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RESEARCH ARTICLE

Joint Effects of Dispersal and Trophic Interactions on the Biodiversity of Species

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Abstract A bifurcation analysis and numerical simulation of a partial differential equations model is performed to have a better understanding of the combined influences of local dispersal and trophic interactions on species range limits (i.e., the boundaries of locations where species is found). This system consists of prey-predator interactions, environmental suitability, and local dispersal terms. The main objective of this investigation is to examine the joint effects of distinct ecological factors on population dynamics and also species ranges. In the absence of dispersal, our results show that variations in abiotic environments and handling times of predator cause distinct outcomes of species interactions (i.e., stable limit cycles, species coexistence, and species exclusion). The inclusion of dispersal into this system reduces the predation pressure and stabilizes this ecological community to mediate species biodiversity. Local dispersal also induces intriguing dynamical behaviour in the system such as bistability, stable and unstable limit cycles.

Keywords: prey-predator interactions, partial differential equations, numerical bifurcation analysis.

Introduction

With the increasing concern about biological invasion, climate change and environmental disturbance problems, a need exists for quantification of invasive and our vulnerable native species geographical ranges and their borders [1-2]. Often, these native and invasive species would interact with each other (i.e., biotic interactions) through predation (or competition) in order to survive in the natural communities [3]. Generally, predation is an example of trophic interactions whereby it describes the feeding relationship between interacting species and the food web dynamics [4]. Predator species will also require time to capture and consume during the process of digesting their prey species; this is referred to as handling time [5]. Typically, the trophic levels would include a variety of species that are linked together by their eating habits. For instance, there are prey, specialist predators (i.e., species with a restricted diet that can only survive by feeding on prey species), and generalist predators (i.e., species that can consume a variety of food resources, including specialist species) [1,4].

Biotic interactions have been documented to affect species distributions and remains one of the ubiquitous forces that structures biodiversity across heterogeneous environments [6]. In the absence of biotic interactions, a species has a range of environments (or habitats) that it can inhabit (i.e., fundamental niches). When encountered with other species through biotic interactions, however, this situation restricts each species from certain areas and permits them to inhabit a smaller fraction of their core ranges. (i.e., realized niche) [7]. The significant impacts of biotic interactions have also been illustrated to limit the realized niches of many ecological communities: for instance, some recent studies show that the predatory marine species like ditch shrimp and fish appear to restrict mosquito larvae distributions through predation [8]. Different ecological studies [2,3,4] have also demonstrated that generalist predator can play an influential role in mediating distinct dynamics of ecological system. This is because the generalist species can attack intermediate specialist predators as well as prey species. Thus, generalist species is also able to regulate the biodiversity of ecological communities [4,9].

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Abiotic environmental factors such as climate have also caused the range expansions (and contractions) of different species, leading to the assumption that climatic variables are the main determinants of species range limits [10,11]. In many cases, the change in ambient temperature is supposed to be a direct cause for the range expansions in the natural communities [12]. Different studies have also discovered that the variations in temperature can affect species distributions in terrestrial and marine communities [13,14]. The change in climate would have an immediate effect on natural communities, and consequently in the spread of these distinct species [15]. Besides biotic interactions and abiotic environments that can shape species distributions, dispersal process is also a salient feature of range shifting dynamics and some biological invasions of natural communities [16,17]. Hence, better understanding on the dispersal behaviour of species is fundamental to improve the biological surveillance and to target control efforts [18]. For example, some insect species have been thought as a poor flyer as its range of local dispersal is generally assumed to be limited to a few hundred meters only; nevertheless, recent studies suggest that these insects can fly further than the limit that is usually deemed sufficient for containment and control measures [19,20]. This insight illustrates that dispersal behaviour of species is a critical element to be considered in estimating the spread of certain ecological species and provide essential information for defining effective biological control strategies, which rely on a clear understanding of dispersal patterns of ecological communities [21].

Incorporating biotic and abiotic interactions, as well as local dispersal processes, is an essential first step in creating accurate models of species distributions [22]. Due to the complexities of examining the impacts of trophic interactions and species' dispersal process across heterogeneous environments, we employed a mathematical model using partial differential equations (PDEs) consisting of biotic interactions between prey and specialist predator species using Holling type-II functional and numerical responses [23]. Generalist predation force is incorporated into the model using a mortality term, which we assume to be a density-independent death rate across a range of environmental conditions. This ecological system is solved using numerical simulation and bifurcation analysis techniques to demonstrate how distinct ecological forces like predator handling time and the magnitude of local dispersal interact to determine community compositions.

This paper is structured as follows. First, some theoretical analysis of this trophic interactions system is described. We then solve this model using numerical simulation and bifurcation analysis and highlight our main findings in terms of species coexistence, species exclusion, and oscillatory dynamics outcomes. Finally, some of the ecological implications of our results are also discussed.

Trophic interactions iodel: A partial differential equation system

As a way to describe the effects of prey-predator interactions and local dispersal on species biodiversity along a one-dimensional environmental gradient of $0 \leq x \leq 1$, we employ a partial differential equation model for predator $\left(P(x,t)\right)$ and prey species $\left(N(x,t)\right)$:

$$\frac{\partial N}{\partial t} = (r - cN - gx)N - \frac{aNP}{1+akN} + D_N \frac{\partial^2 N}{\partial x^2},$$
$$\frac{\partial P}{\partial t} = \frac{baNP}{1+akN} - (m + gx)P + D_P \frac{\partial^2 P}{\partial x^2}. \quad (1)$$

where r is the intrinsic growth rate of density N, c is the strength of intraspecific density dependence, and g is the strength of mortality gradient for both prey and predator, and m is the mortality force (i.e., death rate) mediated by generalist predation. The parameter a describes the attack rate on prey, the parameter b indicates the rate of conversion of prey into the birth of new predator species, and the term

k reflects the handling time for predator to consume prey species. Model (1) is made up of a prey-predator system (with Holling type-II functional response) that is extended along an environmental gradient, x. The reaction terms of the model (1) are comparable to those of the Rosenzweig-MacArthur model [24,25], which becomes a PDE when the diffusion terms are included. The terms D_N and D_P are the diffusion coefficients of prey and predator species, respectively.

Consistent with some ecological literature [4,26,28,31], we set zero-flux boundary conditions on each species to simulate a situation in which no species can migrate across boundaries:

$$D_N \frac{\partial N}{\partial x}\Big|_{x=0,1} = D_P \frac{\partial P}{\partial x}\Big|_{x=0,1} = 0. \quad (2)$$

Without dispersal ($D_N = D_P = 0$), model (1) corresponds to an ordinary differential equations (ODE) system in which the dynamical behaviour at a specific environment x in independent of the behavior at all other environments. The steady states and local stability analysis can be computed, and the model possesses three different steady states (S_i) in the form of (N^*, P^*) where i specifies the type of steady states that occur in the system:

$$S_0 = (0,0)\,, S_1 = \left(\frac{(r-gx)}{c}, 0\right),$$

$$S_2 = \left(\frac{m+gx}{a[b-k(m+gx)]}, \frac{(r-cN^*-gx)(1+akN^*)}{a}\right).$$

The steady state S_0 represents the extinction of both prey and predator species. In the absence of predator, the prey density is $N^*(x) = (r-gx)/c$. As a result, the highest prey density is achieved at $x = 0$ which is $N^*(0) = r/c$. The steady state S_1 represents the survival of prey species and exclusion of predator species. Meanwhile, in the steady state S_2, prey and predator species coexist.

In the presence of local dispersal ($D_N, D_P > 0$), the PDE model is represented by the trophic system (1). To solve this system, we performed numerical simulation using MATLAB ode15s solver for an adequate time (e.g., t = 1000) until steady state is obtained. We also verified that steady state is stable (i.e., all the real parts of the eigenvalues are negative). The Jacobian matrix and the eigenvalues are calculated numerically using MATLAB fsolve and eig functions, and readers who are interested in the PDE stability analysis method is directed to the following work [4,26,27,28]. In general, a stable PDE system steady state is the one in which all of the real components of the obtained eigenvalue spectrum are negative. We also use the numerical continuation software Auto to track both stable and unstable steady states, as well as bifurcation points, as the magnitude of a specific parameter value changes. The parameter values of this PDE model are presented in Table 1 unless otherwise mentioned, and they are inspired by several ecological studies [29,30].

Results and discussion

The dynamical behavior of the model under various dispersal scenario

Now, we illustrate how the changes in local dispersal strength, trophic interactions, and abiotic environments affect the dynamical behaviour of prey-predator populations using numerical simulation. To explain the difference in the steady states observed and to better understand the underlying ecological mechanisms behind the emergence and exclusion of certain dynamics in the system (1) under varying dispersal strength and handling times of predator, we also perform bifurcation analysis on the PDE system (1) and the findings are presented in the next sub-sections.

Table 1. Parameter values.

Symbol	Description	Parameter
r	The intrinsic growth rate of density prey species	1
c	Strength of intraspecific density dependence of the prey species	0.02
g	Strength of mortality gradient for both prey and predator	1
a	The attack rate on prey species	0.1
b	Prey conversion rate into the birth of predator	1
k	The handling time of predator	0.4
m	The death rate of predator	0.2
$D_N = D_P = D$	The strength of symmetric dispersal of prey and predator species	Vary

No-dispersal (D= 0): The roles of generalist predation and environments

Without dispersal $(D = 0)$, we discover that range limits are influenced by trophic interactions between species, abiotic environments, and their handling times, k. The density of prey along an environmental gradient, x, is depicted in Fig. 1 when $k = 0.4$. Two critical values emerge in this system, corresponding to transcritical (TB) and supercritical Hopf (HB) bifurcations. When two steady state branches of S_1 and S_2 exchange stability after passing through the point $x = 0.7126$ (where S_2 becomes unstable and S_1 becomes stable beyond the TB point), the transcritical bifurcation occurs. The mortality force induced by generalist predation gets more severe as the magnitude of x increases, i.e., $x > 0.7126$, the exclusion of specialist predator is observed (i.e., through steady state S_1); only the prey species survives in this situation, and the other species are displaced. Ecologically, a transcritical bifurcation represents a species' invasion (or extinction) boundary in the ecological system.

Based on Fig. 1, a supercritical Hopf bifurcation is another type of bifurcation that occurs in this system, which appears at x = 0.269. As the generalist predation force decreases with magnitude of x (i.e., $x <$ *0.269)*, then coexistence of species through oscillatory dynamics is possible. Although there occur stable limit cycles in this trophic system (green curve), the amplitude of oscillations of these limit cycles increases, causing the specialist predator and prey species to fluctuate. In certain environments where the prey-predator species fluctuate to extremely low densities over time, this could increase the risk of some species to go extinct due to demographic factors. In general, lower population densities are more vulnerable to such random extinction and could result is destabilization of species biodiversity. Contrarily, when generalist predation force is rather moderate (i.e., *0.269* < x < *0.7126*), a two-species stable steady state appears near the central portions of x, which can enhance species biodiversity; in this case, coexistence of prey-predator species is observed

Apart from generalist predation and abiotic environments, other ecological factors such as local dispersal and handling times can shape species biodiversity in this ecosystem. We now investigate how predator handling times and local dispersal affect distinct dynamical behaviours in this ecological model (1). We highlight our findings by employing bifurcation analysis and numerical simulation approaches under several dispersal scenarios.

The effects of low and moderate dispersal levels on community dynamics

Inclusion of low and moderate dispersal levels (e.g., $D = 0.0002$) into the model causes intriguing spatio-temporal observations as the values of k vary. As shown in Figure 2 below, this PDE model represents the occurrences of: (i) species coexistence when $k = 0.2$ (Fig. 2a) and $k = 2.4$ (Fig. 2c); (ii)

oscillatory dynamics when $k = 0.7$ (Fig. 2b); and (iii) exclusion of predator when $k = 5.0$ (Fig. 2d) in some portions of x, particularly towards the left end of spatial domain. Closer examination of our spatio-temporal observations also suggests that there occur several critical values of k beyond which distinct ecological outcomes emerge in this system. These threshold phenomena influence some bifurcation changes in dynamics in the PDE model as k evolves

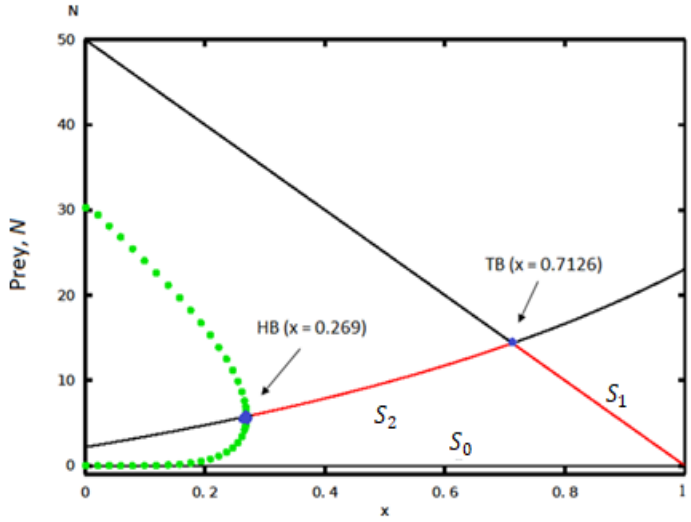

Figure 1. Bifurcation analysis of the model with no dispersal $(D = 0)$ as x changes. Curves in red (or black) represent steady states, while curves in green represent oscillatory dynamics. The HB and TB thresholds represent supercritical Hopf (HB point) and transcritical bifurcations (TB point), respectively.

One-parameter bifurcation analysis is then performed as predator handling times varied to better understand why certain dynamical behaviours appear (or disappear) in the PDE model at low and moderate dispersal levels. For instance, Fig. 3 depicts the density of specialist predator species $(P14)$ when $D = 0.0002$ at environment $x = 0.2$ as k varies. Multiple attractors exist: middle branches (two species coexistence steady state) and lower branches (single species steady state with prey survives) can be either stable (red curves) or unstable (black curves) depending on k values; oscillatory dynamics (green curves) occur, resulting in the coexistence of prey and predator species via stable limit cycles. From the bifurcation analysis of the no-dispersal scenario, we discovered that supercritical Hopf bifurcation can mediate the stable oscillatory dynamics in this model (Fig. 1). In our PDE model, this phenomenon (supercritical Hopf bifurcations, i.e., k_l and k_r), is still evident, but Fig. 2 shows the emergence of subcritical Hopf bifurcations (grey points) when $k_{cl} < k < k_{cr}$; in this case, unstable limit cycles (blue curves) are created in some regions of k, leading to bistability between stable limit cycles and two-species coexistence steady state. A basin boundary, which corresponds to unstable limit cycles (blue curves), separates these two bistable attractors with the long-term dynamics are determined by the initial distributions of species. In addition, coexistence outcome can also occur via two-species steady states when $k < k_l$ or $k_r < k < k_t$, where k_t denotes transcritical bifurcation (black point). In the long run, as k increases further (i.e., $k > k_t$), specialist predators can be displaced and only prey species survive. Furthermore, we also discover that, in some regions of x, inclusion of local dispersal into the model stabilizes trophic dynamics and mediates more outcomes with species coexistence (via two-species steady state and oscillatory dynamics), as compared to the no-dispersal scenario (Fig. 1).

Additionally, it is discovered that the presence of low and moderate local dispersal fundamentally affects the response of this ecological system, resulting in intriguing dynamical behaviours. These ideas may be seen in our findings as stable limit cycles alternate with unstable ones when handling times change. Because of this, the system attractors can emerge in various stable or unstable states, and these outcomes are made possible by incorporating local dispersal and the spatial dimension.

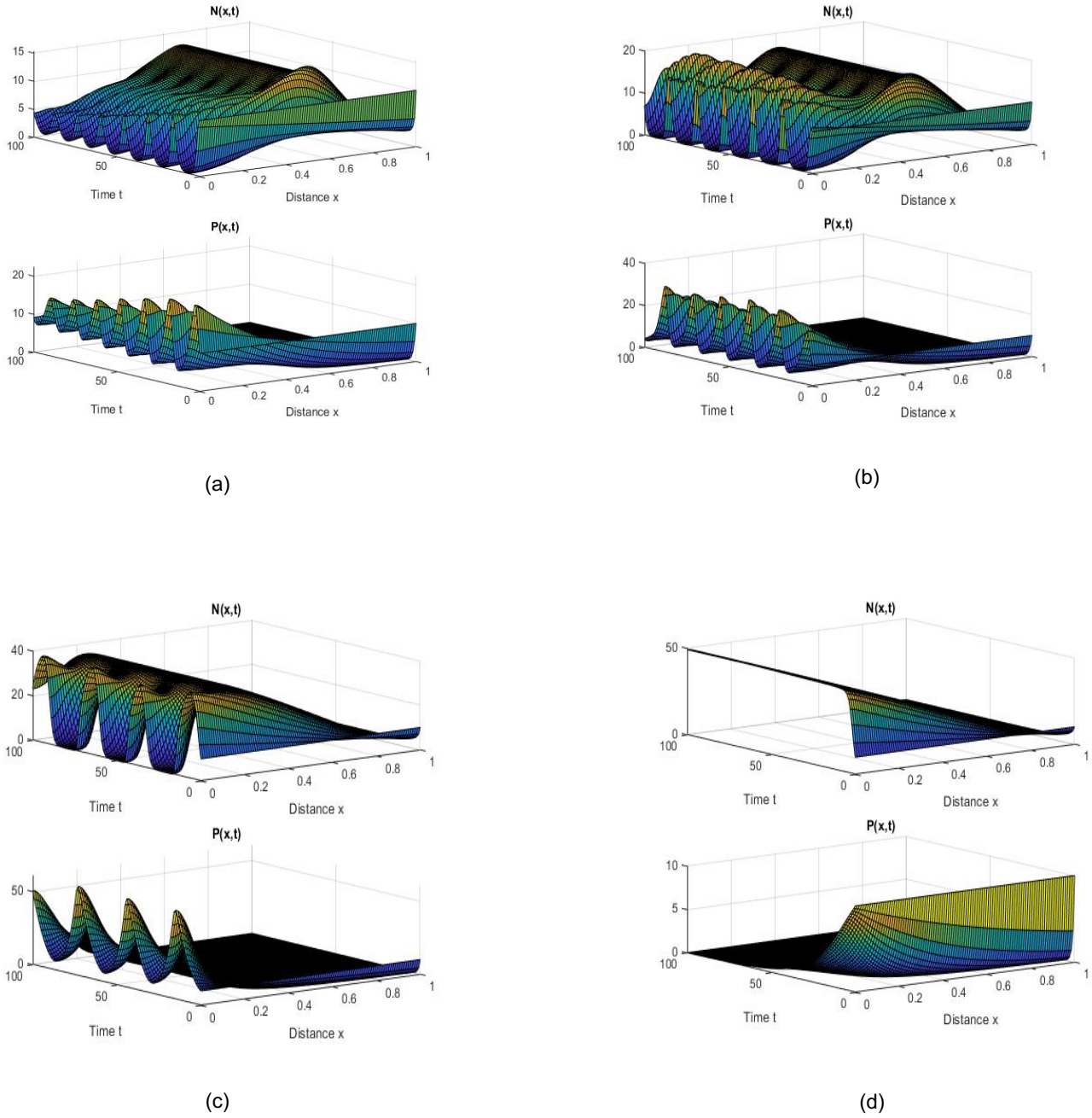

Figure 2. Numerical simulation of a PDE model for predator $\left(P(x,t)\right)$ and prey species $\left(N(x,t)\right)$ with low and moderate dispersal, $D = 0.0002$. (a) The system's spatial-temporal behaviour when $k = 0.2$. (b) The system's spatial-temporal behaviour when $k = 0.7$. (c) The system's spatial-temporal behaviour when $k = 2.4$. (d) The system's spatial-temporal behaviour when $k = 5.0$.

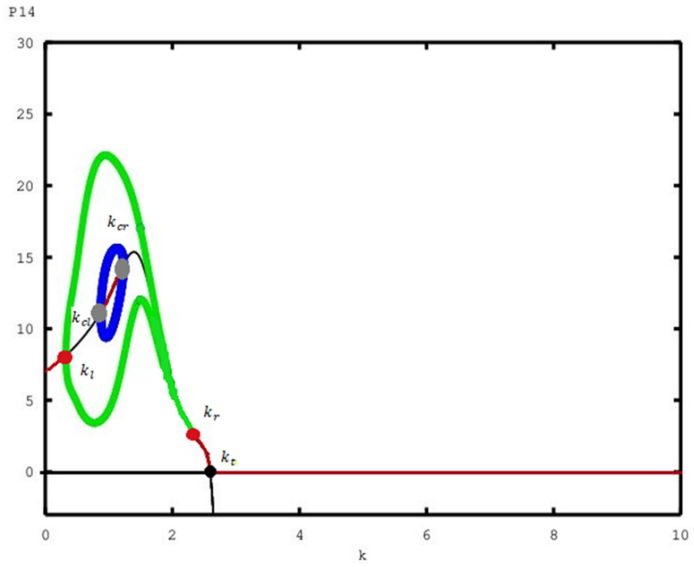

Figure 3. The density of specialist predator species for the PDE model, $(P14)$ at $D = 0.0002$, $x = 0.2$ and $m = 0.3$ as handling time, k, changes. k_l and k_r are the threshold values for supercritical Hopf bifurcation (red point), while k_{cl} and k_{cr} are the threshold values for subcritical Hopf bifurcation (grey point). Transcritical bifurcation is indicated by the critical point k_t (the black dot). Stable (or unstable) steady states are shown by red (or black) lines, and stable (or unstable) limit cycles are denoted by green (or blue) curves. The middle (two-species steady state) and bottom (single-species steady state with prey survival) branches can be either stable or unstable, depending on the values of k.

The effects of rapid dispersal levels on community dynamics

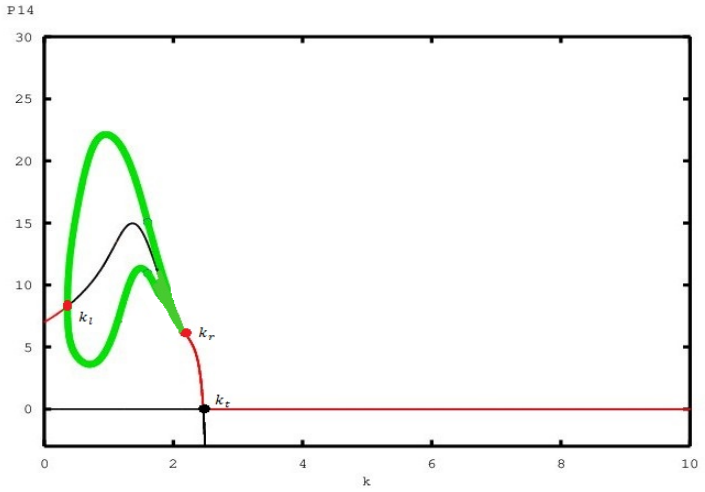

Figure 4. The density of specialist predator, $(P14)$ as handling time, k, varies in the PDE model for $D = 0.0005$, $x = 0.2$ and $m = 0.3$. The supercritical Hopf bifurcation is represented by the threshold values k_l and k_r (red points), whereas the transcritical bifurcation is represented by k_t (black point). Stable (or unstable) steady states can emerge in the system, and they are represented by red (or black) curves, whereas stable limit cycles are represented by green curves. The middle (two-species steady state) and bottom (single-species steady state with prey survival) branches can be either stable or unstable, depending on the values of k. The other parameter values are shown in the Table (1).

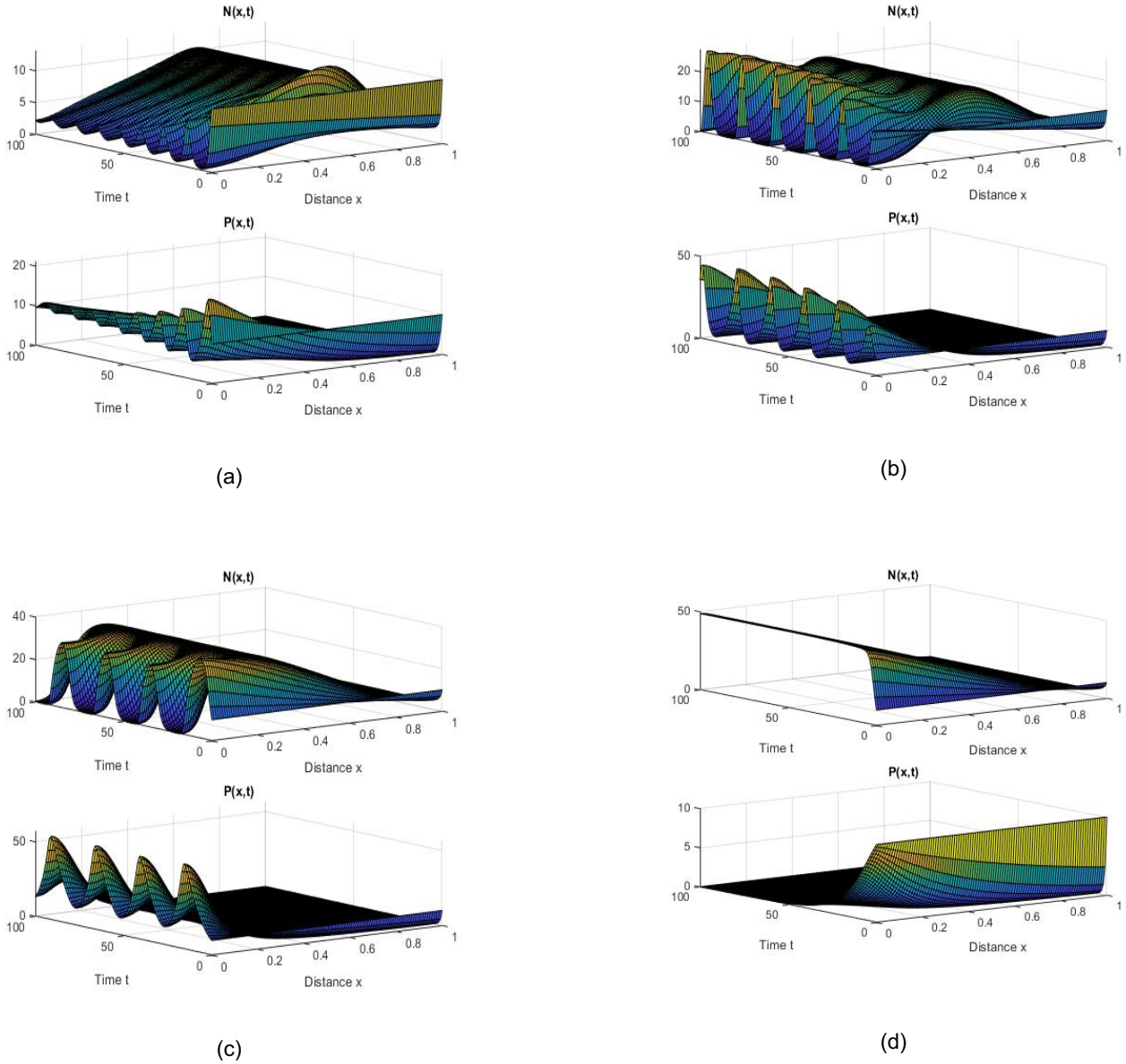

Figure 5. Numerical simulation of a PDE model for specialist predator $(P(x,t))$ and prey species $(N(x,t))$ with strong dispersal, $D = 0.0005$. (a) The system's spatial-temporal behaviour when k= 0.2. (b) The system's spatial-temporal behaviour when k= 1.0. (c) The system's spatial-temporal behaviour when k= 2.3. (d) The system's spatial-temporal behaviour when k= 5.0.

Increasing the intensity of local dispersal reduces the bifurcational changes in the dynamics of this ecological system even further. The density of specialist predator species $(P14)$ under k-parameter variation in the presence of rapid dispersal scenarios (e.g., $D = 0.0005$) is shown in Fig. 4, which can be compared to our findings in Fig. 3. Supercritical Hopf bifurcations (red points) and transcritical bifurcations are both associated with certain k threshold values, such as k_l, k_r and k_t (black point). Crossing some of these thresholds would lead to a change in qualitative dynamics; (i) coexistence via stable steady state of two species (when $k < k_l$ or $k_r < k < k_t$); (ii) stable limit cycle $(k_l < k < k_r)$; (iii) prey species survival and the exclusion of a specialist predator $(k > k_t)$. These observations are evident when we scrutinize the spatio-temporal diagrams of the PDE model. As shown in Fig. 5, we observe the occurrences of species coexistence via steady state (when $k = 0.2$ and 2.3, as shown by Fig. 5a and 5c,

respectively), oscillatory dynamics (when $k = 1.0$, as shown by Fig. 5b) and exclusion of predator species (when $k = 5$, as shown by Fig. 5d) in some portions of x. We also notice that the subcritical Hopf bifurcations and unstable limit cycles are not evident in our bifurcation analysis of the rapid dispersal process. When local dispersal levels are strong, some intriguing dynamical behaviours in this prey-predator system cease to emerge. As a result, the bistability phenomena found at low (or moderate) dispersal levels disappears, resulting in the exclusion of unstable state of population oscillations for higher dispersal scenarios.

It is also observed that the phenomena of species biodiversity destabilization is weakened in the presence of local dispersal, as compared to no-dispersal scenario (compared green curves in Fig. 1 with Fig. 3 and Fig. 4). Because local dispersal plays a significant role in interactions with handling times and predation pressure, these ecological processes increase the likelihood of maintaining population densities to oscillate further away from zero, thereby decreasing the likelihood of a population becoming extinct (due to demographic factors).

Conclusions

In this work, a bifurcation analysis and numerical simulation studies have been carried out to reveal the effects of local dispersal and trophic (prey-predator) interactions on species biodiversity using a PDE model (1). This ecological system exhibits a wide range of dynamics that correspond to the different outcomes of species interactions in ecological communities, such as species coexistence, species exclusion, bistability, and oscillatory dynamics. Our findings also demonstrate that inclusion of local dispersal into the model stabilizes trophic dynamics and mediates additional observations about species coexistence. Species dispersal reduces the impact of population fluctuations on species biodiversity by reducing their amplitudes. This condition enhances the possibility to keep population densities further away from zero, therefore lowering the chance of a species population to go extinct. Finally, local dispersal also induces intriguing dynamical behaviour in the system such as bistability and unstable limit cycles.

Acknowledgments

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