



NUMERICAL ANALYSIS OF ORDINARY DIFFERENTIAL EQUATIONS OF ECOLOGICAL COMPETING SPECIES ACROSS DIVERSE ENVIRONMENTS

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ABSTRACT: *In a geographical region, species have their range margins (i.e., the geographic boundaries where species can be found). Several species distribution models have shown that environmental factors (i.e., abiotic factors) and species interactions (i.e., biotic interactions) are responsible for shaping the distributions of species. Yet, most of the models often focus on one of these factors and ignore their joint effects. Consequently, predicting which species will exist and at what range margins is a challenge in ecology. Thus, in this paper, the combined influences of these ecological factors on multi-species community structures are studied. An ordinary differential equations (ODE) model is employed to study multi-species competition interactions across diverse environments. The model is numerically analysed for the range margins of the species and threshold values of competition strength which leads to the presence-absence of species. It is observed that the range margins are influenced by competition between species combined with environmental factors and the threshold values of competition strength correspond to transcritical bifurcation. Depending on the species' competition strengths, the model exhibits coexistence and exclusion of species, mediated by weak and aggressive biotic interactions, respectively. It is observed that ecologically similar species competitively affect each other more than dissimilar species.*

KEYWORDS: Ordinary Differential Equations, Competition Strength, Diverse Environments, Range Margins, Threshold Values



INTRODUCTION

Generally, all species have natural geographic range margins; however, the range margins can be shifted if the species are affected by ecological factors (Williams & Blois, 2018). For instance, the range margins of the species can be shifted due to biotic interactions (Martin & Bonier, 2018; Ravenek et al., 2016) and changes in environmental factors (Anderegg & HilleRisLambers, 2019; Lamprecht et al., 2018). However, these factors most often, do not act in isolation but they interact with one another to influence the distributions of species in their habitats (Dormann et al., 2018; Lewis et al., 2017). Consequently, predicting which species will coexist and at what range is a challenge in ecology (Amundrud & Srivastava, 2019). Therefore, a research study as in this paper, which focuses on the combined influence of ecological factors such as biotic and abiotic factors on the species distribution is important in the field of ecology.

As stated above, species distributions can be influenced by the combined effects of biotic interactions and abiotic factors (Connell, 1961; Mittelbach, 2012; Ojonubah & Mohd, 2020). This is because the interactions of the biotic and abiotic factors are observed to determine how each factor affects the competing species (Amundrud & Srivastava, 2019; Gilman et al., 2010; Meier et al., 2011; Thurman & Garcia, 2019). For instance, environmental factor was demonstrated to mask the effect of biotic interactions among species (Godsoe et al., 2017). Such interactions between biotic and abiotic factors may alter community structures. The interplay of biotic and climate factors in an earlier study was reported to influence the range margins of species in grassland communities (Suttle et al., 2007). Wittmann et al. (2013) experimentally studied the competition of two species and reported that the outcomes of the interactions of the two species hinge on competitive interactions and climate change. It is still not clear how the combined effects of competition interactions and environmental changes may influence the outcomes of multi-species interactions. However, the combined influence of biotic and environmental factors in determining the species' community structures is also confirmed in recent studies (Darwell et al., 2017; Freeman et al., 2018; Ojonubah & Mohd, 2020).

Motivated by these observations, this paper investigates the coexistence, range margins of species and threshold values of competition strength which leads to the presence-absence of species due to influences of species competition interactions across diverse environments; using the ordinary differential equations (ODE) model. To gain insight into the interplay of biotic interactions and environmental factors, these factors are combined in the ODE model with the assumption that the competitive strengths of the species are asymmetrical. Thus, the competition models (Godsoe et al., 2014; MacLean & Holt, 1979; Mohd et al., 2017; Roughgarden, 1979), are extended to investigate the outcomes of multi-species competition interactions. The models are for four species and it is an extension of the Lotka-Volterra competition (LVC) model based on Mohd et al. (2017).

Thus, this paper is organized as follows: After the introduction is the description of the deterministic model, which combines the biotic and abiotic factors. This is followed by the description of numerical methods. Then, the results on the range margins of the species are illustrated using numerical simulations. Thereafter, summary plots and bifurcation analyses are presented to show the presence-absence of the species across a geographical region as a model parameter varies. Based on the results, the ecological implications are discussed.



MATERIALS AND METHODS

The models

A deterministic model is presented in this section to study the distributions of n -species with densities $N_i(t)$ across diverse environments. It is a competition model, which is a system of ODEs in $0 \leq x \leq 1$, written as in Equation (1) and in Ojonubah and Mohd (2020).

$$\frac{dN_i}{dt} = \frac{r_i N_i}{K_i(x)} \left(K_i(x) - \sum_{j=1}^n \alpha_{ij} N_j \right), (i = 1, 2, \dots, n). \quad (1)$$

Here, r_i is the intrinsic growth rate, $K_i(x)$ is the carrying capacity of species i , α_{ij} is the interspecific competition coefficient of species j on species i (a measure of the strength of competition of one species on another), α_{ii} is the intraspecific competition coefficients (a measure of the strength of the competition within the same species) and N_i is the densities of species i at time t . The densities of species i are rescaled with respect to α_{ii} , which is set as 1 and $\alpha_{ij} \neq \alpha_{ji}$ imply an asymmetry in the competitive strengths of the species. For simplicity, α_{ij} henceforth will be written as α_j . In this paper, competition of four species (i.e., $n = 4$) is investigated, such that $\alpha_1, \alpha_2, \alpha_3, \alpha_4$ and $K_1(x), K_2(x), K_3(x), K_4(x)$ represent species 1, 2, 3 and 4 interspecific coefficients of competition and carrying capacities respectively (Ojonubah & Mohd, 2020).

The suitability of the environments is modelled into the carrying capacities $K_i(x)$, such that the effect of environmental factors on each species is dependent on $K_i(x)$. In this case, x represents geographical locations or serves as a proxy for representing abiotic components like temperature, humidity, salinity, pH, altitude, etc. However, since it is easier to examine the effects of a limited number of abiotic factors, the results in this paper use temperature as a proxy for component x . In this case, since x is the varying parameter in $K_i(x)$, it implies that each species' carrying capacity also depends on x . Thus, the effects of biotic interactions on the range margins of species depend on how the species respond to environmental factors. To illustrate these effects in the interactions of multi-species communities, the carrying capacity $K_i(x)$ of the species is modelled to vary linearly with x (Ojonubah & Mohd, 2020). Thus, the carrying capacity of species i is given as:

$$K_i(x) = m_i x + b_i, \quad (2)$$

In this case, m_i represents species i response to environmental gradients (i.e., the slope of species i carrying capacity), and it serves as a measure of the environmental suitability of different locations with respect to x , b_i is the point of intercept of species i carrying capacity when $x = 0$. Thus, the minimum or maximum densities that can be achieved by species i is at $x = 1$, depending on whether m_i is negative or positive respectively.

In this paper, competition among the species is localised. This means, ecological competition between species for the same resources occurs at the same location and does not involve the species moving from one location to another. In this case, the species compete with each other at a particular location without migration. This also, implies that Equation (1) dynamical behaviour in one location is independent of other locations.



Numerical Methods

To understand the dynamics of the system, dN_i/dt in Equation (1) is set to zeros and we solved numerically for the steady states. The stability analysis of the steady states is also carried out, using the MAPLE package. Thus, the steady state whose real parts of the eigenvalues are negative is stable. The numerical simulation results on the range margins of the species are obtained by employing MATLAB *ode45* solver for $t = 1000$ to solve Equation (1) until steady states are achieved. Also, summary plots are generated using MATLAB *ode45* solver, to show different species present and their range margins across the geographical locations as the model parameter, α_1 changes. MAPLE package is also used to verify that the simulation results are stable.

To further cross-check the simulation results, the numerical simulation package XPPAUT is employed. Thus, the steady states of Equation (1) are computed with the aid of *cvsolve* solver for $t = 1000$. We then continued the steady states in AUTO, where the stable and unstable steady states, as well as the bifurcation points, are tracked as the model parameter, α_1 changes at a particular location x . The value $10^{-1}/10^{-6}$ is used as the maximum/minimum allowable step size.

Parameterisation of the Models and Units

The values of α_j that are used in this paper are obtained from Table 1 of Ayala et al. (1973), when they conducted an experimental study using pairs of *Drosophila* species in eight experiments to determine the abundances of the species at equilibrium. α_j are estimated between 0.33 and 5.32, except for one outrageous value which is 12.37 (Ayala et al., 1973). The unit of α_j is resources consumed/day. However, due to the uncertainty of competition coefficients, the model behaviour is analysed for a realistic range of α_j . Also, the competition between two pairs of ecologically similar species is investigated in this paper as in Ojonubah and Mohd (2020). Based on the carrying capacities, species 1 and 2 are similar and warm-tolerant species. This is because the two species have the same environmental requirements (i.e., their carrying capacities increase as x increases from 0 to 1). Warm tolerant species refers to species that have the ability to grow and produce optimally under warm temperatures. For example, Davis et al., (1998b) experimentally studied three species of *Drosophila* (i.e., *D. melanogaster*, *D. simulans* and *D. subbobscura*). In closed single-species clines, the abundances of *D. melanogaster* and *D. simulans* are observed to increase as temperature increases from 10°C – 25°C. Thus, they are regarded as warm tolerant species similar to species 1 and 2 in this paper. Species 3 and 4 are also another set of similar species. Their carrying capacities are both homogeneously distributed across the locations x , which means that both species have the same environmental tolerance. As stated in Table 1, species 1, 2, 3 and 4 carrying capacities are given as $K_1(x) = m_1x$, $K_2(x) = m_2x$, $K_3(x) = b_3$, and $K_4(x) = b_4$ respectively. The carrying capacities are chosen similarly to Davis et al. (1998) experimental demonstrations of the abundances of *Drosophila* species at equilibrium, which in single-species closed clines, are linearly distributed across temperature gradients. The parameter values of the carrying capacities as stated in Table 1 are chosen based on previous theoretical studies (Godsoe et al., 2014; Mohd et al., 2017; Ojonubah & Mohd, 2020). The units of the parameter values are as follows: m_i is °C⁻¹, r_i is day⁻¹ and b_i is the number of species/Km².

**Table 1: Symbols with the descriptions and parameter values**

Symbol	Items description	Parameter value	Reference
r_i	Intrinsic growth rates of species i	1	Godsoe et al. (2014) and Mohd et al. (2017)
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

Numerical results are presented in this section to illustrate the range margins and coexistence of species across locations x and threshold values (i.e., bifurcation points) of competition strength, which leads to presence-absence of species due to combined influences of species competition interactions and environmental gradients. The circles in Figure 1 correspond to the invasion points of the species and can also be calculated using the invasion analysis method (Ojonubah & Mohd, 2020).

To show the impacts of competition strengths on multi-species community assembly, the numerical results are obtained separately for different competition strengths of the species as in Figure 1 and Figure 2, which show the range margins and densities of the species. Also, summary plots are presented in Figure 3, which illustrate the presence-absence of the species across the locations as species 1 competition strength (i.e., α_1) varies with respect to the locations x . Bifurcation analysis results are also presented in Figure 4, which shows the stable and unstable steady states of species, as well as bifurcation points present at a particular location x as α_1 varies. The bifurcation analysis and the summary plot results also agreed on the presence-absence of the species. A detection threshold value of 0.5% of the maximum observed density of the species is employed for the numerical results. The detection threshold value determines when a species is to be considered absent if its density is below the critical value (i.e., a species will not be considered present if its density is below the critical value). The value of 0.5% used in this paper is based on a previous ecological study by Gaston (2003); (Mohd et al., 2016, 2018; Ojonubah & Mohd, 2020).

Range margins of species due to biotic interactions

Figure 1 and Figure 2 illustrate interactions outcomes (e.g., range margins) of the species resulting from relatively weak (i.e., $\alpha_j < 1$) and aggressive (i.e., $\alpha_j > 1$) biotic interactions



respectively, among the species as predicted by Equation (1). The competition strengths, initial abundances and carrying capacities of the species used for the computation of both results (i.e., Figure 1 and Figure 2) are stated below the Figures. The same carrying capacities and initial abundances are used for the figures except in Figure 1(b) and Figure 2(b), where $K_2(x) = 2x - 0.8$ to demonstrate influences of environmental difference (particularly as the $K_2(x)$ changes). Thick lines are used to represent the steady states of the species and the range margins are shown on the horizontal axis for species 1, 2, 3 and 4, which are denoted as blue, dark green, red and black coloured circles respectively (see Figure 1).

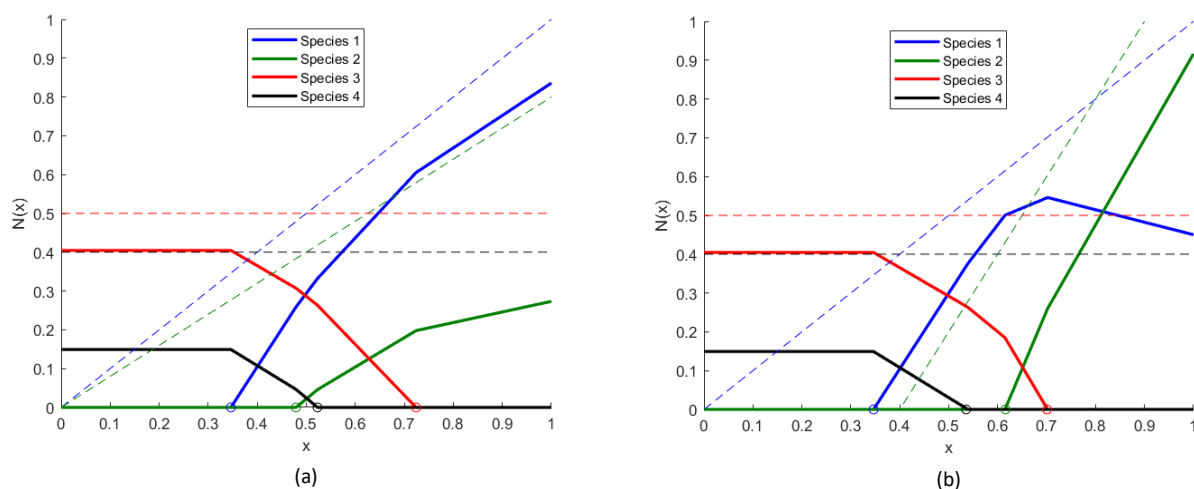


Figure 1. The steady states of species i . Solid lines indicate steady states and the dotted lines represent the carrying capacities as parameterisation of linear environmental gradient changes. The figures are computed with $\alpha_1 = 0.63$, $\alpha_2 = 0.60$, $\alpha_3 = 0.62$, $\alpha_4 = 0.64$; $K_1(x) = x$, $K_2(x) = 0.8x$, $K_3(x) = 0.5$, $K_4(x) = 0.4$ and initial abundances: $N_1(x) = 0.1K_1(x)$, $N_2(x) = 0.9K_2(x)$, $N_3(x) = 0.1K_3(x)$, $N_4(x) = 0.9K_4(x)$. In Figures 1(a) and (b), $K_2(x) = 0.8x$ and $K_2(x) = 2x - 0.8$ respectively. Circles on the horizontal axis represent the invasion points (x_i) of the species.

It is observed that in Figure 1(a) for instance, two or more species coexisted at the same locations, with multi-species coexistence centrally located. Because of competition from species 3 and 4, the range margins of species 1 and 2 are shifted from their fundamental niche (i.e. the full range of environment that a species can occupy and use without the presence of biotic interactions). In this paper, the full range of the environment occupied by species 1, 2, 3 and 4 without biotic interactions is $0 < x \leq 1$. Thus, in the presence of biotic interactions, the new location points (i.e., the invasion points) for species 1 and 2 are at $x_1 = 0.3463$ (blue circles) and $x_2 = 0.4791$ (dark green circles) respectively. In the same way, species 3 and 4 are excluded by species 1 and 2 from the right-hand side of the locations x , such that species 4 and 3 range margins are respectively at $x_4 = 0.5229$ (black circles) and $x_3 = 0.7239$ (red circles). In this case, the invasion points, divide the spatial domain of the species into regions of two-species, three-species and four-species coexistence. Based on Figure 1(a) for instance, the regions of two-

species coexistence correspond to two domains. Considering from the left to the right, there exists a region (i.e., $x \leq x_1$) where species 3 and 4 coexist and exclude species 1 and 2. Also, from the right, is the region (i.e., $x_3 \leq x$) where species 1 and 2 coexist with the extinction of species 3 and 4. These are followed by two regions (i.e., $x_1 \leq x \leq x_2$ and $x_4 \leq x \leq x_3$) of three-species coexistence. In the first region, species 1, 3 and 4 are present and exclude only species 2. Similarly, in the second region, species 1, 2 and 3 are present with species 4 absent. The last region is the central domain (i.e., $x_2 \leq x \leq x_4$), where all four species coexisted. The multi-species coexistence at the centre, suggests that the central region is likely to be the most favourable environment for all the species.

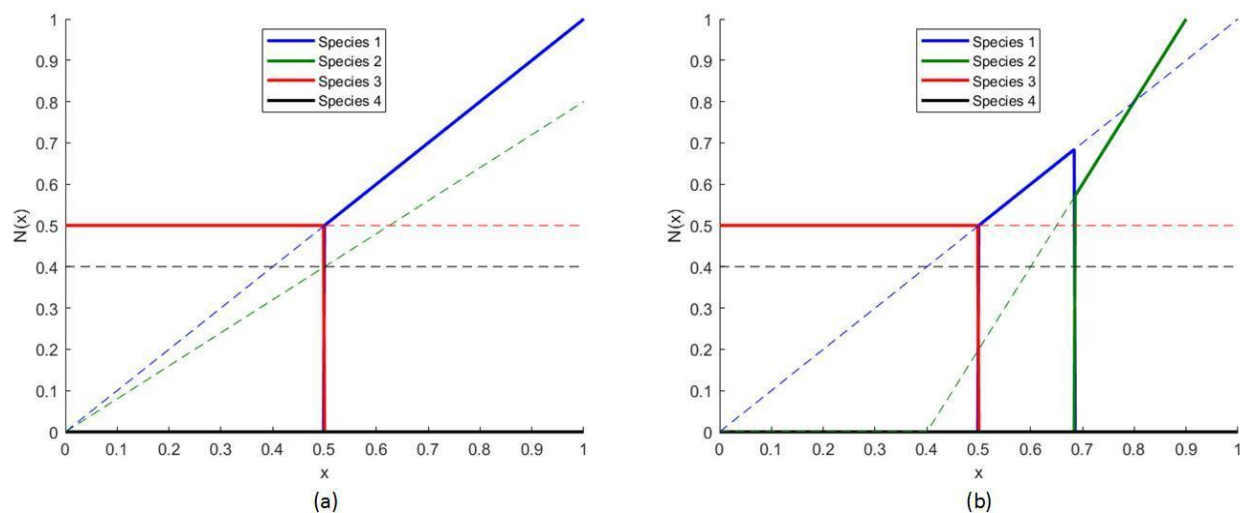


Figure 2. The steady states of species i . Figures 2(a) and (b) are computed with $\alpha_1 = 1.33$, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$; $K_1(x) = x$, $K_2(x) = 0.8x$, $K_3(x) = 0.5$, $K_4(x) = 0.4$ and initial abundances: $N_1(x) = 0.1K_1(x)$, $N_2(x) = 0.9K_2(x)$, $N_3(x) = 0.1K_3(x)$, $N_4(x) = 0.9K_4(x)$. In Figures 2(a) and (b), $K_2(x) = 0.8x$ and $K_2(x) = 2x - 0.8$ respectively.

However, when the competitive strengths of all the species are relatively aggressive (i.e., $\alpha_j > 1$) as illustrated in Figure 2, the qualitative outcomes of the competition will also change (compare Figure 1 to Figure 2). The range margins of the species in Figure 2 as predicted by Equation (1) depict that coexistence of species is generally impossible when the competition is aggressive. The dynamical behaviour of the model leads to exclusion of all species except one, due to aggressive biotic interactions. Consequently, the competitive region is partitioned into smaller units, where each location is occupied by a stable steady state of single species, which exists to the maximum density of the carrying capacity.

Similarly, the presence-absence of the species may also depend on the magnitude of the environmental gradients (i.e., carrying capacities) and biotic interactions. Thus, Figure 1(a) and Figure 2 (a) (left column) and Figure 1(b) and Figure 2(b) (right column) are computed to illustrate the influence of different environmental gradients on the presence-absence of species. The same parameter values are used to compute the two columns except that, in Figure 1(a)



and Figure 2(a), the environmental gradient for species 2 is $K_2(x) = 0.8x$ and $K_2(x) = 2x - 0.8$ in Figure 1(b) and Figure 2(b).

Due to slight changes in the environmental gradient of species 2, the community assembly observed in Figure 1(a) and Figure 2(a) are not the same as in Figure 1(b) and Figure 2(b). Thus, in Figure 1(b) for instance, the order of invasion points (x_i) of the species becomes x_1, x_4, x_2 and x_3 (compare Figures 1(a) with (b)). In this case, multi-species (i.e., four species) coexistence is not attainable in Figure 1(b), which is quite different from the observations in Figure 1(a). A similar observation is true in Figures 2(a) and (b), which, due to differences in environmental gradients, depict different species' presence-absence across the locations x . In Figure 2(b) for instance, location x is separated into three parts with the presence of species 3 on the left and species 1 and 2 present on the right side (compare Figure 2(b) with (a)). Species 2, now with the advantage of the environmental gradient, dominated the right region and shifted species 1 to a narrower region towards the centre (see Figure 2(b)).

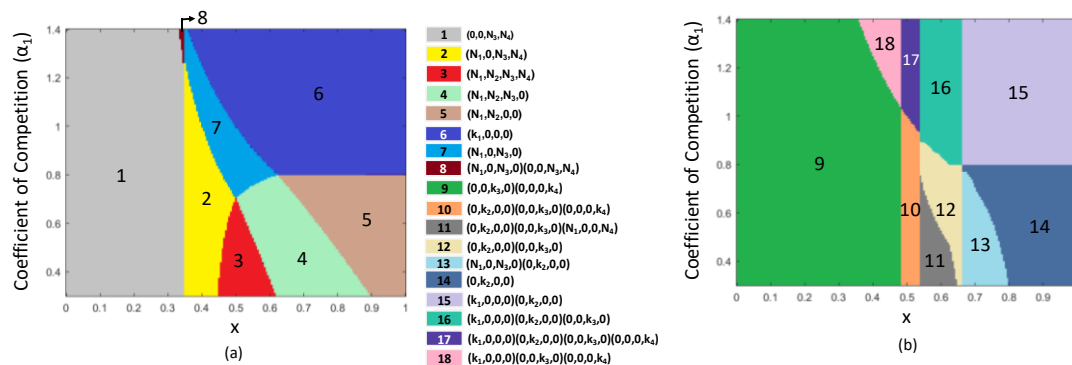


Figure 3. The summary plots show the presence-absence of the species as the competition strength of species 1 (i.e., α_1) varies with respect to the environmental gradients x . Figure 3(a) is computed with $\alpha_1 = 0.3 - 1.4$, $\alpha_2 = 0.60$, $\alpha_3 = 0.62$, $\alpha_4 = 0.64$ and Figure 3(b) 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 Locations as Competition Strength of Species 1 Varies

Figures 3(a) and (b) are the summary plots of 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 environmental gradients as described in Table 1. To detect the presence-absence of the four species, four sets of initial abundances are used to generate Figure 3, each favouring one of the four species at a time. Each set of the initial conditions is run independently before the presence/absence of the species is combined using summary plot techniques (Mohd et al., 2017, 2018; Ojonubah & Mohd, 2020). Colours are used to represent the range margins of species present at a particular location (α_1, x) (Mohd et al., 2017; Ojonubah & Mohd, 2020). Changes in colour, illustrate different stable combinations of species present across the geographical locations. Also, the boundary where one colour changes to another, corresponds to the critical value of the competition coefficient, α_1 (i.e., transcritical bifurcation), where one stable combination of species lost its stability for another stable combination of species. Apart from the colours used to differentiate the presence



of species in a particular location (α_1, x) , each location is also distinguished by a number. The numbers are nominal scales used basically for easy identification. Thus, the stable combination of species that each colour or number represents in a particular location is indicated in the colour legend in Figure 3.

Figure 3 (i.e., (a) and (b)) illustrates the model predictions as α_1 varies (i.e., $\alpha_1 = 0.3 - 1.4$) with the competitive strengths of other species kept constant at $\alpha_2 = 0.60$, $\alpha_3 = 0.62$, $\alpha_4 = 0.64$ in Figure 3(a) and $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$ in Figure 3(b). The $k_1 - k_4$ in the legend represent the presence of species 1 - 4 as single-species, existing to their carrying capacities; while $N_1 - N_4$ represent the presence of species 1 - 4 at a particular location. The regions labelled 8, 9, 12, 13 and 15; 10, 11, 16 and 18; and 17 correspond to the presence of *bistable*, *tristable* and *tetrastable* steady states of species respectively at the same location (α_1, x) , as indicated in the colour legend in Figure 3. *Bistable* and *tristable* imply the presence of two and three stable steady states of species respectively at a particular location (α_1, x) , which may consist of single-species, single- and multi-species or multi-species coexistence. Similarly, *tetrastable* region implies the presence of four stable steady states of single species in the region, each existing to the maximum density of the carrying capacity.

When $\alpha_1 < 1$ in Figure 3(a), multi-species coexistence is observed (region label 3), especially near the central location, which is similar to the observation in Figure 1(a). However, as competition strength, α_1 increases, the four species' coexistence simultaneously excludes species 2 and 4 giving rise to the coexistence of species 1 and 3 (region labelled 7). Also, as α_1 increases further, the model exhibits the coexistence of relatively weaker species 3 with stronger and dissimilar species 1 without species 2, as evident in Figure 3(a) (see region labelled 8). For instance, at $\alpha_1 > 1.24$, Figure 3(a) depicts *bistable* steady states of two-species coexistence (region labelled 8), where species 1 at that location is a stronger competitor relative to other species. This observation is an indication of priority effects (i.e., alternative stable states) at that location.

Also, when other species' competition strengths become stronger relative to species 1 as illustrated in Figure 3(b), a higher priority effect is observed. This situation leads to a higher variation in species composition, particularly at the central locations. Thus, *bistable* (region labelled 12 and 13) and *tristable* (region labelled 10 and 11) steady states of single-species or single- and multiple-species are observed when $\alpha_1 < 0.8$. However, as $\alpha_1 > 0.8$ (see Figure 3(b)), the co-occurrence of 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 the existence of *tristable* and *tetrastable* steady states of single species (region labelled 16, 18, and 17). The single species it may converge to will depend on the initial abundance of the species. The results show the prevalence of priority effects throughout the range of $\alpha_1 = 0.3 - 1.4$ except in Figure 3(a), where evidence of priority effects is observed only at $\alpha_1 > 1.24$. This illustrates that in multi-species interactions, priority effects can occur if at least, the competition coefficient of one of the competing species is greater than 1 (Ojonubah & Mohd, 2020).

Presence-absence of Species at a Location as Competition Strength of Species 1 Varies

To give further clarifications on different species' presence-absence in the summary plots (i.e., Figure 3), numerical continuation is employed. The idea is to track the stable and unstable steady states of the species and bifurcation points in Equation (1) at a particular location x as α_1 varies. For instance, Figures 4(a) and (b) and Figures 4(c) and (d) illustrate the stable steady



state densities of species 1 (i.e., N_1) at two locations $x = 0.5$ and $x = 0.9$ respectively. Any of the species other than species 1 can be used for these plots. The carrying capacities of the species used for the plots are as specified in Table 1. Figure 4(a) and Figure 4(c) are computed at the locations $x = 0.5$ and $x = 0.9$ respectively with $\alpha_1 = 0.3 - 1.8$, $\alpha_2 = 0.60$, $\alpha_3 = 0.62$, $\alpha_4 = 0.64$ and Figure 4(b) and Figure 4(d) are computed at the locations $x = 0.5$ and $x = 0.9$ respectively with $\alpha_1 = 0.3 - 1.8$, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$. The results illustrate several stable and unstable steady states of species presence-absence and the existence of threshold values (α_1). The threshold values in the results correspond to the critical values in the summary plots. Figures 4(a) and (c) and Figures 4(b) and (d) correspond to the summary plots in Figure 3(a) and Figure 3(b) respectively.

The threshold values (i.e., α_{q1} , α_{q2} , α_{q3} in Figures 4(a) and (c) and α_{t1} , α_{t2} in Figures 4(b) and (d)) correspond to transcritical bifurcation points, which lead to different branches of stable (red lines) and unstable (black lines) steady states of the species. Solid lines indicate feasible solutions and dotted lines represent infeasible solutions (i.e., one of the densities of the species is negative). In Figure 4(a) for instance, there exists one stable steady-state branch of four-species coexistence when $\alpha_1 < \alpha_{q1}$. This is followed by another stable steady-state branch of species 1 and 3 coexistence (i.e., $\alpha_{q1} < \alpha_1 < \alpha_{q2}$) with the simultaneous exclusion of species 2 and 4. Beyond this steady state, is another stable steady-state branch (i.e., $\alpha_1 > \alpha_{q2}$) of species 1, existing as a single species to its carrying capacity. Similarly, in Figure 4(c) with one stable steady-state branch (i.e., $\alpha_1 < \alpha_{q3}$) of species 1 and 2 coexistence, which gives rise to species 1 single-species branch for $\alpha_1 > \alpha_{q3}$.

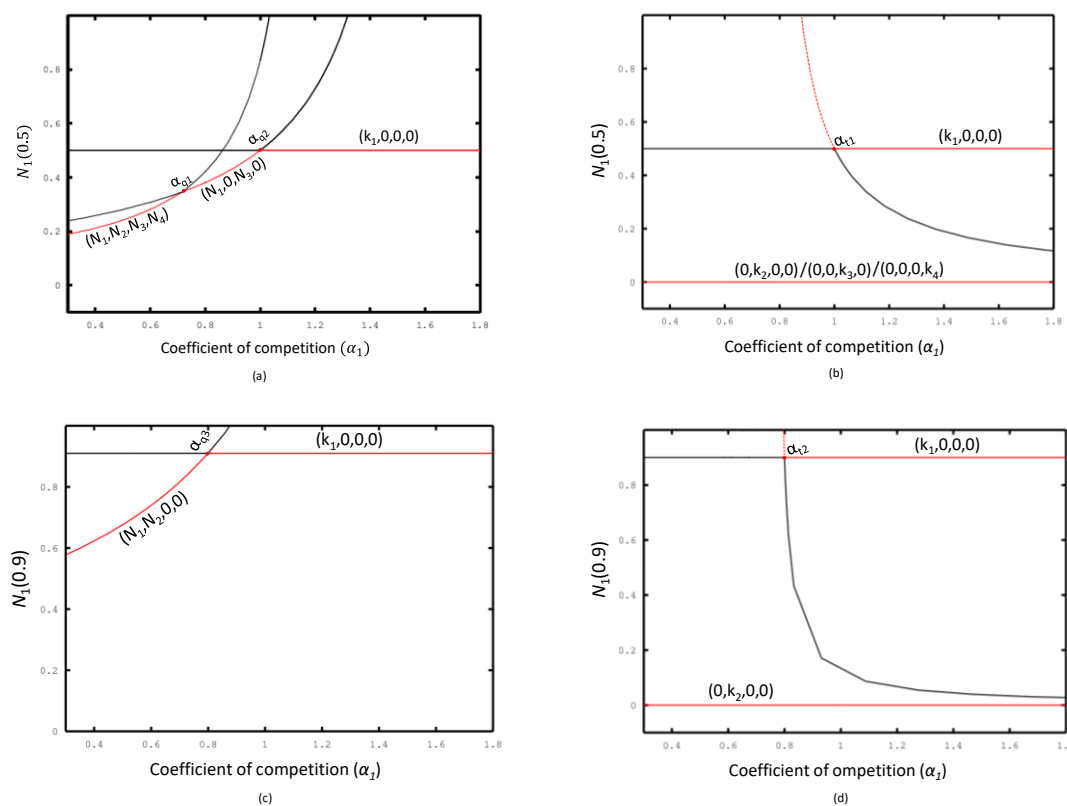


Figure 4. The density plots at location x of species 1 as α_1 varies. Figures 4(a) and (b) and Figures 4(c) and (d) represent the density of species 1 at the locations $x = 0.5$ and x



= 0.9 respectively. Red and black solid curves indicate stable and unstable steady states respectively. The dotted lines represent infeasible solutions. Figures 4(a) and (c) are computed with $\alpha_1 = 0.3 - 1.8$, $\alpha_2 = 0.60$, $\alpha_3 = 0.62$, $\alpha_4 = 0.64$ and Figures 4(b) and (d) are computed with $\alpha_1 = 0.3 - 1.8$, $\alpha_2 = 1.30$, $\alpha_3 = 1.32$, $\alpha_4 = 1.34$.

Also, in Figure 4(b), the model exhibits priority effects throughout the range of α_1 . Consequently, this leads to many branches of stable and unstable steady states. For instance, there exist *tristable* steady states of single species (lower red line) with species 2, 3 and 4 present, each existing as a single specie. Above these stable steady states (i.e., $\alpha_1 > \alpha_{t1}$) is another stable steady state of species 1 single-species, which is separated from the *tristable* steady states by an unstable steady state (i.e., four species) branch. A similar behaviour is also observed in Figure 4(d), where species 2 exists as a single specie (lower red line), and then, separated from another single specie of species 1 for $\alpha_1 > \alpha_{t2}$ by unstable steady state (i.e., black middle line) of two-species coexistence.

DISCUSSIONS

In this paper, the influences of environmental factors combined with competition interactions on multi-species community structures are investigated. The numerical simulation results generated give a detailed prediction of species distributions and the results are found to be consistent with previous studies (Godsoe et al., 2014; Mohd et al., 2017). The findings are significant as they improve the understanding of the mechanism through which biotic interactions and environmental factors combined to determine multi-species community structures. For instance, environmental components alone, determine the range margins and then, defines the fundamental niche of the species (Geijzendorffer et al., 2011). The inclusion of competition interactions shifts the range margins of the species to a realized niche. Therefore, the presence-absence of the species depends on how the species respond to the competition intensity of one another, combined with the changes in the environment.

The results show that different values of the competition coefficients can lead to the different dynamical behaviour of the model. For instance, when $\alpha_j < 1$, the coexistence of multiple species is observed near the central region with the exclusion of some species in the peripheral regions. This form of community structure has earlier been observed in other studies, which also observed maximum biodiversity at mid-elevations (Beck et al., 2017; Dong et al., 2017). The implication is that the diversity of species will be at its peak, where the environment is moderately suitable 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 unfavourable environments on some species, coupled with competition interactions from the environmentally favoured species. Connell (1961) reported in his experimental research that, competition interactions and environmental factors can 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 favourably compete for space and resources without anyone being excluded.

However, with strong competition interactions among the species combined with environmental factors, exclusion of the species from some locations is observed and



coexistence is impossible. This observation agreed with experimental research using *Daphnia* species by Loureiro et al. (2013), who observed that community dynamics can be altered by environmental factors. Yet, the coexistence of weaker competitors with other stronger competitors as indicated in the result implies that species whose ecological needs are not very similar can possibly afford to coexist, in-respective of their competitive strengths. Although locally coexisting species should be expected to be more similar, the coexistence of dissimilar species may be possible because they may not compete enough with one another (Pinsky, 2019). This suggests that similar species may compete more with one another, such that ecologically similar species during intense competition may exact stronger priority effects on one another than dissimilar species, which may have implications for conservation management. Godsoe et al. (2014) disclosed that if two interacting species are ecologically similar, then, a little change in the biology of either species can radically change the range margins of the species. This accounts for species 1 coexistence independently with weaker and dissimilar species 3 at the same locations (e.g., see Figure 3) without the ecologically similar species 2 due to priority effects.

Ecologically, these qualities could be implemented in biocontrol management, either for preserving the weaker species among the stronger ones or to minimise the excesses of a species whose activities are undesirable in the habitat. In this paper, it is illustrated that species 1 and species 2 are ecologically similar species and species 3 and 4 are another set of ecologically similar species. In this instance, species 1 could be sustained in the habitat by having more of species 3 or 4 instead of species 2 in the habitat. Similarly, if all the species are relatively strong, the activities of species 1 and species 2 affect each other more (respectively species 3 and 4). Consequently, species 1 for instance, can be sustained in the habitat by introducing more of it against species 2. Similarly, if species 4 activities are not desirable in the habitat, the activities can be curtailed by introducing more of species 3. It has previously been observed that initial abundance can be used in biocontrol management, to regulate the presence-absence of species (Jones et al., 1999; Tang et al., 2010).

Also, the numerical continuation results which illustrate both stable and unstable steady states and bifurcation points of the models, proffer detailed clarifications for the different species presence-absence observed in the numerical simulation results. The existence of threshold values for competition strength, α_1 is illustrated. The threshold values correspond to critical values (or colour change) in the summary plots, where one combination of species presence exchanges its stability for another combination of species. The bifurcation points, therefore, lead to different dynamical behaviours of the models such as coexistence, simultaneous exclusion of species and priority effects.

CONCLUSIONS

A deterministic model is used in this paper, which is a system of ODEs, to investigate the combined effects of competition interactions and environmental factors on multi-species community structure. The model is analysed using numerical methods for the range margins of the species. The numerical simulation results are found to be consistent with each other. The results show that environmental factors can combine with species interactions to determine multi-species community assembly (Little & Altermatt, 2018). Although, the outcomes depend on the species' competition strengths, which may lead to the coexistence or exclusion of species



mediated by weak and/or aggressive interactions, respectively, as also observed in the theoretical studies of three species (Mohd et al., 2017) and four species (Ojonubah and Mohd, 2020).

However, the findings of the four species investigated in this paper differ from that of the three species. Most intuitively is the finding in this paper that ecologically similar species, competitively affect each other more than the dissimilar species (Ojonubah and Mohd, 2020). A weaker species is observed in this paper to coexist with dissimilar and stronger species at the same location in the absence of similar species. Also observed in this paper is the priority effects occurrence, when the interspecific competition strength of at least one of the species interspecific competition is greater than intraspecific competition.

Hence, based on the findings, it is suggested that adequate knowledge of biotic interactions and changes in the environment is essential for the successful maintenance of biodiversity and conservation management (Ojonubah and Mohd, 2020). Also, ecological factors such as dispersal with the nonlinear carrying capacity of species may change the outcomes of the competition dynamics presented in this paper. Therefore, the inclusion of dispersal with nonlinear carrying capacity in the deterministic model in this paper may be an interesting extension of this paper. This may lead to robust predictions of the range margins of species across a geographical region.

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Conflict of Interest Statement

- None of the authors of this paper has a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

- No competing interests are at stake and there is No Conflict of Interest with other people or organisations that could inappropriately influence or bias the content of the paper.

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