

Dynamical implications of bi-directional resource exchange within a meta-ecosystem

Marisabel Rodriguez Messan^a, Darin Kopp^b, Daniel C. Allen^b, Yun Kang^{*,c}

^a School of Mathematical and Statistical Sciences, Arizona State University, Tempe, AZ 85281, USA

^b Department of Biology, University of Oklahoma, Norman, OK 73019, USA

^c College of Integrative Sciences and Arts, Arizona State University, Mesa, AZ 85212, USA

ARTICLE INFO

Keywords:

Bi-directional resource exchange
Meta-ecosystem
Terrestrial ecosystems
Aquatic ecosystems
Multiple alternative stable states
Amensalistic interactions
Antagonistic interactions
Competitive interactions
Mutualistic interactions

ABSTRACT

The exchange of resources across ecosystem boundaries can have large impacts on ecosystem structures and functions at local and regional scales. In this article, we develop a simple model to investigate dynamical implications of bi-directional resource exchanges between two local ecosystems in a meta-ecosystem framework. In our model, we assume that (1) Each local ecosystem acts as both a resource donor and recipient, such that one ecosystem donating resources to another results in a cost to the donating system and a benefit to the recipient; and (2) The costs and benefits of the bi-directional resource exchange between two ecosystems are correlated in a nonlinear fashion. Our model could apply to the resource interactions between terrestrial and aquatic ecosystems that are supported by the literature. Our theoretical results show that bi-directional resource exchange between two ecosystems can indeed generate complicated dynamical outcomes, including the coupled ecosystems having amensalistic, antagonistic, competitive, or mutualistic interactions, with multiple alternative stable states depending on the relative costs and benefits. In addition, if the relative cost for resource exchange for an ecosystem is decreased or the relative benefit for resource exchange for an ecosystem is increased, the production of that ecosystem would increase; however, depending on the local environment, the production of the other ecosystem may increase or decrease. We expect that our work, by evaluating the potential outcomes of resource exchange theoretically, can facilitate empirical evaluations and advance the understanding of spatial ecosystem ecology where resource exchanges occur in varied ecosystems through a complicated network.

1. Introduction

It is increasingly recognized that material fluxes across ecological boundaries can have substantial consequences for ecosystem structure and function by mediating ecological processes across multiple temporal and spatial scales [18,27,37,39]. Processes operating over multiple spatial scales (e.g. landscape, region) have been considered in the study of population persistence and species coexistence [27]. The metapopulation and metacommunity frameworks have contributed much towards understanding spatial relationships in ecology by focusing on the movement of organisms [4,13,27,32,49]. A metapopulation, defined as a set of local populations in which individuals move from one place (population) to another [10,14], has provided insight into how the spatial coupling of local populations through dispersal permits the regional persistence of species that experience local extinctions and colonizations [27]. A metacommunity is a set of local communities connected by dispersal of multiple interacting species at different spatial scales [24,27], which has an exclusive focus on the biotic

components of ecosystems [27]. The concept of a meta-ecosystem — a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries [27] — builds upon these frameworks by embracing flows of biotic and abiotic elements [11,26,27]. This study investigates the theoretical consequences of reciprocal resource exchange between two ecosystems influencing functional characteristics such as energy flow and nutrient cycling.

Resources refer to any object or substance that contributes positively to the growth, reproduction, or maintenance of an organism. Resource flows in the form of inorganic nutrients in terrestrial-aquatic ecosystems [7] have gained much attention as essential nutrients can limit primary production of individual plants and entire ecosystems [1,8,51,52]. For instance, energy exchange in stream-riparian meta-ecosystems play an important role in the ecological functions by linking aquatic and terrestrial food webs [1,2]. In streams, different forms of energy flow affect fish production, which is directly affected by detritus or indirectly by the aquatic food chain (e.g. terrestrial and aquatic insects feeding on riparian vegetation) [2]. Within this stream-riparian

* Corresponding author.

E-mail addresses: marisabel@asu.edu (M.R. Messan), dcallen@ou.edu (D.C. Allen), yun.kang@asu.edu (Y. Kang).

meta-ecosystem context, the importance of resource unidirectional transfers from a donor ecosystem to a recipient ecosystem has been studied [6]. For instance, much research has focused on the flow of terrestrial-derived resources (e.g., leaf litter) to recipient aquatic ecosystems [42]. On the other hand, the flow of energy, detritus, and organisms from the water to the land can also have large effects on terrestrial community structure [38,42] as many studies have shown that aquatic insects have strong effects on terrestrial consumer abundance [36,43], distribution [33,41], and behavior [12]. These studies have shown that aquatic insects can represent a substantial portion (25%–100%) of energy supplied to terrestrial consumers [3,42]. Thus, resource movements between ecosystems are bi-directional in general and can play an important role in regulating nutrient availability and ecosystem productions [1,47].

Adjacent ecosystems rarely function independently of each other [11,27]. Instead, their habitats interact extensively, with each system being inherently linked by the cross-habitat transfer of energy or nutrients [21]. Resource exchange between two adjacent ecosystems, such as terrestrial and aquatic ecosystems, typically have high temporal and spatial variation and can enter each other's habitats at any trophic level, which could have dramatic influences on food web dynamics (e.g., predation) and regulating nutrient availability and productions in each ecosystem [1,39]. For example, terrestrial invertebrate inputs play important roles in streams. Depending on the season, invertebrates falling into a stream can make up as much as 50% of the annual consumption in some fish species [3]. Similarly, emerging aquatic insects are an important food source for riparian predators such as birds, lizards, and spiders [3,5,28]. They can comprise up to 90% of a riparian predator's diet [23]. Motivated by this, we aim to develop a simple model to investigate dynamical outcomes of bi-directional resource exchange between two ecosystems through trophic interactions across ecosystem boundaries. We expect that our model can be applied to ecosystems such as adjacent terrestrial and aquatic ecosystems.

Mathematical models have been useful to help us gain deeper biological insights on how resource exchange across ecosystem boundaries can have huge impacts on ecosystem structures and functions at local and regional scales. Recent theoretical work (e.g. [11,27,42]) based on the meta-ecosystem concept has been an important and timely extension to existing approaches in spatial ecology, which provides a powerful theoretical framework to address novel questions including the effects of bi-directional resource exchange in spatial ecosystem ecology [11,27]. In [27], they developed a simple theoretical meta-ecosystem model to demonstrate how significant global source-sink constraints arise from spatial coupling of ecosystems through nutrient flows. In [11], they analyzed a model for meta-ecosystem dynamics in a heterogeneous environment to study how the spatial flows of materials such as inorganic nutrients and nutrients sequestered into producers, herbivores, and detritus affect the community dynamics by extending the source-sink concept with an ecosystem perspective. In [42], they developed a model of resource exchange between rivers and watersheds to predict the spatial extent of material and nutrient fluxes from aquatic portions of watershed ecosystems based on a geomorphic template that includes river network structure, topography, and channel sinuosity along with important biological attributes such as productivity and dispersal ability. There is no doubt that the framework of meta-ecosystem theoretical approach [11,27] has the potential to integrate the perspectives of community, ecosystem, and landscape ecology to provide important and novel fundamental insights into the dynamics and functioning of ecosystems from local to global scales.

In this article, motivated by the work of Leroux and co-workers [11,27], we develop and analyze a simple meta-ecosystem model to explore how bi-directional resource exchanges and interactions between two adjacent ecosystems such as terrestrial and aquatic ecosystems affect ecological community structures and their productions. Interactions between multiple trophic levels are an important starting point in the prediction of the effects of resource loss and (or) gain in

ecosystems that can prompt sudden changes in the functioning of complex ecosystems. Our model focuses on the resource exchange between two ecosystems mainly driven by trophic interactions such as predation. More specifically, our model resembles a meta-ecosystem in which the individual ecosystem compartments function as both donors and recipients; each compartment exchanges resources reciprocally and ecosystem production is determined by in situ resource levels and the balance between inputs and outputs of materials through trophic interactions.

The rest of the article is organized as follows: In Section 2, we provide a short review on similar models in varied topics of ecological systems to gain deeper insights on the applications of our proposed model and the related dynamical outcomes. In Section 3, we provide the detailed model derivation of the proposed model. In Section 4, we perform local and global mathematical analysis to obtain theoretical results along with the related biological implications, and implement numerical simulations and bifurcation analysis to gain more insights on the dynamical effects of the cost and benefit of resource exchange. In Section 5, we discuss our results and potential future work. Lastly, we provide an appendix with detailed proofs of our theoretical results.

2. Comparisons to applications of similar models in two-species interactions

Mathematical models can help us understand the complexity of ecosystems in a quantitative way through simplifications. In this section, we will provide a short review on similar but different models that have been applied to population dynamics of two species interactions with potentially different dynamical outcomes than our proposed model due to modeling assumptions.

Holland and DeAngelis [17] proposed a bi-directional consumer-resource (C-R) mutualism model, where each species can be mutualistic (i.e., beneficial) and parasitic (i.e., costly) to the other species with the related interactions modeled through Holling type II functional responses. This model explains when and how mutualism transitions into parasitism, and the related results show that overexploitation (amensalistic interaction) may be beneficial to a species in the short-term or lead to extinction of one or both species; however, densities of both species are greater in the absence of overexploitation in the long term. Our proposed model (3) models benefits through increasing its carrying capacity and cost through Holling Type I functional responses. These different modeling approaches give different dynamical outcomes. Even though both our model and the model proposed in [17] potentially carry the same number of interior equilibria, their stability differs.

Zhang presents a competition-mutualism combined model by using a parabolic function in [57] extending his work with a two-species model in [56] to describe mutualism (or cooperation) occurring at low density while competition occurs at high density. The model in [57] shows the six kinds of interactions between two species in community or ecosystem level including competition, mutualism, predation, commensalism, amensalism, and neutralism through simple phase-plane analysis. Similar to our model, the work in [56,57] also observe competition, mutualism, predation, amensalism as well as commensalism. The study of Zhang et al. [56] also focuses on the stability conditions of boundary equilibria (one species goes extinct), and the related stability results of boundary equilibria support opinion of Zhang [57] about mutualism can promote two-species coexistence with implications that the evolution of mutualism may contribute to the multiple species coexistence and stability of ecosystem, and that mutualism may be favored by natural selection. The analytical work in [56,57] has been limited.

One of the recent work by Wang and Wu [53] proposed a mutualism-competition combined model modified from the Lotka–Volterra model which assumes that species i has positive effects on species j when it is at low density, while it has negative effects on species j when it is at high density. The interval of low density of species j , represents

the region of net mutualism of species j to species i . This assumption is using a definition by Hernandez and Barradas [16], i.e., the mutualism-competition interaction among multiple species means that mutualism happens when the species are at low population density while competition happens when they are at high population density, which is opposite to our proposed model due to the fact that we are modeling on the nutrient exchange between ecosystems instead of organism interactions. Wang and Wu [53] focuses on mutualism and competition, and gives some useful insights as to which degree mutualism has more influence on either a higher competitive species or both species on reaching a density larger than its carrying capacity by displaying regions of net mutualism, through simple analysis such as stability analysis and phase plane graphs.

As a summary, the models studied in [53,56,57] are similar and show that: mutualism at low population density brings a positive effect on the system by promoting coexistence and making the species achieve high densities; species that compete so intensely that they cannot coexist in the pure competition model, but can coexist if they are mutualistic at low densities; when in coexistence, the species with strong competitive ability and/or high initial density would benefit from the mutualism by approaching a density larger than its carrying capacity; when mutualism occurs in certain domains, a win-win situation emerges in which both species approach densities larger than their carrying capacities, respectively.

Our proposed meta-ecosystem model (3) models nutrient exchanges between two ecosystems by using the similar modeling approach in [34] that developed a mutualism-parasitism continuum model and its application to plant-mycorrhizae interactions. The model incorporates the gain to the host from the interaction with the symbiont and the symbiont's density independent and dependent death rates. Our model (3) does not assume a density independent nutrient depletion in each ecosystem, but does assume a density dependent resource exchange.

The comparisons above suggest that different functional responses of benefits and costs of interactions can produce different dynamical outcomes. For example, the stability of equilibria of the model proposed in [17] is different than the other models presented here including our model (3). Also, the models in [53,56,57] are similar but their study focuses are slightly different: Zhang [57] addressed interior equilibria; Zhang et al. [56] provided mathematical definitions of different interactions and studied the boundary equilibria; and Wang and Wu [53] studied mutualism and competition interactions only. All of these study are using simple stability analysis along with phase plane portraits.

3. Model derivation

In this section, we present a simple meta-ecosystem model to examine the dynamical outcomes of bi-directional resource exchanges between two nutrient-limited ecosystems. Bi-directional resources exchange occurs when an ecosystem acts as a bioreactor and transforms a resource from an unavailable form to an available one [15,50]. As a consequence, each ecosystem is both a resource donor and a recipient. In the proposed model, we use benefits and costs to refer to the positive effect of resource gain and negative effect of resource loss on biomass production, respectively. These general terms incorporate the suite of possible direct and indirect effects of resource exchanges that could be mainly driven by trophic interactions. Thus, the production of each ecosystem is a nonlinear function of local environments and the balance between resource inputs and outputs.

Let $P(t)$, $Q(t)$ be the production of two adjacent ecosystems that have resource exchange at time t . Resource exchange between P and Q ecosystems cause simultaneous benefits and costs which affect the ecosystem growth. Each ecosystem acts as a recipient by receiving resources (benefit) and as a donor by contributing with resources (cost) in a nonlinear fashion. We represent the meta-ecosystem dynamics of two ecosystems with bi-directional resource exchange with the following equations (see Fig. 1 for a schematic presentation):

$$\begin{aligned}\frac{dP}{dt} &= r_p P \left[1 - \frac{P}{K_p + a_p Q} \right] - b_p Q P \\ \frac{dQ}{dt} &= r_q Q \left[1 - \frac{Q}{K_q + a_q P} \right] - b_q Q P\end{aligned}\quad (1)$$

where r_i , $i = p, q$ is the intrinsic growth rate of biomass in ecosystem i ; K_i is the in situ resource availability (i.e. carrying capacity) of ecosystem i in the absence of the resource exchange; a_i indicates the quantity of resource from the donor ecosystem that is transferred to the recipient system i ; and b_i represents the depletion rate of resources of the donor ecosystem i at the ecosystem level. More specifically, the ecological assumptions of the proposed model (1) can be stated as follows:

1. In the absence of resource exchange, the production dynamics of ecosystem P and Q are described by the following logistic growth model (2):

$$\begin{aligned}\frac{dP}{dt} &= r_p P \left[1 - \frac{P}{K_p} \right] \\ \frac{dQ}{dt} &= r_q Q \left[1 - \frac{Q}{K_q} \right]\end{aligned}\quad (2)$$

which implies that either ecosystem P or Q could have persistent production at their carrying capacity $(P^*, Q^*) = (K_p, K_q)$ without resource exchange.

2. In our meta-ecosystem model (1), the cost (or contribution) of each ecosystem is modeled through the Holling Type I functional response, i.e. $b_i Q P$, $i = p, q$, as we assume that the resource exchange between two ecosystems P and Q is mainly driven by the trophic interactions such as predation. This assumption is supported by the resource exchange occurring at the interface between the terrestrial and aquatic ecosystems. A classic article by Jackson and Fisher [22] shows that 97% of the biomass of adult insects emerging from streams into riparian ecosystems do not return to the aquatic ecosystem due to environmental stress and predation pressure.
3. In our meta-ecosystem model (1), the benefit or resource that recipient ecosystem i receives from the donor ecosystem j is measured as a linear function of the production of the donor ecosystem. For example, due to the resource exchange, the potential carrying capacity of the ecosystem P increases to $K_p + a_p Q$ where the term $a_p Q$ incorporates the gain to the recipient ecosystem P from the resource exchange with the donor ecosystem Q . This modeling approach uses the framework of a mutualism-parasitism continuum model developed in [34] that considers the costs and benefits of two interacting species.

Following [30], we rescaled the meta-ecosystem model (1) by letting $p = \frac{P}{K_p}$, $q = \frac{Q}{K_q}$, $\tau = r_p t$. Thus it yields

$$\frac{dp}{d\tau} = \frac{1}{K_p}, \quad \frac{dq}{d\tau} = \frac{1}{K_q}, \quad \frac{d\tau}{d\tau} = \frac{1}{r_p}$$

which gives the following meta-ecosystem model (see the detailed rescaling steps in the last section):

$$\begin{aligned}p' &= \frac{dp}{d\tau} = p \left[1 - \frac{p}{1 + \alpha_p q} - \beta_p q \right] \\ q' &= \frac{dq}{d\tau} = \gamma q \left[1 - \frac{q}{1 + \alpha_q p} - \beta_q p \right],\end{aligned}\quad (3)$$

where p and q represent the resource stock of each ecosystem relative to its own carrying capacity; $\alpha_i = \frac{a_i K_j}{K_i}$ and $\beta_i = \frac{b_i K_j}{r_i}$ encompass the relative benefits and costs of resource exchanges for ecosystem i , respectively; $\frac{\alpha_i}{\beta_i} = \frac{a_i r_i}{b_i K_i}$ is the relative ratio of benefit to cost for ecosystem i . Increasing

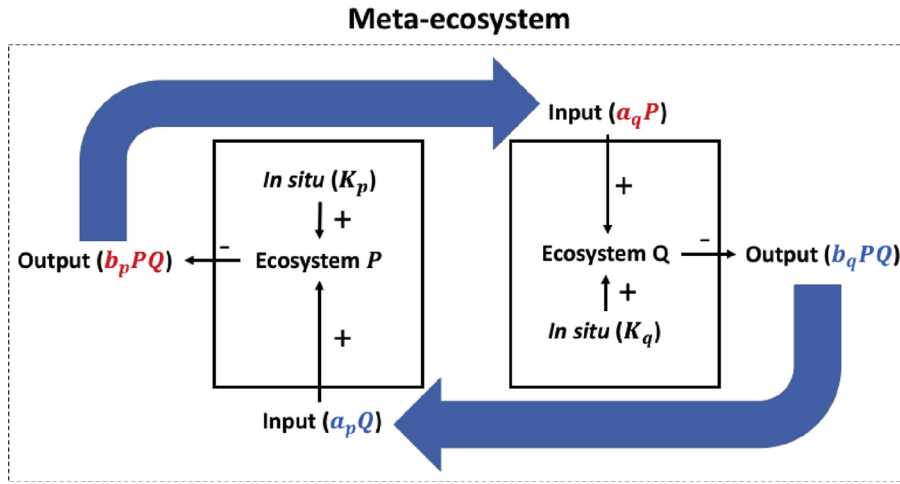


Fig. 1. A schematic representation of our meta-ecosystem model.

the carrying capacity K_p of ecosystem p will increase the relative benefits of ecosystem q causing a decrease of the relative benefits for ecosystem p . The exchange of resources, in this case favoring ecosystem q , has a cost. Therefore, the parameter describing the cost of resource exchange in ecosystem p increases as K_p increases. Also, we notice that the ratio for ecosystem q , $q = \frac{Q}{K_q}$ is not affected by the increase of K_p . This could be explained by the fact that ecosystem q is undergoing an equal proportion of the relative benefits and costs due to the resource exchange, so the ecosystem q is not affected by the change of K_p . Moreover, $\gamma = \frac{r_q}{r_p}$ represents the relative growth rate of resources in q relative to those in p , e.g. if $\gamma > 1$, then $r_p < r_q$. Note that, for convenience, we use *relative* to denote the parameters that have been re-scaled. In the rest of this article, we will investigate how the *relative benefits (costs) of resource exchanges*, α_i (β_i), and the *relative ratio of benefit to cost* $\frac{\alpha_i}{\beta_i}$ of each ecosystem affect ecological community structure and the production of each ecosystem.

4. Mathematical analysis

We first provide the following theorems regarding the general dynamical properties of our proposed model (3):

Theorem 1 (Positivity and Boundedness). *The meta-ecosystem model (3) is positive invariant and bounded in $\mathbb{R}_+^2 = \{p \geq 0; q \geq 0\}$ and only has equilibrium dynamics.*

Theorem 1 indicates that our meta-ecosystem is biologically well-defined with simple dynamics (i.e. it has no limit cycles according to Dulac–Bendixson Criterion).

Theorem 2 (Persistence of ecosystems). *Ecosystem i in the meta-ecosystem (3) is persistent if its relative cost is less than 1, i.e., $\beta_i = \frac{b_i}{r_i} K_j < 1$.*

Theorem 2 indicates the persistence of each ecosystem requires its relative cost to be less than 1, i.e.

$$\beta_i = \frac{b_i}{r_i} K_j < 1 \Leftrightarrow K_j < \frac{r_i}{b_i}.$$

This implies that ecosystem i can persist if its effective growth rate $\frac{r_i}{b_i}$ is greater than the original carrying capacity K_j of ecosystem j . The results of **Theorem 2** also imply that the meta-ecosystem (3) is permanent when $\beta_i < 1$ for both $i = p, q$, i.e., both Ecosystem p and Ecosystem q are persistent. Then according to the fixed point theorem [20], we can conclude that the meta-ecosystem (3) has at least one interior equilibrium when $\beta_i < 1$ for both $i = p, q$.

Now we study the number of equilibria and their stability for Model (3). First, the model always has the following three boundary equilibria:

$E_{00} = (0, 0)$, $E_{01} = (0, 1)$, $E_{10} = (1, 0)$, and it can have up to three interior equilibria that are determined with the isoclines (4) and (5) by setting $p' = 0$ and $q' = 0$:

$$p^* = g(q^*) = (1 - \beta_p q^*)(1 + \alpha_p q^*) \quad (4)$$

$$q^* = f(p^*) = (1 - \beta_q p^*)(1 + \alpha_q p^*). \quad (5)$$

Notice that $f(p)$ has a maximum $f(M_q) = \frac{(\alpha_q + \beta_q)^2}{4\alpha_q\beta_q} = \frac{(\frac{\alpha_q}{\beta_q} + 1)^2}{4\frac{\alpha_q}{\beta_q}} \geq 1$ at

its critical point $M_q = \frac{\frac{\alpha_q}{\beta_q} - 1}{2\alpha_q}$ and $g(q)$ a maximum $g(M_p) = \frac{(\frac{\alpha_p}{\beta_p} + 1)^2}{4\frac{\alpha_p}{\beta_p}} \geq 1$

at its critical point $M_p = \frac{\frac{\alpha_p}{\beta_p} - 1}{2\alpha_p}$.

We denote each of these maxima as the composite cost-benefit term for ecosystems q and p , respectively. That is, for a given α_i and β_i , $i = p, q$, it describes the maximum resource stock a given ecosystem can achieve and the stock of the neighboring ecosystem. The resource stock of ecosystem i reaches a maximum value of $\frac{(\frac{\alpha_i}{\beta_i} + 1)^2}{4\frac{\alpha_i}{\beta_i}} \geq 1$ when the re-

sources of ecosystem j are at $\frac{\frac{\alpha_j}{\beta_j} - 1}{2\alpha_j}$, for $i, j = p, q$, $i \neq j$. Now we present the following theorem regarding the number of equilibria and their stability for Model (3):

Theorem 3 (Equilibria and Stability Dynamics). *Let $\alpha_p, \alpha_q, \beta_p, \beta_q$ and γ be positive parameters. Our meta-ecosystem model (3) always has three boundary equilibria: $E_{00} = (0, 0)$, $E_{01} = (0, 1)$, $E_{10} = (1, 0)$ where the extinction equilibrium E_{00} is always a source; the boundary equilibrium $E_{01} = (0, 1)$ is locally asymptotically stable (LAS) if $\beta_p > 1$; and the boundary equilibrium $E_{10} = (1, 0)$ is LAS whenever $\beta_q > 1$. Model (3) can have up to three interior equilibria provided the following sufficient conditions are satisfied:*

1. No interior equilibrium (see Fig. 5): Model (3) has no interior equilibrium if the following inequalities hold

$$\frac{\alpha_i}{\beta_i} < 1, 1 < \beta_j < \frac{\alpha_j + \frac{1}{\beta_i - \alpha_i}}{1 + 2\alpha_j}$$

$$\text{and } \frac{\alpha_j \beta_j (\alpha_i - \beta_i)^2}{\alpha_i \beta_i (\beta_j + 2\alpha_j \beta_j - \alpha_j)} = \frac{(\frac{\alpha_i}{\beta_i} - 1)^2}{\frac{\alpha_i}{\beta_i} (\frac{1}{\alpha_j} + 2 - \frac{1}{\beta_j})} > 1$$

- for $i = p, j = q$ or $i = q, j = p$.
- One interior equilibrium (see Fig. 3a): Model (3) has a unique interior equilibrium if $\frac{\alpha_i}{\beta_i} < 1, \beta_i < 1$ for both $i = p, q$ and
$$\beta_j < \frac{\alpha_j}{1 + 2\alpha_j} \text{ for } j = p \text{ or } j = q \text{ but } j \neq i.$$
 - Two interior equilibria (see Fig. 6): Model (3) has two interior equilibria if the following inequalities hold
$$\frac{4\frac{\alpha_j}{\beta_j}}{\left(1 + \frac{\alpha_j}{\beta_j}\right)^2} < \beta_i < 1 < \beta_j < \alpha_j$$
for either $i = p, j = q$ (see Fig. 6 a) or $i = q, j = p$ (see Fig. 6b).
 - Three interior equilibria (see Fig. 4): Model (3) has three interior equilibria if the following inequalities hold
$$\frac{\alpha_j}{\beta_j} > 1 \text{ and } \frac{4\frac{\alpha_j}{\beta_j}}{\left(1 + \frac{\alpha_j}{\beta_j}\right)^2} < \beta_i < 1$$
for both $i, j = p, q, i \neq j$.

Theorem 3 suggests that with resource exchanges, the meta-ecosystem (3) could have very complicated dynamics such as multiple alternative states depending on local environments.

Based on our theoretical results (Theorems 1–3) along with the aid of the two-dimensional bifurcation diagram (see Fig. 2 when $\alpha_p = \alpha_q = 3$ and $\gamma = 1$), we conclude that the relative cost $\beta_i, i = p, q$ and the relative ratio of benefit to cost $\frac{\alpha_i}{\beta_i}, i = p, q$ determine the dynamical outcomes of the meta-ecosystem (3) as follows:

- Relative costs of resource exchange of both ecosystems are less than 1: the meta-ecosystem (3) is permanent with either one (the blue region on the left corner of Fig. 2) or three interior equilibria (the yellow region on the left corner Fig. 2) where the separation of these two cases is determined by curves approximated by $\frac{4\frac{\alpha_j}{\beta_j}}{\left(1 + \frac{\alpha_j}{\beta_j}\right)^2} = \beta_i$ for

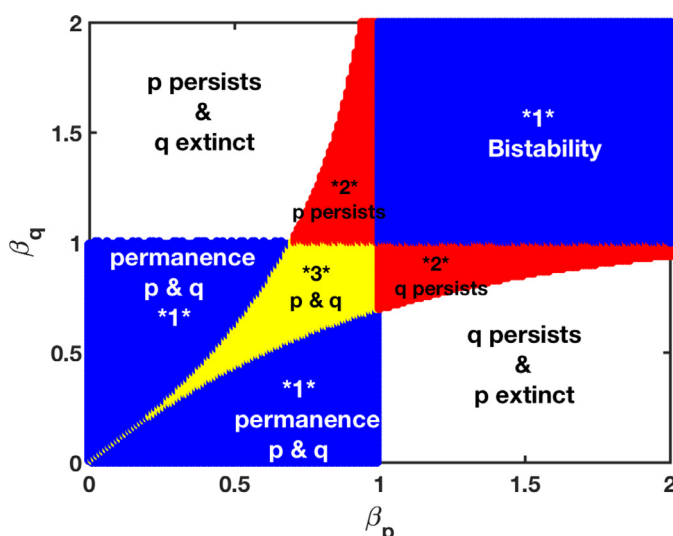


Fig. 2. Bifurcation diagram of β_p versus β_q showing the number of interior equilibria of our proposed model (3) when $\alpha_p = \alpha_q = 3$ and $\gamma = 1$. No interior (white), One interior (blue), Two interior (red), Three interior (yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

both $i, j = p, q$ and $i \neq j$.

- One interior equilibrium (see Fig. 3a): Based on sufficient conditions from Theorem 3, the meta-ecosystem (3) has global stability at the unique interior equilibrium when the following inequalities hold

$$\frac{\alpha_i}{\beta_i} < 1, \beta_i < 1 \text{ for both } i = p, q$$

$$\text{and } \beta_j < \frac{\alpha_j}{1 + 2\alpha_j} \text{ for } j = p \text{ or } j = q$$

but $j \neq i$.

These conditions imply that this type of permanence of the meta-ecosystem (3) occurs when both ecosystems have low relative costs (i.e., $\beta_i < 1$) and low relative ratio of benefit to cost (i.e., $\frac{\alpha_i}{\beta_i} < 1$).

- Three interior equilibria (see Fig. 4): The meta-ecosystem (3) can have three interior equilibria $E_{pq}^1, E_{pq}^2, E_{pq}^3$ when the relative costs of resource exchange between ecosystem p and q have intermediate values, i.e. $\beta_i < 1, i = p, q$, but the relative cost of resource exchange β_i is greater than $\frac{4\frac{\alpha_j}{\beta_j}}{\left(1 + \frac{\alpha_j}{\beta_j}\right)^2}$, for both $i, j = p, q$ and

$i \neq j$. In this case, the meta-ecosystem (3) is permanent and has two interior alternative states where initial conditions determine when the system approaches to the interior stable state at which one ecosystem will have the advantage for a given outcome. We define this dynamical outcome as a **Type Three** bi-stability.

- Relative costs of resource exchange for both ecosystems are greater than 1 (see the blue region in the upper right corner of Fig. 2): the meta-ecosystem (3) has a **Type One** bi-stability between the two boundary equilibria E_{01} and E_{10} (see Fig. 3b), where the meta-ecosystem has a unique interior equilibrium E_{pq}^1 which is a saddle. In this case, initial conditions determine which boundary equilibrium the system will approach to.
- One of the relative costs of resource exchange of ecosystems is less than 1 (i.e., $(\beta_i - 1)(\beta_j - 1) < 0$): the meta-ecosystem (3) has either no interior equilibrium (white regions in Fig. 2) or two interior equilibria (red regions in Fig. 2) where the separation of these two cases is determined by curves approximated by $\frac{4\frac{\alpha_j}{\beta_j}}{\left(1 + \frac{\alpha_j}{\beta_j}\right)^2} = \beta_i$ for both

$i, j = p, q$ and $i \neq j$.

- No interior equilibrium (see Fig. 5): According Theorem 3, the meta-ecosystem (3) has global stability at the boundary equilibrium (i.e., the ecosystem j goes extinct due to resource exchange) when the following inequalities hold

$$\frac{\alpha_i}{\beta_i} < 1, 1 < \beta_j < \frac{\alpha_j + \frac{1}{\beta_i - \alpha_i}}{1 + 2\alpha_j}$$

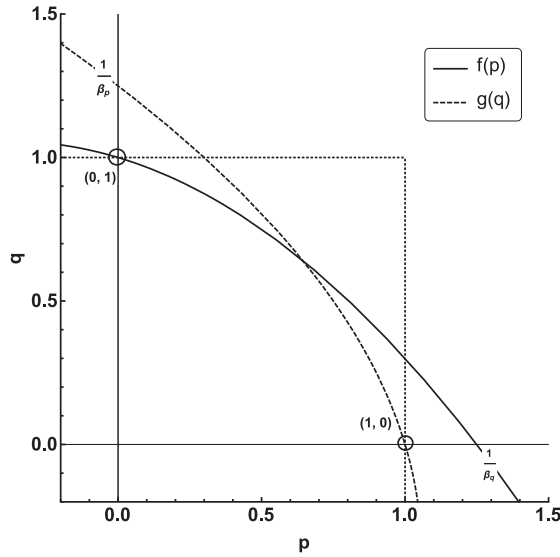
$$\text{and } \frac{\alpha_i \beta_j (\alpha_i - \beta_i)^2}{\alpha_i \beta_i (\beta_j + 2\alpha_j \beta_j - \alpha_j)} = \frac{\left(\frac{\alpha_i}{\beta_i} - 1\right)^2}{\frac{\alpha_i}{\beta_i} \left(\frac{1}{\alpha_j} + 2 - \frac{1}{\beta_j}\right)} > 1$$

where the conditions $\beta_j < \frac{\alpha_j + \frac{1}{\beta_i - \alpha_i}}{1 + 2\alpha_j}$ and

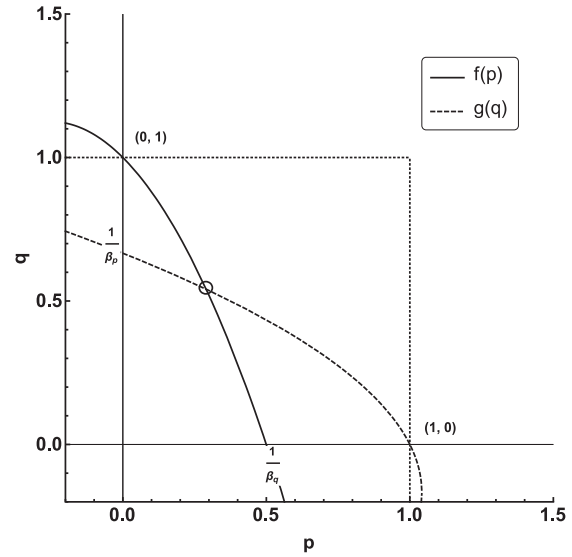
$$\frac{\alpha_j \beta_j (\alpha_i - \beta_i)^2}{\alpha_i \beta_i (\beta_j + 2\alpha_j \beta_j - \alpha_j)} = \frac{\left(\frac{\alpha_i}{\beta_i} - 1\right)^2}{\frac{\alpha_i}{\beta_i} \left(\frac{1}{\alpha_j} + 2 - \frac{1}{\beta_j}\right)} > 1 \text{ requires that } \beta_i < 1. \text{ This implies}$$

that Ecosystem i is persistent and drives Ecosystem j to extinction based on Theorem 2. This case occurs when the relative cost of resource exchange for Ecosystem j is high, i.e., $\beta_j > 1$, while the relative cost of resource exchange β_i and the relative ratio of benefit to cost $\frac{\alpha_i}{\beta_i}$ for Ecosystem i are low.

Biologically, bi-directional resource exchange between two ecosystems, leads to the depletion of the resource stock in one ecosystem and persistence in the other. With the exclusion of one

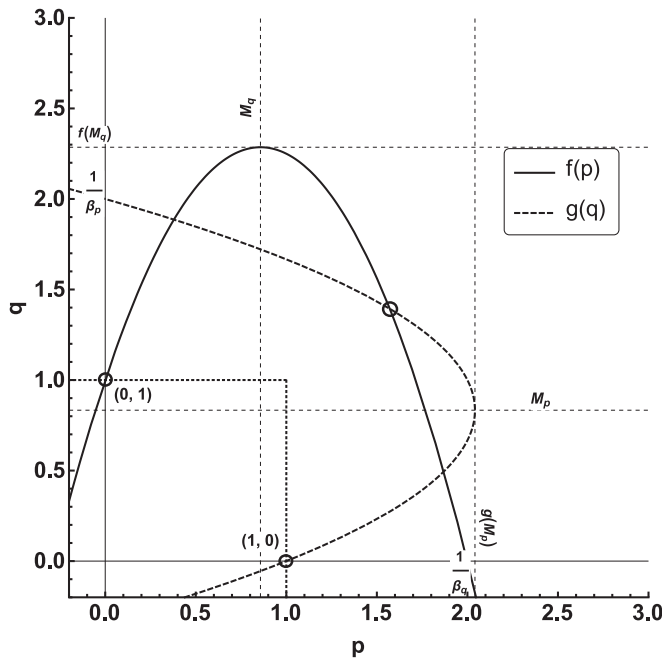


(a) $\beta_i < 1, i = p, q$, E_{pq} is global asymptotically stable.



(b) $\beta_i > 1, i = p, q$, Type One bi-stability: E_{10} and E_{01} are local asymptotically stable.

Fig. 3. Phase plane showing one interior equilibrium and stability of equilibria using isoclines (4) and (5). • - Stable, ○ - Unstable.



(a) $\beta_p, \beta_q < 1$, E_{pq}^1 and E_{pq}^3 are local asymptotically stable.

Fig. 4. Phase plane showing three interior equilibria and Type Three bi-stability of equilibria using isoclines (4) and (5). • - Stable, ○ - Unstable.

ecosystem, the resource stock of the meta-ecosystem converges to that of the persistent ecosystem with the low relative cost. This dynamical outcome is analogous to the *competition exclusion* scenario of the traditional two species competitive Lotka–Volterra model even though both ecosystems act as a donor and recipient.

- *Two interior equilibria* (see Fig. 6): This is the case when the meta-ecosystem (3) has a **Type Two** bi-stability dynamical outcome between one boundary equilibrium and one stable interior equilibrium if the inequalities

$$\frac{4\frac{\alpha_j}{\beta_j}}{\left(1 + \frac{\alpha_j}{\beta_j}\right)^2} < \beta_i < 1 < \beta_j < \alpha_j \text{ hold.}$$

Biological implications of conditions that lead to this type of alternative stable states are that: (1) The relative cost for resource exchange of Ecosystem i is less than one but larger than

$\frac{4\frac{\alpha_j}{\beta_j}}{\left(1 + \frac{\alpha_j}{\beta_j}\right)^2} < \beta_i < 1$ which guarantees that Ecosystem i is persistent with two different production outcomes depending on initial conditions; (2) Ecosystem j has high relative cost (i.e., $\beta_j > 1$) and relative ratio of benefit to cost (i.e., $\frac{\alpha_j}{\beta_j} > 1$) for resource exchange which provides an opportunity for the production of Ecosystem j to be greater than one for proper initial conditions.

In the following two subsections, we explore how the relative cost and benefit of resource exchange for each ecosystem, i.e., $\alpha_i, \beta_i, i = p, q$, affect the dynamical structure and production of the meta-ecosystem (3) through two and one dimensional bifurcation diagrams, respectively.

4.1. Effects of the relative benefits of resource exchange on model dynamics

Fig. 2 is a two-dimensional bifurcation diagram of $\beta_p \in (0, 2)$ versus $\beta_q \in (0, 2)$ with all possible scenarios of the number of interior equilibria of the meta-ecosystem (3) by setting $\alpha_p = \alpha_q = 3$ and $\gamma = 1$. To explore how the relative benefits α_p and α_q affect the geometry structure of $\beta_p - \beta_q$ regions with no (white), one (blue), two (red) and three (yellow) interior equilibria, we compare the case of $\alpha_p = \alpha_q = 3$ (Fig. 2) to the cases of $\alpha_p = .6, \alpha_q = 3$ (Fig. 7b) and $\alpha_p = 15, \alpha_q = 3$ (Fig. 7a). The following observations arise:

Increasing the value of the relative benefit α_i of bi-directional resource exchange for Ecosystem i , we expect that **Type Two** and **Type Three** bi-stability regions (i.e., alternative stable states) are increased while the extinction region for Ecosystem i is decreased. For example, by comparing Fig. 7a ($\alpha_p = 15$) to Fig. 2 ($\alpha_p = 3$) where α_p increases from 3 to 15, we can observe that the yellow (**Type Three** bi-stability) and the red (**Type Two** bi-stability) region in Fig. 7a are increased while the white region in the right bottom corner in Fig. 7a (where the global extinction of Ecosystem p occurs) is decreased. Biologically speaking, this implies that increasing values of the relative benefit α_i of bi-directional resource exchange for Ecosystem i can potentially increase the complexity of the dynamics of the meta-ecosystem (3) by

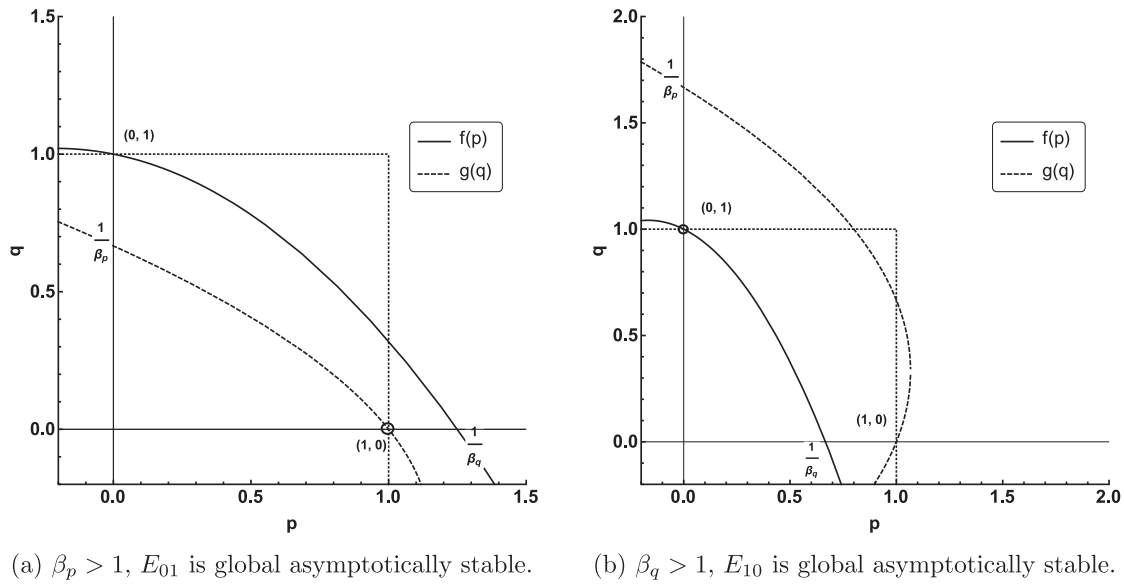


Fig. 5. Phase plane showing no interior equilibrium and stability of possible equilibria using isoclines (4) and (5). • - Stable, ○ - Unstable.

generating alternative states (the increased yellow region confined in $[0, 1] \times [0, 1]$ of Fig. 7a) and promote the survivorship for Ecosystem i by shrinking the extinction region of Ecosystem i and expanding Type Two bi-stability region in return shown in Fig. 7a.

Decrease the value of the relative benefit α_i of bi-directional resource exchange for Ecosystem i , we expect that Type Two and Type Three bi-stability regions are decreased while the extinction region for Ecosystem i is increased. As an example, we compare Fig. 7b ($\alpha_p = .6$) to Fig. 2 ($\alpha_p = 3$) where α_p decreases from 3 to 0.6, we can observe that the yellow (Type Three bi-stability) and the red (Type Two bi-stability) region in Fig. 7b are shrunk while the white region in the right bottom corner in Fig. 7b (where the global extinction of Ecosystem p occurs) has been increased. Thus, this implies that decreasing values of the relative benefit α_i of bi-directional resource exchange for Ecosystem i can potentially decrease the complexity of the dynamics of the meta-ecosystem (3) by eliminating bistable regions (see the decreased yellow and red region in the right bottom of Fig. 7b) and suppress the survivorship for Ecosystem i by expanding the extinction region of

Ecosystem i (see the white region shown in Fig. 7b).

4.2. Interactions generated by the bi-directional resource exchange within ecosystems

In the absence of the bi-directional resource exchange, the two ecosystems of the meta-ecosystem (3) are uncoupled and both approach the rescaled carrying capacity 1, i.e., the meta-ecosystem (3) has a globally stable equilibrium at $(p^*, q^*) = (1, 1)$. However, with the bi-directional resource exchange, the dynamics and the ultimate productions of the meta-ecosystem (3) (i.e., its stable equilibria (p^*, q^*)) could be very complicated. To illustrate all potential interactions, we define the following terminologies:

Amensalistic Interaction: This is the case when one ecosystem goes extinct while the other achieves its rescaled original carrying capacity 1, i.e., $(p^*, q^*) = (1, 0)$ or $(p^*, q^*) = (0, 1)$ is either globally or locally stable for the meta-ecosystem (3). For example, $(p^*, q^*) = (1, 0)$ is globally stable in the white region of the left bottom corner in Figs. 2

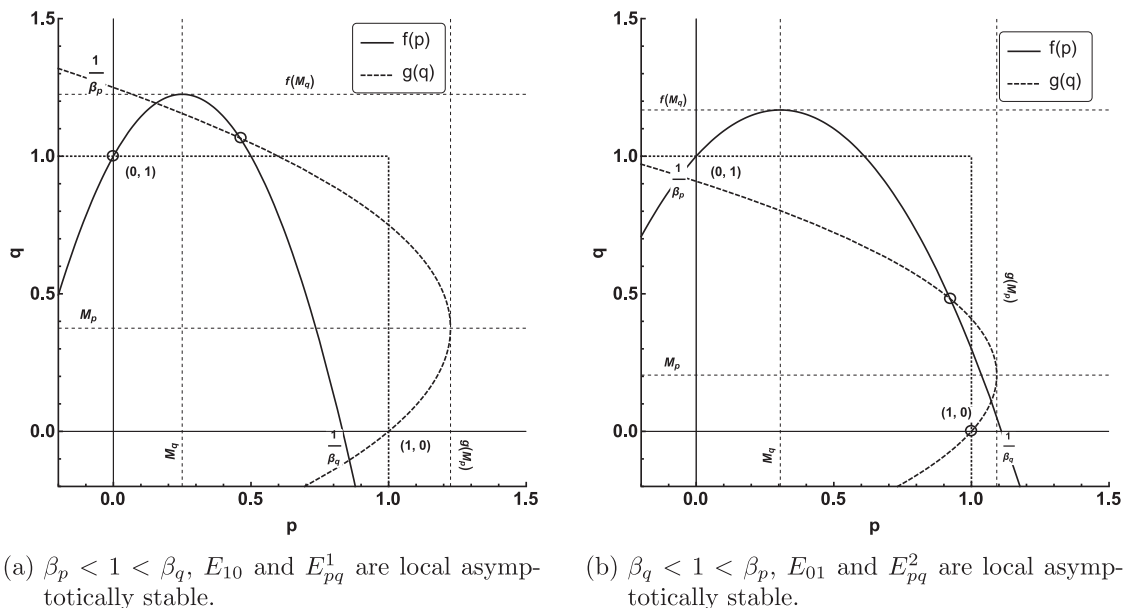


Fig. 6. Phase plane showing two interior equilibria and Type Two bi-stability of equilibria using isoclines (4) and (5). • - Stable, ○ - Unstable.

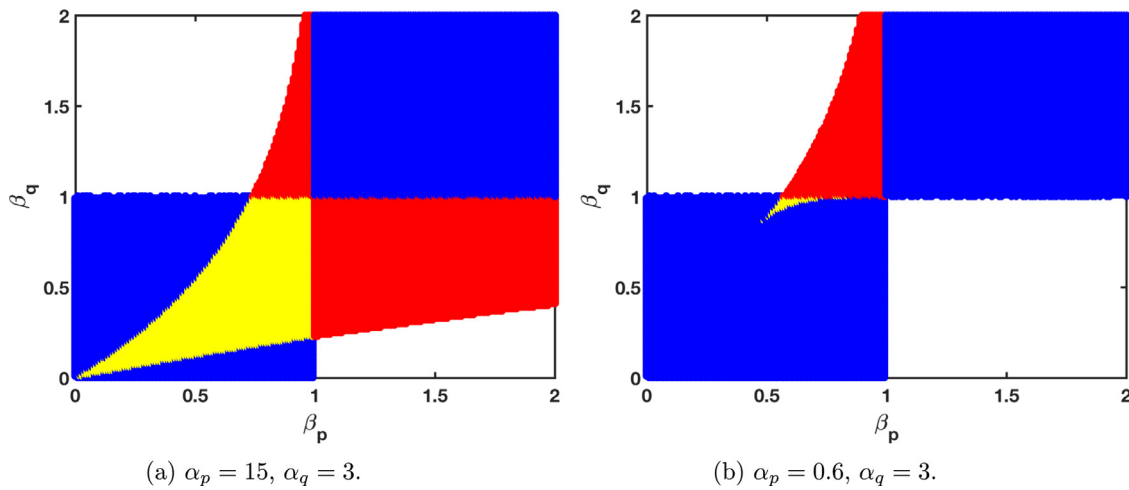


Fig. 7. Bifurcation diagrams of β_p versus β_q showing the number of interior equilibria of our proposed model (3). No interior (white), One interior (blue), Two interior (red), Three interior (yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and 7 while it is locally stable in the blue region of the right top corner in Figs. 2 and 7 (i.e., $\beta_i > 1$ for both $i = p$ and q); and $(p^*, q^*) = (0, 1)$ is globally stable in the white region of the right bottom corner in Figs. 2 and 7 while it is locally stable in the blue region of the right top corner in Figs. 2 and 7. The outcome of this *Amensalistic Interaction* leads to no harm to Ecosystem i but drives Ecosystem j extinct where $i, j = p, q$ and $i \neq j$. **Mutualistic Interaction:** This is the case when the ultimate productions of both ecosystems in the meta-ecosystem (3) are larger than their rescaled carrying capacity 1, i.e., $(p^*, q^*) > (1, 1)$. This could occur when the meta-ecosystem (3) has either one (i.e., blue regions of left bottom corner in Figs. 2 and 7) or three interior equilibria (i.e., the yellow region in Figs. 2 and 7). The outcome of this *Mutualistic Interaction* provides the benefits to each ecosystem such that their productions are larger than the case without resource exchange. **Competitive Interaction:** This is the case when the ultimate productions of both ecosystems in the meta-ecosystem (3) are smaller than their rescaled original carrying capacity 1, i.e., $(p^*, q^*) < (1, 1)$. This could occur when the meta-ecosystem (3) has one interior equilibrium (i.e., blue regions of left bottom corner in Figs. 2 and 7). The outcome of this *Competitive Interaction* produces some harm to each ecosystem such that their productions are smaller than the case without resource exchange.

Antagonistic Interaction: This is the case when the production of one ecosystem is above its rescaled carrying capacity 1 while the other is below, i.e., (p^*, q^*) with $p^* \in (0, 1)$ and $q^* > 1$ or (p^*, q^*) with $q^* \in (0, 1)$ and $p^* > 1$. This could occur when the meta-ecosystem (3) has either one (i.e., blue regions of left bottom corner in Figs. 2 and 7) or two interior equilibria (i.e., the red regions in Figs. 2 and 7) or three interior equilibria (i.e., the yellow region in Figs. 2 and 7). The outcome of this *Antagonistic Interaction* produces some harm to one ecosystem but benefits the other.

Commensalistic Interaction: This is the case when the production of one ecosystem is above its rescaled carrying capacity 1 while the other is equal to 1, i.e. (p^*, q^*) with $p^* = 1$ and $q^* > 1$. This case occurs when the meta-ecosystem (3) has either one, two or three interior equilibria (i.e., blue, red or yellow region in Figs. 2 and 7) and under the condition that $\alpha_q = \frac{\alpha_p - \beta_p}{\alpha_p \beta_p (1 - \beta_q)} - 1$ and $\alpha_p > \beta_p$, for any arbitrary

positive $\alpha_p, \beta_p, \beta_q$. The outcome of this *Commensalistic Interaction* produces neither benefit nor harm to one ecosystem but benefits the other. An example when $p^* = 1$ and $q^* > 1$ occurs with parameter values $\gamma = 1, \alpha_p = 2, \beta_p = .4, \beta_q = 0.5, \alpha_q = 3$ generating equilibria: $(p^*, q^*) = \{(0, 0), (0, 1), (1, 0), (1, 2), (1.0967, 1.9376), (1.7559, 0.7651)\}$ with $(p^*, q^*) = (1, 2)$ being locally stable.

Other Interactions: If $p^* = 1$, it is possible that the meta-ecosystem

(3) has the coexistence state with $q^* < 1$. This is the case when the production of one ecosystem is below its rescaled carrying capacity 1 while the other is equal to 1. An numerical example of the case $p^* = 1$ and $q^* < 1$ occurs with parameter values $\gamma = 1, \alpha_p = 2, \beta_p = 0.9, \beta_q = 0.5, \alpha_q = 0.222$, generating equilibria: $(p^*, q^*) = \{(0, 0), (0, 1), (1, 0), (1, 0.6111)\}$ with $(p^*, q^*) = (1, 0.6111)$ being globally stable.

Naturally, we would like to explore how local environment of the meta-ecosystem (3) that lead to the ultimate production of one ecosystem is above or below its original carrying capacity due to resource exchange. We have the following corollary from the graphic analysis of Theorem 3:

Corollary 1. Assume that (p^*, q^*) is a locally stable interior equilibrium of the meta-ecosystem (3), then we have the following statements:

1. If $\beta_q > 1$, then the production of Ecosystem p has $p^* \in (0, 1)$. On the other hand, if $\frac{4\frac{\alpha_p}{\beta_p}}{\left(1 + \frac{\alpha_p}{\beta_p}\right)^2} < \beta_q < 1, \frac{\alpha_p}{\beta_p} > 1$, then the production of Ecosystem p is $p^* > 1$.
2. If $\beta_p > 1$, then the production of Ecosystem q has $q^* \in (0, 1)$. On the other hand, if $\frac{4\frac{\alpha_q}{\beta_q}}{\left(1 + \frac{\alpha_q}{\beta_q}\right)^2} < \beta_p < 1, \frac{\alpha_q}{\beta_q} > 1$, then the production of Ecosystem q is $q^* > 1$.

The production of Ecosystem p would be negatively affected from the bi-directional resource exchange if $\beta_q = \frac{b_q}{r_q} K_p > 1$ (i.e., $K_p > \frac{r_q}{b_q}$) which implies that the large original carrying capacity K_p in Ecosystem p is greater than the large relative growth rate $\frac{r_q}{b_q}$ in Ecosystem q . However, in order for Ecosystem p to benefit from the resource exchange, it requires to have a large value of the relative benefit to cost $\frac{\alpha_p}{\beta_p} > 1$, and the relative benefit for the other ecosystem q should be in the intermediate range that is constrained by the relative benefit to cost $\frac{\alpha_p}{\beta_p}$ for Ecosystem p , i.e.,

$$\frac{4\frac{\alpha_p}{\beta_p}}{\left(1 + \frac{\alpha_p}{\beta_p}\right)^2} < \beta_q < 1.$$

When the meta-ecosystem (3) experiences the *Type Two* bi-stability between one boundary equilibrium and one interior stable coexistence equilibrium (see the red region of Figs. 2 and 7), then it has *Antagonistic Interaction* where the production of one ecosystem is above its rescaled

carrying capacity 1 while the other is below. More specifically, if the conditions of the meta-ecosystem (3) having two interior equilibria are met, i.e.,

$$\frac{4\alpha_j}{\beta_j} < \beta_i < 1 < \beta_j < \alpha_j,$$

then Ecosystem i is persistent so that it could have either the ultimate production being at its rescaled carrying capacity 1, or a production that is below its rescaled carrying capacity 1 depending on initial conditions; and Ecosystem j is approaching to either extinction or a production that is above its rescaled carrying capacity 1 depending on initial conditions. For example, in the case of $\beta_p < 1 < \beta_q$, the meta-ecosystem (3) has bi-stability between $(p^*, q^*) = (1, 0)$ and (p^*, q^*) with $p^* \in (0, 1), q^* > 1$. Thus, Ecosystem p does not benefit from the resource exchange while Ecosystem q may go to extinct. However, as a tradeoff, Ecosystem q has an opportunity to have its production beyond its rescaled carrying capacity under the proper initial conditions.

If the meta-ecosystem (3) experiences the *Type Three* bi-stability between two interior stable coexistence equilibria (see the yellow region in Figs. 2 and 7), then it has either *Antagonistic Interaction* or *Mutualistic Interaction* where at least the production of one ecosystem in each stable interior equilibrium is beyond its rescaled carrying capacity 1. More specifically, the meta-ecosystem (3) has two stable interior equilibria (p_1^*, q_1^*) and (p_2^*, q_2^*) with $p_1^* > 1$ and $q_2^* > 1$.

The relative benefit and cost of bi-directional resource exchange for each ecosystem play an important role in its production of the meta-ecosystem (3). To explore the detailed impacts on production size along with stability dynamics, we use one dimensional bifurcation diagrams to investigate the potential effects of the relative benefit β_i (e.g., Figs. 8 and 9) and the relative cost α_i (e.g., Figs. 10–13) by setting $\gamma = 1$.

First, we study the effects of the relative cost of bi-directional resource exchange in the following two cases by setting $\alpha_p = \alpha_q = 3$:

1. Let $\beta_q = 0.2 < 1$ and β_p varies in $(0, 2)$ (see Fig. 8): This is the case when Ecosystem q is persistent since its relative cost β_q is less than 1. We can observe that there are three critical points $0 < \beta_p^1 < \beta_p^2 < \beta_p^3 < 1$ of β_p such that:

- $\beta_p \in (0, \beta_p^1)$: The meta-ecosystem (3) has a unique interior globally stable equilibrium $(p^*, q^*) > (1, 1)$ where it has *Mutualistic Interaction* in which both ecosystems benefit from resource exchange. In the range $(0, \beta_p^1)$, increasing the value of the

relative cost β_p for Ecosystem p leads to the decreased production p^* of Ecosystem p and the increased production q^* of Ecosystem q . In the range (β_p^1, β_p^2) , increasing β_p leads to the decreased production p_1^* of Ecosystem p for both $i = 1, 2$; however, increasing β_p can lead to the increased production q_1^* and the decreased production q_2^* of Ecosystem q . In the range (β_p^2, β_p^3) , increasing β_p leads to the decreased productions for both ecosystems p, q .

- $\beta_p \in (\beta_p^3, 1)$: The meta-ecosystem (3) has a unique interior globally stable equilibrium (p^*, q^*) where it has *Antagonistic Interaction* with $p^* \in (0, 1)$ and $q^* > 1$. In this range, increasing β_p leads to the decreased productions for both ecosystems p, q .
 - $\beta_p > 1$: The meta-ecosystem (3) has no interior equilibrium and it approaches to $(p^*, q^*) = (0, 1)$ globally, i.e., it has *Amensalistic Interaction* where Ecosystem p goes extinct while Ecosystem q achieves its rescaled carrying capacity 1.
2. Let $\beta_q = 1.4 > 1$ and β_p varies in $(0, 2)$ (see Fig. 9): The meta-ecosystem (3) has local stability at $(p^*, q^*) = (1, 0)$ since the relative cost β_q of Ecosystem q is greater than 1. We can observe that there is a critical point $0 < \beta_p^1 < 1$ of β_p such that:
 - $\beta_p \in (0, \beta_p^1)$: The meta-ecosystem (3) has no interior equilibrium and it approaches to $(p^*, q^*) = (1, 0)$ globally, i.e., it has *Amen-salistic Interaction* where Ecosystem q goes extinct while Ecosystem p achieves its rescaled original carrying capacity 1.
 - $\beta_p \in (\beta_p^1, 1)$: The meta-ecosystem (3) has one stable interior equilibrium (p^*, q^*) (i.e., the *Type Two* bi-stability) where it has *Antagonistic Interaction* with $p^* \in (0, 1)$ and $q^* > 1$. In this range, increasing β_p leads to the decreased productions for both ecosystems p, q .
 - $\beta_p > 1$: The meta-ecosystem (3) has a unique unstable interior equilibrium (p^*, q^*) (i.e., the *Type One* bi-stability) where it has *Antagonistic Interaction* such that one ecosystem goes extinct while the other achieves its rescaled original carrying capacity 1, i.e., both $(p^*, q^*) = (1, 0)$ and $(p^*, q^*) = (0, 1)$ are locally stable for the meta-ecosystem (3).

In summary, we conclude that increasing the value of the relative cost β_p for Ecosystem p can always lead to the decreased production p^* of Ecosystem p ; however, depending on local environment conditions,

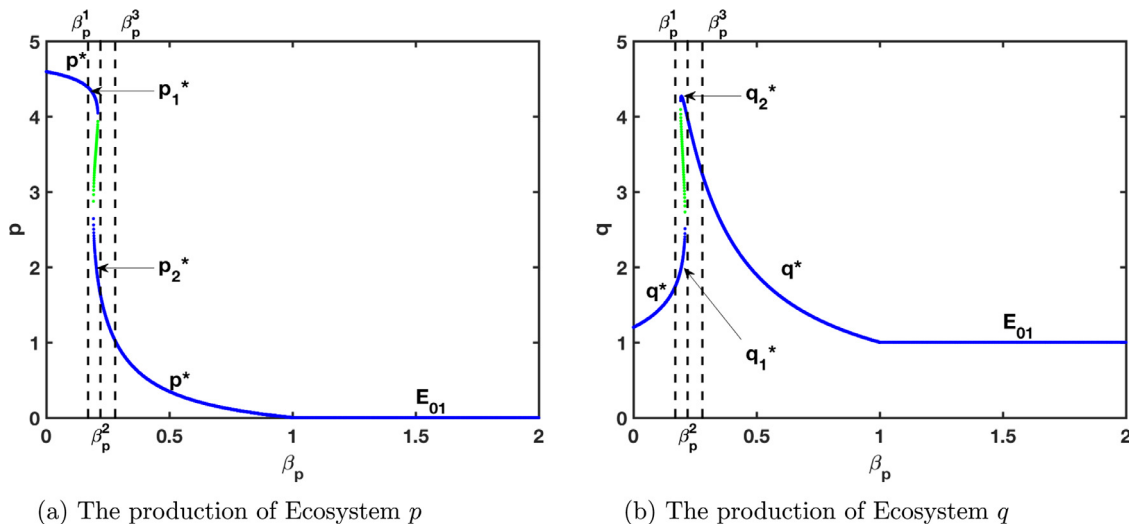


Fig. 8. Bifurcation diagram showing the stability of interior equilibria of the meta-ecosystem (3) when $\gamma = 1$; $\alpha_p = \alpha_q = 3$; $\beta_q = 0.2$, $\beta_p \in (0, 2)$. Stable; Unstable.

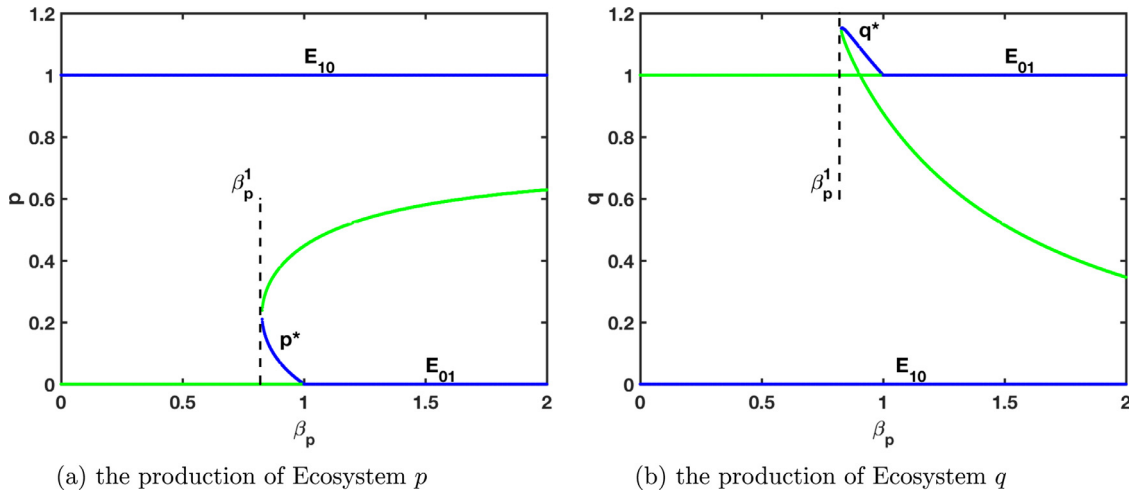


Fig. 9. Bifurcation diagram showing the stability of interior equilibria of the meta-ecosystem (3) when $\gamma = 1$; $\alpha_p = \alpha_q = 3$; $\beta_q = 1.4$; $\beta_p \in (0, 2)$. Stable; Unstable.

increasing β_p may increase or decrease the production q^* of Ecosystem q .

Now we explore the effects of the relative benefit of bi-directional resource exchange in the following four cases:

1. $\beta_q = 0.9 < 1 < \beta_p = 1.2$ and $\alpha_q = 1.5$ such that $\frac{\alpha_q}{\beta_q} > 1$ (see Fig. 10): This is the case when Ecosystem q is persistent since its relative cost β_q is less than 1 and the meta-ecosystem (3) is locally stable at $(p^*, q^*) = (0, 1)$ with the relative cost β_p of Ecosystem p being greater than 1. We can observe that there is a critical point $0 < \alpha_p^1 < 3$ of α_p such that:
 - $\alpha_p \in (0, \alpha_p^1)$: The meta-ecosystem (3) has no interior equilibrium and it approaches to $(p^*, q^*) = (0, 1)$ globally, i.e., it has *Amen-salistic Interaction* where Ecosystem p goes extinct while Ecosystem q achieves its rescaled carrying capacity 1.
 - $\alpha_p > \alpha_p^1$: The meta-ecosystem (3) has one stable interior equilibrium (p^*, q^*) (i.e., the *Type Two-bi-stability*) where it has *Antagonistic Interaction* with $p^* > 1$ and $q^* \in (0, 1)$. In this range, increasing the relative benefit α_p of resource exchange for Ecosystem p leads to the increased production p^* for Ecosystem p and the decreased production q^* for Ecosystems q .
2. $\beta_p = .9 < 1 < \beta_q = 1.2$ and $\alpha_q = 1.2$ such that $\frac{\alpha_q}{\beta_q} > 1$ (see Fig. 11): This is the case when Ecosystem p is persistent, i.e., its relative cost β_p being less than 1 and the meta-ecosystem (3) is locally stable at

$(p^*, q^*) = (1, 0)$ since the relative cost β_q of Ecosystem q is greater than 1. We can observe that there is a critical point $0 < \alpha_p^1 < 3$ of α_p such that:

- $\alpha_p \in (0, \alpha_p^1)$: The meta-ecosystem (3) has one stable interior equilibrium (p^*, q^*) (i.e., the *Type Two-bi-stability*) where it has *Antagonistic Interaction* with $p^* \in (0, 1)$ and $q^* > 1$. In this range, increasing α_p leads to the increased production p^* for Ecosystem p and the decreased production q^* for Ecosystems q .
 - $\alpha_p > \alpha_p^1$: The meta-ecosystem (3) has no interior equilibrium and it approaches to $(p^*, q^*) = (1, 0)$ globally, i.e., it has *Amensalistic Interaction* where Ecosystem q goes extinct while Ecosystem p achieves its rescaled carrying capacity 1.
3. $\beta_p = \beta_q = 0.9 < 1$ and $\alpha_q = 0.5$ such that $\frac{\alpha_q}{\beta_q} < 1$ (see Fig. 12): This is the case when the meta-ecosystem (3) is permanent with a unique interior globally stable equilibrium (p^*, q^*) since $\beta_i < 1$ for both $i = p, q$ and $\frac{\alpha_q}{\beta_q} < 1$. We can observe that there is a critical point $0 < \alpha_p^1 < 1$ of α_p such that:
 - $\alpha_p \in (0, \alpha_p^1)$: The meta-ecosystem (3) has a unique globally stable interior equilibrium (p^*, q^*) where it has *Competitive Interaction* with $p^* \in (0, 1)$ and $q^* \in (0, 1)$. In this range, increasing α_p leads to the increased production p^* for Ecosystem p and the decreased production q^* for Ecosystems q .
 - $\alpha_p > \alpha_p^1$: The meta-ecosystem (3) has a unique globally stable interior equilibrium (p^*, q^*) where it has *Antagonistic Interaction*

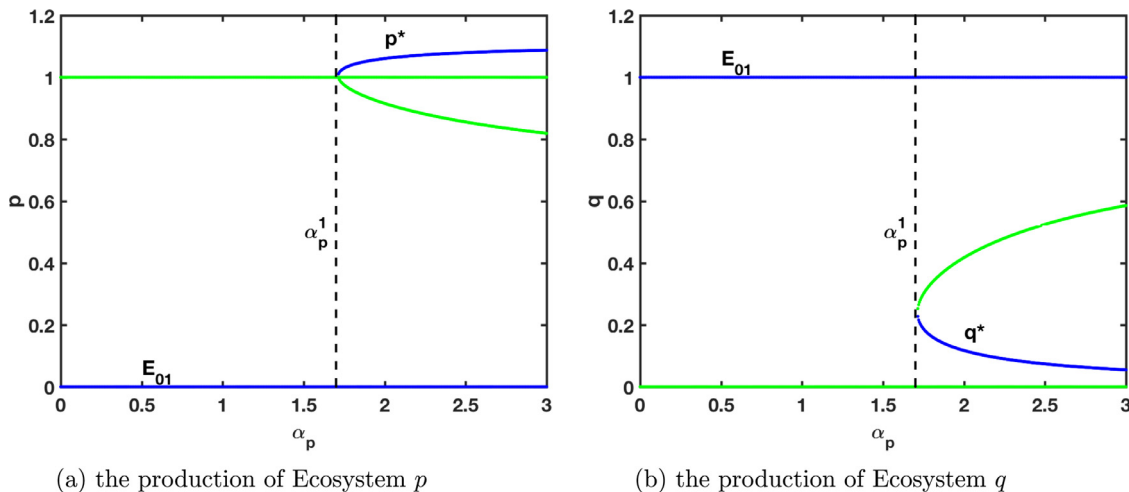


Fig. 10. Bifurcation diagram showing the stability of interior equilibria of the meta-ecosystem (3) when $\gamma = 1$; $\beta_p = 1.2$; $\beta_q = 0.9$; $\alpha_q = 1.5$ and $\alpha_p \in (0, 3)$. Stable; Unstable.

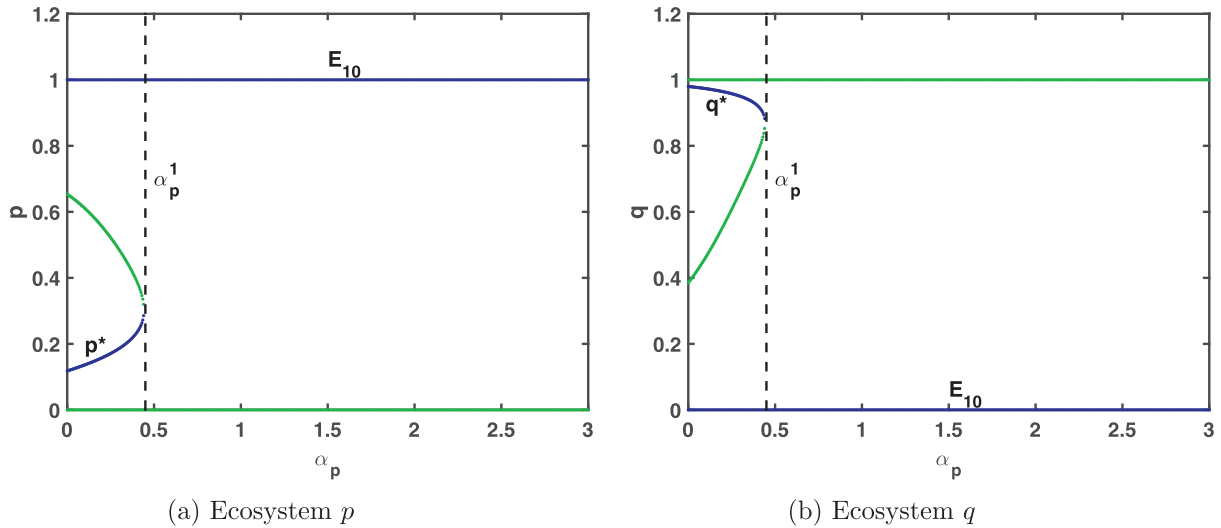


Fig. 11. Bifurcation diagram showing the stability of interior equilibria of the meta-ecosystem (3) when $\gamma = 1$; $\beta_p = .9$; $\beta_q = 1.2$; $\alpha_q = 1.2$ and $\alpha_p \in (0, 3)$. Stable; Unstable.

with $p^* > 1$ and $q^* \in (0, 1)$. In this range, increasing α_p leads to the increased production p^* for Ecosystem p and the decreased production q^* for Ecosystems q .

4. $\beta_p = \beta_q = 0.9 < 1$ and $\alpha_q = 1.5$ such that $\frac{\alpha_q}{\beta_q} > 1$ (see Fig. 13): This is the case when the meta-ecosystem (3) is permanent with either a unique globally stable interior equilibrium (p^*, q^*) or two stable interior equilibria (p_i^*, q_i^*) , $i = 1, 2$ (i.e., the *Type Three* bi-stability) since $\beta_i < 1$ for both $i = p, q$ and $\frac{\alpha_q}{\beta_q} > 1$. We can observe that there are two critical points $0 < \alpha_p^1 < \alpha_p^2 < 6$ of α_p such that:
 - $\alpha_p \in (0, \alpha_p^1)$: The meta-ecosystem (3) has a unique globally stable interior equilibrium (p^*, q^*) where it has *Antagonistic Interaction* with $p^* \in (0, 1)$ and $q^* > 1$. In this range, increasing α_p leads to the increased production p^* for Ecosystem p and the decreased production q^* for Ecosystems q .
 - $\alpha_p \in (\alpha_p^1, \alpha_p^2)$: The meta-ecosystem (3) has two stable interior equilibria (p_i^*, q_i^*) (i.e., the *Type Three* bi-stability) where it has *Antagonistic Interaction* with $p_1^* \in (0, 1)$; $q_1^* > 1$ and $p_2^* > 1$; $q_2^* \in (0, 1)$. In this range, increasing α_p can increase the production p_i^* for both $i = 1, 2$ of Ecosystem p and q_2^* for Ecosystem q . However, increasing α_p can decrease the production q_1^* of Ecosystem q .

– $\alpha_p > \alpha_p^2$: The meta-ecosystem (3) has a unique globally stable interior equilibrium (p^*, q^*) where it has *Antagonistic Interaction* with $p^* > 1$ and $q^* \in (0, 1)$. In this range, increasing α_p can increase the production p^* for Ecosystem p and decrease the production q^* for Ecosystems q .

In summary, we conclude that increasing the value of the relative benefit α_p for Ecosystem p can increase the production p^* of Ecosystem p . Increasing α_p can decrease the production q^* of Ecosystem q but it could also increase the production q^* in some cases.

5. Discussion

The meta-ecosystem concept has been used to study substantial consequences of bi-directional resource exchange across ecosystem boundaries on ecosystem structure and function [11,18,27,37,39,42]. Resource exchange between two adjacent ecosystems, such as terrestrial and aquatic ecosystems, can act on each other's habitats through trophic interactions such as predation, which could have dramatic impacts on the dynamics of each ecosystem [11,27,37,42]. For example, terrestrial invertebrates can make up as much as 50% of the annual consumption in some fish species and emerging aquatic insects

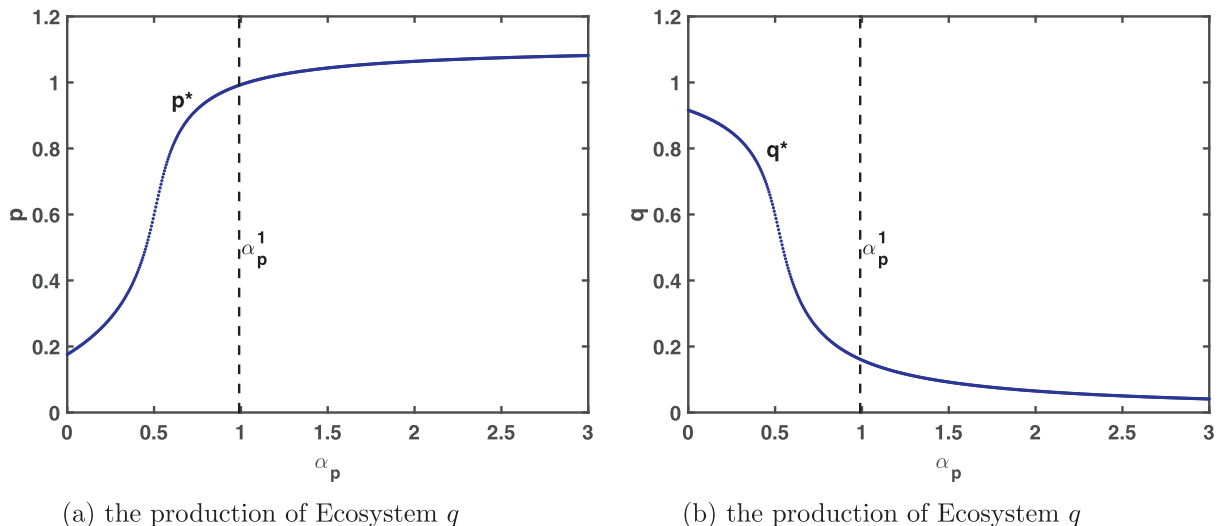


Fig. 12. Bifurcation diagram showing the stability of interior equilibria the meta-ecosystem (3) when $\gamma = 1$; $\alpha_q = 0.5$; $\beta_p = \beta_q = 0.9$ and $\alpha_p \in (0, 3)$. Stable; Unstable.

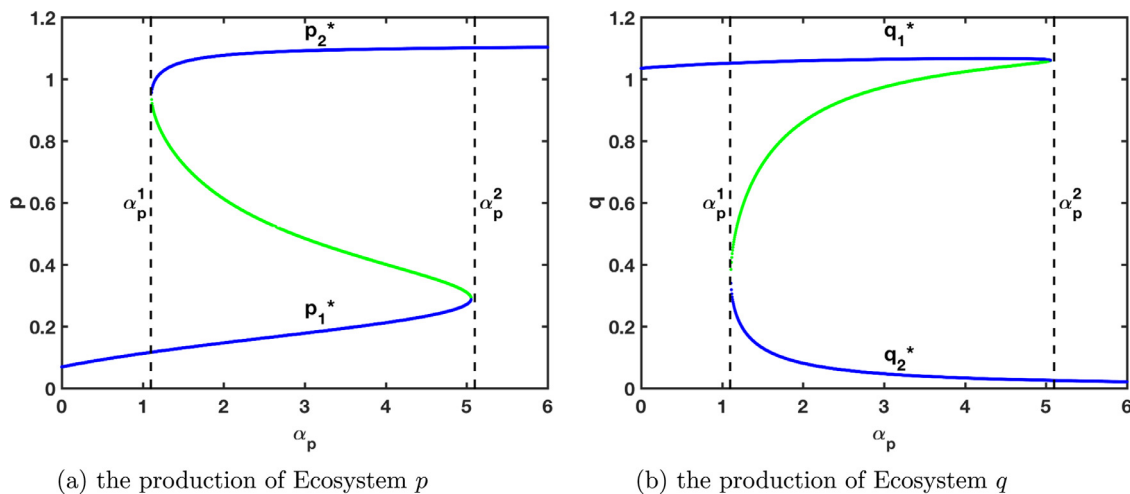


Fig. 13. Bifurcation diagram showing the stability of interior equilibria of the meta-ecosystem (3) when $\gamma = 1$; $\alpha_q = 1.5$; $\beta_p = \beta_q = 0.9$. Stable; Unstable.

can comprise up to 90% of a riparian predator's diet [3,23,28]. Motivated by this, our study aims to develop a simple meta-ecosystem model to explore potential dynamical outcomes of bi-directional resource exchange through trophic interactions between two adjacent ecosystems such as terrestrial-aquatic ecosystems.

Our model describes a situation in which each ecosystem directly facilitates the use of a resource that is otherwise unavailable to the recipient ecosystem. We assume that the main driver of bi-directional resource exchange between two ecosystems are species interactions such as predation and related nutrients crossing ecosystem boundaries where each ecosystem benefits from the newly available resource but at a cost of losing resources important for local growth. As a result, each ecosystem experiences benefits and costs from bi-directional resource exchange. After rescaling, our analysis implies that our proposed meta-ecosystem can have rich dynamics due to resource exchange, and the relative costs and benefits of bi-directional resource exchange of both ecosystems determine its dynamical outcomes.

Our work proposes a more in depth study of the effects of the interactions of two ecosystems by using one- and two-dimensional bifurcations, which shows examples of critical points where increasing or decreasing the relative benefit of resource exchange can change the interactions, say, from mutualistic to antagonistic to amensalistic. The results of Zhang and co-workers [53,56,57] show the possibility of switching from one kind of inter-specific interaction to another due to variation in population densities. In our study, we show that the specific interactions depend on the relative cost and benefit of resource exchange. Using two-dimensional bifurcations, we provide regions of persistence and permanence of the ecosystems, and identify the effects of the relative benefit and/or cost with respect to the area that provides decrease (or increase) of extinction of one of the ecosystems and co-existence of both ecosystems. Using one-dimensional bifurcations, we are able to capture how the relative cost and benefit that can determine the production size at the different interactions we present. We also classify different types of bi-stability exhibited in our model.

In summary, our theoretical results imply: (1) The persistence of an ecosystem in the meta-ecosystem is determined by its relative cost of bi-directional resource exchange which below one, the ecosystem is persistent; above one, the other ecosystem goes extinct locally. (2) The ratio of the relative benefit to cost of resource exchange for each ecosystem contributes greatly on whether the meta-ecosystem has alternative stable states (i.e., bi-stability). (3) If the relative costs of bi-directional resource exchange for both ecosystems are less than 1, then the meta-ecosystem is permanent with either one or two interior stable equilibria where the latter case occurs when the relative costs are not too small and the relative ratio of benefits to costs for both ecosystems

are greater than 1. The case of two interior stable equilibria refers to the *Type Three* bi-stability. (4) If the relative costs of bi-directional resource exchange for both ecosystems are larger than 1, then one of the two ecosystems in the meta-ecosystem will go extinct, and initial conditions determine which ecosystem goes extinct (*Type One* bi-stability). (5) If the relative cost of resource exchange for one ecosystem is less than 1 while the other one is greater than 1. Then the meta-ecosystem either has one ecosystem going extinct globally and the other ecosystem approaching its original carrying capacity; or experiences the *Type Two* bi-stability where both ecosystems can co-exist or one of the two ecosystems goes extinct locally depending initial conditions. Although each ecosystem acts as a donor and recipient, the case of the meta-ecosystem having the persistence of one ecosystem and the global extinction of the other can be analog to the *Competition Exclusion* scenario of the traditional Lotka-Volterra two species competition model. Also, numerical results showed that increasing (Decreasing) values of the relative benefit of bi-directional resource exchange for one ecosystem can potentially increase (compress) the complexity of the dynamics of the meta-ecosystem by generating (eliminating) alternative states (i.e., the *Type Two* and *Type Three* bi-stability) and promote (suppress) the survivorship of this ecosystem.

In addition to the impacts on ecological communities, bi-directional resource exchange between two ecosystem can affect their productions tremendously. Two ecosystems of the meta-ecosystem can experience **Amensalistic Interaction, Mutualistic Interaction, Competitive Interaction, Antagonistic Interaction, Commensalistic Interaction**, or the combinations of these interactions when the meta-ecosystem has alternative stable states, depending on their relative benefits and costs. In summary, *Amensalistic Interaction* emerges when one ecosystem goes extinct while the other achieves its rescaled original carrying capacity 1, occurs when at least one ecosystem has its relative cost of resource exchange less than 1. For example, the meta-ecosystem has the *Type One*-bi-stability or experiences *Competition Exclusion*. *Competitive Interaction* emerges when the productions of both ecosystems are smaller than their rescaled original carrying capacity 1, only occurs when the meta-ecosystem is permanent with a unique coexistence equilibrium. *Antagonistic Interaction* can occur when the meta-ecosystem has a unique coexistence equilibrium, or the *Type Two* bi-stability, or the *Type Three* bi-stability. However, if the meta-ecosystem has the *Type Two* bi-stability, then it definitely experiences *Antagonistic Interaction* when one ecosystem achieves an equilibrium biomass resource stock greater than its scaled carrying capacity and the other reaches an equilibrium below this level closed to exhaustion of resources (see Fig. 6). This scenario is similar to the hypothesis of Margalef [29] that mature forests exploit earlier successional stages due to

foraging by consumers from late-successional ecosystems [27]. It follows that mobile consumers can reciprocally transport nutrients between the ecosystems (e.g. feeding in one and defecating (or dying) in the other [46]. For instance, the quality of forage differs between ecosystems but the consumer feeds and defecates in each equally. Over time, differences in forage quality might equate to one ecosystem paying a higher cost of herbivory (i.e. exporting higher quality and importing lower quality) and perpetually keeping the ecosystem with the higher cost of resource loss in an early successional stage. Priority effects on equilibrium dynamics may need further support to this interpretation. Currently it is unclear whether material transfers are great enough to drive successional change [27]. Moreover, *Mutualistic Interaction* emerges when the productions of both ecosystems being greater than 1, can only occur when the meta-ecosystem is permanent with the *Type Three* bi-stability under proper conditions. In our model, we found that this scenario occurs when both ecosystems have high relative ratios of benefit to cost and have low relative costs for both ecosystems (see Fig. 3a). This type of interaction may underlie observations of over-yielding present in diverse forests relative to monocultures [44] and could result from ecosystems utilizing different forms of the same resource or from the redistribution of resources among trees limited by different nutrients. Sapijanskas et al. [44] recently proposed that litter exchange was responsible for over yielding (i.e. higher community level yields in mixtures relative to monocultures) in tropical forests and Pretzsch and Schütze [40] documented facilitation between Norway spruce and European. Lastly, Wood et al. [54] found trees responded to leaf litter nutrients by increasing leaf production within months of addition, but did not provide information regarding the effects of reciprocal litter exchange. In addition, positive effects of litter are typically observed after longer periods of time (i.e. 15 years [55]).

Furthermore, due to a nonlinear relationship in the trade-off of benefits and costs between the exchange of resources, our model suggests that increasing the value of the relative cost for an ecosystem can always decrease its production (see Figs. 8 and 9); however, depending on the local environment, it may increase or decrease the production of the other ecosystem. If we increase the value of the relative benefit for one ecosystem, then the ecosystem has an increased production; however, the other ecosystem may have decreased production most cases but increased production in some cases (see Figs. 10–13). For instance, the latter can occur when the relative cost of bi-directional resource exchange of both ecosystems are less than one. In this case, we have $\alpha_i > \beta_i$, i.e., $\frac{\alpha_i}{\beta_i} > \frac{K_i}{r_i}$, for $i, j = p, q, i \neq j$, which implies that the ratio of the quantity of resource received from donor ecosystem to the depletion rate of resources must be greater than the ratio of its carrying capacity to the intrinsic growth rate of biomass. Other interesting outcomes in our model are shown by increasing the carrying capacity K_i of ecosystem i . This will increase the relative benefits causing a decrease of the relative benefits for ecosystem i . The exchange of resources, in this case favoring ecosystem j , has a cost. Therefore, the parameter describing the cost of resource exchange increases as K_i increases. Also, we notice that the ratio for ecosystem j is not affected by the increase of K_i .

Appendix A. Theoretical proofs

A1. Rescaling

Rescaling Model (1) by letting $p = \frac{P}{K_p}$, $q = \frac{Q}{K_q}$, $\tau = r_p t$,

$$\frac{dP}{dt} = r_p P \left[1 - \frac{P}{K_p + a_p Q} - \frac{b_p}{r_p} Q \right], \quad \frac{dQ}{dt} = r_q Q \left[1 - \frac{Q}{K_q + a_q P} - \frac{b_q}{r_q} P \right]$$

This is explained by the fact that ecosystem j is undergoing an equal proportion of the relative benefits and costs due to the resource exchange, so the ecosystem j is not affected by the change of K_i .

Despite the theoretical results presented here seem to be supported by empirical evaluations, we make a number of simplified assumptions. First, our meta-ecosystem is closed to the inputs of external inputs (e.g. atmospheric N) and losses (e.g. recalcitrant litter; [31]), processes which can have an important role in nutrient availability in a local ecosystem. Secondly, our model assumes resources needed to be processed (conditioned) by the donor ecosystem before they are made available to the recipient ecosystem. More specifically, we assume that resource exchange is mainly driven by the trophic interactions. However, this simplified assumption may not be completely unreasonable. For instance, leaf litter conditioning in the stream ecosystem may affect its decomposition after deposition in the riparian ecosystem by a flood. Similarly, terrestrial insects fallen into aquatic environments are sometimes considered more profitable for consumers than *in situ* prey [3]. Further, in our model, resources flow freely between ecosystems (i.e. no preferential movement due to wind or topography or concentration gradients resources). In reality, there may be a preferential movement of resources between ecosystems. For instance, litter typically depend on the predominant wind or water direction, downslope topography and litter characteristics (e.g. leaf geometry and specific weight; [9,25,35,47]). Lastly, there is no distinction in factors governing the transformation of a resource within a donor or its use in recipient ecosystem (e.g. decomposition). Instead, the model aggregates these effects into general costs and benefits for analytical tractability. The abstractness of the cost-benefit terms in the model may, to say the least, be difficult to measure empirically and further discrimination between the many, complex and possibly interacting factors may be necessary to evaluate these theoretical results empirically.

Although this is a highly simplified model of bi-directional resource exchanges, it seems to be supported by a number of empirical observations (e.g. [9,45,55]). It is becoming increasingly known that the exchange of resources between ecosystems is important and the ecosystem function and structure cannot be separated from the context in which takes place. Investigating the potential responses of the biomass resource stocks in two ecosystems using a theoretical approach allowed us to drastically reduce the complexity found in nature and therefore provides an acceptable foundation on which to base future theoretical evaluations. Integrating theoretical and empirical ecology is a fruitful area of research and a necessary step towards a complete understanding of spatial ecosystem ecology [27].

Acknowledgments

This research is partially supported by NSF-DMS (1313312&1716802); NSF-IOS/DMS (1558127); and *Scholar Award in Complex Systems* from The James S. McDonnell Foundation (UHC 220020472).

$$\begin{aligned}
\frac{dp}{d\tau} &= \frac{dp}{dP} \frac{dP}{dt} \frac{dt}{d\tau} \\
&= \frac{1}{K_p} r_p P \left[1 - \frac{P}{K_p + a_p Q} - \frac{b_p}{r_p} Q \right] \frac{1}{r_p} \\
&= \frac{P}{K_p} \left[1 - \frac{\frac{P}{K_p}}{1 + a_p \frac{K_q Q}{K_p}} - \frac{b_p K_q}{r_p K_q} Q \right] \\
&= p \left[1 - \frac{p}{1 + \frac{a_p K_q Q}{K_p}} - \frac{b_p K_q}{r_p} \frac{Q}{K_q} \right] \\
&= p \left[1 - \frac{p}{1 + \alpha_p q} - \beta_p q \right]
\end{aligned}$$

$$\begin{aligned}
\frac{dq}{d\tau} &= \frac{dq}{dQ} \frac{dQ}{dt} \frac{dt}{d\tau} \\
&= \frac{1}{K_q} r_q Q \left[1 - \frac{Q}{K_q + a_q P} - \frac{b_q}{r_q} P \right] \frac{1}{r_p} \\
&= \frac{r_q Q}{r_p K_q} \left[1 - \frac{\frac{Q}{K_q}}{1 + a_q \frac{K_p P}{K_q}} - \frac{b_q K_p}{r_q K_p} P \right] \\
&= \gamma q \left[1 - \frac{q}{1 + \frac{a_q K_p P}{K_q}} - \frac{b_q K_p}{r_q} \frac{P}{K_p} \right] \\
&= \gamma q \left[1 - \frac{q}{1 + \alpha_q p} - \beta_q p \right],
\end{aligned}$$

$$\begin{aligned}
p' &= \frac{dp}{d\tau} = p \left[1 - \frac{p}{1 + \alpha_p q} - \beta_p q \right] \\
q' &= \frac{dq}{d\tau} = \gamma q \left[1 - \frac{q}{1 + \alpha_q p} - \beta_q p \right]
\end{aligned}$$

Proof of Theorem 1. Note that

$$p'|_{p=0} = 0, \quad q'|_{q=0} = 0,$$

hence according to Theorem A.4 (p.423) in Thieme (2003), we conclude that the system (3) is positively invariant in $\mathbb{R}_+^2$. It follows that the set $\{(p, q), \in \mathbb{R}_+^2: p, q = 0\}$ is invariant. Consider the following:

$$\begin{aligned}
p' &= p \left[1 - \frac{p}{1 + \alpha_p q} - \beta_p q \right] = p \left[\frac{1 - p + (\alpha_p - \beta_p)q - \alpha_p \beta_p q^2}{1 + \alpha_p q} \right] \\
q' &= \gamma q \left[1 - \frac{q}{1 + \alpha_q p} - \beta_q p \right] = \gamma q \left[\frac{1 - q + (\alpha_q - \beta_q)p - \alpha_q \beta_q p^2}{1 + \alpha_q p} \right].
\end{aligned}$$

Then, by the property of positive invariance we have the following cases:

Case 1: $\alpha_p \leq \beta_p$:

$$p' \leq \frac{p(1-p)}{1 + \alpha_p q} \quad \text{which implies} \quad \limsup_{t \rightarrow \infty} p(t) \leq 1.$$

$$q' \leq \frac{\gamma q(1-q)}{1 + \alpha_q p} \quad \text{which implies} \quad \limsup_{t \rightarrow \infty} q(t) \leq 1.$$

Case 2: $\alpha_p > \beta_p$:

$$\begin{aligned}
p' &= \frac{p}{1 + \alpha_p q} \left[1 - p + (\alpha_p - \beta_p) q \left(1 - \frac{\alpha_p \beta_p}{\alpha_p - \beta_p} q \right) \right] \\
&\leq p \left[1 - p + \underbrace{(\alpha_p - \beta_p) q \left(1 - \frac{\alpha_p \beta_p}{\alpha_p - \beta_p} q \right)}_{N_q} \right] \\
&< p(1 + N_q - p), \quad \limsup_{t \rightarrow \infty} p(t) \leq 1 + N_q, \\
q' &= \gamma q \left[1 - q + \underbrace{(\alpha_q - \beta_q) p \left(1 - \frac{\alpha_q \beta_q}{\alpha_q - \beta_q} p \right)}_{N_p} \right] \\
&< \gamma q(1 + N_p - q), \quad \limsup_{t \rightarrow \infty} q(t) \leq 1 + N_p.
\end{aligned}$$

where

$$N_i = \max_{0 \leq i \leq \frac{\alpha_j - \beta_j}{\alpha_j \beta_j}} \left\{ (\alpha_j - \beta_j) i \left[1 - \frac{\alpha_j \beta_j}{\alpha_j - \beta_j} i \right] \right\},$$

for $i = p, q, i \neq j$.

This shows that system (3) is bounded in $\mathbb{R}_+^2$.

Next, we show system (3) has only equilibrium dynamics. Define $\Phi(p, q) = \frac{1}{pq}$ which is positive in $\mathbb{R}_+^2$, then we have

$$\begin{aligned}
\nabla \cdot (\Phi(p', q')) &= \frac{\partial}{\partial p} (\Phi \cdot p') + \frac{\partial}{\partial q} (\Phi \cdot q') \\
&= \frac{\partial \left(\frac{1}{q} - \frac{p}{q(1 + \alpha_p q)} - \beta_p \right)}{\partial p} + \frac{\partial \left(\frac{\gamma}{p} - \frac{\gamma q}{p(1 + \alpha_q p)} - \gamma \beta_q \right)}{\partial q} \\
&= -\frac{1}{q(1 + \alpha_p q)} - \frac{\gamma}{p(1 + \alpha_q p)} < 0.
\end{aligned}$$

This shows that system (3) has no limit cycle (i.e. only equilibrium dynamics) according to Dulac–Bendixson Criterion (Theorem A.12 on [48]). $\square$

Proof of Theorem 2. According to Theorem 1, we know that Model (3) is attracted to a compact set C in $\mathbb{R}_+^2$. First, we focus on the persistence conditions for y . Notice that when $q = 0$, $\frac{dp}{dt} = p(1 - p)$. Then we conclude that the ω -limit set is $(1, 0)$. Therefore, we have

$$\left. \frac{dq}{dt} \right|_{p=1, q=0} = \gamma \left[1 - \frac{q}{1 + \alpha_q p} - \beta_q p \right] \Big|_{p=1, q=0} = \gamma[1 - \beta_q].$$

Since $\frac{dq}{dt} > 0$ if and only if $\beta_q < 1$, according to Theorem 2.5 of Hutson [19], we can conclude that q is persistent if $\beta_q < 1$.

Now, when $p = 0$, $\frac{dq}{dt} = \gamma q[1 - q]$, then the ω -limit set in this case is $(0, 1)$. Therefore, we have

$$\left. \frac{dp}{dt} \right|_{p=0, q=1} = \left[1 - \frac{p}{1 + \alpha_p q} - \beta_p q \right] \Big|_{p=0, q=1} = 1 - \beta_p.$$

Since $\frac{dp}{dt} > 0$ if and only if $\beta_p < 1$, according to Theorem 2.5 of Hutson [19], we can conclude that p is persistent if $\beta_p < 1$. $\square$

Proof of Theorem 3. It is clear that for all positive values of the parameters, Model (3) always has three boundary equilibria: $E_{00} = (0, 0)$, $E_{01} = (0, 1)$, and $E_{10} = (1, 0)$.

The local stability of each of the boundary equilibria follow from the analysis of the Jacobian matrix:

$$J(p, q) = \begin{pmatrix} 1 - \frac{2p}{1 + \alpha_p q} - \beta_p q & p \left(\frac{\alpha_p p}{(1 + \alpha_p q)^2} - \beta_p \right) \\ \gamma q \left(\frac{\alpha_q q}{(1 + \alpha_q p)^2} - \beta_q \right) & \gamma \left(1 - \frac{q}{1 + \alpha_q p} - \beta_q p \right) - \frac{\gamma q}{1 + \alpha_q p} \end{pmatrix} \quad (\text{A.1})$$

For each of the three equilibria we have:

1. **E₀₀** – The Jacobian matrix associated with the extinction equilibrium is:

$$J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & \gamma \end{pmatrix},$$

with eigenvalues $\lambda_1 = 1$ and $\lambda_2 = \gamma$. Therefore, we conclude E_{00} is always unstable.

2. E_{01} – The Jacobian matrix associated with this equilibrium is:

$$J(0, 1) = \begin{pmatrix} 1 - \beta_p & 0 \\ \gamma(\alpha_q - \beta_q) & -\gamma \end{pmatrix}.$$

Notice that $\lambda_1 + \lambda_2 = -\gamma + (1 - \beta_p) < 0$ if and only if $\beta_p > 1$ and $\lambda_1 \lambda_2 = -\gamma(1 - \beta_p) > 0$ if and only if $\beta_p > 1$. Hence this boundary equilibria is stable whenever $\beta_p > 1$.

3. E_{10} – The Jacobian matrix associated with this equilibrium is:

$$J(1, 0) = \begin{pmatrix} -1 & \alpha_p - \beta_p \\ 0 & \gamma(1 - \beta_q) \end{pmatrix}.$$

Notice that $\lambda_1 + \lambda_2 = -1 + \gamma(1 - \beta_q) < 0$ if and only if $\beta_q > 1$ and $\lambda_1 \lambda_2 = -\gamma(1 - \beta_q) > 0$ iff $\beta_q > 1$. Hence this boundary equilibria is stable whenever $\beta_q > 1$.

Now we show the sufficient conditions of the existence and the number of interior equilibria of Model (3). If (p^*, q^*) is an interior equilibrium, then it satisfies the following two quadratic equations:

$$q = (1 - \beta_q p)(1 + \alpha_q p) = f(p)$$

$$p = (1 - \beta_p q)(1 + \alpha_p q) = g(q)$$

with restrictions that $p^* < \frac{1}{\beta_q}$ and $q^* < \frac{1}{\beta_p}$. Since

$$f'(p) = -(2\alpha_q \beta_q p - (\alpha_q - \beta_q))$$

$$g'(q) = -(2\alpha_p \beta_p q - (\alpha_p - \beta_p)),$$

then we have

$$\left. \frac{df}{dp} \right|_{p < M_q} > 0, \quad \left. \frac{df}{dp} \right|_{p = M_q} = 0, \quad \text{and} \quad \left. \frac{df}{dp} \right|_{p > M_q} < 0$$

and

$$\left. \frac{dg}{dq} \right|_{q < M_p} > 0, \quad \left. \frac{dg}{dq} \right|_{q = M_p} = 0, \quad \text{and} \quad \left. \frac{dg}{dq} \right|_{q > M_p} < 0$$

where

$$M_q = \frac{\alpha_q - \beta_q}{2\alpha_q \beta_q} \quad \text{and} \quad M_p = \frac{\alpha_p - \beta_p}{2\alpha_p \beta_p}.$$

The expressions of M_i , $i = p, q$ imply that the quadratic equation $f(p)$ has $M_q < 0$ if $\frac{\alpha_q}{\beta_q} < 1$ and $M_q > 0$ if $\frac{\alpha_q}{\beta_q} > 1$. Similarly, we can conclude that the quadratic equation $g(q)$ has $M_p < 0$ if $\frac{\alpha_p}{\beta_p} < 1$ and $M_p > 0$ if $\frac{\alpha_p}{\beta_p} > 1$. Therefore, according to the geometry of $q = f(p)$ and $p = g(q)$ (see Figure 6–4), we can conclude the following:

1. Two interior equilibria (see Fig. 6): Model (3) has two interior equilibria if the following inequalities hold

$$\frac{\alpha_j}{\beta_j} > 1 \quad \text{and} \quad \frac{4 \frac{\alpha_j}{\beta_j}}{\left(1 + \frac{\alpha_j}{\beta_j}\right)^2} < \beta_i < 1 < \beta_j$$

for either $i = p, j = q$ (see Fig. 6a) or $i = q, j = p$ (see Fig. 6b).

2. Three interior equilibria (see Fig. 4): Model (3) has three interior equilibria if the following inequalities hold

$$\frac{\alpha_j}{\beta_j} > 1 \quad \text{and} \quad \frac{4 \frac{\alpha_j}{\beta_j}}{\left(1 + \frac{\alpha_j}{\beta_j}\right)^2} < \beta_i < 1$$

for both $i, j = p, q, i \neq j$.

On the other hand, if (p^*, q^*) is an interior equilibrium, then it satisfies the following equation subject to $p^* < \frac{1}{\beta_q}$ and $q^* < \frac{1}{\beta_p}$

$$q = (f \circ g)(q) = [1 + \alpha_q(1 + \alpha_p q)(1 - \beta_p q)][1 - \beta_q(1 + \alpha_p q)(1 - \beta_p q)],$$

which can be rewritten in the following form

$$F(q) = q - (f \circ g)(q) = c_4 q^4 + c_3 q^3 + c_2 q^2 + c_1 q + c_0$$

where:

$$\begin{aligned}
c_4 &= \alpha_p^2 \beta_p^2 \alpha_q \beta_q > 0 \\
c_3 &= 2\alpha_p \beta_p \alpha_q \beta_q (\beta_p - \alpha_p) \\
c_2 &= \alpha_q \beta_q (\alpha_p - \beta_p)^2 + \alpha_p \beta_p (\alpha_q - \beta_q - 2\alpha_q \beta_q) \\
c_1 &= 1 + (\beta_p - \alpha_p)(\alpha_q - \beta_q - 2\alpha_q \beta_q) \\
c_0 &= (1 + \alpha_q)(\beta_q - 1)
\end{aligned}$$

This implies the following:

1. $c_3 > 0$ if $\beta_p > \alpha_p$
2. $c_2 > 0$ if $\alpha_q > \beta_q + 2\alpha_q \beta_q \Leftrightarrow \beta_q < \frac{\alpha_q}{1+2\alpha_q}$ or the following inequalities hold

$$\beta_q > \frac{\alpha_q}{1+2\alpha_q} \text{ and } \frac{\alpha_q \beta_q (\alpha_p - \beta_p)^2}{\alpha_p \beta_p (\beta_q + 2\alpha_q \beta_q - \alpha_q)} > 1.$$

3. $c_1 > 0$ if $\beta_p > \alpha_p$ and $\beta_q < \frac{\alpha_q}{1+2\alpha_q}$ or the following inequalities hold

$$\beta_p > \alpha_p, \beta_q > \frac{\alpha_q}{1+2\alpha_q} \text{ and } \beta_q < \frac{\alpha_q + \frac{1}{\beta_p - \alpha_p}}{1+2\alpha_q}.$$

4. $c_0 > 0$ if $\beta_q > 1$ while $c_0 < 0$ when $\beta_q < 1$.

Therefore, we could have the following conclusions

1. No interior equilibrium (see Fig. 5): Model (3) has no interior equilibrium when $c_i > 0$ for all $i = 0, 1, 2, 3, 4$, e.g., if the following inequalities hold

$$\begin{aligned}
\frac{\alpha_p}{\beta_p} < 1, \quad 1 < \beta_q < \frac{\alpha_q + \frac{1}{\beta_p - \alpha_p}}{1+2\alpha_q} \\
\text{and } \frac{\alpha_q \beta_q (\alpha_p - \beta_p)^2}{\alpha_p \beta_p (\beta_q + 2\alpha_q \beta_q - \alpha_q)} > 1.
\end{aligned}$$

2. One interior equilibrium (see Fig. 3): Model (3) has a unique interior equilibrium when $c_0 < 0$ and $c_i > 0$ for all $i = 1, 2, 3, 4$, e.g., if $\frac{\alpha_p}{\beta_p} < 1$, $\beta_q < \frac{\alpha_q}{1+2\alpha_q}$ and the following inequalities holds

$$\begin{aligned}
\beta_p < 1 \text{ and } \frac{\alpha_q}{\beta_q} < 1 \\
\Rightarrow F(q)|_{q=1} = (1 + \alpha_p)(1 - \beta_p)(\alpha_q \beta_q (1 + \alpha_p)(1 - \beta_p) + \beta_q - \alpha_q) > 0.
\end{aligned}$$

Similarly, due to the symmetric properties of $f(p)$ and $g(q)$, we could have the conclusions on the cases of no or one interior equilibrium by looking at the equations in terms of p :

$$G(p) = p - (g \circ f)(p) = d_4 p^4 + d_3 p^3 + d_2 p^2 + d_1 p + d_0$$

where:

$$\begin{aligned}
d_4 &= \alpha_q^2 \beta_q^2 \alpha_p \beta_p > 0 \\
d_3 &= 2\alpha_q \beta_q \alpha_p \beta_p (\beta_q - \alpha_q) \\
d_2 &= \alpha_p \beta_p (\alpha_q - \beta_q)^2 + \alpha_q \beta_q (\alpha_p - \beta_p) - 2\alpha_q \beta_q \alpha_p \beta_p \\
d_1 &= 1 + (\alpha_q - \beta_q)(\beta_p - \alpha_p + 2\alpha_p \beta_p) \\
d_0 &= (1 + \alpha_p)(\beta_p - 1).
\end{aligned}$$

Therefore, combined the equations of $G(p)$ and $F(q)$, we have the following conclusions

1. No interior equilibrium (see Fig. 5): Model (3) has no interior equilibrium if the following inequalities hold

$$\frac{\alpha_i}{\beta_i} < 1, \quad 1 < \beta_j < \frac{\alpha_j + \frac{1}{\beta_i - \alpha_i}}{1+2\alpha_j} \text{ and } \frac{\alpha_j \beta_j (\alpha_i - \beta_i)^2}{\alpha_i \beta_i (\beta_j + 2\alpha_j \beta_j - \alpha_j)} > 1$$

for $i = p, j = q$ or $i = q, j = p$.

2. One interior equilibrium (see Fig. 3a): Model (3) has a unique interior equilibrium if $\frac{\alpha_i}{\beta_i} < 1$, $\beta_i < 1$ for both $i = p, q$ and

$$\beta_j < \frac{\alpha_j}{1 + 2\alpha_j} \text{ for } j = p \text{ or } j = q \text{ but } j \neq i.$$

□

Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.mbs.2018.05.006.

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