

The interplay between mutualism, competition and dispersal promotes species coexistence in a multiple interactions type system

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ABSTRACT

The stability and maintenance of species biodiversity in the multiple interactions type systems have attracted much attention. Regardless of their nature, several forms of interactions are discovered to exhibit oscillatory behaviour. This large-amplitude oscillation also de-stabilizes populations of multiple species and raises species' chances of extinction. A central question in ecology is how do we maintain community stability and species coexistence mechanisms in a multiple interactions type community. It is thought that the dynamics of mutualism support multi-species coexistence in a complex ecological system. Here, we extend a four-species multiple interactions type (e.g., resource-competitor-exploiter-mutualist) system by incorporating a local dispersal component. We then employ this model to assess how the combined impacts of dispersal, mutualism and competition shape species coexistence and community stability in this ecological system. Our findings show that the interplay of mutualism and competition affects the complexity of ecological dynamics in this multiple interactions type system with local dispersal. Using numerical simulation, we demonstrate how strong mutualism could stabilize the spatio-temporal dynamics. Employing bifurcation analysis, we also discover that mutualism essentially modifies this ecological community's response to increasing competitive pressure on the resource species. These insights are evident in our findings through the emergence of intriguing dynamics where stable limit cycles alternate with unstable ones as competitive pressure varies. While alternative stable states are common in different ecological systems with mutualistic interactions, they are often stable, whereas, in our studies, we realize that there can be alternative stable or unstable states if the spatial dimension is considered through the incorporation of the diffusion component. Consequently, the long-term dynamics converge to multi-species coexistence outcomes either via a stable steady state or a limit cycle depending on species' initial abundances. It is also observed that this complexity ceases when mutualism becomes strong enough. Additionally, the destabilization of species biodiversity phenomenon through the occurrence of limit cycles increasing in the amplitude of oscillations (with some species population densities approaching zero) is weakened in the presence of strong mutualistic strength and local dispersal. Overall, the joint effects of mutualism, competition and local dispersal result in different community compositions, and these insights may have significant consequences in conservation management and biological control strategies.

1. Introduction

Mutualism is a win-win interspecific interaction between two species in which each benefit from the interaction in the community (Bronstein et al., 2004). Several studies have demonstrated the distinct role of mutualism in the ecosystem (Bronstein, 2001b; Holland et al., 2002; Bever, 2003; Bruno et al., 2003; Fath, 2007). Previous work on mutualism focus on one- or two-species systems, and in the natural ecosystems, several species are known to interact in various ways. Holland et al. (2002) sum up the effects of mutualism in the multi-species communities: the coexistence of interacting species are

influenced by how the positive feedback from mutualism balance the negative feedback (Bever, 2003; Chesson, 2000); in this case, mutualism provides cost and benefit effects that are dependent on the densities of species (Addicott, 1979; Morales, 2000; Bronstein, 2001a). The benefits derived from mutualism supports the maintenance of the ecological structure, ecosystem and biodiversity (Aslan et al., 2013; Aliyu and Mohd, 2021). Mutualism has been reported to destabilize ecological systems as reported by some researchers before (Takimoto and Suzuki, 2016), which has led to divergence views as a result of population explosion (Iwata et al., 2011). Thus, we hypothesized

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that some essential mechanisms support the coexistence of a complex ecological system (Tubay et al., 2013; Kakishima et al., 2015). The important ecological question is, how do mutualism shape multi-species coexistence and community stability in a multiple interactions type system? One possible way is through the impact of mutualism on interspecific competition, as the competition among interacting species is an important interaction in nature.

Species are known to compete for scarce resource in order to survive (Gause, 1932). Consistent with this observation, the Lotka–Volterra model is a foundational competition model known in mathematical biology (Grover et al., 1997). This study's findings show that multi-species coexistence is only feasible when the interspecific competition is less than intraspecific competition (Case, 1999; Gotelli, 2008; Mittelbach and McGill, 2019). On the contrary, when the intraspecific competition is less than the interspecific competition, the principle of competitive exclusion occurs (Hardin, 1960). However, this situation can be perceived as a paradoxical effect as multiple species can coexist in nature; this point of view supports the “paradox of phytoplanktons” (i.e., limited resources supports a wide range of plankton species). The pertinent question is, can stable coexistence occur when competition interacts with other biotic factors and how mutualism force structures the outcomes of an ecological system? Several studies have examined the combined impact of mutualism and competition in shaping multi-species ecological dynamics and found that communities with mutualism and competition are inherently unstable (Mougi and Kondoh, 2015, 2012; Suweis et al., 2014; Kondoh and Mougi, 2015; Mougi and Kondoh, 2014a; Mougi, 2016).

Numerous studies have shown a synergistic effect between species diversity and biotic interactions (Kondoh and Mougi, 2015; Mougi and Kondoh, 2012, 2014a; Mougi, 2016). Nevertheless, there is no definite answer on how the interplay between mutualism, competition, and dispersal shapes species diversity in a multiple interactions type system. Transfer, settlement, and emigration have been reported as the main contributions in species dispersal (Lidicker and Stenseth, 1992). Mohd et al. (2017) report that the effect of abiotic and biotic factors combined with local dispersal can influence species range margin; it is also discovered that coexistence of multi-species is feasible due to the movement of species even in the presence of intense biotic interactions (Mohd et al., 2017; Mohd and Noorani, 2021).

Strong biotic interactions often cause the appearance of alternative stable states (or ecologically known as priority effects) in the absence of dispersal (Mohd, 2016; Mohd et al., 2016). The presence of dispersal diminishes the pervasiveness of priority effects and consequently affects species coexistence mechanisms (Mohd et al., 2018). Some researchers have studied the effects of local dispersal and competition on multi-species coexistence structure (Salau et al., 2012; Mohd et al., 2017; Godsoe et al., 2017). However, all these studies are focused on single interaction (i.e., competition) among interacting species. An important ecological question is what effects do local dispersal have on distinct biotic interactions in multi-species communities? Specifically, it is still unknown what impacts local dispersal, mutualism and competition have on the community stability and species coexistence mechanisms in the multi-species systems.

To explore the impact of mutualism on competition in the presence of dispersal, we extend the previous multiple interactions type (e.g., resource-competitor-exploiter-mutualist) system by incorporating a spatial diffusion term. This ecological system is investigated to ascertain the combined impacts of mutualism and competition between dispersing species, affecting the community stability and species coexistence mechanisms. We demonstrate how the interplay between mutualism, competition and local dispersal shape the community structure and complexity of ecological dynamics using our numerical findings. Finally, we propose some ecological implications of our results from species conservation and biodiversity management.

2. Model description and analysis

To study how the impacts of mutualism and competition interact with local dispersal to shape community stability and species coexistence, we extend a simple multiple interactions type model (Mitani and Mougi, 2017) with a spatial diffusion component. The conceptual framework of this ecological system can be represented by Fig. 1. We use a Lotka–Volterra predator–prey model that is globally stable, which has a controlled prey growth rate in the presence of antagonistic interaction (Mougi and Kondoh, 2014b). Also, the type II functional response represents the mutualistic interaction, to eliminate the unbounded and unrealistic population growth (Mitani and Mougi, 2017). The multiple interactions type model is represented with the following coupled nonlinear partial differential equations (PDE):

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

where X , W , Y , Z are the population variables of resource, competitor, exploiter and mutualist species, respectively. The parameter r_X is the level of the growth rate of resource species; r_W is the level of the growth rate of competitor species, and r_Z is the level of the growth rate of mutualist species. Also, 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 unity for simplicity. The terms D_X , D_W , D_Y and D_Z are diffusion coefficient of X , W , Y and Z , respectively. The diffusion term models local dispersal along spatial locations, x . We assume distinct dispersal strength for each of the interacting species to reflect on the dynamics of multi-species systems. The parameter values used in the numerical simulation are defined in Table 1, which are motivated by the ecological studies of Mitani and Mougi (2017) and Mohd et al. (2017). Also, we apply zero-flux boundary conditions for each of the species (i.e., assuming no movement can occur across the boundaries):

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

2.1. Existence of equilibria

In this subsection, the existence of equilibrium points and the stability analysis of these equilibria are examined in the model (1) without dispersal (i.e., $D = 0$). To do this, let us call each of these equations as follows:

$$F1 = \frac{dX}{dt} = X \left(r_X - X - \beta W - aY + \frac{uZ}{h_Z + Z} \right), \quad (3)$$

$$F2 = \frac{dW}{dt} = W(r_W - W - \alpha X), \quad (4)$$

$$F3 = \frac{dY}{dt} = Y(gaX - d), \quad (5)$$

$$F4 = \frac{dZ}{dt} = Z \left(r_Z - Z + \frac{vX}{h_X + X} \right). \quad (6)$$

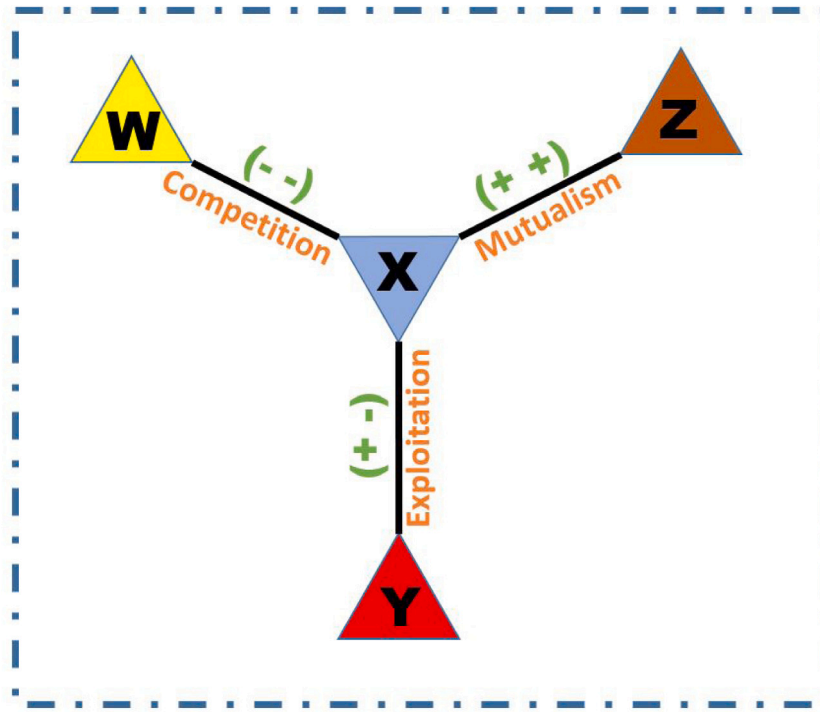


Fig. 1. The conceptual framework of a multiple interactions type system consisting of resource (X), competitor (W), exploiter (Y) and mutualist (Z) species.

Table 1

Parameter values are motivated by the previous studies of Mitani and Mougil (2017) and Mohd et al. (2017).

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	1.8
g	Conversion efficiency of the exploiter species	0.25
d	Death rate of the exploiter	0.005
h_X	Half saturation constant	1
h_Z	Half saturation constant	1
β	Competitive strength of the competitor species	0.7
α	Competitive strength of the resource species	0.2
D_X	Dispersal strength of resource species	0.003
D_W	Dispersal strength of competitor species	0.002
D_Y	Dispersal strength of exploiter species	0.004
D_Z	Dispersal strength of mutualist species	0.0038

Setting $F_1 = F_2 = F_3 = F_4 = 0$, we can solve for equilibrium point (X^*, W^*, Y^*, Z^*) .

From Eq. (5),

$$X^* = \frac{d}{ga}. \quad (7)$$

From Eq. (4),

$$W^* = \left(r_W - \frac{ad}{ga} \right). \quad (8)$$

From Eq. (6),

$$Z^* = \left(\frac{r_Z(gah_X + d) + vd}{gah_X + d} \right). \quad (9)$$

From Eq. (3),

$$Y^* = \frac{1}{a} \left(r_X - \frac{d}{S^*} - \beta r_W - \frac{N^*}{S^*} + \frac{uM^*}{Q^*} \right), \quad (10)$$

where:

$$M^* = r_Z(gah_X + d) + vd,$$

$$N^* = \alpha\beta d,$$

$$Q^* = gah_X + d,$$

$$S^* = ga.$$

Therefore, we have the following biologically relevant equilibrium points:

1. Extinction equilibrium,

$$E_0 (0, 0, 0, 0). \quad (11)$$

2. Extinction of resource species equilibrium,

$$E_1 \left(0, r_W, \frac{1}{a} \left(-\beta r_W + \frac{uZ^*}{h_Z + Z^*} \right), r_Z \right). \quad (12)$$

3. Extinction of competitor species equilibrium,

$$E_2 \left(\frac{d}{S^*}, 0, \frac{1}{a} \left(r_X - X^* + \frac{uZ^*}{h_Z + Z^*} \right), r_Z + \frac{vX^*}{h_X + X^*} \right). \quad (13)$$

4. Extinction of exploiter species equilibrium,

$$E_3 \left(\frac{d}{S^*}, r_W - \alpha X^*, 0, r_Z + \frac{vX^*}{h_X + X^*} \right). \quad (14)$$

5. Extinction of mutualist species equilibrium,

$$E_4 \left(\frac{d}{S^*}, r_W - \alpha X^*, \frac{1}{a} (r_X - X^* - \beta r_W), 0 \right). \quad (15)$$

6. Four-species coexistence equilibrium,

$$E_* \left(\frac{d}{S^*}, \left(r_W - \frac{ad}{ga} \right), \frac{1}{a} \left(r_X - \frac{d}{S^*} - \beta r_W - \frac{N^*}{S^*} + \frac{uM^*}{Q^*} \right), \left(r_Z + \frac{vd}{Q^*} \right) \right), \quad (16)$$

where $X(t) > 0$, $W(t) > 0$, $Y(t) > 0$ and $Z(t) > 0$.

2.2. Local stability analysis

Though the system (1) can possess up to six equilibria, based on the parametrization as in Table 1, we can observe the appearance of two of these equilibria e.g., E_2 and E_* in our numerical simulation results later on. The stability of these two equilibria can be analysed as follows:

Proposition 2.2.1. *The competitor species extinction equilibrium point, E_2 , is locally stable in \mathfrak{R}_+^4 if:*

$$\begin{aligned} r_X + r_W + \frac{uZ^*}{h_Z + Z^*} - aY^* &< X^*(\alpha + 2), \\ r_W &< \alpha X^*, \\ r_Z - 2Z^* &< \frac{vX^*}{h_X + X^*}, \end{aligned} \quad (17)$$

hold.

Proof. First, we calculate the Jacobian matrix of the system (1) evaluated at E_2 :

$$J(E_2) = \begin{bmatrix} k_1 & -\beta X^* & -aY^* & k_2 \\ 0 & k_3 & 0 & 0 \\ k_4 & 0 & -d & 0 \\ k_5 & 0 & 0 & k_6 \end{bmatrix},$$

We then calculate the characteristic equation from this matrix:

$$J(E_2) - \lambda I = \begin{bmatrix} k_1 - \lambda I & -\beta X^* & -aY^* & k_2 \\ 0 & k_3 - \lambda I & 0 & 0 \\ k_4 & 0 & -d - \lambda I & 0 \\ k_5 & 0 & 0 & k_6 - \lambda I \end{bmatrix},$$

where:

$$\begin{aligned} k_1 &= r_X - 2X^* - aY^* + \frac{uZ^*}{h_Z + Z^*}, \\ k_2 &= X^* \left(\frac{u}{h_Z + Z^*} - \frac{uZ^*}{(h_Z + Z^*)^2} \right), \\ k_3 &= r_W - \alpha X^*, \\ k_4 &= gaY^*, \\ k_5 &= Z^* \left(\frac{v}{h_X + X^*} - \frac{vX^*}{(h_X + X^*)^2} \right), \\ k_6 &= r_Z - 2Z^* + \frac{vX^*}{h_X + X^*}. \end{aligned}$$

The eigenvalues obtained by solving characteristic equations above will satisfy the following equations:

$$\begin{aligned} \lambda_1 + \lambda_2 &= \left((r_X - 2X^*) - \beta W^* - aY^* + \frac{uZ^*}{h_Z + Z^*} \right) + (r_W - \alpha X^*), \\ \lambda_1 \cdot \lambda_2 &= \left((r_X - 2X^*) - \beta W^* - aY^* + \frac{uZ^*}{h_Z + Z^*} \right) (r_W - \alpha X^*), \\ \lambda_3 &= -d, \\ \lambda_4 &= r_Z - 2Z^* + \frac{vX^*}{h_X + X^*}, \end{aligned} \quad (18)$$

where λ_1 , λ_2 , λ_3 , and λ_4 represent the eigenvalues of E_2 . We observe that Eqs. (18) will have all eigenvalues with negative real part if and only if the inequalities (17) hold, and thus, E_2 will be locally stable in \mathfrak{R}_+^4 (otherwise E_2 is unstable).

Proposition 2.2.2. *The four-species coexistence equilibrium point E_* is locally asymptotically stable in \mathfrak{R}_+^4 if:*

$$\begin{aligned} r_X + r_W &< 2(X^* + W^*) + \beta W^* + \alpha X^* + aY^* + \frac{uZ^*}{h_Z + Z^*}, \\ r_W &< 2W^* + \alpha X^*, \\ X^* &< \frac{d}{ga}, \\ r_Z - 2Z^* &< \frac{vX^*}{h_X + X^*}, \end{aligned} \quad (19)$$

hold.

Proof. We calculate the Jacobian matrix of the system (1) evaluated at E_* :

$$J(E_*) = \begin{bmatrix} k_1 & k_2 & k_3 & k_4 \\ k_5 & k_6 & 0 & 0 \\ k_7 & 0 & k_8 & 0 \\ k_9 & 0 & 0 & k_{10} \end{bmatrix},$$

where:

$$\begin{aligned} k_1 &= r_X - 2X^* - \beta W^* - aY^* + \frac{uZ^*}{h_Z + Z^*}, \\ k_2 &= -\beta X^*, \\ k_3 &= -aY^*, \\ k_4 &= X^* \left(\frac{u}{h_Z + Z^*} - \frac{uZ^*}{(h_Z + Z^*)^2} \right), \\ k_5 &= -\alpha W^*, \\ k_6 &= r_W - 2W^* - \alpha X^*, \\ k_7 &= gaY^*, \\ k_8 &= gaX^* - d, \\ k_9 &= Z^* \left(\frac{v}{h_X + X^*} - \frac{vX^*}{(h_X + X^*)^2} \right), \\ k_{10} &= r_Z - 2Z^* + \frac{vX^*}{h_X + X^*}. \end{aligned}$$

We obtain the characteristics equation as follows:

$$\lambda^4 + A_1 \lambda^3 + A_2 \lambda^2 + A_3 \lambda + A_4 = 0, \quad (20)$$

where: $A_1 = k_1 + k_6 + k_8 + k_{10}$,
 $A_2 = k_8(k_1 + k_2) + (k_1 k_6 - k_2 k_5) - k_3 k_7$,
 $A_3 = k_8(k_1 k_6 - k_2 k_5) + k_3 k_6 k_7$,
 $A_4 = k_8 k_{10}(k_1 k_6 - k_2 k_5)$.
Also,

$$\Delta = A_1 A_2 A_3 - A_3^2 - A_1^2 A_4. \quad (21)$$

Using the Routh–Hurwitz criteria and given that the inequalities (19) hold, then all the real parts of the eigenvalues of E_* will be negative. Thus, E_* will be locally asymptotically stable in \mathfrak{R}_+^4 (otherwise E_* is unstable).

The stability analysis for the other equilibria can be calculated using similar techniques. When dispersal is included (i.e., $D > 0$), then the ecological system is represented by the PDE model (1). Since the PDE system's attractors cannot be obtained analytically, numerical simulations are performed, and these aspects are discussed in the following sections.

2.3. Numerical methods for solving the PDE system

To numerically solve the model (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 (Mohd et al., 2017). Using this numerical scheme, the spatial domain ($0 \leq x \leq 1$) 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 the model (1):

$$\begin{aligned} \frac{\partial^2 X}{\partial x^2} &= \frac{X_{i+1} - 2X_i + X_{i-1}}{h^2}, \\ \frac{\partial^2 W}{\partial x^2} &= \frac{W_{i+1} - 2W_i + W_{i-1}}{h^2}, \\ \frac{\partial^2 Y}{\partial x^2} &= \frac{Y_{i+1} - 2Y_i + Y_{i-1}}{h^2}, \\ \frac{\partial^2 Z}{\partial x^2} &= \frac{Z_{i+1} - 2Z_i + Z_{i-1}}{h^2}. \end{aligned} \quad (22)$$

The zero-flux boundary conditions (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 . A standard ODE solver, `ode15s`, is employed to solve the resulting system of ODE until an equilibrium is achieved (e.g., the simulation is performed till $t = 1000$). The mesh size $h = 0.02$ is used in the numerical simulation. The stability of these equilibria can also be calculated numerically and interested readers are referred to the following work (Mohd, 2018b,a) on the methodology to conduct this computation. In short, the Jacobian matrix and the eigenvalues can be calculated numerically using MATLAB `fsolve` and `eig` functions, respectively; similar to our previous discussion, an equilibrium of the PDE system can be classified as stable if all the real parts of the spectrum of eigenvalues are negative. Similarly, for numerical simulation in XPP, we also discretized the 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 perform bifurcation analysis and continue the steady states of the model (1). In particular, we tracked the stable, unstable, and bifurcation points that emerge in this ecological system as the parameters are varied (Ermentrout, 2012; Omaiye and Mohd, 2018). It is also checked that the numerical results are insensitive to a reduction in grid spacing (i.e., as the number of grid points changed).

3. Results

Based on our numerical simulation experiments performed, we highlight the salient observations of the ecological model (1) in the presence of distinct ecological factors such as mutualism, competition and local dispersal. For instance, Fig. 2 depicts the existence of a multi-species coexistence equilibrium in this ecological system as parameter values fixed as in Table 1. We observed that the system coexistence dynamics converge to the four-species steady state for different initial conditions when the mutualistic interactions are strong ($u = 3$). Similar observations can be seen from the model's spatio-temporal behaviours illustrated by Fig. 3(a)–(d). These plots depict the coexistence dynamics of this multi-species ecological system, including local dispersal and strong mutualistic strength. When mutualism force is high, this situation can mediate the stabilization of the ecological community. The system demonstrates a damped transient oscillation, and in the long run, species' spatial distributions settle to a stable steady state across locations x . We also discover that reducing the strength of mutualistic interactions u lead to the destabilization of this multiple interactions type system. As an example, Fig. 4(a)–(d) shows the effects of weak mutualistic strength ($u = 0.5$) and local dispersal on species distribution in this ecological system. We observe that weak mutualistic force destabilizes the multiple interactions type system. In this case, the population densities of interacting species fluctuate with the increasing amplitude of oscillations in this multi-species community. To understand species coexistence mechanisms and community stability in this multiple interactions type system, we performed a co-dimension one bifurcation analysis and some of the findings are presented below.

3.1. Effects of competition in the multiple interactions type model without dispersal ($D = 0$)

Here, we first aim to demonstrate the effects of competition and other biotic factors on the species coexistence and community stability of this ecological system in the absence of dispersal ($D = 0$). To achieve this, we conduct a co-dimension one bifurcation analysis using α as our bifurcation parameter in the presence of strong mutualistic interactions u . For instance, Fig. 5(a)–(d) shows some intriguing bifurcation dynamics that occur to resource (X), competitor (W), exploiter (Y) and mutualist (Z) species, respectively. We observe the emergence of two supercritical Hopf bifurcations (HB_1 and HB_2), a subcritical Hopf bifurcation (HB_3), period-doubling bifurcation (PD_1 and PD_2) and limit point bifurcations of cycles (LPC_1 to LPC_5). The community

stability and species coexistence are influenced by these bifurcations changes in dynamics that occur in this multi-species system. As the parameter α is varied, there exists several threshold phenomena and also the appearance of distinct stable and unstable attractors: (i) four-species coexistence steady-state ($\alpha < HB_1$ and $HB_2 < \alpha < HB_3$) and (ii) stable limit cycles ($HB_1 < \alpha < HB_2$) and (iii) unstable limit cycles (in the vicinity of LPC and HB_3). We also observe transcritical bifurcation (BP) where there is an exchange of stability between two steady states at this bifurcation point. For example, transcritical bifurcation occurs at (BP) as four-species steady state (given by Eq. (16)) exchanges its stability with three-species steady-state with competitor species absent (given by Eq. (13)). This transcritical bifurcation results in the extinction of the community's competitor species when the resource species competitive strength is rather high.

Additionally, the phenomenon related to the destabilization of species biodiversity through the occurrence of limit cycles that increases the amplitude of oscillations (with distinct species densities approach zero) is also evident in this multiple interactions type model without local dispersal ($D = 0$). This situation increases the likelihood of extinction and consequently leads to destabilization of species biodiversity (i.e., interacting species with lower population densities are more prone to such random chances). In the absence of dispersal, we also realize some complex transitions between stable limit cycles and unstable ones through limit point bifurcations of cycles and period-doubling bifurcations. These kinds of dynamics can engender interesting population behaviours such as alternative stable states and non-equilibrium dynamics. In this situation, the long-term distributions of species can converge to distinct outcomes depending on initial abundances.

3.2. Combined effects of mutualism, competition and local dispersal in the multiple interactions type model

In the absence of dispersal ($D = 0$), we further investigate the effects of distinct mutualistic forces and competition between species on the bifurcation dynamics of this ecological system. For instance, Fig. 6(a)–(d) illustrates the density of resource species (X) as competitive pressure α changes under various mutualism scenarios e.g., $u = 0.5, 1.5, 3$ and 5 , respectively. Without dispersal, we observe that the destabilization of species biodiversity phenomenon through the occurrence of limit cycles increasing in the amplitude of oscillations (with some species population densities approaching zero) is still prevalent in this ecological system when the positive effects of mutualism (u) increase. Similar to our previous observations before, there are several thresholds of supercritical and subcritical Hopf bifurcations, period-doubling bifurcations and the limit point bifurcations of cycles as the competitive pressure and mutualistic strength change in this multiple interactions type system without dispersal.

Now, we highlight the combined effects of competition and mutualistic interactions on the ecological system's outcomes with the incorporation of local dispersal. For instance, Fig. 7(a)–(d) shows the species coexistence and community stability of this multi-species system for distinct values of mutualistic strength (e.g., $u = 0.5, 1.5, 3, 5$) using α as our bifurcation parameter. In particular, we observe that strong mutualism can interact with the dispersal process to stabilize the spatio-temporal dynamics of this ecological system. As an example, for $u = 0.5$, we observed the occurrence of two supercritical Hopf bifurcation (HB_1 and HB_2), a subcritical Hopf bifurcation (HB_3), a period-doubling bifurcations (PD) and numerous limit point bifurcations of cycles (LPC_1 to LPC_{12}). These bifurcation dynamics determine this multiple interactions type system's community compositions as the threshold values of α vary. It is also observed that for $u = 1.5$, the bifurcation dynamics simplify further i.e., two supercritical Hopf bifurcations (HB_1 and HB_2), a subcritical Hopf bifurcation (HB_3) and six limit point bifurcations of cycles (LPC_1 to LPC_5). We also discover that mutualism essentially modifies this ecological community's response

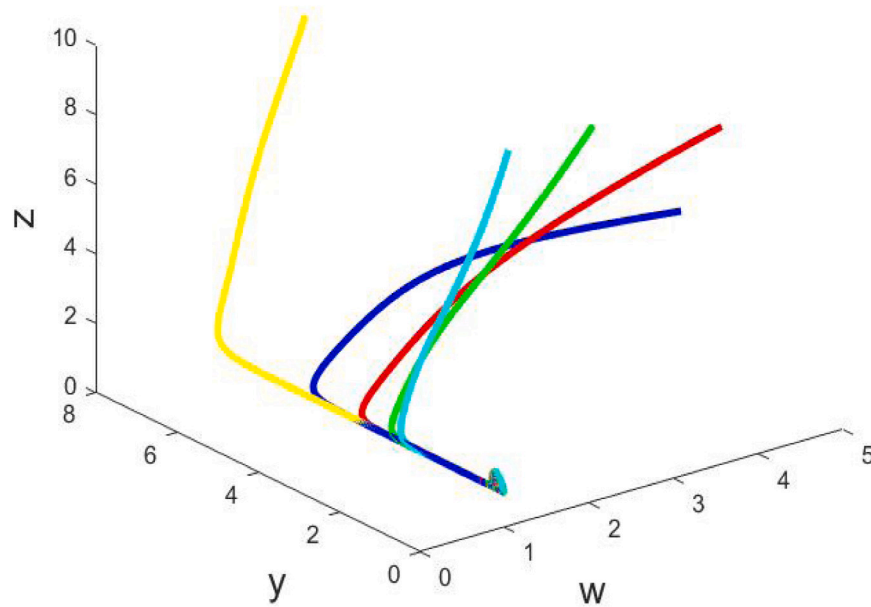


Fig. 2. Stability properties of the multi-species system for different initial conditions. Initial population densities: $X = 0.9$, $W = 0.7$, $Y = 0.6$, $Z = 0.8$. The diagram is plotted using MATLAB and the parameter values as in Table 1.

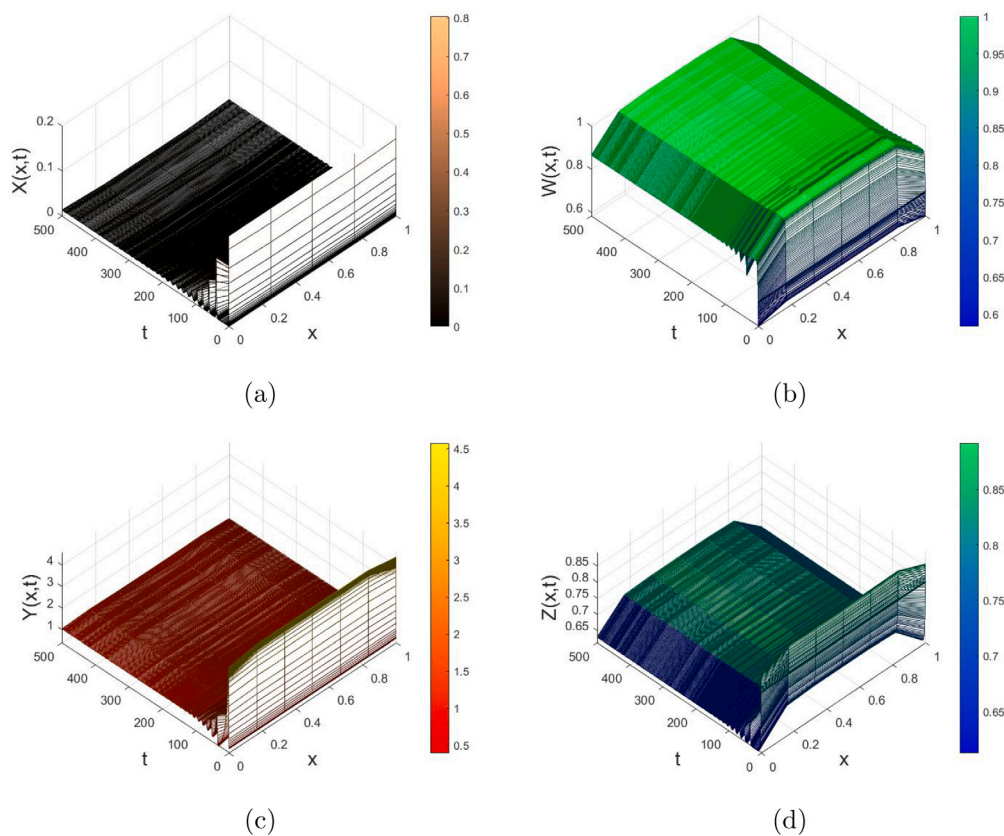


Fig. 3. Spatio-temporal diagrams showing the effects of strong mutualistic strength ($u = 3$) and dispersal on the interacting species. (a) resource species, (b) competitor species, (c) exploiter species, (d) mutualist species. Initial condition: $X(x, t = 0) = 0.3$, $W(x, t = 0) = 0.2$, $Y(x, t = 0) = 0.2$, $Z(x, t = 0) = 0.4$. Initial population densities: $X = 0.9$, $W = 0.7$, $Y = 0.6$, $Z = 0.8$. The number of grid point used is 40. The diagrams are plotted using MATLAB Ode15s solver and the parameter values as in Table 1.

(with local dispersal) towards the increase of the competitive pressure on the resource species. These insights are evident in our findings through the emergence of intriguing dynamics where stable limit cycles alternate with unstable ones as competitive pressure varies. Due to this reason, there can be alternative stable or unstable states, and these

outcomes are possible through the incorporation of local dispersal and also the spatial dimension into the system. Consequently, the long-term dynamics converge to multi-species coexistence outcomes either via a stable steady state or a limit cycle depending on species' initial abundances.

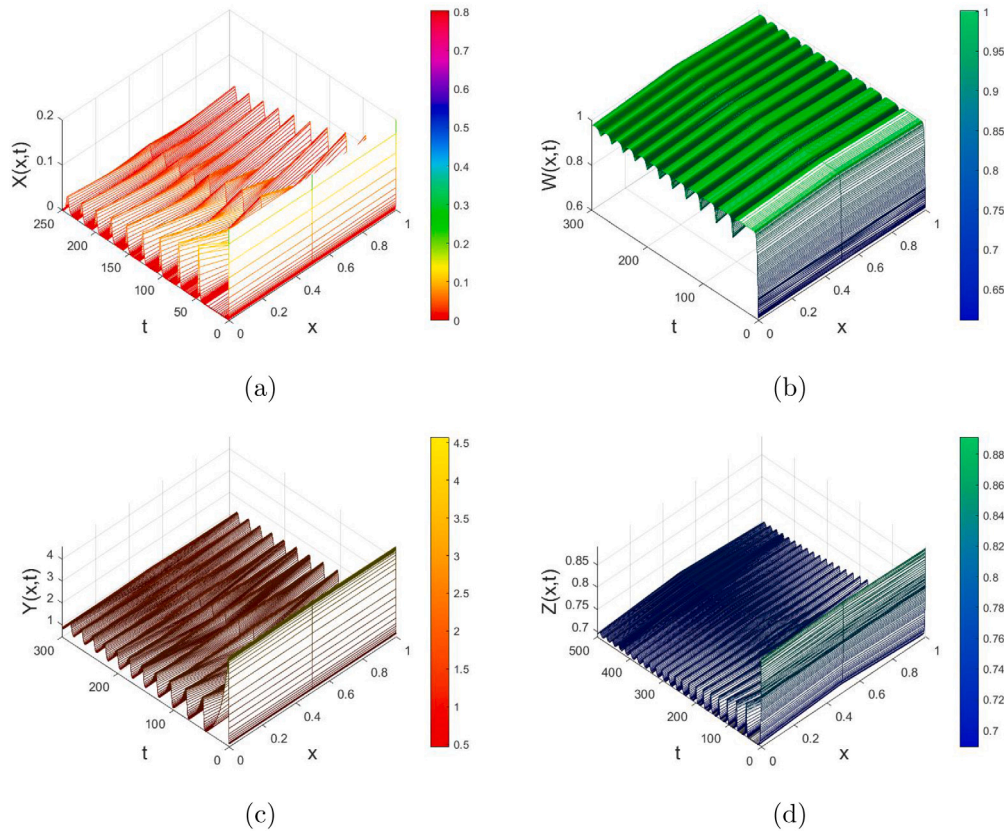


Fig. 4. Spatio-temporal diagrams showing the effects of weak mutualistic strength ($u = 0.5$) and dispersal on the interacting species. (a) resource species, (b) competitor species, (c) exploiter species, (d) mutualist species. Initial condition: $X(x, t = 0) = 0.3$, $W(x, t = 0) = 0.2$, $Y(x, t = 0) = 0.2$, $Z(x, t = 0) = 0.4$. Initial population densities: $X = 0.9$, $W = 0.7$, $Y = 0.6$, $Z = 0.8$. The number of grid point used is 50. The diagrams are plotted using MATLAB Ode15s solver and the parameter values as in Table 1.

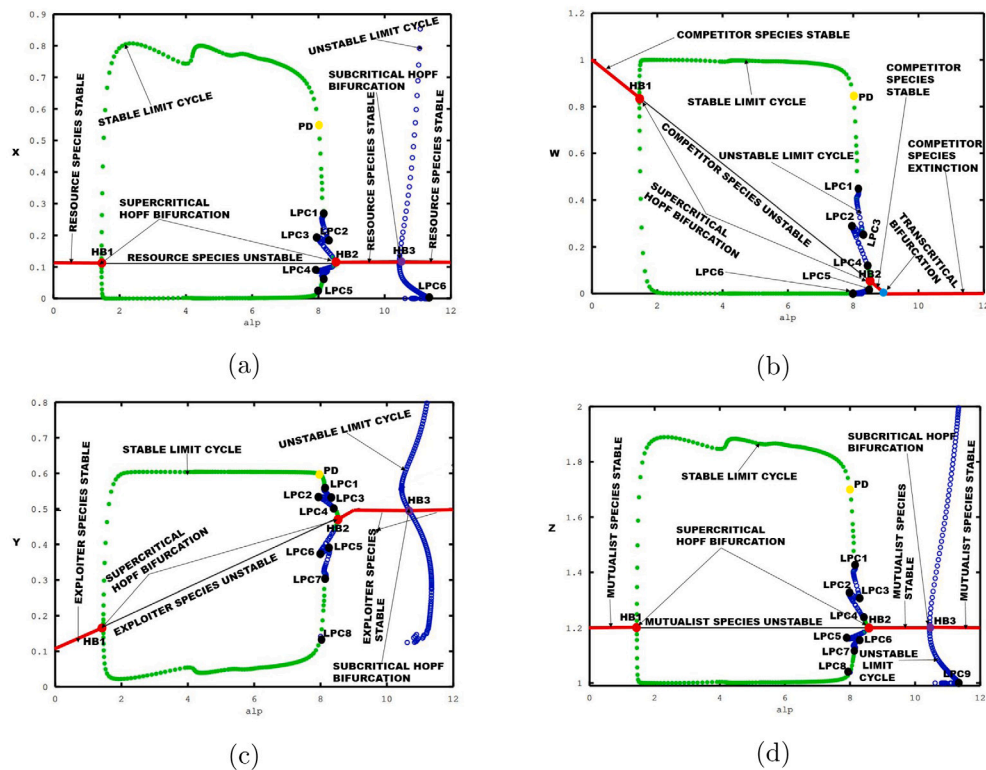


Fig. 5. Co-dimension one bifurcation as we vary α without dispersal ($D = 0$). Initial condition: $X(x, t = 0) = 0.3$, $W(x, t = 0) = 0.2$, $Y(x, t = 0) = 0.2$, $Z(x, t = 0) = 0.4$. Initial population densities: $X = 0.9$, $W = 0.7$, $Y = 0.6$, $Z = 0.8$. The diagrams are plotted using XPPAUT package and the parameter values as in Table 1.

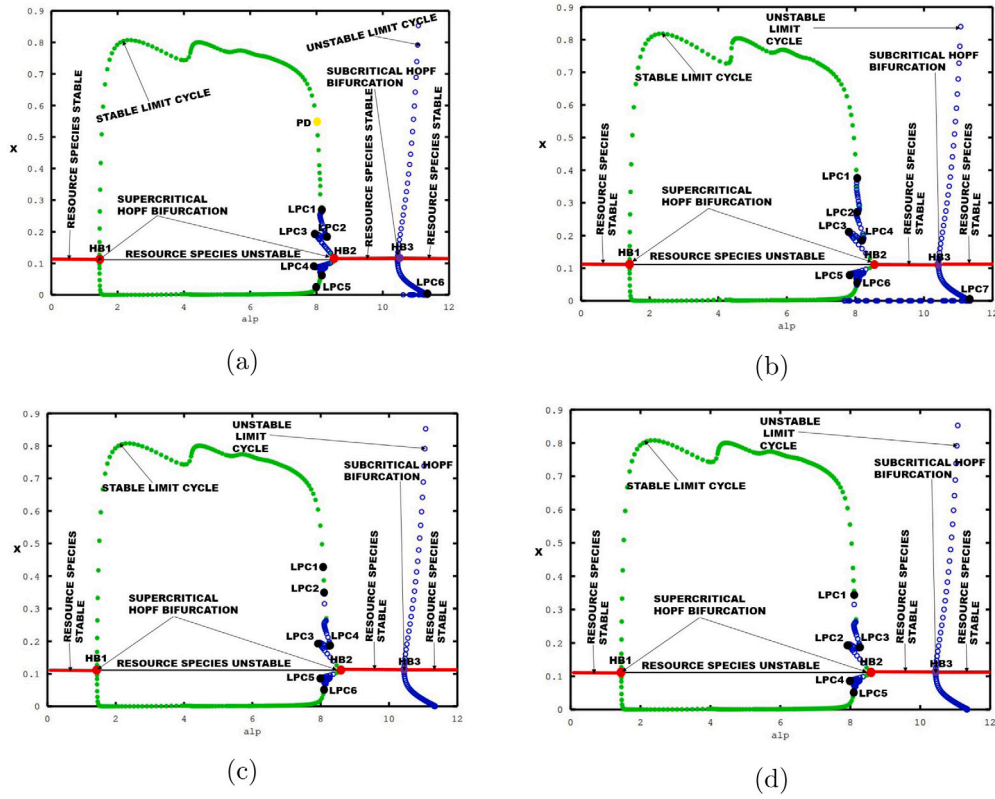


Fig. 6. Co-dimension one bifurcation as we vary α without dispersal ($D = 0$) and for distinct mutualistic strength. (a) $u = 0.5$, (b) $u = 1.5$, (c) $u = 3$ and (d) $u = 5$. Initial condition: $X(x, t = 0) = 0.3$, $W(x, t = 0) = 0.2$, $Y(x, t = 0) = 0.2$, $Z(x, t = 0) = 0.4$. Initial population densities: $X = 0.9$, $W = 0.7$, $Y = 0.6$, $Z = 0.8$. The diagrams are plotted using XPPAUT package and the parameter values as in Table 1.

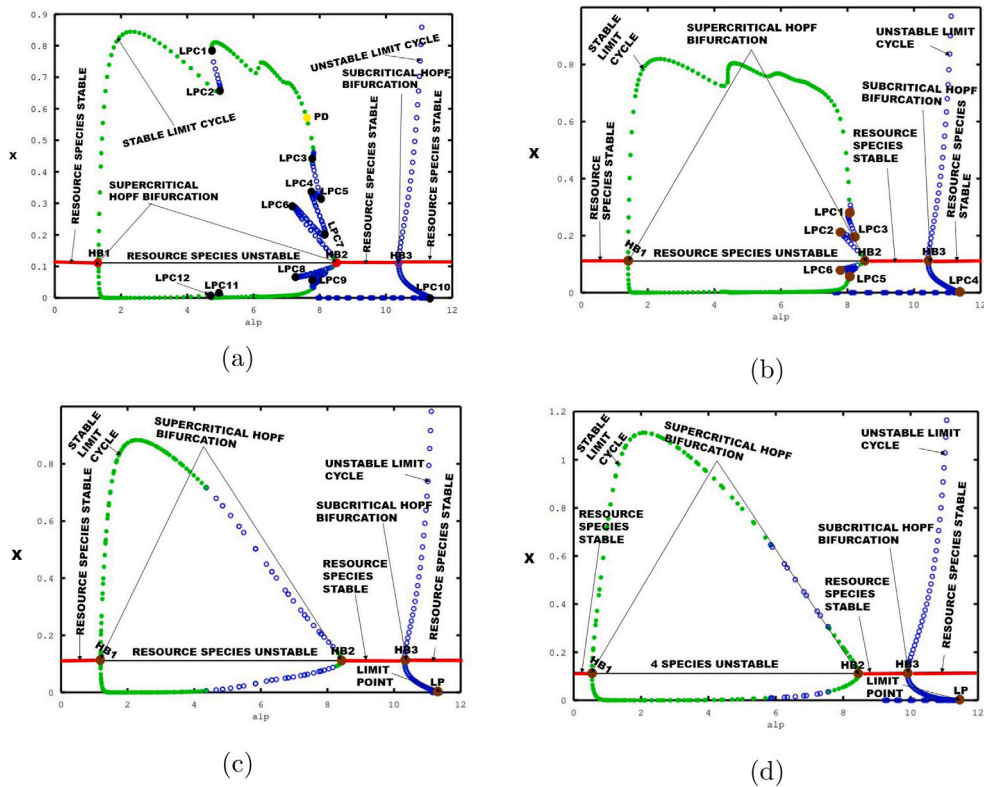


Fig. 7. Co-dimension one bifurcation as we vary α for distinct dispersal and mutualistic strength. (a) $u = 0.5$, (b) $u = 1.5$, (c) $u = 3$ and (d) $u = 5$. Initial condition: $X(x, t = 0) = 0.3$, $W(x, t = 0) = 0.2$, $Y(x, t = 0) = 0.2$, $Z(x, t = 0) = 0.4$. Initial population densities: $X = 0.9$, $W = 0.7$, $Y = 0.6$, $Z = 0.8$. The diagrams are plotted using XPPAUT package and the parameter values as in Table 1.

Increasing the intensity of mutualistic strength causes further reduction to the bifurcation changes in dynamics of the system: for stronger mutualism scenarios (e.g., $u = 3$ and $u = 5$), we notice the emergence of two supercritical Hopf bifurcations (HB_1 and HB_2) and a subcritical Hopf bifurcation (HB_3); in these cases, period-doubling (PD) and limit point of cycle bifurcations (LPC) are not evident in our analysis. It is observed that the complexity in ecological dynamics ceases to exist when mutualism becomes strong enough. We also observe that the destabilization of species biodiversity phenomenon is weakened in the presence of strong mutualistic strength, and this situation is also mediated by the influences of local dispersal in this multiple interactions type system (compared Fig. 7(c)-(d) with Fig. 6(c)-(d)). Due to the positive impacts of strong mutualism in interaction with the dispersal process, this condition increases the tendency of maintaining population densities to oscillate further away from zero (i.e., in some regions of α in Fig. 7(c)-(d)), and thus decreasing the likelihood that a population will become extinct in the presence random chances.

4. Discussion and ecological implications

In this work, we have examined the combined impacts of mutualism and competition in the presence of local dispersal and how these different ecological factors shape community stability and species coexistence mechanisms in this multiple interactions type system. We demonstrate that this ecological model has a rich repertoire of dynamical behaviours, including different species coexistence equilibria, alternative stable states and stable (or unstable) limit cycles. We also show that this extended ecological model can well capture these distinct attractors and several outcomes of species interactions. This system can also depict further insights on the reality of complex ecological interactions consisting of resource, competitor, exploiter and mutualist species. Using the extended model (1), we seek to better understand the joint effects of simultaneous presence of a mutualistic and a competitive relationship in a multiple interactions type system. When several species compete for limited resources, Gause's competitive exclusion principle predicts that coexistence is impossible and exclusion of species will occur in the long term. This principle inspired Hutchinson's paradox of the phytoplankton, which refers to the surprisingly large diversity of multiple species supported by ecosystems' limited resources. Several solutions to this paradox have been suggested in ecological theory. Apart from some biological factors like asymmetrical biotic interactions (Mohd, 2019; Kerr et al., 2002), abiotic components (Saidin et al., 2020; Guisan et al., 2013), dispersal process (Reichenbach et al., 2007; Mohd et al., 2018), stochasticity (Hubbell, 2001; Mohd et al., 2016) and memory effects (Moustafa et al., 2018, 2020), this work also helps to shed some light on another plausible mechanism of species richness: diversity in interaction types and the influential roles of mutualism. Our findings show that multi-species coexistence becomes more pronounced in this multiple interactions type system due to strong mutualistic forces; additionally, species diversity is enhanced by allowing these interacting species to coexist dynamically e.g., via oscillatory solutions and non-equilibrium dynamics.

Our bifurcation analysis results show that the resource species' competitive strength can induce ecological complexity in this multiple interactions type system. These bifurcation dynamics can sometimes lead to complex behaviours in the ecological systems under consideration. Though competition can lead to the extinction of certain species, its interplay with mutualism shows some exciting observations essential for the maintenance of species biodiversity. Our findings are important because the interplay between mutualism and competition results in different outcomes of species interactions in this ecological community. Further comparing the bifurcation analysis results also shows a qualitative change in the ecological system's overall dynamics with and without dispersal. These result can be attributed to the significant

influences of mutualism, competition and local dispersal in this multi-species system. The incorporation of local dispersal into this multiple interactions type model stabilizes the spatio-temporal dynamics and mediates more outcomes that are favourable to species diversity. The destabilization of species biodiversity phenomenon that occurs through the emergence of population fluctuations with increasing amplitude of oscillations is also weakened due to dispersal. This inclusion increases the tendency to maintain population densities further away from zero, thus decreasing the likelihood that a population will become extinct (due to random chances). These results also suggest that the destabilizing phenomenon of the "paradox of enrichment" postulated by some ecological models with a nonlinear functional response may be resolved and could be inverted into stabilizing effects with the addition of local dispersal and the diversity in interaction types into ecological communities.

In parallel with some theoretical studies (Kooi et al., 2004; Valdovinos et al., 2016, 2018), which show the (de-) stabilizing effects of mutualism on the community compositions, these previous findings are in agreement with our results. However, our analysis also reveals the influential roles of mutualism and competition in structuring multi-species ecosystems. It is observed that strong mutualism could stabilize the spatio-temporal dynamics, and this positive force essentially modifies the response of the ecological community towards the increase of the competitive pressure on the resource species. These insights are evident in our findings through the emergence of intriguing global dynamics where stable limit cycles alternate with unstable ones as competitive pressure varies. While alternative stable states are common in distinct ecological systems with mutualistic interactions, they are often stable, whereas, in our studies, we realize that there can be alternative stable or unstable states. Consequently, the long-term behaviours converge to multi-species coexistence outcomes either via a stable steady state or a limit cycle depending on species' initial abundances. Closer examination of our bifurcation analysis findings also reveals some significant insights: as mutualism and competition forces become stronger in the system, this situation can induce complex ecological dynamics simplification. In general, our analysis shows that strong mutualistic strength influences the ecological dynamics exerted by competition in this multiple interactions type community. Owing to this reason, the complexity of ecological outcomes is reduced further by the positive effects of mutualism on the competition. Interestingly, the long term behaviour converge to stable multi-species coexistence equilibrium and also limit cycles as competitive pressure increases. We also observe that this complexity ceases when mutualism becomes strong enough.

The interplay between mutualism and competition in a multiple interactions type system can shape species biodiversity from the species conservation viewpoint. These findings are consistent with previous observations of some ecological studies, which documented that different ecological forces such as mutualism and competition can promote species richness (Pascual-García and Bastolla, 2017; Chomicki et al., 2019; Bascompte, 2019; Martignoni et al., 2020). With regards to the findings on the inclusion of local dispersal into the ecological system, our current results also suggest that enhancing the connectivity between habitat patches, e.g., through the construction of artificial movement corridors (Brudvig et al., 2009; Mohd et al., 2018) in specific natural ecosystems, may provide some degree of protection to the sink populations in degrading habitats and increase the chance of species survival. As local dispersal is allowed between habitat patches, this mechanism leads to higher resource-competitor-exploiter-mutualist ratios and greater species ranges overlap between these interacting species; consequently, this situation can result in the maintenance of species richness. In general, dispersal may provide rescue effects for declining populations, which is in line with the crucial phenomenon observed in metapopulation theory. In metapopulation models, interacting species are assumed to occupy habitat patches that are connected by dispersal. In this case, the coexistence of interacting species can

occur in the metapopulation systems due to the rescue effects; in particular, dispersal of individuals from other habitat patches rescues the inferior species from being excluded by the superior species. These observations are also in tandem with some ecological studies (Massol et al., 2017; Godsoe et al., 2017; Di Musciano et al., 2020; Jiménez-Valverde et al., 2021), which demonstrate that local dispersal can maintain the abundance of species within patches, and thus prevent species exclusion.

Overall, this work should serve as a starting point for studying how the impacts of mutualism, competition and local dispersal can combine to result in community stability and species coexistence outcomes. We conclude that the diversity in interaction types and also local dispersal process are among critical factors driving multi-species community dynamics. A better understanding of the combined effects of these distinct ecological factors will lead to a better estimate of species distributions and will build greater confidence in the models' predictions.

CRedit authorship contribution statement

Murtala Bello Aliyu: Conceptualization, Methodology, Software, Writing - original draft, Writing - revised draft. **Mohd Hafiz Mohd:** Writing - original draft, Writing - revised draft, Investigation, Supervision.

Declaration of competing interest

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

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