Effects of asymmetrical biotic interactions on multispecies dynamics

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Abstract. One of the key challenges in ecology is to predict multispecies spatial distributions in the future. The influence of biotic interactions in the form of competition and environmental change such as climate are thought to have significant impacts on the distribution of species. To ascertain this, we study a multispecies community assembly with asymmetrical competition across heterogeneous environments using mathematical modelling. With the aid of analytical and simulation analyses, we achieved the predictions of the species range margins (comprising the geographic boundary beyond which a species is not present). We also perform bifurcation analysis in order to understand the competitive dynamics across location. Our results show that the combined influence of the biotic and abiotic factors lead to coexistence of species when competition is relatively weak and existence of single dominant species territory during aggressive competitions. Also, the threshold values observed in the bifurcation analysis correspond to transcritical bifurcation points.

1. Introduction

In nature, species range margins and biodiversity across geographical locations may be changing due to the combine influences of ecological factors such as climate change and biotic interactions. The consequence is that the prediction of the future presence-absence of species in a geographical location may be a challenging task to ecologists. This aspect is thought to have dramatic effects on the conservation plans that can alleviate biodiversity. Therefore, anticipation and management of these effects are among the most crucial problems in ecology [1, 2]. As such, the presence-absence of species by which we refer to the boundary where a species is present or absent and also means the range margins or limits of species is one of the main thrusts of this study. In this study, we are also concerned with ecological forces that influence species community assemblies across geographical region and the mechanisms that can induce coexistence of species and the occurrence of priority effects. Environmental factors (such as climate change) and biotic interactions (such as interactions among species) [2, 3] are known to have significant impacts on the distributions and range margins of species. Although range shifts of species have earlier been attributed to biotic interactions by researchers in the past [4], emphases are frequently placed on climate change by contemporary ecologists to be another responsible factor [5-7]. Generally, species over time and space, respond differently to environmental changes and as well as biotic interactions [8]. Therefore, since biotic interactions among species simultaneously take place with the changes in the environment, species distribution study which focus on the joint effects of climate change and biotic interactions, may be in the right direction.
There are several empirical evidences which inspired this study to show that species distribution can jointly be shaped by biotic interactions and climate change. For instance, Connell [9] investigated interspecific competition between Balanus and Chthamalus species in rocky intertidal zone along Scottish coast. He observed vertical distribution between the two species due to competition where Chthamalus occupied the upper region but was limited from above by desiccation and Balanus occupied the immediate region below. In addition, Park et al. [10] conducted experimental studies which also show the importance of interaction between biotic factor and abiotic environments (e.g. temperature and humidity) can determine species distribution with the occurrence of priority effects. According to Gilman et al. [11] climate change effect on species can intensely be determined by species biotic interactions. Also, Meier et al. [12] stated that species interactions with each other can impact species response to changes in the environment and in a similar way, environmental changes can as well determine the trend of species interactions in a community. These observations may be due to the fact that factors that affect species interactions either directly or indirectly most often vary systematically across environmental gradients [13].

However, how biotic interactions combined with environmental factors to influence species distributions in their community remains not clear and need to be investigated further. For instance, Wisz et al. [2] reviewed examples where plant distributions are shaped by biotic interactions, agreed that we lack the data to estimate the relative significance of biotic and abiotic factors in plants. Nevertheless, the empirical limitations can be resolved through mathematical modelling approach. There are existing mathematical models which give better understanding of how biotic interactions can influence distributions of species [14-17]. In addition, Godsoe et al. [13] and Mohd et al. [18] investigated the combined effects of biotic interactions and abiotic environments on the range margins of species using modelling approach. However, few of these studies consider the asymmetrical interactions aspect of species competitions. For instance, the range margin predictions from the model assumptions of [13, 18] that interspecific competition is symmetric may require further investigations. They assumed equal competition strengths for all the species which is rarely true in nature. According to Roughgarden [19] asymmetrical models prediction differ from those of symmetrical models. In this regards, Mohd et al. [18] further suggested that the analysis of the range margins of species can be carried out with consideration for asymmetric competitions. The empirical research on snail species in two streams in the western United States to measure biotic interaction strengths between the snail species by [20] demonstrates that asymmetric interactions could be responsible for the patterns of dominance by one of the snails species. Also, Morin [21] reported that asymmetric strengths of each type of competitions can lead to different outcomes.

In this view, asymmetrical competition models may give competition outcomes different from that of symmetrical models. The question is, does asymmetrical competition model really give different predictions from symmetrical models? To gain insights into this question, we extend previous mathematical models of [13] and [18], which model biotic interactions and climate change with the assumption that biotic interactions among species are symmetrical. The purpose is to investigate additional competition outcomes that may arise from an asymmetrical model. We focus on competition between multiple species, example, four species. Thus, our model consists of four systems of ordinary differential equations, which represent asymmetric interspecific competitions among four species in a heterogeneous environment. To model abiotic components, we incorporate the suitability of the environments into the carrying capacities of each species. The inclusion therefore combined the effects of biotic interactions and abiotic factors (environmental gradients) on multispecies community dynamics.

This study is organised as follows. After this introduction is the model descriptions which combine biotic and abiotic factors. This is followed by analytical results on the range margins of species, simulation results and the bifurcation analysis. Based on our results, we discuss the ecological implications of the results.
2. Methodology

2.1. Species Competition Model

To predict the distribution of competing species across heterogeneous environments, we use mathematical model for the densities $N_i(x, t)$ of $n$ species. The model is an extension of Lotka-Voltera competition model [22, 23] extended along one dimensional environmental gradient $x$, where $0 \leq x \leq 1$ such that:

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

where $r_i$ is the intrinsic growth rate, $k_i(x)$ is the carrying capacity, $\alpha_{ij}$ is the strength of competition of species $j$ on species $i$, $a_i$ is the intraspecific coefficients and $N_i$ is the densities of species $i$ at time $t$. By rescaling the density of species $i$ relative to its competition coefficients $a_i$, we set $a_i$ to equal 1, such that competition coefficients, $\alpha_{ij}$ signify the ratio of interspecific to intraspecific competition.

The effect of environmental gradients on species competition outcomes is determined by $k_i(x)$ in the presence of biotic interactions. Thus, the maximum number of species that an environment can accommodate at a time, depends on the carrying capacity of the environment. In this case, $x$ is the varying parameter of $k_i(x)$ and it can represent the abiotic environmental features like climate, humidity, salinity and any other environmental factors that affect the species in a geographical location. In this study, our model is a reflection of laboratory research of [24, 25] such that $x$ strictly denote temperature. Therefore, the effects of biotic interactions on range margins of species may depend on how the species respond to environmental factors. To show these effects in the interactions of multispecies communities, the carrying capacity term (i.e $k_i(x)$) is modelled such that it varies linearly with $x$ as shown in (2):

$$k_i(x) = m_ix + b_i \quad (2)$$

Here $c_i$ is the intercept of species $i$ carrying capacity when $x = 0$, $m_i$ is the slope of species $i$ carrying capacity which is a measure of a change in the suitability of the environment with respect to abiotic component $x$ and $k_i(x)$ is as earlier defined. Since $x$ is a function of the carrying capacity $k_i(x)$ of species $i$, it’s therefore restricted by the abiotic environment; such that the distribution of the species $i$ in the absence of competition reaches its maximum at $x = 1$ for all positive $m_i$. Thus, for four competing species (i.e $n = 4$), equation (1) becomes:

$$\frac{dN_1}{dt} = \frac{r_1 N_1}{k_1} (k_1(x) - N_1 - \alpha_{12} N_2 - \alpha_{13} N_3 - \alpha_{14} N_4)
= a_1$$

$$\frac{dN_2}{dt} = \frac{r_2 N_2}{k_2} (k_2(x) - N_2 - \alpha_{21} N_1 - \alpha_{23} N_3 - \alpha_{24} N_4)
= a_2$$

$$\frac{dN_3}{dt} = \frac{r_3 N_3}{k_3} (k_3(x) - N_3 - \alpha_{31} N_1 - \alpha_{32} N_2 - \alpha_{34} N_4)
= a_3$$

$$\frac{dN_4}{dt} = \frac{r_4 N_4}{k_4} (k_4(x) - N_4 - \alpha_{41} N_1 - \alpha_{42} N_2 - \alpha_{43} N_3)
= a_4$$

In equation (3), the model represents the population dynamics of competing species such that $N_1, N_2, N_3$ and $N_4$ respectively represent species 1-4 densities. For model simplification, we will consider $a_{ij} = a_j$ in our analysis and so, $a_1, a_2, a_3$ and $a_4$ denote species 1-4 competition coefficients.

2.2. Steady states and stability analysis

To understand the dynamics of the system, we compute the steady states of equation (3) and then analyse the stability of the steady states. The steady states are computed by setting $\frac{dN_1}{dt}, \frac{dN_2}{dt}, \frac{dN_3}{dt}$ and $\frac{dN_4}{dt}$ to zeros and the stability of the steady states are performed with the aid of MAPLE package. Thus, only the relevant stable steady states will be discussed here. The stability status is obtained by analysing the nature of eigenvalues of the Jacobian matrices and since $k_i(x)$ are functions of $x$, the stability analysis of
the steady states depends on the location \( x \). Therefore, a steady state with all negative real parts of the eigenvalues is stable.

2.3 Numerical methods

Based on the steady states, we used the techniques of invasion analysis to derive analytical results on species’ range margins for model (3). Numerical simulation results on the range margins of the species are obtained by employing MATLAB ode15 solver for \( t = 1000 \) to solve model (3); i.e until steady states were achieved. The stability of the steady states is checked using MAPLE package. The numerical simulations were carried out separately for relatively weak \( (\alpha_{ij} < 1) \) and relatively strong \( (\alpha_{ij} > 1) \) interspecific competition cases. The parameters values used for our analyses are presented in Table 1. The numerical continuation package XPPAUT to compute bifurcation diagrams of model (3) and the stable and unstable steady states are tracked using AUTO as competition coefficient \( (\alpha_{ij}) \) changes. The bifurcation analyses illustrate occurrence of different threshold phenomena, which determine the outcomes of biotic interactions such as species coexistence and priority effects.

Table 1. Symbols with the descriptions and parameter values used for computation of figures.

| Symbol | Items description | Parameter value |
|--------|------------------|-----------------|
| \( r_i \) | 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 \( k_3 \) | -1 |
| \( m_4 \) | Gradient of \( k_4 \) | -0.8 |
| \( b_1 \) | 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 \( x = 0 \) | 1 |
| \( b_4 \) | Carrying capacity of species 4 at \( x = 0 \) | 0.8 |

3. Results

3.1 Analytical results on Range margins of species

In this section, we derive and present analytical results of the model (3) using the method of invasion analysis. The results are specifically based on illustration from figure 1A. The method of invasion analysis is such that a species can invade if the growth rate of the species is greater than zero (i.e \( \frac{dN_i}{dt} > 0 \)) [26]. Thus, boundary invasion of an invading species requires that \( \frac{dN_i}{dt} \) in (3) to be greater than zero for the species to invade. For instance, at the invasion point of species 1, only species 3 and 4 are present and so, species 1 can only invade if

\[
k_1(x) > \alpha_{33}N_3^* + \alpha_{44}N_4^*
\]

and the point \( x \) where \( k_1(x) = \alpha_{33}N_3^* + \alpha_{44}N_4^* \) satisfy the invasion point of species 1; which corresponds to \( N_3^* \) and \( N_4^* \) stabilities. Since species 1 and 2 are absent at the invasion point of species 1, their densities (i.e \( N_1 \) and \( N_2 \)) are taken to be zero at the invasion point of species 1. In this case, \( N_1 \) and \( N_2 \) are unstable at the species 1 invasion point. From our stability analysis results, the steady state
\[(0,0,N_3^*,N_4^*) = (0,0,\frac{\alpha_4 k_4 - k_3}{\alpha_4 \alpha_4 - 1}, \frac{\alpha_4 k_3 - k_2}{\alpha_4 \alpha_4 - 1}) \text{ where } k_3 = m_1 x + b_3, \ k_4 = m_4 x + b_4 \text{ and } k_1 = m_1 x; \text{ when substituted into equation (4) gives the invasion point of species 1 as}
\]
\[x_1 = \frac{(\alpha_3 \alpha_4 - \alpha_2) b_3 + (\alpha_3 \alpha_4 - \alpha_2) b_4}{(\alpha_2 \alpha_4 - 1)m_1 - (\alpha_2 \alpha_4 - \alpha_2)m_1 - (\alpha_2 \alpha_4 - \alpha_2)m_1} \]
\[(5)\]

In a similar way, species 2 invasion point corresponds to the presence of species 1, 3 and 4 in the simulation results such that species 2 can invade if
\[k_2(x) = (\alpha_1 N_1^* + \alpha_3 N_3^* + \alpha_4 N_4^*) \]
and the point where \[k_2(x) = (\alpha_1 N_1^* + \alpha_3 N_3^* + \alpha_4 N_4^*) \] satisfies the invasion point of species 2. In this case, the only stable steady state becomes
\[\left( \frac{-a_2 a_2^3 + a_2 a_2^3 - a_2 a_4^4 + a_2^4}{2 a_2 a_2^3 - a_2 a_2^3 - a_2 a_4^4 + 1}, \frac{-a_2 a_2^3 + a_2 a_2^3 - a_2 a_4^4 + a_2^4}{2 a_2 a_2^3 - a_2 a_2^3 - a_2 a_4^4 + 1}, \frac{-a_2 a_2^3 + a_2 a_2^3 - a_2 a_4^4 + a_2^4}{2 a_2 a_2^3 - a_2 a_2^3 - a_2 a_4^4 + 1}, \frac{-a_2 a_2^3 + a_2 a_2^3 - a_2 a_4^4 + a_2^4}{2 a_2 a_2^3 - a_2 a_2^3 - a_2 a_4^4 + 1} \right) \]
with \[k_3 = m_1 x + b_1, \ k_4 = m_4 x + b_4 \text{ and } k_2 = m_2 x \]. Thus, species 2 invasion point on substitution is given as
\[x_2 = \frac{(\alpha_2 a_4^4 - \alpha_2 a_4^4 - \alpha_2 a_4^4 + a_2^4 + a_2 m_1 + (\alpha_2 a_4^4 - \alpha_2 a_4^4 + a_2 m_1)}{(2 a_2 a_2^3 - a_2 a_2^3 - a_2 a_4^4 + 1)} \]
\[(7)\]

As we move towards the right along the environmental gradients \( x \) are the invasion points of species 4 and then species 3 which respectively correspond to the presence of species 2, 3 and 4 and then species 1 and 2. Thus, we can derive the invasion point of species 3 and 4 similar to that of species 1 and 2 to give
\[x_4 = \frac{(2 a_4 a_3^4 - a_4 a_3^4 - a_4 a_3^4 - a_4 a_3^4 + 1)b_3 - (\alpha_4 a_2 - \alpha_2 - \alpha_2 + 1\alpha_4 a_3)}{(a_3 a_4^4 - a_3 a_4^4 + 1)a_4 m_1 + (a_3 a_4^4 - a_3 a_4^4 + 1)a_4 m_2} \]
\[(8)\]
and
\[x_3 = \frac{(a_4 a_4 - 1)b_3}{(a_3 - 1)a_4 m_1 + (a_4 - 1)a_4 m_2} \]
\[(9)\]

All the invasion points stated above correspond to transcritical bifurcation points where each species exchange its stability from being unstable to become stable.

**Figure 1.** The steady states of equation (3) resulting from environmental gradients (2). In both figures, solid lines indicate steady states of species 1 and the dotted lines represent their carrying capacities (i.e \( k(x) \)). The invasion points \( (x) \) of the species are on the horizontal axis. Figures 1a and b represent asymmetric competition with \( \alpha_1 = 0.6, \alpha_2 = 0.62, \alpha_3 = 0.61, \alpha_4 = 0.63 \) and figure 1c represents symmetric competition with \( \alpha_1 = 0.63 \). Initial abundance used for the figures: \( N_1(x) = 0.1 k_1(x), N_2(x) = 0.9 k_2(x), N_3(x) = 0.1 k_3(x), N_4(x) = 0.9 k_4(x) \). Other parameters values used for the computation of these results are
given in table 1 except in figure 1b where species 2 carrying capacity is $k_2(x) = 2x - 0.8$ and MATLAB ode 15s solver is used to compute the results.

3.2 Range margins of species for relatively weak competitions (i.e $a_i < 1$)

Figure 1a and b shows the asymmetrical competition outcomes of four species for $a_i < 1$ as predicted by equation (3) and figure 1c is presented to illustrate symmetrical competition outcomes for comparison with asymmetrical results. Parameter values used to illustrate the dynamical outcomes of the competitions are listed in table 1 and in figure 1 caption. In figure 1a, the range margins of species 1 for example is at $x = 0.4068$ (blue circle); compared with figure 1c where the range margins of the species 1 is at $x = 0.412$ (blue circle). The range margins of the four species are on the $x$-axis for species 1 – 4; respectively labelled as blue, green, black and red circles. The numerical results of the range margins of the four species computed for only asymmetrical competition, correspond to the analytical results of the range margins $x_i$ stated in (5), (7), (8) and (9). As a result, the spatial domain of the species is divided into regions of two species, three species and four species coexistence. In figure 1a for instance, the regions of two species coexistence correspond to two domains. Thus, from the left, we have the region (i.e $x \leq x_1$) where species 3 and 4 coexist and displace species 1 and 2 to invasion points of 0.4068 and 0.4845 respectively. Also, from the right is the region (i.e $x \leq x_3$) where species 1 and 2 coexist and displace species 3 and 4 to extinction points of 0.5956 and 0.5161 respectively. These are followed by two regions (i.e $x_1 \leq x \leq x_2$ and $x_3 \leq x \leq x_4$) 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 and exclude only species 4. The last region is the middle domain (i.e $x_2 \leq x \leq x_4$), where all the four species coexist. These observations illustrate that for relatively weak competition, coexistence of two (2) or more species is possible. In this case, both the carrying capacity and competition strengths of the species combined to determine the dynamical competition outcomes of the species.

Similar observations are possible in the case of figure 1b, which is computed to illustrate the importance of environmental gradients in the species competition dynamics. In order to demonstrate this significance, only species 2 environmental gradient is altered from $k_2 = 0.8x$ to $2x - 0.8$; while other parameters remain the same with figure 1a. In this way, the community assemblies observed in figure 1a are not possible in figure 1b due slight change in the environmental gradient of species 2. As a result, the order of invasion points ($x_i$) of the species in figure 1b becomes $x_1$, $x_4$, $x_2$, and $x_3$; respectively labelled as blue, black, green and red circles. In this case, multispecies (i.e four species) coexistence is not possible which is quite different from our observations in figure 1a.

Also, figure 1c shows a similar qualitative result when compared with figure 1a. However, their range margins predictions differ. For example, species 1 invasion point in figure 1a is at $x = 0.4068$ which is shifted to $x = 0.412$ in figure 1c. As a result, species 3 is observed to occupy a region beyond species 4 carrying capacity (compare figure 1a and 1c).

**Figure 2.** The steady state of model (3) following environmental gradient (2). Solid lines indicate steady states of species $i$ and the dotted lines indicate their carrying capacities. Figure 2a and b represent relatively strong competitions with: $a_1 = 1.10, a_2 = 1.31, a_3 = 1.11, a_4 = 1.32$. Figure 2a initial abundance: $N_i(x) = 0.1k_i(x), N_2(x) = 0.9k_2(x), N_3(x) = 0.1k_3(x), N_4(x) = 0.9k_4(x)$ and 2b initial abundance: $N_i(x) = 0.08k_i(x), N_2(x) = 0.7k_2(x), N_3(x) = 0.1k_3(x), N_4(x) = 0.7k_4(x)$.
3.3 Range margins of species for relatively strong competitions (i.e \( \alpha_i > 1 \))

Figure 2a and b illustrate the model (3) predictions on four species competition outcomes for relatively strong competitions (i.e \( \alpha_i > 1 \)). Parameter values used to illustrate the dynamical outcomes of the competitions are outlined in table 1 and in figure 2 caption. For this case of strong competition, coexistence of species is impossible such that the dynamical behaviour of the model leads to exclusion of other competitors from a particular region with only dominant species occupying the region to its carrying capacity. In this situation, the outcomes of the competition depend on competition strength and initial abundance of the species [27]; where initially more abundant species have more potentials to dominate the competition.

Thus, figure 2a and b are respectively computed to illustrate the impacts of competition strength and initial abundance on competition outcomes. As a result of aggressive competitions among the four species, the spatial domain in the two figures are divided into four regions of single species each to its carrying capacity. Observe that in figure 1a, the regions of single species from the left correspond to the domain (black) where only species 4 is present and dominates species 1, 2 and 3. This is followed by the region (red) with only species 3 present. Also, to the right of this region is the species 1 dominant domain (blue) where it excludes other competitors. The last region on the right, is where species 2 dominates (green) the competition and exist as single species. Similarly, in figure 2b the spatial domain is also divided into regions of single species, but the width of the area occupied by each species either increases or decreases as initial abundance of the species is varied compared with figure 2a.

![Figure 3](image)

**Figure 3.** The bifurcation analysis of density steady state of species at a location \( x = 0.5 \) for equation (3) resulting from environmental gradients (2) with varied species 1 competition strength \( \alpha_1 \). Solid red lines represent stable steady states, dotted red line denote infeasible solution (i.e one of the densities of species is negative) and dotted black lines indicate unstable steady states. Figure 3a is computed using: \( \alpha_1 = 0.3-1.5, \alpha_2 = 0.62, \alpha_3 = 0.61, \alpha_4 = 0.63 \); while figure 3b is computed using: \( \alpha_1 = 0.3-1.5, \alpha_2 = 1.12, \alpha_3 = 1.11, \alpha_4 = 1.13 \) and other parameters values used for the computation of the results are given in table 1. The threshold values correspond to transcritical bifurcation points (i.e \( \alpha_{1A}, \alpha_{2A} \) and \( \alpha_{1B} \)) and XPPAUT is used to compute the results with the aid of AUTO.

3.4 Bifurcation analysis

We performed bifurcation analyses at a location \( x = 0.5 \) in order to further understand the diverse species that are present or absent at this location \( x \) as species 1 competition strength \( \alpha_1 \) changes. The bifurcation analysis, therefore, reveals the threshold value of species 1 competition strength \( \alpha_1 \). Thus, figure 3a and b is constructed to track the stable and unstable steady states of the species that are present or absent in model (3). Figure 3a is the model bifurcation outcomes of varying species 1 competition strength \( \alpha_1 \) while other species competition strengths are kept constant at relatively weak competitions (i.e below \( \alpha_i \).
edions and environmental factors on multispecies distribution is persistently a challenge in ecology. As a result, our model prediction revealed predictions of asymmetrical biotic interactions of multispecies differ quantitatively from that of symmetrical interactions. Such variation is attributed to dynamics of abundance and competition strength. Existence of single species to its’ carrying capacity whose area occupied can be determined both initial abundance and competition strength. We observe that figure 3a and figure 3b give different dynamics at the location $x = 0.5$. Thus, we have in figure 3a coexistence of the four species at relatively weak competition $a_1$ and exclusion of species as competition gets stronger; which lead to coexistence of only two species (i.e species 1 and 3) and then single-species (i.e species 1). In the case of figure 3b, we have existence of single-species (i.e species 3) and as competition becomes stronger, priority effects occur where two different single-species (i.e species 3 and species 1) exist at the same location $x$. Notice in figure 3a that coexistence of species is only possible at $a_i < 1$ and as competition strength becomes aggressive (i.e $a_i > 1$) all other competitors are excluded with only species 1 existing as single species to its’ carrying capacity. However, due to impacts of strong competitions from other species in figure 3b, coexistence of species is impossible at the location. Also, the threshold values (i.e $a_{1A}$, $a_{2A}$ and $a_{1B}$) in the figures corresponds to transcritical bifurcation points where one combination of species exchange its stability for another combination of species.

4. Discussion

We study the combined effects of biotic interactions and environmental factors on multispecies asymmetric competition outcomes in heterogeneous environments. Although, it is no longer a new idea that environmental factors such as climate change [5-7] and biotic interactions [2, 3, 28] can individually impacts species range margins, but their studies is still relevant in ecology. This is because, the extent to which the two factors relatively combined to determine species distribution (i.e the presence-absence) in a geographical location is persistently a challenge in ecology [2]. However, through mathematical modelling approach, we show that multispecies community assembly can be influenced by combined influence of biotic interactions and environmental factors. Our finding is robust because, it shows that both the two factors are significant in species distribution. As a result, our model prediction revealed coexistence of species at the central region of the geographical location than at the peripheral of the location where exclusion of species is observed even at relatively weak competition. This form of species distribution was also observed in the empirical study of small mammal species along elevational gradients. This is because, some species that are not favoured in an environment can easily be excluded in the presence of biotic interactions; such that multispecies coexistence is only possible where all the species are favoured by the environment.

When competition becomes aggressive, we observed that competition outcomes are determined by the initial abundance of the species and can be influenced by species competition strengths. This observation may add value to existing knowledge which claimed that initial abundance of the species is the sole determinant of competition outcomes during intense competition [13, 18]. It is possible that species competition strength to be the umpire of competition alongside with initial abundance depending on parametrization. In this case, only one species dominates the competition in a particular location and exist as a single species to its’ carrying capacity whose area occupied can be determined by both initial abundance and competition strength.

These observations are qualitatively consistent with symmetrical biotic interactions of multispecies dynamics [18]. However, the range margins predictions of asymmetrical biotic interactions of multispecies differ quantitatively from that of symmetrical interactions. Such variation is attributed to unequal interaction strengths with which the species interact with one another, which obviously, is not the case in symmetrical interactions.

Our work also revealed the importance of tracking the stable and unstable steady states of the model using bifurcation analysis. This is because, bifurcation analysis gives detailed theoretical explanation of the observed differences of species presence-absence in our numerical simulation results at a particular location $x$, while competition strength changes. Our bifurcation results revealed existence of threshold
values of competition strengths which lead to coexistence and priority effects. The threshold values correspond to transcritical bifurcations which are the points where one combination of species gradually exchange its’ stability for another one.

5. Conclusion
Environmental change may continue to impact on range margins of species community assembly. As a result, identifying that biotic interactions can mediate species responses to environmental effects is important in multispecies ecological dynamics. This has been achieved through our theoretical models which is used to study the combined effects of biotic interactions with the environmental factors. Consequently, our result shows that the combined influence of biotic and abiotic factors can lead to coexistence of species when competition strengths are relatively weak. However, in the presence of relatively aggressive competition, mediated by the initial abundance of the species, coexistence is impossible; such that only dominant single species occupying a particular region to it carrying capacity. The challenge for researchers in this direction, is to extend this model for accurate predictions and forecasts of future species distributions under climate change. Efforts in this direction, requires appropriate model assumptions and parameterization.

6. References
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