Journal of Theoretical Biology 515 (2021) 110600

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

# Sharp boundary formation and invasion between spatially adjacent periodical cicada broods

Geunho Kye [a], Jonathan Machta [b,c], Karen C. Abbott [d], Alan Hastings [c,e], William Huffmyer [f], Fang Ji [d], Andrew M. Liebhold [g,h], Julie C. Blackwood [a,*]

[a] Department of Mathematics and Statistics, Williams College, Williamstown, MA 01267, USA
[b] Department of Physics, University of Massachusetts Amherst, Amherst, MA 01003, USA
[c] Santa Fe Institute, Santa Fe, NM 87501, USA
[d] Department of Biology, Case Western Reserve University, Cleveland, OH 44106, USA
[e] Department of Environmental Science and Policy, University of California Davis, Davis, CA 95616, USA
[f] Department of Mathematics, Applied Mathematics, and Statistics, Case Western Reserve University, Cleveland, OH 44106, USA
[g] USDA Forest Service Northern Research Station, Morgantown, WV 26505, USA
[h] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Praha 6 – Suchdol, Czech Republic

ARTICLE INFO

*Article history:*
Received 16 September 2020
Revised 17 January 2021
Accepted 18 January 2021
Available online 26 January 2021

*Keywords:*
Magicicada spp.
Leslie matrix
Synchrony

ABSTRACT

Periodical cicadas, *Magicicada* spp., are a useful model system for understanding the population processes that influence range boundaries. Unlike most insects, these species typically exist at very high densities (occasionally $>1000/\ m^2$) and have unusually long life-spans (13 or 17 years). They spend most of their lives underground feeding on plant roots. After the underground period, adults emerge from the ground to mate and oviposit over a period of just a few days. Collections of populations that are developmentally synchronized across large areas are known as "broods". There are usually sharp boundaries between spatially adjacent broods and regions of brood overlap are generally small. The exact mechanism behind this developmental synchronization and the sharp boundary between broods remain unknown: previous studies have focused on the impacts of predator-driven Allee-effects, competition among nymphs, and their impacts on the persistence of off-synchronized emergence events. Here, we present a nonlinear Leslie-type matrix model to additionally consider cicada movement between spatially separated broods, and examine its role in maintaining brood boundaries and within-brood developmental synchrony that is seen in nature. We successfully identify ranges of competition and dispersal that lead to stable coexistence of broods that differ between spatial patches.



## 1. Introduction

With increasing interest in the effects of climate change on the geographical distribution of species, as well as the increasing numbers of biological invasions, there is a growing need to improve our knowledge of mechanisms that determine the range boundaries of populations and species. Climate is a well-known driver of species range boundaries and there have been extensive efforts to understand and model the climatic niche of various species (Peterson, 2003; Morin et al., 2007; Thomas, 2010). But climate forms just one part of a species' ecological niche; species ranges are also affected by biotic interactions such as competition, predation and herbivory (Holt, 2009; Roux et al., 2012). Despite the fact that many theoretical and empirical works have contributed to the understanding of coexistence and geographic overlap of organisms, the biotic mechanisms that form sharp range boundaries are complex and difficult to identify in natural systems.

Periodical cicadas (*Magicicada* spp.) are ideal model organisms to examine ecological processes that lead to sharp spatial boundaries, due to their long lifespans, exceptionally high densities, unique spatial distributions and developmental synchronization. For more than 350 years (Unnamed Observer, 1667), periodical cicadas have captured the interest of biologists, naturalists, and entomologists. Their life cycles were first outlined in detail in the early 20th century (Marlatt, 1907; Snodgrass, 1919; Marlatt, 1898). After hatching from eggs, which are laid in the twigs of trees, periodical cicada nymphs burrow underground, feeding on xylem fluids from tree roots. At the end of their 13th or 17th year underground (periodical cicadas have a 13 year life span in portions of their range and 17 years in other regions), they emerge

* Corresponding author.

https://doi.org/10.1016/j.jtbi.2021.110600
0022-5193/

en masse and spend about a month as adults, during which time they mate and oviposit. Periodical cicada populations typically exist at exceptionally high densities (as high as >1000/ $m^2$) and their loud buzzing mating calls can be heard from hundreds of meters away.

In any one part of the range of periodical cicadas, annual development of populations is synchronized and these synchronized populations, termed "broods", extend over several hundred $km^2$ (Fig. 1). Because of the sudden, regular, and periodic emergence and mating patterns, a cicada brood is defined as a population of temporally isolated cicadas: a single-aged cohort of individuals that live together underground and emerge together in the same year. Broods generally consist of 3–4 different sympatric species that are phenotypically very similar. This means that every 13th or 17th year, the entire region experiences a single mass emergence event in the early summer. Studies have theorized that this synchronous emergence of cicadas allows for satiation of predators, giving a sufficient number of adults the chance to survive, mate and reproduce (Karban, 1982). Their disappearance underground also prevents the occurrence of a long-term numerical response in above ground predators (Koenig and Liebhold, 2013), allowing populations to maintain high densities from generation to generation. In addition, the regions that the broods occupy and the boundaries between them appear to be stable over multiple generations (Williams and Simon, 1995), implying some type of synchronous ecological equilibrium.

Given their long lifespans that are spent almost entirely underground, multi-generational time-series data on periodical cicada populations takes decades to procure and reveal little about their lives as nymphs. What is known is that periodical cicada nymphs experience competition-driven mortality over time (although the details of how this competition works are unknown (Karban, 1984; Karban, 1997)) and adults experience predation-driven mortality once they emerge. In addition, periodical cicadas are sometimes observed emerging four years early, one year early, or one year late. This phenomenon is referred to as "stragglers" (regardless of whether emergence is late, as this term would imply, or early) and it provides a mechanism by which individuals effectively leak into another brood. What meditates these leakage events, how large they usually are, or how commonly they occur, however, are all poorly understood (Heath, 1968; Lloyd and White, 1976; White and Lloyd., 1979; White et al., 1979). Taking into account these uncertainties, Blackwood et al. (2018) built a model to capture the effects of competition and leakage that lead to single cicada broods at a single spatial location. Specifically, they considered the cicada population dynamics assuming either a steady annual rate of leakage among nymphs or a single large leakage event and determined the conditions that lead to replacement of the dominant brood. In both of these scenarios, they varied the form of competitive interaction between nymphs to reflect uncertainty in the details of nymphal competition. Assuming a steady leakage rate, under all forms of inter-brood competition, they found that a single brood persists for sufficiently low levels of leakage and over a range of competition intensity. This finding is consistent with the observation that locations typically contain only a single brood (Fig. 1), despite the existence of stragglers. They also discovered that the magnitude of a large leakage event (i.e. the proportion of cicadas in a brood that accelerate or delay development) determines whether and when a leaked brood outcompetes and supplants the parent brood in a single patch.

Previous work thus indicates that the predation on adults creates a strong Allee effect and this play a key role in limiting the presence of only a single brood at most locations (Lehmann-Ziebarth et al., 2005; Tanaka et al., 2009). But why do single broods occupy large, spatially-distinct regions (Cooley et al., 2009) with sharp boundaries between regions with different broods (Williams and Simon, 1995)? To answer this, we build and expand upon the framework presented in Blackwood et al. (2018) by looking at multiple spatial locations (hereafter, "patches") and introducing dispersal between them. We focus on periodical cicadas that have a 17 year life span and explore the processes that affect interactions between spatially adjacent periodical cicada broods and their spatial dynamics. We examine the conditions that lead to different types of equilibrium, such as the persistence of only the native brood in its original patch, the invasion of one brood into the other's patch, or coexistence of multiple broods in a single patch. We also consider a two-patch version of Machta et al. (2019) analytical approximation to the Blackwood et al. model, to examine the generality of our results. Our study provides insights into the formation of range boundaries in periodical cicadas as well as other interacting populations.

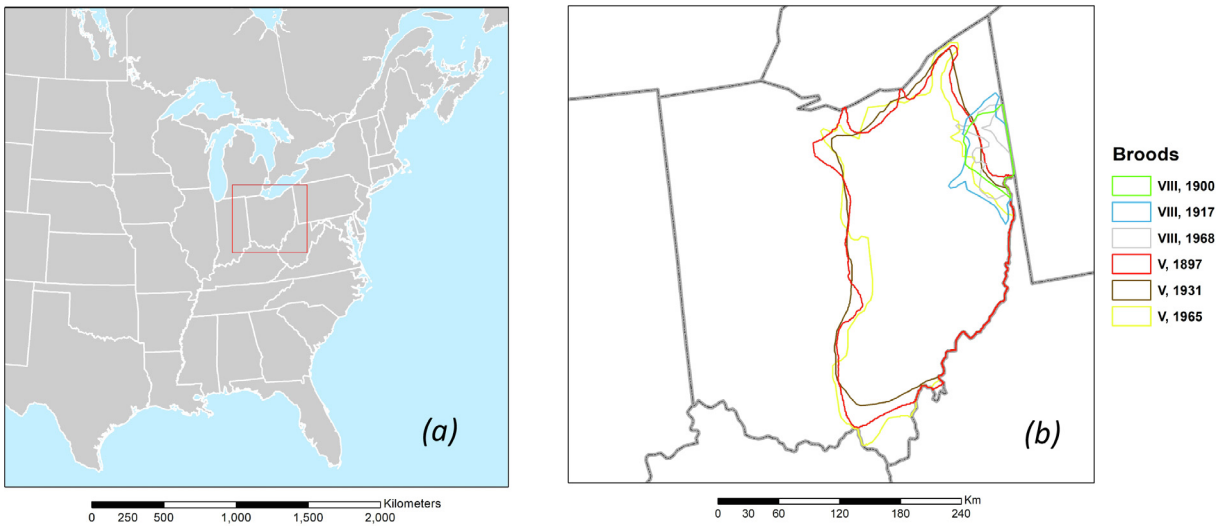



**Fig. 1.** Map showing the boundaries of periodical cicada broods V and VIII in Ohio, USA during emergence years spanning a ca. 70 year period. Note that both broods continue into neighboring Pennsylvania and West Virginia but survey data used to draw maps were only available from Ohio. Map redrawn from Forsythe (1976). Map in (a) is a reference map of eastern North America and (b) shows detail of brood distribution.

## 2. Model formation

### 2.1. Growth and reproduction

Our model follows (Blackwood et al., 2018), but with the addition of a second patch and dispersal between patches (as explained below). To model population size in a 17-year cicada population, we let the population density of age $i$ individuals ($i = 0, 1, \dots 16$) in patch $A$ and at time $t$ be $x_{i,t}$. We then build a 17-dimensional vector, $\mathbf{x}_t$, that describes the population density of every age group within patch $A$ at time $t$.

Two types of life history processes occur each year (Fig. 2). First, the nymphs experience competition-driven mortality during each year of development. We represent this by setting the proportion of cicadas who survive from year $i$ to year $i+1$ as $s_i(\mathbf{x}_t)$, so that $x_{i+1,t+1} = s_i(\mathbf{x}_t)x_{i,t}$. Second, if the cicadas are in their 17th year, they can reproduce and disperse to a neighboring patch. We let $x_e = s_{16}(\mathbf{x}_t)x_{16,t}$ be the population density of cicadas that survive their 17th year and emerge, and $R(x_e)$ be the fecundity rate, the average number of adult eggs laid per emerging cicada. Multiplying these by the current population size gives $\tilde{x}_{0,t+1}$, the new age-0 cicada population density before accounting for dispersal, as opposed to $x_{0,t+1}$, the post-dispersal age-0 cicada population density. To summarize, we have

$$x_{i+1,t+1} = s_i(\mathbf{x}_t)x_{i,t}, \qquad \text{for} \qquad 0 \leqslant i < 16 \tag{1}$$

$$\tilde{x}_{0,t+1} = R(s_i(\mathbf{x}_t)x_{i,t})s_i(\mathbf{x}_t)x_{i,t} = R(x_e)x_e, \qquad \text{for} \qquad i = 16. \tag{2}$$

Putting this into a Leslie matrix yields

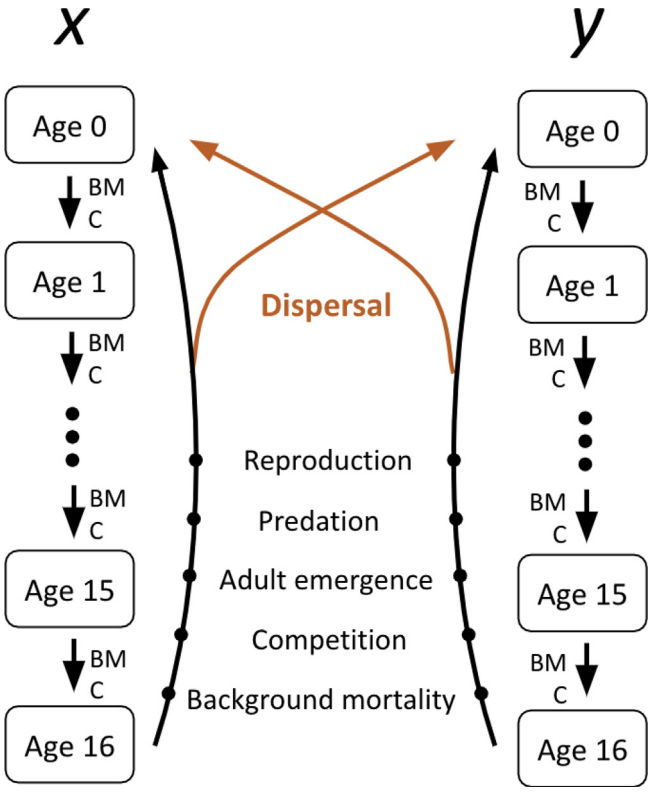



**Fig. 2.** Schematic representation of the life cycles of two spatially disjoint cicada populations, X and Y. Each population undergoes background mortality (BM) and competition (C) each year, and adults additionally undergo emergence, predation mortality, reproduction, and dispersal in their 17th year. Processes shown in black are modeled following Blackwood et al. (2018). Dispersal, in orange, is new to this model.

$$\begin{bmatrix} \tilde{x}_{0,t+1} \\ x_{1,t+1} \\ x_{2,t+1} \\ \vdots \\ x_{16,t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & \dots & 0 & R(x_e)s_{16}(x_{16,t}) \\ s_0(x_{0,t}) & 0 & \dots & 0 & 0 \\ 0 & s_1(x_{1,t}) & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_{15}(x_{15,t}) & 0 \end{bmatrix} \begin{bmatrix} x_{0,t} \\ x_{1,t} \\ x_{2,t} \\ \vdots \\ x_{16,t} \end{bmatrix}.$$

More simply, if we define our Leslie matrix as $\mathbf{L}(\mathbf{x}_t)$, then we have $\tilde{\mathbf{x}}_{t+1} = \mathbf{L}(\mathbf{x}_t)\mathbf{x}_t$.

We also model the impact of cicada movement (dispersal) to patches other than the ones where they emerged. Because broods can be both temporally and geographically offset, emerging cicadas in one brood can theoretically move unimpeded to a geographically distinct brood's patch. To represent this, we use a second 17-dimensional population vector, $\mathbf{y}_t$, which behaves exactly as $\mathbf{x}_t$ does, but represents the population in a second patch $B$, and we define $d$, the dispersal, which is the proportion of the population that emerges from one patch but lays their eggs in the other. Thus, given $\tilde{\mathbf{x}}_{t+1}$ and $\tilde{\mathbf{y}}_{t+1}$, the pre-dispersal populations, we have

$$x_{0,t+1} = (1-d)\tilde{x}_{0,t+1} + d(\tilde{y}_{0,t+1}), \tag{3}$$

$$y_{0,t+1} = (1-d)\tilde{y}_{0,t+1} + d(\tilde{x}_{0,t+1}) \tag{4}$$

and the time step from $(\mathbf{x}_t, \mathbf{y}_t)$ to $(\mathbf{x}_{t+1}, \mathbf{y}_{t+1})$ is completed.

Finally we account for leakage ("stragglers"), the early or late emergence of certain individuals within a brood. Given that we know little about leakage except for that it occurs, we assume that each year a fixed proportion $\phi$ of individuals will leak to the brood one year younger, one year older, and four years older. We also assume that cicadas cannot join broods that do not exist, and adjust accordingly: for example, a 15th-year cicada can no longer join the brood four years older, since there is no 19th-year brood. We add this to our model by defining a leakage matrix $\mathbf{C}$, with

$$\begin{aligned} c_{0,0} &= 1 - 2\phi \\ c_{i,i} &= 1 - 3\phi \text{ for } 1 \leqslant i \leqslant 12 \\ c_{i,i} &= 1 - 2\phi \text{ for } 13 \leqslant i \leqslant 15 \\ c_{16,16} &= 1 - \phi \\ c_{i+4,i} &= \phi \text{ for } 0 \leqslant i \leqslant 12 \\ c_{i+1,i} &= \phi \text{ for } 0 \leqslant i \leqslant 15 \\ c_{i-1,i} &= \phi \text{ for } 1 \leqslant i \leqslant 16, \end{aligned}$$

and all other entries 0. Note that if $\phi$, our proportion of cicadas that leak, is 0, then $\mathbf{C}$ reduces to the identity matrix. Put together, we have

$$\tilde{\mathbf{x}}_{t+1} = \mathbf{CL}(\mathbf{x}_t)\mathbf{x}_t \tag{5}$$

with dispersal again implemented according to Eqs. 3,4. To summarize,a schematic representation of the full life cycle is shown in Fig. 2.

### 2.2. Model parameters

We assume that cicadas undergo density dependent mortality due to competition. In the absence of rigorous empirical data on underground cicada competition dynamics, we assume that all cicadas compete equally with all other cicadas, regardless of age (Blackwood et al., 2018). We model competition by setting survivorship to be proportional to the inverse exponential of the sum of population densities of all cicada nymphs in a patch; higher total population density leads to lower *per capita* survivorship. Together with density-independent survivorship (Karban, 1997) of a proportion $s$ of nymphs that survive competition,

$$s_i(\mathbf{x}_t) = s\ \exp\left(-\sum_{j=0}^{16} a x_{j,t}\right), \tag{6}$$

where $a$ is a competition coefficient. Note that in this case, because all cicadas compete equally, the effects of competition are the same for each age group in a given year, but change from year to year as population densities shift.

To define fecundity, $R(x_e)$, we account for both predation-driven Allee effects and reproductive output. Given the high densities of cicadas that emerge at once, we assume a Holling Type II functional response in order to account for satiation of predators (Karban, 1982; Karban, 1984). Then the proportion of cicadas that survive predation is

$$\max\left[0, 1 - \frac{P_{\max}}{A_{\text{half}} + x_e}\right], \tag{7}$$

where $P_{\max}$ is the maximum density of cicadas per square meter that can be consumed by predators, and $A_{\text{half}}$ is the population density at which $P_{\max}/2$ cicadas per square meter are consumed by predators. When $x_e < P_{\max} - A_{\text{half}}$, predators would theoretically be able to consume more cicada adults than currently exist; the max function prevents this.

To find the total number of eggs laid per cicada that emerges, we can simply multiply the survival rate after emergence by the per capita fecundity of adult cicadas that have survived predation, $m$. This gives us the final equation

$$R(x_e) = \max\left[0, m\left(1 - \frac{P_{\max}}{A_{\text{half}} + x_e}\right)\right], \tag{8}$$

where $m, P_{\max}$, and $A_{\text{half}}$ have been fit using empirical field data (Karban, 1984).

For analytical purposes, it becomes convenient to nondimensionalize the population density. We do so by dividing the population densities $x_{i,t}$ by $A_{\text{half}}$ so that the nondimensional form of Eq. (8) is given by:

$$R(x_e) = \max\left[0, m\left(1 - \frac{P}{1 + x_e}\right)\right], \tag{9}$$

where $P$ is the nondimensional term $P_{\max}/A_{\text{half}}$. Hereafter, we refer only to the nondimensional form of population density.

In nondimensionalizing the population density, we must also use the new nondimensional competition coefficient $\alpha$, where $\alpha = aA_{\text{half}}$. For consistency with Blackwood et al. (2018), we report all parameter values in their nondimensional forms. Parameters are summarized in Table 1.

**Table 1**
Parameters and their values. $P_{\max}, A_{\text{half}}, m$, and $s$ are from Blackwood et. al., calculated from Karban (1997), Karban (1984), Karban (1997). We also nondimensionalize $\alpha$, the competition coefficient.

| Parameter | Definition | Value |
|---|---|---|
| $P_{\max}$ | Maximum cicadas killed by predation per square meter | 3.929 |
| $A_{\text{half}}$ | Density at which $P_{\max}/2$ cicadas are killed per square meter | 3.285 |
| $P$ | Dimensionless quantity $P_{\max}/A_{\text{half}}$ | 1.1916 |
| $m$ | Offspring per surviving adult cicada | 56.18 |
| $\phi$ | Proportion of cicadas that leak | 0–0.02 |
| $s$ | Density-independent survivorship | 0.915 |
| $\alpha$ | Competition coefficient (nondimensional) | 0–0.03 |
| $d$ | Proportion of cicadas that disperse to neighboring patch | 0–0.2 |
| $n$ | Difference in age of cicada broods | 0–17 |
| $\gamma$ | Initial Ratio of sizes of cicada broods | 0.8–1.2 |

### 2.3. Initial conditions

In addition to parameters, we also define initial conditions from which to run the model. Since we are modeling two separate geographic patches and allowing for interaction between them, it becomes especially important to keep track of exactly how the two systems vary. If we start with the same initial condition in two patches, then the population dynamics of each patch are the same as they would have been if they were independent of each other, with no spatial interaction.

Let $\mathbf{x}_t$ and $\mathbf{y}_t$ be the population densities in patches $A$ and $B$, respectively, with initial conditions $\mathbf{x}_0$ and $\mathbf{y}_0$. Then

$$\tilde{\mathbf{x}}_1 = \mathbf{CL}(\mathbf{x}_0)\mathbf{x}_0 \tag{10}$$
$$\tilde{\mathbf{y}}_1 = \mathbf{CL}(\mathbf{y}_0)\mathbf{y}_0 \tag{11}$$

and $\tilde{\mathbf{x}}_1$ interacts with $\tilde{\mathbf{y}}_1$ as described in Eqs. (3) and (4) to get $\mathbf{x}_1$ and $\mathbf{y}_1$.

For simplicity, and because it is most biologically relevant (Cooley et al., 2009), we always begin with a single brood in each patch. We initialize the model with 10 age-0 nymphs/m$^2$ in patch A and refer to this brood as "brood-0." Then we have

$$\mathbf{x}_0 = \begin{bmatrix} x_{0,0} \\ x_{1,0} \\ x_{2,0} \\ \vdots \\ x_{16,0} \end{bmatrix} = \begin{bmatrix} 10 \\ 0 \\ 0 \\ \vdots \\ 0 \end{bmatrix}.$$

Then using $\mathbf{x}_0$ as a reference, we construct $\mathbf{y}_0$ with two initial condition parameters, $n$, the difference in age of the broods that initially populate each patch, and $\gamma$, the ratio of population densities B:A of the initial broods in each patch (Table 1). Cicadas that emerge as adults in the same year as the cohort initialized in patch $A$ (or patch $B$) will hereafter be referred to as "brood-0" (or "brood-$n$"), regardless of whether those individuals remain in their patch of origin. This is consistent with real cicada broods, which are defined by their emergence year and not by their geographic location per se. Note that if $n = 0$ and $\gamma = 1$, we end up with $\mathbf{x}_0 = \mathbf{y}_0$ and there is only one brood that occupies both patches.

As an example, if $n = 1$ and $\gamma = 1.1$, then we have

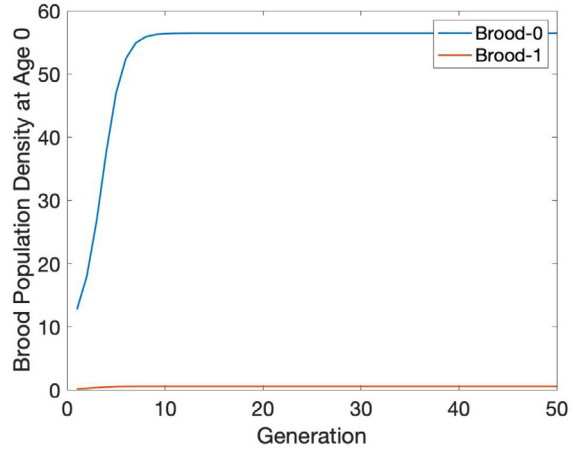
$$\mathbf{x_0} = \begin{bmatrix} 10 \\ 0 \\ 0 \\ \vdots \\ 0 \end{bmatrix}, \quad \mathbf{y_0} = \begin{bmatrix} 0 \\ 11 \\ 0 \\ \vdots \\ 0 \end{bmatrix}.$$

Thus, given a complete set of parameters (all those included in Table 1), we can analyze how the cicada populations change over time by examining $\mathbf{x}_t$ and $\mathbf{y}_t$ as $t$ changes.

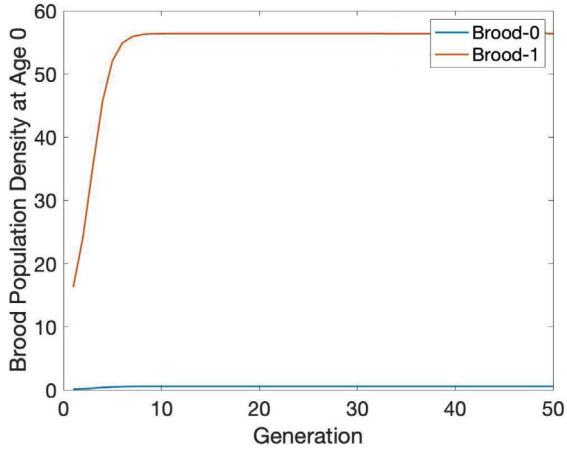
### 2.4. Tracking broods

We are interested in the population dynamics of the broods in the two patches. That is, we are interested in what conditions may lead to patterns of invasion of one brood's patch by another, stable coexistence of broods in a single patch, or extinction of broods.

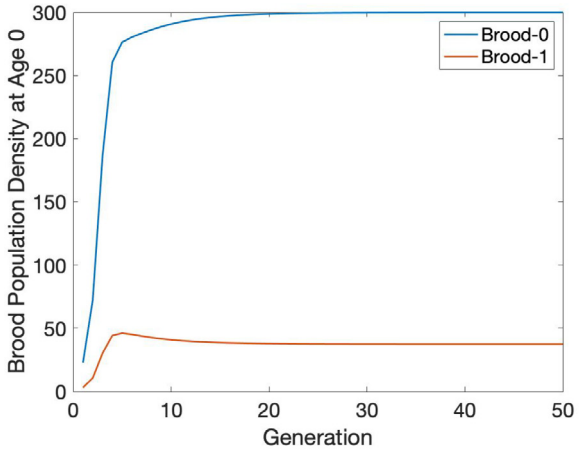
In order to track broods over time, we must account for the fact that populations of adults are absent and then emerge every 17th year. A simple way to do so is to only count age-0 cicadas every 17th year, so that the size of the brood can be accurately compared every generation. If we want to track the size of brood-$k$ in patches A and B, we let



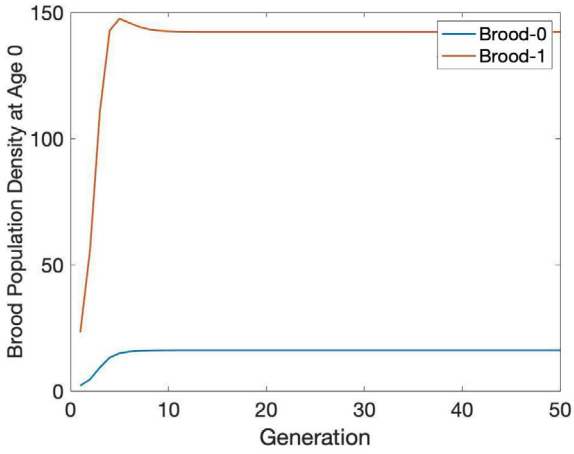

(a) Population Density in Patch A Equilibrium Type 1




(b) Population Density in Patch B Equilibrium Type 1




(c) Population Density in Patch A Equilibrium Type 2




(d) Population Density in Patch B Equilibrium Type 2

**Fig. 3.** Population density change over time, for conditions that lead to an equilibrium in which each brood remains dominant in its native patch. In (a) and (b), equilibrium type 1, the native broods explode in size for the first 5–10 generations before leveling off, while no immigrating brood establishes itself. In (c) and (d), equilibrium type 2, while the native broods still explode in size, an immigrating brood is also able to establish itself in the same territory and the two broods coexist locally. In both cases, population size reaches equilibrium when background mortality and deaths due to competition and predation are exactly balanced with fecundity. In general, time to reach equilibrium is short, less than 15 generations, although this can vary greatly based on model parameters and initial conditions.

$$f_k(T) = x_{0,17T-k} \tag{12}$$

$$g_k(T) = y_{0,17T-k} \tag{13}$$

so $f_k(T)$ and $g_k(T)$ represent the population density of the initial age-k cicadas in their $T^{\text{th}}$ generation. Thus, $f_k(x)$ and $g_k(x)$ also serve as proxies for the size of the $T^{\text{th}}$ generation of brood-k (how large a given generation was). Also important to note is that this model census occurs immediately after basic mortality, reproduction, and dispersal have occurred and age-0 cicada nymphs have been newly hatched.

For simplicity, we also prevent stragglers from occurring ($\phi = 0$), before returning to them at the end of the section. Thus, if $n = 1$, cicadas can only emerge in years 15, 16, 32, 33, 49, 50, and so on. So, for any set of parameters, $f_0(T)$ and $g_0(T)$ are, respectively, the population sizes of brood-0 in its home patch ($A$) and the neighboring patch ($B$) at the start of generation $T$. Similarly, $g_n(x)$ and $f_n(x)$, are the population sizes of brood-$n$ in its home patch ($B$) and neighboring patch ($A$), respectively. This almost always results in some type of equilibrium. We find three different types of equilibrium, which we will discuss in the following section. In each of these examples, we begin with an initial condition of $n = 1$ and $\gamma = 1$, so that

$$\mathbf{x}_0 = \begin{bmatrix} 10 \\ 0 \\ 0 \\ \vdots \\ 0 \end{bmatrix}, \quad \mathbf{y}_0 = \begin{bmatrix} 0 \\ 10 \\ 0 \\ \vdots \\ 0 \end{bmatrix},$$

and only varying the competition ($\alpha$) and dispersal ($d$) to achieve different equilibria.

## 3. Results

### 3.1. Types of equilibrium

In their non-spatial model, Blackwood et al. found that without stragglers ($\phi = 0$), at most one brood could persist in any one patch (Blackwood et al., 2018). However, the identity of this brood may

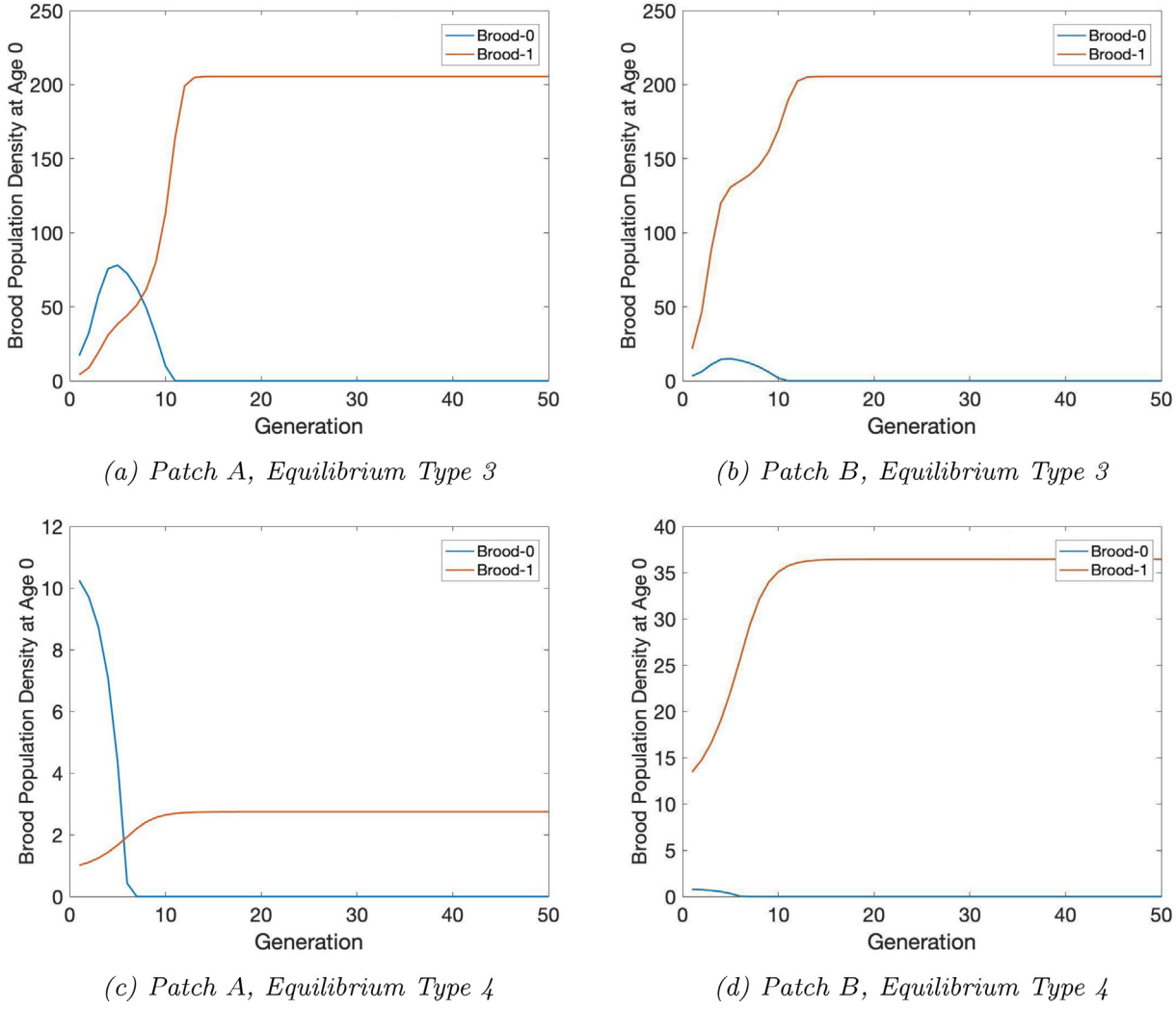



**Fig. 4.** Population density change over time, for conditions that lead to an invasion equilibrium. At high enough levels of dispersal, individuals from one brood are able to emigrate to a neighboring patch in great enough numbers to outcompete the native brood. In (a) and (b), equilibrium type 3, brood-1 from patch *B* has been able to outcompete not only the immigrating brood-0 in its own patch, but also the established brood-0 in the neighboring patch. The result is a spatially-uniform invasion of one brood into its neighboring patch and the extinction of its neighboring brood. In (c) and (d), equilibrium type 4, at higher levels of competition and lower levels of dispersal, brood-1 again completely outcompetes brood-0 in both patches, but is unable to establish an equally populous brood in the invaded patch *A*. Like in Fig. 3, time to equilibrium is short, generally less than 15 generations.

depend on initial conditions. Because we recover Blackwood et al.'s model by setting $d = 0$, this is also the behavior we observe in each patch in the absence of any dispersal. Following the arguments of Karlin and McGregor (1972) – who noted that due to continuity in both the locations of equilibria and in the eigenvalues that determine their stability, small parameter changes cannot have large effects on equilibrium behaviors – we can also expect to see at most one brood per patch when dispersal, $d$, is sufficiently small. Indeed, equilibrium type 1 (described in detail below) illustrates that, for low dispersal, the results of our model can be deduced from Blackwood et al.'s results. However, this logic cannot tell us how low dispersal must be to be "sufficiently small", nor what new qualitative behaviors emerge when our dispersal parameter $d$ exceeds this level. Characterizing these new qualitative behaviors (equilibrium types 2–4 below) is therefore a central contribution of our analysis.

The first two equilibrium types occur when each brood exists steadily in its own patch, shown in Fig. 3. At moderately low levels of dispersal and high levels of competition, an immigrating brood appears, but only as a result of dispersal – cicadas that disperse to a neighboring patch are outcompeted and die out before having the chance to reproduce (type 1). In a type 1 equilibrium, the immigrating brood never establishes a self-sustaining population in the new patch and every cicada nymph from the immigrating brood has not previously dispersed.. At lower levels of competition or higher levels of dispersal, however, emigrating individuals are able to establish themselves in great enough numbers to survive and reproduce in their neighboring patch, although they remain less dense than the native broods (type 2). In a type 2 equilibrium, some cicada nymphs from the immigrating broods may be offspring of nymphs that had dispersed previously, combining with the newly dispersed immigrating cicada nymphs to produce a larger brood.

Another set of equilibrium conditions occur when one brood "invades" another, shown in Fig. 4. In this case, a brood from one patch will migrate to another in great enough numbers to outcompete the extant brood there, eliminating it. Thus, we end up with only one brood that has taken over both patches (types 3 and 4).

In the equilibrium conditions in Fig. 4, brood-1, initially from patch *B*, is the brood that invades, eliminating brood-0 from patch *A*. This occurs because of the initial conditions: patch *A* began with 10 age-0 cicadas per square meter, and patch *B* began with

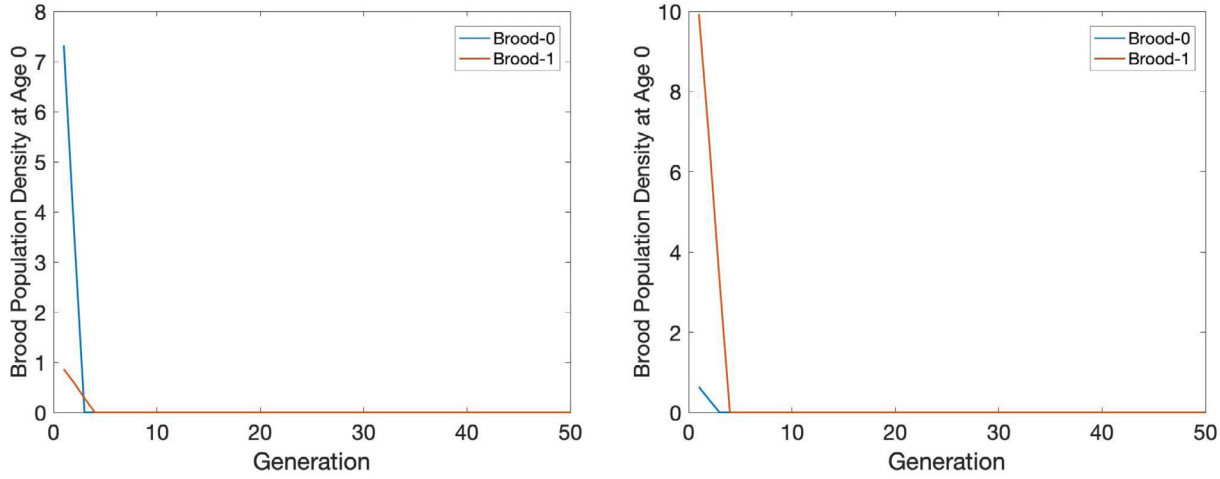
10 age-1 cicadas per square meter. Since cicadas undergo annual mortality, brood-1 experiences fewer rounds of nymphal mortality and its first emergence is thus larger and reproduces in greater numbers than brood-0. These slightly greater numbers allow brood-1 from patch *B* to eventually outcompete brood-0 in both patches. Equilibrium types 3 and 4 differ in their spatial distribution of broods. In Fig. 4a and b (type 3), brood-1 has survived in its initial patch B and also invaded patch A, creating a spatially homogeneous distribution of cicadas across patches A and B. In Fig. 4c and d (type 4), brood-1 has survived in its initial patch B and also invaded patch A, but is unable to establish an equally dense population in patch B, creating a spatially heterogeneous distribution. In this case, no cicadas that were originally hatched in patch A survive to reproduce, but some eggs are still laid in patch A by cicadas immigrating (dispersing) in from patch B.

The simplest and final equilibrium condition, type 5, occurs when all broods go extinct. We see this type of equilibrium in Fig. 5. Extinction is driven by competition and predation; at high levels of either process, the cicadas are unable to survive long enough to reproduce and maintain a population. It should be noted that from these initial conditions, an immigrating brood does briefly establish itself in each territory. While the population density of the immigrating brood is small, so too is the population density of the native brood, resulting in low competition that allows for the immigrating brood to decline over a few generations before going extinct.

### 3.2. Effects of $\gamma$ on equilibrium

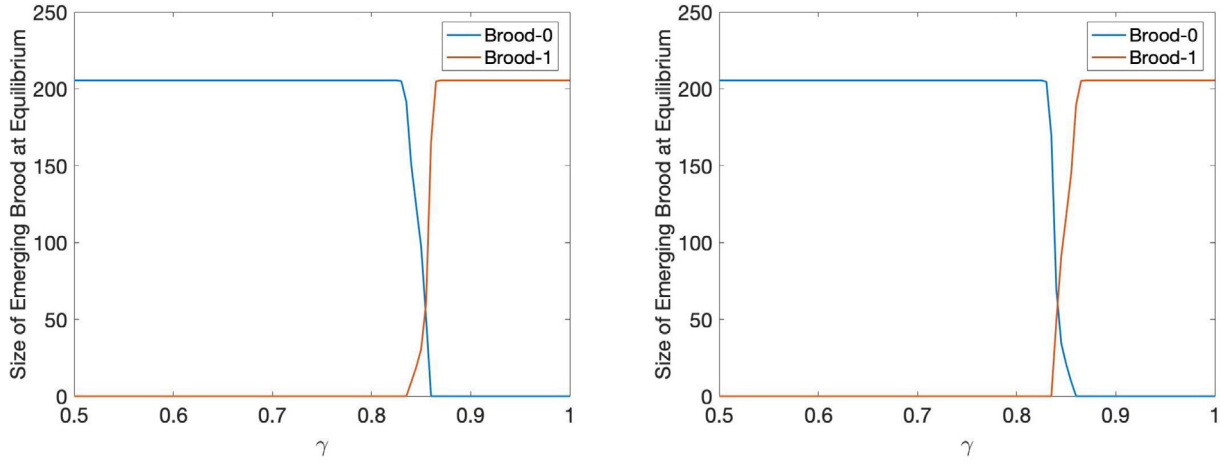
To illustrate all five of these cases, we began with initial conditions of $\gamma = 1$, meaning that both patches had the same population density in the first year. However, unless $n = 0, \gamma = 1$ will always result in different 17-year average brood sizes, because brood-$n$ reproduces after $n$ fewer rounds of nymphal mortality in the first modeled generation. Because density-dependent competition and predation are the primary drivers of brood viability, these two parameters ($n$ and $\gamma$) become especially important when determining to what extent a brood is able to establish itself in both patches.

We focus here specifically on $\gamma$, before returning to $n$ later on. We fix $n = 1$, so varying $\gamma$ gives the initial condition




(a) Patch A, Equilibrium Type 5 (b) Patch B, Equilibrium Type 5

**Fig. 5.** Extinction, equilibrium type 5. Each brood is driven to extinction in its own territory, although each brood briefly immigrates to the neighboring territory before also dying out.




(a) Patch A (b) Patch B

**Fig. 6.** Effects of varying $\gamma$ on equilibrium population density, captured after 50 generations, or 850 years. The abruptness of the switch at approximately $\gamma = 0.85$ is purely a function of how long the model runs (i.e running for infinite time would result in a vertical line).

$$\mathbf{x}_0 = \begin{bmatrix} 10 \\ 0 \\ 0 \\ \vdots \\ 0 \end{bmatrix}, \quad \mathbf{y}_0 = \begin{bmatrix} 0 \\ 10\gamma \\ 0 \\ \vdots \\ 0 \end{bmatrix},$$

In Fig. 6 (an invasion case), we show an example of how $\gamma$ affects equilibrium. While the parameter values will always lead to some sort of invasion (same parameters as in Fig. 4), $\gamma$ will directly impact which brood invades the other. In our example in Fig. 4, $\gamma = 1$, and we see brood-1 from patch $B$ invade patch $A$ and eliminate the brood-0. As we decrease $\gamma$, however, Fig. 6 suggests that around $\gamma = 0.85$, the invasive brood switches from brood-1 to brood-0. This suggests that $\gamma \approx 0.85$ is the point at which the population densities of brood-0 and the brood-1 are equal upon their first emergence as adults.

Also worth noting is that varying $\gamma$ has no impact on the equilibrium population density of the invasive brood. We see a sharp switch at $\gamma = 0.85$, but otherwise equal population density across all values of $\gamma$. In other words, varying $\gamma$ impacts which brood "wins," but not how much they win by, and different initial conditions still lead to the same equilibrium population density.

### 3.3. Interactions between competition and dispersal

We have fixed $\phi = 0, n = 1, \gamma = 1$, modeling a simplified but ecologically relevant situation of two geographically separated but adjacent cicada broods, one year apart in age, with no leakage. As such, in the absence of leakage, competition ($\alpha$) and dispersal ($d$) are the primary drivers of cicada brood equilibrium. Fig. 7 shows every combination of values of $\alpha$ and $d$ at which we get each of the 5 equilibrium types outlined in the previous section.

Fig. 7a and b show the phase diagrams for patches $A$ and $B$, respectively. In each graph, regions 1 and 2 (where the regions are numbered to match the equilibrium type that occurs there) represent parameter conditions in which each patch's respective initial brood is the dominant brood. Regions 3 and 4, however, represent parameter conditions in which the same brood (in this case, brood-1) dominates in both patches.

Region 1 in Fig. 7 represents broods in their respective native patches with no self-sustaining immigrating brood (type 1, Fig. 3a and b). This occurs at low to moderate dispersal values and at almost all competition values in our range. In the absence of leakage, and if the two broods fail disperse to each other's patches in great enough numbers, then individuals from each brood will have difficulty surviving until reproduction in any other patch but their own. This is also consistent with Blackwood et. al., who found this type of equilibrium at low leakage and at all competition values.

Region 2 in Fig. 7 represents multiple brood coexistence (type 2, Fig. 3c and d). This occurs at low to moderate dispersal values and intermediate competition values. Beginning in this region, decreasing dispersal or increasing competition moves the equilibrium back to region 1, since an immigrating brood is no longer viable. Increasing dispersal moves the equilibrium to region 3 (invasion), since the immigrating brood is now immigrating in much larger numbers and is able to outcompete the extant brood. Also note that while regions 3 and 4 both represent invasion, they differ in the population sizes of broods: region 3 represents one brood that is equally populous in both patches, while region 4 represents one brood with different population densities in the two patches (see Fig. 4).

Coexistence regions 1 (regional coexistence) and 2 (local coexistence) are sandwiched above and below by regions 3 and 4 (invasion). This suggests that multiple brood coexistence only occurs in a "sweet spot" of competition, where it is low enough that the smaller brood can immigrate and exist in the larger brood's native patch, but high enough so that the larger brood does not take over the smaller brood's patch upon immigrating.

Region 5 represents extinction, which occurs universally across all values of dispersal, given high enough competition. Increased competition will always reduce population density, until population density reaches 0.

### 3.4. Effects of n on equilibrium

Having examined the impacts of $\alpha, d$, and $\gamma$, we turn our attention to $n$, which is simply the initial age of the brood in patch $B$. Much like $\gamma, n$ defines our initial conditions and indirectly impacts the size of broods. As an example, if we let $\gamma = 1$ and $n = 2$, we have the initial condition

$$\mathbf{x}_0 = \begin{bmatrix} 10 \\ 0 \\ 0 \\ 0 \\ \vdots \\ 0 \end{bmatrix}, \mathbf{y}_0 = \begin{bmatrix} 0 \\ 0 \\ 10 \\ 0 \\ \vdots \\ 0 \end{bmatrix}.$$

Recall that because of the annual mortality of cicadas, a year-0 brood with a population density of 10 cicadas per square meter is actually smaller than a year-1 brood with the same population density, when measured by 17-year average brood population density. Thus, increasing $n$ has a similar effect as increasing $\gamma$, which is to change the ratio of initial sizes of the two broods.

Fig. 8 shows the impact of varying $n$ on the entire phase diagram. First, we note that the boundary between regions 2 (coexistence) and 3 (invasion) shift leftward (toward lower dispersal) as $n$ increases. This indicates that at greater values of $n$, the larger brood is able to invade the neighboring patch at lower values of dispersal: increasing $n$ increases the difference in size between initial broods, and broods with larger population size advantages are more easily able to invade a neighboring patch.

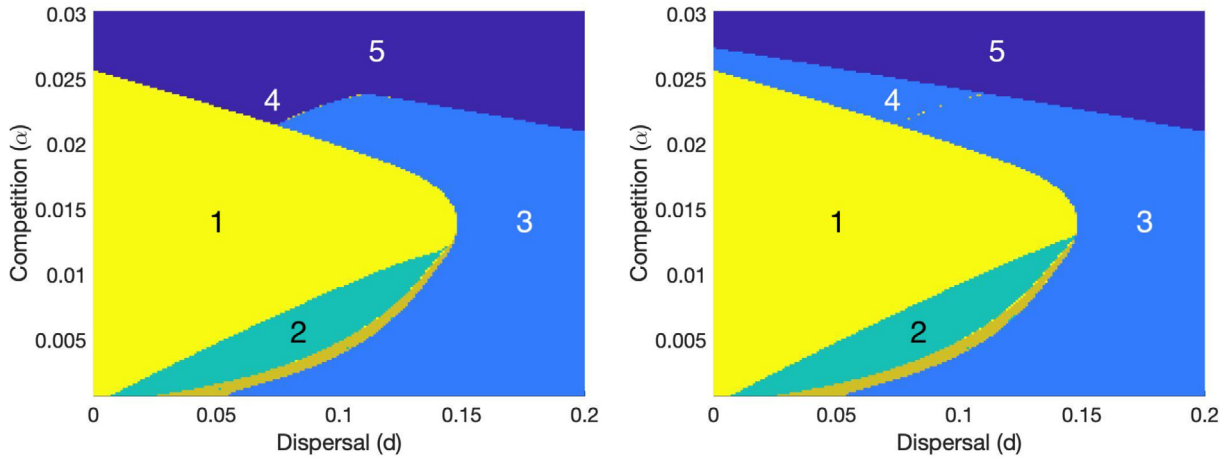
In addition, we also see the boundary between equilibrium region 5 (extinction) and equilibrium region 3 (invasion) shift upward (toward higher competition) as $n$ increases. This occurs for a similar reason: broods with larger population size advantages are more able to withstand higher competition.

For comparison, Fig. 9 shows the impact of increasing $\gamma$ on the entire phase diagram. We note the impact is almost identical to that of increasing $n$, for similar reasons: at greater values of $\gamma$, the larger brood is gains a greater advantage over the smaller brood, shifting the boundaries of the phase diagram accordingly.

### 3.5. Comparing dispersal and leakage

Up until now, we have focused on the effects of $\alpha, d, n$, and $\gamma$, while leaving leakage ($\phi$) ("stragglers") fixed at 0. We now turn to comparing the effects of dispersal with those of leakage on equilibrium. While not initially obvious choices for direct comparison, dispersal and leakage represent the only ways in which individuals or their offspring can leave their brood and join another one, so we are interested in understanding whether these two distinct processes have similar dynamical effects.

A simple way to break down leakage for more direct comparison to dispersal is to investigate cases in which individuals can only leak in one of three ways (four years ahead, one year ahead, one year behind), instead of in all three ways simultaneously as observed in nature. This comparison is also not perfect: namely, dispersal represents back-and-forth interaction between two




(a) Patch A Equilibrium (b) Patch B Equilibrium

**Fig. 7.** Phase diagram of each patch, showing the type of equilibrium that results from each set of parameters. We vary competition ($\alpha$) and dispersal ($d$), while fixing $\phi = 0, n = 1, \gamma = 1$. Regions 1 and 2 represent equilibria in which each brood persists in its native patch, with or without the other brood (as in Fig. 3), regions 3 and 4 represent invasion equilibria (as in Fig. 4), and region 5 represents extinction equilibria (as in Fig. 5). Note that region 4 (invasion) is subsumed into region 5 (extinction) in patch A into region 3 (invasion) in patch B, indicating the heterogeneity of cicada distribution between patches A and B; no cicadas survive long enough to reproduce in patch A, so emergence appears similar to extinction, but some do in patch B, so emergence remains similar to that under region 3. Dark yellow regions are areas where equilibrium has not yet been reached. All simulations were run for 50 generations, or 850 years.

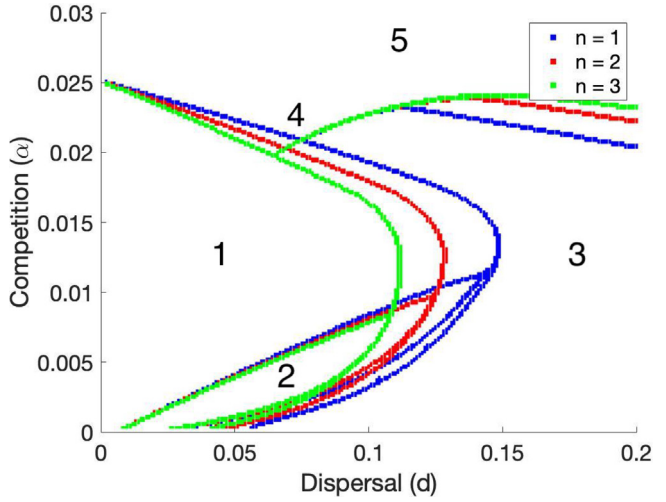



**Fig. 8.** Overlaid phase diagrams of patches A and B, for $n = 1, 2$ and 3. We keep fixed $\phi = 0, \gamma = 1$ for easy comparison. All simulations were run for 50 generations, or 850 years.

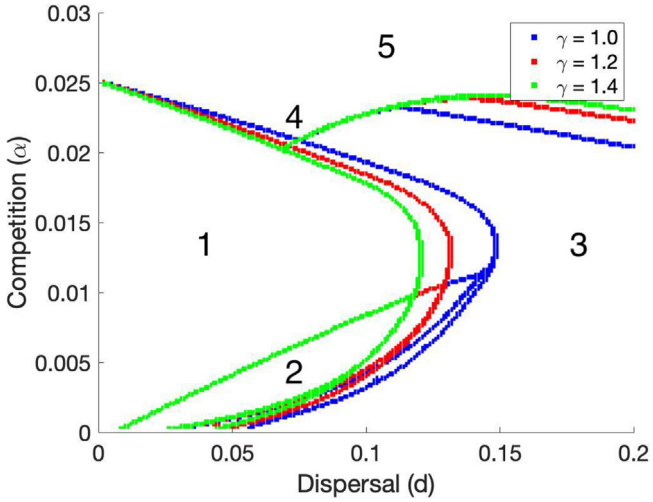



**Fig. 9.** Overlaid phase diagrams of patches A and B, for /$gamma = 1, 2$ and 3. We keep fixed $\phi = 0, n = 1$ for easy comparison. All simulations were run for 50 generations, or 850 years.

broods, whereas leakage represents only the one-way flow of individuals from one brood to another, then another, and then theoretically to all 17 broods. Still, +1, −1, and +4 leakage, shown in Fig. 10 are roughly analogous to dispersal from a neighboring patch that is one year ahead or behind (occurs in patch $A$ or $B$, respectively, when $n = 1$) and 4 years ahead (occurs in patch $A$ when $n = 4$).

In all three scenarios, we see single-brood equilibria (region 1) at almost all values of competition and at low values of leakage. This is the exact same trend as in Fig. 7, where we see equilibrium region 1 at almost all values of competition and at low values of dispersal; just as low levels of dispersal prevent sufficient immigration to form another locally-viable brood, low levels of leakage prevent sufficient numbers of stragglers to form another viable brood.

Another shared feature of the competition-dispersal and competition-leakage phase diagrams (Figs. 7 and 10, respectively) is the presence of a region of coexistence equilibria (equilibrium type 2) to the right of region 1. In both cases, if we begin in region 1 at sufficiently low competition values (the lower leftmost region of both Figs. 7 and 10) and and increase either dispersal or leakage, we see equilibrium shift to region 2. The same reasoning as in competition-dispersal phase diagram applies here: that individuals are now able to leave their brood at high enough rates to allow for a viable second brood.

Further increasing leakage from equilibrium region 2 (moving right from the green region to the dark yellow region in Fig. 10, and from the green region to the blue region in Fig. 7), however, has a different effect in the competition-leakage phase diagram than in the competition-dispersal phase diagram. Increasing dispersal in the competition-dispersal plane results in the smaller, invading brood becoming large enough to outcompete and replace the native brood, moving the equilibrium to a single-brood state. Increasing leakage in the competition-leakage plane also results in the new brood outcompeting and replacing the resident brood,

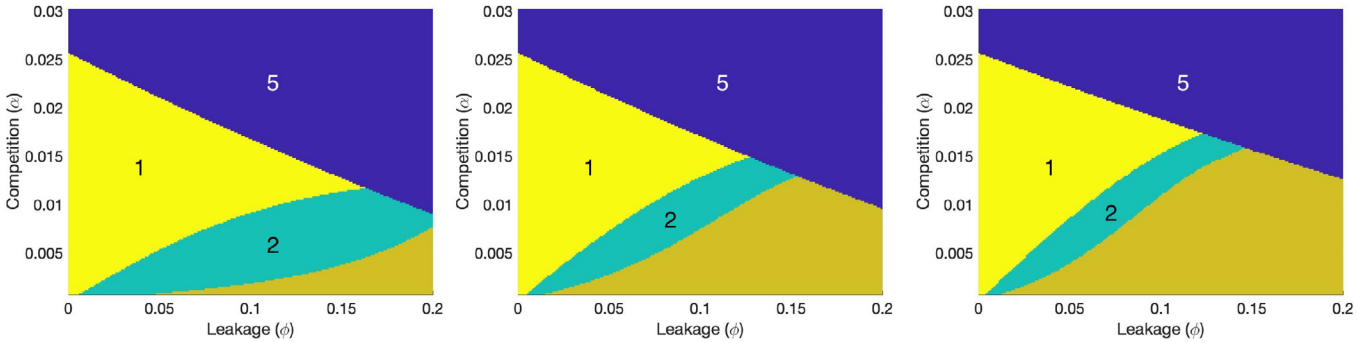



**Fig. 10.** Equilibrium phase diagrams, plotting leakage against competition, with no dispersal occuring. Region 1 represents single brood existence, region 2 represents multiple brood coexistence, region 5 represents extinction, and dark yellow regions represent no equilibrium within the time frame of our simulations.

but rather than establishing a new equilibrium, the new brood in turn spawns a subsequent brood, and the cycle repeats itself. As such, at high enough leakage new broods will always form and die out, and no constant single-brood equilibrium is ever reached.

Finally, we also see that at high levels of competition, at any levels of leakage or dispersal, we get extinction. Beyond this, we also see the negatively sloped boundary between equilibrium region 5 and all the other regions, which implies that lower leakage, like lower dispersal, allows for greater brood tolerance to competition.

## 4. Equilibria in the hybrid model approximation

Machta et al. (2019), derived an approximation to the Blackwood et al. (2018) Leslie matrix model that yields qualitatively similar results and can be solved analytically. The key approximation in this hybrid approximation is to replace the discrete age-structured matrix model by a continuous time differential equation while retaining reproduction as a discrete event. To facilitate an analytic solution we also use a simplified functional response. The phase diagram in the dispersal–competition plane for the two-patch version of the hybrid model with a simplified functional response, described in detail in Appendix B, is shown in Fig. 11.

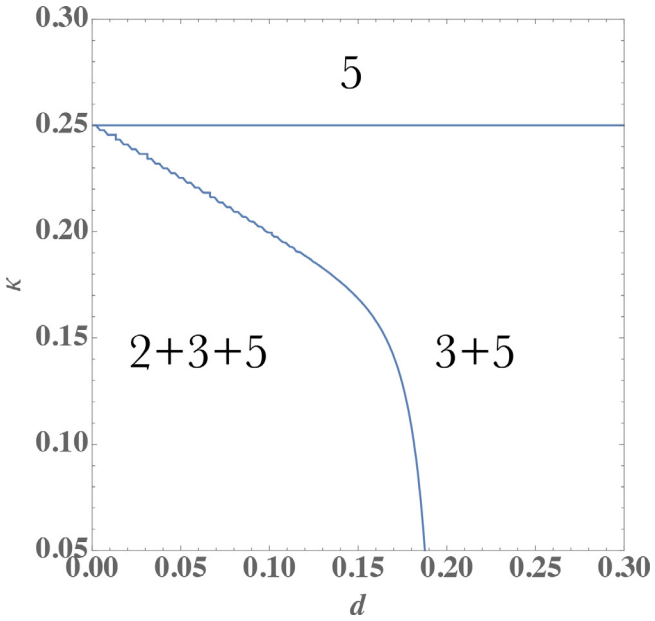



**Fig. 11.** The regions in the $\kappa$–$d$ phase diagram in the hybrid model approximation with simplified functional response. $\kappa$ is a dimensionless ratio proportional to competition strength and $d$ is dispersal. In region 5 no broods can exist in equilibrium. In region 3 + 5, in addition to extinction, a single brood can stably exist with the same population size in both patches. In region 2 + 3 + 5, in addition to the zero and one brood stable equilibria, it is also possible for two broods to stably coexist in both patches with each brood in the majority in its home patch and in the minority in the other brood's home patch. The simplified functional response breaks down for sufficiently small $\bar{\kappa}$ and the two-brood equilibrium becomes unstable. This region is not shown.

While Figs. 7 and 11 both show phase diagrams in the dispersal–competition plane, they have different interpretations. Fig. 11 shows what is *possible* in each region, for biologically relevant values of competition and dispersal. For example, in the region of Fig. 11 labeled "2 + 3 + 5", local coexistence (equilibrium type 2), spatially-uniform invasion (type 3) and extinction (type 5) are all possible. The specific initial conditions will determine which of the possible equilibria is the stationary state. In general, whenever a two-brood equilibrium (type 2) is possible, so too is spatially uniform invasion (type 3) and extinction, and whenever spatially uniform invasion is possible, so too is extinction. By contrast, Fig. 7 shows the final state that results from a specific initial condition. This difference explains why the lower boundary of region 5 slopes downward in Fig. 7, where as in Fig. 11, it is horizontal at the limit of existence for the single brood state in a single patch.

Although the quantitative features of the phase diagram depend on the various approximations made here, there are two qualitative features that are quite robust and will apply to a broad class of models with symmetric dispersal and no leakage ("stragglers") including the Leslie matrix model studied here. The first robust feature is the fact that dispersal cannot rescue a brood that would not, due to the strength of competition, be able to persist in either patch. This explains the horizontal (dispersal-independent) boundary above which extinction is the only possible outcome (region 5). The second robust feature is that in the limit of small dispersal, the two-brood equilibrium (type 2) is possible, and is stable for all parameter values for which the one brood equilibrium is possible. This result follows from continuity and the fact that if there is no dispersal then two broods may coexist, each in its own patch with a density that is identical to a single patch system.

There are also notable differences between Figs. 7 and 11. Equilibrium type 4 (invasion with spatially heterogeneous final densities) is never seen in the approximate model, due to an assumption in the calculation of a symmetry between the two patches when the two broods are interchanged. Another notable qualitative difference between Fig. 7 and Fig. 11 is that some of region 3 undercuts region 2 in Fig. 7, suggesting that two-brood

equilibria are unstable for sufficiently weak competition. This undercutting does not occur in Fig. 11, because the simplified functional response breaks down when competition is sufficiently weak and population densities are very high. In Appendix B we consider the other limit of very weak competition and very high population densities and show that the two-brood, two-patch equilibrium (of type 2) is always unstable in this limit. Thus, by continuity, sufficiently near the horizontal axis ($\tilde{\kappa} = 0$), the only stable equilibria in the analytical model are a single brood, as in Fig. 7, and extinction.

The details of the calculation and method of plotting the phase diagram are presented in Appendix A and a Mathematica file found in the supplement.

## 5. Discussion

Understanding the different processes that affect interactions between spatially adjacent periodical cicada populations and their spatial dynamics was the primary goal of this study. These types of interactions between adjacent broods and influences on brood boundaries provides insight into the role of competitive interspecific interactions and their influences on species range boundaries. Boundaries of periodical cicada broods are in some ways analogous to species range boundaries; in some cases, competitive exclusion between two species may lead to non-overlapping ranges (Case and Taper, 2000), resembling the case for periodical cicada broods. However, unlike two competing species, two periodical cicada broods occupy identical ecological niches so niche differences can be eliminated as a factor contributing to their boundaries.

The most biologically relevant equilibrium for cicada broods is the one with regional, but not local, coexistence (Figs. 3a and b, region 1 in Fig. 7) since this describes the situation seen through most of the range of periodical cicadas. Empirical studies (Cooley et al., 2009) have shown that it is quite rare for multiple temporally separated cicada broods to exist together in the same region and broods tend to be geographically distinct, with sharp brood boundaries and little overlap between the areas which different broods occupy (Cooley et al., 2007). Based on our model, this implies either that the interaction between neighboring broods is so low (i.e. dispersal between the patches is low) that no new brood can be viable, or that the competition within a region is high enough that newly entering individuals are driven below the Allee threshold set by predation before they can form a new brood.

Invasion equilibria (Fig. 4, regions 3 and 4 in Fig. 7) are also biologically relevant, at least theoretically. The existence of these regions indicates that under specific combinations of competition and dispersal, it is possible for one brood to invade and replace a geographically adjacent brood. Given that long-term, multigenerational population data on cicadas takes decades to gather, we have virtually no empirical evidence for or against invasion occurring in cicada broods. However, it is conceivable that some larger broods today were once two temporally and geographically separated broods and under specific levels of brood dispersal and competition, one brood invaded and replaced the other.

While two or more periodical cicada broods rarely overlap or coexist sympatrically, this situation has occasionally been observed at or near boundaries between two broods (Cooley et al., 2007). Our model suggests a specific level of dispersal from one patch to another is necessary for coexistence to occur. We defined dispersal as the proportion of cicadas in one patch that emerge and lay their eggs in a neighboring patch (Fig. 3c and d, region 2 in Fig. 7). While framed as an intrinsic property of the cicada broods themselves, dispersal can also serve as a proxy for the inverse distance between two broods; the closer two broods are geographically, the more likely individuals from the patch occupied by one brood will be to disperse to the other patch. Thus given the results of our model, we might expect to see some coexistence of broods when two broods are initially temporally separate but geographically close together.

A limitation of the model, of course, is that it only includes two similarly sized geographic regions, when in reality cicada broods often border multiple others and can occupy differently sized spaces. For example, we might expect a brood occupying a very large patch to behave differently when invading and surviving in other patches than a brood occupying a relatively small patch, even with similar cicada density. Further investigations into the nature of cicada dispersal across varied and more than two geographic regions of should prove interesting. We are also limited by the dearth of research on underground cicadas; we assumed a standard background mortality rate, a nonlinear competition-based survivorship, and a constant leakage term to maintain consistency with Blackwood et al. (2018), but these assumptions may not necessarily hold true in all cases.

Beyond providing insight into the population interactions that govern range boundaries in peridoical cicadas, results presented here provide additional understanding of the formation of range boundaries for other species. Specifically, these results are potentially applicable to other systems in which the population dynamics of two or more competing species are affected by Allee effects and competition (Keitt et al., 2001; Clerc et al., 2010). They illustrate how the existence of an Allee effect can amplify competitive interactions between two species and thereby impose range limits on competing species. These findings can be described as a type of "range-pinning" in which density-dependent dynamics interact with a strong Allee effect to constrain species from occupying areas of potentially suitable habitat.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## CRediT authorship contribution statement

**Geunho Kye:** Conceptualization, Formal analysis, Methodology, Writing - original draft. **Jonathan Machta:** Conceptualization, Writing - review & editing, Analysis in Sec. 4. **Karen C. Abbott:** Conceptualization, Writing - review & editing. **Alan Hastings:** Conceptualization, Writing - review & editing. **William Huffmyer:** Conceptualization, Writing - review & editing. **Fang Ji:** Conceptualization, Writing - review & editing. **Andrew M. Liebhold:** Conceptualization, Writing - review & editing. **Julie C. Blackwood:** Conceptualization, Methodology, Writing - review & editing, Supervision.

## Acknowledgements

AML was funded by grant EVA4.0, No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by OP RDE. We also thank two anonymous reviewers for their thoughtful comments which have led to an improved manuscript.

## Appendix A. Hybrid model two-brood calculation

The calculation of the phase diagram, Fig. 11 is carried out within the hybrid model introduced in Machta et al. (2019). In this model, reproduction is at a single time as in the full Leslie matrix model but juvenile survivorship is replaced by a linear form,

$$s_i(x_{i,t}) = (1-\sigma/q)\sum_{j=0}^{q-1}\frac{\beta}{q}x_{j,t}, \tag{14}$$

where $q$ is the lifespan of cicadas in years, $\sigma$ is mortality and $\beta$ is a competition parameter. In the hybrid model, the calculation is carried out in the limit $q \gg 1$ which yields a differential equation in time for juvenile competition that permits an analytic solutions to the model. However, as shown in Sec. 9.2 of Machta et al. (2019), results from the hybrid model calculation are in reasonably good quantitative agreement with Leslie matrix model results for $q = 17$, using the exponential form of competition, Eq. (6). The relation of hybrid model parameters to the parameters defined in Sec. 2.2 is $\beta = 17a = 17\alpha/A_{\text{half}}$and $\sigma = 17(1-s)$.

In order to proceed further without unnecessary complications, we introduce a simplified functional response where reproduction is quadratic in the adult population density as described in Section 6 of Machta et al. (2019). In this approximation, the equation that relates the dimensionless adult population density for a single brood, $\tilde{\chi}$ at the current emergence to the density at the subsequent emergence $\tilde{\chi}'$ is

$$\left(\frac{1}{\tilde{\chi}'}-1\right)^{-1} = \frac{\tilde{\chi}^2}{\tilde{\kappa}}, \tag{15}$$

where $\tilde{\kappa}$ is a dimensionless combination of the parameters $A_{\text{half}}, \beta, \sigma$ and $m$, controlling predation, competition, juvenile mortality and fecundity, respectively,

$$\tilde{\kappa} = \left(\frac{A_{\text{half}}\beta}{m}\right)e^{\sigma}(e^{\sigma}-1)/\sigma. \tag{16}$$

The dimensionless population density is defined from the actual population density $x$ via,

$$\tilde{\chi} = \beta x(e^{\sigma}-1)/\sigma. \tag{17}$$

Note that if $A_{\text{half}}, \sigma$ and $m$ are held fixed, $\tilde{\kappa}$ is simply a dimensionless competition parameter. The simplified functional arises from the full functional response in the limit that $P_{\max} = A_{\text{half}}$ $(P = 1)$ and $A_{\text{half}} \gg x_e$, where $x_e$ is the density of emerging juveniles. The simplified function response yields results that are qualitatively similar to the full model. However, because there is no Allee threshold in the simplified function response, a type 1 equilibrium does not exists in this approximation. Given the definition of parameters in the hybrid model and the parameter choices used elsewhere in the paper (see Table 1) we can relate $\tilde{\kappa}$ to the dimensionless competition parameter $\alpha$ as

$$\tilde{\kappa} = 2.88\alpha. \tag{18}$$

To analyze the a two-brood, two-patch system, we make similar assumptions as made in Section 7 of Machta et al. (2019), which analyzes the unstable two-brood equilibrium in a single patch. We assume that each brood emerges at nearly the same time (in comparison to their full lifecycle, perhaps separated by one year). Each brood suffers predation and reproduces independently. Because of these assumptions, there will be symmetric solutions where the population density of the majority and minority broods in each territory patch is the same in both patches. We do not attempt to find asymmetric solutions due to the complexity of the mathematics. Finally, we assume that dispersal of adults comes first and that predation and reproduction occur after dispersal. The order of dispersal compared to predation and reproduction do not make a significant difference.

We first note that the single-brood steady state in two patches is identical to the single-brood steady state in a single patch for any value of dispersal. The solution of Eq. (15) for the dimensionless adult population is given by

$$\tilde{\chi} = \frac{1}{2}\left(1+\sqrt{1-4\tilde{\kappa}}\right). \tag{19}$$

The solution exist only if $\tilde{\kappa} < 1/4$ and it is shown in Ref. Machta et al. (2019) that the solution is stable for all $\tilde{\kappa} < 1/4$. The cicada limit of existence of $\tilde{\kappa} = 1/4$ in the hybrid model with quadratic functional response then yields a limit of existence $\alpha \approx 0.087$, which is an overestimate. In Machta et al. (2019) it was shown that this failing is a result of the simplified functional response and that the hybrid model solved with the full functional response Eq. (8) yields an accurate estimate for the limit of existence.

For the two-brood, two-patch solution we assume a symmetric situation in which each brood is in the majority in its home patch and has the same dimensionless population density, $\tilde{\chi}$ in its home patch. Similarly the minority brood has the the same density, $\tilde{\psi}$ in each patch. Because of the symmetry assumption, we do not identify a region where a type 4 equilibrium might exist.

We begin by solving for the ratio of the minority to majority densities, $r = \tilde{\psi}/\tilde{\chi}$. In Section 3 of Machta et al. (2019) it was shown that, within the assumption of symmetric competition, the ratio of population densities of two competing broods does not change as the juveniles grow underground thus the ratio of emerging adults is the same as the ratio of the preceding first year juveniles, yielding a steady state equation for $r$,

$$r = \left(\frac{d\tilde{\chi}+(1-d)\tilde{\psi})}{(1-d)\tilde{\chi}+d\tilde{\psi}}\right)^2 \tag{20}$$

$$= \left(\frac{d+(1-d)r}{(1-d)+dr}\right)^2. \tag{21}$$

The numerator and denominator are, respectively, the number of juveniles in the minority and majority brood given the adult populations $\tilde{\psi}$ and $\tilde{\chi}$ whose ratio is $r$ before dispersal and reproduction. Dispersal yields the two terms in the numerator and denominator and reproduction explains the square. The second line follows from the definition, $r = \tilde{\psi}/\tilde{\chi}$. The relevant solution to this equation is,

$$r = \frac{2d^2-4d+1+(2d-1)\sqrt{1-4d}}{2d^2}. \tag{22}$$

The fact that the equation for $r$ depends only on dispersal is a feature of the simplified response. Qualitatively, the behavior of this solution is that $r = 0$ when $d = 0, r$ increases monotonically with $d$ and reaches one when $d = 1/4$. For $d > 1/4$ the solution is complex and not biologically relevant. The second solution is the inverse of this solution and refers to the equivalent situation that $\tilde{\chi}$ $(\tilde{\psi})$ is defined as the minority (majority) brood. The third solution has $r = 1$ for all $d$ and represents the unstable two-brood equilibrium that is also present in a one patch system (see Section 3 of Machta et al. (2019)).

To complete the solution of the two-patch, two-brood steady state we need to find the total population density in each patch, $\tilde{\tau} = \tilde{\chi}+\tilde{\psi}$. Since the entire population competes underground but reproduces separately, the steady state equation for $\tilde{\tau}$ take the form,

$$\left(\frac{1}{\tilde{\tau}}-1\right)^{-1} = \frac{(d\tilde{\chi}+(1-d)\tilde{\psi})^2}{\tilde{\kappa}} + \frac{((1-d)\tilde{\chi}+d\tilde{\psi})^2}{\tilde{\kappa}}. \tag{23}$$

After some algebra that combines the fact that $\tilde{\chi} = \tilde{\tau}/(1+r)$ and $\tilde{\psi} = r\tilde{\tau}/(1+r)$, and the solution for $r$ as a function of $d$ we can simplify this equation to,

$$\left(\frac{1}{\tilde{\tau}}-1\right)^{-1} = \frac{(1-2d)}{\tilde{\kappa}}\tilde{\tau}^2, \tag{24}$$

whose solution is the same as the solution, Eq. (19) for the single-territory, single-brood steady state except that $\tilde{\kappa}$ is increased by dispersal to the value $\tilde{\kappa}/(1-2d)$. The region where the two patch, two-brood, solution exists then satisfies the two requirements that $\tilde{\kappa} < (1-2d)/4$ and $d < 1/4$. For small $d$, the initial linear segment of the upper boundary of region 2 in Fig. 11 nearly follows this existence line but increasingly deviates below it because the solution loses linear stability before it ceases to exist.

To determine the region of existence and stability of the two-brood solution we must investigate the linearized map for the four variable system, $\tilde{\chi}_a, \tilde{\psi}_a, \tilde{\chi}_b, \tilde{\psi}_b$ where, as before, $\tilde{\chi}$ and $\tilde{\psi}$ refer to the minority and majority brood sizes, respectively, and the subscripts $a$ and $b$ label the patch.

The largest eigenvalue of the linearized map can be found analytically but is a quite complex algebraic expression that was obtained using Mathematica. The curve in the figure separating regions 3 + 5 and 2 + 3 + 5 was found numerically by solving for the values of $\tilde{\kappa}$ and $d$ where the largest eigenvalue is equal to one. Within region 2 + 3 + 5 this eigenvalue is less than one and the symmetric two-patch, two-brood solution is linearly stable. The Mathematica notebook that implements the calculation can be found in the supplement.

The simplified functional response is valid when $A_{\text{half}} \gg x_e$. As competition decreases, the population density increases and eventually becomes larger than $A_{\text{half}}$. In the limit of very weak competition, the inequality is reversed, $A_{\text{half}} \ll x_e$. In this limit predators are satiated after consuming only a tiny fraction of the population and there is effectively no functional response so that $R(x_e) \to m$. In this limit, it is again straightforward to calculate the population densities of the two-patch, two-brood equilibrium and, in particular, the equation for the ratio, $r$ of the sizes of the minority and majority broods in each patch is now given by

$$r = \left( \frac{d\tilde{\chi} + (1-d)\tilde{\psi})}{(1-d)\tilde{\chi} + d\tilde{\psi}} \right) \tag{25}$$

$$= \left( \frac{d + (1-d)r}{(1-d) + dr} \right). \tag{26}$$

This equation is almost identical to Eq. 21 except for the absence of the square. This difference results from the fact that the reproduction is now linear rather than quadratic in the limit of weak competition. This equation reduces to $r^2 = 1$ and the relevant solution is $r = 1$, which, together with the symmetry assumptions about the equilibrium, implies that each brood is the same size in both patches. However, since each brood has the same population density in each patch, this equilibrium is identical to the two-brood equilibrium in a single patch, which has been shown to be unstable in Ref. Machta et al. (2019). Thus, for sufficiently weak competition, there can be no stable two-brood equilibrium.

## References


Peterson, A.T., 2003. Predicting the geography of species' invasions via ecological Niche modeling. Q. Rev. Biol. 78 (4), 419–433.

Morin, X., Augspurger, C., Chuine, I., 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries?. Ecology 88 (9), 2280–2291.

Thomas, C.D., 2010. Climate, climate change and range boundaries. Divers. Distrib. 16 (3), 488–495.

Holt, R.D., 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proc. Nat. Acad. Sci. 106 (Suppl. 2), 19659–19665.

Roux, P.C.L., Virtanen, R., Heikkinen, R.K., Luoto, M., 2012. Biotic interactions affect the elevational ranges of high?Latitude plant species. Ecography 35 (11), 1048–1056.

Unnamed Observer, 1667. Some observations of swarms of strange insects, and the mischiefs done by them. Philos. Trans. Roy. Soc. 1 (8), 137–138.

Marlatt, C.L., 1907. The periodical cicada. U.S. Dep. Agric. Bur. Entomol. Bull. 71, 1–181.

Snodgrass, R.E., 1919. The "17-year locust" in 1919. U.S. Dep. Agric. Circ. 127, 1–10.

Case, T.J., Taper, M.L., 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. Am. Nat. 155, 583–605.

Marlatt, C.L., 1898. The periodical cicada. U.S. Dep. Agric. Div. Entomol. Bull. 14, 1–148.

Cooley, J.R., Kritsky, G., Marshall, D.C., Hill, K.B.R., Bunker, G., Neckermann, M.L., Yoshimura, J.I.N., Cooley, J.E., Simon, C., 2007. A GIS-based map of periodical cicada brood XIII in 2007, with notes on adjacent populations of broods III and X (Hemiptera: Magicicada spp.). Bull. Entomol. Soc. Am. 62, 241–246.

Williams, K.S., Simon, C., 1995. The ecology, behavior, and evolution of periodical cicadas. Annu. Rev. Entomol. 40, 269–295.

Karban, R., 1982. Increased reproductive success at high densities and predator satiation for periodical cicadas. Ecology 63, 321–328.

Koenig, W.D., Liebhold, A.M., 2013. Avian predation pressure as a potential driver of periodical cicada cycle length. Am. Naturalist 181, 145–149.

Cooley, J., Kritsky, G., Edwards, M., Zyla, J., Marshall, D., Hill, K., Krauss, R., Simon, C., 2009. The distribution of periodical cicada. Am. Entomol. 55, 106–112.

Karban, 1984. Opposite density effects of nymphal and adult mortality for periodical cicadas. Ecology 65, 1656–1661.

Karban, 1997. Evolution of prolonged development: a life table analysis for periodical cicadas. Am. Naturalist 150, 446–461.

Heath, J.E., 1968. Thermal synchronization of emergence in periodical "17-year" cicadas (Homoptera, Cicadidae, Magicicada). Am. Midl. Nat. 80, 440–448.

Lloyd, M., White, J.A., 1976. Sympatry of periodical cicada broods and the hypothetical four-year acceleration. Evolution 30, 786–801.

White, J., Lloyd, M., 1979. 17-year cicadas emerging after 18 years: a new brood?. Evolution 33, 1193–1199.

White, J., Lloyd, M., Zar, J.H., 1979. Faulty eclosion in crowded suburban periodical cicadas: populations out of control. Ecology 60, 305–315.

Blackwood, J.C., Machta, J., Meyer, A.D., Noble, A.E., Hastings, A., Liebhold, A.M., 2018. Competition and stragglers as mediators of developmental synchrony in periodical cicadas. Am. Natrualist 192 (4), 479–489.

Machta, J., Blackwood, J.C., Noble, A.E., Liebhold, A.M., Hastings, A., 2019. Hybrid model for the population dynamics of periodical cicadas. Bull. Math. Biol. 81, 1122–1142.

Forsythe Jr., H.Y., 1976. Distribution and species of 17-year cicadas in broods V and VIII in Ohio. Ohio J. Sci. 76, 254–258.

Karlin, S., McGregor, J., 1972. Polymorphisms for genetic and ecological systems with weak coupling. Theor. Popul. Biol. 3, 210–238.

Lehmann-Ziebarth, N., Heideman, P.P., Shapiro, R.A., Stoddart, S.L., Hsiao, C.C.L., Stephenson, G.R., Milewski, P.A., Ives, A.R., 2005. Evolution of periodicity in periodical cicadas. Ecology 86, 3200–3211.

Tanaka, Y., Yoshimura, J., Simon, C., Cooley, J.R., Tainaka, K.I., 2009. Allee effect in the selection for prime-numbered cycles in periodical cicadas. Proc. Nat. Acad. Sci. 106, 8975–8979.

Keitt, T.H., Lewis, M.A., Holt, R.D., 2001. Allee effects, invasion pinning, and species' borders. Am. Nat. 157, 203–216.

Clerc, M.G., Escaff, D., Kenkre, V.M., 2010. Analytical studies of fronts, colonies, and patterns: combination of the Allee effect and nonlocal competition interactions. Phys. Rev. E 82, 036210.