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Authors

Arroyo-Esquivel, Jorge

Hastings, Alan

Baskett, Marissa L

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Jorge Arroyo-Esquivel (✉ jarroyoe@ucdavis.edu)

University of California-Davis <https://orcid.org/0000-0003-4399-954X>

Alan Hastings

University of California Davis

Marissa L. Baskett

University of California Davis

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Local interactions affect spread of resource in a consumer-resource system with group defense

Jorge Arroyo-Esquivel¹, Alan Hastings², and Marissa L. Baskett²

¹ *Department of Mathematics, University of California Davis*

² *Department of Environmental Science and Policy, University of California Davis*

Abstract

Integrodifference equations are a discrete time spatially explicit model that describes dispersal of ecological populations through space. This framework is useful to study spread dynamics of organisms and how ecological interactions can affect their spread. When studying interactions such as consumption, dispersal rates might vary with life cycle stage, such as cases with dispersive juveniles and sessile adults. In the non-dispersive stage, resources may engage in group defense to protect themselves from consumption. These local nondispersive interactions may limit the number of dispersing recruits that are produced and therefore affect how fast populations can spread.

We present a spatial consumer-resource system using an integrodifference framework with limited movement of their adult stages and group defense mechanisms in the resource population. We model group defense using a Type IV Holling functional response, which limits survival of adult resource population and enhances juvenile consumers production. We find that high mortality levels for sessile adults can destabilize resource at carrying capacity. Furthermore, we find that at high resource densities, group defense leads to a slower local growth of resource in newly invaded regions due to intraspecific competition outweighing the effect of consumption on resource growth.

Keywords: consumer-resource, integrodifference equations, group defense, nondispersing, life stages

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9 on previous versions of the manuscript. All authors read and approved the
10 final manuscript.

11 1. Introduction

12 Integrodifference equations (IDEs) are a modelling framework that de-
13 scribes a population density in continuous space and discrete time by ex-
14 ploring the growth and dispersal processes separately [20]. They have been
15 successfully used to study the spread dynamics of annual plants [4], popula-
16 tions in a river system [24], and populations with moving habitats [34]. This
17 approach have also been expanded to consider population interactions such
18 as consumption [27], parasitism [9], and competition [23].

19 In a variety of organisms such as perennial plants, echinoderms [7, 31],
20 and colonial insects [14], dispersal happens at some stages in their life history,
21 with other stages being more sessile. The IDE framework can be expanded
22 to consider these dynamics by explicitly adding a non-dispersing stage of a
23 population. Such IDE models find that local interactions of these organisms
24 may limit the number of dispersing recruits that are produced, which may
25 lead to a slower spread rate. For example, [9] and [25] found that parasitism of
26 more sessile stages destabilize the spatial distribution of the entire population
27 and reduce the spread rate. In a model of competition of different green crab
28 genotypes [16], an increased sessile adult survival of the entire population
29 leads to an increased spread rate of the top competitor and a decrease in
30 the spread rate of the lower competitor. However, this dynamic has not
31 been previously included in consumer-resource systems, which includes both
32 herbivore-plant and predator-prey interactions.

33 When considering consumer-resource dynamics in organisms with limited
34 movement, group defense mechanisms may allow resource to become more
35 resistant to consumption. These group defense mechanisms reduce consump-
36 tion intensity as resource density increases [11]. This behavior occurs in var-
37 ious taxa where adults have limited movement. For example, bees produce
38 social waves that repel predators [18], and kelp provide habitat for predators
39 of their grazers, which induces cryptic behavior in grazers with subsistence

40 off of kelp detritus rather than active grazing [17]. A previous model with-
 41 out stage-dependent dispersal considered the spatial dynamics of a resource
 42 using group defense [33], where they found oscillatory spatial distributions
 43 at high initial resource densities caused by group defense. The potential
 44 for group defense to qualitatively affect dynamical outcomes of interacting
 45 species raises the question of how group defense in a sessile stage might affect
 46 overall spread given dispersive juveniles.

47 In this paper we present and analyze an IDE model of the spatiotemporal
 48 dynamics of a consumer-resource system where adults have limited movement
 49 and resource present group defense. In Section 2 we introduce the model,
 50 which is based on the ideas presented by [16], and provide a nondimensional
 51 version which we will analyze. In Section 3 we analyze two features of the
 52 spatiotemporal dynamics: the dispersal induced instabilities of the resource-
 53 only system and the spread rate of resource. Finally in Section 4 we discuss
 54 how these results lead to a further understanding of how local interactions
 55 affect the spread of organisms.

56 2. Model

57 In this section we extend an integrodifference model to consider motile,
 58 dispersing juveniles and the local interactions between sessile adult stages. A
 59 similar extension was previously considered in [16] and a formal construction
 60 of this model is analogous to that in [6]. Consider a region in space denoted
 61 by Ω . At each time step m and point in space $x \in \Omega$, our model follows
 62 populations densities of consumer $P_m(x)$ and resource $N_m(x)$ populations at
 63 reproductive age (hereafter adults).

64 For each population $i = P, N$, at each time step m a fraction δ_i of the
 65 adult population survives to the next time step in absence of consumption.
 66 consumers consume adult resource following a unimodal, Type IV Holling
 67 functional response [5]. This functional form models group defense of resource
 68 with lower consumption strength at high resource density. Let γ_N be the
 69 attack intensity of the consumer and $1/\sqrt{\sigma_N}$ the density of resource at which
 70 consumption intensity is the highest.

71 Juveniles of both populations disperse following a kernel $k_i(x, y)$ for $i =$
 72 P, N , and a fraction of those juveniles survive and become adults at the
 73 next time step. Consumers produce juveniles that survive to become adults
 74 proportional to their consumption intensity with a factor γ_P . Resources
 75 produce juveniles by a constant factor R , where $R > 1 - \delta_N$ for population

76 persistence. The fraction of newly-setting resource juveniles that survive to
 77 become adults depends on local consumer and resource densities. Consumers
 78 consume settling resources with a constant intensity γ_S . Local resources
 79 further limits resource settlement through intraspecific competition with a
 80 carrying capacity proportional to $1/\beta$.

81 These assumptions lead to the system of equations:

$$\begin{aligned}
 P_{m+1}(x) &= \delta_P P_m(x) + \gamma_P \int_{\Omega} k_P(x, y) \frac{P_m(y) N_m(y)}{1 + \sigma_N N_m(y)^2} dy, \\
 N_{m+1}(x) &= \delta_N N_m(x) \exp\left(-\frac{\gamma_N P_m(x)}{1 + \sigma_N N_m^2(x)}\right) \\
 &\quad + R \frac{\exp(-\gamma_S P_m(x))}{1 + \beta N_m(x)} \int_{\Omega} k_N(x, y) N_m(y) dy.
 \end{aligned} \tag{1}$$

82 To simplify our analysis, we first nondimensionalize the model. We use the
 83 same nondimensionalization than in [6]. For each m , let $p_m = \gamma_S P_m$, $n_m =$
 84 βN_m . Then, if $\gamma_p = \gamma_P/\beta$, $\gamma_n = \gamma_N/\gamma_S$, $\sigma = \sigma_N/\beta^2$, our nondimensional
 85 version of the model is

$$\begin{aligned}
 p_{m+1}(x) &= \delta_p p_m(x) + \gamma_p \int_{\Omega} k_p(x, y) \frac{p_m(y) n_m(y)}{1 + \sigma n_m(y)^2} dy, \\
 n_{m+1}(x) &= \delta_n n_m(x) \exp\left(-\frac{\gamma_n p_m(x)}{1 + \sigma n_m^2(x)}\right) \\
 &\quad + R \frac{\exp(-p_m(x))}{1 + n_m(x)} \int_{\Omega} k_n(x, y) n_m(y) dy.
 \end{aligned} \tag{2}$$

86 Note that we have also changed the indices of δ_i and k_i in order to preserve
 87 clarity.

88 3. Results

89 3.1. Overview of nonspatial results

90 In [6] we study the dynamics of the nonspatial version of Model 2 given
 91 by the system:

$$\begin{aligned}
p_{m+1} &= \delta_p p_m + \gamma_p \frac{p_m n_m}{1 + \sigma n_m^2}, \\
n_{m+1} &= \delta_n n_m \exp\left(-\frac{\gamma_n p_m}{1 + \sigma n_m^2}\right) + R \frac{\exp(-p_m)}{1 + n_m} n_m.
\end{aligned} \tag{3}$$

92 Here we summarize our main findings relevant to the analysis of the rest
93 of this paper. Model 3 has four fixed points: an unstable extinction fixed
94 point $(0, 0)$, a resource-only fixed point $(0, n^*)$ where n^* is

$$n^* = \frac{R}{1 - \delta_n} - 1, \tag{4}$$

95 and, when $\sigma \neq 0$, two coexistence fixed points (p^\wedge, n^\wedge) and (p^\vee, n^\vee) . The
96 lower coexistence fixed point (p^\vee, n^\vee) is always unstable, whereas the positive
97 coexistence point (p^\wedge, n^\wedge) exchanges stability with the resource-only point
98 $(0, n^*)$ at the bifurcation value for γ_p :

$$\gamma_p^* = (1 - \delta_p) \frac{1 + \sigma n^{*2}}{n^*}. \tag{5}$$

99 The resource-only fixed point is stable when consumer conversion inten-
100 sity is under a given threshold γ_p^* (i.e. $\gamma_p < \gamma_p^*$) and unstable otherwise. In
101 addition, the positive coexistence fixed point becomes biologically infeasible
102 as it becomes stable as p^\wedge becomes negative. We can thus say that the posi-
103 tive coexistence fixed point is unstable whenever it is biologically feasible.

104 In the case the resource-only equilibrium is stable (when $\gamma_p < \gamma_p^*$), this
105 stability is global, i.e. all trajectories converge to the equilibrium. In the
106 case there are no stable fixed points (when $\gamma_p > \gamma_p^*$), the system converges
107 globally to a quasiperiodic consumer-resource cycle.

108 3.2. Dispersal-induced instabilities

109 In this section we explore how dispersal affects the stability of the consumer-
110 resource dynamics by analyzing Model 2. Dispersal can induce instabilities
111 in stable population densities, a mechanism first observed by [30] and fur-
112 ther analyzed by [22]. In the case of IDEs, this mechanism can be analyzed
113 following the linearization process of [27]. We can write Model 2 in the same
114 form as the model presented in [16]:

$$\begin{aligned}
p_{m+1}(x) &= P_p(p_m(x), n_m(x)) + S_p(p_m(x), n_m(x)) \int_{\Omega} k_p(x, y) R_p(p_m(y), n_m(y)) dy, \\
n_{m+1}(x) &= P_n(p_m(x), n_m(x)) + S_n(p_m(x), n_m(x)) \int_{\Omega} k_n(x, y) R_n(p_m(y), n_m(y)) dy.
\end{aligned} \tag{6}$$

115 In addition, we will assume that dispersing juveniles do not die or escape
116 the habitat during the dispersal process, i.e.

$$\int_{\Omega} k_i(x, y) dy = 1$$

117 for both $i = p, n$. Using this assumption, we linearize the system near a
118 stable equilibrium as follows. Let (\bar{p}, \bar{n}) be a stable equilibrium of System 3,
119 then if $p_m = \bar{p} + \xi_m, n_m = \bar{n} + \eta_m$, where (ξ_m, η_m) is a small perturbation
120 around \bar{p} , we linearize the first equation of System 6 as

$$\begin{aligned}
\bar{p} + \xi_{m+1} &= P_p(\bar{p}, \bar{n}) + \left(\frac{\partial P_p}{\partial p_m} \xi_m + \frac{\partial P_p}{\partial n_m} \eta_m \right) \\
&+ \left(S_p(\bar{p}, \bar{n}) + \left(\frac{\partial S_p}{\partial p_m} \xi_m + \frac{\partial S_p}{\partial n_m} \eta_m \right) \right) \int_{\Omega} k_p(x, y) \left(R_p(\bar{p}, \bar{n}) + \left(\frac{\partial R_p}{\partial p_m} \xi_m + \frac{\partial R_p}{\partial n_m} \eta_m \right) \right) dy.
\end{aligned}$$

121 Multiplying the terms around the integral, and disregarding higher order
122 terms yields

$$\begin{aligned}
\xi_{m+1} &= \left(\left(\frac{\partial P_p}{\partial p_m} + R_p(\bar{p}, \bar{n}) \frac{\partial S_p}{\partial p_m} \right) \xi_m + \left(\frac{\partial P_p}{\partial n_m} + R_p(\bar{p}, \bar{n}) \frac{\partial S_p}{\partial n_m} \right) \eta_m \right) \\
&+ \int_{\Omega} k(x, y) S_p(\bar{p}, \bar{n}) \left(\frac{\partial R_p}{\partial p_m} \xi_m + \frac{\partial R_p}{\partial n_m} \eta_m \right) dy
\end{aligned}$$

123 and a similar equation for η_{m+1} . Then, given $J(F)$ as the Jacobian matrix of
124 a given function F evaluated at (\bar{p}, \bar{n}) , our linearized system, in matrix form,
125 is

$$\begin{aligned}
\begin{pmatrix} \xi_{m+1}(x) \\ \eta_{m+1}(x) \end{pmatrix} &= J \begin{pmatrix} P_p + R_p(\bar{p}, \bar{n}) S_p \\ P_n + R_n(\bar{p}, \bar{n}) S_n \end{pmatrix} \begin{pmatrix} \xi_m(x) \\ \eta_m(x) \end{pmatrix} \\
&+ \int_{\Omega} K(x, y) J \begin{pmatrix} S_p(\bar{p}, \bar{n}) R_p \\ S_n(\bar{p}, \bar{n}) R_n \end{pmatrix} \begin{pmatrix} \xi_m(y) \\ \eta_m(y) \end{pmatrix} dy
\end{aligned} \tag{7}$$

126 where $K(x, y) = \text{diag}(k_p(x, y), k_n(x, y))$ and the integral represents rowwise
 127 integration. To study how dispersal leads to instabilities in the system, let
 128 $\gamma_p < \gamma_p^*$ and $(\bar{p}, \bar{n}) = (0, n^*)$. Then, the linearized system (Equation 7 is

$$\begin{aligned} \xi_{m+1}(x) &= \delta_p \xi_m(x) + \int_{\Omega} k_p(x, y) \frac{\gamma_p n^*}{1 + \sigma n^{*2}} \xi_m(y) dy, \\ \eta_{m+1}(x) &= - \left(\frac{\delta_n \gamma_n}{1 + \sigma n^{*2}} + \frac{R}{1 + n^*} \right) n^* \xi_m(x) + \left(\delta_n - \frac{R n^*}{(1 + n^*)^2} \right) \eta_m(x) \\ &\quad + \int_{\Omega} k_n(x, y) \frac{R \eta_m(y)}{1 + n^*} dy. \end{aligned} \quad (8)$$

129 We then take the Fourier transform of Equation 8. Doing this, our system
 130 simplifies to

$$\begin{pmatrix} \hat{\xi}_{m+1}(\omega) \\ \hat{\eta}_{m+1}(\omega) \end{pmatrix} = (\mathbf{A} + \mathbf{KJ}) \begin{pmatrix} \hat{\xi}_m(\omega) \\ \hat{\eta}_m(\omega) \end{pmatrix} \quad (9)$$

131 where \hat{f} corresponds to the Fourier transform of a given function f , i.e.

$$\hat{f}(\omega) = \int_{-\infty}^{\infty} \exp(i\omega x) f(x) dx, \quad (10)$$

132 and the matrices $\mathbf{A}, \mathbf{K}, \mathbf{J}$ satisfy

$$\begin{aligned} \mathbf{A} &= \begin{pmatrix} \delta_p & 0 \\ - \left(\frac{\delta_n \gamma_n}{1 + \sigma n^{*2}} + \frac{R}{1 + n^*} \right) n^* & \delta_n - \frac{R n^*}{(1 + n^*)^2} \end{pmatrix} \\ \mathbf{K} &= \begin{pmatrix} \hat{k}_p(\omega) & 0 \\ 0 & \hat{k}_n(\omega) \end{pmatrix} \\ \mathbf{J} &= \begin{pmatrix} \frac{\gamma_p n^*}{1 + \sigma n^{*2}} & 0 \\ 0 & \frac{R}{1 + n^*} \end{pmatrix}. \end{aligned} \quad (11)$$

133 Decay of $\hat{\xi}_m(\omega)$ and $\hat{\eta}_m(\omega)$ for all ω guarantees the decay of $\xi_m(x)$ and
 134 $\eta_m(x)$, which would imply stability of the carrying capacity equilibrium. The
 135 matrix $\mathbf{A} + \mathbf{KJ}$ has a triangular form, and thus the eigenvalues are

$$\begin{aligned} \lambda_1 &= \delta_p + \hat{k}_p(\omega) \frac{\gamma_p n^*}{1 + \sigma n^{*2}}, \\ \lambda_2 &= \delta_n - \frac{R n^*}{(1 + n^*)^2} + \hat{k}_n(\omega) \frac{R}{1 + n^*}. \end{aligned} \quad (12)$$

136 If both populations disperse following a Laplace kernel:

$$k_i(x - y) = \frac{a_i}{2} \exp(-a_i|x - y|) \quad (13)$$

137 for $i = p, n$, then the Fourier transform of these kernels is

$$\hat{k}_i(\omega) = \frac{a_i^2}{a_i^2 + \omega^2}. \quad (14)$$

138 Note that $\hat{k}_i(\omega) \geq 0$ for all ω , which implies that if $\gamma_p < \gamma_p^*$, then $0 <$
 139 $\lambda_1 < 1$ for all ω . For λ_2 , for any $R, \delta_n > 0$, the inequality $\lambda_2 < -1$ does not
 140 have a real solution. This implies that dispersal of a Laplace kernel will not
 141 induce instabilities in a resource-only state.

142 If we choose instead a double-gamma distribution:

$$k_i(x - y) = \frac{a_i^2}{2} |x - y| \exp(-a_i|x - y|) \quad (15)$$

143 for $i = p, n$, then their Fourier transform is

$$\hat{k}_i(\omega) = \frac{a_i^2(a_i^2 - \omega^2)}{(a_i^2 + \omega^2)^2}. \quad (16)$$

144 Equation 16 has a global minimum of $-\frac{1}{8}$. If $\hat{k}_p(\omega) = \frac{-1}{8}$, then we find
 145 that $\lambda_1 < -1$ is satisfied when

$$\gamma_p > \frac{8(1 + \delta_p)(1 + \sigma n^{*2})}{n^*} > \gamma_p^*$$

146 which implies that $\lambda_1 > -1$ for $\gamma_p < \gamma_p^*$. If $\hat{k}_n(\omega) = \frac{-1}{8}$, then the expression
 147 $\lambda_2 < -1$ has a solution whenever

$$R > (1 - \delta_n) \left(\frac{9}{8} - \frac{1 + \delta_n}{1 - \delta_n} \right)^{-1}$$

148 provided that $\frac{9}{8} - \frac{1 + \delta_n}{1 - \delta_n} > 0$. This last inequality occurs only for $\delta_n < \frac{1}{17}$,
 149 and thus instabilities will only be caused by dispersal for high local resource
 150 mortalities. We can compare that, at low local mortalities of resource, the
 151 eigenvalue λ_2 is almost unchanged as the frequency ω changes (Figure 1a),
 152 whereas at high local mortalities, the eigenvalue has a wider range of change
 153 and crosses the -1 line (Figure 1b). This suggests that dispersal of resource

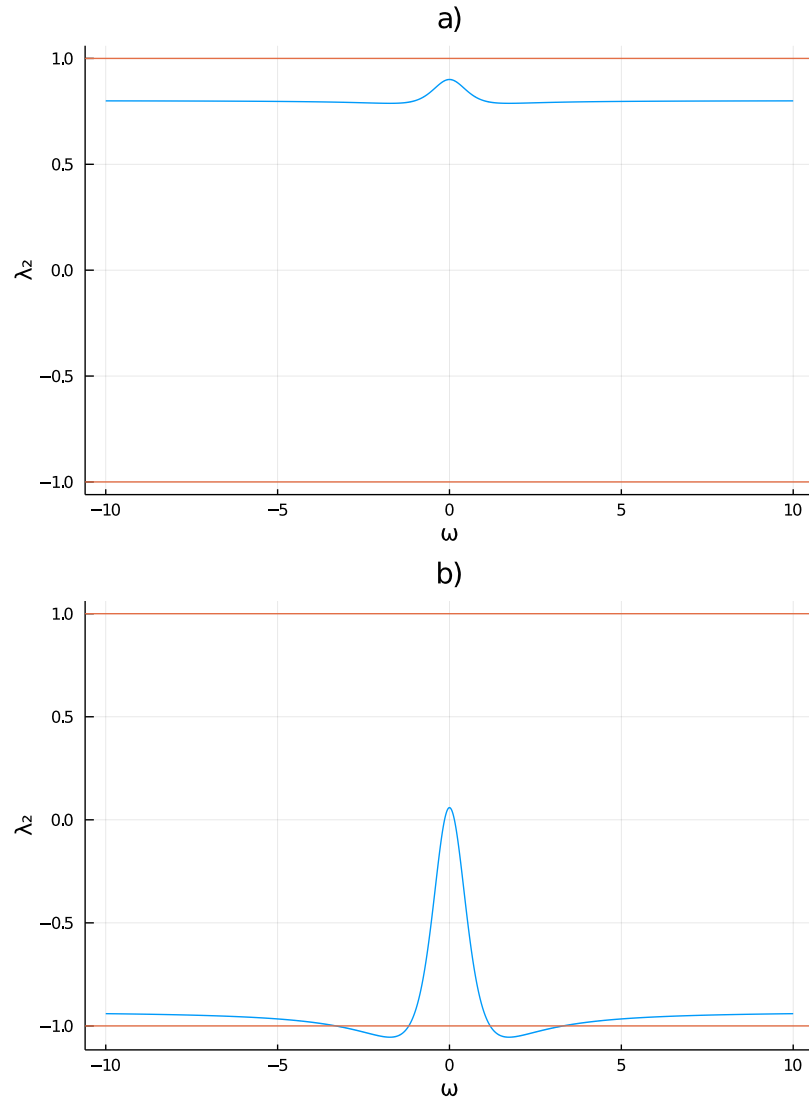


Figure 1: Values of λ_2 in Equation 12 as the Fourier transform frequency ω varies, when k_n follows the double-gamma distribution kernel (Equation 15). In these figures we use $R = 20$, and $a_n = 1$ with two values for resource adult survival: **a)** $\delta_n = 0.9$, and **b)** $\delta_n = 0.01$.

154 does not affect its stability when most of the reproductive adults can survive
155 more than one time step.

156 The spatial pattern formation presented by these dynamics is in Figure
157 2. Even in the presence of instabilities caused by dispersal of resources,
158 consumers are not able to invade. This shows that although resource density
159 is varying, a low consumer conversion rate ($\gamma_p < \gamma_p^*$) makes it impossible for
160 consumers to invade and have any influence over the resource population,
161 making this system essentially a resource-only system.

162 3.3. Spread rate of resource

163 In a general integrodifference framework, the spread rate of a population
164 is calculated by analyzing when the extinction equilibrium of the travelling
165 wave solution of the system becomes unstable [35]. This also works in the
166 case of a single-population dynamics system with sessile stages [10]. In the
167 case of System 2, the extinction equilibrium of resource is always unstable,
168 which implies that the resource is always able to invade when rare. Instead
169 of explicitly calculating the spread rate, we numerically estimate the time
170 it takes for the population to reach a specific population density at a given
171 point in space.

172 To do this, let $\Omega = [-L/2, L/2]$ for habitat length L . In addition, let the
173 initial conditions be a constant consumer density p_0 (i.e. $p_0(x) = p_0$) and
174 the resource at carrying capacity at a single point at 20% of the length of
175 the habitat (i.e. $n_0(x) = n^*\delta(x - a)$, where $\delta(x)$ is the Kronecker delta, and
176 a is the point that represents 20% of the length of Ω). We then calculate
177 the time it takes for the resource to reach a population density of 80% its
178 carrying capacity at 80% of the habitat length, i.e. we find the time M that
179 satisfies

$$M = \min_m \{n_m(b) = 0.8n^*\} \quad (17)$$

180 where b is the point that represents the 80% of the length of the habitat.
181 An example of this procedure is in Figure 3. In this case $M = 28$. We then
182 explore how does changing different parameters of the model makes these
183 transient times vary.

184 The results of these numerical experiments are in Figure 4. Intuitively,
185 as more consumers are present in the environment (higher initial consumer
186 density p_0 (a), consumer survival δ_p (b) and dispersal a_p (d)), the time to
187 spread increases, and that, as more resource juveniles are produced (higher

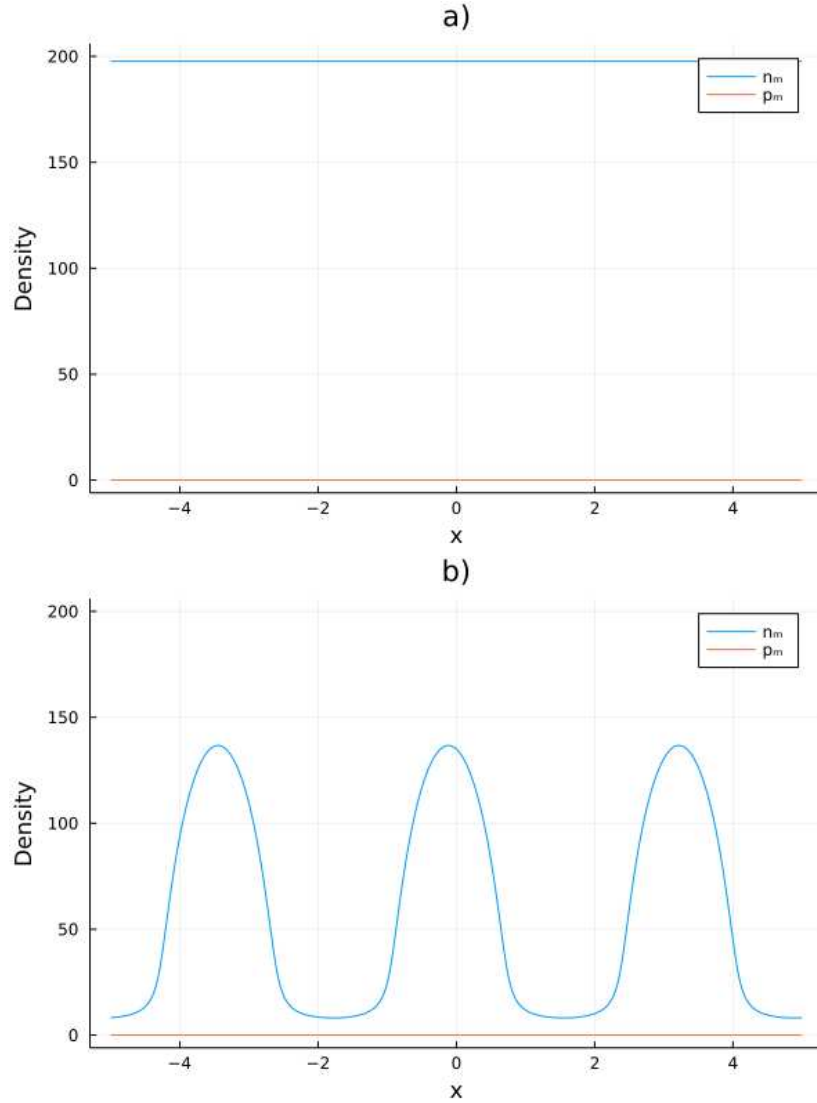


Figure 2: Distributions of consumers $p_t(x)$ and resources $n_t(x)$ after 1000 time steps with an initial distribution being a random perturbation of the uniform distributions $p_0(x) = 0$ and $n_0(x) = n^*$. In these simulations we use a double-gamma kernel (Equation 15) with $a_n = 1$ and $a_p = 5$. The other parameters of the model are $\delta_p = 0.8$, $\gamma_N = 0.1$, $\sigma = 1$, $R = 20$, $\gamma_p = 0.7$, and γ_p^* with two values for prey adult survival: **a)** $\delta_n = 0.9$ and **b)** $\delta_n = 0.01$.

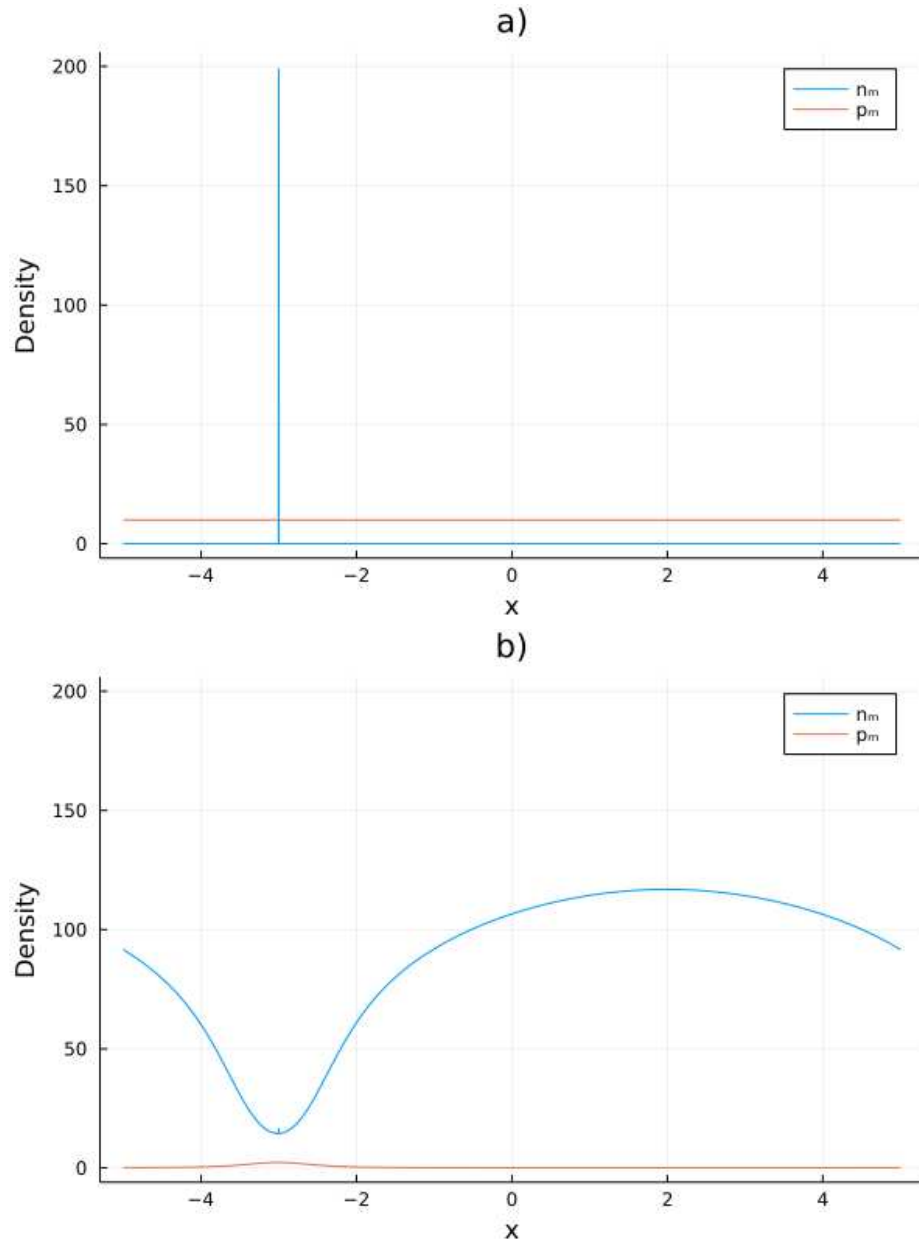


Figure 3: Distributions of consumers $p_t(x)$ and resources $n_t(x)$ at **a)** initial setup described in Section 3.3, and **b)** after 30 time steps. In these simulations we use a Laplace kernel (Equation 13) with $a_n = 1$ and $a_p = 5$. The other parameters of the model are $L = 10$, $\delta_p = 0.8$, $\gamma_N = 0.1$, $\sigma = 1$, $R = 20$, $\gamma_p = 0.7\gamma_p^*$, and $\delta_n = 0.9$.

188 R (h)) and disperse further (higher a_n (i)), the time to spread decreases.
189 More surprisingly, increasing adult resource survival (higher δ_n (f)) or group
190 defense intensity (higher σ (e)) leads to a longer time to spread, increasing
191 the attack intensity (γ_n (g)) does not have an impact over the time it takes
192 to spread, and consumer conversion intensity (γ_p (c)) has a minimal impact,
193 even after crossing the bifurcation value γ_p^* .

194 To explain these results, note that a higher adult resource survival δ_n
195 leads to a higher value of n^* in Equation 4. This higher value of n^* takes
196 longer to be reached, thus making the conditions of Equation 17 take longer
197 to be satisfied. For increasing group defense intensity σ , albeit having a
198 smaller but potentially counter-intuitive impact, arises from the fact that,
199 as σ increases, consumption intensity reaches its peak at a lower resource
200 density. This causes intraspecific competition at a local scale to play a bigger
201 role as a limiting factor of resource growth at lower densities, thus slowing
202 down the spread process. Analogously, attack intensity might not have an
203 impact over the time to spread because group defense makes consumption
204 less important at high resource densities, which means the source population
205 at the left of the habitat is not impacted by consumption and allows to source
206 new juveniles that will eventually overcome consumption at a similar density.
207 A similar argument explains the low impact of consumer conversion intensity
208 γ_p over the spread time.

209 4. Discussion

210 In this paper we explored how local interactions of sessile organisms in
211 a consumer-resource system affect the spread rate of resource. Two main
212 results arise from this exploration: sessile resource adults stabilize the spatial
213 distribution of resource, and group defense leads to a slower spread rate.

214 We find that, when the consumers cannot invade the resource, and when
215 most adults survive to the next reproduction period (high δ_n), these sessile
216 adults stabilize the distribution of resource and prevent the resource carrying
217 capacity to be destabilized by dispersal. This destabilization required a fat-
218 tailed kernel, which leads to accelerated invasions [19]. These stability results
219 also provide more evidence to the argument that increased dispersal leads to
220 a negative correlation between spatial stability and synchrony in population
221 densities between patches [1].

222 In the case of resource spread when rare, we found a higher group defense
223 (σ) leads to a higher time to reach carrying capacity at the other end of

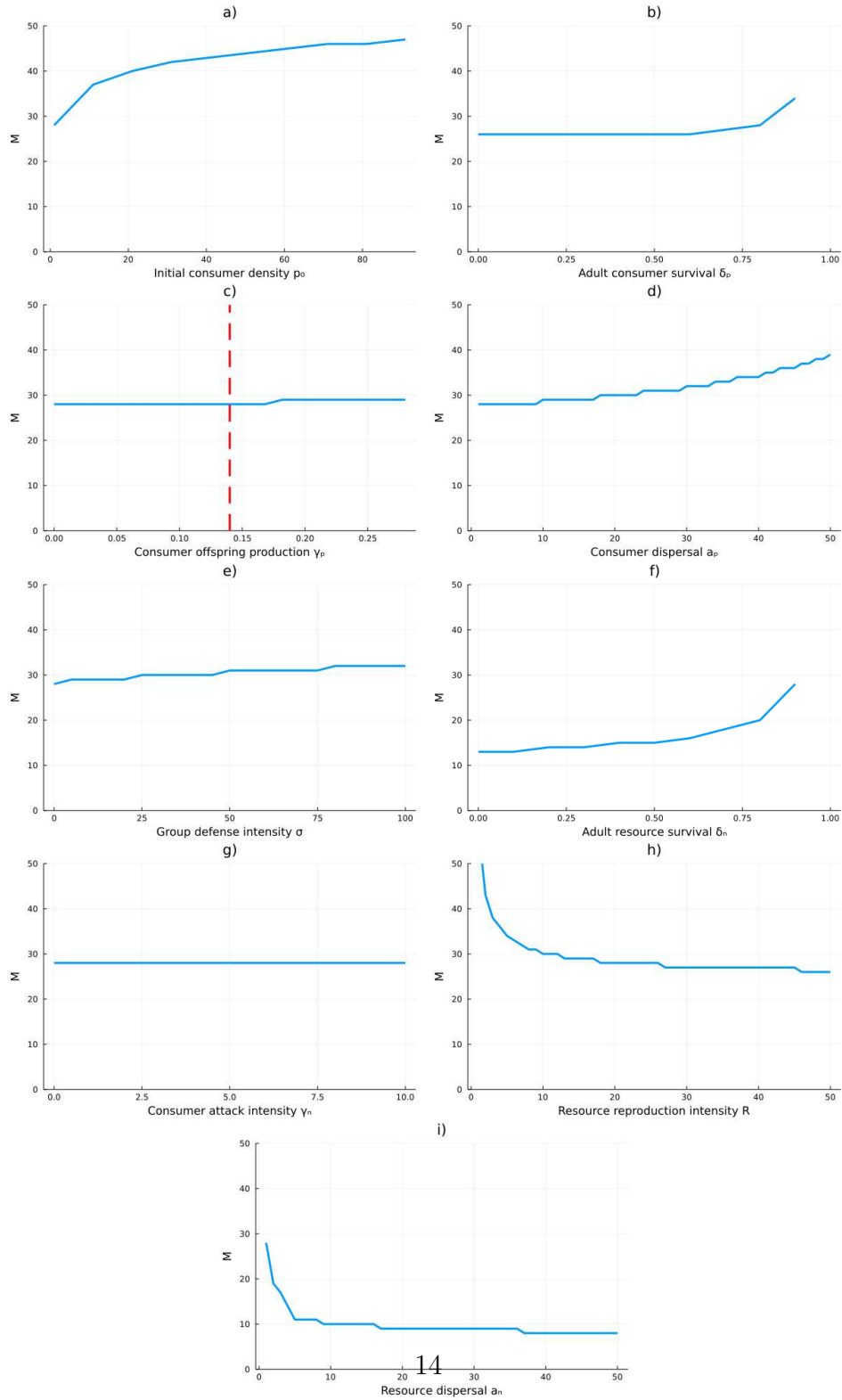


Figure 4: Number of time steps M required for the population to reach 80% of its carrying capacity at 80% of the habitat Ω (Equation 17). Unless it's the parameter being changed, in these simulations we use a Laplace kernel (Equation 13) with $a_n = 1$ and $a_p = 5$. The other parameters of the model are $L = 10$, $\delta_p = 0.8$, $\gamma_N = 0.1$, $\sigma = 1$, $R = 20$, $\gamma_p = 0.7\gamma_p^*$, and $\delta_n = 0.9$. In the figure where γ_p varies, the red vertical dashed line represents $\gamma_p = \gamma_p^*$.

224 a habitat. One explanation for this trend is a greater role of intraspecific
225 competition at lower consumption intensity compared to a higher intensity.
226 Previous empirical studies have found that at low consumption intensities,
227 intraspecific competition can have a bigger impact on juvenile survival [26?
228] and spread [?]. However, none of these studies looked at this question
229 in the context of organisms presenting group defense. Another way that
230 group defense might decrease spread rate, not modelled here but biologically
231 feasible, is if resources' energy investment in group defense reduces energy
232 availability for reproduction [29].

233 Another feature of our model is the implicit inclusion of stage structure in
234 the spatial dynamics. The importance of stage structure in dispersal dynam-
235 ics was first observed by [15] using spatially explicit models with continuous
236 space and continuous time, and with discrete space and discrete time. In the
237 case of continuous space and discrete time, previous analyses that expand
238 the IDE framework to consider stages with limited movement also implicitly
239 included stage structure [16, 32]. We find a similar general result to those
240 previous analyses, where local interactions in the stages with limited move-
241 ment affect the spread rate of the population. In our model, intraspecific
242 competition slows down spread, in contrast to competitive systems, where
243 a high survival of adults promotes spread of the top competitor[16], and
244 analogous to single population dynamics where high mortality of stages with
245 limited movement can lead to an Allee effect which slows spread rates [32].

246 As with any model, we made a number of simplifying assumptions in our
247 model. First, we only consider the case where consumers resource upon adult
248 resource or settling juveniles. Growth of species with limited movement as
249 adults such as urchins [3] and tunicates [28] has been linked to consumption
250 of their dispersing larvae. We suspect dispersing larvae consumption will re-
251 duce the impact of local interactions and give more emphasis on the dispersal
252 dynamics. Second, we assume that the dispersing individuals are the juve-
253 niles. This assumption doesn't capture populations where larvae have limited
254 movement ability compared to their adult stages such as a consumer-resource
255 interaction between dragonflies and frogs [?]. We speculate the model that
256 captures those dynamics would have a similar structure to this one, which
257 would imply that juvenile interactions would be the main constraint on of
258 spread dynamics.

259 Another limitation is that our environment is spatially homogeneous. In
260 reality, spatial heterogeneity may lead to different dynamics than the ones
261 observed in our model. In our model the only factor that produces habi-

262 tat heterogeneity for resource is the distribution of consumer population.
263 However, other potential factors of heterogeneity not accounted by our anal-
264 ysis are substratum topography [12, 21] and resource availability [13]. These
265 factors can be included in our model with spatially variable survival or repro-
266 ductive functions. This could render our problem intractable, which would
267 require numerical analysis to be well explored.

268 Finally, we assumed both consumer and resource have limited movement
269 as adults. However, by setting the proportion of sessile adults that survive (δ_i
270 for $i = p, n$) equal to 0, our model allows only one of the two species to have
271 limited movement as adults. As seen in the dispersal-induced instabilities
272 (Section 3.2), this is a sufficient condition for instabilities of resource at
273 carrying capacity.

274 In conclusion, in a consumer-resource system, local interactions between
275 sessile adults are key to determining the ability of resource to spread by lim-
276 iting their production of offspring through consumption. Similar results were
277 obtained when modelling invasive algae, where the consumption of the sub-
278 strate in the soil slowed the spread rate of the algae [8]. These observations
279 contrast with those seen in competitive models, where competition acts on
280 a more regional scale by allowing coexistence of competitors in space [2] or
281 stopping the invasion front of the higher competitor [16]. These models ex-
282 emplify the use the IDE framework in a wider range of interactions between
283 species such as perennial plants and animals with limited movement.

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