

Joint Effects of Symmetric and Asymmetric Dispersal on the Complex Dynamics of a Multiple Interactions Type System

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Abstract This paper extends a multiple interactions type ecological system by incorporating both symmetric and asymmetric dispersal mechanisms. Using this partial differential equations model, we numerically show different spatio-temporal dynamics of interacting species. We then examine the dynamical behaviours of the system for a wide range of parameter values, thereby permitting an investigation of the interplay between local dynamics due to mutualist-resource-competitor-exploiter interactions on the one hand and dispersal rate and its (a)symmetry, on the other. To do this, a co-dimension one bifurcation analysis is performed using the magnitude of competitor and resource species interactions under various dispersal scenarios. In the absence of dispersal, our analysis by varying the competitive pressure uncovers some bifurcational changes in dynamics such as supercritical Hopf and transcritical bifurcations. The interactions between these two local bifurcations result in intriguing outcomes, namely coexistence steady states, stable limit cycles and alternative stable states. Inclusion of low (or moderate) levels of symmetric dispersal into the system modifies the response of this ecological community towards the change in competitive pressure and mediates distinct multiple species coexistence steady states. As symmetric dispersal increases to rapid migration levels, a greater stabilising impact on the dynamics of the system is observed and this situation enhances the likelihood of species diversity. In the case of asymmetric dispersal, alternative stable states phenomenon has been found to be more pronounced due to the emergence of different bistable attractors, which include two coexisting stable limit cycles. Owing to this reason, we predict sensitivity of dynamics to small perturbations in initial densities of mutualist-resource-competitor-exploiter species. It is also unveiled that the

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(in)direct effects exerted by resource species can interact with dispersal asymmetry to engender subcritical Hopf, period-doubling and limit point bifurcations of cycles: these phenomena also exhibit complex dynamical behaviours such as alternative stable states or unstable dynamics, which can stabilise or destabilise this multi-species community.

Keywords Partial differential equations · Hopf bifurcation · Transcritical bifurcation · Period-doubling bifurcation · Saddle-node bifurcation · Numerical bifurcation analysis

1 Introduction

The dispersal dynamics has received much attention in mathematical biology and ecology [1–4]. The stabilisation of multiple species communities by dispersal plays a crucial role in reducing the extinction of vital species from the ecosystem and supporting the recolonisation process of rare species [5–9]. Several studies have illustrated the importance of symmetric [10, 11] and asymmetric [12–16] dispersal strength in (di)stabilising multiple species system. The stability of this system where based on the strength of dispersal among interacting species. However, these studies focus on two habitat patches and in real life, more than two habitat patches interacts. More importantly, it remain unknown what effect do symmetric and asymmetric dispersal strength have on multiple interactions type community.

Several studies have described population oscillation as a consequence of antagonistic interactions and affect the change in species fitness [17, 18]. The dispersal strength determines the synchronisation of the multi-species communities across space [19, 20]. Spatial synchronisation reduces the positive effects of dispersal in stabilising multi-species system with population oscillation [21, 7]. There are conflicting reports on the stabilisation effects of dispersal on multi-species communities. For instance, Hudson and Cattadori [22] report dispersal as a sword with double-edge, i.e., it can have both synchronisation and stabilising effects on multiple species communities. Some theoretical studies report that the synchronisation effects of dispersal destabilise (i.e., affects species persistence and coexistence) multi-species ecosystem [23, 24]. Also, several theoretical and experimental studies report the effects of dispersal on community stabilisation (i.e., either stabilising, destabilising or no-effects) [25–27]. An essential ecological question is what effects do the interplay between local dispersal and competition have on the community stabilisation and species coexistence mechanisms in a multiple interactions type model?.

Competition is a vital biotic interaction among interacting species in the natural ecosystem [28]. The Lotka-Volterra competition model form the basis of competition among interacting species in the ecosystem [29, 30]. In this model, species coexistence is possible if and only if the intraspecific competition is stronger than interspecific competition [31–33]. However, species coexistence

is not possible if the interspecific competition is stronger than the intraspecific competition (i.e., "competitive exclusion principle occur") [34]. However, this situation is paradoxical as species coexistence are observed in nature. Hence the ecological question, what mechanisms allow stabilisation of multi-species communities and species coexistence in a multiple interactions type system? One possible way is through the interplay between multiple biotic interactions and dispersal. Kondoh [35] report that multiple interactions type model provide a good framework for understanding multi-species communities. Some studies report that there is a synergistic relationship between species diversity and interactions type [36–38].

Simulation studies of multiple interactions type model show some complex dynamical behaviours (e.g., chaotic dynamics and oscillations) [39]. In another study of the four-species system, dispersal mechanisms influence the population dynamics of the interacting species in the communities [40]. Shabunin [41] report that species interactions strength and distinct dispersal mechanisms induce various amplitude of cycles in the general community structure. Given these divergent views, we investigate the combined effects of symmetric, asymmetric dispersal and competition on multiple interactions type system. Specifically, it remains unknown what effects symmetric, asymmetric dispersal and competition has on the coexistence dynamics of multiple interactions type system.

To address this knowledge gap, we extend the ecological system of [42] by incorporating local dispersal mechanisms. This incorporation of dispersal mechanisms transforms nonlinear ordinary differential equations into the system of nonlinear partial differential (PDE). We employ numerical simulations and bifurcation analysis techniques to explore the joint effects of local dispersal and its (a)symmetry together with distinct biotic interactions on the dynamics of this ecological model.

2 Model description

We employ a system of PDE for the densities $X(x, t)$, $W(x, t)$, $Y(x, t)$ and $Z(x, t)$ in one-dimension $0 \leq x \leq 1$ [42–44]:

$$\begin{aligned}
 \frac{\partial X}{\partial t} &= X \left(r_X - X - \beta W - aY + \frac{uZ}{h_x + Z} \right) + D_X \frac{\partial^2 X}{\partial x^2}, \\
 \frac{\partial W}{\partial t} &= W(r_W - W - \alpha X) + D_W \frac{\partial^2 W}{\partial x^2}, \\
 \frac{\partial Y}{\partial t} &= Y(gaX - d) + D_Y \frac{\partial^2 Y}{\partial x^2}, \\
 \frac{\partial Z}{\partial t} &= Z \left(r_Z - Z + \frac{vX}{h_x + X} \right) + D_Z \frac{\partial^2 Z}{\partial x^2}.
 \end{aligned} \tag{1}$$

where X , W , Y , Z are the time-dependent population densities of resource,

competitor, exploiter and mutualist species, respectively. The term r_X is the growth rate of the resource species; r_W is the growth rate of the competitor species; r_Z is the growth rate of the mutualist species; α and β represent the competition strength; a represents the rate at which the exploiter captures the resource species; g represents the conversion efficiency; d represents the death rate of the exploiter; u and v represent the benefits from the mutualistic interactions; h_X and h_Z represent the half-saturation constant. The strength of mutualist species self-regulation is set to unity for simplicity. The system (1) is a spatial extension of the multiple interactions type model [42]. In general, the system of ordinary differential equations (ODE) becomes systems of PDE with the addition of the diffusion term. The term D_i ($i = X, W, Y, Z$) represents the local dispersal strength along spatial domain x . We assume distinct dispersal strength to reflect on the dynamics of multi-species. Also, we apply zero-flux (or Neumann) boundary conditions for each of the species (i.e., no movement can occur across the boundaries):

$$\begin{aligned}
 D_X \frac{\partial X(0,t)}{\partial x} &= D_X \frac{\partial X(1,t)}{\partial x} = 0, \\
 D_W \frac{\partial W(0,t)}{\partial x} &= D_W \frac{\partial W(1,t)}{\partial x} = 0, \\
 D_Y \frac{\partial Y(0,t)}{\partial x} &= D_Y \frac{\partial Y(1,t)}{\partial x} = 0, \\
 D_Z \frac{\partial Z(0,t)}{\partial x} &= D_Z \frac{\partial Z(1,t)}{\partial x} = 0.
 \end{aligned} \tag{2}$$

While there are several boundary conditions (e.g., Dirichlet, zero-flux, periodic) [45–49] that can be used in modelling natural ecosystems, we have employed zero-flux boundary conditions primarily because it is ecologically a more realistic choice, which mimics the island biogeography scenario where the interacting species cannot escape from this isolated (or closed) community. Therefore, the local dynamics and species diversity are merely affected by different interaction types (e.g., competition, exploitation and mutualism) and also dispersal process between neighbouring habitats, which is the main focus of this work. This kind of boundary condition is also chosen to emphasise parallel with other ecological and theoretical studies [43, 44, 50, 51], which have also used zero-flux boundary conditions to model their biological populations. This certainly provides an advantage to compare (and contrast) our findings with these published results, together with allowing us to extend previous knowledge and highlight the novelty of the work in light of previous studies. Indeed, we have made a deliberate choice to consider Neumann boundary conditions as shown in equations (2), and we acknowledge that other boundary conditions such as periodic boundary can be employed to avoid introducing boundary effects. Additionally, the spatial domain x can also be extended to larger domain so as to eliminate these effects. Based on the preliminary analysis conducted, we have tried to eliminate these effects in our simulation before and we seen qualitatively similar dynamics to those observed in the

findings of this work. One of the plausible reasons between the similarity in qualitative behaviour might be due to the ecological system considered here is spatially-homogeneous. Consistent with the ecological mid-domain effect (i.e., increasing overlap of species ranges towards the center of an ecosystem domain) [52], we also focus our analysis on the dynamical behaviours near the central regions (which is further away from the boundaries of spatial domain); thus, we do not expect to observe any noticeable difference between the results with (e.g., using zero-flux) and without (e.g., using periodic) boundary effects.

3 Numerical Method

To solve equations (1) with the boundary conditions defined in equations (2), we use the method of lines. This numerical method is implemented in MATLAB and it provides a good platform for solving systems of PDE in both spatial variable x and time t [53]. Using the method of line, the $0 \leq x \leq 1$ spatial domain is divided into meshes with $M + 1$ equal points with $x_i = ih$ for $i = 0, 1, \dots, M$. The central difference approximation is used to replace the spatial derivative in equations (1):

$$\begin{aligned}\frac{\partial^2 X}{\partial x^2} &= \frac{X_{i+1} - 2X_i + X_{i-1}}{h^2}, \\ \frac{\partial^2 W}{\partial x^2} &= \frac{W_{i+1} - 2W_i + W_{i-1}}{h^2}, \\ \frac{\partial^2 Y}{\partial x^2} &= \frac{Y_{i+1} - 2Y_i + Y_{i-1}}{h^2}, \\ \frac{\partial^2 Z}{\partial x^2} &= \frac{Z_{i+1} - 2Z_i + Z_{i-1}}{h^2}.\end{aligned}\tag{3}$$

Further, the zero-flux boundary conditions equations (2) are encoded into this numerical scheme using the finite difference approximation. The resulting transformation leads to a $4(N + 1)$ systems of ODE, one for each species across spatial locations x . Standard ODE solver, `ode15s`, is employed to solve the resulting system of ODE for $t = 1000$. The mesh size $h = 0.09$ is used in the numerical simulation. Similarly, for numerical simulation in XPPAUT, we also discretised model (1) using the method of lines where the PDE is transformed into a large system ODE, and the resulting system is solved using `cvsolve` solver for $t = 1000$. Furthermore, we also employed AUTO to continue the steady-state, in which case we tracked the stable, unstable and bifurcation points that emerge in this ecological system as the parameters are varied [54]. It is also checked that the numerical results are insensitive to a reduction in grid spacing (i.e., as the magnitude of different finite points is increased). The parameter values used in the numerical simulation are defined in Table 1, which are motivated by the ecological studies of [42, 43]. For the stability analysis of the model in the absence of dispersal ($D = 0$), interested readers are referred to [55].

Table 1: Parameter values

Parameter	Definition	Values
r_X	The intrinsic growth rate of resource species	1
r_W	The intrinsic growth rate of competitor species	1
r_Z	The intrinsic growth rate of the mutualist species	1
u	Maximum benefit of the mutualistic interaction	3
v	Maximum benefit of the mutualistic interaction	2
a	Capture rate	2.8
g	Conversion efficiency of the exploiter species	0.25
d	Death rate of the exploiter	0.05
h_X	Half saturation constant of the hyperbolic functional response	1
h_Z	Half saturation constant of the hyperbolic functional response	1
β	Competitive strength of the competitor species	0.7 (Vary)
α	Competitive strength of the resource species	0.2 (Vary)
D_X	Dispersal strength of resource species	0.005
D_W	Dispersal strength of competitor species	0.003
D_Y	Dispersal strength of exploiter species	0.0027
D_Z	Dispersal strength of mutualist species	0.004

4 Results

Using this multiple interactions type system with parameter values as specified in Table 1, we first numerically show different spatio-temporal dynamics of interacting species. For instance, the existence of multi-species coexistence steady state (Figure 1 and Figure 3) and stable limit cycles (Figure 2 and Figure 4) are illustrated for different choices of initial condition (i.e., represented by distinct colour trajectories). For distinct initial densities, the system dynamics converge to an ecologically feasible state and this demonstrates the stability property of the attractor under consideration. We also discover that multiple coexistence state outcomes and oscillatory dynamics are the inherent characteristics of this ecological system consisting of mutualist-resource-competitor-exploiter species. In the following subsections, we examine the dynamical behaviours of the system for a wide range of parameter values, thereby permitting an investigation of the interplay between local dynamics due to different interaction types on the one hand, and dispersal rate and its (a)symmetry, on the other.

4.1 Bifurcational changes in dynamics mediated by competitor species under distinct dispersal scenarios

Since one of the goals of this work is to improve our understanding of how competitive strength and dispersal process affect biodiversity of species in a complex ecological system, we perform a co-dimension one bifurcation analysis as parameter β (i.e., the strength of competitor species) varies under various dispersal scenarios. These findings are illustrated in Figure 5 where we consider no-dispersal case (Figure 5 (a)), symmetric (Figure 5 (b)-(c)) and asymmetric

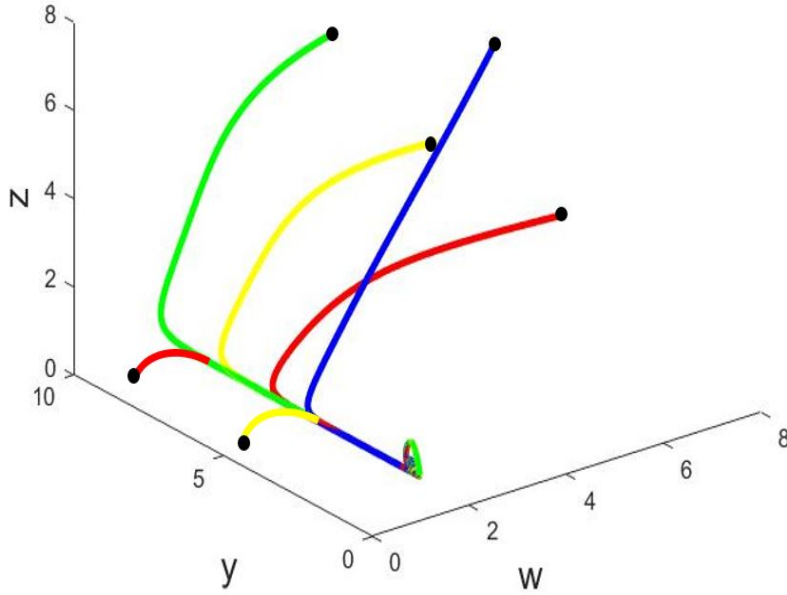


Fig. 1: Global stability of the system for different initial conditions. Initial population densities: $X(x, t = 0) = 0.9$, $W(x, t = 0) = 0.7$, $Y(x, t = 0) = 0.6$, $Z(x, t = 0) = 0.8$. The diagram is plotted using MATLAB package and the parameter values as in Table 1.

(Figure 5 (d)) dispersal processes. We compare the outcomes of these different dispersal scenarios to examine how dispersal process interacts with competitive dynamics in this mutualist-resource-competitor-exploiter system.

In the absence of dispersal ($D = 0$), Figure 5 (a) shows the dynamical behaviour of this multi-species system as competitive strength, β , changes. There occur some threshold values of β corresponding to supercritical Hopf bifurcation (i.e., HSB : red point) and transcritical bifurcations (i.e., $TB1$ and $TB2$: black points). The existence of some branches of steady states is also observed, particularly unstable (black curves) and stable (red, yellow and blue curves) steady states. As β changes, the emergence of different stable attractors are realised: (i) four-species steady-state (red curve) i.e., when $\beta < HSB$; (ii) bistable outcomes between three- (yellow curve) and two- (blue curve) species steady states i.e., when $TB2 < \beta < TB1$; (iii) two-species (blue curve) steady state i.e., when $\beta > TB1$. When $HSB < \beta < TB2$, oscillatory behaviour

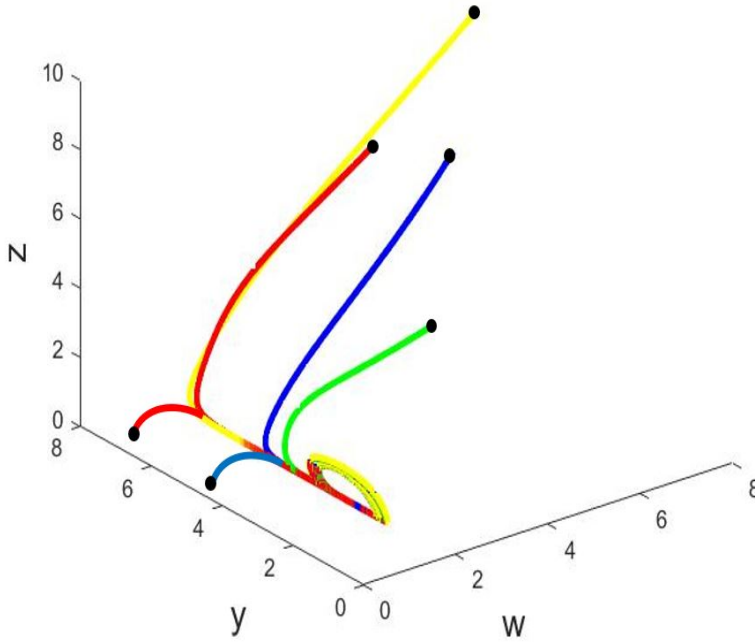


Fig. 2: The existence of limit cycle dynamics for distinct choice of initial condition. Initial population densities: $X(x, t = 0) = 0.9$, $W(x, t = 0) = 0.7$, $Y(x, t = 0) = 0.6$, $Z(x, t = 0) = 0.8$. The diagram is plotted using MATLAB package and the parameter values as in Table 1.

(green dots) emerges with population fluctuations in this four-species system are observed; in this case, stable limit cycles appear with all steady states of the system become unstable. Due to this reason, the trajectories do not converge to any steady state as it converges to a stable limit cycle from positive initial densities.

Next, we establish the effects of symmetric dispersal process in this multi-species model, as demonstrated by Figure 5 (b). Inclusion of low (or moderate) levels of symmetric dispersal (e.g., $D = 0.0027$) into the system modifies the response of this ecological community towards the change in competitive pressure and mediates distinct multiple species coexistence steady states: (i) four-species steady state (red curve); (ii) three-species steady state (yellow curve); (iii) two-species steady state (blue curve). While the occurrences of Hopf bifurcation and oscillatory dynamics are not evident in this case, we observe that transcritical bifurcation plays an important factor in determining

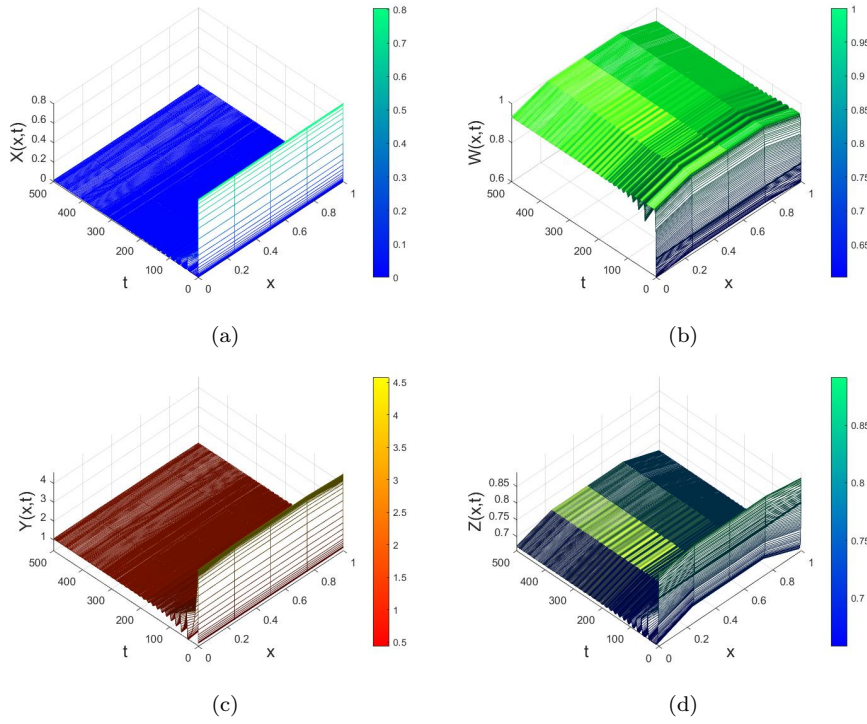


Fig. 3: Spatio-temporal diagram of the system with distinct dispersal strength i.e., $D_X = 0.005$, $D_W = 0.003$, $D_Y = 0.0027$ and $D_Z = 0.004$. Initial population densities: $X(x, t = 0) = 0.9$, $W(x, t = 0) = 0.7$, $Y(x, t = 0) = 0.6$, $Z(x, t = 0) = 0.8$. The diagrams are plotted using MATLAB ode15s solver and the parameter values as in Table 1.

the survival (and exclusion) of different interacting species in this multiple interactions type system. It is also discovered that the strength of multiple interactions type arising from distinct ecological populations such as resource, competitor and exploiter species is amplified in the presence of dispersal, which can weaken the chance of species survival in this ecological system.

An increased in symmetric dispersal level (e.g., $D = 0.005$) leads to a greater stabilising impact on the dynamics of the system, as shown by Figure 5 (c). It is observed that rapid dispersal process between interacting species shifts the critical values of competitive pressure ($TB1$ and $TB2$) to higher thresholds and promotes more outcomes with multiple species coexistence (compare Figure 5 (c) with Figure 5 (b)); for example, the four-species coexistence steady state (red curve) occurs at more values of β , which enhances the likelihood of species diversity. As the dispersal rate increased, the onset of oscillatory dynamics through Hopf bifurcations (HSB) are observed again. It is also realised that there are two small ranges of bistability characterised by the

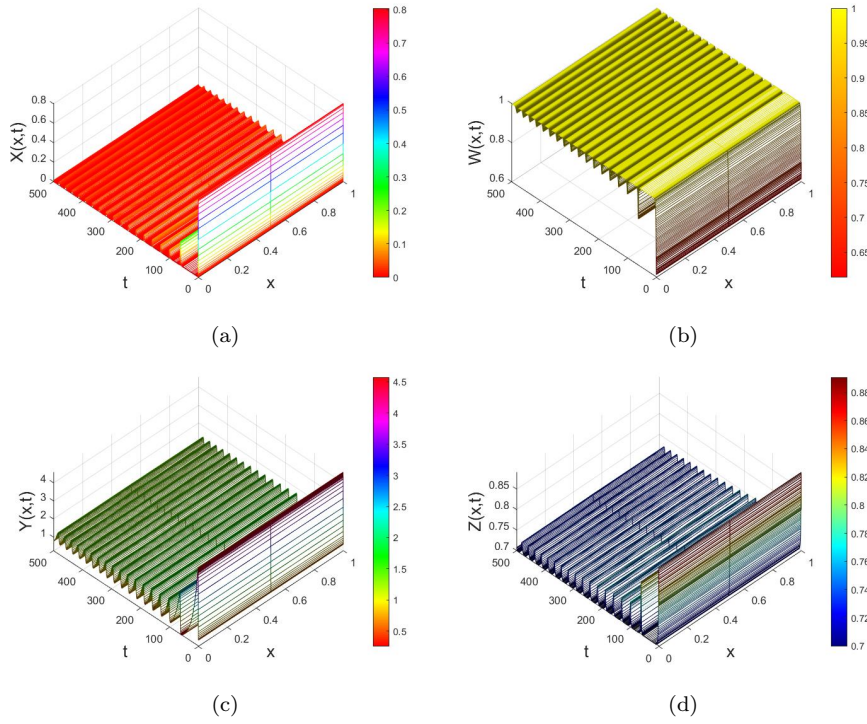


Fig. 4: Spatio-temporal diagram of the system in the absence of dispersal (i.e., $D_X = D_W = D_Y = D_Z = 0$). Initial population densities: $X(x, t = 0) = 0.9$, $W(x, t = 0) = 0.7$, $Y(x, t = 0) = 0.6$, $Z(x, t = 0) = 0.8$. The diagrams are plotted using MATLAB ode15s solver and the parameter values as in Table 1.

coexistence of: (i) a stable steady states and a stable limit cycle; and (ii) two stable steady states. These onset of sustained oscillations and bistability phenomena have been seen more prominently in our extensive simulations (data not shown) with higher rates of migration than shown in Figure 5 (c). This observation can be explained by the fact that increasing rates of symmetric dispersal between populations of resource, competitor, exploiter and mutualist species modify its local interactions such that the bifurcational changes in dynamics occur under relatively moderate ranges of competitive pressure (β), compared to the finding with low dispersal levels.

In the case of asymmetric dispersal (Figure 5 (d)), qualitatively similar dynamical behaviours are seen for certain values of competitive pressure (β). However, unlike in the symmetric dispersal cases (Figure 5 (b)-(c)), the alternative stable states phenomenon has been found to be more pronounced under some medium ranges of β . Apart from bistability outcomes between different stable steady states and steady state-limit cycle attractors, we observe two coexisting stable limit cycles that occur due to asymmetry in dis-

persal rates. In this case, the amplitude of the fluctuations in population size and also species distributions differ, as revealed by inspection of our bifurcation diagram. This situation can induce uncertainties in the predictions of the long-term species distributions since the outcomes are determined by initial abundances of species. As a consequence of alternative stable states, we predict sensitivity of dynamics to small perturbations so that slightly distinct initial densities of mutualist-resource-competitor-exploiter species may lead to several different outcomes of community compositions. Additionally, this destabilising effect can also be ameliorated by the degree of asymmetry in dispersal rates and also the effects of (in)direct interactions from the resource species. This issue warrants further investigation and is the subject of our analysis in the next section.

4.2 Bifurcational changes in dynamics due to (in)direct interactions induced by the resource species and asymmetric dispersal

Based on our analysis, the community compositions of this ecological system are affected by interactions between dispersal process (in terms of strength and asymmetry) and local dynamics induced by the competitor species. The salient features of this multiple interactions type model are realised under asymmetric dispersal scenario and we hypothesised that the dynamical behaviours of the model would also be affected by the effects of (in)direct interactions mediated by the resource species. In this ecological system, the resource species shares a mutualist, a competitor and an exploiter. Thus, the presence of this species is important as it would provide a balance between mutualistic and antagonistic interactions (e.g., competition and exploiter) at the autotrophic level. To examine how the (in)direct effects exerted by this species interact with dispersal asymmetry, we performed bifurcation analysis using the strength of interactions of the resource species (α) and the result is shown in Figure 6. In the presence of asymmetric dispersal levels, we discover rich dynamical behaviours, which can stabilise or destabilise this multi-species community as the magnitude of α changes. In particular, the appearances of two supercritical Hopf bifurcations (*HSB*), a subcritical Hopf bifurcation (*HB*), a period-doubling bifurcations (*PD*) and numerous limit point bifurcations of cycles (*SNBC*) are uncovered through our bifurcation analysis. This part of the finding reveals interesting global dynamics where stable limit cycles (emanated from the *HSB* bifurcations) alternate with unstable ones (emanated from the *HB*, *PD* and various *SNBC* bifurcations) as the strength of resource species varies. The implications of this finding are interesting because, although alternative states are common in the multiple interaction types models, they are usually stable, whereas our finding shows that there can be alternative stable or unstable states if the asymmetric dispersal strength is considered. In this case, the fate of interacting species can fall into a stable steady state or a limit cycle depending on the initial abundances.

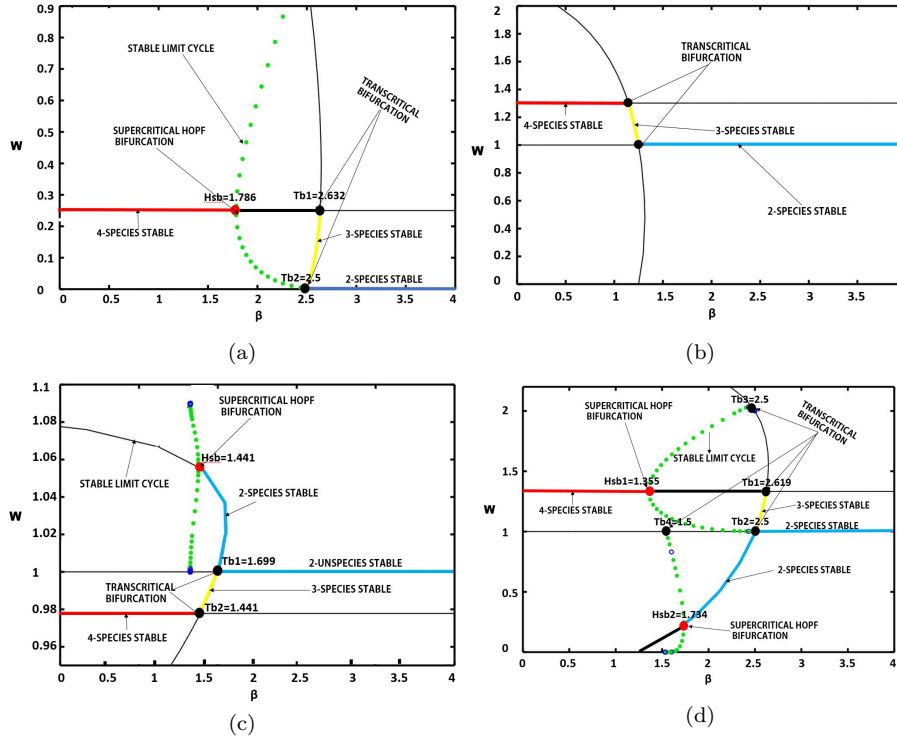


Fig. 5: Co-dimension one bifurcation analysis using β as the bifurcation parameter. (a) without dispersal ($D = 0$), (b) with symmetric dispersal strength (i.e., $D_X = D_W = D_Y = D_Z = 0.0027$), (c) with symmetric dispersal strength (i.e., $D_X = D_W = D_Y = D_Z = 0.005$ and (d) with asymmetric dispersal strength (i.e., $D_X = 0.005$, $D_W = 0.003$, $D_Y = 0.0027$ and $D_Z = 0.004$). Four species stable (red lines), three species stable (yellow lines), two species stable (blue lines) and stable limit cycles (black lines). Red dots represent supercritical Hopf bifurcation and black dots represent transcritical bifurcation. Initial species population densities: $X(x, t = 0) = 0.9$, $W(x, t = 0) = 0.7$, $Y(x, t = 0) = 0.6$, $Z(x, t = 0) = 0.8$. The diagrams are plotted using XPPAUT package and the parameter values as in Table 1.

5 Discussion and Ecological Implications

In this work, we have extended a multiple interactions type system [42] by incorporating spatial dispersal process. We examined the dynamical behaviours of the system for a realistic range of parameter values to demonstrate the generality of our ecological observations. This also permit us to investigate the interplay between local dynamics induced by the interactions of mutualist-resource-competitor-exploiter species on the one hand, and dispersal rate and its (a)symmetry, on the other hand. Overall, our findings reveal that the na-

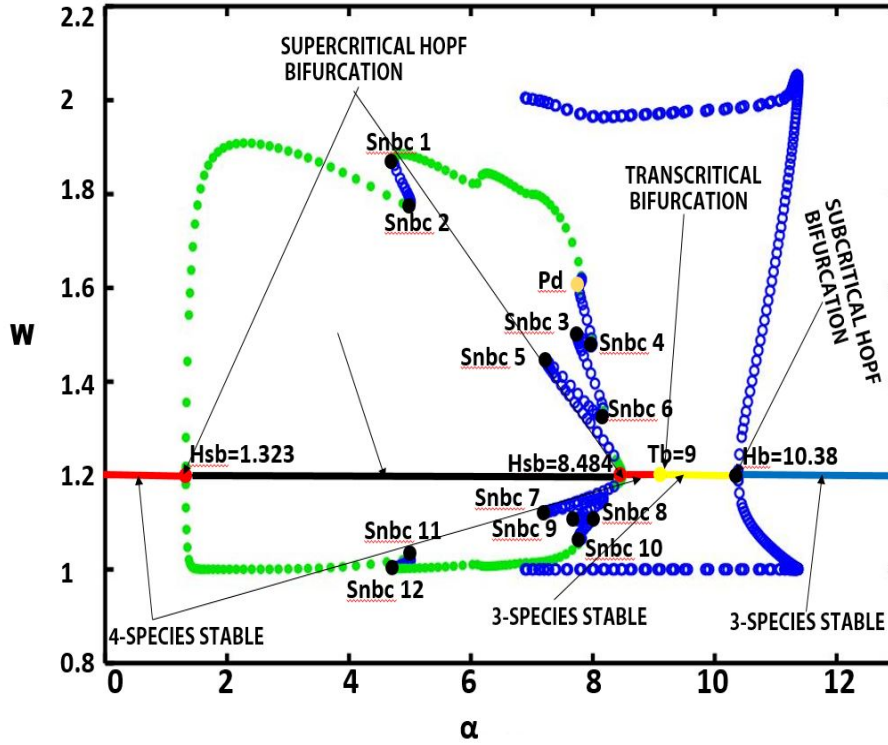


Fig. 6: Co-dimension one bifurcation analysis as the density of species varies against α in the presence of asymmetric dispersal. Initial population densities: $X(x, t = 0) = 0.9$, $W(x, t = 0) = 0.7$, $Y(x, t = 0) = 0.6$, $Z(x, t = 0) = 0.8$. The dispersal strength are : $D_X = 0.005$, $D_W = 0.003$, $D_Y = 0.0027$ and $D_Z = 0.004$. The diagram is plotted using XPPAUT package and the parameter values as in Table 1.

ture of direct and indirect interactions between interacting species, as well as complex ecological dynamics engendered, depend on the (a)symmetry in dispersal rates and the magnitude of interaction strengths among species.

We also discover the stabilising, and occasionally destabilising, effects of dispersal process on the dynamics of multiple interactions type system. These double-edged sword effects of dispersal [56] have also been pointed out in previous studies [57–59, 9, 60, 61] using metapopulation models, and are again demonstrated by our partial differential equations (PDE) system. Given this consistency, we propose that the (de)stabilising effects of dispersal process seem to be robust to changes in models specification, ecological interactions and also migration schemes considered [16]. By examining related work and distinct models together with trying to obtain similar predictions between

these ecological systems, we establish that the dispersal effects observed are in fact robust, and they are not restricted to specific details and assumptions of the modelling frameworks. These notions are also in parallel with findings from experimental setup using spatially structured bacterial populations [8]. It has also been experimentally verified in *Drosophila* metapopulations [25], and supported by the modelling verification of the underlying dispersal mechanisms, which can determine the fruitfly species persistence [11].

It should be noted that different effects of dispersal have also been observed in competitive systems using PDE models [43, 44, 50, 51]: while dispersal mechanism can stabilise community dynamics and promote coexistence outcomes, in certain cases, this process can also cause destabilisation of multi-species coexistence state, and lead to dispersal-induced extinction phenomenon. These contrasting observations occur under symmetric dispersal scenarios and depend on the intensity of dispersal, which also affect the community stability [53, 44]. By extending a simple classical model [62, 63] and making this ecological system to be more realistic with the inclusion of spatial dispersal process, recent studies [64] also found that coexistence state which would be stable without spatial effects can be destabilised by dispersal. The results of our investigation corroborate most of these basic prior findings about the dynamics of simple ecological interactions with local dispersal and generalise these insights to complex interactions type model consisting of mutualist-resource-competitor-exploiter species.

Additionally, our work also re-emphasises the importance of bifurcation analysis in understanding the qualitative behaviour of ecological models and their overall dynamics [65, 66]. Our bifurcation analysis results demonstrate the occurrences of supercritical Hopf and transcritical bifurcations under symmetric dispersal scenarios, which mediate multi-species coexistence state and sustained oscillations. Other dynamical behaviours are realised under asymmetric dispersal strength where alternative stable states phenomenon has been found to be more pronounced due to the emergence of different bistable attractors. The (in)direct effects exerted by resource species can also interact with dispersal asymmetry to engender some intriguing dynamics such as subcritical Hopf, period-doubling and limit point bifurcations of cycles. Consequently, several complex transitions between stable limit cycles and unstable ones occur through the interactions of these different bifurcation phenomena. These kinds of transitions can engender interesting population behaviours such as alternative stable (or unstable) states and non-equilibrium dynamics; in this case, the sensitivity of dynamics to small perturbations in initial densities of species are evident.

From an ecological viewpoint, this work also demonstrates the diversity in ecological modules, in interaction with dispersal rate and its (a)symmetry, will be vital for the conservation and management of the real multi-species communities for which human activities are altering natural dispersal rates of species. Our results also suggest that migration corridors should be designed with appreciation of dispersal (a)symmetry mechanisms in population dynamics in order to optimise the chance of species survival. Different disper-

sal scenarios and magnitudes considered in this work can provide a technique for the manipulation of migration rates (e.g., by facilitating the movement of species through the construction of conservation corridors) in order to ensure the persistence of interacting species. This strategy may also be used in order to minimise the risk of extinction of an endangered species, or to maximise the efficiency of an eradication campaign.

In conclusion, given that biological conservation do sometimes involve enforcing or facilitating dispersal among interacting species, a better understanding on the effects of dispersal (a)symmetry and local dynamics induced by different ecological species might help in planning effective conservation strategies. Knowledge of dispersal process and information on distinct biotic interactions can be incorporated in developing robust predictive models for estimating potential distributions of species. We recommend the use of modelling frameworks such as PDE models to predict the combined effects of dispersal (a)symmetry and complex ecological interactions between species. We also suggest that the overall dynamics of ecological communities will be revealed better by scrutinising the systems under consideration using the techniques from dynamical systems and bifurcation analysis.

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