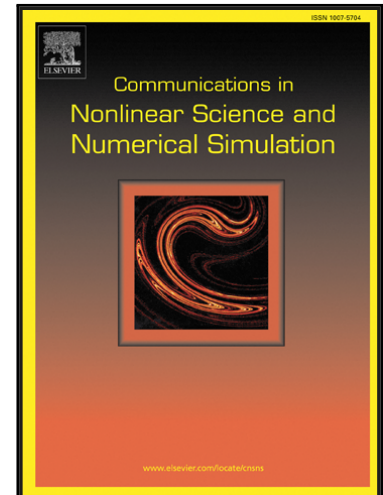


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HIGHLIGHTS

- 1 • The effects of different dispersal patterns on
2 priority effects (PE) are examined.
- 3 • Local and non-local dispersal models are used to
4 predict PE and species coexistence.
- 5 • PE are more prevalent in the non-local dispersal
6 than in the local dispersal models.
- 7 • Very long-range dispersal can lead to exclusion
8 of species.
- 9 • Moderate dispersal permits multi-species coexis-
10 tence versus short-range dispersal.

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Effects of different dispersal patterns on the presence-absence of multiple species

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ABSTRACT: Predicting which species will be present (or absent) across a geographical region remains one of the key problems in ecology. Numerous studies have suggested several ecological factors that can determine species presence-absence: environmental factors (i.e. abiotic environments), interactions among species (i.e. biotic interactions) and dispersal process. While various ecological factors have been considered, less attention has been given to the problem of understanding how different dispersal patterns, in interaction with other factors, shape community assembly in the presence of priority effects (i.e. where relative initial abundances determine the long-term presence-absence of each species). By employing both local and non-local dispersal models, we investigate the consequences of different dispersal patterns on the occurrence of priority effects and coexistence in multi-species communities. In the case of non-local, but short-range dispersal, we observe agreement with the predictions of local models for weak and medium dispersal strength, but disagreement for relatively strong dispersal levels. Our analysis shows the existence of a threshold value in dispersal strength (i.e. saddle-node bifurcation) above which priority effects disappear. These results also reveal a co-dimension 2 point, corresponding to a degenerate transcritical bifurcation: at this point, the transcritical bifurcation changes from subcritical to supercritical with corresponding creation of a saddle-node bifurcation curve. We observe further contrasting effects of non-local dispersal as dispersal distance changes: while very long-range dispersal can lead to species extinctions, intermediate-range dispersal can permit more outcomes with multi-species coexistence than short-range dispersal (or purely local dispersal). Overall, our results show that priority effects are more pronounced in the non-local dispersal models than in the local dispersal models. Taken together, our findings highlight the profound delicacy in the mediation of priority effects by dispersal processes: “big steps” can have more influence than many “small steps”.

KEYWORDS: local and non-local dispersal; biotic and abiotic factors; priority effects; coexistence

1. INTRODUCTION

36 Are ecological communities with non-local dispersal (i.e. dispersal process that occurs over non-adjacent or
37 larger spatial locations) more likely to exhibit priority effects^{1,2} (i.e. where relative initial abundances determine
38 the long-term presence-absence of each species) than localised dispersal, and when does the occurrence of
39 priority effects depend on dispersal distance and its magnitude? Answering these questions requires better
40 understanding of species dispersal mechanisms³⁻⁶ in conjunction with consideration of the roles of biotic
41 interactions⁷⁻¹⁰ and abiotic environments¹¹⁻¹⁴. Some studies^{8,15} have demonstrated contrasting effects of local
42 dispersal on the occurrence of priority effects: when dispersal exceeds a threshold value, priority effects vanish
43 and lead to exclusion of species; as dispersal decreases below this threshold value, priority effects occur, which
44 can promote the dominance of interacting species depending on initial abundances; consequently, this situation
45 can mediate coexistence of multiple species in the presence of moderate dispersal levels. Other studies have
46 also demonstrated that priority effects and local dispersal can be important drivers of community assembly over
47 small spatial scales^{16,17} but the persistence of this phenomenon is unclear under non-local dispersal process.

48 In this paper, we investigate the interaction of priority effects with non-local dispersal in determining the
49 range limits of species. While the importance of priority effects in shaping community compositions is likely
50 to be influenced by biotic interactions¹⁸⁻²², abiotic environments²³⁻²⁵ and dispersal process⁴, much remains
51 unknown about how priority effects and non-local dispersal interact to shape presence-absence of multiple
52 species. Specifically, it remains unclear whether the effects of non-local dispersal can lead to the persistence or
53 exclusion of priority effects across heterogeneous environments with biotic interactions among multiple species.
54 To fill part of this knowledge gap, we employ various models of dispersal to explore the possible occurrence
55 of priority effects in community assembly. This investigation is inspired by the dispersal biology of species:
56 for example, some plant seeds are often dispersed over short distances and near to their parents' locations^{26,27}.
57 Consistent with this observation, theoretical models are developed with the assumptions that species can move
58 locally between adjacent sites while interacting with other species. These assumptions serve as a basis of several
59 modelling frameworks with local dispersal process such as partial-differential equations (PDE) models^{8,16,28}
60 and stochastic (random walk) models^{15,29-31}. However, there are some plant seeds that are transported longer
61 distances by dispersal vectors such as animals, wind and water^{26,27,32-34}. Some animal species also show a
62 non-local dispersal pattern^{35,36}: for instance, Drobzhansky and Wright³⁷ discovered that the spatial dispersal
63 distribution of fruit flies illustrates a long-distance dispersal movement.

64 The observation of non-local dispersal pattern between animal species is also evident in other studies^{38,39};
65 for instance, Etienne et al.³⁸ show how the incorporation of non-local dispersal processes using a dispersal

66 kernel (i.e. the distribution function that describes the probability of dispersal to different locations) into a
67 modelling framework can affect the predicted population dynamics of species. They find that the establishment
68 and persistence of species are determined by the modes of dispersal, where non-local dispersal can further
69 enhance the chance of species survival³⁸. Conversely, some experimental studies discover that species richness
70 is rapidly lost when ecological processes such as dispersal occur over relatively large spatial scales⁴⁰, whereas
71 coexistence of species are possible when ecological processes are localized^{40,41}. Given these contrasting
72 observations on non-local dispersal, its effects on community assembly is not well understood in the presence
73 of priority effects, which are mediated by intense biotic interactions.

74 To address this problem, we extend previous deterministic theoretical studies involving two interacting
75 species^{42,43} to model biotic interactions and dispersal among multiple species across heterogeneous envi-
76 ronments. We first model dispersal between adjacent locations by incorporating a diffusion equation into
77 our systems. This inclusion leads to a system of PDE consisting of interspecific competition, environmental
78 suitability (carrying capacity) and local dispersal terms. We then examine the impacts of non-local dispersal
79 on community dynamics, in the presence of biotic and abiotic forces that can limit the presence-absence of
80 species. For such situations, some non-local dispersal models have been formulated⁴⁴⁻⁴⁶, but the interaction
81 of priority effects with non-local dispersal in shaping species range limits has not been investigated explicitly.
82 For instance, Hetzer et al.⁴⁶ study a two-species model with long-distance dispersal; they discover that non-
83 local dispersal process can affect community dynamics with faster disperser leading to extinction. Motivated by
84 these studies, we incorporate a dispersal kernel into our multi-species models; this inclusion leads to a system
85 of integro-differential equations (IDE). By comparing results of non-local dispersal (IDE) with local dispersal
86 (PDE) models, we explore the consequences of different dispersal patterns on priority effects under varying
87 dispersal intensity. Additionally, we investigate the effects of different dispersal distance on species coexistence
88 in multi-species communities. We also aim to provide theoretical explanations for the effects of dispersal on
89 multi-species community assembly.

90 The article is organised as follows. After describing the two models, we illustrate local and non-local
91 dispersal effects under various dispersal distances and magnitude using our simulation results. We highlight
92 the similarities and differences between the predictions of the two models, with respect to the occurrence of
93 priority effects and the possibility of species coexistence. By using numerical continuation, we discuss some
94 mathematical insights on the contrasting effects of dispersal on presence-absence of species. Finally, we discuss
95 several ecological implications of our results.

4

2. THE MODELS

2.1. Local Dispersal Model: Partial Differential Equations

To model a local dispersal process across heterogeneous environments where biotic interactions among multiple species are present, we consider a partial differential equation (PDE) model for the densities $N_i(x, t)$ of m species in a one-dimensional domain $a_L \leq x \leq a_R$ ¹⁵:

$$\frac{\partial N_i}{\partial t} = \frac{r_i N_i}{K_i(x)} \left(K_i(x) - \sum_{j=1}^m \alpha_{ij} N_j \right) + D_i \frac{\partial^2 N_i}{\partial x^2} \quad (i = 1, 2, \dots, m) \quad (1)$$

where r_i is the intrinsic growth rate, K_i is the carrying capacity in the absence of competitors, D_i is the diffusion coefficient of species i , and α_{ij} is the coefficient for competition of species j on species i . All intraspecific competition coefficients $\alpha_{ii} = 1$, and the remaining competition coefficients α_{ij} represent the ratio of intraspecific to interspecific competition. In the case of single-species (e.g. $m = 1$), equation (1) reduces to a standard logistic growth model. In general, equation (1) is a spatially extended Lotka-Volterra competition model^{8,10,43}, which becomes a PDE with the addition of the diffusion term.

In the absence of dispersal ($D_i = 0$), the dynamical behaviour of equation (1) at a specific location x is independent of the behaviour at all other locations. Competition is assumed to be local (meaning that species only compete with other species at the same location) and we also assume that interspecific competition is symmetric e.g. $\alpha_{ij} = \alpha_{ji} = \alpha$ (for $i \neq j$). Following these assumptions, the simplest equation of type (1) is in the case of two-species (e.g. $m = 2$): competitive interactions within each location x lead to several outcomes, depending on the competition coefficient α (with $\alpha \neq 1$ a necessity) and the ratio of the carrying capacities $\frac{K_1}{K_2}$: local coexistence (when $\alpha < \frac{K_1}{K_2} < \frac{1}{\alpha}$) and priority effects (when $\frac{1}{\alpha} < \frac{K_1}{K_2} < \alpha$). The analysis can also be extended for the cases of asymmetric competition ($\alpha_{ij} \neq \alpha_{ji}$) and multiple competing species; the reader is referred to⁴⁷⁻⁵¹ for further details and extensions of these dynamical systems results. Because of the uncertainty in choosing the competition coefficient α , we have examined the dynamics of equation (1) for a realistic range of values of α .

The suitability of a particular environment or location is modelled by incorporating a spatial dependence x into the carrying capacity term; each species' carrying capacity $K_i(x)$ can vary with spatial location x . x could be a location within a geographical region, or used as a proxy for representing abiotic environmental factors such as temperature, moisture or elevation that affect the presence-absence of species. The effects of biotic interactions on range limits can depend on how each species responds to the environmental gradient. To illustrate these effects in a multi-species community, we use nonlinear environmental gradients (i.e. carrying

124 capacity varies nonlinearly with x in a three-species model ($m = 3$). We could use a linear function for
 125 carrying capacity as discussed by^{10,52}, but there can be two limitations of this kind of function: (i) carrying
 126 capacity changes unboundedly as x varies; (ii) theoretically, species' fundamental niches extend for an infinite
 127 distance. These limitations can be removed by using a quadratic function:

$$128 \quad K_i(x) = \max \left\{ K_{i,max} \left(1 - \frac{(x - x_i)^2}{w_i^2} \right), 0.001 \right\} \quad (2)$$

129 where x_i is the location at which the carrying capacity for species i is at its maximum $K_{i,max}$ and w_i is the
 130 width of the fundamental niche. To ensure equation (1) is well defined, we set $K_i(x)$ to a small but non-zero
 131 value (0.001) outside the fundamental niche. For visualisation of carrying capacity described by equation (2),
 132 refer to Fig. 2A. We have also examined the outcomes of our models using different parametrisation of carrying
 133 capacity (e.g. linear function, Gaussian function, different set of parameter values); the main lesson that we
 134 learned from this investigation is that the dynamical behaviours of the models are qualitatively similar to the
 135 ones observed in this paper. We refer the interested readers to^{15,43,53-55} for further details and discussion on this
 136 matter.
 137

138 The diffusion term models dispersal among locations, with the parameter D_i representing the strength
 139 of local dispersal for species i . We also assume that interacting species have the same local dispersal rate
 140 ($D_i = D$).

141 2.2. Non-Local Dispersal Model: Integro-Differential Equations

142 For a non-local dispersal process, we consider a system of integro-differential equations (IDE) for the densities
 143 $N_i(x, t)$ of m species in a one-dimensional domain $a_L \leq x \leq a_R$:

$$144 \quad \frac{\partial N_i}{\partial t} = \frac{r_i N_i}{K_i(x)} \left(K_i(x) - \sum_{j=1}^m \alpha_{ij} N_j \right) + \rho_i \left[\int k(x-y) N_i(y) dy - N_i(x) \right] \quad (i = 1, 2, \dots, m) \quad (3)$$

145 where ρ_i is the the dispersal rate of non-local dispersal process and $k(x-y)$ is the probability density function
 146 of species moving from location y to x (i.e. dispersal kernel). Since interacting species are assumed to have the
 147 same local dispersal rate ($D_i = D$), this assumption corresponds to all species have the same non-local dispersal
 148 rate ($\rho_i = \rho$) in IDE models. Equation (3) is a spatially extended Lotka-Volterra competition model^{8,10,43},
 149 which becomes an IDE with the addition of a dispersal kernel.
 150

151 The dispersal kernel models movement of species to non-adjacent spatial locations, with the parameter ρ_i
 152 representing the strength of non-local dispersal for species i . We employ a finitely supported dispersal kernel

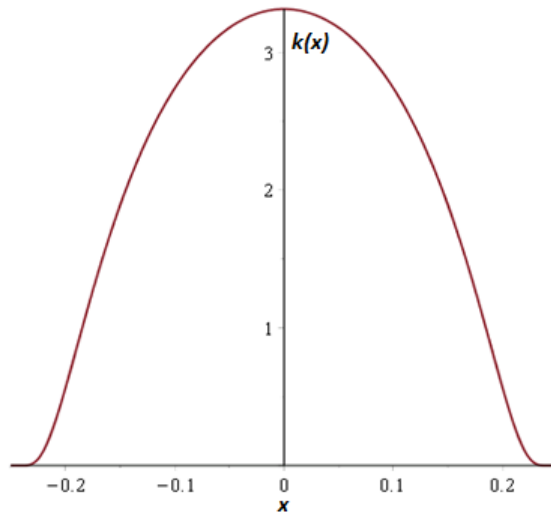


Fig. 1 The dispersal kernel described by equation (4) with dispersal distance $b = 0.25$ and normalisation constant $c_b = 9.009134488$.

153 similar to^{44,45} as an example, in order to illustrate the effects of non-local dispersal in a multi-species community
 154 dynamics:

155

$$k(x) = \begin{cases} c_b e^{\frac{b^2}{x^2 - b^2}}, & |x| < b \\ 0, & \text{otherwise} \end{cases} \quad (4)$$

156

157 where b characterises dispersal distance and c_b is a normalisation constant such that $\int k(x)dx = 1$. For
 158 illustration of the dispersal kernel described by equation (4), refer to Fig. 1. Other types of function for the
 159 non-local dispersal could also be chosen⁵⁶, but we chose the dispersal kernel given by (4) primarily because
 160 of the convenient interpretation of the distance parameter, b , in the exponent. Since the kernel is symmetric,
 161 all odd moments (such as mean) equal 0, and the kernel shape is encoded by even moments (such as mean-
 162 squared displacement). To fairly compare non-local dispersal models (3) and local dispersal models (1), we
 163 impose the condition that their mean-squared displacements (per unit time) are equal. Note that the mean-
 164 squared displacement for the diffusion model is $2D_i$, while the mean-squared displacement for the dispersal
 165 kernel, $\rho_i \sigma^2$, is calculated numerically (i.e. by using second moment with $\sigma^2 = \int x^2 k(x)dx$). The relationship
 166 between the dispersal rate ρ_i of the IDE model with the diffusion coefficient D_i of the PDE model⁵⁷⁻⁶⁰ is given

Table 1 Parameter values.

Symbol	Description	Parameter Values
r_i	The intrinsic growth rate of species i	1
$K_{1,max}$	As indicated in equation (2)	3500
$K_{2,max}$	As indicated in equation (2)	5000
$K_{3,max}$	As indicated in equation (2)	5000
x_1	As indicated in equation (2)	0.8
x_2	As indicated in equation (2)	0.2
x_3	As indicated in equation (2)	0.5
w_1	As indicated in equation (2)	0.6
w_2	As indicated in equation (2)	0.7
w_3	As indicated in equation (2)	0.25
D_i	Diffusion coefficient	0-0.0025
b	Dispersal distance	0-2
ρ_i	Dispersal rate of IDE (calculated using equation (5))	
α_{ij}	Competition coefficient (values given in figure captions)	

167 by:

168

169

$$\rho_i = \frac{2D_i}{\sigma^2} \quad (5)$$

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and we measure strength of dispersal via D_i in both models.

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Numerical simulations are conducted for the local and non-local dispersal models and the results of the two models are compared in the next sections. Unless otherwise stated, parameter values used in the simulation are given in Table (1). In all cases, we employed numerical simulation using MATLAB `ode15s` solver for sufficient time until steady state is reached. We also verified that steady state is stable (i.e. all the real parts of the eigenvalues are negative). To do this, the Jacobian matrix and the eigenvalues are calculated numerically using MATLAB `fsolve` and `eig` functions. We also used numerical continuation package XPPAUT to check our simulation results; the stable and unstable steady states are tracked as a model parameter changes.

3. RESULTS

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In the absence of dispersal ($\rho_i = D_i = 0$), the presence-absence of species depend on the strength of biotic interactions in a delicate manner⁵¹. When interspecific competition is relatively weak, multiple species can coexist at the same location; for instance, Fig. 2B shows modelling results with no dispersal, with coexistence of species possible near the central region. Competition from species 2 (green) and species 3 (red) eliminates species 1 (blue) from some locations x and shifts the range limit of species 1 from $x = 0.2$ (blue square, Fig. 2A) to the right (blue circle, Fig. 2B); similarly, the range limits of species 2 (green circle) and species 3

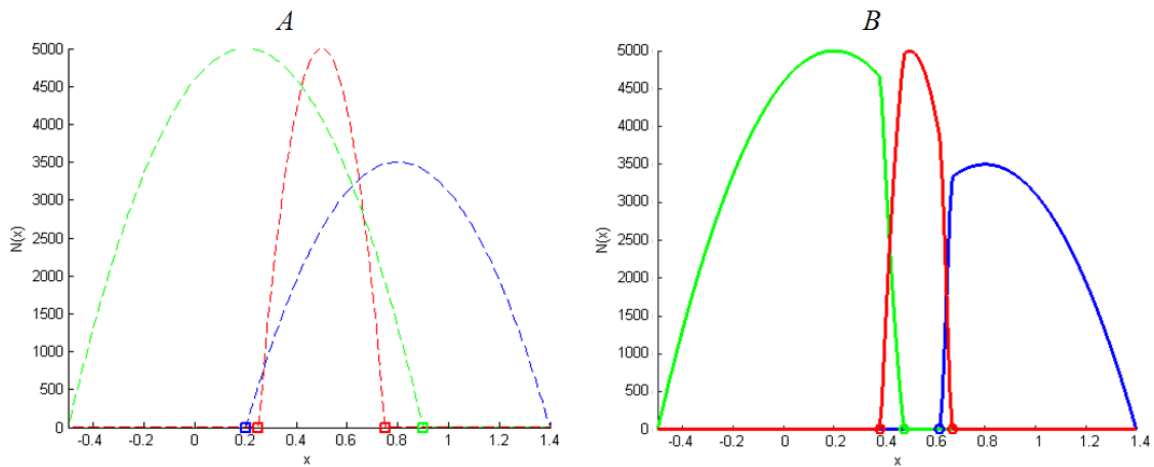


Fig. 2 A, The nonlinear carrying capacities (dotted lines) following equation (2) for species 1 (blue), species 2 (green) and species 3 (red) with squares representing the range limits of species in the absence of biotic interactions. B, Modelling results with no-dispersal ($D_i = \rho_i = 0$) with circles representing the range limits of species in the presence of biotic interactions. Competition coefficient: $\alpha_{ij} = 0.8$. Other parameter values as in Table (1).

184 (red circles) are affected due to biotic interactions.

185 When $\alpha > 1$ (i.e. interspecific competition is stronger than intraspecific), priority effects occur with the
 186 range limits of species depend on initial abundances and also the strength of dispersal (i.e. when $\rho_i, D_i > 0$).
 187 In the following sections, we demonstrate the effects of different modes of dispersal on the presence-absence
 188 of species, and we highlight the similarities and differences between the simulation results from non-local and
 189 local dispersal models, with respect to the occurrence of priority effects and species coexistence. By means of
 190 numerical continuation, we find that there are threshold values for ecologically-relevant parameters (e.g. D , α
 191 and b), which lead to the (dis-)appearance of priority effects in the models.

192 3.1. The Effects of Different Modes of Dispersal on Priority Effects (Short-Range Dispersal)

193 When dispersal is incorporated into the models ($\rho_i, D_i > 0$), the presence-absence of species is influenced
 194 by movement of individuals from other locations. For example, Fig. 3 shows the range limits of species
 195 predicted by the local dispersal model (1) with zero (first row), weak (second row), medium (third row), strong
 196 (fourth row) and stronger (fifth row) dispersal levels, with two different initial conditions: initial abundances
 197 favour species 3 (left column); and initial abundances favour species 1 and 2 (right column). To understand
 198 the dynamical behaviour of equation (1) for a range of values of the interspecific competition coefficient α
 199 across locations x , we constructed summary plots of the local dispersal model, which are shown in Fig. 5 (left
 200 column). These plots depict which combination of species is present at each location x and are generated using
 201 three different initial abundances, each favouring one of the three species. Consistent with previous ecological

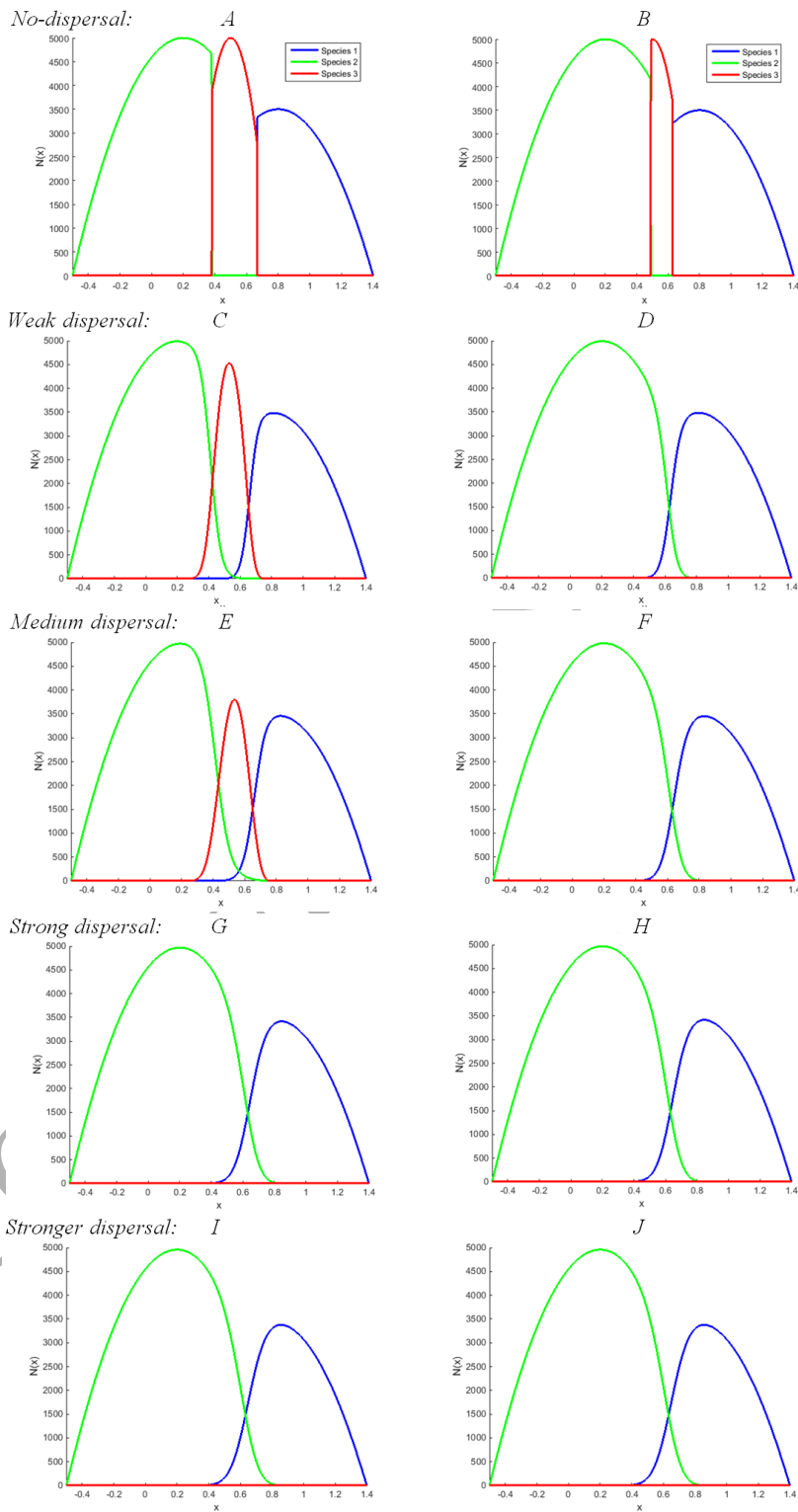


Fig. 3 Results of the PDE model under various dispersal strength: $D = 0$ (A,B); $D = 0.0005$ (C,D); $D = 0.001$ (E,F); $D = 0.0015$ (G,H); $D = 0.002$ (I,J). *Left column*, species densities at $\alpha = 1.28$ when initial abundances favour species 3: $N_1(x) = 0.1K_1(x)$, $N_2(x) = 0.1K_2(x)$, $N_3(x) = 0.9K_3(x)$. *Right column*, species densities at $\alpha = 1.28$ when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x)$, $N_2(x) = 0.9K_2(x)$, $N_3(x) = 0.1K_3(x)$. Carrying capacities are as in Fig. 2. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

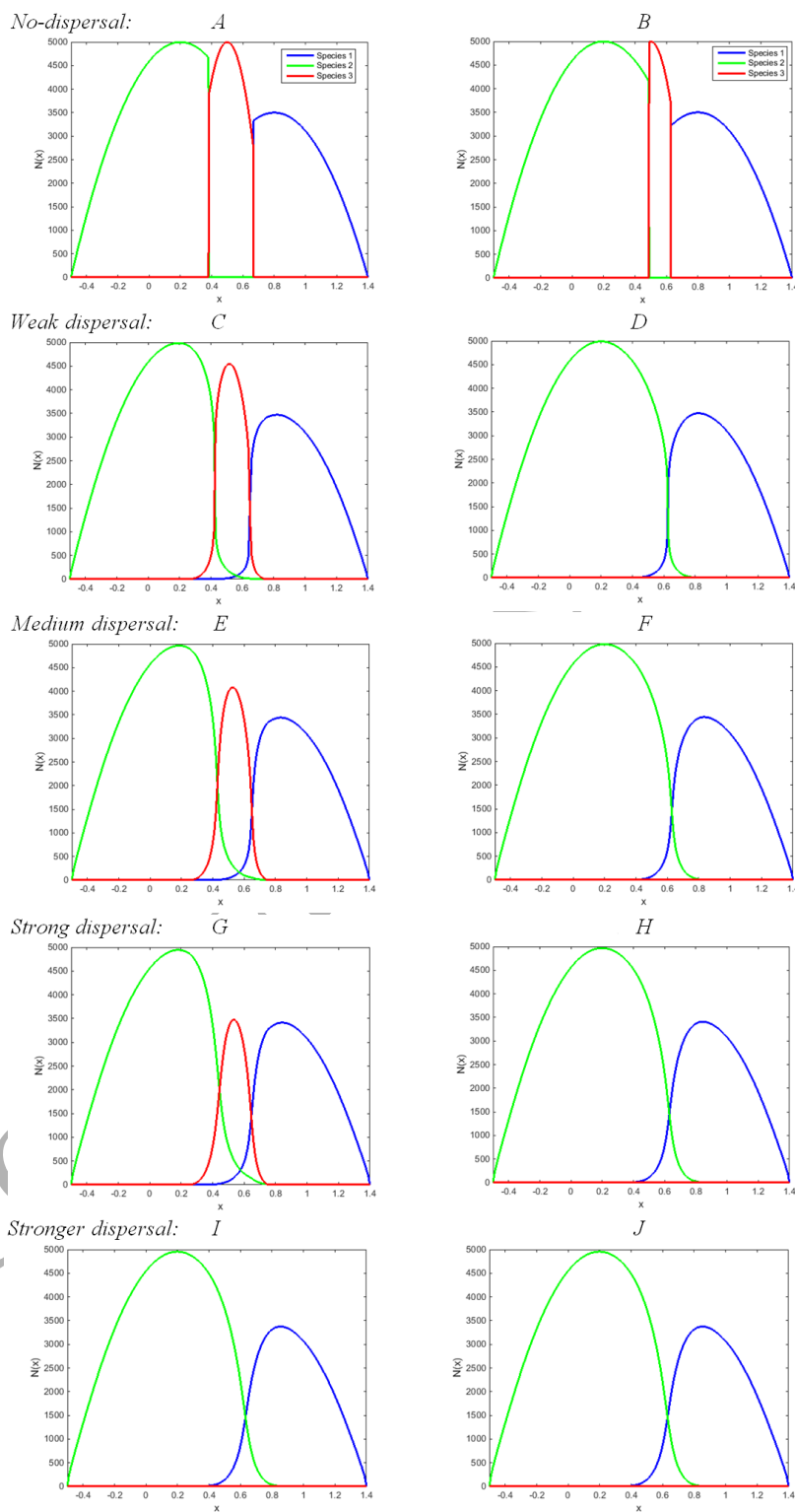


Fig. 4 Results of the IDE model with $b = 0.25$ under various dispersal strength: $D = 0, \rho = 0$ (A,B); $D = 0.0005, \rho = 0.1011$ (C,D); $D = 0.001, \rho = 0.2024$ (E,F); $D = 0.0015, \rho = 0.3036$ (G,H); $D = 0.002, \rho = 0.4048$ (I,J). *Left column*, species densities at $\alpha = 1.28$ when initial abundances favour species 3: $N_1(x) = 0.1K_1(x), N_2(x) = 0.1K_2(x), N_3(x) = 0.9K_3(x)$. *Right column*, species densities at $\alpha = 1.28$ when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x), N_2(x) = 0.9K_2(x), N_3(x) = 0.1K_3(x)$. Carrying capacities are as in Fig. 2. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

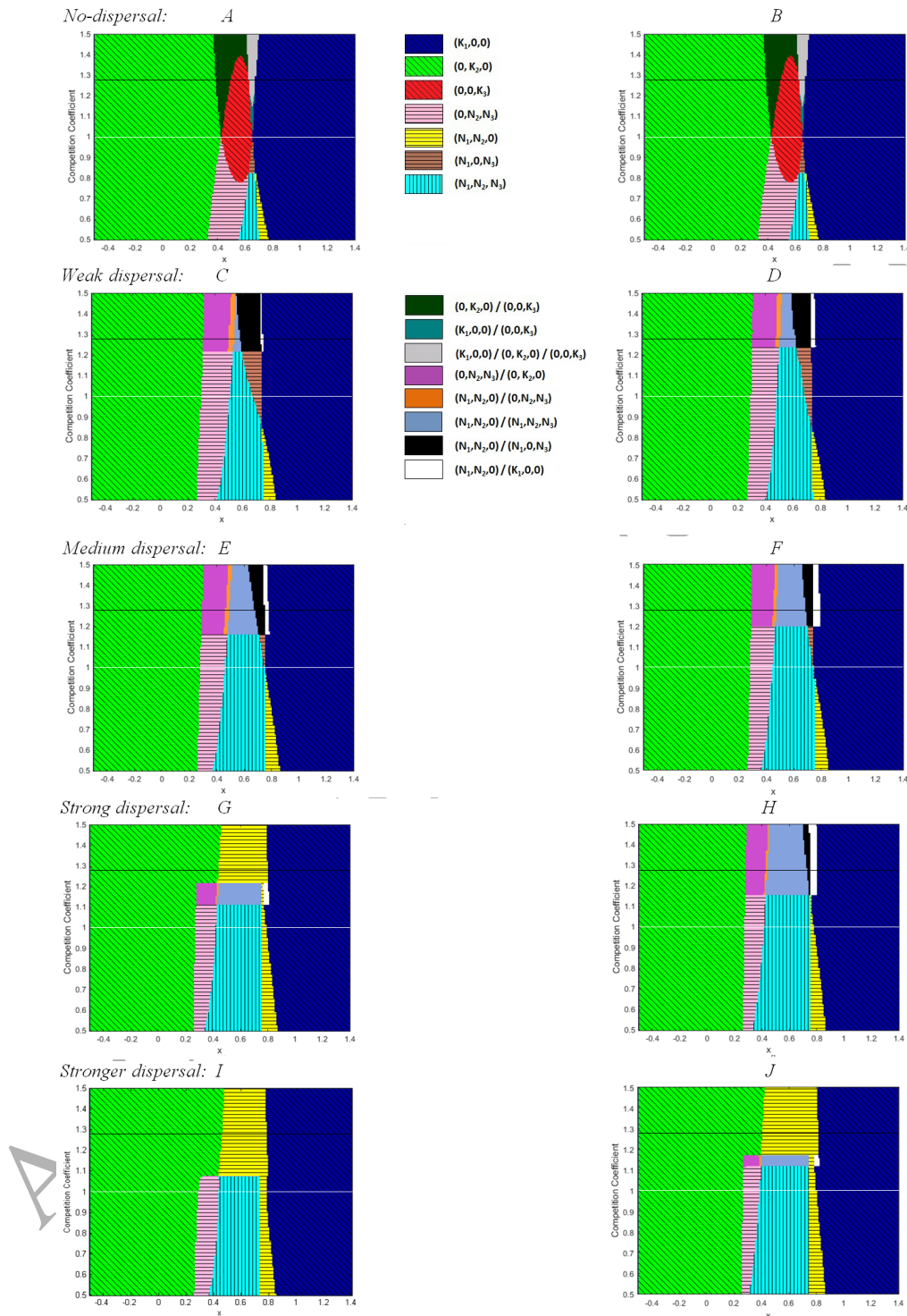


Fig. 5 Results of the PDE (1) and IDE (3) models: $D = 0$ (A,B); $D = 0.0005$ (C,D); $D = 0.001$ (E,F); $D = 0.0015$ (G,H); $D = 0.002$ (I,J). *Left (respectively, Right) column*, summary plots of the PDE model (respectively, IDE). Black lines correspond to the value of $\alpha = 1.28$ shown in Fig. 3 and Fig. 4; white lines correspond to the value of $\alpha = 1$. Colours correspond to combinations of species presences and the meaning of these colours are described in a graphical legend. Carrying capacities are as in Fig. 2.

202 studies^{61–63}, we define a species to be present if its density is greater than 0.5% of the maximum density of
 203 that species. This can be thought of as a detection threshold (i.e. meaning that we would not observe a species
 204 that is present at a sufficiently low density). The colours of the regions in Fig. 5 are as follows: (i) diagonal
 205 shaded correspond to single species presence with: *blue*, $(K_1, 0, 0)$; *green*, $(0, K_2, 0)$; and *red*, $(0, 0, K_3)$;
 206 (ii) horizontal shaded correspond to two-species coexistence with: *pink*, $(0, N_2, N_3)$; *brown*, $(N_1, 0, N_3)$; and
 207 *yellow*, $(N_1, N_2, 0)$; (iii) vertical shaded corresponds to three-species coexistence with: *cyan*, (N_1, N_2, N_3) ;
 208 (iv) unshaded correspond to priority effect regions, where in Fig. 5 (A,B) *dark green*, $(0, K_2, 0)$ or $(0, 0, K_3)$;
 209 *teal*, $(K_1, 0, 0)$ or $(0, 0, K_3)$; *light grey*, $(K_1, 0, 0)$ or $(0, K_2, 0)$ or $(0, 0, K_3)$; Fig. 5 (C,D,E,F,G,H,I,J) *purple*,
 210 $(0, N_2, N_3)$ or $(0, K_2, 0)$; *orange*, $(N_1, N_2, 0)$ or $(0, N_2, N_3)$; *grey blue*, $(N_1, N_2, 0)$ or (N_1, N_2, N_3) ; *black*,
 211 $(N_1, N_2, 0)$ or $(N_1, 0, N_3)$; *white*, $(N_1, N_2, 0)$ or $(K_1, 0, 0)$. We have also investigated the outcomes of the
 212 models using various ecological criteria (e.g. 0.5% of the maximum carrying capacity of that species, $K_{i,max}$;
 213 0.5% of the maximum density of any species; and 0.5% of the maximum total density of species); the results
 214 presented in this section are robust to reasonable choices of presence-absence criterion. To illustrate the effects
 215 of non-local dispersal on the presence-absence of species, we constructed Fig. 4 using IDE model (3) with
 216 short-range dispersal (e.g. $b = 0.25$), which has similar layout and comparable to the local dispersal results
 217 (Fig. 3). For comparison, the summary plots of IDE model are shown in Fig. 5 (right column).

218 Overall, the results of the IDE are in agreement with those of the PDE models, particularly for weak and
 219 medium dispersal levels: when $\alpha > 1$, we observe priority effects that depend on initial abundances in both
 220 models. Increasing the intensity of dispersal from weak to medium dispersal levels enhances the occurrence of
 221 priority effects (compare unshaded regions in Fig. 5C, E and Fig. 5D, F). This situation promotes coexistence
 222 of two (Fig. 3D, F and Fig. 4D, F) or three species (Fig. 3C, E and Fig. 4C, E) near the centre of the region.
 223 The main difference between these two models is observed under strong dispersal: there are more occurrences
 224 of priority effects in the IDE than in the PDE models (compare unshaded regions in Fig. 5G and Fig. 5H). For
 225 instance, the IDE models show that either two-species coexistence or three-species coexistence is possible near
 226 the centre of the domain (Fig. 4G, H), whereas three-species coexistence is no longer possible in the PDE model
 227 (Fig. 3G, H) under strong dispersal scenario. These results show that priority effects persist when dispersal is
 228 strong in the non-local dispersal models, and they are eliminated at higher values of dispersal in the IDE than in
 229 the PDE models.

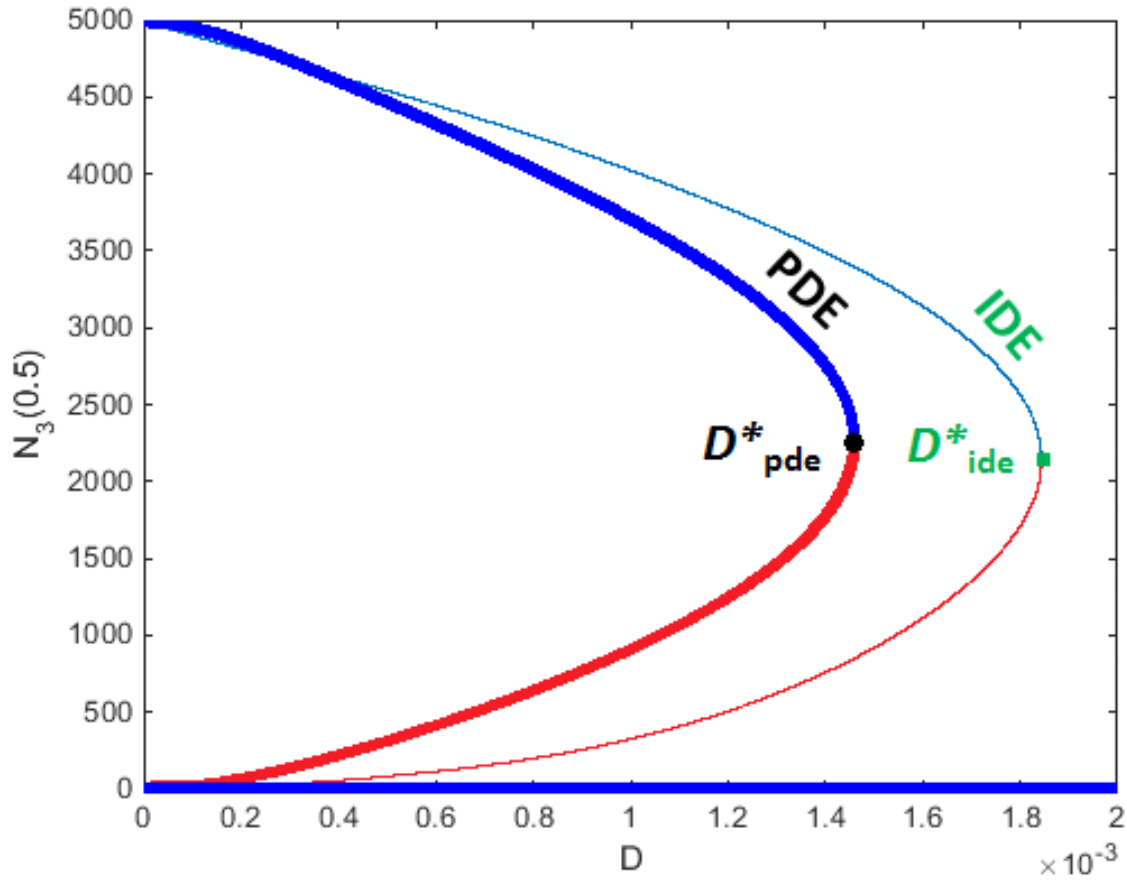


Fig. 6 The density of a focal species (species 3) at $x = 0.5$ and $\alpha = 1.28$ for PDE model (thick lines) and IDE model with $b = 0.25$ (thin line) as the dispersal strength D changes. The threshold values D_{pde}^* (black point) and D_{ide}^* (green point) correspond to diffusion coefficients for PDE and IDE, respectively (for IDE, the corresponding diffusion coefficients D and ρ are related by equation (5)); these thresholds also correspond to saddle-node bifurcation points. There are three branches of N_3 : (i) unstable three-species steady-states (red curves); (ii) stable three-species steady-state, with species 3 present (upper blue curves); (iii) stable two-species steady-state, with species 3 absent (lower blue curves). Other parameter values as in Table (1). These plots are computed by numerical continuation using XPPAUT.

230 3.2. Theoretical Explanations on the (Dis-)Appearance of Priority Effects in the Non-Local and Local 231 Dispersal Models

232 To clarify the persistence or exclusion of the priority effect in some regions for rapid dispersal levels in both
233 models (Fig. 5G, I and Fig. 5H, J), we employed numerical continuation to track the steady states of the models
234 as dispersal strength D changes. Fig. 6 shows the steady-state density of species 3 at $x = 0.5$ for PDE (thick
235 lines) and IDE (thin lines) models when $\alpha = 1.28$ as dispersal intensity D are varied. There are three branches
236 of steady states: the upper (three-species coexistence) and lower branches (two-species coexistence with species
237 3 absent) of steady states are stable (blue curves); these are separated by an unstable steady state (red curve).

238 There is a threshold dispersal strength D_{pde}^* (respectively, D_{ide}^*) for PDE (respectively, IDE), corresponding
 239 to a saddle-node bifurcation, beyond which the three-species coexistence state vanishes and priority effects
 240 disappear; for values of dispersal $D < D_{pde}^*$ (respectively, $D < D_{ide}^*$), the density N_3 tends toward upper or
 241 lower steady-state, depending on initial species abundances; for values of dispersal $D > D_{pde}^*$ (respectively,
 242 $D > D_{ide}^*$), priority effects disappear and there is only one stable steady state, in which species 3 is absent. The
 243 main difference between the two bifurcation curves in Fig. 6 is that the saddle-node bifurcation point for the
 244 IDE (i.e. D_{ide}^*) is shifted to stronger dispersal levels at this location, as compared to the PDE model (i.e. D_{pde}^*).

245 The steady states of the systems are also tracked as the strength of competition α changes under different
 246 dispersal scenarios (Fig. 7) in order to gain better understanding of the dynamics of PDE and IDE simulation
 247 results (Fig. 3 and Fig. 4). For moderate dispersal levels, as α increases from 0.5 to 1.5 near the central
 248 location, our summary plots (unshaded regions of Fig. 5E and Fig. 5F) show that there is a threshold value
 249 for competitive strength, beyond which priority effects appear. Continuation results in Fig. 7A are consistent
 250 with the aforementioned simulation results. Fig. 7A depicts the steady-state density of species 3 at $x = 0.5$ for
 251 the PDE (thick lines) and the IDE (thin lines) models as α changes under medium dispersal. There are threshold
 252 competitive strengths α_{pde}^- and α_{ide}^- for the PDE and IDE models (respectively), corresponding to transcritical
 253 bifurcations, beyond which priority effects occur: for competitive strength $\alpha > \alpha_{pde}^-$ (respectively, $\alpha > \alpha_{ide}^-$),
 254 the density N_3 tends toward upper or lower steady-state (blue curves), depending on initial species abundances;
 255 for values of competitive strength $\alpha < \alpha_{pde}^-$ (respectively, $\alpha < \alpha_{ide}^-$), the priority effects vanish and there is only
 256 one stable steady state, in which species 3 is present in three-species coexistence. We note that the threshold
 257 value of competitive strength is higher in the IDE (i.e. α_{ide}^-) than in the PDE (i.e. α_{pde}^-) models under moderate
 258 dispersal levels.

259 We also observe qualitatively different dynamics between the PDE and IDE models in our summary plots for
 260 strong dispersal (unshaded regions of Fig. 5G and Fig. 5H). In particular, there are critical values for competitive
 261 strength in which priority effects appear and then vanish in some regions of the PDE summary plot as α increases
 262 (Fig. 5G). Our continuation results (Fig. 7B: thick curves) reveal that there are threshold values of α (black
 263 points) in the PDE models: the lower and upper thresholds α_{pde}^- , α_{pde}^+ correspond to transcritical and saddle-
 264 node bifurcations (respectively), and priority effects occur for the range of competitive strength where $\alpha_{pde}^- <$
 265 $\alpha < \alpha_{pde}^+$. In the IDE models, for the range of competition coefficient α that we investigated, there is a threshold
 266 competitive strength α_{ide}^- (corresponding to a transcritical bifurcation) beyond which priority effects occur. In
 267 this situation, priority effects persist for a bigger range of competitive strength α (i.e. when $\alpha > \alpha_{ide}^-$); this is
 268 consistent with the IDE simulation results (Fig. 5H).

269 As dispersal intensity increases to stronger dispersal, we notice that priority effects region shrinks in the

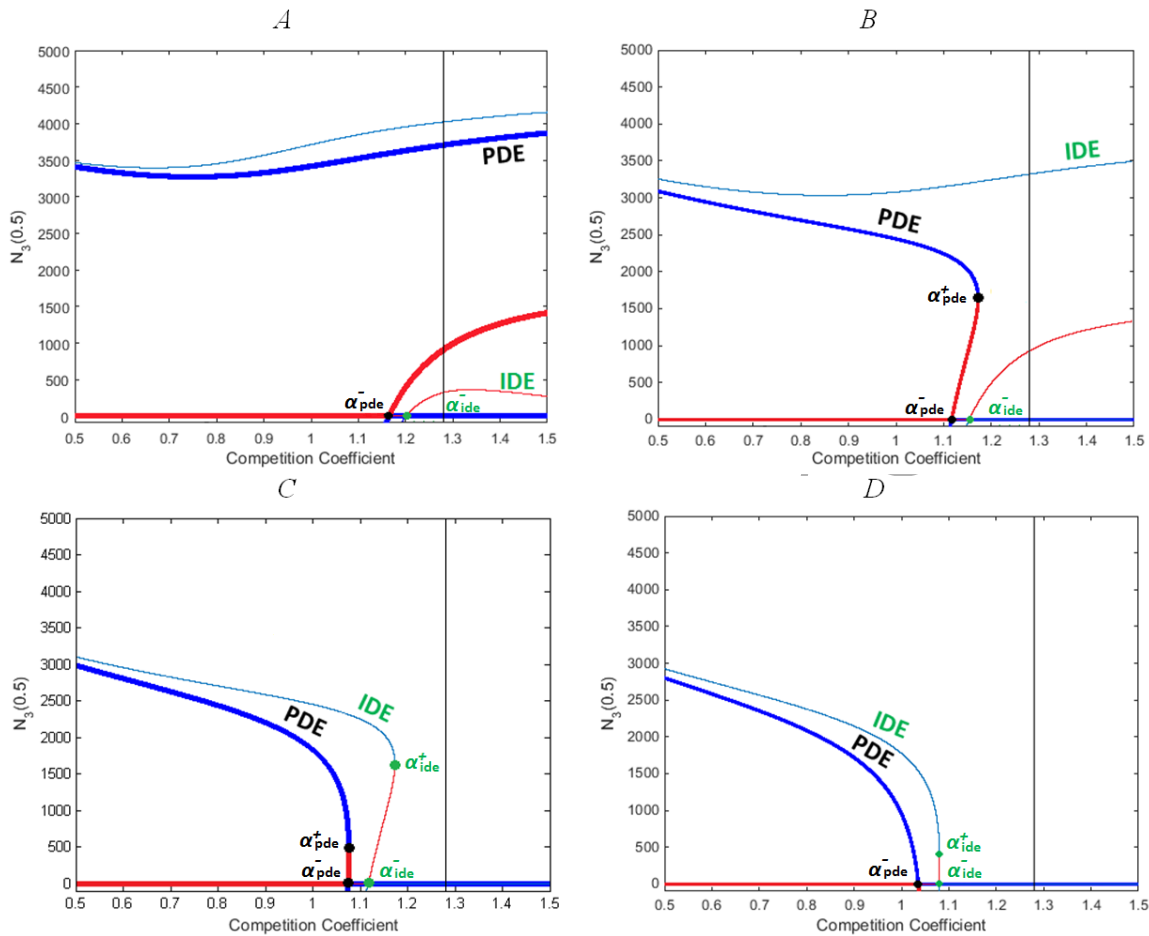


Fig. 7 The density of species 3 (N_3) for PDE model (thick lines) and IDE model with $b = 0.25$ (thin line) at $x = 0.5$ as the strength of biotic interactions α change under various dispersal scenarios: (A) $D = 0.001$, (B) $D = 0.0015$, (C) $D = 0.002$, (D) $D = 0.0025$. The points α_{pde}^- and α_{ide}^- correspond to transcritical bifurcations and α_{pde}^+ and α_{ide}^+ correspond to saddle-node bifurcation points in the PDE and the IDE, respectively. Three branches of N_3 : (i) unstable three-species steady-states (red curves); (ii) stable three-species steady-state, with species 3 present (upper blue curves); (iii) stable (respectively, unstable) two-species steady-state, with species 3 absent, which emerges to the right (respectively, left) of transcritical bifurcations α_{pde}^- and α_{ide}^- (lower blue (respectively, red) curves). The black lines correspond to the value of competition coefficient $\alpha = 1.28$ shown by the simulation results in Fig. 3 (PDE) and Fig. 4 (IDE). Other parameter values as in Table (1). These plots are computed by numerical continuation using XPPAUT.

270 summary plots of both models (unshaded regions of Fig. 5I, J). Closer investigation of PDE (respectively,
 271 IDE) continuation results in Fig. 7C, D demonstrates that the two bifurcation points, namely transcritical
 272 bifurcation α_{pde}^- (respectively, α_{ide}^-) and saddle-node bifurcation α_{pde}^+ (respectively, α_{ide}^+), come closer and
 273 closer to one another and, finally, coalesce (compare black (bifurcation) points in Fig. 7C with Fig. 7D). To
 274 investigate the interaction of transcritical and saddle-node bifurcations and to clarify the disappearance of
 275 priority effects as dispersal strength D and competition coefficient α change, we constructed two-parameter

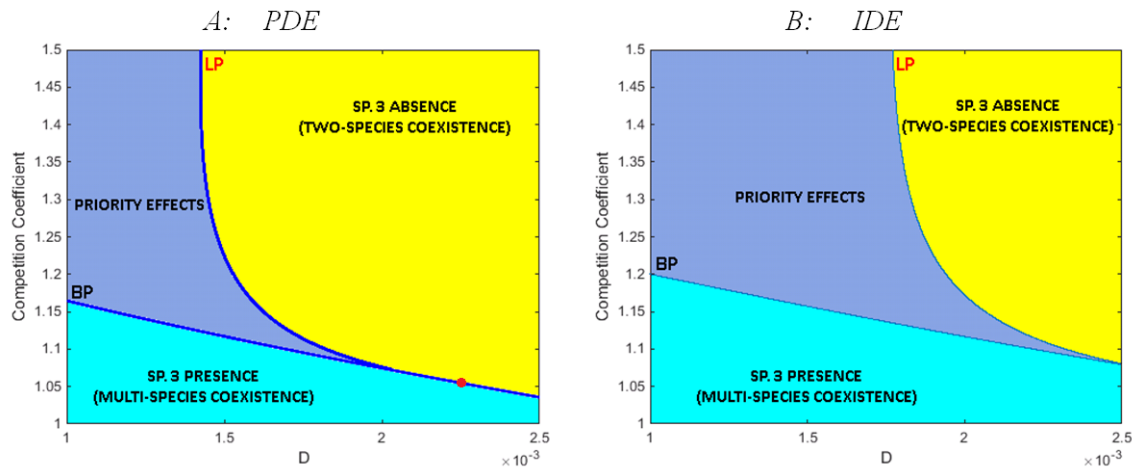


Fig. 8 Parameter space diagram, which summarises different dynamics at location $x = 0.5$ for the PDE (left) and IDE (right) models, as dispersal strength D and competitive strength α are varied. Colours correspond to combinations of species presences: (i) three-species coexistence (cyan); (ii) two-species coexistence with species 3 absence (yellow); (iii) priority effect regions (blue-grey). LP curves correspond to saddle-nodes bifurcations and BP curves correspond to transcritical bifurcations. Points of intersection between BP and LP curves correspond to degenerate transcritical bifurcation point (red point). These co-dimension two bifurcation plots are computed by varying two parameters using numerical continuation package XPPAUT.

276 bifurcation diagrams, as shown in Fig. 8. These plots illustrate the dynamics at the central region ($x = 0.5$) as
 277 the strength of competition α and magnitude of dispersal D are varied in both models. There is a co-dimension
 278 2 point (red point) for PDE (Fig. 8A), corresponding to a degenerate transcritical bifurcation: at this point, the
 279 transcritical bifurcation (BP) changes from subcritical to supercritical with corresponding creation of a saddle-
 280 node bifurcation curve (LP). This co-dimension 2 bifurcation acts as an organising centre and separates the
 281 parameter space into three different regions: inside the wedge there are priority effects (blue-grey colour) with
 282 two stable steady states (i.e. three-species coexistence with species 3 presence or two-species coexistence with
 283 species 3 absence), and outside the wedge there is one stable steady state (i.e. three-species coexistence with
 284 species 3 presence (cyan colour) and two-species coexistence with species 3 absence (yellow colour)). Similar
 285 observations are possible in the IDE (Fig. 8B) as competitive strength α and dispersal intensity D changes (i.e.
 286 degenerate transcritical bifurcation occurs when dispersal strength D increases further than the values shown in
 287 Fig. 8B).

288 Overall, we find that bistable region (blue-grey colour) is larger in the IDE as compared to PDE models,
 289 which leads to more occurrences of priority effects under rapid dispersal levels. The three-species coexistence
 290 region (cyan colour) is also larger in IDE, where for different parameter values investigated, we observe stable
 291 coexistence of focal species (e.g. species 3) with its neighbouring competitors (e.g. species 1 and 2). We

292 also notice that the width of the (yellow colour) region supporting two-species coexistence (e.g. with species 3
 293 absence) outcome is wider in the PDE than IDE models.

294 **3.3. Contrasting Observations of Non-Local Dispersal on Species Presence-Absence** 295 **(Intermediate-Range and Long-Range Dispersal)**

296 In the previous section, we observe that the coexistence of species is enhanced when dispersal occurs over non-
 297 adjacent spatial locations, whereas exclusion of some species occurs when dispersal is localised. This finding
 298 is illustrative, but it may not be general. The opposite observation is also possible: it has been observed in
 299 experimental studies⁶⁴ that species coexistence is rapidly lost when dispersal occurs over larger scales, whereas
 300 species coexistence is possible when dispersal occurs over intermediate or short distances; in the latter case,
 301 coexistence of species peaks at intermediate-range dispersal. Motivated by this experimental observation, we
 302 investigate the consequences of intermediate-range and long-range dispersal on species coexistence using our
 303 non-local dispersal model (3). To do this, we conducted numerical experiments by considering various dispersal
 304 distance b and also different initial species abundances. For example, Fig. 9 shows the presence-absence of
 305 species at $\alpha = 1.28$ for stronger dispersal levels ($D = 0.002$) predicted by the PDE (first row), and the IDE
 306 models with $b = 0.25$ (second row), $b = 0.5$ (third row), $b = 0.9$ (fourth row) and $b = 2$ (fifth row). These
 307 plots are generated using two different initial conditions: initial abundances favour species 3 (left column);
 308 and initial abundances favour species 1 and 2 (right column). We also constructed stack graphs for the IDE
 309 models, which are shown in Fig. 10, for a range of values of dispersal distance b . These plots summarise the
 310 proportion of different species present across sites x (e.g. single-species present (blue squares), two-species
 311 present (green squares) and three-species present (red squares)) as dispersal distance b changes. To generate
 312 these stack graphs, we used two different initial conditions: initial abundances favour species 3 (left column);
 313 and initial abundances favour species 1 and 2 (right column). As with the summary plots, we define a species
 314 to be present if its density is greater than 0.5% of the maximum density of that species.

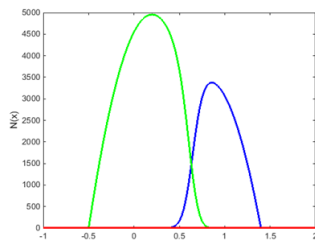
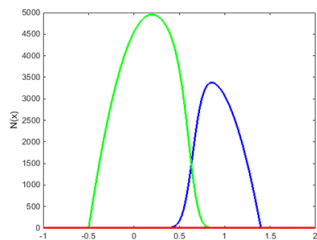
315 When b is relatively small, the predictions of the IDE (Fig. 9C, D) are in agreement with those of the PDE
 316 (Fig. 9A, B); in the case of stronger dispersal, priority effects are absent and only two-species coexistence is
 317 possible near the central region. When b increases to intermediate levels, we find that priority effects emerge
 318 with coexistence of three (Fig. 9E, G) or two species (Fig. 9F, H) near the centre of the region depending on
 319 initial abundances. The occurrence of priority effects is still evident when b is relatively large (Fig. 9I, J), but we
 320 observe more outcomes where species exclusions are possible; in this situation, mostly one species dominating
 321 at any given location x , depending on initial abundances. This observation can clearly be seen from our stack
 322 graphs (Fig. 10A): when non-local dispersal process occurs over very large spatial scales (e.g. $b = 2$), multi-

Species Presence-Absence for Stronger Dispersal Levels ($D = 0.002$)

PDE

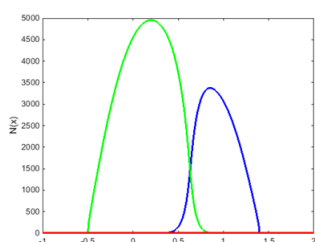
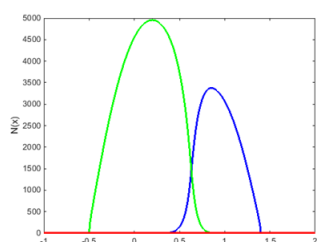
A

B

IDE ($b = 0.25$)

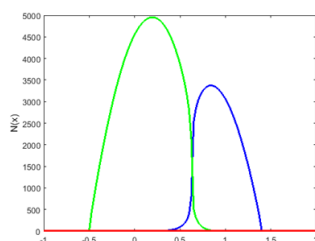
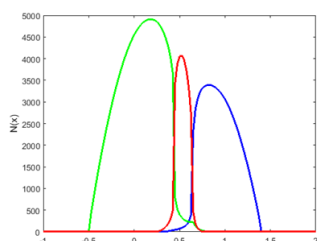
C

D

IDE ($b = 0.5$)

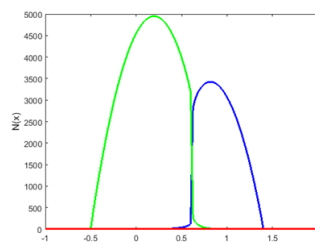
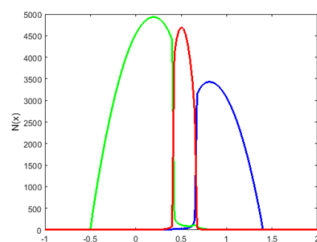
E

F

IDE ($b = 0.9$)

G

H

IDE ($b = 2$)

I

J

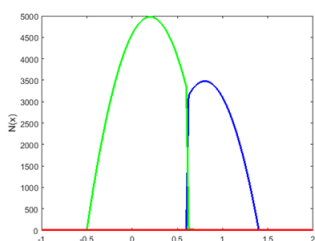
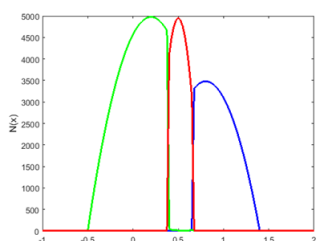


Fig. 9 Results for stronger dispersal levels ($D = 0.002$) predicted by the PDE models (A,B); and the IDE models with $b = 0.25$ (C,D); $b = 0.5$ (E,F); $b = 0.9$ (G,H); $b = 2$ (I,J). *Left column*, species densities at $\alpha = 1.28$ when initial abundances favour species 3: $N_1(x) = 0.1K_1(x)$, $N_2(x) = 0.1K_2(x)$, $N_3(x) = 0.9K_3(x)$. *Right column*, species densities at $\alpha = 1.28$ when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x)$, $N_2(x) = 0.9K_2(x)$, $N_3(x) = 0.1K_3(x)$. Carrying capacities are as in Fig. 2. These plots are computed by numerical simulation with MATLAB ode15s solver.

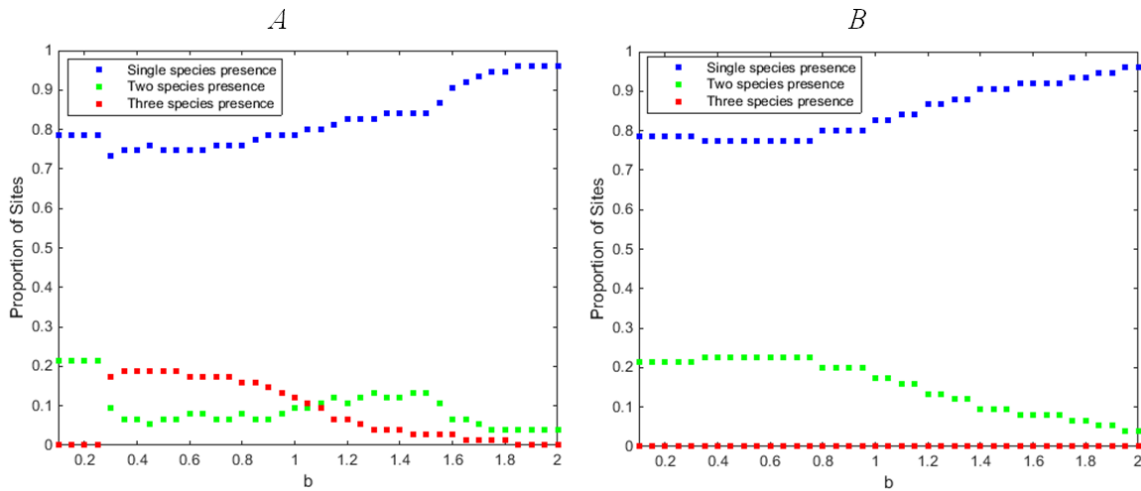


Fig. 10 Proportion of different species present across sites x for different values of b : single-species present (blue squares); two-species present (green squares); three-species present (red squares). Stack graphs for the IDE models with stronger dispersal levels ($D = 0.002$) at $\alpha = 1.28$ as dispersal distance b changes. *Left column*, IDE results when initial abundances favour species 3: $N_1(x) = 0.1K_1(x)$, $N_2(x) = 0.1K_2(x)$, $N_3(x) = 0.9K_3(x)$. *Right column*, IDE results when initial abundances favour species 1 and 2: $N_1(x) = 0.9K_1(x)$, $N_2(x) = 0.9K_2(x)$, $N_3(x) = 0.1K_3(x)$. Carrying capacities are as in Fig. 2. These plots are computed by numerical simulation with MATLAB `ode15s` solver.

323 species coexistence is impossible. In this situation, the proportion of sites with only one-species (blue squares)
 324 present increases rapidly, while the sites with two-species (green squares) and three-species (red squares) present
 325 reduce to low proportions. We also observe that non-local dispersal that occurs over intermediate distances (e.g.
 326 $b = 0.5$) can promote multi-species coexistence in comparison to non-local dispersal over short distances (e.g.
 327 $b = 0.25$) or purely local dispersal. For short-range dispersal, priority effects vanish in our stack graphs, and
 328 only two-species coexistence is possible for different initial abundances (Fig. 10A, B).

329 To investigate the (dis-)appearance of priority effects as the values of b change, we performed numerical
 330 continuation to track the steady states of the IDE models. Fig. 11 depicts the steady-state density of species 3
 331 at $x = 0.5$ for stronger dispersal levels ($D = 0.002$) when $\alpha = 1.28$ as parameter b in the IDE is varied. For
 332 instance, there are three branches of steady states: the upper (three-species coexistence, with species 3 present)
 333 and lower branches (two-species coexistence, with species 3 absent) of steady states are stable (blue curves);
 334 these are separated by an unstable three-species steady state (red curve). There is a threshold dispersal distance
 335 b_T , corresponding to a saddle-node bifurcation, below which the upper branch of steady states vanishes and
 336 priority effects vanish. For values of dispersal distance $b < b_T$, the priority effects disappear and there is only
 337 one stable steady state, in which species 3 is absent. For values of dispersal distance $b > b_T$, priority effects
 338 occur and the density N_3 tends toward upper or lower steady-state, depending on initial species abundances.

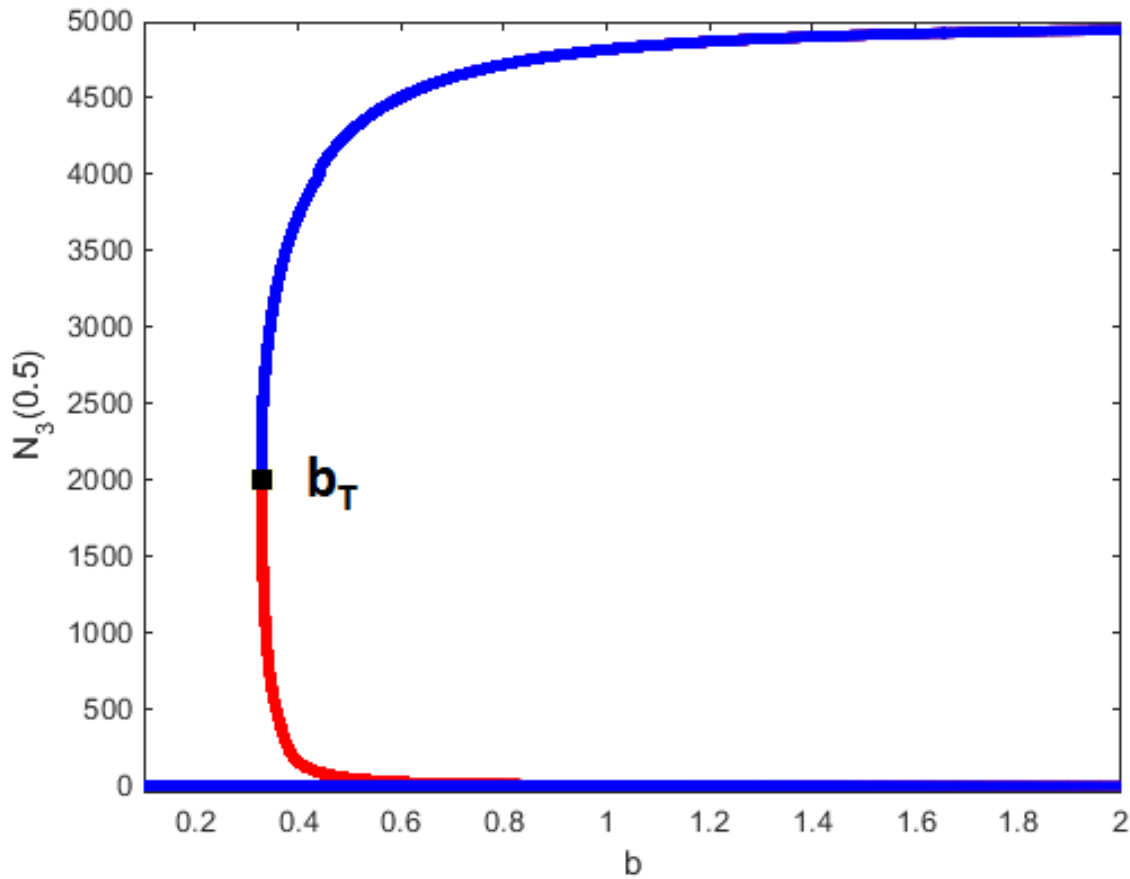


Fig. 11 The density of a focal species (species 3) at $x = 0.5$ and $\alpha = 1.28$ for IDE models with stronger dispersal levels ($D = 0.002$) as the dispersal distance b changes. The threshold value b_T (black square) corresponds to saddle-node bifurcation point. There are three branches of N_3 : (i) unstable three-species steady-states (red curves); (ii) stable three-species steady-state, with species 3 present (upper blue curves); (iii) stable two-species steady-state, with species 3 absent (lower blue curves). Other parameter values as in Table (1). These plots are computed by numerical continuation using XPPAUT.

4. DISCUSSION AND ECOLOGICAL IMPLICATIONS

339 In this work, we have used PDE and IDE models to study the influences of different dispersal patterns on
 340 the occurrence of priority effects, which are mediated by intense biotic interactions across heterogeneous
 341 environments. We discover that the occurrence of priority effects vary with dispersal strategies and strength;
 342 they are eliminated at stronger values of dispersal in the IDE than in the PDE models. Our summary plots show
 343 that the regions supporting dispersal-mediated coexistence and/or priority effects are wider in the IDE models
 344 under rapid dispersal scenarios. These findings demonstrate that the interaction of priority effects and dispersal,
 345 which can mediate multi-species coexistence, are more pronounced in the IDE models. It has been shown that
 346 non-local dispersal process can enhance the chance of species survival across heterogeneous environments³⁸.

347 Biologically, non-local dispersal increases the possibility of migrating species to escape the effects of intense
348 biotic interactions from other species by dispersing further away; this situation enhances the establishment and
349 persistence of species^{38,65}. We also notice that dispersal-induced extinction phenomenon is more evident in the
350 PDE models, which leads to extinction of some species near the centre for more values of D . Local dispersal
351 generates a clumped spatial distribution, which increases the effects of competition among species and enhances
352 the possibility of extinction of some species⁶⁵.

353 Our findings also highlight the important roles of the spatial scale of ecological processes in maintaining
354 community compositions (Fig. 9, Fig. 10 and Fig. 11). Some experimental studies^{40,41} have illustrated that
355 allowing ecological processes such as dispersal to occur locally can promote coexistence in a community
356 assembly⁴¹; however, when ecological processes occur over very large spatial scale, species coexistence is
357 rapidly lost and extinction is possible⁴⁰. Our findings are in line with the aforementioned observations:
358 we observe that while very long-range dispersal can lead to an exclusion effect (of all but one species),
359 short-range and intermediate-range dispersal can promote coexistence of two and three species, respectively.
360 Ecologically, long-distance dispersal increases the risk of landing in unsuitable habitats outside species
361 fundamental niches^{66,67}. In our models, this effect can be seen in the exclusion of neighbouring competitors
362 (e.g. species 1 and 2) near the central region; consequently, this situation reduces the possibility of multiple
363 species to coexist, and in turn benefit focal species (e.g. species 3), in which they can exclude other competitors.

364 We also discover qualitatively similar observations of priority effects between the consequence of increasing
365 dispersal distance b and the effect of decreasing dispersal strength D . As D is decreased in the PDE models
366 (Fig. 6), this situation corresponds to limited dispersal events, and thus the dynamics resemble those observed
367 in no-dispersal case. In the presence of intense biotic interactions, competitive exclusion (of all but one species)
368 occurs due to priority effects. Ecologically, when species have lower migration rates, this situation can result in
369 a crowding effect and increased competition, which in turn leads to species exclusion. As dispersal distance b
370 increases (Fig. 11), this situation corresponds to infrequent long range dispersal events. In this case, dispersal of
371 species over larger distances is possible but rare, which may result in species presence-absence to resemble those
372 observed in no-dispersal scenario (i.e. in the presence of intense biotic interactions, priority effects emerge with
373 only one species can exist at any given locations). Consequently, we observe that there are more occurrences of
374 priority effects in the IDE models as dispersal distance b increases.

375 The continuation results further reveal the bifurcation structure of the PDE and IDE models and they are
376 consistent with simulation results. We find that (Fig. 6) there is a threshold dispersal strength D : this threshold
377 value depends on the modes of dispersal and we show that this value is higher in the IDE model than in the
378 PDE model by considering the dynamics near the central region. Consequently, priority effects persist for

379 stronger dispersal in IDE model, as opposed to PDE model. Additionally, we observe the conditions under
380 which co-dimension 2 bifurcation (Fig. 8) occurs as a result of the interaction between transcritical and saddle-
381 node bifurcations. In general, the interaction of transcritical and saddle-node bifurcations is also studied in
382 other biological systems, such as in Kooi et al.⁶⁸, Van Voorn and Kooi⁶⁹, Saputra et al.⁷⁰ and Landi et al.⁷¹.
383 These findings also demonstrate the possibility of dramatic changes on species presence-absence in response
384 to small variations in the ecologically-relevant parameters, which can induce an uncertainty in the range-limit
385 predictions.

386 From a species conservation perspective, a qualitative implication of our results is that connecting local
387 habitats via movement corridors can have negative impacts for community compositions at several spatial scales.
388 This observation is in line with research on metacommunities, which illustrates negative effects of dispersal on
389 coexistence of species at larger spatial scale⁷². In practice, conservationists believe that increasing connectivity
390 between habitat patches enhances the possibility of species survival⁷³⁻⁷⁵. Our results show that an increase in
391 connectivity, however, can increase the risk of species extinction due to the rapid spread of superior species
392 (e.g. competitors or invasive species) into local habitats; when dispersal occurs over larger spatial scales, this
393 situation can also jeopardise species coexistence due to the risk of landing in unsuitable habitats. Based on these
394 observations, we suggest that the risk of dispersal-induced extinction should be taken into account in
395 the design of such corridors as a conservation tool. This may require detailed knowledge of dispersal rates and
396 biotic interactions, as well as information on dispersal patterns of species.

397 In conclusion, this study serves as a first step in demonstrating how incorporation of different dispersal
398 patterns can improve our predictions of priority effects that strongly determine the presence-absence of species.
399 Knowledge of local and non-local dispersal mechanisms can be incorporated in developing robust predictive
400 models for estimating potential presence-absence of species. We recommend the use of local dispersal (PDE)
401 models to predict the combined effects of dispersal, environment and biotic interactions on range limits when
402 species' dispersal ability are localised. However, we suggest that the range-limit predictions will be revealed
403 better by non-local dispersal (IDE) models when considering certain species that can disperse larger distances
404 via non-local dispersal.

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