



Research article

Biodiversity and ecosystem stability in a four-species prey-predator food chain with meta-communities

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Abstract: In this study, we examine tri-trophic food chain dynamics within meta-communities to understand how ecological interactions sustain biodiversity and ecosystem stability. A mathematical model is developed to capture trophic interactions among species across interconnected habitats, incorporating harvesting effects and management strategies. Stability analyses identify conditions for system stability, while simulations show how key ecological parameters influence species persistence. Integrating maximum sustainable yield (MSY) policies reveals optimal harvesting levels that ensure sustainability, whereas excessive harvesting causes population decline or instability. Comparisons with rice–fish co-culture systems demonstrate that biodiversity enhances tri-trophic interactions and ecosystem resilience. The findings provide insights into ecological balance and sustainable management for preserving biodiversity and ecosystem health.

Keywords: Tri-trophic food chain; meta-communities; positivity; boundedness; harvesting methods; sustainability; management policies

1. Introduction

In ecosystems, organisms form food chains where energy is transferred from plants to herbivores and then predators [1–4]. The top consumer typically occupies the highest trophic level, while decomposers are often excluded. Food chains can be modeled to study biodiversity, species coexistence, and system stability. Top predator extinction can occur due to efficient energy transfer at low temperatures and starvation at high temperatures [5–7]. Introducing meta-food webs, which combine complex communities with multiple trophic levels and habitats. Large species on higher trophic levels are at the highest risk of extinction due to fragmented landscapes, as smaller species cannot support their predators. The meta community proposes a self-organized mechanism for maintaining biodiversity, which is sensitive to habitat loss and fragmentation, emphasizing the need to consider changing habitats in ecosystem modeling [8–12].

Natural food webs are complex, with energy flow pathways determined by basic consumer-resource interactions. However, our knowledge of the structure of the food web affects these flows, and community dynamics are limited. Accurate predictions of community effects require understanding bottom-up and top-down forcing, with evidence suggesting apex predators play a crucial role [13, 14]. Current food web models assume linear or saturating feeding rates, but generalist top consumers may exhibit more complex feeding behavior through "switching" between prey [14, 15]. Living organisms acquire and lose energy through consumption, gathering resources, and respiration, with feeding interactions being the primary force in shaping communities. Food webs depict the network of interactions among populations, trophic units, or functional groups [16, 17]. The interactions among populations determine the structure of a food web and impact population dynamics. Therefore, to predict the community's response, a dynamic investigation is necessary as the properties of individual parts alone cannot make accurate predictions [18, 19].

Elton (1927) and Lindeman (1942) are endorsed with the origins of food web theory. Elton's work introduced the concept of community perspective, highlighting the interdependence of abundance patterns across different trophic levels. He visually represented this interdependence in the form of the "Eltonian pyramid." Lindeman provided an explanation for this occurrence by using biomass as a measure of energy, asserting that energy is lost at each progression to a higher trophic level in accordance with the second law of thermodynamics. As a result, the amount of available energy diminishes as trophic levels increase [20–22]. The energetic approach resulted in the belief that communities are largely controlled from the bottom up, with higher trophic levels being reliant on the abundance of lower trophic levels. The modeling approach by Lotka (1925) and Volterra (1926) led to the development of the food chain theory, with Rosenzweig and MacArthur (1963) using mathematical reasoning to link the "green world hypothesis" to predator-prey relationships. They laid the foundation for concepts like predator control and primary productivity. This theory was further developed by Hairston et al. (1977) and Oksanen et al. (1981) who projected a comprehensive framework pertaining to food webs consisting of more than three trophic levels. According to this theory, there is an oscillating pattern of resource-driven regulation and consumer-driven regulation from the highest to the lowest trophic level [23–28].

According to the theory proposed by Oksanen et al. (1981), the control in food chains with more than three trophic levels alternates between bottom-up and top-down. The top predators, which are totally constrained by their food supply, control the sub-terminal species. This leads to the release of

the prey from predation pressure, and this pattern continues down the food chain. As a result, the top trophic level and even levels are bottom-up controlled, and their equilibrium biomass increases with primary producer enrichment. However, odd levels are top-down controlled and remain constant regardless of enrichment. The theory also predicts that the food chain will lengthen with increasing enrichment, indicating that a higher trophic level's successful establishment requires sufficient productivity of the food chain. Feeding interactions cause a major effect on food web dynamics. Predators' consumption rates typically depend on prey density, as described by the functional response. The functional response can be classified into three types, with type 2 and type 3 being most relevant for a wide range of consumers. However, differentiating between these types using empirical data is often difficult because the functional response's shape is sensitive to feeding rates at low prey densities, which are seldom observed [29–31]. Vennila and Karthikeyan [32] investigated an EOQ model incorporating food waste circularity to minimize costs, emissions, and waste while maximizing profits. They analyzed how system parameters and product circularity influence sustainability and economic strategies.

Reserved zones and unreserved zones are areas designated for conservation purposes or not. Patches refer to distinct areas of habitat within a larger landscape. Meta-communities are groups of species that occur in multiple patches and can be affected by the spatial arrangement of these patches. Conservation efforts focus on connecting reserved zones through corridors to support meta-communities and promote ecosystem health and resilience [33–35]. In addition to ecological models, bifurcation and stability analysis have also been extensively studied in epidemiological systems. The disease transmission models are determined by the role of transcritical and Hopf bifurcations in predicting epidemic outbreaks and persistence [36–39]. These studies demonstrate that similar mathematical tools are effective in understanding the qualitative changes of ecological and epidemiological systems. Inspired by these works, we extend such bifurcation analysis to our ecological setting, where the reserve zone plays an analogous role to intervention strategies in disease models, influencing persistence and stability of populations.

Naik et al. [40] investigated complex bifurcation phenomena in a novel discrete-time predator-prey model with Holling-type response, validated through MATLAB simulations. The results deepen our understanding of dynamic behaviors and bifurcation structures in ecological systems. Singh et al. [41] studied stability, bifurcations, and solution behavior in a predator-prey system with extra food and anti-predator behavior, supported by numerical simulations. Some researchers [42, 43] utilize fractional-order models to account for memory and hereditary effects in predator-prey interactions, resulting in a more accurate depiction of biological systems. Others [44–49] use discrete-time and continuous models to examine complicated dynamics such as chaos and bifurcations in population systems. Recent experimental and field studies emphasize that empirical data are essential to validate theoretical food web models. For instance, Wan et al. [51] demonstrated that spatial aggregation of herbivores and predators intensifies tri-trophic cascades in rice–fish co-culture systems, while rice–fish integration promotes ecosystem multifunctionality and yield stability [52, 53]. These findings motivate the use of real ecological data to fit and test our model, ensuring that simulated trophic interactions reflect observed biodiversity–stability relationships in managed ecosystems. Recent advances in ecological mathematical modeling have explored complex trophic interactions, harvesting strategies, and sustainability under uncertain environments [54–58]. These studies emphasize the growing importance of integrating realistic ecological factors, which our present model extends by

incorporating meta-community effects and sustainable management perspectives. The scientific motivation of this study arises from the need to understand how biodiversity and spatial heterogeneity influence the long-term stability of ecosystems through multi-trophic interactions. Although several tri-trophic food chain models have been developed to investigate predator–prey relationships, most neglect the role of meta-communities and reserve zones that represent spatial connectivity among habitats. Such factors are increasingly recognized as key drivers of ecological persistence and resilience. Motivated by this gap, we introduce a novel four-species food web model that integrates bottom-up (resource-driven) and top-down (predator-driven) regulatory mechanisms across interconnected patches. The proposed model explicitly incorporates reserve zone effects, harvesting pressures, and migration dynamics, providing a more realistic representation of biodiversity processes in spatially structured ecosystems. The major novelty of this study lies in combining analytical approaches, including boundedness, bifurcation, and persistence analyses with global sensitivity and numerical simulations, to explore how meta-community structure affects ecological stability. This comprehensive framework advances our theoretical understanding of biodiversity–stability relationships and offers insights relevant for ecosystem management and conservation planning.

We also introduce a representation of interconnected feeding relationships comprising four species that account for the influence of the reserve zone on prey. The third level predator (z) is a specialist predator that feeds only on the first-level prey (x), while the fourth level predator (w) is a generalist predator that feeds on species from both the first and third levels. We investigate the boundedness of the model's solution, as well as the stability analysis. The solution's dynamic behavior is observed to be highly dependent, particularly the steadiness of balance points.

2. Mathematical model

Model (2.1) describes the dynamics of a four-species food web consisting of primary producers (x), primary consumers (y), secondary consumers (z), and tertiary consumers (w). The first equation models the growth of producers through a logistic term $rx(1 - x/k)$ with carrying capacity k , reduced by self-limitation $-a_1x$ and exploitation by secondary consumers $-b_1xz$, while primary consumers contribute positively to producers via $+a_2y$. The second equation represents the dynamics of primary consumers, which grow logistically with rate s and carrying capacity l , gain resources from producers through $+a_1x$, and are regulated by competition and mortality $-a_2y$. The third equation accounts for secondary consumers, which increase due to feeding on producers $+b_2xz$, decline naturally in the absence of resources $-b_0z$, and are suppressed by predation from tertiary consumers $-d_1zw$. Finally, the last equation describes tertiary consumers, which benefit from consuming secondary consumers $+d_2zw$, but also suffer natural mortality $-cw$. Functions $p(x) = b_1x$ and $q(z) = d_1z$ are used to simplify the functional responses of the producer–secondary consumer and secondary–tertiary consumer interactions, respectively. This formulation incorporates bottom-up effects (resource-driven growth) and top-down effects (predation and competition), providing a realistic representation of multi-trophic ecological interactions. Thus, the equation is,

$$\begin{aligned}
\frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - a_1x + a_2y - b_1, \\
\frac{dy}{dt} &= sy \left(1 - \frac{y}{l}\right) + a_1x - a_2y, \\
\frac{dz}{dt} &= b_2xz - b_0z - d_1zw, \\
\frac{dw}{dt} &= d_2zw - cw.
\end{aligned} \tag{2.1}$$

Here, model (2.1) is analyzed with the initial conditions $x(0) \geq 0$, $y(0) \geq 0$, $z(0) \geq 0$, and $w(0) \geq 0$. The functions $p(x) = b_1x$ and $q(z) = d_1z$.

Table 1. Description of model parameters.

Parameter	Description
r	Rate of growth of primary producers
k	Carrying capacity of primary producers
a_1	Self-limitation coefficient of primary producers
a_2	Competition coefficient of primary consumers
s	Growth rate of primary consumers
l	Carrying capacity of primary consumers
b_1	Mutualism coefficient between producers and secondary consumers
b_2	Competition coefficient between producers and secondary consumers
b_0	Death rate of secondary consumers in the absence of primary producers
d_1	Competition coefficient of secondary and tertiary consumers
d_2	Growth rate of tertiary consumers

Analyzing the dynamics of each trophic level can describe the general dynamics exhibited by the system. The population dynamics of the food web model exhibit various patterns. Primary producers (x) exhibit logistic growth, which eventually stabilizes at a population size constrained by the carrying capacity k . Due to their predation on (x), the major consumers (y) experience oscillations, which cause changes in the size of their population. Intricate dynamics emerge from mutualism, competition with (x), predation from both y and w , and effects on the population size of the secondary consumers (z). The tertiary consumers (w) reach a steady-state, with the population size stabilizing at an equilibrium level dependent on the competition term cw .

The present system (2.1) does not explicitly include a harvesting term; however, the concept of Maximum Sustainable Yield (MSY) is incorporated conceptually to assess sustainable harvesting within the proposed food-web framework. The MSY represents the critical harvesting level h^* that maximizes the long-term yield without driving any species to extinction. In this study, h^* is interpreted as the equilibrium harvesting rate that would maintain species persistence if proportional harvesting took place.

3. Boundedness

Theorem 3.1. Assume that the conditions $b_1 \geq b_2$ and $r_1 \geq r_2$ hold, then every solution of system (2.1) remains within a bounded subset of $\mathbb{R}_+^4$.

Proof. Consider $x(t), y(t), z(t), w(t)$ as a solution of system (2.1) corresponding to a non-negative initial condition. Thus,

$$U(t) = x(t) + y(t) + z(t) + w(t).$$

We have,

$$\frac{dU}{dt} = rx - \frac{rx^2}{k} + sy - \frac{sy^2}{l} - (b_1 - b_2)xz - (d_1 - d_2)zw - b_0z - cw$$

Now, using $b_1 \geq b_2$ and $d_1 \geq d_2$, we can write:

$$\frac{dU}{dt} \leq rx - \frac{rx^2}{k} + sy - \frac{sy^2}{l} - b_0z - cw$$

Adding and subtracting suitable terms, we get:

$$\frac{dU}{dt} + \alpha U \leq rk - \frac{r}{k}(x - k)^2 + sl - \frac{s}{l}(y - l)^2 \leq rk + sl = \mu$$

Applying Gronwall's Inequality [50]:

$$0 \leq U(t) = x(t) + y(t) + z(t) + w(t) \leq \frac{\mu}{\alpha}(1 - e^{-\alpha t}) + U(0)e^{-\alpha t}$$

Hence,

$$0 \leq \limsup_{t \rightarrow \infty} U(t) \leq \frac{\mu}{\alpha}$$

Thus, these solutions are bounded.

4. Meta-food web model

The dynamics of a meta-community consisting of M patches, where each patch contains N ecological species and has uniform species densities across the network, can be described through the application of the generalized modeling approach. The spatial interconnectivity of the patches further contributes to the system's complexity.

$$\begin{aligned} \dot{X}_l^k &= G_l^k(X_l^k) - M_l^k(X_l^k) + \epsilon_1 F_l^k(X_1^k, \dots, X_S^k) \\ &\quad - \sum_j D_{lj}^k(X_1^k, \dots, X_S^k) + \sum_l [E_l^{kl}(X_1^k, \dots, X_S^k, X_1^l, \dots, X_S^l) \\ &\quad - E_l^{lk}(X_1^l, \dots, X_S^l, X_1^k, \dots, X_S^k)] \end{aligned}$$

The system can be represented by

$$X^k = [X_1^k, \dots, X_S^k],$$

where the lower index l refers to a species and the upper index k refers to the patch. This representation is comparable to the previous one, but with the added complexity that species can interact with multiple other species and move between different patches.

$$\dot{X}_l^k = z_l^k(X^k) + \sum_j \left[E_l^{kl}(X^k, X^l) - E_l^{lk}(X^k, X^l) \right]$$

To ascertain the overall prey biomass available to a predator, we make use of $R_{jl}^k(X_l^k)$, which indicates the specific contribution of species j to the total prey biomass. This division enables us to break down the equation into local interaction terms z_l^k and dispersal terms.

$$T_l^k(X^k) = \sum_j R_{jl}^k(X_l^k)$$

Determining the total biomass available to a predator involves considering the individual contribution of species j to the overall prey biomass, which is denoted as $R_{jl}^k(X_l^k)$. This contribution influences the local interactions:

$$\begin{aligned} z_l^k = \dot{X}_l^k = & G_l^k(X^k) - M_l^k(X^k) + \epsilon_l F_l^k(X_1^k, T_l^k(X^k)) \\ & - \sum_j \frac{R_{jl}^k(X_l^k)}{T_j^k(X^k)} F_j(X_j^k, T_l^k(X^k)) \end{aligned}$$

By utilizing the precise dynamics of z_l^k for the case of a meta-food web without any dispersal, we can compute the Jacobian. This results in a block matrix structure for the local Jacobian, denoted by J_p :

$$J_p = \begin{pmatrix} p^1 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & p^N \end{pmatrix}$$

Upon expressing the diagonal elements op^k in scale and exponent parameters, we get

$$P_{ii}^k = \alpha_i^k \left[\bar{v}_i^k \delta_i^k \phi_i^k + v_i^k \delta_i^k (\gamma_i^k \chi_{ii}^k \lambda_{ii}^k + \psi_i^k) - \rho_i^k \sigma_i^k \mu_i^k - \rho_i^k \sigma_i^k \left(\beta_{ii}^k \psi_i^k + \sum_n \beta_{ni} \lambda_{ni} [(\gamma_n^k - 1) \chi_{ni}^k + 1] \right) \right]$$

The non-diagonal elements can be obtained in the case of cross-diffusion, where there are dependencies in the migration behavior between species using the matrices C^{km} . The migration terms for dispersal from patch m to patch k are contained in the exponent parameters in the equation.

$$P_{ij}^k = \alpha_i^k \left[\bar{v}_i^k \delta_i^k \gamma_i^k \chi_{ij}^k \lambda_{ij}^k - \rho_i^k \sigma_i^k \left(\beta_{ji}^k \psi_j^k + \sum_n \beta_{ni} \lambda_{nj} (\gamma_n^k - 1) \chi_{nj}^k \right) \right]$$

The Jacobian can be expressed based on the patch structure as follows:

$$J_C = \begin{pmatrix} \ddots & -\sum_m C^{km} & \dots & C^{kl} \\ \vdots & \ddots & \ddots & \vdots \\ C^{lk} & \dots & -\sum_m C^{lm} & \ddots \end{pmatrix}$$

In the context of patch dynamics in meta-food webs, the exponent parameters for the migration terms from one patch to another are contained in matrix C^{km} . Each element of this matrix captures the outcome of species dispersal on the system's population dynamics.

When there is simple diffusion, the migration matrix C is diagonal. In contrast, if the migration behavior between species is interdependent, known as cross-diffusion, then matrix C includes non-diagonal elements.

$$J_C = \begin{pmatrix} {}^*p - \sum_m c^{km} & \dots & C \\ \vdots & \ddots & \vdots \\ C & \dots & P - \sum_m c^{lm} \end{pmatrix}$$

which can be simplified to

$$J = \begin{pmatrix} {}^*p - \sum_m C & \dots & C \\ \vdots & \ddots & \vdots \\ C & \dots & P - \sum_m C \end{pmatrix}$$

When the food web and dispersal conditions across all patches are homogeneous, a steady state can be observed in nature by taking into account biomass per area instead of absolute biomass. This state is commonly observed when the dispersal is proportional to the connectivity per spatial node in place of the patch size.

We may express the summation of m as equivalent to the degree d^k of patch k , which represents the number of patches it is connected to. Hence, we can express it as follows:

$$J = \begin{pmatrix} {}^*p - d^k C & \dots & C \\ \vdots & \ddots & \vdots \\ C & \dots & P - d^l C \end{pmatrix}$$

The Jacobian of the meta-food web can be simplified by understanding that the Laplace matrix is the result of subtracting the degree matrix from the adjacency matrix.

$$J = I \otimes P - L \otimes C$$

and

$$(P - \kappa L)q = \lambda q$$

From the eigenvalue sets of each Laplace matrix that contain the eigenvalue κ , we can identify the set of eigenvalues for the Jacobian of the full meta-community. The collection of all these sets forms the union that encompasses all the eigenvalues of the Jacobian.

$$EV(J) = \bigcup_{n=1}^N EV(P - \kappa_n C)$$

The above equation defines the stability equation for the meta-community, which enables us to derive the eigenvalue sets of the Jacobian and, consequently, assess the system's stability.

$$S(\kappa) = \operatorname{Re}(\lambda_{\max}(\kappa))$$

A multifaceted mathematical function, known as the stability function, is used to ascertain the system's stability. This function takes into account various factors such as the network structure, species interactions, and dispersal dynamics to assess the stability of the system. The stability function is examined to understand the system's dynamic behavior of the meta-community and its possible response to environmental variation or disturbance.

5. Bifurcation analysis

The dynamics of system (2.1) about each equilibrium point are affected by variations in parameter values. To study this effect, we employ Sotomayor's hypothesis to conduct bifurcation analysis. This approach enables us to examine how fluctuations in the parameter values can cause qualitative changes within the system dynamics *may result in the formation of additional equilibrium points or limit cycles*. In contrast, the stability function determines the overall stability of the system, taking into account all equilibrium points and their associated dynamics. However, by varying the parameter values and examining their effect on the system's behavior, we can gain insight into how to achieve desired outcomes and improve the system's stability.

$$J = \begin{pmatrix} r - a_1 - \frac{2rx}{k} - b_1z & a_2 & -b_1x & 0 \\ a_1 & s - a_2 - \frac{2sy}{l} & 0 & 0 \\ b_1z & 0 & b_2x - b_0 - d_1w & -d_1z \\ 0 & 0 & d_2w & d_2z - cl \end{pmatrix}$$

Here, the system's dynamic behavior around equilibrium points is analyzed using Sotomayor's theorem, which explores the impact of varying parameter values. The theorem establishes that Pitchfork bifurcation is absent at the points F_i , $i = 0, 1, 2, 3$.

- (i) If $(r - a_1)^2 - la_1^3 \neq 0$, the equilibrium points F_0 in system (2.1) will undergo a transcritical bifurcation for the parameter value $a_2^* = \frac{s(r-a_1)}{r}$.
- (ii) If $v_3^{[1]} \neq 0$, then for the parameter value $b_2^* = \frac{b_0}{x}$ system (2.1) has a transcritical bifurcation at the equilibrium point F_1 .
- (iii) If $v_3^{[2]} \neq 0$, then for the parameter value $\gamma_2^* = \frac{a}{z^*}$, system (2.1) at the equilibrium point F_2 undergoes a transcritical bifurcation.

From the Jacobian matrix $J(F_3)$, all the eigenvalues of $J(F_3)$ have negative real parts at the equilibrium point F_3 . As a result, F_3 is classified as a hyperbolic equilibrium point, and consequently, there is no occurrence of bifurcation in system (2.1) at F_3 .

Also, $\operatorname{Re}(\lambda_{01}) = \operatorname{Re}(\lambda_{02}) = \lambda_{01} + \lambda_{02} \neq 0$ and λ_{03} and λ_{04} are real eigenvalues. Hence, Hopf bifurcation does not occur at F_0 .

Upon analyzing the Jacobian matrix, it has been determined that $J(F_1)$ and $J(F_2)$ possess four real eigenvalues. Therefore, it is concluded that Hopf bifurcation does not occur at these equilibrium points. In conclusion, the bifurcation analysis of system (2.1) highlights the critical role of parameter thresholds in shaping the system dynamics. Specifically, transcritical bifurcations are observed at the equilibria F_0 , F_1 , and F_2 for the critical parameter values. These bifurcations indicate that small changes in ecological parameters may exchange the stability between trivial and non-trivial equilibria, thereby determining whether species populations persist, decline, or collapse. In contrast, the absence of Hopf bifurcation at all equilibrium points confirms that the system does not give rise to periodic oscillations such as limit cycles under parameter variation. The main contribution of this analysis is therefore twofold: (i) identify the precise parameter regimes that separate stability from instability, and (ii) to establish that the long-term dynamics of the system are governed by equilibrium states rather than oscillatory behavior. Ecologically, this means that controlling key parameters can help maintain coexistence of species and prevent instability, thereby ensuring the sustainability of the food web system.

6. Persistence of the model

To examine the persistence of all species in system (2.1) over time, the persistence conditions are analyzed using the approach of Freedman and Waltman. The concept of persistence pertains to trajectories that originate from within the interior of $\mathbb{R}_+^4$ and stay strictly positive with no ω -limit sets located on the boundary planes, reflecting the continued existence of species over time. The stability of F_1 and F_2 on the boundary subsets defined by the xy and xyz planes is examined using the lemma.

Theorem 6.1. *System (2.1) can persist if the conditions $b_2x < b_0$ and $d_2z < c$ are not satisfied.*

Proof. We denote the orbit passing through a point q located inside the positive octant of $\mathbb{R}_+^4$ as $O(q)$, and we represent its omega limit set as $\Omega(q)$. The boundedness of system (2.1) ensures that $\Omega(q)$ is constrained. It is claimed that $F_0 \notin \Omega(q)$. By contradiction, we assume that F_0 is a saddle point that is not the only element in $\Omega(q)$. According to the Butler–McGehee lemma, another point exists in the omega-limit set $p \in \omega^s(F_0) \cap \Omega(q)$, where $\omega^s(F_0)$ is the stable point of F_0 . Then, $\omega^s(F_0)$ is either $\mathbb{R}_+^3(xzw)$ or $\mathbb{R}_+^3(yzw)$, and the orbit $o(p)$ passing through p is contained in $\Omega(q)$.

Assuming that $\omega^s(F_0)$ represents the space $\mathbb{R}_+^3(xzw)$ (similar proof applies when $\omega^s(F_0)$ represents the space $\mathbb{R}_+^3(yzw)$), if p belongs to the boundary axes of $\mathbb{R}_+^3(xzw)$, i.e., $p \in \mathbb{R}_+^3(xzw)$, this implies that the positive axis containing p forms a component of $\Omega(q)$, which contradicts the boundedness of $\Omega(q)$. p lies in the interior of $\mathbb{R}_+^3(xzw)$, and no equilibrium exists in the interior, so the orbit $o(p)$ passing through p , as a subset of $\Omega(q)$, must be unbounded, thereby contradicting the fact that $F_0 \notin \Omega(q)$. We now demonstrate that $F_1 \notin \Omega(q)$. As F_1 is a saddle point, by the Butler–McGehee lemma, there occurs a point, say p_1 , such that $p_1 \in \omega^s(F_1) \cap \Omega(q)$, where $\omega^s(F_1)$ is the space $\mathbb{R}_+^3(xzw)$, provided that $b_2x < b_0$ is violated. If $p_1 \in \mathbb{R}_+^3(xzw)$, then this contradicts our assumption. Therefore, we assume that p_1 belongs to $\mathbb{R}_+^3(xzw)$. Hence, there is no equilibrium point in the interior of $\mathbb{R}_+^3(xzw)$, $o(p_1) \subset \Omega(q)$, which is unbounded, contradicting our assumption. Thus, $F_1 \notin \Omega(q)$. Now, F_2 is a saddle point in $\mathbb{R}_+^4$ for $d_2z < c$. Hence, $F_2 \notin \Omega(q)$. Therefore, $\Omega(q)$ is in the interior of $\mathbb{R}_+^4$, which demonstrates the persistence of system (2.1).

7. Global sensitivity analysis

To evaluate the influence of model parameters on the system's dynamics, a global sensitivity analysis is conducted using the Partial Rank Correlation Coefficient (PRCC) method. This approach quantifies the strength and direction of the monotonic relationship between each parameter and selects output variables while controlling for the effects of all other parameters. The analysis is performed using Latin Hypercube Sampling (LHS) to generate $N = 1000$ samples across specified ranges for all 12 parameters involved in the system (see Table 2). The ranges are chosen as $\pm 10\%$ of the nominal values to reflect reasonable biological variability. Each sampled parameter set is used to numerically integrate the system of equations (Equation 2.1) over a time interval $[0, 100]$ using the Runge-Kutta method.

The state variables $x(t)$, $y(t)$, $z(t)$, and $w(t)$, representing the populations of primary producers, primary consumers, secondary consumers, and tertiary consumers, respectively, are recorded at the final time point $t = 100$. These terminal values are used as output metrics for the PRCC computation.

The resulting PRCC values indicate the relative sensitivity of each output to variations in the input parameters. A positive PRCC suggests a direct relationship between the parameter and the output variable, whereas a negative PRCC implies an inverse relationship. PRCC values close to $+1$ or -1 indicate a strong influence, while values near zero suggest minimal impact. Figure 1 shows that the PRCC analysis reveals that output x is positively influenced by the growth rate and carrying capacity of primary producers (r , k , d_2), and negatively by the interaction term b_1 and clearance rate c . Output y is most sensitive to the carrying capacity of primary consumers (l), with negative contributions from a_2 , b_1 , and c . Output z increases with c and decreases with the tertiary consumer growth rate (d_2). For output w , parameters b_2 and d_2 exert positive effects, while b_1 , d_1 , and c have strong negative influences. Overall, parameters related to consumer-resource interactions and top-down effects exhibit the most significant control over system dynamics.

Table 2. Partial rank correlation coefficients (PRCC) for model outputs.

Parameter	Value Range	PRCC (x)	PRCC (y)	PRCC (z)	PRCC (w)
r	[1.0, 1.8]	0.38	0.16	0.05	0.30
k	[40, 60]	0.23	0.01	0.00	0.20
a_1	[0.3, 0.5]	-0.09	0.14	0.00	-0.08
a_2	[0.5, 0.7]	0.18	-0.30	0.01	0.15
s	[1.2, 1.8]	0.07	0.25	0.00	0.06
l	[30, 50]	0.26	0.87	0.00	0.21
b_1	[0.6, 0.8]	-0.46	-0.14	0.02	-0.40
b_2	[0.7, 0.9]	-0.01	-0.02	0.06	0.42
b_0	[0.01, 0.03]	-0.01	0.03	-0.03	-0.03
d_1	[0.3, 0.5]	0.03	-0.02	-0.02	-0.39
d_2	[0.2, 0.4]	0.45	0.16	-0.71	0.35
c	[0.4, 0.6]	-0.46	-0.15	0.70	-0.33

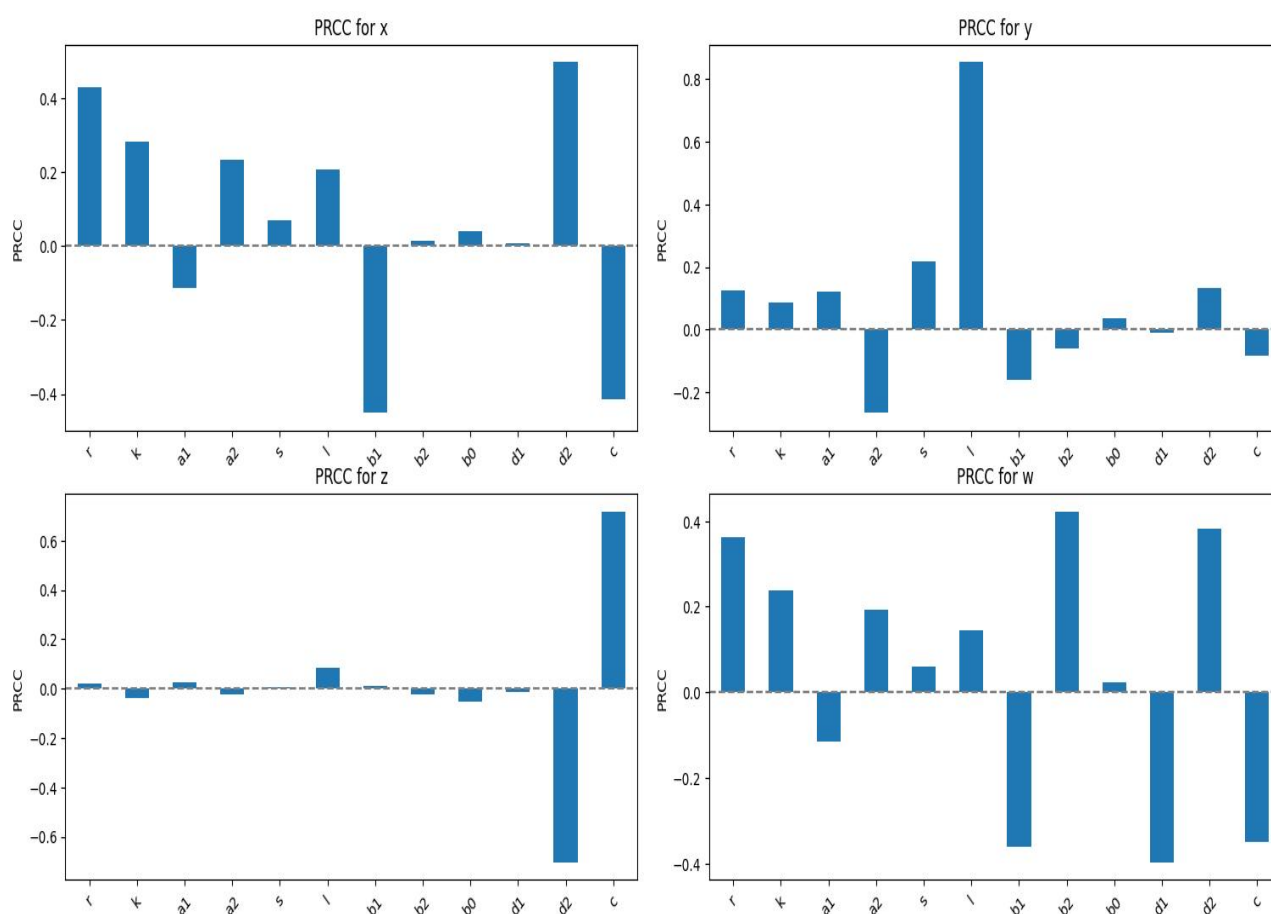


Figure 1. Partial Rank Correlation Coefficients (PRCC) indicating the sensitivity of each model parameter to the four system outputs: x , y , z , and w . Positive and negative values represent the direction and strength of monotonic influence each parameter has on the respective output. Parameters with PRCC values closer to ± 1 have a stronger influence on the output variable.

8. Numerical analysis

To assess the biological relevance of the proposed model, parameter ranges are selected to qualitatively match empirical observations from tri-trophic rice–fish ecosystems, where increased biodiversity enhances trophic regulation and productivity. The observed stability of our model under varying predator–prey interaction strengths aligns with field evidence that diversified systems, such as rice–fish co-cultures, support stronger top-down control and improved resilience to perturbations [51–53].

8.1. Impact of the meta community due to the migration rate of prey

A food web model incorporates parameter m , to represent the migration rate of prey species (x) to the meta community. The magnitude of this parameter would have an impact on the population size of x in the meta community. If the migration rate is increased, it would cause a greater influx of prey

to the meta community. This could potentially result in an increase in the populations of primary (y) and secondary consumers (z) that rely on x as a food source. Consequently, the population of the top predator (w), which feeds on z , could be affected. Figure 2 shows the varying migration rates of prey to the meta-community.

$$r = 1.4, \quad k = 50, \quad a_1 = 0.4, \quad a_2 = 0.6, \quad b_1 = 0.7, \quad b_2 = 0.8, \quad b_0 = 0.02$$

$$s = 1.5, \quad l = 40, \quad c = 0.5, \quad d_1 = 0.4, \quad d_2 = 0.3$$

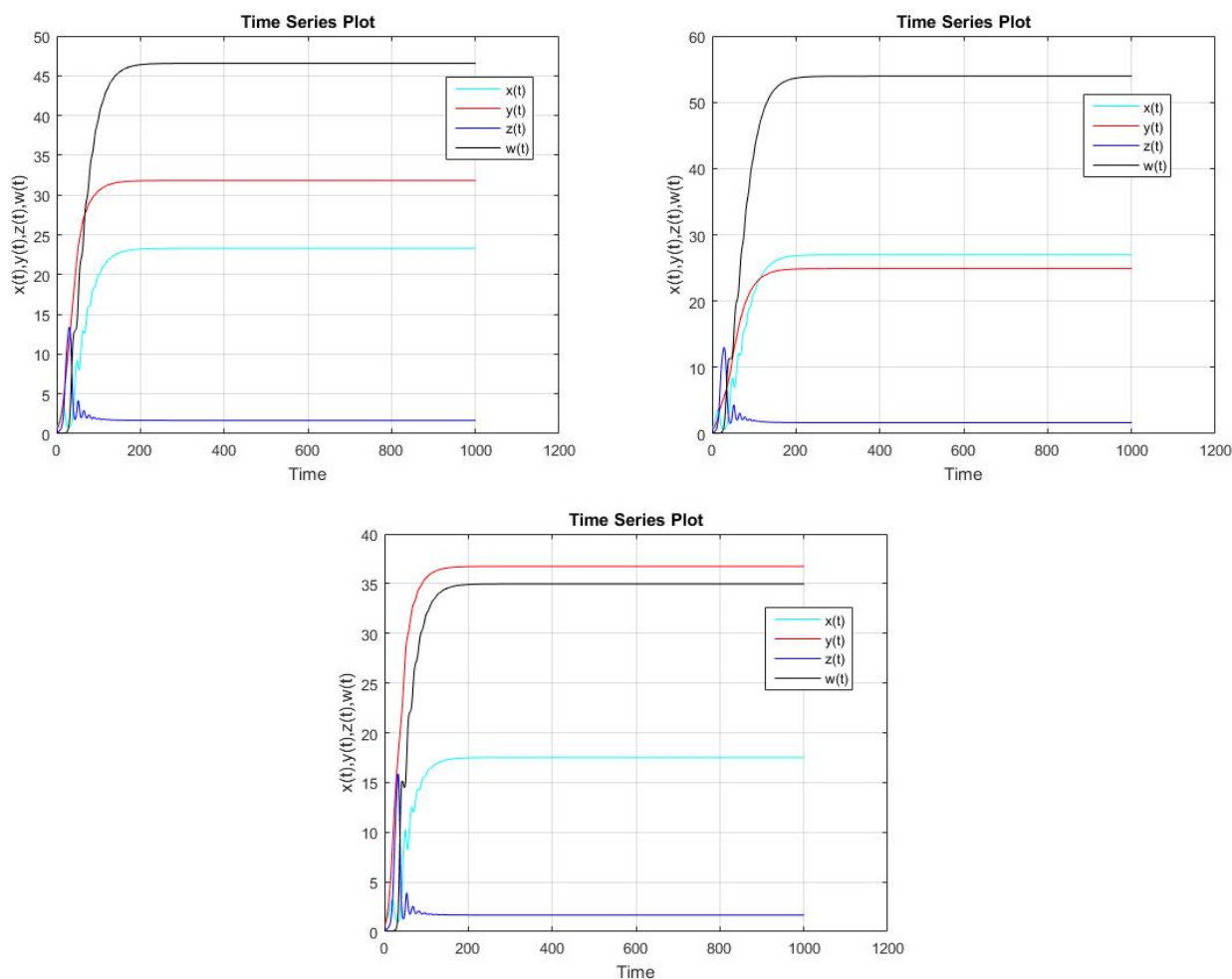


Figure 2. Dynamics of the system under varying migration rates of prey to the meta-community.

8.2. Impact of the meta community due to the natural death rate of predator (y)

In the food web model, the natural death rate of the predator (y) can be represented by a parameter such as d , which would affect the death rate of y . Increasing natural death rate would lead to a decline in the size of population y , which would affect the population size of the secondary consumer (z) that feeds on y , and ultimately affect the population of the top predator (w) that feeds on z . Figure 3 shows the dynamical effect of increased natural death rate of the predator.

- (a) $b_0 = 1$ to the stable point (15.45, 28.02, 1.95, 20.96)
 (b) $b_0 = 0.002$ to the stable point (15.45, 28.02, 1.95, 22.96) in the interior of $\mathbb{R}_+^4$.

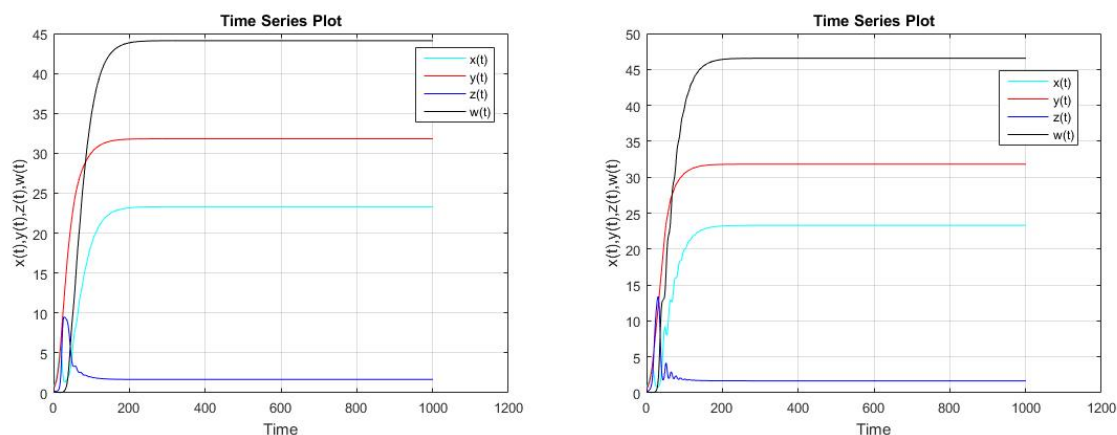


Figure 3. System behavior at equilibrium under the effect of increased natural death rate of the predator.

8.3. Impact of the meta community due to the natural death rate of top predator (w)

Parameter e can be used to denote the natural death rate of the top predator (w) in the food web model. An increase in e would result in a decrease in population size of the top predator, thereby affecting the population size of secondary consumer (z) that is preyed upon by the top predator. This could also potentially affect the population size of the primary consumer (y) that feeds on the secondary consumer. Figure 4 shows the system response changes in the natural death rate of the top predator.

- (a) When $c = 1$, model reaches a stable point at (5.05, 21.95, 4.95, 7.06) in interior of $\mathbb{R}_+^4$.
 (b) When $c = 0.1$, model reaches a stable point (39.45, 36.02, 0.95, 59.96) in interior of $\mathbb{R}_+^4$.
 (c) When $c = 0.01$, model reaches a stable point (44.45, 39.02, 0.05, 75.06) in interior of $\mathbb{R}_+^4$.
 (d) When $c = 0.001$, model reaches a stable point (51.45, 39.02, 0.005, 77.96) in the interior of $\mathbb{R}_+^4$.

8.4. Impact of the meta community due to attack rate of the top predator (w) on predator (y)

In the food web model, the attack rate of the top predator (w) on the predator (y) can be represented by a parameter such as h , which would affect death rate of y due to predation by w . Increasing attack rate would lead to a higher predation pressure on y , potentially leading to a decrease in population size of y and affecting population sizes of z and w that are higher in the food chain. Figure 5 shows the dynamical effect of the top predator's attack rate on the predator within the meta-community.

- (a) When $d_1 = 0.001$, the model reaches a stable point (15.45, 28.02, 1.95, 11.96) in the interior of $\mathbb{R}_+^4$.
 (b) When $d_1 = 0.002$, the model reaches a stable point (15.45, 28.02, 1.95, 16.96) in the interior of $\mathbb{R}_+^4$.

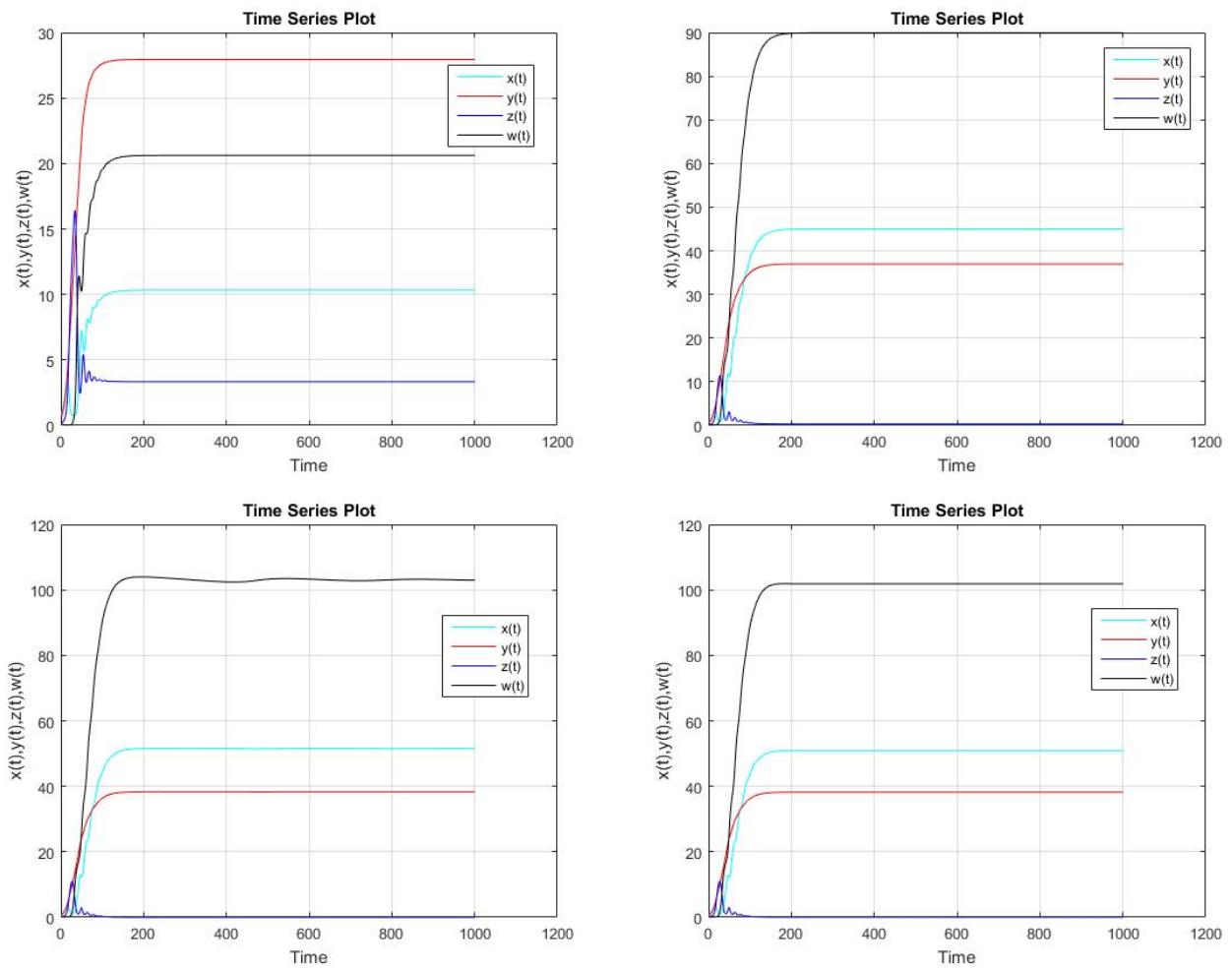


Figure 4. System response to changes in the natural death rate of the top predator.

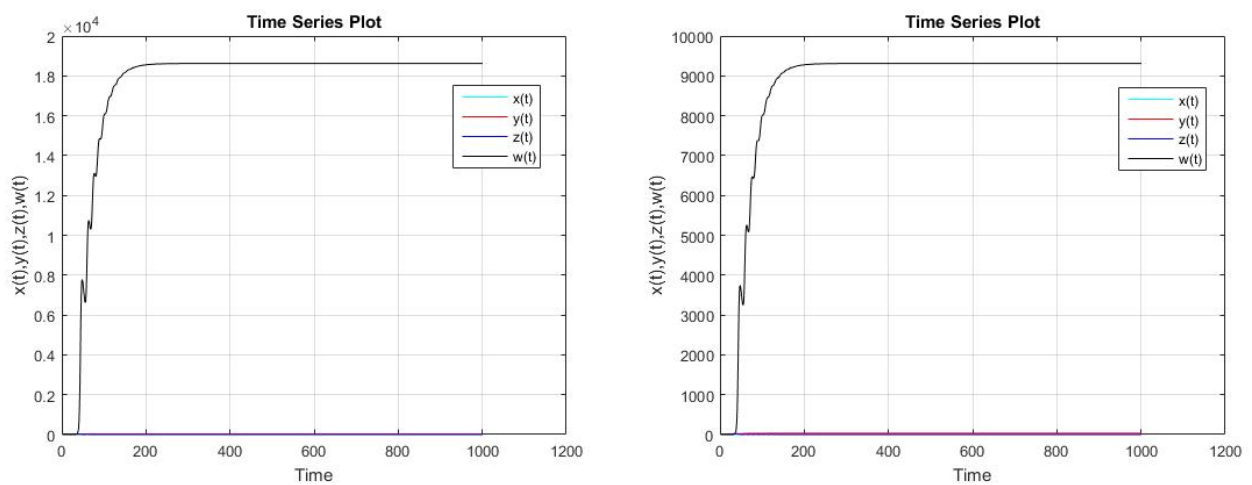


Figure 5. Effect of the top predator's attack rate on the predator within the meta-community.

8.5. Impact of the meta community due to the rate at which the predator (y) is transformed into the top predator (w)

In the food web model, conversion rate of the predator (y) to the top predator (w) can be represented by a parameter such as p , which would affect the growth rate of w due to predation on y . Increasing the conversion rate would lead to a higher growth rate of w , potentially resulting in growth of the population of w and affecting the population sizes. Figure 6 shows the system outcome based on the conversion rate of the predator to the top predator.

- (a) When $d_2 = 1$, the model reaches a stable point (42.05, 37.02, 0.95, 6311.06) in the interior of $\mathbb{R}_+^4$.
- (b) When $d_2 = 0.01$, the model reaches a stable point (0.45, 21.02, 39.95, 0.96) in the interior of $\mathbb{R}_+^4$.
- (c) When $d_2 = 0.004$, the model reaches a stable point (0.02, 20.02, 999.05, 0.006) in the interior of $\mathbb{R}_+^4$.
- (d) When $d_2 = 0.0004$, the model reaches a stable point (0.02, 21.0, 1024.95, 0) in the interior of $\mathbb{R}_+^3$.

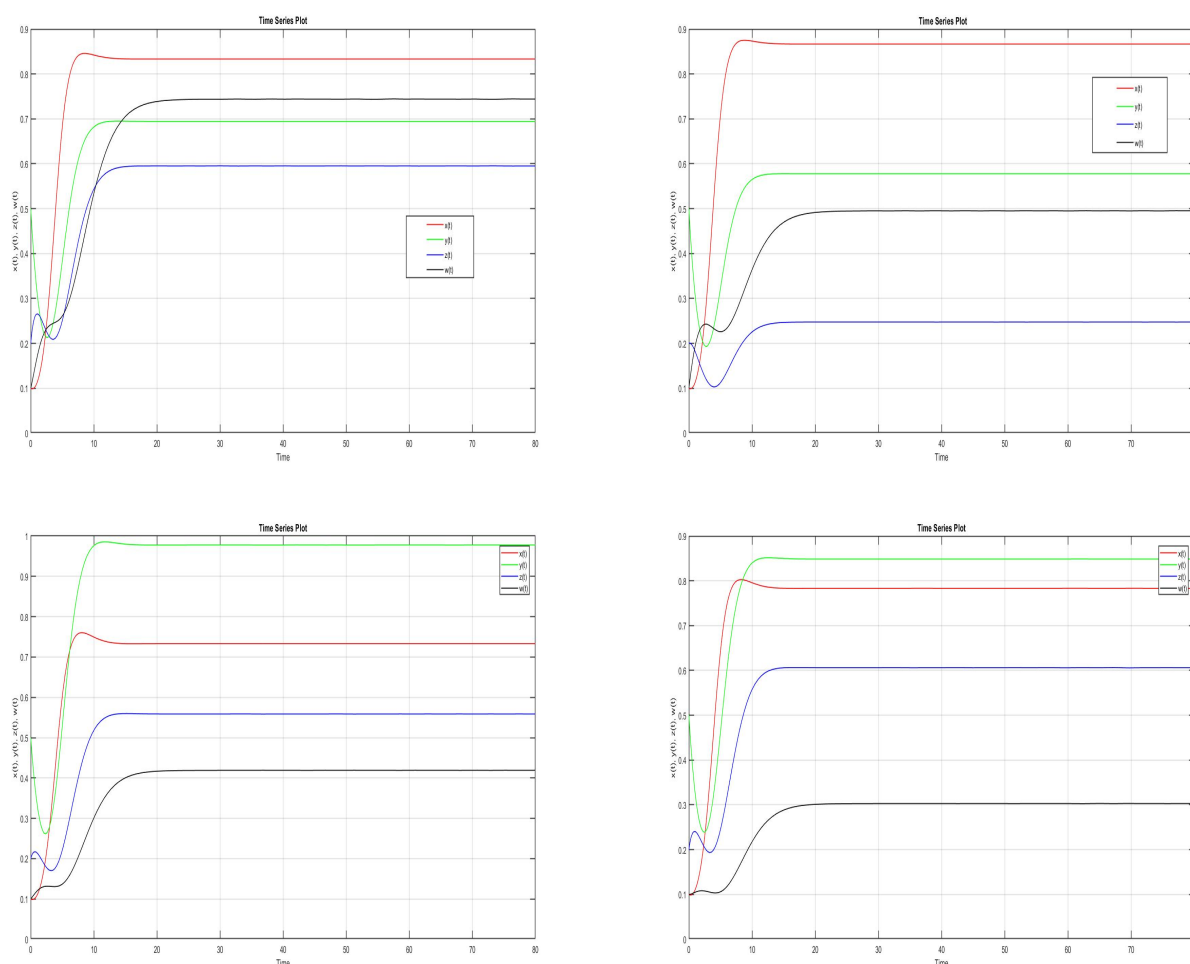


Figure 6. System outcome based on the conversion rate of the predator to the top predator.

8.6. Impact of the meta community due to the carrying capacity of the meta community

In the food web model, the carrying capacity of the meta community can be represented by a parameter such as K , which would disturb the maximum population size of all species in the meta community. Increasing the carrying capacity would enable higher populations of all species in the meta community, potentially affecting the abundances of species within the food web. Figure 7 shows the influence of the carrying capacity of the meta-community on species populations.

- (a) When $a_2 = 1$, the model reaches a stable point (15.05, 27.02, 1.95, 23.06) in the interior of $\mathbb{R}_+^4$.
- (b) When $a_2 = 0.001$, the model reaches a stable point (0.05, 40.02, 1.95, 0.06) in the interior of $\mathbb{R}_+^4$.
- (c) When $a_2 = 0.003$, the model reaches a stable point (0.02, 40.02, 2.05, 0.003) in the interior of $\mathbb{R}_+^4$.
- (d) When $a_2 = 0.0004$, the model reaches a stable point (0.02, 40.0, 1.95, 0) in the interior of $\mathbb{R}_+^3$.

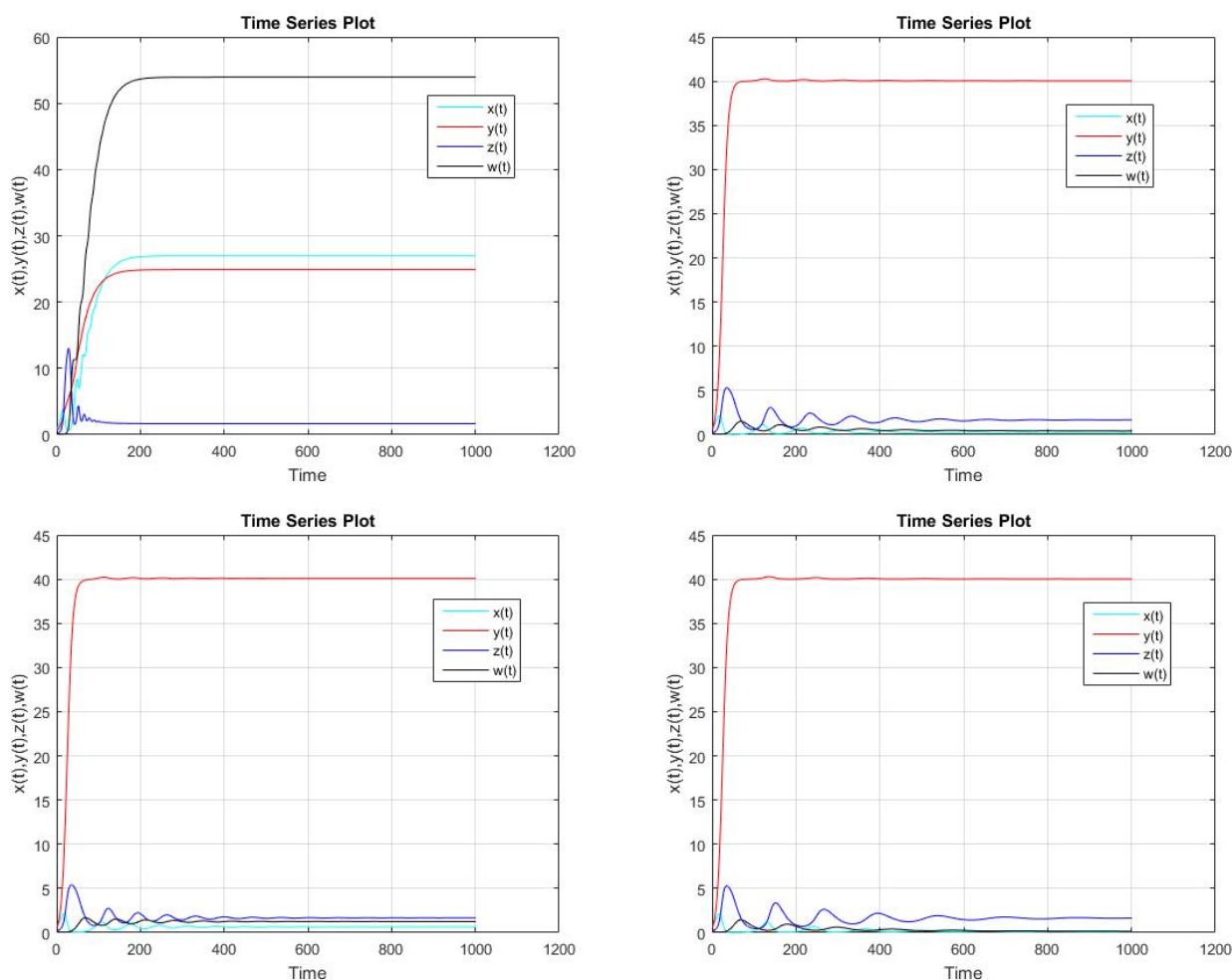


Figure 7. Influence of the carrying capacity of the meta-community on species populations.

8.7. Impact of the meta community due to the transformed rate of prey (x) to predator (y)

In the food web model, the transformed rate of prey (x) to predator (y) in a meta community can be represented by a parameter such as a , which would affect the growth rate of y due to predation on x . Increasing the conversion rate would lead to a higher growth rate of y in the meta community, potentially affecting population dimensions of species in the food web. Figure 8 shows the effect of the conversion rate of prey to predator on the population structure in the meta-community

- (a) When $b_2 = 1$, the model reaches a stable point (15.05, 27.02, 1.95, 31.06) in the interior of $\mathbb{R}_+^4$.
- (b) When $b_2 = 0.01$, the model reaches a stable point (15.05, 27.02, 1.95, 0.26) in the interior of $\mathbb{R}_+^4$.
- (c) When $b_2 = 0.0003$, the model reaches a stable point (15.05, 27.02, 1.95, 0.06) in the interior of $\mathbb{R}_+^4$.
- (d) When $b_2 = 0.0002$, the model reaches a stable point (15.05, 39.02, 0, 0) in the interior of $\mathbb{R}_+^2$.

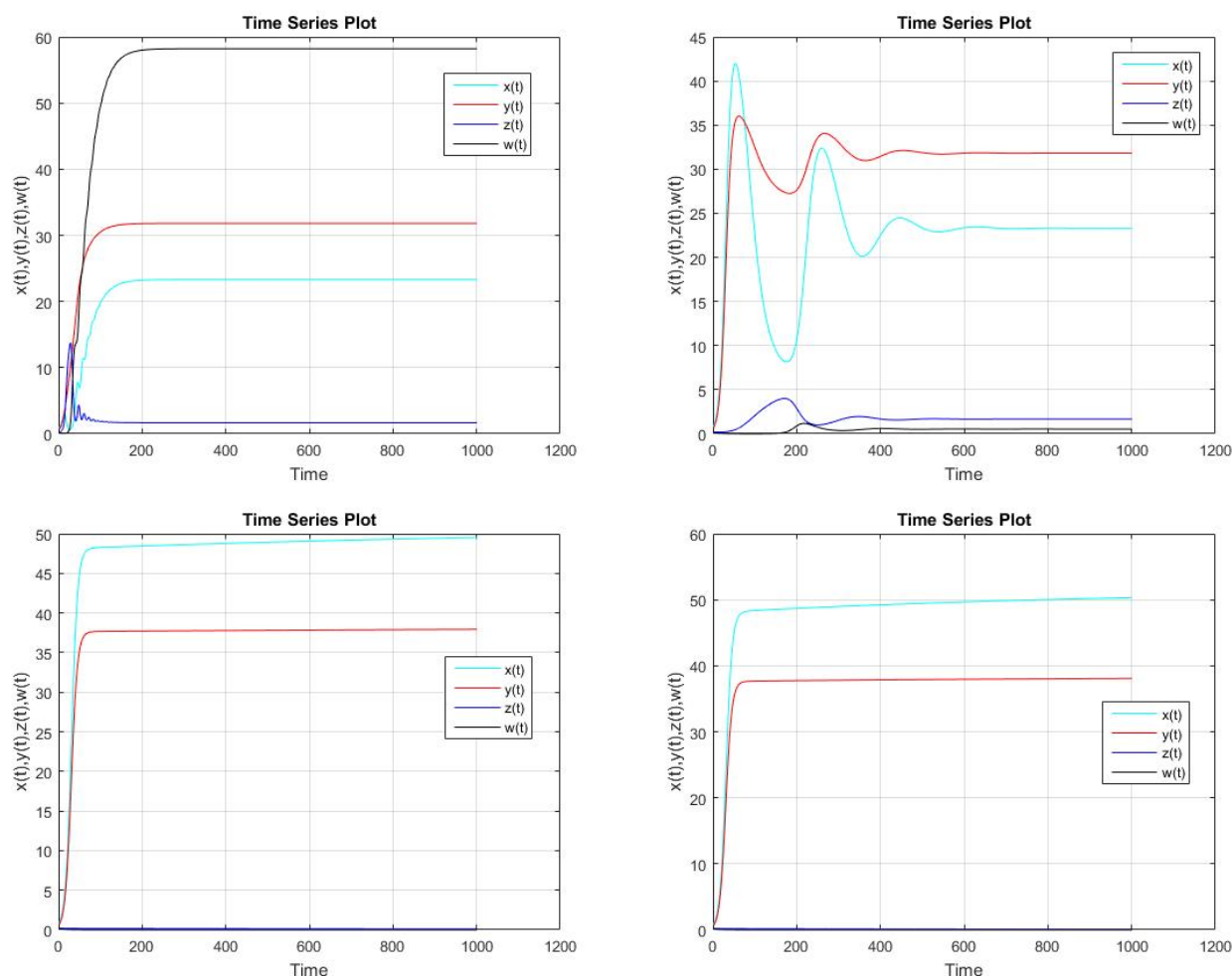


Figure 8. Effect of the conversion rate of prey to predator on population structure in the meta-community.

8.8. Impact of the meta community due to the attack rate of predator (y) on prey (x)

The dynamics of the system are influenced by variations in the attack rate of predator (y) on prey (x) within the meta-community. An increase in attack rate diminishes the prey population, which may subsequently reduce the predator population due to limited food availability. This reduction can further affect the top predator population due to decreased access to its prey. Conversely, a reduced attack rate may rise the prey population, which can support higher population levels of both predator and top predator due to increased resource availability. Figure 9 shows the dynamics influenced by changes in the predator's attack rate on the prey.

For $b_1 = 0.1$

$$\lambda_1 = -0.367 + 3.96i, \quad \lambda_2 = -0.297 - 4.96i, \quad \lambda_3 = -1.036, \quad \lambda_4 = -2.367$$

For $b_1 = 0.01$

$$\lambda_1 = -0.087 + 3.96i, \quad \lambda_2 = -0.047 - 4.06i, \quad \lambda_3 = -2.036, \quad \lambda_4 = -3.67$$

For $b_1 = 0.0001$

$$\lambda_1 = -0.0039 + 3.96i, \quad \lambda_2 = -0.007 - 3.919i, \quad \lambda_3 = -2.6, \quad \lambda_4 = -1.367$$

For $b_1 = 0.00001$

$$\lambda_1 = -0.367 + 3.96i, \quad \lambda_2 = -0.007 - 3.96i, \quad \lambda_3 = -1.036, \quad \lambda_4 = -2.367$$

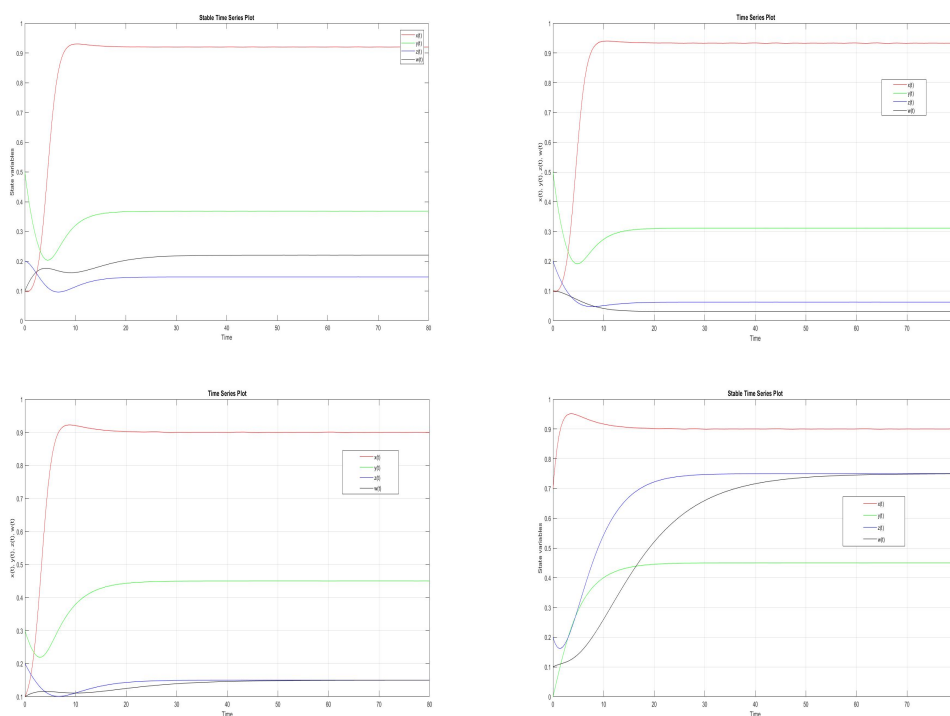


Figure 9. Dynamics influenced by changes in the predator's attack rate on the prey.

9. Conclusions

The food web model combined with a system of differential equations represents a dynamic and complex ecosystem where trophic level interactions drive the system's dynamics. Studying this model can provide knowledge into the underlying mechanisms driving population growth, competition, and predation observed in real-world ecosystems. A proposed ecological model has elucidated how a reserved zone can impact the dynamical behavior of a food chain prey-predator model. Analyzing equilibrium points of the system has demonstrated the boundedness and led to an investigation of its potential dynamical behavior. Conditions for persistence have been established, indicating that the system exhibits transcritical bifurcation. Numerical simulations validate the analytical findings, and the influences of various parameters on the behavior of the proposed system are examined. The top predator's persistence depends on parameters b_2 , a_2 , and d_2 , and predator's z existence relies on the translation rate b_2 of the prey in the unreserved zone. Under all circumstances, prey species x in an unreserved area and prey species y in a reserved area remain persistent. For a broad spectrum of parameters, the system that incorporates the reserved zone approaches a stable state. The full range of predator-prey interactions across trophic levels, including those with varying time scales of interaction, is incorporated into the dynamics of generalized meta-food webs, resulting in non-linear dynamics. The main contribution of this study is the formulation and rigorous analysis of an ecological model that integrates the effects of a reserve zone into a prey-predator food chain. Our analysis establishes that the system is bounded, admits transcritical bifurcations at specific equilibrium points, and excludes the occurrence of Hopf bifurcations. These findings provide a clearer understanding of how reserve zones and prey capture rates influence the long-term coexistence and persistence of species within meta-food webs. This contribution strengthens the theoretical foundation for managing biodiversity in spatially structured ecosystems.

Numerous factors, such as the structure of the food web and coupling matrix, influence the dynamics of the system. To make comprehensive claims about the network's resilience, information on spatial networks in natural settings is required. Additionally, the use of meta-communities on discrete patches can provide insights into cyclical population dynamics and heterogeneous steady states, stabilizing biomass and offering potential means for repopulation. The fourth-order Runge-Kutta (RK4) method employed in this study provides several advantages over existing lower-order numerical schemes. First, it offers higher accuracy in approximating the nonlinear dynamics of the prey-predator system with relatively small step sizes. Second, the RK4 scheme ensures better stability properties, which are particularly important for capturing long-term dynamics such as bifurcations and equilibrium transitions. Third, the method is computationally efficient, striking a balance between accuracy and cost, making it more suitable than simple schemes such as Euler or modified Euler methods. These features enable us to effectively capture the complex nonlinear interactions present in the proposed model, thereby ensuring the reliability of the obtained results. Our theoretical findings are consistent with recent field evidence from rice-fish co-culture systems, which demonstrate that increased biodiversity amplifies tri-trophic cascades and stabilizes ecosystem functions. Therefore, the model provides a mechanistic framework for understanding biodiversity-function relationships observed in real agricultural and natural ecosystems. Overall, while the generalized modeling approach is an effective tool for gathering insights, conventional methods are necessary to validate predictions.

10. Results and discussions

The study demonstrates that the proposed ecological model, considering a reserve zone's impact on a prey-predator food chain, exhibits boundedness and possesses transcritical bifurcation at equilibrium points. The prey populations in both zones remain stable under all conditions. The system reaches a steady state across parameter values. The generalized meta-food webs encompass a complete range of predator-prey interactions across trophic levels with varying time scales, resulting in non-linear dynamics. The system's behavior is inclined by the structure of the food web and its coupling matrix, highlighting the need for data on spatial networks in natural environments to make robust general statements. The approach applied helps examine the persistence conditions of the system, ensuring that all species have strictly positive trajectories originating in the interior of the state space, guaranteeing their long-term survival. The study reveals the potential effects of the fluctuating rate at which the predator captures prey in the meta-community, impacting the overall dynamics of the system. Additionally, Sotomayor's theorem shows that Hopf bifurcation does not occur at specific points in the system. The findings indicate significant implications, including the following: The proposed model shows stable behavior and persistence conditions, ensuring a sustainable ecosystem; both prey species persist in different zones, contributing to overall stability; the system converges to a steady state across parameters, highlighting its robustness; the incorporation of meta-food webs provides insights into predator-prey interactions; considering the food web's structure is vital for understanding system behavior; varying the predator's attack rate impacts overall dynamics; and Sotomayor's theorem reinforces stability and suitability for analyzing the food chain in meta-communities. The study's results inform effective conservation and management practices, supporting ecosystem sustainability and species diversity.

Use of AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

Conflict of interest

All authors declare no conflicts of interest in this paper.

Authors contributions

R. Geetha: Investigation, Writing- Original draft preparation, Methodology, Validation. M. Sivabalan: Supervision, Writing - Review & Editing. Mehmet Yavuz: Resources, Writing - Review & Editing. T. Megala: Formal analysis, Data collection. M. Siva Pradeep: Conceptualization, Writing - Review & Editing.

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