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Impacts of Asymmetric Biotic Interactions and Environmental Factors on the Presence-Absence of Multispecies

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ABSTRACT

Interactions between multispecies are usual incidence in their habitats. Such interactions among the species are thought to be asymmetric in nature, which combine with environmental factors can determine the distributions and abundances of the species. Most often, each species responds differentially to biotic interactions and environmental factors. Therefore, predicting the presence-absence of species is a major challenge in ecology. In this paper, we used mathematical modelling to study the combined effects of biotic interactions (i.e. asymmetric competition) and environmental factors on the presence-absence of the species across a geographical region. To gain better insight on this problem, we performed invasion and numerical simulation analyses of the model of multispecies competitive dynamics. Different threshold values of competition coefficients were observed, which result in different phenomena; such as coexistence of species and priority effects. Consequently, we propose that asymmetric biotic interactions, combined with environmental factors can allow coexistence of relatively weak and strong species at the same location x.

*Keywords***:** Coexistence, competition, invasion point, priority effects, threshold values

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INTRODUCTION

Generally, all species have natural geographic range margins (i.e. the geographic boundary of species presence-absence). Most often, the range margins of the species can be shifted due to biotic interactions (e.g.

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competitions) and environmental factors (e.g. climate change) (Freeman et al., 2018). These factors, are recognized as part of ecological forces that have significant impacts on the distributions and range margins of species (Godsoe et al., 2015). Climate change may persist and biotic interactions in a multispecies habitat, usually, is unavoidable due to limited resources. Consequently, the prediction of the presence-absence of the species in a geographical region is still one of the challenges in ecology (Amundrud, & Srivastava, 2019). Therefore, a research study which focuses on the influence of these factors on the species distribution, will continue to fascinate the ecologists.

Environmental factors often act as a limiting factor on species distributions and its range margins (Hill & Preston, 2015) and can lead to the presence-absence of the species across a geographical region (Kearney & Porter, 2009; Wiens, 2011). Environmental factors have been demonstrated to determine the distributions of species in a habitat. For example, species in intertidal communities are shown to have altered their range margins due to shore temperature changes (Barry et al., 1995). Also, Perry et al. (2005) illustrated that fish species distributions had shifted in mean depth (or latitude) due to temperature increase. In a similar way, Rowe et al. (2015) demonstrated that extreme cold spells had strong impacts on the distributions and abundances of tropical species.

Similar to environmental factors, biotic interactions in the form of competition among the species, have significant effects on the distributions and range shifts of the species (Gause, 1932). Empirical studies have shown that biotic interactions is a key factor affecting species distributions (Wisz et al., 2013). Also, there are suggestions which also acknowledged that competitive interactions can regulate species range margins in geographic environments (Mohd et al., 2017). They observed that, weak biotic interactions lead to coexistence of species, while strong biotic interactions result in exclusion of species; i.e. multiple coexistence of these interacting species is impossible. Consequently, only single-species can be observed at a particular location. In this case, initial abundance of the species determines the competitive outcomes of the species (Hiscox et al., 2015) and the phenomenon is known as priority effects. However, the occurrence of priority effects can be influenced by environment factors. Empirical study on Daphnia species has shown how environmental factors (e.g. temperature, salinity and humidity) altered priority effects outcomes (Loureiro et al., 2013). Other experimental evidences exist which used initial abundance to illustrate the occurrence of priority effects (Park et al., 1965).

Also, species distributions can be influenced by the combined effects of biotic interactions and abiotic environments (Alexander et al., 2016). This is because the effects of climate change on species can strongly be influenced by species' interactions (Gilman et al., 2010). Similarly, environmental components can also influence the nature of biotic interactions (Meier et al., 2011). Experimental studies conducted on fruits fly species distributions, confirmed that competitive interactions could lead to different responses of species to environmental perturbations (Davis et al., 1998a; Davis et al., 1998b). Connell (1961) also, demonstrated empirically the combined effects of biotic interactions and environmental factors in shaping community assembly. Similarly, Park (1954) in experimental study illustrated the importance of interactions between biotic and abiotic factors in species distributions. It was also confirmed that the roles of both biotic and abiotic factors were significant in shaping range margins of species (Darwell et al., 2017).

However, there are few theoretical researches which investigate the interplay of biotic interactions and environmental factors on species range margins, using mathematical modelling. One obvious limitation of the existing models is the assumptions that species competitive strength is symmetrical (Godsoe et al., 2014; Mohd et al., 2017), which may not be true. The strength of competition among species is often asymmetrical (Lawton & Hassell, 1981). These differences may modify the outcomes of species interactions and then, the presence-absence of species across a geographical region. On this basis, Mohd et al. (2017) suggested that the analysis of multispecies competition could be extended to asymmetric competition, which was the main thrust of this paper.

To gain insight on the presence-absence of interacting multispecies across a heterogeneous geographical region, we used mathematical model which incorporated biotic and environmental factors. Hence, we performed analytical and numerical simulations analyses of the model, to observe the range margins of multispecies communities. To further illustrate the presence-absence of the species across the geographical locations, we constructed summary plots and then bifurcation analyses of the model as a parameter value varies.

Thus, this paper is organized as follows. After this section, is another section with the presentation and description of the model. This is followed by derivations of our analytical results on the range margins of species using invasion analysis. Then, we illustrate our results on the range margins of species using numerical simulations. We then, present the results of our summary plots and bifurcation analyses to show the presence-absence of the species across a geographical location as a model's parameter varies. Based on our results, we highlight our observations and then discuss the ecological implications of the results.

MATERIALS AND METHODS

The Models

In the 1920s and 1930s, Lotka (1925) and Volterra (1926) developed competition model between two-species, which is popularly referred to as Lotka-Volterra competition (LVC) model. The well-known LVC, which becomes the framework for studying competition in ecology (Gavina et al., 2018), is spatially implicit, and does not explicitly incorporate environmental changes. However, the analysis of the LVC have revealed fundamental predictions. These include coexistence of two species when competition is weak and bi-stability of single-species, which converges to one species and the other excluded when competition is strong. The existence of bi-stability gave rise to the question of what additional ecological forces lead to convergence to one single-species. To answer this question, resulting in several possibilities of studies, which include the effects of environmental heterogeneity (Godsoe et al., 2017; Birand & Barany, 2014). Therefore, we extended LVC model to study the distributions of *n*-species with densities $N_i(x,t)$ across heterogeneous environments. The competition model is a system of ordinary differential equations (ODEs) in one-dimensional domain with $0 \leq x \leq 1$, which is written as Equation 1:

$$\frac{dN_i}{dt} = \frac{r_i N_i}{k_i(x)}\left(k_i(x) - \sum_{j=1}^{n} \alpha_{ij} N_j\right), \ (i = 1,2, \ldots, n) \qquad [1]$$

where r_i is the intrinsic growth rate, $k_i(x)$ is the carrying capacity at location, α_{ij} is the coefficient of the competition of species *j* on species *i*, α_{ii} is the intraspecific coefficients and N_i is the densities of species *i* at time *t*. For simplifying the model, α_{ii} is rescaled to equal 1 and $\alpha_{ij} \neq \alpha_{ji}$ implies asymmetric competition strengths between the interacting species. Subsequently, we would simply denote α_{ij} as α_j; such that for a system of four species interactions (i.e. $n = 4$), α_1, α_2, α_3, and α_4 represent species 1, 2, 3 and 4 interspecific competition coefficients respectively.

The suitability of the environments is modelled into the carrying capacity of each species, such that the effects of environmental factors on the species, depend on $k_i(x)$. The term x represents a geographical location and it is used as a proxy for abiotic components like temperature, humidity and salinity. Thus, we modeled $k_i(x)$ to vary linearly with x; such that in Equation 2:

$$k_i(x) = m_i x + b_i \qquad [2]$$

Here, m_i is the slope of species *i*'s carrying capacity and it serves as a measure of the environmental suitability with respect to x, b_i is the intercept of species *i* carrying capacity when $x = 0$.

To understand the dynamics of the system, we solved numerically for the steady states of Equation [1] by setting $\frac{dN_i}{dt}$ to zeros. The stability analysis of the steady states was then performed using MAPLE package. Thus, at a location x, the steady state who's all the real parts of the eigenvalues are negative is considered stable. Based on the steady states, we used the techniques of invasion analysis to derive analytical results on the species' range margins. Numerical simulation results on the range margins of the species were obtained by employing MATLAB ode15s solver (Higham & Higham, 2016) for $t = 1000$ to solve Equation [1] until steady states were achieved. We also generated summary plots using MATLAB ode15s solver and then computed bifurcation analyses of the Equation [1] using XPPAUT package, as the model parameter (α_1) varies. The numerical simulations were carried out separately at categorized levels of species coefficients of competition. The values of α_j were determined from Table 1 of Ayala et al. (1973), when they conducted empirical study using pairs of *Drosophila species* in eight experiment to determine the abundances of the species at equilibrium. α_j was estimated between 0.33 and 5.32; except one outrageous value which was 12.37 (Ayala et al., 1973). In this study, we assumed that competition strengths of the species were asymmetrical and because of the uncertainty of competition coefficients, our model's behavior was analyzed for a range of α_j. However, modifying the values of α_j used this study, could alter the range margins of the species. Also, the parameter values b_i and m_i of the carrying capacities of the species in Table 1, were determined from the linear regression analysis of Figure 3 of Davis et al. (1998b) by Godsoe et al. (2014). Similarly, the intrinsic growth rate, r_i of the species was obtained. The parameters values used in the analyses are shown in Table 1 and parameter values not presented in Table 1 are written below the Figures.

Table 1

Symbols with the descriptions and parameter values used for the computation of the figures

Symbol	**Items description**	**Parameter value**
r_i	The intrinsic growth rates of species *i*	1
m_1	Gradient of k_1	1
m_2	Gradient of k_2	0.8
m_3	Gradient of k_3	0
m_4	Gradient of k_4	0
b_1	Carrying capacity of species 1 at $x = 0$	0
b_2	Carrying capacity of species 2 at $x = 0$	0
b_3	Carrying capacity of species 3 at $x = 0$	0.5
b_4	Carrying capacity of species 4 at $x = 0$	0.4

RESULTS

This section consists both analytical and numerical simulation results of the Equation [1]. The analytical results are based on numerical simulation results on the species' range margins illustrated in Figure 1A and both results broadly agreed with each other.

Analytical Results on the Range Margins of Species

Here, we used the method of invasion analysis to derive analytical results of the Equation [1]. The invasion analysis method was based on the derivation of species' range margins using the criterion that a species that could invade at a location must be rare at that point and its growth rate had to be greater than zero (i.e. $\frac{dN_i}{dt} > 0$) (Hastings & Gross, 2012).

Godsoe et al. (2014) analyzed the invasion points (denoted by x_i) of Equation [1] with $n = 2$. The technique is by setting the right-hand side of Equation [1] greater than zero; then, substitute the steady states and the values of the carrying capacities in it. We extended their method to derive the invasion points for four-species. The method of our analysis was based on tracking the species that are present in the numerical result, and the species that can invade when rare at a location *x*. Based on Figure 1A, only species 3 and 4 were present at the locations where species 1 and 2 were rare. In this case, either species 1 or 2 could invade in the presence of species 3 and 4; depending on the magnitude of the carrying capacities of species 1 and 2. From Table 1, $k_1 > k_2$; so that species 1 had higher potentials to invade in the presence of species 3 and 4 than species 2. Thus, for species 1 to invade it required that the right-hand side of $\frac{dN_1}{dt}$ in Equation [1] be greater than zero. Species1 was considered rare at its invasion point and so, its density (i.e. N_1) was set to zero. Similarly, the density of species 2 (i.e. N_2) was also considered to be zero, since at the invasion point of species 1 only species 3 and 4 were present. Thus, species 1 could invade if $k_1(x) = \alpha_3 N_3^* + \alpha_4 N_4^*$ $k_1(x)$. Therefore, the point *x* satisfying $k_1(x) = \alpha_3 N_3^* + \alpha_4 N_4^*$ corresponds to species1 invasion point which is denoted as x_1. But $k_1(x) = m_1 x$ and for stable steady state $(0, 0, N_3^*, N_4^*)$, with $k_3 = b_3$ and $k_4 = b_4$, we have the invasion point of species 1 given as in Equation 3:

$$x_1 = \frac{\alpha_3\alpha_4(b_3 + b_4) - (\alpha_3 b_3 + \alpha_4 b_4)}{m_1(\alpha_3\alpha_4 - 1)} \qquad [3]$$

Moving along the environmental gradient *x* to the right of x_1 (see Figure 1A), we observed the presence of species 1, 3 and 4 with species 2 absent. Thus, we can derive species 2 invasion point in a similar manner to species 1. In this case, $\frac{dN_2}{dt}$ in Equation [1] must be greater than zero for species 2 to invade. Also, at the invasion point of species 2, its density (i.eN_2) was zero, so that $k_2(x) > \alpha_1 N_1^* + \alpha_3 N_3^* + \alpha_4 N_4^*$. Thus, invasion point of species 2 satisfies $k_2(x) = \alpha_1 N_1^* + \alpha_3 N_3^* + \alpha_4 N_4^*$ and for stable steady state $(N_1^*, 0, N_3^*, N_4^*)$ where $k_2(x) = m_2 x$, $k_3 = b_3$ and $k_4 = b_4$, the invasion point of species 2 becomes Equation 4:

$$x_2 = \frac{\alpha_1\alpha_3\alpha_4(b_3 + b_4) + \alpha_3 b_3(1 - \alpha_1 - \alpha_4) + \alpha_4 b_4(1 - \alpha_1 - \alpha_3)}{m_2(2\alpha_1\alpha_3\alpha_4 - \alpha_1\alpha_3 - \alpha_1\alpha_4 - \alpha_3\alpha_4 + 1) - \alpha_1 m_1(\alpha_3\alpha_4 - \alpha_3 - \alpha_4 + 1)} \qquad [4]$$

In this case, the scenarios by which species 2 range margin can increase depends on strong interspecific competition from species 1, 3 and 4 at the boundary of species 2 fundamental niche. For instance, increase in $\alpha_3 b_3$ or $\alpha_4 b_4$ or both can shift species 2 from its fundamental niche and increase the range of *x* for which species 2 can be present or absent. However, since species 2 is ecologically different from species 3 and 4 due to their carrying capacities vary differently as the environmental gradient changes; so, we expect a modest change in species 1, 3 and 4 to bring about a modest change in the range margin of species 2 (Godsoe et al., 2014) . Also, species 2 range margin can also increase when the denominator in Equation [4] becomes rather small. As the denominator tends to zero, the range margin of species 2 also tends to infinity. This second mechanism is associated with two species (e.g. species 1 and 2) that are ecologically similar (i.e. their carrying capacities vary directly as the environmental gradient changes).

In a similar way, species 4 invasion point can be computed in the presence of species 1, 2 and 3. Thus, invasion point of species 4 is given as in Equation 5.

$$x_4 = \frac{b_4(2\alpha_1\alpha_2\alpha_3 - \alpha_1\alpha_2 - \alpha_1\alpha_3 - \alpha_2\alpha_3 + 1) - \alpha_3 b_3(\alpha_1\alpha_2 - \alpha_1 - \alpha_2 + 1)}{\alpha_1 m_1(\alpha_2\alpha_3 - \alpha_2 - \alpha_3 + 1) + \alpha_2 m_2(\alpha_1\alpha_3 - \alpha_1 - \alpha_3 + 1)} \qquad [5]$$

Similarly, we have the invasion point of species 3 computed to give in Equation 6:

$$x_3 = \frac{b_3(\alpha_1\alpha_2 - 1)}{\alpha_1 m_1(\alpha_2 - 1) + \alpha_2 m_2(\alpha_1 - 1)} \qquad [6]$$

Numerical Results on the Range Margins of Species

Numerical results are presented to illustrate the influence of biotic interactions and environmental gradients on the range margins of species across locations *x*. To show the impacts of asymmetrical competition strengths on multispecies community structures, the numerical results were obtained separately for different competitive strengths of the species. A detection threshold value of 0.5% was employed for these results, such that a species was considered absent if its density was below the expected value (Gaston, 2003).

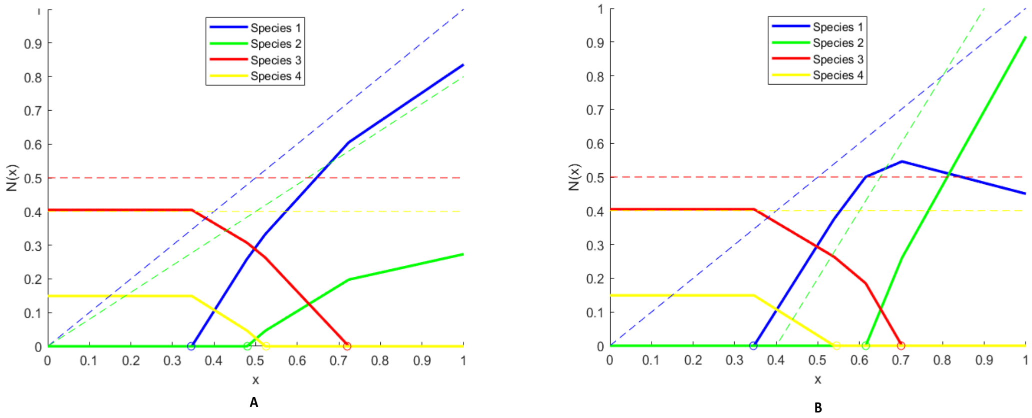


Figure 1. The steady states of species i due to weak interactions ($\alpha_j < 1$). Solid lines indicate steady states and the dotted lines represent the carrying capacities of species i. Circles on the horizontal axis of the Figures, represent the invasion points (x_i) of the species. Figures 1A and B are computed with $\alpha_1 = 0.63$, $\alpha_2 = 0.60$, $\alpha_3 = 0.62$, $\alpha_4 = 0.64$; $k_1(x) = x$, $k_2(x) = 0.8x$, $k_3(x) = 0.5$, $k_4(x) = 0.4$ and initial abundance: $N_1(x) = 0.1k_1(x)$, $N_2(x) = 0.9k_2(x)$, $N_3(x) = 0.1k_3(x)$, $N_4(x) = 0.9k_4(x)$. In Figure 1B, $k_2(x) = 2x - 0.8$

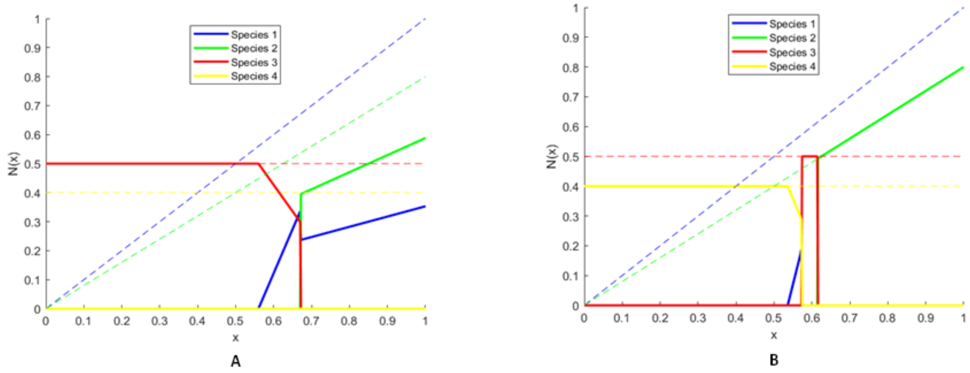
Multispecies Range Margins due to Weak Interactions ($\alpha_j < 1$)

Figures 1A and B illustrate interactions outcomes of multispecies with relatively weak interaction strengths (i.e. $\alpha_j < 1$) of all the species. The same carrying capacities (dotted lines) and initial abundances are used for the two Figures except in Figure 1B where $k_2(x) = 2x - 0.8$. We observed multispecies coexistence and the range margins of the species depended on the interaction strengths and carrying capacities of the species. For instance, in Figure 1A, two or more species coexisted at the same locations x, with multiple species coexistence was possible near the central location. However, due to impacts of competition interactions, the region of coexistence between the four-species was rather very small. This observation is also illustrated in Figure 4A, where the region of four-species (i.e. red colored region) also decreased as α_1 varies from 0.3 – 1.4. The range margins of the species are indicated as circles, according to the colors of the species on the horizontal axis and they correspond to the invasion points of our analytical results.

To illustrate the influence of environmental components on the community assembly, we compute Figure 1B. In this case, the community structures differ from that observed in Figure 1A. Due to changes in the environmental gradient, only two and three species coexistence are possible. However, in both cases illustrated, species 1 and 2 occupied the right-hand side of the locations x; while species 3 and 4 occupied the left-hand side. This community structures are possible because, species 1 and 2 are both warm tolerant species and so, they are regarded as similar species. Also, species 3 and 4 are also another set of similar species with homogenous distributions throughout the locations x. Thus, they can easily be displaced from the upper locations by species 1 and 2. This also, accounts for species 1 and 2 being rare at the lower part of the locations and multispecies coexistence at the centre, where the environment is most suitable for all the species. Generally, competing species coexist for relatively weak (i.e $\alpha_j < 1$) biotic interactions.

Multispecies Range Margins due to Weak ($\alpha_1 < 1$) and Strong ($\alpha_j > 1$) Biotic Interactions

Figure 2 is computed to illustrate competition outcomes between relatively weaker ($\alpha_1 < 1$) species 1 and other relatively stronger ($\alpha_j > 1$) species. Thus, Figures 2A and C and Figures 2B and D, are computed with $\alpha_1 = 0.60$, $\alpha_2 = 1.10$, $\alpha_3 = 1.12$, $\alpha_4 = 1.14$ and $\alpha_1 = 0.60$, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$ respectively. The same carrying capacities are used for the figures



A

B

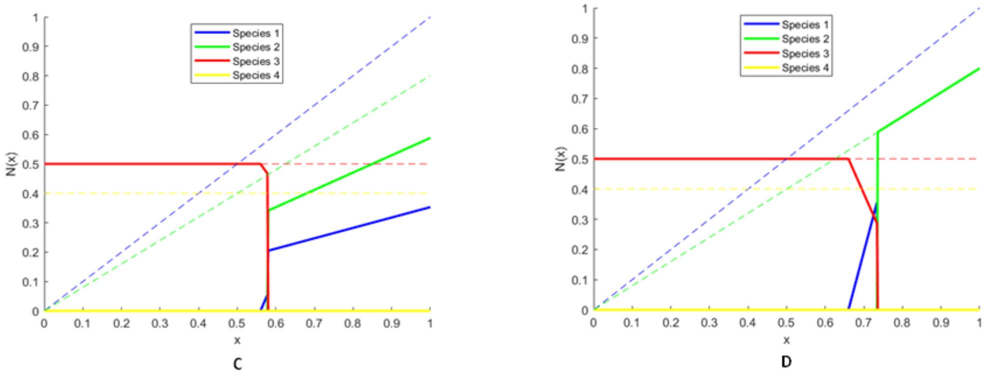
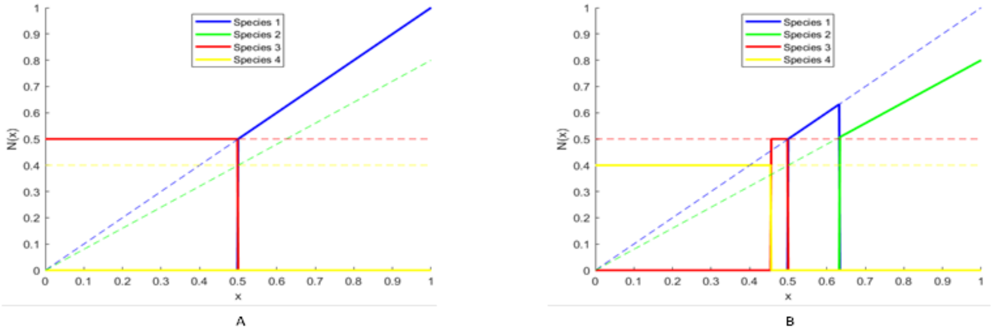
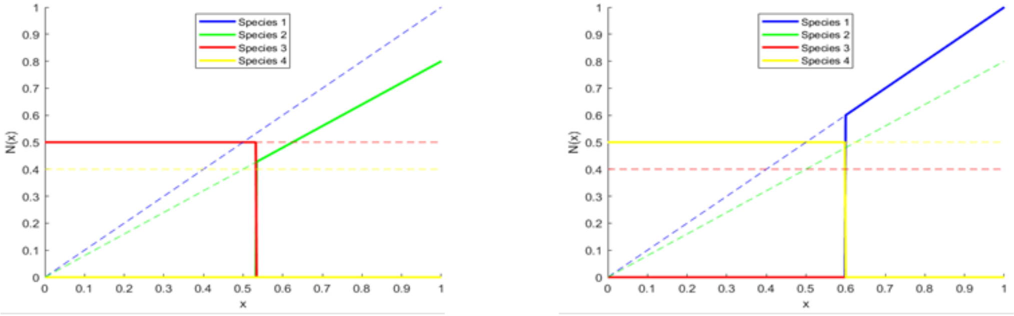


Figure 2. The steady states of species i due to weak ($\alpha_1 < 1$) and strong ($\alpha_j > 1$) interactions. Solid lines indicate steady states and the dotted lines represent the carrying capacities of species i. Figures 2A and C are computed with $\alpha_1 = 0.60$, $\alpha_2 = 1.10$, $\alpha_3 = 1.12$, $\alpha_4 = 1.14$ and Figures 2B and D are computed with $\alpha_1 = 0.60$, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$. The Figures are computed with the same carrying capacities: $k_1(x) = x$, $k_2(x) = 0.8x$, $k_3(x) = 0.5$, $k_4(x) = 0.4$ and varied initial abundance.

with varying initial abundance to show the range margins where a species may be present or absent. In both cases, we observed exclusion of species and coexistence of competitively weaker species 1 with other stronger species at the same location *x*. For instance, Figures 2A and C show *bistable* coexistence of species 1 with species 2 and 3 (i.e. $(N_1, 0, N_3, 0)$ and $(N_1, N_2, 0, 0)$) at the same location *x* (e.g. see location $x = 0.6$). To further illustrate these results, we computed Figures 2B and D which also show coexistence of relatively weaker species 1 with other stronger species at the same location *x*. However, due to high priority effects (see Figures 2B and D), the weaker species 1 lost its coexistence with the similar stronger species 2 and maintained its coexistence with the dissimilar stronger species 3 and 4. These observations illustrate that, ecologically similar species (e.g. 1 versus 2 and 3 versus 4) competitively affect each other more than the dissimilar species.





C

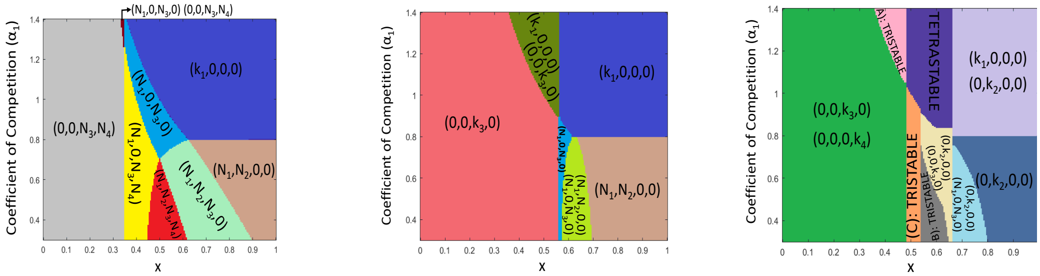
D

Figure 3. The steady states of species i due to intense biotic interactions ($\alpha_j > 1$). Solid lines indicate steady states and the dotted lines represent the carrying capacities of the species i. Figure 3A is computed with $\alpha_1 = 1.33$, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$; $k_1(x) = x$, $k_2(x) = 0.8x$, $k_3(x) = 0.5$, $k_4(x) = 0.4$ and initial abundance: $N_1(x) = 0.1k_1(x)$, $N_2(x) = 0.9k_2(x)$, $N_3(x) = 0.1k_3(x)$, $N_4(x) = 0.9k_4(x)$. Figure 3B is computed with $\alpha_1 = 1.43$, $\alpha_2 = 1.40$, $\alpha_3 = 1.42$, $\alpha_4 = 1.44$; $k_1(x) = x$, $k_2(x) = 0.8x$, $k_3(x) = 0.5$, $k_4(x) = 0.4$ and initial abundance: $N_1(x) = 0.1k_1(x)$, $N_2(x) = 0.9k_2(x)$, $N_3(x) = 0.1k_3(x)$, $N_4(x) = 0.9k_4(x)$. Figure 3C is computed with $\alpha_1 = 1.33$, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$; $k_1(x) = x$, $k_2(x) = 0.8x$, $k_3(x) = 0.5$, $k_4(x) = 0.4$ and initial abundance: $N_1(x) = 0.001k_1(x)$, $N_2(x) = 0.9k_2(x)$, $N_3(x) = 0.1k_3(x)$, $N_4(x) = 0.9k_4(x)$. Figure 1D is computed with $\alpha_1 = 1.33$, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$; $k_1(x) = x$, $k_2(x) = 0.8x$, $k_3(x) = 0.4$, $k_4(x) = 0.5$ and initial abundance: $N_1(x) = 0.1k_1(x)$, $N_2(x) = 0.9k_2(x)$, $N_3(x) = 0.1k_3(x)$, $N_4(x) = 0.9k_4(x)$.

Multispecies Range Margins due to Intense Biotic Interactions ($\alpha_j > 1$)

We observed that when competitive strengths of species are relatively intense, $\alpha_j > 1$, coexistence of species is impossible, and the dynamical outcomes of the model depend on initial abundances, interaction strengths and carrying capacities of the species. For instance, Figure 3A illustrate interactions outcomes of the multispecies, where species 1 and 3 occupied the geographical region as single-species; each to its carrying capacity and exclude species 2 and 4. To illustrate the effects of interaction strengths on competition outcomes, we compute Figure 3B with different competition coefficients, $\alpha_1 = 1.43$, $\alpha_2 = 1.40$, $\alpha_3 = 1.42$, $\alpha_4 = 1.44$ but with the same carrying capacities and initial abundances as in Figure 3A. Due to increase in the competition coefficients, we observe the presence of the four single-species. However, species 2 with higher initial abundance dominated the larger part of the right region and then shifted species 1 with smaller initial abundance towards a smaller right center. Similarly, species 4 with higher initial abundance than species 3 occupied a larger region on the left.

To further illustrate the importance of initial abundance, we compute Figure 3C with the same competition coefficients and carrying capacities as in Figure 3A but with different initial abundances: $N_1(x) = 0.001k_1(x)$, $N_2(x) = 0.9k_2(x)$, $N_3(x) = 0.1k_3(x)$, $N_4(x) = 0.9k_4(x)$. We observed the presence of species 2 in the place of species 1 (compare Figure 3A with Figure 3C). The result demonstrates the influence of initial abundance in the presence-absence of species. This situation where the dynamical behavior of the model depends on initial abundance is known as alternative stable states; ecologically refer to as priority effects (Gilman et al., 2010). Lastly, Figure 3D was computed to illustrate the influence of the environmental gradients on the presence-absence of the species. Thus, we computed the Figure with the same parameters as in Figure 3A except that, the carrying capacities of species 3 and 4 were interchanged with each other. Species 4 now with the advantage of the carrying capacity and initial abundance, excluded species 3 and occupied the region as a single-species (compare Figure 3A and Figure 3D). Generally, ecologically similar species have more impacts on one another than the reverse.



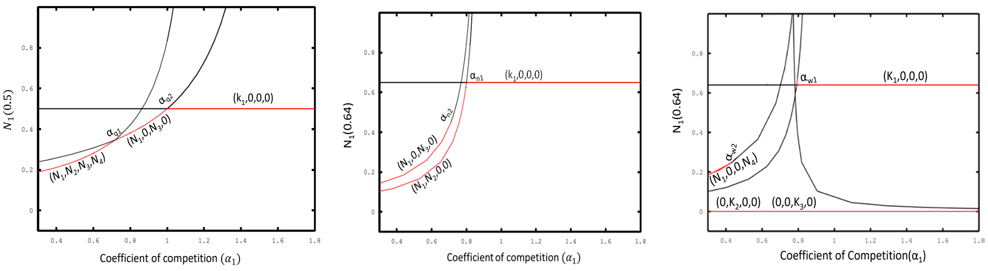
A *B* *C*

Figure 4. The summary plots of the presence-absence of the species as competitive strength of species 1 (i.e. α_1) varies with respect to environmental gradients x. Different colors are used to represent different combinations of species present and the change in color represent a change in stability of one combination of species for another one. Figure 4A is computed with $\alpha_1 = 0.3 - 1.4$, $\alpha_2 = 0.60$, $\alpha_3 = 0.62$, $\alpha_4 = 0.64$; Figure 4B is computed with $\alpha_1 = 0.3 - 1.4$, $\alpha_2 = 1.10$, $\alpha_3 = 1.12$, $\alpha_4 = 1.14$ and Figure 4C is computed with $\alpha_1 = 0.3 - 1.4$, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$

Presence-Absence of Species Across Geographical Locations as Competition Strength (α_1) Varies

Figures 4A-C are summary plots of the Equation [1] generated to show the presence-absence of species as competition strength of species 1 (i.e. α_1) changes with respect to environmental locations x. The plots are generated using four sets of initial abundances, each favoring one of the four species. Changes in colors illustrate different combinations of species present across the geographical region. Each color represents the range margins of species present at a given location x. Also, the boundary where one-color changes to another correspond to the critical value of the competitive strength of species 1 (i.e. α_1); where one stable combination of species lost its stability for another stable combination of species. In Figures 4A-C, α_1 varies from 0.3 - 1.4 with competitive strengths of other species kept constant at $\alpha_2 = 0.60$, $\alpha_3 = 0.62$, $\alpha_4 = 0.64$ in Figure 4A, $\alpha_2 = 1.10$, $\alpha_3 = 1.12$, $\alpha_4 = 1.14$ in Figure 4B and $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$ in Figure 4C. The regions label (*A*):, (*B*): and (*C*): *tristable* in Figure 4C respectively correspond to the presence of three stable combinations of species at the same location x.

When $\alpha_1 < 1$ in Figure 4A, we observed multispecies coexistence especially near the central location x. However, as competition strength α_1 increases, species 2 and 4 are simultaneously exclude, such that only species 1 and 3 coexistence can be observed. As earlier observed in our numerical simulations in Figure 2, coexistence of relatively weaker species with stronger species is also evident in Figure 4. For instance, Figure 4A illustrates *bistable* coexistence of species (i.e. $(N_1,0,N_3,0)$ and $(0,0,N_3,N_4)$) where species 1 is a stronger competitor at that location relative to other species. The same *bistable* coexistence of species (i.e. $(N_1,0,N_3,0)$ and $(N_1,N_2,0,0)$) is also observed in Figure 4B, where species 1 is a weaker competitor at that location compared to other competitors. These results show the leading roles of asymmetric interactions among multispecies; through which the coexistence of weaker species with stronger species is illustrated. Further, as other species competition strengths become stronger relative to species 1 as in Figure 4C, we observed higher priority effects which result to more species diversity. Thus, we observe single- and multiple- species and two or three single species co-occurrences at the same location x when $\alpha_1 < 0.8$. However, as $\alpha_1 > 0.8$ (see Figure 4C), co-occurrence of multiple species and single- and multiple- species (e.g. $(0,k_2,0,0)$, $(N_1,0,N_3,0)$) is impossible due to higher priority effects. This situation leads to existence of *bistable*, *tristable* and *tetratable* single-species steady states. These results show the persistence of priority effects throughout the range of $\alpha_1 = 0.3 – 1.4$ except in Figure 4A where evidence of priority effects is observed only at $\alpha_1 > 1.24$. This means that priority effects can occur if at least, the coefficient of competition of one of the competing multispecies is greater than 1.



A *B* *C*

Figure 5. The density plot at a location x of focal species (i.e. species 1) as competitive strength of species 1 (i.e α_1) varies. Figure 5A represents the density of the species 1 at the location x = 0.5. Figures 5B and C represent the density of the species 1 at the location x = 0.64. Red and black solid curves indicate stable and unstable steady states respectively. The threshold values correspond to transcritical bifurcation points (i.e. α_{q1}, α_{q2}, …, α_{w2}). Figure 5A is computed with $\alpha_1 = 0.3$ - 1.8, $\alpha_2 = 0.60$, $\alpha_3 = 0.62$, $\alpha_4 = 0.64$; Figure 5B is computed with $\alpha_1 = 0.3$ - 1.8, $\alpha_2 = 1.10$, $\alpha_3 = 1.12$, $\alpha_4 = 1.14$ and Figure 5C is computed with $\alpha_1 = 0.3$ - 1.8, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$

Presence-Absence of Species at a Location as Competition Strength (α_1) Varies

To improve the understanding of different species presence-absence as α_1 varies, we performed bifurcation analysis (Figure 5) to track the stable and unstable steady states of the species at a location x. Figure 5A and Figures 5B-C illustrate the stable steady states densities of species 1 at locations $x = 0.5$ and $x = 0.64$ respectively. The same results are expected if any of the species, other than species 1 is used for the plots. The red and black curves represent stable and unstable steady states respectively.

The results show threshold values which correspond to the critical values in the summary plots in Figure 4 and transcritical bifurcation points (i.e. α_{q1}, α_{q2}, ... α_{w2}) that illustrate different species presence-absence. Thus, we have the region of four species coexistence as illustrated in Figure 5A for $\alpha_1 < \alpha_{q1}$. This region is followed by another region (i.e. $\alpha_{q1} < \alpha_1 < \alpha_{q2}$) where we have simultaneous exclusion of species 2 and 4 with only species 1 and 3 coexisting as competition gets stronger. Beyond the region, $\alpha_1 > \alpha_{q2}$ is the region of stable steady states of single species ($k_1,0,0,0$). We also observe (Figure 5B) that at the location $x = 0.64$, the model exhibits *bistable* coexistence of species (i.e. ($N_1,0,N_3,0$) and ($N_1,N_2,0,0$)) which undergoes transcritical bifurcation at $\alpha_1 > \alpha_{n1}$ to show one stable single-species (k_1,0,0,0). Also, Figure 5C illustrate co-occurrence of *bistable* single-species and coexisting species (i.e ($0,k_2,0,0$), ($0,0,k_3,0$) and ($N_1,0,0N_4$)) at the same location $x = 0.64$. The presence of *bistable* and *tristable* species respectively in Figures 5B and C further illustrate evidence of priority effects for $\alpha_1 < 1$.

DISCUSSIONS

We studied multispecies competition in an environmentally changing habitat with asymmetrical competitive strengths of the species. The numerical simulation results generated provide an easier and accurate predictions of species distributions; and the results are found to be consistent with previous studies (Connell, 1961). Our findings are significant as they improve the understanding on the combined effects of biotic interactions and environmental factors, in determining multispecies community structures. For instance, environmental components alone can determine the range margins and then, defines the fundamental niche of the species (Geijzendorffer et al., 2011). The inclusion of competition interactions can shift the range margins of the species to a realized niche. Therefore, the presence-absence of species depends on the competitive intensity on one another and the response of species to environmental changes.

Our results show that different values of the competition coefficients can lead to different dynamical behavior of the model. For instance, when $\alpha_j < 1$, we observe coexistence of multispecies near the central region with the exclusion of some species at the peripheral regions. This form of community structure has earlier been observed in empirical study of small mammal species along elevational gradients (McCain, 2004;

McCain, 2005). The implication is that, diversity of species will be at its peak where the environment is moderately suitability with low competition intensity on the species. Thus, exclusion of the species at the lower and upper environments of the locations is expected due to unfavorable environments on some species, couple with competition interactions from the environmentally favored species. Connell (1961) reported in his empirical research that, competitive interactions and environmental factors could combine to determine the presence-absence of species. Consequently, the conservation of biodiversity can be maintained at relatively weak biotic interactions and moderate environmental components. In this way, both species can favorably compete for space and resources without anyone being eliminated from the community.

However, with strong competition interactions among the species, exclusion of the species from the locations are observed and coexistence is impossible. Consequently, initial abundances determine the presence-absence of the species. However, environmental suitability of the species has also been illustrated in our results to influence priority effects outcomes. This observation agreed with empirical research using Daphnia species (Loureiro et al., 2013) who observed that the outcomes of priority effects and community dynamics can be altered by environmental factors. Also, the coexistence of weaker competitor with other stronger (i.e. $\alpha_j > 1$) competitors as indicated in our result, implies that species whose ecological needs are not very similar can afford to coexist, in-respective of their competition strengths.

Also, our numerical continuation results which illustrate both stable and unstable steady states and bifurcation points of the models, proffer detail explanation on the differences in the presence-absence of species observed in our numerical simulation results. The threshold values of the competitive strengths α_1, correspond to the critical points of gradual exchange of one stable combination of species for another stable one. The bifurcation points therefore, give rise to different dynamical behaviors of the models such as coexistence, simultaneous exclusion of species and priority effects.

CONCLUSIONS

We studied competition interactions dynamics in multispecies using a system of ordinary differential equations to illustrate the competition outcomes in a varying environment. The model analyses revealed different dynamical outcomes such as coexistence of species and priority effects. Our result is significant as it further improved understanding on multispecies community dynamics. Most intuitively, is the coexistence of both weak and strong species at the same location, especially if the species are less ecologically similar. Generally, the findings of our research illustrate how biotic interactions and environmental factors can combined to strongly shape the range margins of multispecies in a habitat (Little & Altermatt, 2018). A previous study (Mittelbach, 2012) had shown that, without biotic interactions, environmental factor alone determined the fundamental niche of the species. Thus, in this research, we have shown that competition interactions can exclude interacting multispecies from some locations in their habitat and then, determine their realized range margins.

However, other ecological factors such as dispersal may change the dynamics of the competitions. Therefore, inclusion of dispersal in our model will be an interesting extension of this paper. Since species response to environmental changes is not always linear, as claimed in this paper, model that expresses the carrying capacities of the species as Gaussian equations, is also a possible extension of our model for future studies.

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