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Dynamic Behaviors of a Two-Species Lotka-Volterra Competition Model with Wind-Dependent Refuge

Guangwen He, Zuzhi Cai and Fengde Chen

***Abstract*—This study investigates the dynamics of a two-species competition model incorporating wind-dependent refuge. Unlike traditional models where refuge are treated as fixed parameters, we propose a wind-speed-dependent refuge parameter $u(w) = u_{\max} e^{-kw}$, which decays exponentially with increasing wind velocity, better reflecting natural ecological dynamics. Through equilibrium analysis and stability evaluation, we demonstrate that heightened wind speeds reduce refuge effectiveness, critically influencing species coexistence. Theoretical results reveal that when $r_1K_1 > \alpha_{12}(1 - u(w))K_2$ and $r_2K_2 > \alpha_{21}(1 - u(w))K_1$, the system admits a unique stable positive equilibrium enabling species coexistence; otherwise, extinction of one species becomes probable. Numerical simulations corroborate that increased wind intensity alters competitive outcomes by impairing refuge functionality. The work provides theoretical support for wind-disturbed ecosystem conservation (e.g., establishing windbreaks) and elucidates complex interactions between environmental factors and species competition, extending classical Lotka-Volterra framework to wind-affected scenarios.**

***Index Terms*—Competition model, refuge, wind speed, stability analysis, numerical simulation**

I. INTRODUCTION

The dynamics of species competition have long been a central focus in ecological research, as they play a crucial role in shaping community structure, biodiversity, and ecosystem stability. The Lotka-Volterra competition model, a cornerstone of theoretical ecology, provides a foundational framework for understanding how two species interact through competition for shared resources [1], [2]. However, natural systems are often influenced by a multitude of environmental factors that can modulate these interactions. Among these factors, the availability of refuges—spatial or temporal refuge that reduce the intensity of competition or predation—has been increasingly recognized as a critical determinant of species coexistence and population dynamics [3], [4].

Refuges can significantly alter competitive outcomes by providing a subset of individuals with protection from interspecific competition. For example, in plant communities, dense vegetation can serve as a refuge for understory species, shielding them from competition with dominant canopy species [5]. Similarly, in animal communities, physical structures such as rock crevices or burrows can offer protection from predators or competitors [6]. Despite their ecological importance, the role of refuges in competition models has often been oversimplified, with most studies assuming static refuge availability [7]. In reality, refuge availability is dynamic and can be influenced by environmental factors such as wind, rainfall, and temperature [8], [9].

Wind, in particular, is a pervasive environmental force that can dramatically alter habitat structure and refuge availability. Strong winds can damage vegetation, uproot trees, or reshape physical landscapes, thereby reducing the availability of refuges [10]. Conversely, wind-driven disturbances can also create new refuges, such as fallen logs or debris piles, which may provide temporary refuge for certain species [11]. The dynamic interplay between wind and refuge availability introduces a layer of complexity to species interactions that has yet to be fully explored in theoretical models [12].

In this study, we extend the classical Lotka-Volterra competition model to incorporate the effects of wind-driven changes in refuge availability. Specifically, we consider a system where one species has access to refuges, while the other does not. The proportion of individuals in the refuge-using species that occupy refuges is modeled as a function of wind speed, reflecting the dynamic nature of refuge availability. This approach allows us to investigate how wind-mediated changes in refuge availability influence competitive outcomes, species coexistence, and population dynamics.

Our model contributes to the growing body of literature on the role of environmental variability in ecological interactions [13], [14]. By integrating wind effects into a competition framework, we provide a more realistic representation of natural systems, where environmental factors and species interactions are inextricably linked. Furthermore, our findings have implications for conservation and management, particularly in habitats prone to wind disturbances, such as coastal ecosystems, forests, and grasslands [15]. Understanding how wind influences refuge availability and species competition can inform strategies for preserving biodiversity and mitigating the impacts of environmental change. For more works on competition model, one could refer to [16]-[42] and the references cited therein.

In the following sections, we present the mathematical formulation of our model, analyze its dynamics, and discuss the ecological implications of our findings. We begin by reviewing the classical Lotka-Volterra competition model and its limitations, then introduce our modifications to incorporate wind-dependent refuge availability. We conclude with a discussion of potential extensions and applications of our

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model in ecological research and management.

II. MODEL FORMULATION

To develop a mathematical model that incorporates the effects of wind on refuge availability and species competition, we make the following assumptions:

1) **Two-species system**: We consider a system of two competing species, denoted as Population 1 (N_1) and Population 2 (N_2). Population 1 has access to refuges, while Population 2 does not. This assumption reflects scenarios where one species can utilize physical structures (e.g., burrows, dense vegetation) for protection, while the other cannot [6].
2) **Refuge use**: A proportion u of Population 1 occupies refuges, where they are protected from competition with Population 2. The remaining proportion $1-u$ of Population 1 competes directly with Population 2. This assumption captures the idea that refuges provide partial protection from competition, as observed in many plant and animal communities [5].
3) **Wind-dependent refuge availability**: The proportion u of Population 1 using refuges is influenced by wind speed w. Specifically, we assume that higher wind speeds reduce refuge availability, leading to a decrease in u. This relationship is modeled as:

$$u(w) = u_{\max} \cdot e^{-kw},$$

where $u_{\max}$ is the maximum refuge proportion (when $w = 0$), and k is a positive constant representing the sensitivity of refuge availability to wind speed. This exponential decay function is chosen to reflect the rapid decline in refuge availability under strong winds, as observed in ecosystems prone to wind disturbances [10].
4) **Population growth**: Both populations grow logistically in the absence of competition, with intrinsic growth rates r_1 and r_2, and carrying capacities K_1 and K_2, respectively. This assumption is consistent with the classical Lotka-Volterra framework and reflects the self-limiting nature of population growth in resource-limited environments [1].
5) **competition**: Competition occurs only between the non-refuge portion of Population 1 ($(1-u(w))N_1$) and Population 2. The competition coefficients α_{12} and α_{21} describe the per capita effect of Population 2 on Population 1 and vice versa, respectively. This assumption reflects the idea that only individuals outside refuges are exposed to direct competition [4].

B. Model equations

Based on the above assumptions, we derive the following system of differential equations to describe the dynamics of the two populations:

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - \frac{\alpha_{12}(1-u(w))}{K_1} N_1 N_2, \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - \frac{\alpha_{21}(1-u(w))}{K_2} N_2 N_1. \end{aligned} \tag{1}$$

Here:

- N_1 and N_2 represent the population densities of Species 1 and Species 2, respectively.
- r_1 and r_2 are the intrinsic growth rates of Species 1 and Species 2, reflecting their ability to reproduce and grow under ideal conditions.
- K_1 and K_2 are the carrying capacities of Species 1 and Species 2, representing the maximum population sizes that the environment can sustain in the absence of competition.
- α_{12} is the competition coefficient describing the per capita effect of Species 2 on Species 1.
- α_{21} is the competition coefficient describing the per capita effect of Species 1 on Species 2.
- $u(w) = u_{\max} \cdot e^{-kw}$ is the wind-dependent refuge proportion, where:
  - $u_{\max}$ is the maximum proportion of Population 1 that can occupy refuges when wind speed $w = 0$.
  - k is a positive constant that determines how rapidly refuge availability decreases with increasing wind speed.

The conceptual framework of our modeling methodology is illustrated in Figure 1.

To demonstrate the impact of wind speed on shelters and consequently on competition coefficients, we present the following numerical example:

Let $u_{\max} = 0.8$, $k = 0.1$, $\alpha_{12} = 0.3$, and $\alpha_{21} = 0.5$.

Figure 2 shows the plots of $u(w)$, $\alpha_{12}^{\text{eff}} = \alpha_{12}(1 - u(w))$, and $\alpha_{21}^{\text{eff}} = \alpha_{21}(1 - u(w))$ as functions of wind speed ω.

From the figure, we can observe that as wind speed ω increases, $u(\omega)$ gradually approaches 0, and the competition coefficients of both populations continuously increase. This indicates intensifying competition between the two populations, which eventually stabilizes.

C. Ecological interpretation of parameters

Each parameter in the model has a specific ecological interpretation, as summarized below:

- **Intrinsic growth rates** (r_1 **and** r_2): These parameters represent the maximum per capita growth rates of Species 1 and Species 2 under ideal conditions (no competition, unlimited resources). Higher values indicate faster population growth, as observed in species with high reproductive potential [13].
- **Carrying capacities** (K_1 **and** K_2): These parameters represent the maximum population sizes that the environment can sustain for each species in the absence of competition. They are influenced by resource availability and environmental conditions, such as nutrient levels in plant communities or habitat size in animal populations [7].
- **Competition coefficients** (α_{12} **and** α_{21}): These parameters quantify the competitive effects between the two species:
  - α_{12} measures the impact of Species 2 on Species 1. A higher value indicates stronger competition from Species 2, as seen in systems where one species dominates resources.
- **Competition coefficients** (α_{12} **and** α_{21})::
  - α_{21} measures the impact of Species 1 on Species 2. A higher value indicates stronger competition

  from Species 1, as observed in systems where one species is more aggressive or efficient in resource use [4].
- **Refuge proportion** ($u(w)$): This function describes the proportion of Population 1 that occupies refuges and is protected from competition with Population 2. It depends on wind speed w:
  - $u_{\max}$ is the maximum refuge proportion when wind speed is zero, representing the ideal refuge availability in calm conditions.
  - k determines how quickly refuge availability decreases as wind speed increases. A higher k indicates greater sensitivity of refuge availability to wind, as observed in ecosystems where wind disturbances are frequent and severe [10].
- **Wind speed** (w): This variable represents the external environmental factor (wind) that dynamically affects refuge availability. It can be modeled as a constant, a time-varying function, or a stochastic process, depending on the ecological context [12].

D. Discussion of model assumptions

The assumptions underlying our model are designed to capture the dynamic interplay between wind and refuge availability in a two-species competitive system. However, it is important to acknowledge the potential limitations of these assumptions:

- **Refuge use**: We assume that only a proportion of Population 1 uses refuges, while Population 2 does not. In reality, both species may have access to refuges, albeit to different extents. Future extensions of the model could explore scenarios where both species utilize refuges, with varying degrees of protection.
- **Wind-dependent refuge availability**: The exponential decay function $u(w) = u_{\max} \cdot e^{-kw}$ is a simplification of the complex relationship between wind and refuge availability. In some ecosystems, wind may have nonlinear effects on refuge availability, or it may create new refuges (e.g., fallen logs) that temporarily increase refuge availability [11]. Future studies could incorporate more complex functional forms to better capture these dynamics.
- **Competition**: We assume that competition occurs only between the non-refuge portion of Population 1 and Population 2. In reality, individuals within refuges may still experience indirect competition (e.g., for shared resources). Future models could incorporate indirect competitive effects to provide a more comprehensive understanding of species interactions.

Despite these limitations, our model provides a valuable framework for exploring the effects of wind-driven changes in refuge availability on species competition and coexistence. By integrating environmental variability into a classical competition framework, we offer a more realistic representation of natural systems, where species interactions are shaped by both biotic and abiotic factors.

III. EXISTENCE OF EQUILIBRIUM POINTS

The equilibrium points are the steady-state solutions of the system, satisfying $\frac{dN_1}{dt} = 0$ and $\frac{dN_2}{dt} = 0$.

Theorem 3.1 *System (1) admits three boundary equilibrium points* $E_0(0,0), E_1(K_1,0), E_2(0,K_2)$*, also, if one of the following conditions are satisfied:*
(1)

$$\begin{array}{rcl} r_1K_1 & > & \alpha_{12}(1-u(w))K_2, \\ r_2K_2 & > & \alpha_{21}(1-u(w))K_1; \end{array} \tag{2}$$

(2)

$$\begin{array}{rcl} r_1K_1 & < & \alpha_{12}(1-u(w))K_2, \\ r_2K_2 & < & \alpha_{21}(1-u(w))K_1; \end{array} \tag{3}$$

then system admits a unique positive equilibrium $E^*(N_1^*, N_2^*)$*, where*

$$\begin{array}{rcl} N_1^* & = & \dfrac{r_2r_1K_1 - r_2\alpha_{12}(1-u(w))K_2}{r_2r_1 - \alpha_{21}\alpha_{12}(1-u(w))^2}. \\ N_2^* & = & \dfrac{r_1r_2K_2 - r_1\alpha_{21}(1-u(w))K_1}{r_2r_1 - \alpha_{21}\alpha_{12}(1-u(w))^2}. \end{array} \tag{4}$$

Proof. We solve the following system of equations:

$$\begin{cases} r_1N_1\left(1-\frac{N_1}{K_1}\right) - \dfrac{\alpha_{12}(1-u(w))}{K_1}N_1N_2 = 0, \\ r_2N_2\left(1-\frac{N_2}{K_2}\right) - \dfrac{\alpha_{21}(1-u(w))}{K_2}N_1N_1 = 0. \end{cases}$$

It is easy to obtain three boundary equilibrium points $E_0(0,0), E_1(K_1,0), E_2(0,K_2)$. For the positive equilibrium (N_1^*, N_2^*), where N_1^* and N_2^* satisfy the following equations:

$$\begin{array}{l} r_1\left(1-\frac{N_1^*}{K_1}\right) - \dfrac{\alpha_{12}(1-u(w))}{K_1}N_2^* = 0, \\ r_2\left(1-\frac{N_2^*}{K_2}\right) - \dfrac{\alpha_{21}(1-u(w))}{K_2}N_1^* = 0. \end{array} \tag{5}$$

Solving this equation, one could finally obtain (2). This ends the proof of Theorem 3.1.

IV. LOCAL STABILITY ANALYSIS OF EQUILIBRIUM POINTS

In this section, we analyze the local stability of equilibrium points of the model.

Theorem 4.1. $E_0(0,0)$ *is unstable;*
Assume that

$$r_2 < \frac{\alpha_{21}(1-u(w))K_1}{K_2}, \tag{6}$$

then E_1 *is locally stable (a sink), and if*

$$r_2 > \frac{\alpha_{21}(1-u(w))K_1}{K_2}, \tag{7}$$

then E_1 *is a saddle point (unstable);*
Assume that

$$r_1 < \frac{\alpha_{12}(1-u(w))K_2}{K_1}, \tag{8}$$

then E_2 *is locally stable (a sink), and if*

$$r_1 > \frac{\alpha_{12}(1-u(w))K_2}{K_1}, \tag{9}$$

then E_2 *is a saddle point (unstable);*
Assume that (2) holds, then $E^*(N_1^*, N_2^*)$ *is locally stable, and if (3) holds, then* $E^*(N_1^*, N_2^*)$ *is unstable.*

Proof. To analyze the local stability of the equilibrium points, we compute the Jacobian matrix J:

$$J = \begin{pmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{pmatrix},$$

where f_1 and f_2 are the right-hand sides of the differential equations for $\frac{dN_1}{dt}$ and $\frac{dN_2}{dt}$ in (1), respectively. The elements of the Jacobian matrix are:

$$\begin{array}{rcl} \frac{\partial f_1}{\partial N_1} & = & r_1\left(1-\frac{2N_1}{K_1}\right)-\frac{\alpha_{12}(1-u(w))}{K_1}N_2, \\ \frac{\partial f_1}{\partial N_2} & = & -\frac{\alpha_{12}(1-u(w))}{K_1}N_1, \\ \frac{\partial f_2}{\partial N_1} & = & -\frac{\alpha_{21}(1-u(w))}{K_2}N_2, \\ \frac{\partial f_2}{\partial N_2} & = & r_2\left(1-\frac{2N_2}{K_2}\right)-\frac{\alpha_{21}(1-u(w))}{K_2}N_1. \end{array} \tag{10}$$

We compute the Jacobian matrix at each equilibrium point and analyze its eigenvalues. At $E_0(0,0)$, the Jacobian matrix is:

$$J(E_0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = r_1$ and $\lambda_2 = r_2$. Since both r_1 and r_2 are positive, E_0 is an unstable equilibrium point (a source).

At $E_1(K_1, 0)$, the Jacobian matrix is:

$$J(E_1) = \begin{pmatrix} -r_1 & -\alpha_{12}(1-u(w)) \\ 0 & r_2-\frac{\alpha_{21}(1-u(w))K_1}{K_2} \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = -r_1$ and $\lambda_2 = r_2 - \frac{\alpha_{21}(1-u(w))K_1}{K_2}$.

- If $r_2 < \frac{\alpha_{21}(1-u(w))K_1}{K_2}$, then $\lambda_2 < 0$, and E_1 is locally stable (a sink).
- If $r_2 > \frac{\alpha_{21}(1-u(w))K_1}{K_2}$, then $\lambda_2 > 0$, and E_1 is a saddle point (unstable).

At $E_2(0, K_2)$, the Jacobian matrix is:

$$J(E_2) = \begin{pmatrix} r_1-\frac{\alpha_{12}(1-u(w))K_2}{K_1} & 0 \\ -\alpha_{21}(1-u(w)) & -r_2 \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = r_1 - \frac{\alpha_{12}(1-u(w))K_2}{K_1}$ and $\lambda_2 = -r_2$.

- If $r_1 < \frac{\alpha_{12}(1-u(w))K_2}{K_1}$, then $\lambda_1 < 0$, and E_2 is locally stable (a sink).
- If $r_1 > \frac{\alpha_{12}(1-u(w))K_2}{K_1}$, then $\lambda_1 > 0$, and E_2 is a saddle point (unstable).

At the positive equilibrium point $E^*(N_1^*, N_2^*)$, the Jacobian matrix is: The Jacobian matrix at the positive equilibrium point $E^*(N_1^*, N_2^*)$ is given by:

$$J(E^*) = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix},$$

where:

$$\begin{array}{rcl} A_{11} & = & r_1\left(1-\frac{2N_1^*}{K_1}\right)-\frac{\alpha_{12}(1-u(w))}{K_1}N_2^*, \\ A_{12} & = & -\frac{\alpha_{12}(1-u(w))}{K_1}N_1^*, \\ A_{21} & = & -\frac{\alpha_{21}(1-u(w))}{K_2}N_2^*, \\ A_{22} & = & r_2\left(1-\frac{2N_2^*}{K_2}\right)-\frac{\alpha_{21}(1-u(w))}{K_2}N_1^*. \end{array} \tag{11}$$

Noting that N_1^*, N_2^* satisfy the equation (3), we can simplify A_{11} and A_{22}:

$$A_{11} = r_1\left(1-\frac{2N_1^*}{K_1}\right) - r_1\left(1-\frac{N_1^*}{K_1}\right) = -\frac{r_1N_1^*}{K_1}.$$

$$A_{22} = r_2\left(1-\frac{2N_2^*}{K_2}\right) - r_2\left(1-\frac{N_2^*}{K_2}\right) = -\frac{r_2N_2^*}{K_2}.$$

Thus, the Jacobian matrix at E^* simplifies to:

$$J(E^*) = \begin{pmatrix} -\frac{r_1N_1^*}{K_1} & -\frac{\alpha_{12}(1-u(w))}{K_1}N_1^* \\ -\frac{\alpha_{21}(1-u(w))}{K_2}N_2^* & -\frac{r_2N_2^*}{K_2} \end{pmatrix}.$$

To analyze the local stability of E^*, we compute the trace (Tr) and determinant (Det) of the Jacobian matrix:

$$\begin{array}{rcl} \mathrm{Tr}(J(E^*)) & = & A_{11}+A_{22} \\ & = & -\frac{r_1N_1^*}{K_1}-\frac{r_2N_2^*}{K_2}, \\ \mathrm{Det}(J(E^*)) & = & A_{11}A_{22}-A_{12}A_{21} \\ & = & \frac{N_1^*N_2^*}{K_1K_2}\left(r_1r_2-\alpha_{12}\alpha_{21}(1-u(w))^2\right). \end{array} \tag{12}$$

According to the Routh-Hurwitz stability criterion, the positive equilibrium point E^* is locally stable if and only if:

$\mathrm{Tr}(J(E^*)) < 0$, $\mathrm{Det}(J(E^*)) > 0$.

Since $N_1^* > 0$, $N_2^* > 0$, $r_1 > 0$, $r_2 > 0$, $K_1 > 0$, and $K_2 > 0$, the trace is always negative:

$$\mathrm{Tr}(J(E^*)) = -\frac{r_1N_1^*}{K_1} - \frac{r_2N_2^*}{K_2} < 0.$$

Thus, the trace condition is always satisfied.

The determinant is positive if:

$$r_1r_2 > \alpha_{12}\alpha_{21}(1-u(w))^2. \tag{13}$$

Noting that if (2) holds, then one could easily verify that (13) holds, hence, (2) is enough to ensure the local stability of the positive equilibrium. However, if (3) holds, then

$$r_1r_2 < \alpha_{12}\alpha_{21}(1-u(w))^2. \tag{14}$$

Consequently, the positive equilibrium point $E^*(N_1^*, N_2^*)$ is unstable.

This ends the proof of Theorem 4.1.

Remark 4.1. Condition (13) shows that the stability of the positive equilibrium depends on the product of the intrinsic growth rates r_1 and r_2, the competition coefficients α_{12} and α_{21}, and the wind-dependent refuge proportion $u(w)$.

(1) Effect of wind speed: As wind speed w increases, the refuge proportion $u(w) = u_{\max}e^{-kw}$ decreases, leading to an increase in $(1-u(w))^2$. This makes the stability condition $r_1r_2 > \alpha_{12}\alpha_{21}(1-u(w))^2$ harder to satisfy, reducing the stability of the positive equilibrium;

(2) Intrinsic growth rates: Higher intrinsic growth rates r_1 and r_2 promote stability by making the stability condition easier to satisfy;

(3) Competition intensity: Lower competition coefficients α_{12} and α_{21} also promote stability by reducing the competitive pressure between the two species.

V. GLOBAL STABILITY ANALYSIS OF EQUILIBRIUM POINTS

In this section, we investigate the global stability of the equilibrium points. Global stability implies that the solutions of the system converge to a specific equilibrium point regardless of the initial conditions. We analyze the global stability using the Dulac criterion.

Theorem 5.1. *System (1) is uniformly bounded, and the system does not have limit cycles.*
Proof.

Firstly we proof that every solution of system (1) that starts in R_+^2 is uniformly bounded. From system (1) one has

$$\frac{dN_i}{dt} \le r_i N_i \left(1 - \frac{N_i}{K_i}\right) \tag{15}$$

By using the differential inequality, we obtain

$$\limsup_{t \to +\infty} N_i(t) \le K_i. \tag{16}$$

From (16), there exists a $\varepsilon > 0$ such that for all $t > T$

$$N_i(t) < K_i + \varepsilon. \tag{17}$$

Let $B = \{(x,y)| \in R_+^2 : N_i < K_i + \varepsilon,\ i = 1,2.\}$. Then every solution of system (1) starts in R_+^2 is uniformly bounded on B.

The Dulac criterion states that if there exists a continuously differentiable function $B(x,y)$ in a region D such that:

$$\frac{\partial (BP)}{\partial x} + \frac{\partial (BQ)}{\partial y} < 0,$$

where

$$P(N_1, N_2) = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - \frac{\alpha_{12}(1 - u(w))}{K_1} N_1 N_2,$$

$$Q(N_1, N_2) = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - \frac{\alpha_{21}(1 - u(w))}{K_2} N_2 N_1.$$

then the system has no periodic solutions in D, and all trajectories converge to an equilibrium point. We choose the Dulac function as $B(N_1, N_2) = \frac{1}{N_1 N_2}$. Then

$$\begin{aligned} & \tfrac{\partial (BP)}{\partial N_1} + \tfrac{\partial (BQ)}{\partial N_2} \\ = \quad & \tfrac{\partial}{\partial N_1}\left(\tfrac{r_1}{N_2}\left(1 - \tfrac{N_1}{K_1}\right) - \tfrac{\alpha_{12}(1-u(w))}{K_1}\right) \\ & + \tfrac{\partial}{\partial N_2}\left(\tfrac{r_2}{N_1}\left(1 - \tfrac{N_2}{K_2}\right) - \tfrac{\alpha_{21}(1-u(w))}{K_2}\right) \\ = \quad & -\tfrac{r_1}{K_1 N_2} - \tfrac{r_2}{K_2 N_1} < 0. \end{aligned} \tag{18}$$

According to Dulac's Criterion, since we have found a function $B(N_1, N_2) = \frac{1}{N_1 N_2}$ such that in the first quadrant of the system:

$$\frac{\partial (BP)}{\partial N_1} + \frac{\partial (BQ)}{\partial N_2} < 0,$$

the system does not have limit cycles in the first quadrant. The proof of Theorem 5.1 is ended.

Remark 5.1. Ecological Implications of Theorem 5.1: This result indicates that the system's dynamic behavior will not exhibit periodic oscillations (i.e., limit cycles) but will instead tend toward an equilibrium point.

Theorem 5.2. *Assume that*

$$r_2 < \frac{\alpha_{21}(1 - u(w))K_1}{K_2}, \tag{19}$$

and

$$r_1 > \frac{\alpha_{12}(1 - u(w))K_2}{K_1}, \tag{20}$$

holds, then E_1 is globally stable.

Proof. Nothing that in this case, from Theorem 3.1 and 4.1 we know that system admits only three equilibrium, $E_0(0,0)$, $E_2(0,K_2)$, those two equilibria are unstable. $E_1(K_1,0)$, which is locally stable, since the system admits no limit cycles, all the solutions will approach to $E_1(K_1,0)$ as $t \to +\infty$. Hence, E_1 is globally stable. The proof of Theorem 5.2 is finished.

Remark 5.2. Ecological interpretations of Theorem 5.2.

1. Wind-dependent refuge collapse

- **Exponential decay of protection:** Refuge efficacy follows
$$\frac{du}{dw} = -k u_{\max} e^{-kw} < 0$$
implying intensified interspecific competition under high wind speeds.
- **Critical thresholds:** Species 2 goes extinct when its growth rate r_2 cannot compensate for:
$$\underbrace{\alpha_{21}}_{\text{Competition}} \cdot \underbrace{(1 - u(w))}_{\text{Exposure}} \cdot \underbrace{\frac{K_1}{K_2}}_{\text{Capacity ratio}}$$

2. Asymmetric competition dynamics

- Species 1 dominates through:
$$\frac{r_1}{r_2} > \frac{\alpha_{12} K_2}{\alpha_{21} K_1} \cdot (1 - u(w))^2$$
establishing an irreversible competitive hierarchy.
- Paradoxically, higher K_2 may accelerate species 2's exclusion by enhancing resource exploitation by species 1.

2. Management implications and conservation strategies

- **Endangered species protection:** If Species 2 is endangered, implement measures (e.g., windbreaks, vegetation restoration) to reduce wind speed w, thereby increasing refuge availability u(w) and alleviating competitive exclusion.
- **Invasive species control:** If Species 1 is invasive, disrupt its growth rate r_1 (e.g., via natural predator introduction) or enhance its competitive coefficient α_{12} (e.g., through competitive intercropping), thereby violating the theorem's conditions to promote coexistence.
- **Habitat design:** In ecological restoration, optimize the K_1/K_2 ratio (e.g., via zoned resource management) to prevent monopolization of habitats by a single species.

Theorem 5.2 establishes that wind regimes (w) modulate competitive exclusion through refuge dynamics ($u(w)$). The critical thresholds in Eqs. (19)-(20) provide quantitative criteria for predicting regime shifts in disturbed ecosystems.

Theorem 5.3. *Assume that*

$$r_2 > \frac{\alpha_{21}(1-u(w))K_1}{K_2}, \tag{21}$$

and

$$r_1 < \frac{\alpha_{12}(1-u(w))K_2}{K_1}, \tag{22}$$

then E_2 is globally stable.

The proof of Theorem 5.3 is similar to that of Theorem 5.2, and we omit the detail here.

Remark 5.3. Ecological interpretations of Theorem 5.3.

1. Critical Transition Conditions

- **Superior regeneration capacity:**

$$r_2 > \underbrace{\alpha_{21}}_{\text{Competition}} \cdot \underbrace{(1-u(w))}_{\text{Exposure}} \cdot \underbrace{\frac{K_1}{K_2}}_{\text{Capacity asymmetry}}$$

Species 2 overcomes competitive suppression through:

  - High intrinsic growth rate (r_2).
  - Efficient resource exploitation (α_{21}).

- **Competitive vulnerability:**

$$r_1 < \alpha_{12}(1-u(w))\frac{K_2}{K_1}$$

Species 1 fails to counterbalance:

  - Amplified competition from exposed populations $(1-u(w))$.
  - Resource pre-emption by species 2 (K_2/K_1).

2. Exponential decay of refuge efficacy The wind-dependent refuge availability follows:

$$u(w) = u_{\max} e^{-k_{\mathrm{w}} w} \tag{23}$$

where:

- $u_{\max}$: Maximum possible refuge proportion (wind-free scenario);
- k_{w}: Wind attenuation coefficient (habitat-specific);
- w: Wind speed (m/s).

This exponential relationship causes:

- **Accelerated exposure of competitors:** The exposed population proportion $1-u(w)$ increases nonlinearly with wind speed:

$$\frac{d}{dw}[1-u(w)] = k_{\mathrm{w}} u_{\max} e^{-k_{\mathrm{w}} w} > 0. \tag{24}$$

- **Geometric amplification of competition:** Effective competition coefficients become:

$$\alpha_{12}^{\mathrm{eff}} = \alpha_{12}(1-u(w)) \tag{25}$$

$$\alpha_{21}^{\mathrm{eff}} = \alpha_{21}(1-u(w)) \tag{26}$$

leading to quadratic intensification of interspecific competition.

A. Critical Wind Speed Threshold

There exists a critical threshold w_c satisfying:

$$w > w_c \Rightarrow u(w) < 1 - \frac{r_1 K_1}{\alpha_{12} K_2} \tag{27}$$

This threshold behavior explains that with the increasing of wind effect, the refuge is ruined, and finally leads to the extinction of the first species.

Theorem 5.3 establishes wind speed (w) as a regime shift trigger through:

- Refuge efficacy collapse ($u(w)$)
- Competitive coefficient amplification ($\alpha_{ij}(1-u(w))$)
- Critical threshold behavior (w_c)

These mechanisms enable predictive management of wind-sensitive ecosystems.

Theorem 5.4. *Assume that*

$$\begin{aligned} r_1 K_1 &> \alpha_{12}(1-u(w))K_2, \\ r_2 K_2 &> \alpha_{21}(1-u(w))K_1, \end{aligned} \tag{28}$$

then $E^*(N_1^*, N_2^*)$ is globally stable.

Proof. Note that in this case, system (1) admits four equilibria, $E_0(0,0)$, $E_1(K_1,0)$, $E_2(0,K_2)$ and $E^*(N_1^*, N_2^*)$. From Theorem 4.1 we know that E_0, E_1, E_2 are all unstable, and only E^* is locally stable, since the system admits no limit cycles, all the solutions will approach to $E^*(N_1^*, N_2^*)$ as $t \to +\infty$. Hence, E_1 is globally stable. The proof of Theorem 5.4 is finished.

Remark 5.4. Ecological interpretations of Theorem 5.4.

1. Resource-conditioned coexistence

- **Effective resource utilization:** The product $r_i K_i$ integrates:

$$\begin{aligned} &\underbrace{r_i}_{\text{Growth potential}} \times \underbrace{K_i}_{\text{Carrying capacity}} \\ = \; &\text{Total resource exploitation capacity.} \end{aligned}$$

- **Competition pressure threshold:** The RHS terms represent:

$$\underbrace{\alpha_{ij}}_{\text{Competition}} \times \underbrace{(1-u(w))}_{\text{Exposure}} \times \underbrace{K_j}_{\text{Opponent's resources}}$$

2. Monitoring framework

- Calculate wind vulnerability index:

$$V_i = \frac{\alpha_{ji} K_j}{r_i K_i} \times (1-u(w)).$$

Coexistence requires $V_1 < 1$ and $V_2 < 1$.

- Establish early-warning thresholds:

$$w_{\text{alert}} = -\frac{1}{k} \ln\left(\frac{1}{u_{\max}}\left(1 - \frac{r_i K_i}{\alpha_{ij} K_j}\right)\right).$$

Theorem 5.4 reveals that wind disturbances (w) modulate species coexistence through:

- Nonlinear refuge decay ($du/dw = -ku$);
- Competition intensity amplification ($\alpha_{ij}^{\mathrm{eff}} = \alpha_{ij}(1-u(w))$);

- Resource-dependent stability criteria (28).

This provides a quantitative framework for climate-resilient ecosystem management.

VI. NUMERIC SIMULATIONS

In this section, numerical simulations are carried out to verify the feasibility of the results we have obtained.

Example 6.1.

Set the following parameters:

$$\begin{aligned} &r_1 = 1.0; K_1 = 100; \alpha_{12} = 0.3;\\ &r_2 = 0.5; K_2 = 40; \alpha_{21} = 0.5; \end{aligned} \tag{29}$$

(1) Assume that the system has no refuge, i.e., $u_{max} = 0$, in this case, since

$$\alpha_{12} = 0.3 < \frac{K_1}{K_2} = \frac{5}{3}, \alpha_{21} = 0.5 > \frac{K_2}{K_1} = \frac{2}{5},$$

it follows from [1], $E_1(K_1, 0) = E_1(100, 0)$ is globally stable. Fig.3 and 4 supports this assertion.

(2) Assume that the system has refuge, i.e., $u_{max} = 0.8$, and no influence of wind effect, i.e., $w = 0$, in this case, since

$$\alpha_{12}(1-u) = 0.06 < \frac{K_1}{K_2} = \frac{5}{3}, \alpha_{21}(1-u) = 0.01 < \frac{K_2}{K_1} = \frac{2}{5},$$

it follows from [1], $E^*(x^*, y^*) = E^*(97.57085020, 40.48582996)$ is globally stable. Fig.5 and 6 supports this assertion. From Fig.1-4, one could see that due to the fact that most of the N_1 population remain in refuge, the competitive pressure on the N_2 population is significantly reduced, allowing the N_2 population to survive in the long term.

(3) Assume that the system has refuge, i.e., $u_{max} = 0.8$, and take wind effect $k = 0.1$, $w = 10$, in this case, since $u = u_{max}\exp\{-k\omega\} = 0.2943$,

$$\begin{aligned} &r_2 = 0.5 < 0.588 = \alpha_{21}(1-u)\tfrac{K_1}{K_2},\\ &\alpha_{12}(1-u)\tfrac{K_2}{K_1} = 0.127 < 1 = r_1, \end{aligned} \tag{30}$$

it follows from Theorem 5.2, $E_1(K_1, 0) = E_1(100, 0)$ is globally stable. Fig.7 and 8 supports this assertion. We observe that although there is a relatively large refuge under windless conditions, its effectiveness is continuously weakened due to the influence of wind speed. As a result, a strong competitive relationship persists between the first population and the second population, ultimately leading to the extinction of the latter.

(4) Assume that the system has refuge, i.e., $u_{max} = 0.8$, and take $k = 0.1$, in this case, from above (3) numeric simulation, we know that the second species will be driven to extinction if $w = 10$. Hence, it is interesting to plot the bifurcation diagram of the density N_1^*, N_2^* about w. Fig. 7 shows that the critical value of w is $w_c = 2.876820725$, for $w > w_c$, then the second species will be driven to extinction, while the first species will approach to its' capacity.

VII. CONCLUSION AND DISCUSSION

In this study, we developed and analyzed a two-species Lotka-Volterra competition model that incorporates wind-dependent refuge availability, a novel approach that extends the classical framework to account for dynamic environmental influences. Our model introduces an exponentially decaying refuge function $u(w) = u_{\max}e^{-kw}$, which captures the reduction in refuge effectiveness as wind speed increases. Through rigorous mathematical analysis, we identified the conditions under which species coexistence or competitive exclusion occurs, demonstrating that wind speed plays a pivotal role in shaping these outcomes.

Theoretical results revealed that the system admits a unique stable positive equilibrium $E^*(N_1^*, N_2^*)$ when the intrinsic growth rates and carrying capacities of both species outweigh the competitive pressures exacerbated by wind-induced refuge loss. Specifically, coexistence is possible when:

$$\begin{aligned} &r_1K_1 > \alpha_{12}(1-u(w))K_2,\\ &r_2K_2 > \alpha_{21}(1-u(w))K_1. \end{aligned} \tag{31}$$

Conversely, if these inequalities are reversed, the system tends toward the extinction of one species, highlighting the fragility of coexistence under high wind conditions. Numerical simulations further validated these findings, illustrating how increased wind speeds disrupt refuge availability and alter competitive hierarchies.

Ecological implications

1) **Wind as a regulator of refuge efficacy**: Our model underscores the nonlinear relationship between wind speed and refuge availability. As wind intensifies, the exponential decay of $u(w)$ rapidly diminishes the protective capacity of refuges, leading to heightened interspecific competition. This mechanism provides a theoretical basis for understanding how wind disturbances, such as storms or seasonal winds, can destabilize ecosystems by eroding niche differentiation.
2) **Conservation strategies**: The results suggest practical measures for biodiversity conservation in wind-prone habitats. For instance, establishing windbreaks or restoring vegetation can mitigate wind effects, preserving refuge availability and promoting coexistence. Conversely, in invasive species management, targeted disruption of refuge conditions (e.g., through controlled wind exposure) could weaken invasive species' competitive advantages.
3) **Species-specific vulnerabilities**: The model highlights the asymmetric impacts of wind on species with differing refuge dependencies. Species reliant on refuges (e.g., understory plants or burrowing animals) are more susceptible to wind-induced competitive exclusion, while non-refuge users may dominate under high wind conditions. This asymmetry necessitates tailored conservation strategies.

Limitations and future directions

While our model advances the integration of environmental variability into competition theory, several limitations warrant attention:

- **Refuge dynamics**: The exponential decay function $u(w)$ simplifies the complex interplay between wind and refuge availability. Future studies could explore non-monotonic or threshold-based relationships, reflecting scenarios where wind initially creates refuges (e.g., fallen debris) before destroying them.

- **Multi-species interactions**: Extending the model to include multiple species with varying refuge dependencies could reveal cascading effects of wind disturbances on community structure.
- **Stochastic wind effects**: Incorporating stochastic or time-varying wind speeds would better mimic natural conditions, allowing for analysis of resilience to unpredictable disturbances.

Broader significance

This work bridges theoretical ecology and environmental science by quantifying how abiotic factors like wind modulate biotic interactions. It also aligns with global concerns about climate change, where increasing wind intensities may exacerbate species declines in vulnerable ecosystems. By elucidating the mechanisms linking wind, refuges, and competition, the model offers a framework for predicting and mitigating the ecological impacts of environmental change.

In summary, our study demonstrates that wind-dependent refuge dynamics are a critical yet understudied factor in species competition. The findings advocate for integrating environmental variability into ecological models to better predict and manage biodiversity in a changing world. Future research should expand on these insights, exploring additional abiotic-biotic interactions and their conservation implications.

AUTHOR CONTRIBUTIONS

G. W. He and Z. Z. Cai contributed equally to analysis and simulations. F. D. Chen supervised the theoretical framework.

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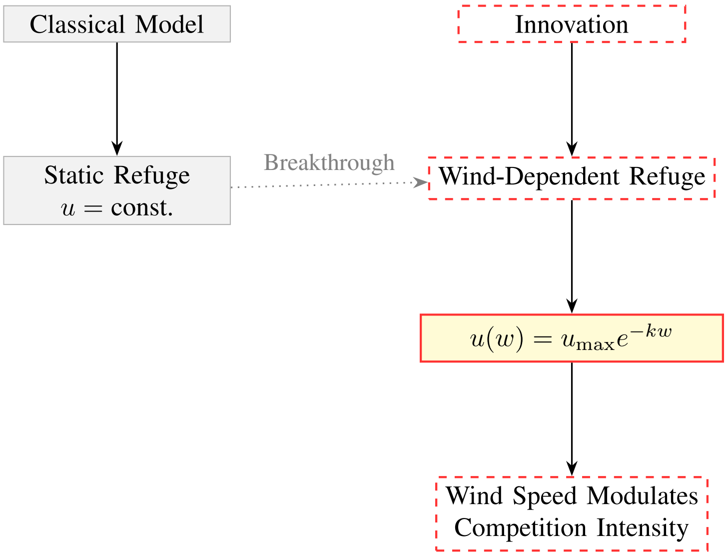

Fig. 1. Conceptual framework of the wind-dependent refuge model. The yellow box highlights the key innovation where refuge availability $u(w)$ becomes a function of wind speed w.

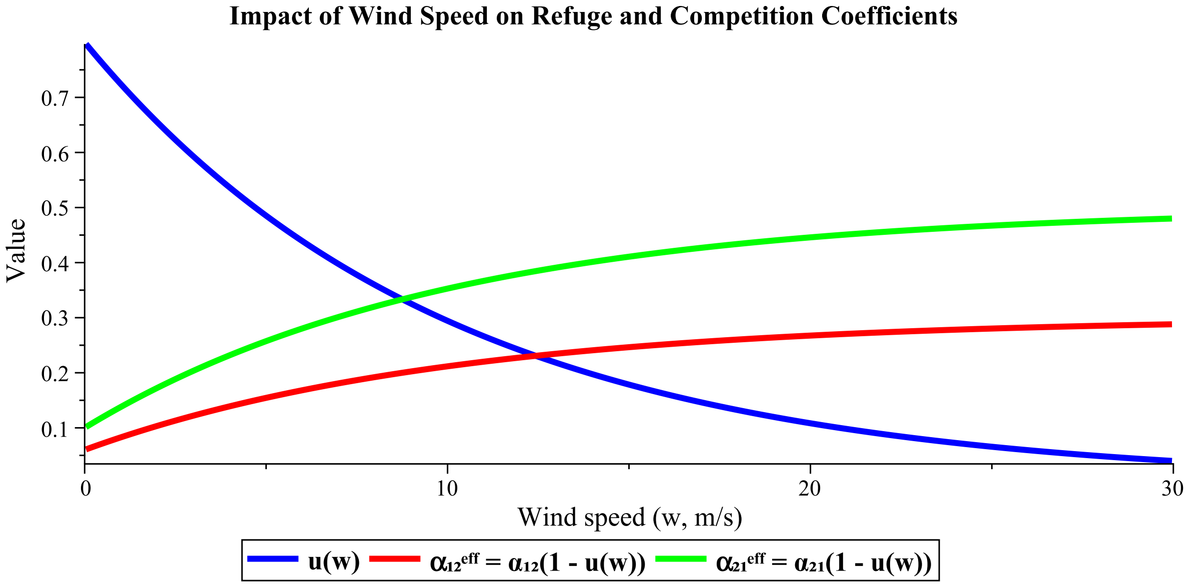

Fig. 2. Impact of Wind Speed on Refuge and Competition Coefficients.

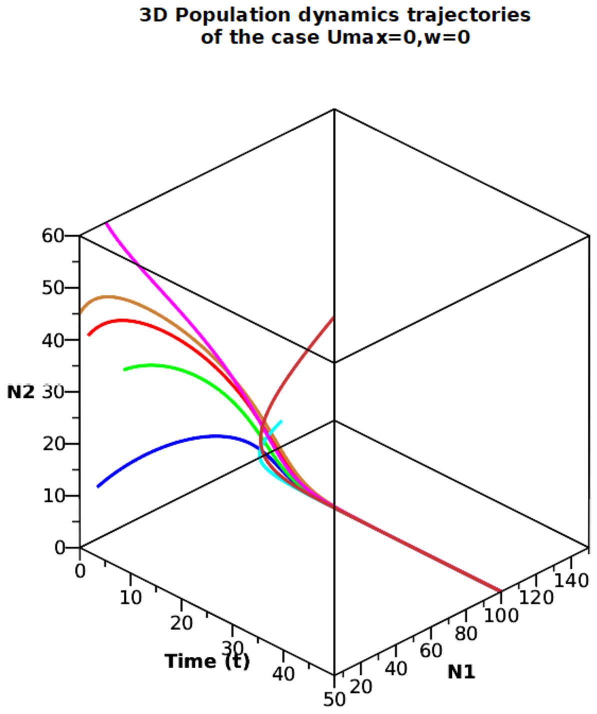

Fig. 3. 3D Population dynamics trajectories of the case $u_{max} = 0$.

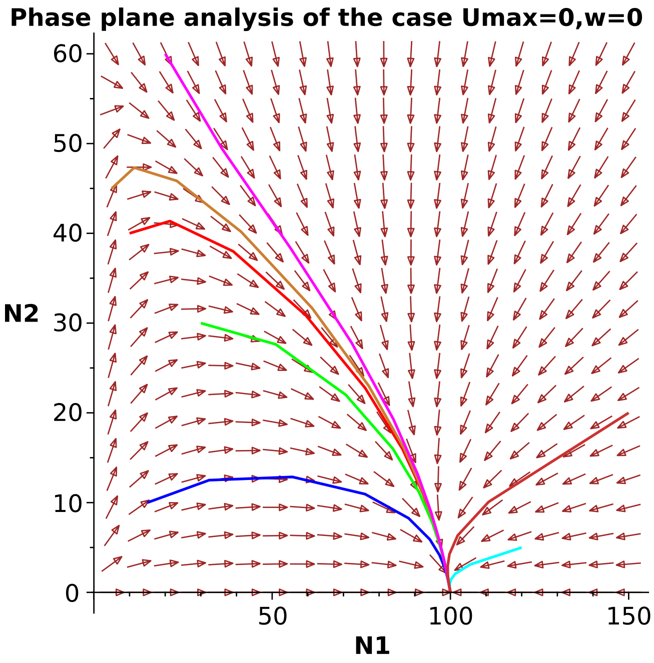

Fig. 4. Phase diagram of the case $u_{max} = 0$:The trajectories under different initial conditions all converge to $E_1(100, 0)$.

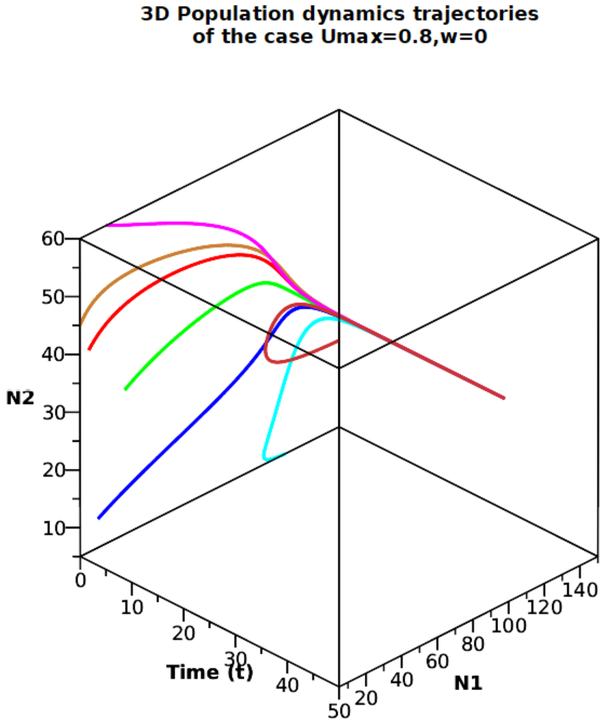

Fig. 5. 3D Population dynamics trajectories of the case $u_{max} = 0.8, w = 0$.

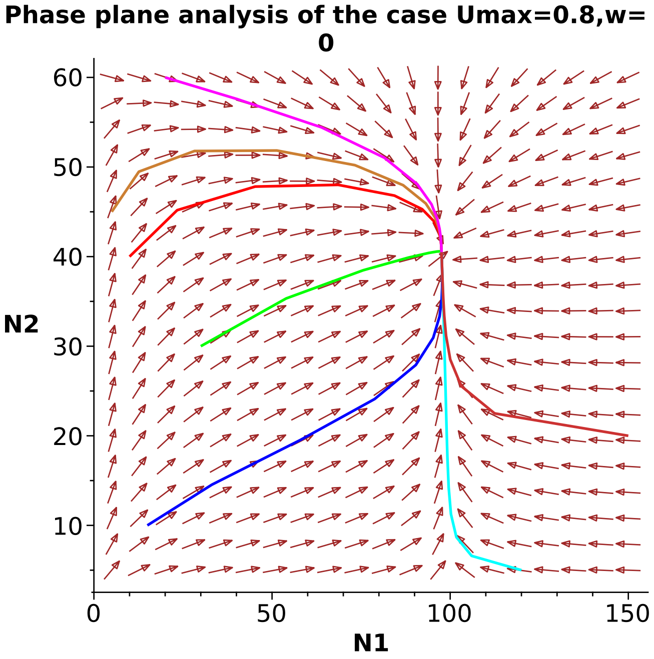

Fig. 6. Phase diagram of the case $u_{max} = 0.8, w = 0$:The trajectories under different initial conditions all converge to $E_1(100, 0)$.

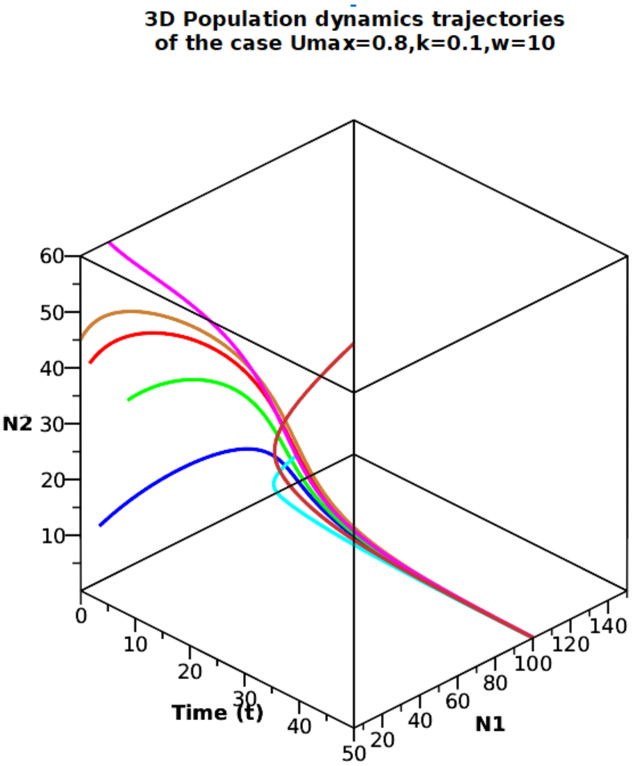

Fig. 7. 3D Population dynamics trajectories of the case $u_{max} = 0.8, k = 0.1, w = 3$.

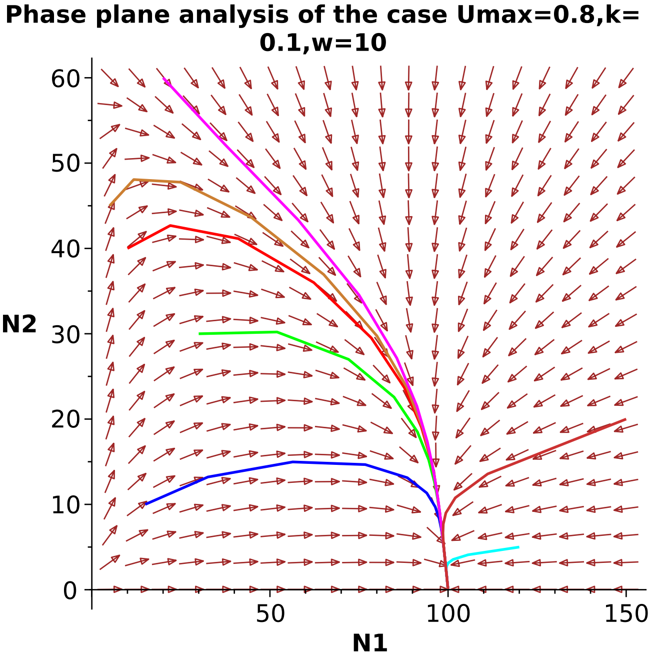

Fig. 8. Phase diagram of the case $u_{max} = 0.8, k = 0.1, w = 0.3$:The trajectories under different initial conditions all converge to $E_1(100, 0)$.

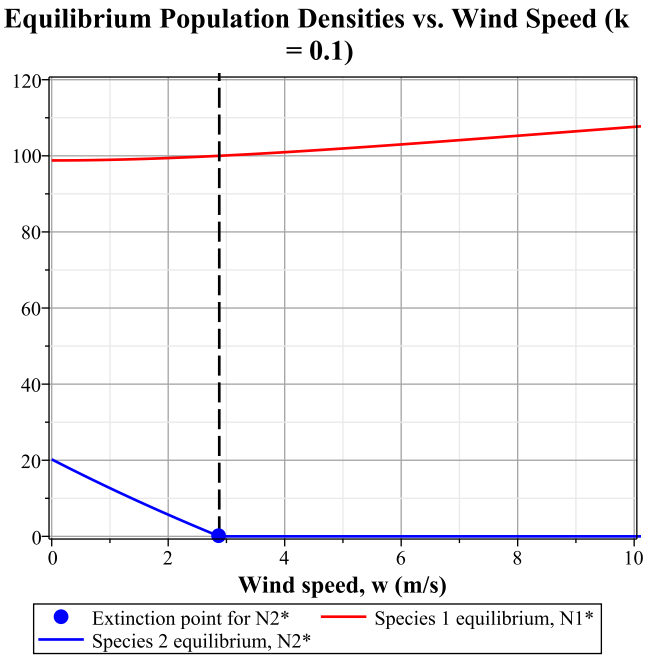

Fig. 9. Bifuction diagram of N_1^*, N_2^* about w.