is optimal in the sense that the species adopting this rate is able to displace its competitor with a similar but different rate. Finally, nine qualitatively different pairwise invasibility plots are obtained by varying the parameter b and the domain size.

1. Introduction. The evolution of dispersal has long fascinated ecologists and evolutionary biologists. The work on reaction-diffusion models started with that of Hastings [15], who showed that slow diffusion evolves in a spatially heterogeneous and temporally constant environment, provided that dispersal is unbiased; see also [10]. An intuitive explanation is that slow dispersal allows the population to better align with resource distribution whereas fast dispersal causes a mismatch between

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population and resource levels. When individuals disperse by a combination of random (diffusion) and active (taxis) movement up the gradient of resource, then the situation changes and the intermediate diffusion rate is sometimes selected [6, 7, 13, 21, 23].

Yet another situation arises in the modeling of spatial population dynamics under the passive action of an environmental drift. Examples include flora and fauna in streams and estuaries [29, 37], coastlines with dominant longshore current, lake water columns with gravitational downward pull [19, 20], as well as gut-dwelling bacteria [1]. For a homogeneous environment with no population loss from the boundary, fast diffusion can sometimes evolve since it enables the population to homogenize and align with the homogeneous resource [26]. In terms of evolutionary dynamics, it was conjectured in [22, 23] that an infinite diffusion rate is evolutionarily stable in some appropriate sense.

When there is net population loss from the boundary, then the question of the persistence of population under the action of environmental drift leads to the so-called drift paradox [32, 33]. In this case, a quantitative answer to the drift paradox can be stated in terms of the critical domain size and its dependence on diffusion rate, advection rate, and population loss rate on the boundary. Here the critical domain size refers to the minimal size of the habitat required for population survival [27, 34, 36]. In particular, when the downstream boundary is lethal, then neither fast nor slowly diffusing population can persist [37]. The intuitive explanation is that the slowly diffusing population is completely washed out by the environmental drift, while the fast diffusing population is also too much exposed to the lethal boundary. In this case, it was conjectured in [22, 25] that there is an intermediate diffusion rate that is evolutionarily stable.

1.1. The model. In this paper, we address the ecological and evolutionary dynamics of populations in the following two-species competition model in a homogeneous, open, advective environment.

$$\begin{cases} U_t = \tilde{\mu}U_{xx} - \tilde{q}U_x + U(\tilde{r} - U - V) & \text{for } 0 < x < L, t > 0, \\ V_t = \tilde{\nu}V_{xx} - \tilde{q}V_x + V(\tilde{r} - U - V) & \text{for } 0 < x < L, t > 0, \\ \tilde{\mu}U_x(0, t) - \tilde{q}U(0, t) = \tilde{\mu}U_x(L, t) + (b-1)\tilde{q}U(L, t) = 0 & \text{for } t > 0, \\ \tilde{\nu}V_x(0, t) - \tilde{q}V(0, t) = \tilde{\nu}V_x(L, t) + (b-1)\tilde{q}V(L, t) = 0 & \text{for } t > 0, \\ U(x, 0) = U_0(x), \quad V(x, 0) = V_0(x) & \text{for } 0 < x < L, \end{cases} \quad (1.1)$$

where $U(x, t), V(x, t)$ are the population densities of two competing species, the coefficients $\tilde{\mu}, \tilde{\nu}, \tilde{q}, \tilde{r}, b, L$ are positive constants. To assess the relative advantage of different diffusion rates, we follow [15] and assume the two species are identical except for their diffusion rates. That is, we take $\tilde{\mu}, \tilde{\nu}$ to be the diffusion rates of the respective species, $\tilde{q}$ is their common advection rate, $\tilde{r}$ is the common local intrinsic growth rate, and b is the boundary loss rate, and L is the length of the habitat.

Next, we discuss the boundary conditions and the parameter b . At the upstream end $x = 0$, the population is assumed to satisfy the no-flux boundary condition, i.e. no individual will pass through the upstream end. At the downstream end $x = L$, there appears an additional nonnegative parameter b . This non-dimensional parameter measures the loss rate of individuals at the boundary relative to the flow rate (see [28] for a detailed derivation). The value of $b \geq 0$ is motivated by the underlying biological scenario. For $b = 0$, we obtain the no-flux condition which is suitable for studying the sinking, self-shading phytoplankton model (see, e.g.

[18, 19, 20]). Whereas $b = 1$ gives the free-flow (or Danckwerts) condition, which describes the stream to lake situation [38]. When b is large, i.e. $b \rightarrow +\infty$, we get the hostile boundary condition, $U(L, t) = 0$, which is suitable for describing the freshwater stream to ocean situation [37]. For $b \geq 1$, the downstream boundary condition can also be understood by extending the differential equations (1.1) to the unbounded domain $(0, \infty)$, by imposing uniform death rates $\tilde{\kappa}_i$ on the exterior domain, i.e.

$$U_t = \tilde{\mu}U_{xx} - \tilde{q}U_x - \tilde{\kappa}_1U, \quad \text{and} \quad V_t = \tilde{\nu}V_{xx} - \tilde{q}V_x - \tilde{\kappa}_2V \quad \text{for } x \geq L, t > 0,$$

and the conditions $\lim_{x \rightarrow +\infty} U(x, t) = 0$ and $\lim_{x \rightarrow +\infty} V(x, t) = 0$ for all t . Then the results in [2, 35] say that the long time dynamics of the problem on the unbounded domain $(0, \infty)$ is equivalent to that of (1.1), provided $\tilde{\kappa}_i$ are chosen such that

$$b = \frac{1}{2} \left(1 + \sqrt{1 + 4 \frac{\tilde{\mu}\tilde{\kappa}_1}{\tilde{q}^2}} \right) = \frac{1}{2} \left(1 + \sqrt{1 + 4 \frac{\tilde{\nu}\tilde{\kappa}_2}{\tilde{q}^2}} \right).$$

Biologically interpreted, it means that the species can move freely between the interior habitat $[0, L]$ and the exterior habitat $[L, \infty)$ beyond the downstream boundary. However, the exterior habitat is a sink with the death rate $\tilde{\kappa}_i$, so there is a positive probability that an individual cannot return to the bounded habitat $[0, L]$. Moreover, for $\tilde{\kappa}_i \rightarrow +\infty$, the probability of not returning is close to 1, which corresponds to the lethal boundary condition being enforced at the downstream boundary.

When there is no advection, i.e. $\tilde{q} = 0$, the set of (degenerate) equilibria $\{(s, 1-s) : 0 < s < 1\}$ attracts all positive solutions, so that neither the slower nor the faster diffuser wins. This can be proved, e.g. by the ideas in [10, 15]. In this paper, we are interested in the case $\tilde{q} > 0$.

To facilitate our discussion, we will non-dimensionalize (1.1) properly by setting

$$u(x, t) = \frac{1}{\tilde{r}} U\left(\frac{\tilde{q}x}{\tilde{r}}, \frac{t}{\tilde{r}}\right), \quad v(x, t) = \frac{1}{\tilde{r}} V\left(\frac{\tilde{q}x}{\tilde{r}}, \frac{t}{\tilde{r}}\right), \quad \mu = \frac{\tilde{\mu}\tilde{r}}{\tilde{q}^2}, \quad \nu = \frac{\tilde{\nu}\tilde{r}}{\tilde{q}^2}, \quad \ell = \frac{\tilde{r}}{\tilde{q}}L.$$

In this way, (1.1) becomes

$$\begin{cases} u_t = \mu u_{xx} - u_x + u(1 - u - v) & \text{for } 0 < x < \ell, t > 0, \\ v_t = \nu v_{xx} - v_x + v(1 - u - v) & \text{for } 0 < x < \ell, t > 0, \\ \mu u_x(0) - u(0) = \mu u_x(\ell) + (b-1)u(\ell) = 0, \\ \nu v_x(0) - v(0) = \nu v_x(\ell) + (b-1)v(\ell) = 0, \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x), \end{cases} \quad (1.2)$$

where μ, ν, b, ℓ are positive parameters. The system (1.2) has a trivial equilibrium $(0, 0)$, and two semitrivial equilibria $(\theta_\mu(x), 0)$ and $(0, \theta_\nu(x))$, where for each $\mu > 0$, $\theta_\mu(x)$ is the unique (whenever it exists) positive solution of the equation

$$\begin{cases} \mu \theta_{xx} - \theta_x + \theta(1 - \theta) = 0 & \text{for } 0 < x < \ell, \\ \mu \theta_x(0) - \theta(0) = \mu \theta_x(\ell) + (b-1)\theta(\ell) = 0. \end{cases} \quad (1.3)$$

In contrast to the situation with no advection, where the slower diffuser prevails, the model sometimes predicts the evolution of fast diffusion as shown by the following result (See [25] for the case $b = 1$ and [26] for the case $0 \leq b < 1$):

Theorem 1.1 ([25, 26]). *Suppose $0 \leq b \leq 1$, and $\mu > \nu > 0$. Then $(\theta_\mu, 0)$ is globally asymptotically stable, whenever it exists.*

However, we do not expect fast diffusion to be selected for all $b \geq 0$, since excessive diffusion is selected against when the boundary is lethal. Indeed, it was conjectured in [26] that the dynamics of (1.2) has some major differences between the case $0 \leq b \leq 1$ and $b > 3/2$. In this paper, we will argue that $b_{crit} = 3/2$ is the critical number that signals the qualitative change in the persistence criterion of a single species, as well as the competition dynamics between the fast and slow diffusers.

1.2. The critical domain size and $b_{crit} = 3/2$. When there is a population loss at the downstream boundary, i.e. $b > 0$, the critical domain size ℓ^* can be used to characterize the ability of a single species to survive [27, 34, 36]. The value of ℓ^* depends on the diffusion rate, advection rate, quality of habitat, and the boundary conditions. While ℓ^* is strictly increasing with respect to the advection rate [26, 35, 38], we will analyze the dependence of ℓ^* on diffusion rate and boundary conditions in detail. We will obtain a necessary and sufficient condition for ℓ^* to depend monotonically on the diffusion rate μ and boundary loss rate b of the species.

Proposition 1.2 ([26, 38]). *For each $b \geq 0$ and $\mu > 0$, there exists a function $\ell^* = \ell^*(\mu, b) \in [0, \infty]$ such that (1.3) has a unique positive solution θ_μ if and only if $\ell > \ell^*$. Moreover, for each $b \geq 0$, $\ell^*(\mu; b)$ is finite if and only if $\mu > \mu_{\min}(b)$, with*

$$\lim_{\mu \searrow \mu_{\min}(b)} \ell^*(\mu, b) = +\infty, \quad \text{and} \quad \lim_{\mu \rightarrow +\infty} \ell^*(\mu, b) = b,$$

where

$$\mu_{\min}(b) = b(1-b) \quad \text{if } 0 \leq b < 1/2 \quad \text{and} \quad \mu_{\min}(b) = 1/4 \quad \text{if } b \geq 1/2. \quad (1.4)$$

In fact, if $\ell \leq \ell^*$, then every nonnegative solution of (1.3) converges to zero uniformly as $t \rightarrow \infty$. If $\ell > \ell^*$, then every nonnegative, nontrivial solution of (1.3) converges to θ_μ uniformly as $t \rightarrow \infty$.

See [38] and [26, Theorem 2.1]. In fact, explicit formula of $\ell^*(\mu, b)$ is given therein. See Proposition 4.1 for details.

Our first new result illustrates the criticality of $b_{crit} = 3/2$ in terms of the critical domain size ℓ^* .

Proposition 1.3. *Let $b \geq 0$ and $\ell^*(\mu, b)$ be given by Proposition 1.2.*

- (a) *Let $b \in (0, \frac{3}{2}]$. Then $\ell^*(\cdot, b)$ is strictly decreasing on $(\mu_{\min}(b), \infty)$. In particular, we have $\min_{\mu} \ell^*(\mu, b) = b$, and that*
 - (i) *If $\ell \leq b$, then the single species goes extinct for all $\mu > 0$;*
 - (ii) *If $\ell > b$, then there exists $\underline{\mu}(\ell, b) > \mu_{\min}(b)$ such that the single species persists if and only if $\mu > \underline{\mu}$.*
- (b) *Let $b > \frac{3}{2}$. Then there exists $\tilde{\mu} \in (\frac{1}{4}, +\infty)$ such that $\ell^*(\cdot, b)$ is strictly decreasing on $(\frac{1}{4}, \tilde{\mu})$ and strictly increasing on $(\tilde{\mu}, +\infty)$. Also,*

$$\ell_{\min}(b) := \min_{\mu > 1/4} \ell^*(\mu; b) = \ell^*(\tilde{\mu}, b)$$

satisfies $\ell_{\min}(b) < b$ so that

- (i) *If $\ell \leq \ell_{\min}(b)$, then the single species goes extinct for all $\mu > 0$;*
- (ii) *If $\ell \in (\ell_{\min}(b), b)$, then there exist finite positive numbers $\frac{1}{4} < \underline{\mu}(\ell, b) < \tilde{\mu}(\ell, b)$ such that the single species persists if and only if $\mu \in (\underline{\mu}, \tilde{\mu})$;*
- (iii) *If $\ell \geq b$, then there exists $\underline{\mu}(\ell, b) > \frac{1}{4}$ such that the single species persists if and only if $\mu > \underline{\mu}$.*

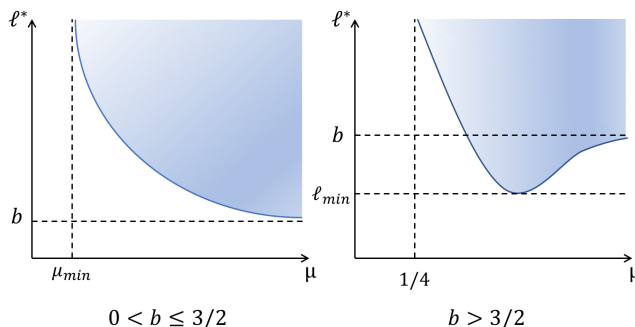


FIGURE 1. Normal form diagrams of ℓ^* against μ for different cases of b , as the illustrations of Proposition 1.3. The value of $\mu_{\min}$ is given in (1.4).

For $b > \frac{3}{2}$ and $\ell \in (\ell_{\min}(b), b)$, Proposition 1.3 says that the single species goes extinct if μ is too large or too small. The faster diffuser can no longer persist and therefore cannot competitively exclude the slower diffuser. In the next section, we will see that even when $b > \frac{3}{2}$ and $\ell \in (b, \infty)$, it is optimal to use some finite diffusion rate.

Remark 1.4. The dependence of critical patch size on parameters in the presence of advection was studied in [35] and subsequently in [2]. Motivated by climate change, the authors studied the case when there is equal boundary loss on both upstream and downstream boundary points. In case Dirichlet conditions are imposed at both ends, the change in monotonicity of ℓ^* in diffusion rate μ was observed in [2]. Here we provide a proof of this fact when the no-flux condition is imposed at the upstream boundary while the population loss rate at the downstream boundary is arbitrary. We conjecture that a similar result holds when population loss is also introduced at the upstream end in the context of [2, 35].

1.3. Evolutionary dynamics. In this paper we will show that the competition and evolutionary dynamics can be organized around the three cases: $b < 3/2$, $b = 3/2$ and $b > 3/2$. The framework of adaptive dynamics uses a game theoretic approach to study the evolution of phenotypes or heritable traits, such as the beak lengths of birds belonging to the same species. The theory of adaptive dynamics has been explored by various authors including Dieckmann and Law [9], Dercole and Rinaldi [8], Geritz et al. [11], McGill and Brown [31] and Waxman and Gavrillets [40].

We are interested in the evolution of dispersal rate, and we will henceforth refer to the values of dispersal rate as *strategies*. A fixed dispersal strategy μ represents all individuals that disperse at a fixed rate of μ . The evolution of dispersal strategy is modeled by a game with strategy function $\lambda(\mu, \nu)$, which is a real-valued function $\lambda(\mu, \nu) = \lambda(\mu, \nu; b, \ell)$ representing the advantage of an individual playing strategy ν against a population of players all playing a common strategy μ . In adaptive dynamics, the strategy function is given by the invasion exponent of a rare mutant population with strategy ν invading a resident population with strategy μ at equilibrium. Here, one must evaluate the linear stability of the equilibrium solution $(u, v) = (\theta_\mu, 0)$ for the system (1.2), which is mathematically characterized by the

principal eigenvalue $\lambda(\mu, \nu)$ of the following problem; see, e.g. [35, 36].

$$\begin{cases} \nu \Psi_{xx} - \Psi_x + (1 - \theta_\mu) \Psi = \lambda \Psi & \text{for } 0 < x < L, \\ \nu \Psi_x(0) - \Psi(0) = \nu \Psi_x(\ell) + (b - 1) \Psi(\ell) = 0, \end{cases} \quad (1.5)$$

where θ_μ is the unique positive solution of (1.3), which is the equilibrium density when the entire population plays the strategy μ . It is easy to see that $\lambda(\mu, \nu) = 0$ when $\mu = \nu$. A rare mutant population with strategy ν can invade the resident population playing strategy μ if $\lambda(\mu, \nu) > 0$. The invasion fails if $\lambda(\mu, \nu) < 0$.

The definition of invasion exponent via the eigenvalue of the (spatially explicit) problem (1.5) is based on the assumption that dispersal and population dynamics of the resident and invader species operate on the same timescale. We refer to the recent work [5] for the situation when the dispersal operates at a faster timescale comparing to population dynamics. Therein a new class of spatially implicit models are derived to discuss evolutionary dynamics.

Theorem 1.1 says that, for $0 \leq b \leq 1$, the faster diffuser always wins the competition. Hence, we expect the strategy $\mu^* = +\infty$ to be advantageous in the evolutionary sense. To facilitate the analysis of the strategy $+\infty$, we perform the following change of variables:

$$\Lambda(\xi, \tau) := \lambda(\mu, \nu), \quad \text{where } \xi := 1/\mu \quad \text{and} \quad \tau := 1/\nu. \quad (1.6)$$

We will henceforth study the evolution of strategies ξ, τ . Note that under such change of variables, θ_μ can be smoothly extended to $\mu = +\infty$, i.e. $\xi = 0$. Hence, $\Lambda(\xi, \tau)$ can be defined as a smooth function for $\xi, \tau \geq 0$. This point of view allows us to extend the classical notions in evolutionary game theory to the case of infinite diffusion rate.

We first define the classical notion of evolutionarily stable strategy (ESS) and convergence stable strategy (CvSS). Since the seminal paper by Maynard Smith and Price [30], game theory and the notion of ESS have been widely used to study problems in animal conflicts. The notion of ESS is the optimal strategy in the population sense: when playing against a population whose vast majority is playing the strategy ξ^* , an individual can maximize its advantage if and only if it plays the same strategy ξ^* . In other words, any individual who plays a strategy $\tau \neq \xi^*$ will be penalized and is expected to decrease in frequency in the long run. In continuous trait models, the definition of an ESS ξ^* is given as a maximum point of the function $\tau \mapsto \Lambda(\xi^*, \tau)$.

Definition 1.5. A strategy ξ^* is a global ESS if it cannot be invaded by any other strategies, i.e.

$$\Lambda(\xi^*, \tau) < 0 \quad \text{for all } \tau \neq \xi^*, \tau \geq 0. \quad (1.7)$$

A strategy ξ^* is a local ESS if (1.7) holds for all $\tau \neq \xi^*$ and sufficiently close to ξ^* .

Adaptive dynamics allows for the formal description of long term evolutionary dynamics of the trait ξ . The underlying idea is that the mean strategy $\bar{\xi}$ evolves in time t according to the advantage or disadvantage derived from playing strategy $\bar{\xi}$ against nearby strategies τ . Indeed, adaptive dynamics assumes that the mean strategy $\bar{\xi}$ increases (resp. decreases) if $\Lambda(\bar{\xi}, \tau) > 0$ for $\tau > \bar{\xi}$ (resp. for $\tau < \bar{\xi}$). Since $\Lambda(\bar{\xi}, \bar{\xi}) = 0$, the sign of $\Lambda(\bar{\xi}, \tau)$ is given (up to the first order) by the sign of the selection gradient $\Lambda_\tau(\bar{\xi}, \bar{\xi}) = \frac{\partial \Lambda}{\partial \tau}(\xi, \tau)|_{(\xi, \tau) := (\bar{\xi}, \bar{\xi})}$, that is

$$\frac{d}{dt} \bar{\xi} = \beta \Lambda_\tau(\bar{\xi}, \bar{\xi}), \quad (1.8)$$

for some $\beta = \beta(t) > 0$.

Definition 1.6. A strategy ξ^* is a convergence stable strategy (CvSS) if ξ^* is a linearly stable equilibrium of (1.8). In particular, $\xi^* > 0$ is a CvSS if

$$\Lambda_\tau(\xi^*, \xi^*) = 0, \quad \text{and} \quad \Lambda_{\tau\xi}(\xi^*, \xi^*) + \Lambda_{\tau\tau}(\xi^*, \xi^*) = \left[\frac{d}{ds} \Lambda_\tau(s, s) \right]_{s=\xi^*} < 0. \quad (1.9)$$

And $\xi^* = 0$ is a CvSS if either (1.9) or $\Lambda_\tau(0, 0) < 0$ holds.

Loosely speaking, a strategy is convergence stable if the mutant is always able to invade a resident population when the mutant strategy is closer to the convergence stable strategy than the resident strategy. In other words, CvSS are those strategies that are attainable via evolution, while ESS are those strategies that are able to persist, once they are achieved.

We now state our main results for evolutionary dynamics. The first result in this subsection resolves a conjecture in [22] concerning the evolutionary stability of $\xi^* = 0$, which corresponds to the diffusion strategy $\mu_* = +\infty$.

Theorem 1.7. *Let $\ell > b$. For $0 \leq b \leq 3/2$, the strategy $\xi^* = 0$ (which corresponds to $\mu_* = +\infty$) is a global ESS. Furthermore,*

- (a) *For $0 \leq b < 3/2$, the strategy $\xi^* = 0$ is a CvSS.*
- (b) *If $b = 3/2$ and $3/2 < \ell < 51/2$, the strategy $\xi^* = 0$ is a CvSS.*
- (c) *If $b = 3/2$ and $\ell > 51/2$, the strategy $\xi^* = 0$ is not a CvSS.*

For $b > 3/2$, $\xi^ = 0$ is neither a local ESS nor a CvSS.*

Remark 1.8. The assumption $\ell > b$ is imposed so that the strategy $\mu^* = +\infty$ is feasible. If $\ell \leq b$, then by Proposition 1.3 there exists $\bar{\mu} > 0$ such that the single species do not persist for all $\mu \geq \bar{\mu}$.

Indeed, Theorem 1.7 shows that the infinite diffusion is ESS if and only if $b \leq \frac{3}{2}$; i.e. as long as $b \leq \frac{3}{2}$, the infinite diffusion rate remains an unbeatable strategy. Though (1.2) is only defined for finite diffusion rates μ, ν , the competition dynamics can be extended to include the case of infinite diffusion in a natural way. Indeed, the population is expected to homogenize in space as $\mu \rightarrow \infty$, so that the following can be identified:

$$\lim_{\mu \rightarrow \infty} u(x, t) = \bar{u}(t) = \lim_{\mu \rightarrow \infty} \frac{1}{\ell} \int_0^\ell u(x, t) dx.$$

So the evolutionary stability of infinite diffusion can be, at least formally, decided by the linear stability of the equilibrium $(1 - b/\ell, 0)$ of the limiting system

$$\begin{cases} \frac{d}{dt} \bar{u}(t) = -\frac{b}{\ell} \bar{u}(t) + \bar{u}(t)(1 - \bar{u}(t) - \frac{1}{\ell} \int_0^\ell v(x, t) dx) & \text{for } t > 0, \\ v_t = \nu v_{xx} - v_x + v(1 - \bar{u}(t) - v) & \text{for } 0 < x < \ell, t > 0, \\ \nu v_x(0, t) - v(0, t) = \nu v_x(\ell, t) - (1 - b)v(\ell, t) = 0 & \text{for } t > 0. \end{cases} \quad (1.10)$$

Interestingly, as shown by Theorem 1.7, determining the linear stability of $(1 - b/\ell, 0)$ is equivalent to determining the sign of $\Lambda(0, 1/\nu)$. Therefore, system (1.10) provides another point of view on the evolutionary stability of the infinite diffusion rate. The evolutionary stability of infinite diffusion has never been established before, even for the case $0 \leq b \leq 1$, for which the competition exclusion between pairs of diffusion strategies was previously shown in [25, 26].

Since $\xi^* = 0$ a global ESS provided $b \leq 3/2$, one may naturally inquire whether the competition exclusion result of Theorem 1.1 can be extended to $b \leq 3/2$; i.e.

the faster diffuser dominates as long as $b \leq 3/2$. The answer is affirmative, with the additional assumption that both diffusion rates are large enough (Theorem 1.13(a)).

The full conclusion of faster diffuser wins, however, cannot be extended up to $b < 3/2$. In fact, our next theorem shows that there can be up to three distinct global ESS, even when $b < 3/2$. Hence, the global dynamics of (1.2) has already undergone a critical change as b varies somewhere between 1 to $3/2$; see Theorem 1.13(c). To the best of our knowledge, this is also the first theoretical result of multiple global ESS in a spatially explicit model for the evolution of dispersal.

Theorem 1.9. (a) For $\ell > \frac{51}{2}$, there exists $\delta > 0$ such that for $b \in (\frac{3}{2} - \delta, \frac{3}{2})$, there is another global ESS, denoted by $\xi_1^*(b) > 0$ (besides $\xi^* = 0$), such that $\xi_1^*(b) \rightarrow 0$ as $b \nearrow \frac{3}{2}$. However, $\xi_1^*(b)$ is not a CvSS.
 (b) More precisely, there exist $c', \delta' > 0$ such that if

$$b < \frac{3}{2}, \quad \ell > \frac{51}{2} \quad \text{and} \quad \left| b - \frac{3}{2} \right| \leq c' \left(\ell - \frac{51}{2} \right)^2 < \delta', \quad (1.11)$$

then there exist at least three global ESS, denoted by ξ^*, ξ_1^*, ξ_2^* , such that

$$0 = \xi^* < \xi_1^* < \xi_2^*.$$

Moreover, $\xi^* = 0$ and ξ_2^* are CvSS but ξ_1^* is not a CvSS.

Remark 1.10. Condition (1.11) describes a cusp region with a vertex at $(b, \ell) = (3/2, 51/2)$.

When $b > 3/2$, we have the following result.

Theorem 1.11. For $\frac{3}{2} < \ell < \frac{51}{2}$, there exists $\delta' > 0$ such that for $b \in (\frac{3}{2}, \frac{3}{2} + \delta')$, there exists $\xi_3^*(b) \in (0, \infty)$ which is both a global ESS and CvSS. Furthermore, $\xi_3^*(b) \rightarrow 0$ as $b \searrow \frac{3}{2}$.

Remark 1.12. When b surpasses $3/2$, Theorem 1.7 says that the strategy $\xi^* = 0$ loses its evolutionary stability. It is conjectured in [22] that, for each $b > 3/2$, there exists a unique intermediate dispersal rate which is evolutionarily stable. We partially resolve this conjecture by showing that a bifurcation at the level of evolutionary stability [8] occurs when the parameter b surpasses $3/2$. The conjecture remains open for general $b > 3/2$.

Next, we systematically study the evolutionary dynamics in terms of the two environmental parameters, namely, the boundary population loss rate b and the domain size ℓ . Our analytical and numerical results reveal a total of 9 qualitatively different pairwise invasibility plots (PIP). These are diagrams in the strategy (ξ, τ) space describing the invasion outcome when a rare mutant playing strategy τ is invading a resident population playing strategy ξ . See Fig. 2 for the normal form diagrams and Fig. 3 for concrete numerical computations, respectively. We suspect that this list has exhausted all possibilities in the particular model, but it will be a nontrivial numerical project to verify this conjecture.

When $b = 0$ and the resources are heterogeneously distributed, the evolutionary dynamics of (1.1) was considered in [12, 23]. In particular, by choosing specific parameters and heterogeneous resource distributions, the existence of evolutionary branching points was proved in [23] (specifically, by the proofs of Lemma 6.8(ii) and Theorem 6.5 of [23]), while some complex PIP's were discovered in [12].

1.4. Ecological dynamics. The evolutionary dynamical results in the previous subsection have various consequences for the two-species competition dynamics governed by (1.2). In fact, the ESS and CvSS can be viewed as critical parameters above which the competition dynamics undergo qualitative changes. The connection of evolutionary dynamics and ecological dynamics has been investigated by Cantrell et al. [4] for a broad class of models including reaction-diffusion equations and nonlocal diffusion equations. It has been shown, for instance, that frequently a species adopting an ESS dispersal strategy can displace a competitor adopting a dispersal strategy that is not an ESS. This is quite unexpected as ESS by its very own definition only guarantees the adopting population to be able to resist invasion. In this subsection, we state our results on the global dynamics of the two-species competition model (1.2), for fixed diffusion rates μ and ν .

Theorem 1.13. (a) *For $0 \leq b < 3/2$ and $\ell > b$, there exists $\underline{\mu} > 0$ large such that for $\mu > \nu \geq \underline{\mu}$, the equilibrium $(\theta_\mu, 0)$, when it exists, is globally asymptotically stable.*
 (b) *For $b > 3/2$, and $\ell \geq b$, there exists $\underline{\mu} > 0$ large such that for $\mu > \nu \geq \underline{\mu}$, the equilibrium $(0, \theta_\nu)$, when it exists, is globally asymptotically stable.*
 (c) *For $b > 3/2$ and $3/2 < \ell < 27/2$, let $\mu_3^* = 1/\xi_3^*$, where ξ_3^* is given by Theorem 1.11. Then there exists $\delta'' > 0$ such that*
 – *for $\mu_3^* + \delta'' \geq \mu > \nu \geq \mu_3^*$, then the equilibrium $(0, \theta_\nu)$, when it exists, is globally asymptotically stable.*
 – *for $\mu_3^* \geq \mu > \nu \geq \mu_3^* - \delta''$, then the equilibrium $(\theta_\mu, 0)$, when it exists, is globally asymptotically stable.*
In particular, if $\mu = \mu_3^$ and $0 < |\nu - \mu_3^*| < \delta''$, then $(\theta_\mu, 0)$, when it exists, is globally asymptotically stable.*

Remark 1.14. Assertion (a) (resp. (b)) is vacuous when $\ell \leq b$ (resp. $\ell < b$), since then θ_μ does not exist for $\mu \gg 1$. Theorem 1.13(c) is due to [4, Theorem 6.2].

Remark 1.15. One can observe from the PIP (Fig. 2(F) and Fig. 3 case $b = 1.51$ and $\ell = 20$) that for fixed $27/2 < \ell < 51/2$ and $b > 3/2$ close enough to b , there are two sequences $(\mu_j, \nu_j) \rightarrow (\mu_3^*, \mu_3^*)$ and $(\mu'_j, \nu'_j) \rightarrow (\mu_3^*, \mu_3^*)$ such that

$$\mu_j > \nu_j > \mu_3^* \quad \text{and} \quad \mu_3^* > \mu'_j > \nu'_j,$$

and

$$\lambda(\mu_j, \nu_j) < 0 \quad \text{and} \quad \lambda(\mu'_j, \nu'_j) < 0,$$

i.e. the semi-trivial equilibria $(\theta_{\mu_j}, 0)$ and $(0, \theta_{\nu_j})$ of the competition model (1.2) are both linearly stable. In other words, the dynamics of (1.2) is bistable. Here $\mu_3^* = 1/\xi_3^*$ and ξ_3^* is given by Theorem 1.11.

Corollary 1.16. *There exists a maximal $b^\dagger \in [1, 3/2)$ such that for any $b < b^\dagger$ and $\ell > 0$, if $\mu > \nu > 0$, then $(\theta_\mu, 0)$, if it exists, is globally asymptotically stable.*

By the results in [25, 26] we have $b^\dagger \geq 1$. Our main contribution is the estimate $b^\dagger < 3/2$, which is a consequence of Theorem 1.13(c). It will be interesting if one can characterize $b^\dagger$, which is closely related to the parameter region in the b - ℓ plane where Fig. 2(G) is valid.

1.5. Organization. In Section 2 we illustrate that there are up to 9 qualitatively different pairwise invasibility plots. In Section 3, we discuss the implications of our results for the original system (1.1). Section 4 is devoted to persistence results of a

single species, where Proposition 1.3 is proved. In Section 5 we prove evolutionary results, including Theorems 1.7, 1.9 and 1.11 concerning the existence of ESS and CvSS. In Section 6 we turn to ecological dynamics. In particular, we will show that the ESS can be seen as the organizing center for the reversal of competition outcomes between the fast and slow diffusers described by system (1.2). Finally, the technical calculations are postponed to Appendix A.

2. Computation of the pairwise invasibility plots. Based on our theoretical results, we can show that there are up to 9 qualitatively different pairwise invasibility plots (PIPs). We provide normal form diagrams in Fig. 2, in which specific theorems proving parts of the diagrams are also referenced.

Our analytical expansion of the invasion fitness function $\Lambda(\xi, \tau)$ confirms the shape of the pairwise invasibility plots near the origin. To test our conjecture of the shape of the pairwise invasibility plots away from the origin, shown in Fig. 2, we also perform numerical computations for the cases $b = 1.49, 1.5, 1.51$ and $\ell = 10, 20, 50$. Our numerical results, shown in Fig. 3 below, confirm our conjecture concerning the shape of the pairwise invasibility plots where analytical conclusions are lacking. To compute these diagrams, we use the 2nd order finite difference scheme to discretize both (1.3) and (1.5) with a uniform grid point ($N = 200$). Since (1.3) is a nonlinear system, we employ Newton's method to solve it with the all-one-vector as an initial guess vector. In Fig. 3, we fix the parameters l and b and track ξ from -0.1 to 0.5 via the homotopy continuation method [14] with $\Delta\xi = 10^{-3}$. Specifically, we solve $\Lambda(\xi, \tau) = 0$ for τ with each given homotopy parameter ξ .

An interesting future direction is to numerically investigate (i) whether there can be more than 9 qualitatively different types of pairwise invasibility plots, and (ii) the exact parameter region in the (b, ℓ) parameter space that corresponds to each type. In this way, the entire adaptive landscape of the model can be fully determined. We believe that it is unlikely that there are more than 9 types of pairwise invasibility plots for this model. One reason is that, by viewing the pairwise invasibility plots as they vary under the two parameters b and ℓ , we expect singularities of at most co-dimension one [39]. We believe it is unlikely that additional singularities, other than the one we have found, exist in this model. For this reason, qualitatively different diagrams are unlikely to occur as β and ℓ vary.

3. Summary and discussion. Our first result gives a global description of how the critical domain size depends on boundary population loss rate b and diffusion rate μ .

- Proposition 1.3 says that the critical patch size remains nonincreasing in μ if and only if $b \leq 3/2$. And as b surpasses $3/2$, the critical patch size ℓ^* is no longer monotone in the diffusion rate μ , and there exists $\ell < b$ such that a single species persists if and only if its diffusion rate is neither too large nor too small.

In contrast to the situation for heterogeneous environments, in which the evolutionary dynamics is likely quite complex (see, [23, Corollary 6.6] for the existence of ESS and evolutionary branching points, and [12] for a combined numerical and theoretical approach to compute pairwise invasibility plots), previous works on homogeneous environments [25, 26, 37] demonstrate that for small population loss at the downstream end (e.g. $0 \leq b \leq 1$) fast diffusion is selected, and suggest that intermediate diffusion is selected when the downstream end becomes lethal ($b = +\infty$).

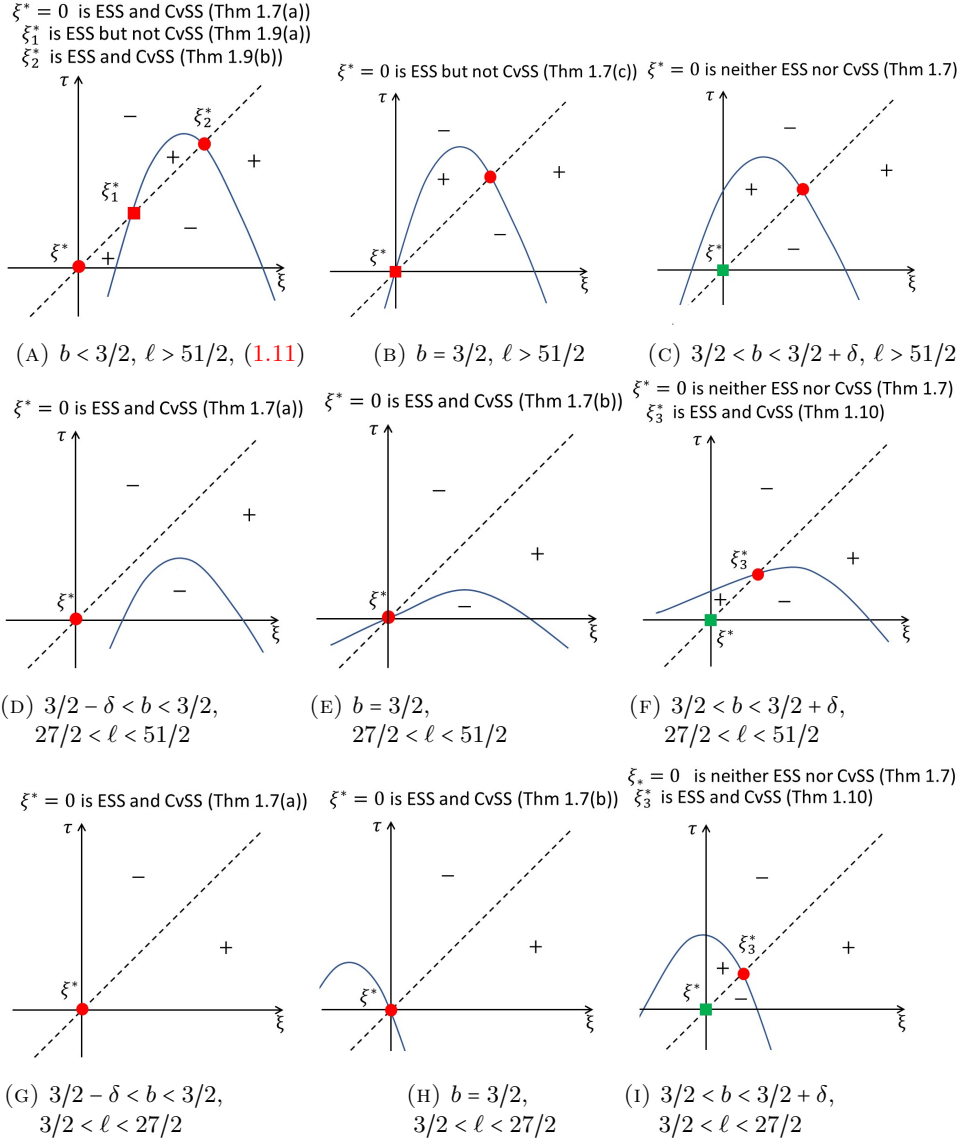


FIGURE 2. The above normal form diagrams summarize the analytical results from Theorems 1.7, 1.9 and 1.11. They illustrate the transition of 9 qualitatively different pairwise invasibility plots, i.e. nullclines of $\Lambda(\xi, \tau)$, as parameters b and ℓ vary. For a pair of strategies (ξ, τ) , if it lies on a region marked with a plus (resp. minus) sign, then it indicates that the species with strategy τ can (resp. cannot) invade the species with strategy ξ when rare. A red circle (●) stands for an ESS and CvSS; a red square (■) stands for an ESS and non-CvSS; a green square (■) stands for a non-ESS and non-CvSS.

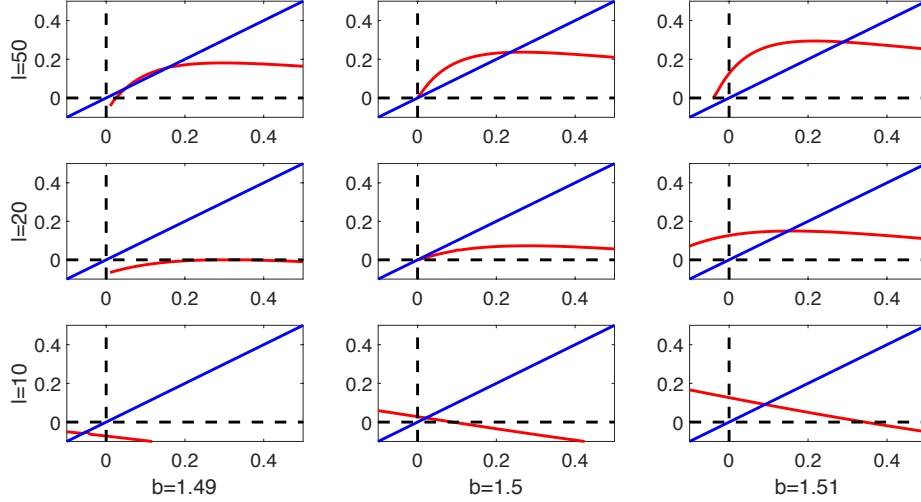


FIGURE 3. Numerical simulation of the pairwise invasibility plots (i.e. the nullclines of $\Lambda(\xi, \tau)$) for parameter values $b = 1.49, 1.5, 1.51$ and $\ell = 10, 20, 50$. The horizontal axis is ξ and the vertical axis is τ .

Our result shows that the evolutionary landscape has an unexpected level of complexity, even for the homogeneous environments in which there is a limited degree of freedom in the environmental parameters.

- For $0 \leq b \leq 3/2$, Theorem 1.7 says that the infinite diffusion rate $\mu^* = +\infty$ is ESS in the sense that the equilibrium $(1 - b/\ell, 0)$ of system (1.10) is linearly stable for any $\nu \in (0, \infty)$. This gives a measure of the advantage of fast diffuser when the population loss on the boundary is less than the critical number $3/2$.
- However, even for $b < 3/2$ (but close to $3/2$), Theorem 1.9(b) says that there exists some $\ell > 51/2$ such that, besides the ESS strategy $\mu^* = \infty$, there are at least two additional ESS strategies $\mu_1^* > \mu_2^* > 0$. In particular, if we take $(\mu, \nu) = (\mu_1^*, \mu_2^*)$ in (1.2), then both semi-trivial equilibria $(\theta_{\mu_1^*}, 0)$ and $(0, \theta_{\mu_2^*})$ are linearly stable, and the competition system (1.2) has a further (unstable) positive equilibrium [16, Proposition 9.1]. This can possibly be attributed to the relatively large size of the domain $\ell \gg b$, so that the patches closest to the upper stream boundary and the downstream boundary are decoupled. In this case, the faster species can better utilize the upstream patch, while the slower species can better utilize the downstream patch. See also [35].
- For $b > 3/2$, our result suggests that fast diffusion rates are selected against. Indeed, when $\ell < b$, the single species can no longer persist for high diffusion rate (Proposition 1.3(b)(ii)), whereas for $\ell \geq b$, $\mu^* = \infty$ is no longer an ESS (Theorem 1.7), despite the fact that $\mu^* = +\infty$ is still a feasible strategy (Proposition 1.3(b)(iii)).
- In fact, Theorem 1.11 suggests that, for $b \searrow 3/2$, there exists $\mu_3^* \in (0, \infty)$ which is both ESS and CvSS. This can be seen as a bifurcation of the ESS in the strategy space [8].
- The formulas of higher derivatives of the strategy function Λ at $(0, 0)$, in terms of the boundary loss rate b and domain size ℓ (see Appendix A), reveal the

critical numbers $b^* = 3/2$ and $\ell^* = 27/2, 51/2$. This leads to 9 qualitatively different pairwise invasibility plots; see Figs. 2 and 3.

The evolutionary dynamics discussed above have immediate consequences on the global dynamics of (1.2) for fixed pairs of strategies (μ, ν) .

- (Fast diffuser wins) For $0 \leq b < 3/2$, the faster diffuser wins in (1.2), provided the minimum of the two diffusion rates is large enough. This extends previous results concerning $0 \leq b \leq 1$. This result is sharp, in view of the possibility of bistability for some b sufficiently close to $3/2$ discussed above.
- (Slow diffuser wins) When $b > 3/2$, then not only $\mu^* = +\infty$ loses its evolutionary stability, we in fact showed that slower diffuser wins in (1.2) as long as both strategies μ, ν are large enough.
- (Edge Effect) The competition reversal can be explained by the effect of the habitat edge due to [35]. On the one hand, for $b < 3/2$, the critical domain size ℓ^* is strictly decreasing in the diffusion rate μ for large μ . Hence for $\mu, \nu \gg 1$, the (relatively) slower diffuser has larger critical domain size and is negatively impacted by the population loss at the downstream edge to a greater extent. This argument predicts that, for $b < 3/2$ and $\mu, \nu \gg 1$, the (relatively) faster diffuser wins. On the other hand, for $b > 3/2$, the critical domain size ℓ^* is strictly increasing in the diffusion rate μ for large μ . Hence the downstream edge negatively impacts the faster diffuser to a greater extent, and leads to the triumph of the slower diffuser.

4. Persistence and the critical domain size $\ell^*(\mu, b)$. The persistence of a single species population with dispersal rate μ is determined by the sign of the principal eigenvalue (i.e. the eigenvalue with the smallest real part), denoted by $\tilde{\lambda}(\mu, \ell, b)$, of the following linearized problem of (1.3) at the trivial equilibrium:

$$\begin{cases} \mu \phi_{xx} - \phi_x + \phi = \tilde{\lambda} \phi & \text{for } 0 < x < \ell, \\ \mu \phi_x(0) - \phi(0) = \mu \phi_x(\ell) - (1-b)\phi(\ell) = 0. \end{cases}$$

On the one hand, if $\tilde{\lambda} > 0$, then the single species persists in the strong sense: the single equation (1.3) has a unique positive equilibrium θ_μ which attracts every nontrivial nonnegative solutions $\theta(x, t)$ of (1.3). On the other hand, if $\tilde{\lambda} \leq 0$, then the species goes to extinction in the sense that $\theta(x, t) \rightarrow 0$ uniformly as $t \rightarrow \infty$; see, e.g. [3].

Proposition 4.1. *Let $\ell^*(\mu, b)$ be given by Proposition 1.2, then $\tilde{\lambda}(\mu, \ell, b) = 0$ if and only if $\ell = \ell^*(\mu, b)$. Moreover,*

- $\lim_{\mu \rightarrow \mu_{\min}(b)} \ell^*(\mu, b) = +\infty$ and $\lim_{\mu \rightarrow +\infty} \ell^*(\mu, b) = b$, where $\mu_{\min}(b)$ is given in (1.4).
- When $b = 0$, $\ell^*(\mu, b) \equiv 0$ for all $\mu > 0$.
- When $0 < b < \frac{1}{2}$, then $\ell^*(\mu, b) < +\infty$ iff $\mu > b(1-b)$. Precisely,

$$\ell^*(\mu, b) = \begin{cases} 2\mu \frac{\arctan \frac{b\sqrt{4\mu-1}}{2\mu-b}}{\sqrt{4\mu-1}} & \text{for } \mu > \frac{1}{4}, \\ \log \left(\frac{2\mu-b+b\sqrt{1-4\mu}}{2\mu-b-b\sqrt{1-4\mu}} \right) \cdot \frac{\mu}{\sqrt{1-4\mu}} & \text{for } b(1-b) < \mu < \frac{1}{4}. \end{cases}$$

- When $b \geq \frac{1}{2}$, then $\ell^*(\mu, b) < +\infty$ iff $\mu > \frac{1}{4}$. Precisely,

$$\ell^*(\mu, b) = \begin{cases} 2\mu \frac{\arctan \frac{b\sqrt{4\mu-1}}{2\mu-b}}{\sqrt{4\mu-1}} & \text{for } \mu \geq \frac{b}{2}, \\ 2\mu \frac{\pi + \arctan \frac{b\sqrt{4\mu-1}}{2\mu-b}}{\sqrt{4\mu-1}} & \text{for } \frac{1}{4} < \mu < \frac{b}{2}. \end{cases}$$

(e) For each $b > 0$ and $\mu > \mu_{\min}(b)$, the scalar quantity $\ell^*(\mu, b)$ is the first positive root and also the unique positive root in $\left(0, \frac{\pi}{2\sqrt{\tau-\tau^2/4}}\right)$ of the equation

$$\frac{\ell^*}{b} \left(1 - \frac{b\tau}{2}\right) = g\left(\sqrt{\tau - \frac{\tau^2}{4}} \ell^*\right), \quad (4.1)$$

where $g(s) = s \cot s$, $\tau = 1/\mu$.

(f) For $b \in (0, \frac{3}{2}]$,

$$\frac{\partial \ell^*}{\partial \mu}(\mu, b) < 0 \quad \text{for } \mu > \mu_{\min}(b).$$

(g) For $b \in (\frac{3}{2}, \infty)$, there exists $\tilde{\mu}(b) > \frac{1}{2}$ such that $\tilde{\mu}(b) \nearrow +\infty$ as $b \searrow \frac{3}{2}$, and

$$\frac{\partial \ell^*}{\partial \mu}(\mu, b) = \begin{cases} < 0 & \text{for } \frac{1}{4} < \mu < \tilde{\mu}, \\ = 0 & \text{for } \mu = \tilde{\mu}, \\ > 0 & \text{for } \mu > \tilde{\mu}. \end{cases}$$

Proof of Proposition 4.1(a)-(e). Assertion (a) is proved in [26, Theorems 2.1]. Assertion (b) is proved in, e.g. [23, Lemma 2.1]. Assertions (c) and (d) follow by taking $L^* = \ell^*$, $r = \alpha = 1$ and $d = \mu = 1/\tau$ in [26, Formulas (2.19), (2.20) and (2.21)]. For assertion (e), observe from the characterization of ℓ^* in [26, Lemmas 2.1 and 2.2] that, for each $b \geq 0$,

$$\frac{\tan\left(\ell^* \sqrt{\tau - \tau^2/4}\right)}{\sqrt{4/\tau - 1}} = \frac{b}{2/\tau - b}.$$

Dividing by $\ell^* \tau/2$ on both sides, we get

$$\frac{\tan\left(\ell^* \sqrt{\tau - \tau^2/4}\right)}{\ell^* \sqrt{\tau - \tau^2/4}} = \frac{b}{\ell^*} \frac{1}{1 - b\tau/2},$$

which is equivalent to (4.1). $\square$

Before we prove the remainder of Proposition 4.1, we first establish a calculus lemma.

Lemma 4.2. For $b \geq \frac{1}{2}$, if $\frac{\partial}{\partial \mu} \ell^*(\mu_0, b) = 0$ for some $\mu_0 > 0$, then $\frac{\partial^2}{\partial \mu^2} \ell^*(\mu_0; b) > 0$.

Proof. In this proof, we fix $b \geq 1/2$ and denote $\mu = 1/\tau$, and set

$$L(\tau) := \ell^*(\mu, b), \quad ' = \frac{\partial}{\partial \tau}, \quad M := \sqrt{\tau - \frac{\tau^2}{4}}, \quad (4.2)$$

to simplify the notations. It remains to show that if $L'(\tau_0) = 0$ for some $0 < \tau_0 < 4$, then $L''(\tau_0) > 0$. Differentiate (4.1) with respect to τ ,

$$L' \cdot \left(\frac{1}{b} - \frac{\tau}{2}\right) - \frac{L}{2} = g'(ML) \left(ML' + \frac{L}{2} \frac{1 - \tau/2}{M}\right). \quad (4.3)$$

Setting $\tau = \tau_0$, so that $L' = 0$, we have

$$-g'(ML)\Big|_{\tau=\tau_0} = \frac{M}{1-\tau_0/2}, \quad \tau_0 \in (0, 2), \quad g'(ML)\Big|_{\tau=\tau_0} < 0. \quad (4.4)$$

Differentiating (4.3) again, we have (using $(ML)' = ML' + \frac{L}{2} \cdot \frac{1-\tau/2}{M}$)

$$\begin{aligned} L'' \cdot \left(\frac{1}{b} - \frac{\tau}{2}\right) - L' = g''(ML) \left[ML' + \frac{L}{2} \cdot \frac{1-\tau/2}{M} \right]^2 \\ + g'(ML) \left\{ ML'' + L' \frac{1-\tau/2}{M} + L \left(-\frac{1}{4M} - \frac{(1-\tau/2)^2}{4M^3} \right) \right\}. \end{aligned}$$

Setting $\tau = \tau_0$, we have $L' = 0$ and

$$L'' \cdot \left(\frac{1}{b} - \frac{\tau_0}{2} - g'(ML)M\right) = g''(ML) \left[\frac{L}{2} \cdot \frac{1-\tau_0/2}{M} \right]^2 - \frac{g'(ML)L}{4M} \left(1 + \frac{(1-\tau_0/2)^2}{M^2} \right).$$

Substituting (4.4), we deduce that

$$L'' \cdot \left(\frac{1}{b} - \frac{\tau_0}{2} + \frac{\tau_0 - \tau_0^2/4}{1-\tau_0/2}\right) = \frac{L^2}{4(g'(ML))^2} \left\{ g''(ML) - \frac{g'(ML)}{ML} [1 + (g'(ML))^2] \right\}. \quad (4.5)$$

Next, observe that $\frac{1}{b} - \frac{\tau_0}{2} + \frac{\tau_0 - \tau_0^2/4}{1-\tau_0/2} = \frac{1}{b} + \frac{\tau_0}{2-\tau_0} > 0$; and that

$$g''(ML) - \frac{g'(ML)}{ML} [1 + (g'(ML))^2] > 0,$$

which follows from $ML \in (0, \pi)$ and Lemma A.12. We can then deduce from (4.5) that $L''(\tau_0) > 0$. This concludes the proof of Lemma 4.2. $\square$

Proof of Proposition 4.1(f) and (g). First, we assume $0 < b \leq 3/2$ and prove assertion (f). For $0 < b \leq 1$, this assertion is proved in [26, Proposition 2.2]. We will now provide a proof for the case $b \geq 1/2$.

Let $L(\tau) = \ell^*(\mu, b)$ be defined as in (4.2). We claim that

$$L'(0) = \frac{b^2}{3} \left(\frac{3}{2} - b \right). \quad (4.6)$$

To this end, rewrite (4.3) as

$$L' \cdot \left(\frac{1}{b} - \frac{\tau}{2}\right) - \frac{L}{2} = \frac{g'(ML)}{ML} \left[M^2 LL' + \frac{L^2}{2} \left(1 - \frac{\tau}{2} \right) \right]. \quad (4.7)$$

Using $L(0) = b$ (i.e. $\ell^*(+\infty, b) = b$) and that $\frac{g'(s)}{s} = -\frac{2}{3} + o(1)$ (which follows from the expansion $g(s) = 1 - s^2/3 - s^4/45 + \dots$), we may set $\tau = 0$ in (4.7) and obtain

$$L'(0) \cdot \frac{1}{b} - \frac{b}{2} = -\frac{2}{3} \cdot \frac{b^2}{2} = -\frac{b^2}{3}.$$

This proves (4.6).

Now, for $b \in (\frac{1}{2}, \frac{3}{2}]$, $L'(0) \geq 0$ and $L(\tau) \rightarrow +\infty$ as $\tau \nearrow 4$ (Proposition 4.1(a)). Lemma 4.2 implies that $L'(\tau) > 0$ for $\tau \in (0, 4)$. This is equivalent to $\frac{\partial}{\partial \mu} \ell^*(\mu, b) < 0$ for $\mu > \frac{1}{4}$. This completes the proof of (f).

For $b > \frac{3}{2}$, $L'(0) < 0$ and $L(\tau) \rightarrow +\infty$ as $\tau \nearrow 4$. Then L achieves a global minimum at some $0 < \tilde{\tau} < 4$. By Lemma 4.2, such $\tilde{\tau}$ is unique, and $L'(\tau) < 0$ for $\tau \in (0, \tilde{\tau})$; and $L'(\tau) > 0$ for $\tau \in (\tilde{\tau}, 4)$. In fact, by (4.4) we have $\tilde{\tau} \in (0, 2)$. This proves (g) and completes the proof of the proposition. $\square$

Proposition 1.3 is a direct consequence of Proposition 4.1.

Proof of Proposition 1.3. To prove (a), let $b \in (0, 3/2]$. Proposition 4.1(f) says that ℓ^* is strictly decreasing in $\mu \in (\mu_{\min}(b), \infty)$, and hence

$$\min_{\mu} \ell^*(\ell, b) = \ell^*(\infty, b) = b,$$

where the last equality follows Proposition 4.1(a). On the one hand, if $\ell \leq b$, then $\ell \leq \ell^*(\infty, b) < \ell^*(\mu, b)$ for all μ , so that the single species goes to extinction for any $\mu > 0$. On the other hand, if $\ell > b$, then by Proposition 4.1(a) again, there exists a unique $\underline{\mu} \in (\mu_{\min}(b), \infty)$ such that $\ell(\underline{\mu}, b) = \ell$, so that the single species persists if and only if $\ell > \ell^*(\mu, b)$. The latter is equivalent to $\mu > \underline{\mu}$. This proves assertion (a). The proof of assertion (b) follows by a similar argument using Proposition 4.1(g). $\square$

5. Evolutionary dynamics. Recall that the invasion exponent $\lambda(\mu, \nu)$ is given by the principal eigenvalue of (1.5). To analyze the situation when μ, ν are very large, we perform the change of coordinates

$$\xi = 1/\mu, \quad \tau = 1/\nu, \quad \Lambda(\xi, \tau) = \lambda(\mu, \nu).$$

Under this transformation, $\Lambda(\tau, \xi)$ can be characterized as the principal eigenvalue of

$$\begin{cases} \phi_{xx} + \tau[\phi_x + (1 - e^{\xi x} \vartheta_{\xi}(\cdot))\phi] = \tau \Lambda \phi, & \text{for } 0 < x < \ell, \\ \phi_x(0) = \phi_x(\ell) + \tau b \phi(\ell) = 0, \end{cases} \quad (5.1)$$

where $\phi(x) = e^{-\tau x} \Psi(x)$, and $\vartheta_{\xi}(x)$ is the unique positive solution of

$$\begin{cases} \vartheta_{xx} + \xi[\vartheta_x + (1 - e^{\xi x} \vartheta)\vartheta] = 0, & \text{for } 0 < x < \ell, \\ \vartheta_x(0) = \vartheta_x(\ell) + \xi b \vartheta(\ell) = 0. \end{cases} \quad (5.2)$$

Remark 5.1. For $\xi > 0$, it is a standard fact that the boundary value problem (5.2) has at most one solution; see e.g. [3, Propositions 3.2 and 3.3].

The smoothness of ϑ_{ξ} up to $\xi = 0$ could be argued by using the uniqueness of the positive solutions to (5.2) when $\xi > 0$ and the Crandall-Rabinowitz Bifurcation Theorem at $\xi = 0$; see [3, Proposition 3.17] and references therein. In particular, the smooth extension of ϑ_{ξ} at $\xi = 0$ is a positive constant. To determine this constant, we observe that, when $\xi > 0$, then integrating (5.2) and using the boundary conditions gives

$$(1 - b)\vartheta(\ell) - \vartheta(0) + \int_0^{\ell} (1 - e^{\xi x} \vartheta(x))\vartheta(x) dx = 0. \quad (5.3)$$

By continuity, we may pass to the limit $\xi \rightarrow 0$ in (5.3) to obtain that $\vartheta|_{\xi=0} \equiv 1 - b/\ell$. This shows that if $\ell > b$, the species reaches the ideal free distribution for $\xi = 0$, which suggests that $\mu = +\infty$ could be an ESS. Theorem 1.7 says that this is true for $b \leq 3/2$ only.

Next, we discuss the domain of definition of Λ . First, define $\bar{\xi} = 1/\underline{\mu}$ and $\underline{\xi} = 1/\bar{\mu}$, where $\underline{\mu}, \bar{\mu}$ are given in Proposition 1.3.

Lemma 5.2. *Let the domain of definition of Λ be $\Gamma_{b,\ell}$, then*

- (a) *If $b \in (0, 3/2]$ and $\ell < b$, or $b > 3/2$ and $\ell < \ell_{\min}(b)$, then ϑ_{ξ} does not exist for any ξ , so that $\Gamma_{b,\ell} = \emptyset$. Here $\ell_{\min}(b)$ is given in Proposition 1.3(b).*
- (b) *If $b \in (0, \infty)$ and $\ell \geq b$, then $\Gamma_{b,\ell} = [0, 1/\underline{\mu}] \times [0, \infty)$.*
- (c) *If $b > 3/2$ and $\ell \in (\ell_{\min}, b)$, then $\Gamma_{b,\ell} = [1/\bar{\mu}, 1/\underline{\mu}] \times [0, \infty)$.*

Moreover,

$$\Lambda(\xi, \tau) < 0 \quad \text{in } [0, 1/\underline{\mu}] \times [1/\underline{\mu}, +\infty), \quad (5.4)$$

and, in case $\bar{\mu} > 0$ (i.e. when $b > 3/2$ and $\ell \in (\ell_{\min}, b)$), then also

$$\Lambda(\xi, \tau) < 0 \quad \text{in } [1/\bar{\mu}, 1/\underline{\mu}] \times [0, 1/\bar{\mu}]. \quad (5.5)$$

Proof. Parts (a)-(c) follow from Proposition 1.3. To show (5.4), we observe that $\tau \geq 1/\underline{\mu}$, so that the single species with strategy τ does not persist. In other words, $\ell \leq \ell^*(\mu, b)$, so that the principal eigenvalue $\hat{\Lambda}$ of

$$\begin{cases} \hat{\phi}_{xx} + \tau[\hat{\phi}_x + \hat{\phi}] = \tau\hat{\Lambda}\hat{\phi}, & \text{for } 0 < x < \ell, \\ \hat{\phi}_x(0) = \hat{\phi}_x(\ell) + \tau b\hat{\phi}(\ell) = 0 \end{cases}$$

is non-positive, and that $\Lambda(\xi, \tau) < \hat{\Lambda} < 0$ by comparison. We omit the proof of (5.5). $\square$

We will expand Λ at $(\xi, \tau) = (0, 0)$ up to one of the third order directional derivatives.

Proposition 5.3. *Let $\ell > b > 0$. Then the single species persists for all sufficiently large μ , so that Λ is well-defined for all small $\xi, \tau \geq 0$, and*

$$\begin{aligned} \text{(i)} \quad \Lambda_\tau(0, 0) &= \frac{b}{3} \left(b - \frac{3}{2} \right), \\ \text{(ii)} \quad \Lambda_{\tau\tau}(0, 0) &= -\frac{b\ell}{90} [b^2 + 15(b-1)^2] < 0. \end{aligned}$$

In case $b = 3/2$, and $\ell > \frac{3}{2}$, then we have

$$\begin{aligned} \text{(iii)} \quad \left[\frac{d}{ds} \Lambda_\tau(s, s) \right]_{s=0} &= \Lambda_{\tau\tau}(0, 0) + \Lambda_{\tau\xi}(0, 0) = \frac{\ell}{240} \left(\ell - \frac{51}{2} \right), \\ \text{(iv)} \quad \Lambda_{\xi\xi}(0, 0) &= -\frac{\ell}{120} \left(\ell - \frac{27}{2} \right). \end{aligned}$$

In case $b = 3/2$, and $\ell = \frac{51}{2}$, then we have

$$\text{(v)} \quad \left[\frac{d^2}{ds^2} \Lambda_\tau(s, s) \right]_{s=0} = \Lambda_{\tau\tau\tau}(0, 0) + 2\Lambda_{\tau\tau\xi}(0, 0) + \Lambda_{\tau\xi\xi}(0, 0) = -\frac{2601}{10}.$$

In case $b = 3/2$, Proposition 5.3 is summarized in the Table 1. See also Fig. 2(B)(E)(F) and the middle column of Fig. 3.

	$\Lambda_{\tau\tau}(0, 0)$	$(\Lambda_{\tau\tau} + \Lambda_{\tau\xi})(0, 0)$	$\Lambda_{\xi\xi}(0, 0)$
$\ell > 51/2$	< 0 (ESS)	> 0 (not CvSS)	< 0
$27/2 < \ell < 51/2$	< 0 (ESS)	< 0 (CvSS)	< 0
$3/2 < \ell < 27/2$	< 0 (ESS)	< 0 (CvSS)	> 0

TABLE 1. Signs of the second derivatives of Λ at $(\xi, \tau) = (0, 0)$ when $b = \frac{3}{2}$.

Proof of Proposition 5.3. This proposition is proved in the Appendix. Specifically, assertions (i) and (ii) are proved in Lemma A.6. Assertions (iii), (iv) and (v) are proved in Proposition A.9, Proposition A.11 and Lemma A.10, respectively. $\square$

Lemma 5.4. *For b, ℓ satisfying $\ell > b \geq 0$, let $\Lambda(\xi, \tau)$ be the principal eigenvalue of (5.1). Then there exists $\delta' > 0$ such that if*

$$\Lambda_\tau(\tilde{\xi}, \tilde{\tau}) = 0 \quad \text{for some } \tilde{\xi} \in [0, \delta'], \text{ and } \tilde{\tau} \geq 0$$

then $\Lambda_{\tau\tau}(\tilde{\xi}, \tilde{\tau}) < 0$. That is, for each $\tilde{\xi} \in [0, \delta']$, exactly one of the followings holds:

- (a) $\Lambda_\tau(\tilde{\xi}, \tau) < 0$ for all $\tau > 0$, or
- (b) there exists $\tilde{\tau} > 0$ such that

$$\Lambda_\tau(\tilde{\xi}, \tau) > 0 \quad \text{for } 0 < \tau < \tilde{\tau}, \quad \text{and } \Lambda_\tau(\tilde{\xi}, \tau) < 0 \quad \text{for } \tau > \tilde{\tau}.$$

Finally, δ' can be chosen to be uniform in compact subsets of $\{(b, \ell) \in \mathbb{R}^2 : \ell > b \geq 0\}$.

Remark 5.5. For fixed $b < \ell$, let $\delta' > 0$ be given by Lemma 5.4. Then any local ESS in $[0, \delta']$ is automatically a global ESS.

Proof of Lemma 5.4. By a compactness argument, we only need to consider the case $\tilde{\xi} = 0$. This proof follows by a similar argument as in the proof of Lemma 4.2. It remains to show that if $\Lambda_\tau(0, \tau_0) = 0$ for some $\tau_0 > 0$, then $\Lambda_{\tau\tau}(0, \tau_0) < 0$. Since $\vartheta_0 = 1 - b/\ell$ (see Remark 5.1), we observe that $\Lambda(\tau, 0)$ is the principal eigenvalue of

$$\begin{cases} \frac{1}{\tau}\phi_{xx} - \phi_x + (b/\ell - \Lambda)\phi = 0 & \text{for } 0 < x < \ell, \\ \frac{1}{\tau}\phi_x(0) - \phi(0) = \frac{1}{\tau}\phi_x(\ell) + (b-1)\phi(\ell) = 0, \end{cases} \quad (5.6)$$

which is the adjoint problem of (5.1) with $\xi = 0$. Since (5.6) says that ℓ is the critical domain size when the local growth rate is $b/\ell - \Lambda$ instead of 1, we can replace in (4.1)

$$\ell^* \text{ by } \ell, \quad 1 - \frac{b\tau}{2} \text{ by } \frac{b}{\ell} - \Lambda - \frac{b\tau}{2}, \quad \text{and} \quad \sqrt{\tau - \frac{\tau^2}{4}} \text{ by } \sqrt{\left(\frac{b}{\ell} - \Lambda\right)\tau - \frac{\tau^2}{4}},$$

and derive the following identity (see Proposition A.5 for further details):

$$\frac{\ell}{b} \left(\frac{b}{\ell} - \Lambda - \frac{b\tau}{2} \right) = g(\ell\sqrt{M}), \quad \text{where} \quad M = \left(\frac{b}{\ell} - \Lambda \right) \tau - \frac{\tau^2}{4}. \quad (5.7)$$

Differentiate (5.7) with respect to τ , we have

$$-\frac{\ell}{b}\Lambda' - \frac{\ell}{2} = g'(\ell\sqrt{M}) \frac{\ell}{2\sqrt{M}} \left[\left(\frac{b}{\ell} - \Lambda \right) - \tau\Lambda' - \frac{\tau}{2} \right]. \quad (5.8)$$

Setting $\tau = \tau_0$, then $\Lambda' = 0$ and we obtain

$$-\frac{1}{g'(\ell\sqrt{M})} = \frac{1}{\sqrt{M}} \left[\left(\frac{b}{\ell} - \Lambda \right) - \frac{\tau_0}{2} \right]. \quad (5.9)$$

Differentiate (5.8) again and set $\tau = \tau_0$,

$$\begin{aligned} -\frac{\ell}{b}\Lambda'' &= g''(\ell\sqrt{M}) \frac{\ell^2}{4M} \left[\left(\frac{b}{\ell} - \Lambda \right) - \frac{\tau_0}{2} \right]^2 - g'(\ell\sqrt{M}) \frac{\ell}{4M^{3/2}} \left[\left(\frac{b}{\ell} - \Lambda \right) - \frac{\tau_0}{2} \right]^2 \\ &\quad + \frac{g'(\ell\sqrt{M})\ell}{2\sqrt{M}} \left[-\tau_0\Lambda'' - \frac{1}{2} \right] \end{aligned}$$

and then using (5.9), we have

$$\begin{aligned}
 & -\Lambda'' \left[\frac{\ell}{b} - \frac{g'(\ell\sqrt{M})\ell\tau_0}{2\sqrt{M}} \right] \\
 &= g''(\ell\sqrt{M}) \frac{\ell^2}{4M} \left[\left(\frac{b}{\ell} - \Lambda \right) - \frac{\tau_0}{2} \right]^2 + \frac{\ell}{4M} \left[\left(\frac{b}{\ell} - \Lambda \right) - \frac{\tau_0}{2} \right] - \frac{g'(\ell\sqrt{M})\ell}{4\sqrt{M}} \\
 &= \ell^2 \left[\frac{g''(\ell\sqrt{M})}{4(g'(\ell\sqrt{M}))^2} - \frac{1}{4(\ell\sqrt{M})g'(\ell\sqrt{M})} - \frac{g'(\ell\sqrt{M})}{4(\ell\sqrt{M})} \right] \\
 &= \frac{\ell^2}{4(\ell\sqrt{M})(g'(\ell\sqrt{M}))^2} \left[(\ell\sqrt{M})g''(\ell\sqrt{M}) - g'(\ell\sqrt{M}) - (g'(\ell\sqrt{M}))^3 \right].
 \end{aligned}$$

Again, using (i) $0 < \ell\sqrt{M} < \pi$, (ii) $g'(\ell\sqrt{M}) < 0$, we deduce that the expression in the square bracket on the top left hand side of the chain of equalities is positive. Since, by Lemma A.12, the right hand side is also positive, we deduce that $\Lambda'' < 0$. This completes the proof of the first part of the lemma. The alternative in the second part follows immediately, as $\tau \mapsto \Lambda(0, \tau)$ can have at most one local minimum in τ . $\square$

Lemma 5.6. *For b, ℓ satisfying $\ell > b \geq 0$, let $\Lambda(\xi, \tau)$ be the principal eigenvalue of (5.1).*

- (i) *For $b \in (0, \frac{3}{2}]$ and $\ell > b$, we have $\Lambda_\tau(0, \tau) < 0$ for all τ ;*
- (ii) *For $b > \frac{3}{2}$ and $\ell > b$, there exists $\tilde{\tau} > 0$ such that*

$$\Lambda_\tau(0, \tau) > 0 \quad \text{for } 0 < \tau < \tilde{\tau}, \quad \text{and} \quad \Lambda_\tau(0, \tau) < 0 \quad \text{for } \tau > \tilde{\tau}.$$

Proof. This follows immediately by using Lemma 5.4 and also Proposition 5.3, which says that $\Lambda_\tau(0, 0) \leq 0$ when $b \in (0, \frac{3}{2}]$ and

$$\Lambda_\tau(0, 0) > 0 \quad \text{and} \quad \Lambda_\tau(0, \tau) < 0 \quad \text{for } \tau \gg 1$$

when $b > \frac{3}{2}$. $\square$

Proof of Theorem 1.7. First, we show that $\xi^* = 0$ is a global ESS when $0 \leq b \leq 3/2$. Indeed, for $b \in [0, 3/2]$, Lemma 5.6 says that $\Lambda_\tau(0, \tau) < 0$ for all $\tau > 0$. Together with the fact that Λ vanishes on the diagonal, i.e. $\Lambda(0, 0) = 0$, we deduce that $\Lambda(0, \tau) < 0$ for all $\tau > 0$, so that $\xi^* = 0$ is a global ESS.

Second, we show that $\xi^* = 0$ is not a local ESS when $b > 3/2$, and thus not a global ESS. This is due to $\Lambda(0, 0) = 0$ and $\Lambda_\tau(0, 0) > 0$ (from Proposition 5.3(i)), so that $\Lambda(0, \tau) > 0$ for some $0 < \tau \ll 1$. It is also clear that $\xi^* = 0$ is not CvSS, since a necessary condition for CvSS is $\Lambda_\tau(0, 0) \leq 0$, according to Definition 1.6.

Next, we prove assertions (a)-(c). Now, by Proposition 5.3(i),

$$\Lambda_\tau(0, 0) = \frac{b}{3} \left(b - \frac{3}{2} \right) < 0 \quad \text{for } 0 \leq b < \frac{3}{2}.$$

Hence $\xi^* = 0$ is a CvSS according to Definition 1.6. This proves assertion (a).

For $b = 3/2$ and $3/2 < \ell < 51/2$, Proposition 5.3(i) and (iii) say that

$$\Lambda_\tau(0, 0) = 0, \quad \text{and} \quad \Lambda_{\tau\tau}(0, 0) + \Lambda_{\tau\xi}(0, 0) = \frac{\ell}{240} \left(\ell - \frac{51}{2} \right) < 0.$$

Hence, $\xi^* = 0$ is a CvSS according to Definition 1.6. This proves assertion (b).

For $b = 3/2$ and $\ell > 51/2$, Proposition 5.3(i) and (iii) say that

$$\Lambda_\tau(0, 0) = 0, \quad \text{and} \quad \Lambda_{\tau\tau}(0, 0) + \Lambda_{\tau\xi}(0, 0) = \frac{\ell}{240} \left(\ell - \frac{51}{2} \right) > 0.$$

Hence, $\xi^* = 0$ is not a CvSS according to Definition 1.6. This establishes the assertion (c). $\square$

Lemma 5.7. *Let $\Lambda(\xi, \tau; b)$ be the principal eigenvalue of (5.1).*

- (i) *For $\ell > \frac{51}{2}$, there exists $\delta > 0$ such that for $b \in (\frac{3}{2} - \delta, \frac{3}{2})$, there exists $\xi^*(b) > 0$ such that $\xi^*(b) \searrow 0$ as $b \nearrow \frac{3}{2}$, and*

$$\Lambda_\tau(\xi^*(b), \xi^*(b); b) = 0, \quad \Lambda_{\tau\tau}(\xi^*(b), \xi^*(b); b) < 0, \quad (\Lambda_{\tau\tau} + \Lambda_{\tau\xi})(\xi^*(b), \xi^*(b); b) > 0.$$

See also ξ_1^ in Lemma 5.8.*

- (ii) *For $\frac{3}{2} < \ell < \frac{51}{2}$, there exists $\delta > 0$ such that for $b \in (\frac{3}{2}, \frac{3}{2} + \delta)$, there exists $\xi^*(b)$ such that $\xi^*(b) \searrow 0$ as $b \searrow \frac{3}{2}$, and*

$$\Lambda_\tau(\xi^*(b), \xi^*(b); b) = 0, \quad \Lambda_{\tau\tau}(\xi^*(b), \xi^*(b); b) < 0, \quad (\Lambda_{\tau\tau} + \Lambda_{\tau\xi})(\xi^*(b), \xi^*(b); b) < 0.$$

Proof. First, observe that when $\ell \neq \frac{51}{2}$, $h(s, b) := \Lambda_\tau(s, s; b)$ satisfies

$$h\left(0, \frac{3}{2}\right) = 0 \quad \text{and} \quad \frac{\partial}{\partial s} h\left(0, \frac{3}{2}\right) = (\Lambda_{\tau\tau} + \Lambda_{\tau\xi})\left(0, 0; \frac{3}{2}\right) \neq 0.$$

Hence for each $\ell \neq \frac{51}{2}$, we may apply the implicit function theorem to yield a smooth function $\xi^*(b)$ for $b \in (-\delta, \delta)$ such that $h(\xi^*(b); b) = 0$, $\xi^*\left(\frac{3}{2}\right) = 0$, and $(\xi^*)'\left(\frac{3}{2}\right)$ satisfies

$$(\xi^*)'\left(\frac{3}{2}\right) = -\frac{\frac{\partial}{\partial b} h\left(0, \frac{3}{2}\right)}{\frac{\partial}{\partial s} h\left(0, \frac{3}{2}\right)} = -\frac{\frac{\partial}{\partial b} \left[\frac{b}{3} \left(b - \frac{3}{2}\right)\right]_{b=\frac{3}{2}}}{(\Lambda_{\tau\tau} + \Lambda_{\tau\xi})\left(0, 0; \frac{3}{2}\right)} = \frac{-1}{2(\Lambda_{\tau\tau} + \Lambda_{\tau\xi})\left(0, 0; \frac{3}{2}\right)},$$

where we have used $h(0, b) = \frac{b}{3} \left(b - \frac{3}{2}\right)$. Taking Proposition 5.3(iii) into account,

$$(\xi^*)'\left(\frac{3}{2}\right) = -\frac{240}{\ell\left(\ell - \frac{51}{2}\right)} = \begin{cases} > 0 & \text{for } \frac{3}{2} < \ell < \frac{51}{2}, \\ < 0 & \text{for } \ell > \frac{51}{2}. \end{cases}$$

This proves the existence of $\xi^*(b)$ that satisfies $\Lambda_\tau(\xi^*(b), \xi^*(b); b) = 0$ for all small b . Finally, the rest of the assertion follows from the values of the respective second derivatives of Λ when $b = \frac{3}{2}$ (Proposition 5.3), and continuity. $\square$

To prove Theorems 1.9 and 1.11, we denote $\Lambda(\xi, \tau) = \Lambda(\xi, \tau; b, \ell)$ to emphasize its dependence in b, ℓ .

Lemma 5.8. *Fix $0 < c' < \frac{10}{2601} \cdot \frac{17^2}{160^2}$, then there exists $\delta' > 0$ such that for parameters b, ℓ satisfying (1.11), the function $g(s, b, \ell) := \Lambda_\tau(s, s; b, \ell)$ has at least two positive roots $\xi_1^* < \xi_2^*$. Furthermore, for such parameters b and ℓ , we have*

$$(\Lambda_{\tau\tau} + \Lambda_{\tau\xi})(\xi_1^*, \xi_1^*) > 0 > (\Lambda_{\tau\tau} + \Lambda_{\tau\xi})(\xi_2^*, \xi_2^*). \quad (5.10)$$

Proof. We write $g(s, b, \ell) = h_0(b, \ell) + sh_1(b, \ell) + s^2h_2(s, b, \ell)$, where by Proposition 5.3(i),

$$h_0(b, \ell) = \Lambda_\tau(0, 0; b, \ell) = \frac{b}{3} \left(b - \frac{3}{2}\right),$$

and, by Proposition 5.3(iii),

$$h_1(b, \ell) = (\Lambda_{\tau\tau} + \Lambda_{\tau\xi})(0, 0; b, \ell) = \frac{\ell}{240} \left(\ell - \frac{51}{2}\right) + O\left(b - \frac{3}{2}\right),$$

and, by Proposition 5.3(v),

$$h_2(s, b, \ell) \leq \frac{1}{2}(\Lambda_{\tau\tau\tau} + 2\Lambda_{\tau\tau\xi} + \Lambda_{\tau\xi\xi})(0, 0; \frac{3}{2}, \frac{51}{2}) = -\frac{2601}{20} < 0.$$

Hence, the function $s \mapsto g(s, b, \ell) = \Lambda_\tau(s, s; b, \ell)$ has two non-degenerate roots if

$$h_1^2 - 4h_0h_2 \geq \left| \frac{\ell}{240} \left(\ell - \frac{51}{2} \right) + O\left(b - \frac{3}{2}\right) \right|^2 - 4 \cdot \frac{b}{3} \left| b - \frac{3}{2} \right| \cdot \frac{2601}{20} > 0. \quad (5.11)$$

Now, if b, ℓ satisfy (1.11), then for some $\epsilon_0 \in (0, 15/160)$,

$$\left| b - \frac{3}{2} \right| \leq \frac{10}{2601} \cdot \left(\frac{17}{160} - \epsilon_0 \right)^2 \left| \ell - \frac{51}{2} \right|^2 \leq \frac{10}{2601} \cdot \left(\frac{\ell}{240} - \epsilon_0 \right)^2 \left| \ell - \frac{51}{2} \right|^2,$$

where we used $c' < \frac{10}{2601} \cdot \frac{17^2}{160^2}$ for the first inequality, and $\ell > 51/2$ for the second inequality. Multiplying both sides by $\frac{2601}{10}$, and using the facts that $b < \frac{3}{2}$ and $\ell > \frac{51}{2}$,

$$4 \cdot \frac{b}{3} \left| b - \frac{3}{2} \right| \cdot \frac{2601}{20} < \frac{2601}{10} \left| b - \frac{3}{2} \right| \leq \left| \left(\frac{\ell}{240} - \epsilon_0 \right) \left(\ell - \frac{51}{2} \right) \right|^2. \quad (5.12)$$

Since it is clear that $|b - \frac{3}{2}| = o(|\ell - \frac{51}{2}|)$, (5.12) implies (5.11). Therefore, for b, ℓ satisfying (1.11), the mapping $s \mapsto g(s, b, \ell) := \Lambda_\tau(s, s; b, \ell)$ has at least two roots $\xi_1^* < \xi_2^*$. Since for $\ell > \frac{51}{2}$ and $b - \frac{3}{2} = o(1)$,

$$g_s(0, b, \ell) = g_s\left(0, \frac{3}{2}, \ell\right) + o(1) = \frac{\ell}{240} \left(\ell - \frac{51}{2} \right) + o(1) > 0,$$

we deduce by the concavity of $s \mapsto g$ that $0 < \xi_1^* < \xi_2^*$ and that (5.10) holds. $\square$

Proof of Theorem 1.9. Let $b \in (3/2 - \delta, 3/2)$ and $\ell > \frac{51}{2}$, and $\xi^*(b) > 0$ be given by Lemma 5.7(i), then it is a local ESS but not a CvSS. By Remark 5.5, it is automatically a global ESS. This proves part (a) of Theorem 1.9.

For part (b), we assume b, ℓ satisfy (1.11). In particular, $b < 3/2$ and $\ell > 51/2$ so that $\xi^* = 0$ is global ESS and CvSS, by Theorem 1.7(b).

Next, by Lemma 5.8, there exists small and positive $\xi_1^* < \xi_2^*$ such that $\Lambda_\tau(\xi_i^*, \xi_i^*) = 0$ for $i = 1, 2$. Thus alternative (b) in Lemma 5.4 holds, and we deduce that ξ_1^*, ξ_2^* are both global ESS. Finally, (5.10) says that ξ_1^* is not a CvSS and ξ_2^* is a CvSS. $\square$

Remark 5.9. According to the classification of [39], $\Lambda(\xi, \tau)$ has a codimension 1 singularity of type $\text{CvSS}_0\text{ESS}_+$. This singularity gives the transition from Fig. 2a to Fig. 2b.

Proof of Theorem 1.11. Fix $3/2 < \ell < 51/2$ and, for $b > 3/2$ and close to $3/2$, let $\xi^*(b)$ be given by Lemma 5.7(ii). Arguing similarly to part (a) of Theorem 1.9, one can show that $\xi^*(b)$ is a global ESS as well as a CvSS. $\square$

6. Proof of ecological dynamics. In this section, we consider the global dynamics of the competition system (1.2).

Lemma 6.1. *Let $0 \leq b < \ell$ be fixed.*

- (a) *If $\Lambda_\tau(0, 0) < 0$, then there exists μ_0 large such that if $\mu > \nu > \mu_0$, then $(\theta_\mu, 0)$ is globally asymptotically stable among all nonnegative, nontrivial solutions of (1.2).*
- (b) *If $\Lambda_\tau(0, 0) > 0$, then there exists μ_0 large such that if $\mu > \nu > \mu_0$, then $(0, \theta_\nu)$ is globally asymptotically stable among all nonnegative, nontrivial solutions of (1.2).*

Proof. First, we assume $\Lambda_\tau(0, 0) \neq 0$ and show that (1.2) has no positive equilibria for μ, ν sufficiently large. Suppose to the contrary that there exist $\mu_j \rightarrow \infty$ and

$\nu_j \rightarrow \infty$, such that (1.2) with $(\mu, \nu) = (\mu_j, \nu_j)$ has positive steady state (u_j, v_j) for all $j \geq 1$. Denoting

$$\xi_j = \frac{1}{\mu_j} \rightarrow 0, \quad \tau_j = \frac{1}{\nu_j} \rightarrow 0, \quad \tilde{u}_j = e^{-\xi_j x} u_j, \quad \tilde{v}_j = e^{-\tau_j x} v_j,$$

the system can be rewritten as

$$\begin{cases} \tilde{u}_{j,xx} + \xi_j [\tilde{u}_{j,x} + (1 - u_j - v_j) \tilde{u}_j] = 0 & \text{for } 0 < x < \ell, \\ \tilde{v}_{j,xx} + \tau_j [\tilde{v}_{j,x} + (1 - u_j - v_j) \tilde{v}_j] = 0 & \text{for } 0 < x < \ell, \\ \tilde{u}_{j,x}(0) = \tilde{u}_{j,x}(\ell) + \xi_j b \tilde{u}_j(\ell) = 0, \\ \tilde{v}_{j,x}(0) = \tilde{v}_{j,x}(\ell) + \tau_j b \tilde{v}_j(\ell) = 0. \end{cases} \quad (6.1)$$

We first observe that

$$\|\tilde{u}_j\|_\infty \leq 1 \quad \text{and} \quad \|\tilde{v}_j\|_\infty \leq 1. \quad (6.2)$$

Indeed, $\tilde{u}_j$ is a subsolution of the single equation

$$u_{xx} + \xi_j [u_x + (1 - e^{\xi_j x} u) u] = 0 \quad \text{in } (0, \ell) \quad \text{and} \quad u_x(0) = u_x(\ell) + \xi_j b u(\ell) = 0,$$

for which the constant function 1 is a supersolution. Hence $\|\tilde{u}_j\|_\infty \leq 1$. The proof for $\|\tilde{v}_j\|_\infty \leq 1$ is similar.

By viewing first and second equations of (6.1) as linear equations in $\tilde{u}_j$ and $\tilde{v}_j$, respectively, we have

$$\tilde{\Lambda}(\xi_j; u_j + v_j) = 0 = \tilde{\Lambda}(\tau_j; u_j + v_j) \quad \text{for } j \geq 1,$$

where $\tilde{\Lambda}(\tau; h(\cdot))$ is the principal eigenvalue of

$$\begin{cases} \phi_{xx} + \tau [\phi_x + (1 - h(x)) \phi] = \tau \tilde{\Lambda} \phi, & \text{for } 0 < x < \ell, \\ \phi_x(0) = \phi_x(\ell) + \tau b \phi(\ell) = 0. \end{cases}$$

Then by Rolle's Theorem, there exists $\tau'_j \rightarrow 0$ (between ξ_j and τ_j) such that

$$\tilde{\Lambda}_{\tau'}(\tau'_j; u_j + v_j) = 0. \quad (6.3)$$

Claim 6.2. *By passing to a subsequence,*

$$\tilde{u}_j \rightarrow C_u, \quad \text{and} \quad \tilde{U}_j := \frac{\tilde{u}_j}{\|\tilde{u}_j\|_\infty} \rightarrow 1 \quad \text{uniformly in } [0, \ell],$$

where C_u is a nonnegative constant and $\|\cdot\|_\infty$ denotes the supremum norm over the interval $[0, \ell]$. A similar conclusion holds for $\tilde{v}_j$ and $\tilde{V}_j = \tilde{v}_j / \|\tilde{v}_j\|_\infty$.

To show the claim, we recall that $\|\tilde{u}_j\|_\infty \leq 1$ and $\|\tilde{v}_j\|_\infty \leq 1$ (by (6.2)). By standard elliptic estimates, we may pass to a subsequence and assume $\tilde{u}_j$ and $\tilde{v}_j$ converge weakly in $W^{2,p}(0, \ell)$, $p > 1$, to some limit functions $\tilde{u}$ and $\tilde{v}$, respectively.

Next, we pass to the limit by letting $\xi_j, \tau_j \rightarrow 0$ in (6.1) to get

$$\tilde{u}_{xx} = 0 \quad \text{for } 0 < x < \ell \quad \text{and} \quad \tilde{u}_x = 0 \quad \text{for } x = 0, \ell,$$

i.e. $\tilde{u} \equiv C_u$ for some nonnegative constant C_u . Next, we observe that $\tilde{U}_j = \tilde{u}_j / \|\tilde{u}_j\|_\infty$ and $\tilde{V}_j = \tilde{v}_j / \|\tilde{v}_j\|_\infty$ satisfy

$$\begin{cases} \tilde{U}_{j,xx} + \xi_j [\tilde{U}_{j,x} + (1 - u_j - v_j) \tilde{U}_j] = 0 & \text{for } 0 < x < \ell, \\ \tilde{V}_{j,xx} + \tau_j [\tilde{V}_{j,x} + (1 - u_j - v_j) \tilde{V}_j] = 0 & \text{for } 0 < x < \ell, \\ \tilde{U}_{j,x}(0) = \tilde{U}_{j,x}(\ell) + \xi_j b \tilde{U}_j(\ell) = 0, & \text{and} \quad \|\tilde{U}_j\|_\infty = 1, \\ \tilde{V}_{j,x}(0) = \tilde{V}_{j,x}(\ell) + \tau_j b \tilde{V}_j(\ell) = 0, & \text{and} \quad \|\tilde{V}_j\|_\infty = 1. \end{cases} \quad (6.4)$$

Hence, $\tilde{U}_j$ also converges to a constant, which must be 1 as $\|\tilde{U}_j\|_\infty = 1$ by construction. By arguing similarly and by passing to a further subsequence, we also have $\tilde{v}_j \rightarrow C_v \geq 0$ and $\tilde{v}_j/\|\tilde{v}_j\|_\infty \rightarrow 1$ uniformly in $[0, \ell]$. This proves the claim.

Next, we show that $C_u + C_v > 0$. Now, divide the first equation of (6.4) by $\tilde{U}_j$ and integrate over $(0, \ell)$, we have

$$\xi_j \int \left[\frac{\tilde{U}_{j,x}}{\tilde{U}_j} + (1 - u_j - v_j) \right] dx = - \int \frac{\tilde{U}_{j,xx}}{\tilde{U}_j} dx.$$

Integrating by parts, we have

$$\xi_j \left\{ [\log \tilde{U}_j]_{x=0}^\ell + \int (1 - u_j - v_j) dx \right\} = - \int \left| \frac{\tilde{U}_{j,x}}{\tilde{U}_j} \right|^2 dx - \left[\frac{\tilde{U}_{j,x}}{\tilde{U}_j} \right]_{x=0}^\ell \leq b \xi_j$$

where we used the boundary conditions of $\tilde{U}_j$. Now, we divide both sides by ξ_j and pass to the limit to get

$$\ell(1 - C_u - C_v) = 0 + \int (1 - C_u - C_v) dx \leq b,$$

where we used $\tilde{U}_j \rightarrow 1$ uniformly and that $u_j + v_j \rightarrow C_u + C_v$ uniformly. This proves $C_u + C_v > 0$ as $b > 0$.

Next, we claim that $C_u + C_v = 1 - b/\ell$. Indeed, integrating (6.1) by parts,

$$\begin{cases} (1 - b)\tilde{u}_j|_{x=\ell} - \tilde{u}_j|_{x=0} + \int_0^\ell (1 - u_j - v_j)\tilde{u}_j dx = 0 \\ (1 - b)\tilde{v}_j|_{x=\ell} - \tilde{v}_j|_{x=0} + \int_0^\ell (1 - u_j - v_j)\tilde{v}_j dx = 0. \end{cases}$$

Letting $j \rightarrow \infty$, we obtain

$$-bC_u + l(1 - C_u - C_v)C_u = -bC_v + l(1 - C_u - C_v)C_v = 0.$$

Adding the above, we obtain $(C_u + C_v)[-b + \ell(1 - C_u - C_v)] = 0$. Since we have already proved $C_u + C_v > 0$, we must have $C_u + C_v = 1 - b/\ell$.

Now, using the continuous dependence of $\tilde{\Lambda}_\tau(\tau, h)$ on τ and h , we may pass to the limit in (6.3) to obtain

$$\Lambda_\tau(0, 0) = \tilde{\Lambda}_\tau(0, 1 - b/\ell) = 0.$$

But this is impossible since $\Lambda_\tau(0, 0) \neq 0$ by assumption. This is a contradiction. Thus (1.2) has no positive equilibria for $\mu, \nu \gg 1$.

Next, we prove part (a). First, we notice that there exists $\delta_1 > 0$ such that for all $(\tau, \xi) \in [0, \delta_1]^2$, (1.2) has no positive steady state and that $\Lambda_\tau(\tau, \xi) < 0$, i.e.

$$\lambda_\nu(\mu, \nu) > 0 \quad \text{for all } \mu, \nu \geq \frac{1}{\delta_1}.$$

Since $\lambda(\mu, \mu) = 0$ for all μ , we deduce that

$$\lambda(\nu, \mu) > 0 > \lambda(\mu, \nu) \quad \text{for } \mu > \nu > 1/\delta_1;$$

i.e. $(\theta_\mu, 0)$ is linearly stable and $(0, \theta_\nu)$ is linearly unstable. Now, since (1.2) has no positive equilibria, we deduce by [17, Theorem B] and [24, Theorem 1.3] that $(\theta_\mu, 0)$ is globally asymptotically stable among all nonnegative, nontrivial solutions of (1.2). The proof of part (b) is analogous and is omitted. $\square$

6.1. Proof of Theorem 1.13.

Proof of Theorem 1.13. First, we show assertion (a). For $b < 3/2$ and $\ell > b$, by Proposition 1.3(a)(ii) we see that there is $\underline{\mu} > 0$ such that the positive solution θ_μ to (1.3) exists iff $\mu > \underline{\mu}$, so that Λ is defined for all $(\xi, \tau) \in [0, 1/\underline{\mu}]^2$. By Proposition 5.3(i), $\Lambda_\tau(0, 0) = \frac{b}{3}(b - \frac{3}{2}) < 0$ for $b < 3/2$. Hence, we deduce from Lemma 6.1(a) that there exists $\underline{\mu}' \geq \underline{\mu}$ such that $(\theta_\mu, 0)$ is globally asymptotically stable whenever $\mu > \nu \geq \underline{\mu}'$. This proves (a).

For $b > 3/2$ and $\ell \geq b$, we check that by Proposition 1.3(b)(iii) that there is $\underline{\mu} > 0$ such that the positive solution θ_μ to (1.3) exists iff $\mu > \underline{\mu}$, so that Λ is defined for all $(\xi, \tau) \in [0, 1/\underline{\mu}]^2$. Next, by Proposition 5.3(i), $\Lambda_\tau = \frac{b}{3}(b - \frac{3}{2}) > 0$ for $b > 3/2$. Hence, we deduce from Lemma 6.1(b) that there exists $\underline{\mu}' \geq \underline{\mu}$ such that $(0, \theta_\nu)$ is globally asymptotically stable whenever $\mu > \nu \geq \underline{\mu}'$. This proves (b).

Next, we apply [4, Theorem 6.2] to prove (c). Let $\mu_3^* = 1/\xi_3^*$, where ξ_3^* is given in Theorem 1.11 (see also Lemma 5.7(ii)). We need to verify conditions (T1)-(T5) for the semiflow generated by (1.2), and (CSS) therein. First, the positive steady state θ_μ is linearly stable and attracts all nonnegative, nontrivial solutions of (1.3). This verifies (T1) and (T4). Also, since $(0, 0)$ is the repeller of (1.2), (T5) holds. Condition (T2) holds by [4, Remark 3.1]. Condition (T3) holds since the inverse of elliptic operators is compact from $C([0, \ell])$ to $C([0, \ell])$. It remains to show (CSS), which can be stated in our situation as

$$\lambda_\nu(\mu_3^*, \mu_3^*) = 0, \quad \lambda_{\nu\nu}(\mu_3^*, \mu_3^*) < 0, \quad \text{and} \quad \lambda_{\mu\mu}(\mu_3^*, \mu_3^*) > 0. \quad (6.5)$$

Indeed, by definition, $\lambda(\mu, \nu) = \Lambda(1/\mu, 1/\nu)$, and

$$\lambda_\nu(s, s) = \Lambda_\tau(1/s, 1/s) \cdot \left(\frac{-1}{s^2} \right) \quad \text{for } s > 0. \quad (6.6)$$

So that we can verify the first condition in (6.5) by using Lemma 5.7(ii), i.e.

$$\lambda_\nu(\mu_3^*, \mu_3^*) = \Lambda_\tau(\xi_3^*, \xi_3^*) \cdot [-(\xi_3^*)^2] = 0. \quad (6.7)$$

Next, we differentiate (6.6) again and set $1/s = \xi_3^*$ to get

$$\begin{aligned} (\lambda_{\nu\nu} + \lambda_{\nu\mu})(\mu_3^*, \mu_3^*) &= (\Lambda_{\tau\tau} + \Lambda_{\tau\xi})(\xi_3^*, \xi_3^*) \cdot [-(\xi_3^*)^2]^2 + \Lambda_\tau(\xi_3^*, \xi_3^*) \cdot [2(\xi_3^*)^3] \\ &= (\Lambda_{\tau\tau} + \Lambda_{\tau\xi})(\xi_3^*, \xi_3^*) \cdot (\xi_3^*)^4 < 0. \end{aligned} \quad (6.8)$$

Finally, differentiating $s \mapsto \lambda(s, \mu_3^*)$ twice at $s = \mu_3^* = 1/\xi_3^*$, we get

$$\begin{aligned} \lambda_{\mu\mu}(\mu_3^*, \mu_3^*) &= \Lambda_{\xi\xi}(\xi_3^*, \xi_3^*) \cdot (\xi_3^*)^4 + \Lambda_\xi(\xi_3^*, \xi_3^*)[-2(\xi_3^*)^3] \\ &= \Lambda_{\xi\xi}(\xi_3^*, \xi_3^*) \cdot (\xi_3^*)^4 > 0, \end{aligned} \quad (6.9)$$

where the second equality follows from the fact that $\Lambda_\xi(s, s) = -\Lambda_\tau(s, s)$ (as it vanishes on the diagonal), and the last inequality follows from $\Lambda_{\xi\xi}(\xi_3^*, \xi_3^*) \approx \Lambda_{\xi\xi}(0, 0) = -\frac{\ell}{120}(\ell - \frac{27}{2}) > 0$ (see Proposition 5.3(iv)). By (6.7), (6.8) and (6.9), we have verified all of (6.5). Hence assertion (c) is a consequence of [4, Theorem 6.2]. $\square$

Appendix A. Computations of derivatives of $\Lambda(\xi, \tau)$ at $(0, 0)$. Recall that $\Lambda(\xi, \tau)$ is the principal eigenvalue of (5.1). We will prove Proposition 5.3 in this section.

A.1. Taylor expansion of the single species equilibrium in ξ . Let $\xi = 1/\mu$ and define $\vartheta_\xi = e^{-x/\mu}\theta_\mu$, where θ_μ is the unique positive solution of (1.3). Then ϑ_ξ satisfies

$$\begin{cases} \vartheta_{xx} + \xi [\vartheta_x + \vartheta(1 - e^{\xi x}\vartheta)] = 0 & \text{for } 0 < x < \ell, \\ (1-b)\vartheta(\ell) - \vartheta(0) + \int_0^\ell \vartheta(1 - e^{\xi x}\vartheta) dx = 0, \\ \vartheta_x(0) = \vartheta_x(\ell) + \xi b\vartheta(\ell) = 0. \end{cases} \quad (\text{A.1})$$

Note that the integral condition can be derived from the equation and the boundary condition when $\xi > 0$. However, when $\xi = 0$, the integral condition is essential to determine the limit $\lim_{\xi \rightarrow 0} \vartheta_\xi = 1 - b/\ell$ uniquely. By the above setting, ϑ_ξ is continuous in $\xi \geq 0$. We will prove that ϑ_ξ depends smoothly on ξ .

Lemma A.1. *For $b \neq \ell$, the steady state ϑ_ξ depends smoothly on $\xi \geq 0$.*

Proof. By [3, Proposition 3.6], the unique positive solution θ_μ of (1.3) depends smoothly on $\mu \in (0, \infty)$. Thus ϑ_ξ depends smoothly on $\xi \in (0, \infty)$.

To show differentiability at $\xi = 0$, we need to show that zero is not an eigenvalue of the following linearized problem of (A.1) at $(\xi, \vartheta_\xi) = (0, 1 - b/\ell)$:

$$\begin{cases} \phi_{xx} + \xi [\phi_x + \phi(1 - 2e^{\xi x}\vartheta_\xi)] = \sigma\phi & \text{for } 0 < x < \ell, \\ (1-b)\phi(\ell) - \phi(0) + \int_0^\ell \phi(1 - 2e^{\xi x}\vartheta_\xi) dx = \sigma \int_0^\ell \phi dx, \\ \phi_x(0) = \phi_x(\ell) + \xi b\phi(\ell) = 0. \end{cases} \quad (\text{A.2})$$

Setting $(\xi, \vartheta_\xi) = (0, 1 - b/\ell)$ and $\sigma = 0$ in (A.2), the first equation and the boundary condition becomes

$$\phi_{xx} = 0 \quad \text{in } (0, \ell), \quad \text{and} \quad \phi_x(0) = \phi_x(\ell) = 0.$$

Hence $\phi = \bar{\phi}$, where $\bar{\phi}$ is a constant. Then the integral condition says

$$-b\bar{\phi} + \int_0^\ell \bar{\phi}[1 - 2(1 - b/\ell)] dx = 0.$$

Since $b \neq \ell$, we deduce $\bar{\phi} = 0$. Hence $\sigma = 0$ is not an eigenvalue of (A.2). By the implicit function theorem, ϑ_ξ is smooth at $\xi = 0$. $\square$

In the following, we will Taylor expand ϑ_ξ in $0 < \xi \ll 1$.

Lemma A.2. *Let $\vartheta_\xi(x) = \tilde{\vartheta}_0(x) + \xi\tilde{\vartheta}_1(x) + \xi^2\tilde{\vartheta}_2(x) + \xi^3\tilde{\vartheta}_3 + O(|\xi|^4)$. Then*

- (i) $\tilde{\vartheta}_0(x) = 1 - \frac{b}{\ell}$.
- (ii) $\tilde{\vartheta}_1(x) = a - \frac{\tilde{\vartheta}_0 b}{2\ell}x^2$, where $a = \frac{b}{3}\left(b - \frac{3}{2}\right) + \left(1 - \frac{b}{\ell}\right)\frac{\ell}{6}(b - 3)$.
- (iii) $(\tilde{\vartheta}_2)_x(x) = -a\left(\frac{2b}{\ell} - 1\right)x + \frac{\tilde{\vartheta}_0}{2}x^2 + \left(\frac{2b}{\ell} - 1\right)\frac{\tilde{\vartheta}_0 b}{6\ell}x^3$.

Proof. First, we observe that $\tilde{\vartheta}_0$ is independent of x , as it satisfies

$$\tilde{\vartheta}_{0,xx} = 0 \quad \text{in } (0, \ell), \quad \tilde{\vartheta}_{0,x}(0) = \tilde{\vartheta}_{0,x}(\ell) = 0.$$

Using this in (A.1), we obtain

$$\begin{aligned} 0 = & (\tilde{\vartheta}_1 + \xi\tilde{\vartheta}_2 + \xi^2\tilde{\vartheta}_3)_{xx} + (\xi\tilde{\vartheta}_1 + \xi^2\tilde{\vartheta}_2 + \xi^3\tilde{\vartheta}_3)_x + O(|\xi|^4) \\ & + (\tilde{\vartheta}_0 + \xi\tilde{\vartheta}_1 + \xi^2\tilde{\vartheta}_2 + \xi^3\tilde{\vartheta}_3) \left[1 - \left(1 + \xi x + \frac{\xi^2 x^2}{2} + \frac{\xi^3 x^3}{6} \right) (\tilde{\vartheta}_0 + \xi\tilde{\vartheta}_1 + \xi^2\tilde{\vartheta}_2 + \xi^3\tilde{\vartheta}_3) \right]. \end{aligned}$$

Consider the first order equation:

$$\begin{cases} \tilde{\vartheta}_{1,xx} = -\tilde{\vartheta}_0(1 - \tilde{\vartheta}_0) & \text{for } 0 < x < \ell, \\ \tilde{\vartheta}_{1,x}(0) = 0 = \tilde{\vartheta}_{1,x}(\ell) + b\tilde{\vartheta}_0. \end{cases} \quad (\text{A.3})$$

The compatibility condition of (A.3) implies (upon integration in x) $-b\tilde{\vartheta}_0 = -\ell\tilde{\vartheta}_0(1 - \tilde{\vartheta}_0)$. This proves (i). Furthermore, we can solve (A.3) and obtain (ii), except for the determination of the constant a .

Next, we compute the constant a by the compatibility condition in the next order equation:

$$\begin{cases} \tilde{\vartheta}_{2,xx} + \tilde{\vartheta}_{1,x} + \tilde{\vartheta}_0(-\tilde{\vartheta}_1 - \tilde{\vartheta}_0x) + \tilde{\vartheta}_1\frac{b}{\ell} = 0 & \text{for } 0 < x < \ell, \\ \tilde{\vartheta}_{2,x}(0) = 0 = \tilde{\vartheta}_{2,x}(\ell) + b\tilde{\vartheta}_1(\ell). \end{cases} \quad (\text{A.4})$$

Using $\int \tilde{\vartheta}_1 dx = \ell a - \ell^2 \tilde{\vartheta}_0 b / 6$, the compatibility condition of (A.4) gives

$$\begin{aligned} & -b\tilde{\vartheta}_1(\ell) + (\tilde{\vartheta}_1(\ell) - \tilde{\vartheta}_1(0)) - \tilde{\vartheta}_0 \int \tilde{\vartheta}_1 dx - \frac{\tilde{\vartheta}_0^2 \ell^2}{2} + \frac{b}{\ell} \int \tilde{\vartheta}_1 dx = 0 \\ & -b \left(a - \frac{\tilde{\vartheta}_0 b \ell}{2} \right) + \left(-\frac{\tilde{\vartheta}_0 b \ell}{2} \right) - \frac{\tilde{\vartheta}_0^2 \ell^2}{2} + \left(\frac{2b}{\ell} - 1 \right) \left(\ell a - \frac{\ell^2 \tilde{\vartheta}_0 b}{6} \right) = 0. \end{aligned}$$

Using $\tilde{\vartheta}_0 = 1 - \frac{b}{\ell}$, we may solve the above to yield

$$a = \frac{b}{3} \left(b - \frac{3}{2} \right) + \left(1 - \frac{b}{\ell} \right) \frac{\ell}{6} (b - 3).$$

This proves the second half of (ii). Next, using (A.4) again,

$$-\tilde{\vartheta}_{2,xx} = \tilde{\vartheta}_{1,x} + \left(\frac{2b}{\ell} - 1 \right) \tilde{\vartheta}_1 - \tilde{\vartheta}_0^2 x = -\frac{\tilde{\vartheta}_0 b x}{\ell} + \left(\frac{2b}{\ell} - 1 \right) \left(a - \frac{\tilde{\vartheta}_0 b x^2}{2\ell} \right) - \tilde{\vartheta}_0^2 x.$$

One then integrate and use the fact that $\tilde{\vartheta}_{2,x}(0) = 0$ to show

$$-\tilde{\vartheta}_{2,x} = -\frac{\tilde{\vartheta}_0 b x^2}{2\ell} + \left(\frac{2b}{\ell} - 1 \right) \left(a x - \frac{\tilde{\vartheta}_0 b x^3}{6\ell} \right) - \frac{\tilde{\vartheta}_0^2}{2} x^2.$$

This proves (iii). (The x^2 terms can be combined using $\tilde{\vartheta}_0 = 1 - b/\ell$.) $\square$

Remark A.3. When $b = 3/2$, then $a = -\tilde{\vartheta}_0 \ell / 4$, and

$$\tilde{\vartheta}_0 = 1 - \frac{3}{2\ell}, \quad \tilde{\vartheta}_1(x) = -\frac{\tilde{\vartheta}_0}{4\ell} (\ell^2 + 3x^2), \quad (\text{A.5})$$

and

$$\tilde{\vartheta}_{2,x} = \frac{\tilde{\vartheta}_0 \ell^2}{4} \left[\left(\frac{3}{\ell} - 1 \right) \frac{x}{\ell} + 2 \left(\frac{x}{\ell} \right)^2 + \left(\frac{3}{\ell} - 1 \right) \left(\frac{x}{\ell} \right)^3 \right].$$

Remark A.4. Define $\vartheta_2^*(x) := \vartheta_2(x) - \vartheta_2(0)$. When $b = 3/2$ and $\ell = 51/2$, then (iii) implies

$$\vartheta_2^*(x) = \vartheta_2(x) - \vartheta_2(0) = -\frac{45}{17}x^2 + \frac{8}{51}x^3 - \frac{10}{17^3}x^4. \quad (\text{A.6})$$

and

$$\begin{cases} 0 & = \vartheta_{3,xx} + \vartheta_{2,x} + \frac{b}{\ell} \vartheta_2 + \vartheta_1[-x\vartheta_0 - \vartheta_1] + \vartheta_0[-\frac{x^2}{2}\vartheta_0 - x\vartheta_1 - \vartheta_2], \\ \vartheta_{3,x}(0) & = 0 = \vartheta_{3,x}(\ell) + (3/2)\vartheta_2(\ell) \end{cases}$$

so that (using $\vartheta_2^* = \vartheta_2 - \vartheta_2(0)$ and $\vartheta_{2,x}^* = \vartheta_{2,x}$)

$$\vartheta_{3,xx} + \vartheta_{2,x}^* = \vartheta_{3,xx} + \vartheta_{2,x} = \frac{\vartheta_0^2}{2}x^2 + 2\vartheta_0x\vartheta_1(x) + \vartheta_1^2(x) + \frac{15}{17}(\vartheta_2^*(x) + \vartheta_2(0)). \quad (\text{A.7})$$

Integrating (A.7) from 0 to x , we get

$$\vartheta_{3,x} = -\vartheta_2^* + \frac{\vartheta_0^2}{6}x^3 + 2\vartheta_0 \int_0^x s\vartheta_1(s) ds + \int_0^x [\vartheta_1^2(s) + \frac{15}{17}\vartheta_2^*(s) + \frac{15}{17}\vartheta_2(0)] ds. \quad (\text{A.8})$$

Setting $x = \ell$ and use the boundary condition of ϑ_3 at $x = \ell = 51/2$, we have

$$\vartheta_{3,x}(\ell) = -b\vartheta_2(\ell) = -b(\vartheta_2(0) + \vartheta_2^*(\ell)),$$

and hence we obtain an equation of $\vartheta_2(0)$:

$$\begin{aligned} & -b(\vartheta_2(0) + \vartheta_2^*(\ell)) \\ &= -\vartheta_2^*(\ell) + \frac{\vartheta_0^2}{6}\ell^3 + 2\vartheta_0 \int_0^\ell s\vartheta_1(s) ds + \int_0^\ell [\vartheta_1^2(s) + \frac{15}{17}\vartheta_2^*(s)] ds + \frac{15\ell}{17}\vartheta_2(0) \end{aligned} \quad (\text{A.9})$$

By the facts that, when $b = 3/2$ and $\ell = 51/2$, $\vartheta_0 = \frac{16}{17}$, $\vartheta_1(x) = -6 - \frac{8}{289}x^2$, and (A.6), we may solve (A.9) to obtain $\vartheta_2(0) = 186.15$.

Hence,

$$\vartheta_2(x) = 186.15 - \frac{45}{17}x^2 + \frac{8}{51}x^3 - \frac{10}{173}x^4, \quad (\text{A.10})$$

$$\vartheta_{2,x}(x) = -\frac{90}{17}x + \frac{8}{17}x^2 - \frac{40}{173}x^3, \quad (\text{A.11})$$

and, when $b = 3/2$ and $\ell = 51/2$, (A.8) implies

$$\begin{aligned} \vartheta_{3,x}(x) &= -\vartheta_2^*(x) + \frac{\vartheta_0^2}{6}x^3 + 2\vartheta_0(-3x^2 - \frac{2}{172}x^4) \\ &\quad + \left[36x + \frac{2 \cdot 6 \cdot 8}{172} \frac{x^3}{3} + \left(\frac{8}{172} \right)^2 \frac{x^5}{5} \right] \\ &\quad + \frac{15}{17} \left[(186.15)x - \frac{15}{17}x^3 + \frac{2}{51}x^4 - \frac{2}{173}x^5 \right]. \end{aligned} \quad (\text{A.12})$$

A.2. Computations of $\Lambda_\tau(0, 0)$ and $\Lambda_{\tau\tau}(0, 0)$.

Proposition A.5. *For each $\tau = \frac{1}{\nu} \geq 0$, the eigenvalue $\Lambda(0, \tau)$ satisfies*

$$\frac{\ell}{b} \left(\frac{b}{\ell} - \Lambda - \frac{b\tau}{2} \right) = g \left(\ell \sqrt{\left(\frac{b}{\ell} - \Lambda \right) \tau - \frac{\tau^2}{4}} \right) \quad (\text{A.13})$$

where $g(s) = s \cot s$.

Proof. In [26] the critical domain size $\ell^*(\nu, b)$, for which there exists a positive solution to

$$\nu\phi_{xx} + \phi_x + r\phi = 0, \quad 0 < x < \ell^*, \quad \phi_x(0) = \nu\phi_x(\ell^*) + b\phi(\ell^*) = 0,$$

is found in terms of ν , r and b (see also Proposition 4.1) by solving

$$\tan \left(\frac{\sqrt{4\nu r - 1}}{2\nu} \ell^* \right) = \frac{b\sqrt{4\nu r - 1}}{2\nu r - b}. \quad (\text{A.14})$$

Now for $\Lambda = \Lambda(0, \nu)$, there exists a positive solution ϕ to

$$\nu\phi_{xx} + \phi_x + (1 - \vartheta_0 - \Lambda)\phi = 0, \quad 0 < x < \ell^*, \quad \phi_x(0) = \nu\phi_x(\ell^*) + b\phi(\ell^*) = 0,$$

where $\vartheta_0 = 1 - b/\ell$. Finally, we deduce the desired result by setting $\ell^* = \ell$, $\nu = 1/\tau$ and $r = 1 - \vartheta_0 - \Lambda = b/\ell - \Lambda$ in (A.14). $\square$

Lemma A.6. *Let $b \geq 0$ and $\ell > b$. Then*

$$\Lambda_\tau(0, 0) = \frac{b}{3} \left(b - \frac{3}{2} \right), \quad \text{and} \quad \Lambda_{\tau\tau}(0, 0) = -\frac{b\ell}{90} [b^2 + 15(b-1)^2]. \quad (\text{A.15})$$

Proof. Fix $b \geq 0$ and $\ell > 0$. Using the expansion $s \cot s = 1 - s^2/3 - s^4/45 + \dots$, we can rewrite (A.13) as

$$1 - \frac{\ell\Lambda}{b} - \frac{\ell\tau}{2} = 1 - \frac{\ell^2}{3} \left[\left(\frac{b}{\ell} - \Lambda \right) \tau - \frac{\tau^2}{4} \right] - \frac{\ell^4}{45} \left[\left(\frac{b}{\ell} - \Lambda \right) \tau - \frac{\tau^2}{4} \right]^2 + O(|\tau|^3), \quad (\text{A.16})$$

where $\Lambda = \Lambda(0, \tau)$. Differentiate (A.16) with respect to τ , and then set $\tau = 0$,

$$-\frac{\ell}{b} \partial_\tau \Lambda(0, 0) - \frac{\ell}{2} = -\frac{\ell^2}{3} \cdot \frac{b}{\ell}, \quad \text{i.e.} \quad \Lambda_\tau(0, 0) = \frac{b}{3} \left(b - \frac{3}{2} \right).$$

Similarly, we deduce

$$\begin{aligned} -\frac{\ell}{b} \frac{\partial^2}{\partial \tau^2} \Lambda(0, 0) &= 2 \left\{ -\frac{\ell^2}{3} \left[-\Lambda_\tau(0, 0) - \frac{1}{4} \right] - \frac{\ell^2 b^2}{45} \right\} \\ &= \ell^2 \left\{ -\frac{2}{3} \left[-\frac{b}{3} \left(b - \frac{3}{2} \right) - \frac{1}{4} \right] - \frac{2b^2}{45} \right\} \\ &= \frac{\ell^2}{90} (16b^2 - 30b + 15) = \frac{\ell^2}{90} [b^2 + 15(b - 1)^2]. \end{aligned}$$

This completes the proof. $\square$

A.3. Expanding $\Lambda_\tau(\xi, \tau)|_{\tau=\xi}$ in powers of ξ .

Lemma A.7. *Let ϑ_ξ be the unique positive solution of (A.1), then*

$$\xi^2 \Lambda_\tau(\xi, \tau)|_{\tau=\xi} = \frac{\int (\vartheta_\xi)_x (e^{\xi x} \vartheta_\xi)_x dx}{\int e^{\xi x} (\vartheta_\xi)^2 dx}.$$

Proof. Fix ξ and differentiate (5.1) with respect to τ , we obtain

$$\begin{aligned} \phi'_{xx} + \tau[\phi'_x + (1 - e^{\xi x} \vartheta_\xi) \phi'] - \tau \Lambda \phi' \\ = -[\phi_x + (1 - e^{\xi x} \vartheta_\xi) \phi - \Lambda \phi] + \tau \Lambda_\tau \phi = \frac{1}{\tau} \phi_{xx} + \tau \Lambda_\tau \phi, \end{aligned}$$

with boundary condition

$$\phi'_x(0) = 0, \quad \text{and} \quad \phi'_x(\ell) + \tau b \phi'(\ell) = -b \phi(\ell).$$

Then, setting $\tau = \xi$ (so that $\Lambda = 0$ and $\phi = \vartheta_\xi$), we have

$$\begin{cases} \phi'_{xx} + \xi[\phi'_x + (1 - e^{\xi x} \vartheta_\xi) \phi'] = \frac{1}{\xi} (\vartheta_\xi)_{xx} + \xi \Lambda_\tau \vartheta_\xi, & \text{for } 0 < x < \ell, \\ \phi'_x(0) = 0, \quad \phi'_x(\ell) + \xi b \phi'(\ell) = -b \vartheta_\xi(\ell). \end{cases} \quad (\text{A.17})$$

Multiply by $e^{\xi x} \vartheta_\xi$, and integrate by parts twice:

$$\begin{aligned} e^{\xi x} [\phi'_x \vartheta_\xi - \phi' (\vartheta_\xi)_x] \Big|_{x=0}^\ell \\ = \frac{1}{\xi} \left\{ [(\vartheta_\xi)_x e^{\xi x} \vartheta_\xi]_{x=0}^\ell - \int (\vartheta_\xi)_x (e^{\xi x} \vartheta_\xi)_x dx \right\} + \xi \Lambda_\tau(\xi, \xi) \int e^{\xi x} (\vartheta_\xi)^2 dx. \end{aligned}$$

It is not hard to verify that the boundary terms cancel exactly, by applying the boundary conditions in (A.1), (A.2) and (A.17). This proves the lemma. $\square$

In the next result, we expand $\Lambda_\tau(\xi, \tau)|_{\tau=\xi}$ in powers of ξ .

Lemma A.8. *The following expansion holds:*

$$\begin{aligned}
 & \Lambda_\tau(\xi, \xi) \int e^{\xi x} (\vartheta_\xi)^2 dx \\
 &= \left[\tilde{\vartheta}_0 \int \tilde{\vartheta}_{1,x} dx + \int (\tilde{\vartheta}_{1,x})^2 dx \right] \\
 &+ \xi \left[\tilde{\vartheta}_0 \int \tilde{\vartheta}_{2,x} dx + 2 \int \tilde{\vartheta}_{1,x} \tilde{\vartheta}_{2,x} dx + \frac{1}{2} \int (\tilde{\vartheta}_1^2)_x dx + \int x (\tilde{\vartheta}_{1,x})^2 dx + \tilde{\vartheta}_0 \int x \tilde{\vartheta}_{1,x} dx \right] \\
 &+ \xi^2 \int \left[\tilde{\vartheta}_{3,x} (\tilde{\vartheta}_0 + 2\tilde{\vartheta}_{1,x}) + \tilde{\vartheta}_{2,x} (x\tilde{\vartheta}_0 + \tilde{\vartheta}_1 + 2x\tilde{\vartheta}_{1,x} + \tilde{\vartheta}_{2,x}) \right. \\
 &\left. + \tilde{\vartheta}_{1,x} \left(\frac{x^2}{2} \tilde{\vartheta}_0 + x\tilde{\vartheta}_1 + \frac{x^2}{2} \tilde{\vartheta}_{1,x} + \tilde{\vartheta}_2 \right) \right] + o(\xi^2). \tag{A.18}
 \end{aligned}$$

Proof. It suffices to expand $\int (\vartheta_\xi)_x (e^{\xi x} \vartheta_\xi)_x dx$ as

$$\begin{aligned}
 & \int (\xi \tilde{\vartheta}_{1,x} + \xi^2 \tilde{\vartheta}_{2,x} + \xi^3 \tilde{\vartheta}_{3,x}) \\
 & \quad \left[\left(1 + \xi x + \frac{\xi^2 x^2}{2} + \frac{\xi^3 x^3}{6} \right) (\tilde{\vartheta}_0 + \xi \tilde{\vartheta}_1 + \xi^2 \tilde{\vartheta}_2 + \xi^3 \tilde{\vartheta}_3) \right]_x dx + o(\xi^4) \\
 &= \xi \int (\tilde{\vartheta}_{1,x} + \xi \tilde{\vartheta}_{2,x} + \xi^2 \tilde{\vartheta}_{3,x}) \left[\tilde{\vartheta}_0 + \xi (x\tilde{\vartheta}_0 + \tilde{\vartheta}_1) + \xi^2 \left(\tilde{\vartheta}_2 + x\tilde{\vartheta}_1 + \frac{x^2}{2} \tilde{\vartheta}_0 \right) \right. \\
 & \quad \left. + \xi^3 \left(\frac{x^3}{6} \tilde{\vartheta}_0 + \frac{x^2}{2} \tilde{\vartheta}_1 + x\tilde{\vartheta}_2 + \tilde{\vartheta}_3 \right) \right]_x dx + o(\xi^4) \\
 &= \xi \int (\tilde{\vartheta}_{1,x} + \xi \tilde{\vartheta}_{2,x} + \xi^2 \tilde{\vartheta}_{3,x}) \left[\xi (\tilde{\vartheta}_0 + \tilde{\vartheta}_{1,x}) + \xi^2 (\tilde{\vartheta}_{2,x} + \tilde{\vartheta}_1 + x\tilde{\vartheta}_{1,x} + x\tilde{\vartheta}_0) \right. \\
 & \quad \left. + \xi^3 \left(\frac{x^2}{2} \tilde{\vartheta}_0 + x\tilde{\vartheta}_1 + \frac{x^2}{2} \tilde{\vartheta}_{1,x} + \tilde{\vartheta}_2 + x\tilde{\vartheta}_{2,x} + \tilde{\vartheta}_{3,x} \right) \right] dx + o(\xi^4) \\
 &= \xi^2 \left\{ \left[\int \tilde{\vartheta}_{1,x} (\tilde{\vartheta}_0 + \tilde{\vartheta}_{1,x}) dx \right] \right. \\
 & \quad + \xi \left[\int \tilde{\vartheta}_{2,x} (\tilde{\vartheta}_0 + \tilde{\vartheta}_{1,x}) dx + \int \tilde{\vartheta}_{1,x} (\tilde{\vartheta}_{2,x} + \tilde{\vartheta}_1 + x\tilde{\vartheta}_{1,x} + x\tilde{\vartheta}_0) dx \right] \\
 & \quad + \xi^2 \left[\int \tilde{\vartheta}_{3,x} (\tilde{\vartheta}_0 + \tilde{\vartheta}_{1,x}) + \tilde{\vartheta}_{2,x} (x\tilde{\vartheta}_0 + \tilde{\vartheta}_1 + x\tilde{\vartheta}_{1,x} + \tilde{\vartheta}_{2,x}) \right. \\
 & \quad \left. + \tilde{\vartheta}_{1,x} \left(\frac{x^2}{2} \tilde{\vartheta}_0 + x\tilde{\vartheta}_1 + \frac{x^2}{2} \tilde{\vartheta}_{1,x} + \tilde{\vartheta}_2 + x\tilde{\vartheta}_{2,x} + \tilde{\vartheta}_{3,x} \right) \right] + o(\xi^2) \Big\},
 \end{aligned}$$

and use Lemma A.7 to complete the proof. $\square$

Proposition A.9. *When $b = \frac{3}{2}$,*

$$\Lambda_{\tau\tau}(0, 0) + \Lambda_{\tau\xi}(0, 0) = \left[\frac{\partial}{\partial s} \Lambda_\tau(s, s) \right]_{s=0} = \frac{\ell}{240} \left(\ell - \frac{51}{2} \right). \tag{A.19}$$

Proof. By Lemma A.8 and the fact that $\Lambda_\tau(0,0) = 0$ when $b = 3/2$, we derive

$$\begin{aligned} \ell \tilde{\vartheta}_0^2 \left[\frac{\partial}{\partial s} \Lambda_\tau(s, s) \right]_{s=0} &= \tilde{\vartheta}_0 \int \tilde{\vartheta}_{2,x} dx + 2 \int \tilde{\vartheta}_{1,x} \tilde{\vartheta}_{2,x} dx + \frac{1}{2} \int (\tilde{\vartheta}_1^2)_x dx + \int x \tilde{\vartheta}_{1,x}^2 dx + \tilde{\vartheta}_0 \int x \tilde{\vartheta}_{1,x} dx. \end{aligned} \quad (\text{A.20})$$

We evaluate individual integrals over the interval $[0, \ell]$ separately:

$$\int \tilde{\vartheta}_{2,x} dx = \frac{\tilde{\vartheta}_0 \ell^2}{4} \left[\left(\frac{3}{\ell} - 1 \right) \frac{\ell}{2} + \frac{2\ell}{3} + \left(\frac{3}{\ell} - 1 \right) \frac{\ell}{4} \right] = \frac{\tilde{\vartheta}_0 \ell^2}{4} \left(-\frac{\ell}{12} + \frac{9}{4} \right). \quad (\text{A.21})$$

$$\int (\tilde{\vartheta}_1^2)_x dx = \tilde{\vartheta}_1^2 \Big|_{x=0}^\ell = \frac{\tilde{\vartheta}_0^2}{16\ell^2} (16\ell^4 - \ell^4) = \frac{15}{16} \tilde{\vartheta}_0^2 \ell^2. \quad (\text{A.22})$$

$$\int x \tilde{\vartheta}_{1,x}^2 dx = \int \frac{9}{4} \frac{\tilde{\vartheta}_0^2}{\ell^2} x^3 dx = \frac{9}{16} \tilde{\vartheta}_0^2 \ell^2. \quad (\text{A.23})$$

$$\int x \tilde{\vartheta}_{1,x} dx = - \int \frac{3}{2} \frac{\tilde{\vartheta}_0}{\ell} x^2 dx = -\frac{\tilde{\vartheta}_0}{2} \ell^2. \quad (\text{A.24})$$

$$\begin{aligned} \int \tilde{\vartheta}_{1,x} \tilde{\vartheta}_{2,x} dx &= \int \left(-\frac{3}{2} \frac{\tilde{\vartheta}_0}{\ell} x \right) \cdot \frac{\tilde{\vartheta}_0 \ell^2}{4} \left[\left(\frac{3}{\ell} - 1 \right) \left(\frac{x}{\ell} \right) + 2 \left(\frac{x}{\ell} \right)^2 + \left(\frac{3}{\ell} - 1 \right) \left(\frac{x}{\ell} \right)^3 \right] dx \\ &= -\frac{3}{8} \tilde{\vartheta}_0^2 \ell^2 \int \left[\left(\frac{3}{\ell} - 1 \right) \left(\frac{x}{\ell} \right)^2 + 2 \left(\frac{x}{\ell} \right)^3 + \left(\frac{3}{\ell} - 1 \right) \left(\frac{x}{\ell} \right)^4 \right] dx \\ &= -\frac{3}{8} \tilde{\vartheta}_0^2 \ell^2 \left(\frac{3-\ell}{3} + \frac{\ell}{2} + \frac{3-\ell}{5} \right) \\ &= \tilde{\vartheta}_0^2 \ell^2 \left(\frac{\ell}{80} - \frac{3}{5} \right). \end{aligned} \quad (\text{A.25})$$

Substituting (A.21) - (A.25) into (A.20), we have

$$\begin{aligned} \ell \tilde{\vartheta}_0^2 \left[\frac{\partial}{\partial s} \Lambda_\tau(s, s) \right]_{s=0} &= \frac{\tilde{\vartheta}_0^2 \ell^2}{4} \left(-\frac{\ell}{12} + \frac{9}{4} \right) + 2 \tilde{\vartheta}_0^2 \ell^2 \left(\frac{\ell}{80} - \frac{3}{5} \right) + \frac{15}{32} \tilde{\vartheta}_0^2 \ell^2 + \frac{9}{16} \tilde{\vartheta}_0^2 \ell^2 - \frac{1}{2} \tilde{\vartheta}_0^2 \ell^2 \\ &= \tilde{\vartheta}_0^2 \ell^2 \left(\frac{9}{16} - \frac{6}{5} + \frac{15}{32} + \frac{9}{16} - \frac{1}{2} - \frac{\ell}{48} + \frac{\ell}{40} \right) \\ &= \frac{\tilde{\vartheta}_0^2 \ell^2}{240} \left(\ell - \frac{51}{2} \right). \end{aligned}$$

This completes the proof. $\square$

Lemma A.10. When $b = 3/2$ and $\ell = 51/2$,

$$\left[\frac{d^2}{ds^2} \Lambda_\tau(s, s) \right]_{s=0} = \Lambda_{\tau\xi\xi}(0,0) + 2\Lambda_{\tau\tau\xi}(0,0) + \Lambda_{\tau\tau\tau}(0,0) = -\frac{2601}{10} < 0.$$

Proof. When $b = 3/2$ and $\ell = 51/2$, we deduce from (A.15) that $\Lambda_\tau(0,0) = 0$, and from (A.19) that

$$\left[\frac{d}{ds} \Lambda_\tau(s, s) \right]_{s=0} = \Lambda_{\tau\xi}(0,0) + \Lambda_{\tau\tau}(0,0) = 0,$$

so the lowest order term on left hand side of (A.18) is

$$\frac{\xi^2}{2} \int_0^{51/2} (\vartheta_0)^2 dx \left[\frac{d^2}{ds^2} \Lambda_\tau(s, s) \right]_{s=0}.$$

Hence, equating the coefficient of ξ^2 on both sides of (A.18), we get

$$\begin{aligned} & \frac{51}{4} \left(\frac{16}{17} \right)^2 \left[\frac{d^2}{ds^2} \Lambda_\tau(s, s) \right]_{s=0} \\ &= \int_0^{\frac{51}{2}} \left[\vartheta_{3,x}(\vartheta_0 + 2\vartheta_{1,x}) + \vartheta_{2,x}(x\vartheta_0 + \vartheta_1 + 2x\vartheta_{1,x} + \vartheta_{2,x}) \right] dx \\ & \quad + \int_0^{\frac{51}{2}} \left[\vartheta_{1,x} \left(\frac{x^2}{2} \vartheta_0 + x\vartheta_1 + \frac{x^2}{2} \vartheta_{1,x} + \vartheta_2 \right) \right] dx. \end{aligned}$$

And the value of $\left[\frac{d^2}{ds^2} \Lambda_\tau(s, s) \right]_{s=0}$ can be evaluated in terms of (A.5), (A.10), (A.11), and (A.12). $\square$

Proposition A.11. *Let $b = \frac{3}{2}$, then*

$$\Lambda_{\xi\xi}(0, 0) = -\frac{\ell}{120} \left(\ell - \frac{27}{2} \right).$$

Proof. Since $\Lambda(\xi, \xi) \equiv 0$ for all ξ , we have

$$\Lambda_{\xi\xi}(0, 0) = -2\Lambda_{\xi\tau}(0, 0) - \Lambda_{\tau\tau}(0, 0) = -2(\Lambda_{\xi\tau}(0, 0) + \Lambda_{\tau\tau}(0, 0)) + \Lambda_{\tau\tau}(0, 0).$$

Setting $b = 3/2$ in Lemma A.6 and using Proposition A.9, we have

$$\begin{aligned} \Lambda_{\xi\xi}(0, 0) &= 2 \left[-\frac{\ell}{240} \left(\ell - \frac{51}{2} \right) \right] - \left\{ \frac{\frac{3}{2}\ell}{90} \left[\left(\frac{3}{2} \right)^2 + 15 \left(\frac{3}{2} - 1 \right)^2 \right] \right\} \\ &= -\frac{\ell}{120} \left(\ell - \frac{51}{2} \right) - \frac{\ell}{60} \left(\frac{9}{4} + \frac{15}{4} \right) \\ &= -\frac{\ell}{120} \left(\ell - \frac{27}{2} \right). \end{aligned}$$

This completes the proof. $\square$

Lemma A.12. *Let $g(s) = s \cot s$, then*

$$g''(s) - \frac{g'(s)}{s} [1 + (g'(s))^2] > 0 \quad \text{for } 0 < s < \pi. \quad (\text{A.26})$$

Proof. Step 1. We claim that

$$\frac{\sin^3 x}{x^3} - \cos x > 0 \quad \text{in } (0, \pi). \quad (\text{A.27})$$

Observe that (A.27) holds trivially in $[\pi/2, \pi)$. For $s \in (0, \pi/2)$, we compute

$$\frac{\sin^3 x}{x^3} - \cos x \geq \left(1 - \frac{x^2}{6} \right)^3 - \left(1 - \frac{x^2}{2} + \frac{x^4}{24} \right) = \frac{x^4}{24} \left(1 - \frac{x^2}{9} \right) > 0.$$

Step 2. It is straightforward to compute

$$g'(s) = \cot s - s \csc^2 s \quad \Longleftrightarrow \quad \frac{g'(s)}{s} - \frac{g(s)}{s^2} = -\csc^2 s,$$

and

$$g''(s) = \frac{g'(s)}{s} - \frac{g(s)}{s^2} + \csc^2 s (-1 + 2g(s)) = 2 \csc^2 s (g(s) - 1).$$

Furthermore,

$$\begin{aligned} 1 + (g'(s))^2 &= 1 + \cot^2 s - 2s \cot s \csc^2 s + s^2 \csc^4 s \\ &= \csc^2 s [1 - 2g(s) + s^2 \csc^2 s] = \csc^2 s [1 - 2g(s) + s^2 (1 + \cot^2 s)] \\ &= \csc^2 s [(1 - g(s))^2 + s^2]. \end{aligned}$$

Step 3. We claim that $-\frac{g'(s)}{s} \geq \frac{2}{3}$ for $s \in (0, \pi)$.

Indeed,

$$\begin{aligned} \frac{d}{ds} \left[-\frac{g'(s)}{s} \right] &= \frac{\cot s}{s^2} - 2 \cot s \csc^2 s + \frac{\csc^2 s}{s} \\ &= \left(\frac{1}{s} - \cot s \right) \left(\csc^2 s - \frac{1}{s^2} \right) + \frac{1}{s^3} - \cot s \csc^2 s \\ &> \frac{1}{s^3} - \cot s \csc^2 s = \csc^3 s \left(\frac{\sin^3 s}{s^3} - \cos s \right) > 0 \end{aligned}$$

for $s \in (0, \pi)$, where we used Step 1 in the last inequality. Hence, the minimum of $-\frac{g'(s)}{s}$ is attained as $s \searrow 0$, so that using the expansion $g(s) = 1 - \frac{s^2}{3} - \frac{s^4}{45} + \dots$, we have

$$-\frac{g'(s)}{s} \geq \lim_{s \searrow 0} -\frac{g'(s)}{s} = \left[\frac{2}{3} + \frac{4s^2}{45} + \dots \right]_{s=0} = \frac{2}{3}.$$

Step 4. We claim

$$g'' - \frac{g'}{s} [1 + (g')^2] \geq \frac{2}{3} (\csc s)^2 [(g-1)^2 + 3(g-1) + s^2] \quad \text{in } (0, \pi).$$

Indeed, by Steps 2 and 3,

$$\begin{aligned} g'' - \frac{g'}{s} [1 + (g')^2] &= 2 \csc^2 s (g-1) + \left(-\frac{g'}{s} \right) \csc^2 s [(1-g(s))^2 + s^2] \\ &\geq 2 \csc^2 s (g-1) + \frac{2}{3} \csc^2 s [(1-g(s))^2 + s^2] \\ &= \frac{2}{3} \csc^2 s [3(g-1) + (1-g(s))^2 + s^2] \end{aligned}$$

Step 5. We claim that (A.26) holds for $s \in [\frac{3}{2}, \pi)$. By completing the square, it is easy to see that

$$h(s) := (g-1)^2 + 3(g-1) + s^2 \geq s^2 - \frac{9}{4}.$$

By Step 4, we deduce that (A.26) holds for $s \in [\frac{3}{2}, \pi)$.

Step 6. It remains to show that $h(s)$ (defined in Step 5) is positive for $s \in [0, \pi/2)$. We first claim

$$g(s) - 1 < -s^2/3 \quad \text{for all } s \in [0, \pi/2). \quad (\text{A.28})$$

Now, for $s \in (0, \pi/2)$,

$$g(s) - 1 = \frac{s \cos s}{\sin s} - 1 < \frac{s(1 - s^2/2 + s^4/24)}{s - s^3/6} - 1 \leq \frac{-s^2/3 + s^4/18}{1 - s^2/6} = -\frac{s^2}{3}$$

This proves (A.28). One can obtain similarly that

$$g(s) - 1 > \frac{-s^2/3 + s^4/30 - s^6/720}{1 - s^2/6 + s^4/120} \quad \text{for all } s \in [0, \pi/2). \quad (\text{A.29})$$

Using (A.28) and (A.29), we have, for $0 < s < \pi/2$,

$$\begin{aligned}
 & (g-1)^2 + 3(g-1) + s^2 \\
 & \geq \frac{s^4}{9} + \frac{-s^2 + s^4/10 - s^6/240}{1 - s^2/6 + s^4/120} + s^2 \\
 & = \frac{(s^4/9 - s^6/54 + s^8/1080) - s^2 + s^4/10 - s^6/240 + (s^2 - s^4/6 + s^6/120)}{1 - s^2/6 + s^4/120} \\
 & = \frac{\frac{4s^4}{90} + \left(-\frac{1}{54} - \frac{1}{240} + \frac{1}{120}\right)s^6 + s^8/1080}{1 - s^2/6 + s^4/120} \\
 & \geq \frac{s^4}{1 - s^2/6 + s^4/120} \left[\frac{4}{90} - \frac{31}{2160} \cdot \left(\frac{\pi}{2}\right)^2 \right].
 \end{aligned}$$

Since the term in the square bracket is positive (≈ 0.009), the lemma follows. $\square$

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