Modeling cooperation and competition in biological communities

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Abstract

The far-reaching consequences of ecological interactions in the dynamics of biological communities remain an intriguing subject. For decades, competition has been a cornerstone in ecological processes, but mounting evidence shows that cooperation also contributes to the structure of biological communities. Here, we propose a simple deterministic model for the study of the effects of facilitation and competition in the dynamics of such systems. The simultaneous inclusion of both effects produces rich dynamics and captures the context-dependence observed in the formation of ecological communities. The approach reproduces relevant aspects of primary and secondary plant succession, the effect of invasive species, and the survival of rare species. The model also takes into account the role of the ecological priority effect and stresses the crucial role of facilitation in conservation efforts and species coexistence.

Keywords: population dynamics, plant succession, competition, facilitation

1. Introduction

A major challenge in the theory of community organization is to understand the origin of species diversity and its impact on the structure of biological communities. The problem still persists to date mainly because of the vast number of abiotic and biotic factors that affect the ability of species to invade and fix their habitat \cite{1,2}. The abiotic factors include environmental constraints which directly affect the demographics of biological communities. The most notable examples are the spatial effects, resource heterogeneity, environmental disturbances such as vegetation fires or other natural phenomena, and events caused or produced by climate changes \cite{3}. In contrast, biotic factors encompass an egregious number of ecological processes and interactions among the various species that constitute the community. The intricate network of inter- and intraspecific interactions ultimately determines the ecological response of species at population and community levels and shapes the formation and stability of ecosystems \cite{4,5}.

Ecological interactions comprise the various types of influence that one organism can exert over another. They are subdivided into positive, neutral, or negative, depending on the outcome onto the target organism. Interspecific predation and competition are, perhaps, the most well-known types of interactions: they embody the natural dispute for resources in ecology and set the cornerstones of the mathematical models developed by Volterra \cite{6}, MacArthur \cite{7}, and Levin \cite{8} to name a few. Together with Gause’s principle of species exclusion \cite{9} – species competing for the same resource cannot coexist – and Hutchinson’s niche separation \cite{10}, their works established the classical theory of ecological communities. In this context, ecologists have investigated the response of ecosystems to...
species invasion and exclusion, stress, environmental changes, and the impact on the structure and functionality of ecosystems [11,12,13,14].

However, the existence of widespread species diversity observed across the globe poses a conceptual challenge to the classical theory. More specifically, to the principle of species exclusion. The empirical observation that different marine species competing for the same set of resources can coexist summarizes what is known as the plankton paradox [15]. According to the classical theory, and assuming homogeneous conditions, only the most competitive species should survive. It turns out that violations of species exclusion occur fairly easily in nature. Palmer lists 120 ecological processes that violate the principle and lead to species coexistence [16]. In that regard, the modern theory of coexistence by Chesson [17] synthesize many of those processes. It states that the suppression of the growth rate is stronger for higher intraspecific densities rather than interspecific ones. This gives a small advantage to invasive species at low densities and promotes coexistence via the decrease of the effective growth rate of the dominant species with their population sizes.

The inability to accommodate small deviations to common assumptions suggests the classical theory still requires adjustments. In particular, the role of positive interactions is generally neglected even though several ecosystems have evolved and still rely on positive interactions. Coral reefs are prime examples. The mutualism between corals and algae (dinoflagellates) allows them to thrive in sub-optimal environmental conditions [18]. Sediments and thermal stress quickly disrupt this delicate interaction, leading to the removal of algae and, eventually, to the characteristic bleaching of coral reefs [19]. This peculiar phenomenon – and linked with climate changes – highlights the dependence of positive interactions in the maintenance of complex ecosystems.

Facilitation can also be an important tool for invasive species, a fact often overlooked in competition-driven models. Based on empirical data, the research team in Ref. [20] found out that seedling strategies for highly invasive trees of the genus Pinus hinge on the mutual relation with mycorrhizal fungi. The positive interaction with the fungi improves the transfer of nutrients and minerals from the soil to the seedling, promoting its growth and increasing the chances of survival. As a result, the invasive trees tend to produce lighter seeds in greater numbers to overcome the reduced chance of finding the fungi. In contrast, the authors of Ref. [20] show that less invasive trees produce seeds that are less dependent on mycorrhizal fungi and thus larger.

The inclusion of facilitation in a framework driven by competitive interactions has proven to be a challenging task so far [21]. A cascade of facilitation processes is known to occur in plant successions at empirical and conceptual levels [22,23]. Plants compete directly for nutrients, water, and sunlight. Early species are more tolerant to poor distribution of nutrients in the soil and, as a result, they facilitate the germination of late-stage plants by either increasing water content or locally reducing the temperature of soil [24]. This positive interaction benefits late species which eventually suppress or replace the early species as they are more efficient to capture sunlight and other resources. The repetition of this process eventually leads to plant or forest succession and the modification of the ecosystem. The key lesson here is that large densities of early species affect the dynamics of late species in different manners depending on their development phase. The behavioral changes figure among one of the factors that complicate a broader formulation of community structures.

Furthermore, the introduction of facilitation processes modifies the basic tenets of niche theory. As discussed in detail [25], interactions that promote facilitation between plants also create paths for species coexistence and increased species richness. The current consensus claims that diversity reduces the effects of abiotic stresses and helps to maintain the stability of ecosystems. At the same time, a larger number of species also implies an increased likelihood of species competing for the same niche, clashing again with Gause’s exclusion principle. The solution for the apparent paradox is that facilitation processes can expand niches while competition reduces them. The expansion of niches can be obtained by merely increasing the output of an existing niche; or by allowing organisms to access species-transformed or mediated resources. The latter actively shape the distribution and accessibility.
of resources in ecosystems instead of merely control their amplitudes (competition). Thus, the inclusion of facilitation forces the departure from the pragmatic view of niche as the representation of locales where species can exist.

Here, we propose a simple dynamical model of plant communities that explicitly contains interspecific competition and facilitation. The inclusion of positive interactions creates a rich dynamics that can reproduce the basic aspects of forest succession, species coexistence, and response to catastrophic events. Our findings show that our model can reproduce the general aspects of experiments testing the stress gradient hypothesis, a phenomenon in which the behavior of interacting species can vary from pure cooperative to pure competition according to their stress level. The paper is organized as follows. In Sec. 2, we revisit some models of population dynamics and the manner in which they approach the interaction between species. Inspired by the Kuno model, in Sec. 3, we extend the formulation to include facilitation as a core part of the dynamics and explain the discrete model for two and three species. The results are shown in Sec. 4 and further discussed in Sec. 5. Our concluding remarks are offered in Sec. 6.

Box 1: Ecological succession

Ecological succession is the natural process that describes the assembling and evolution of species structures in ecological communities. At its core, it describes how the organisms gradually modify their surrounding and create conditions for the establishment of species or their eradication. The process often yields a global increment in biomass and changes the composition of species. The characteristics and ecological functioning of the area also change in order to reflect the new set of dominant species. Forest succession is the prime example: plants grow in an ordered and predictable pattern marked by the progressive dominance of long-living species. In a nutshell, from bare soil to grass, to shrubs and small trees, culminating in mature trees (see Figure 1). In the early stages, pioneer species are dominant under harsh conditions and actively alter the physico-chemical properties of soil and surrounding areas. The presence of pioneers ensures adequate conditions for secondary species to get a foothold and grow. Although secondary species are less adapted to harsh conditions, they exhibit better competitive traits and, thus, tend to replace pioneers, completely or partially. The successional process continues and eventually reaches the climax stage (steady state).

Successional dynamics are classified as primary or secondary. Primary succession concerns the initial colonization of ecosystems. It starts from soil formation and proceeds all the way up to the climax stage. Secondary successions occur shortly after ecosystems are disturbed by natural or human-made events and return to a previous developmental stage. The main difference between secondary and primary succession is the initial distribution of species, with reduced or complete absence of earlier species depending on the intensity and type of disturbance. According to the classical concept by Clements [26], the ecosystem should return to the same steady state prior to the disturbance. However, mounting evidence suggests that secondary successions may lead to different late successional stages, with significant variation of species composition [27, 28]. Possible explanations include reduced biomass and species diversity caused by phosphorus depletion [29, 23], and spatial or priority effects during the colonization [30, 31, 32, 33]. These hypotheses indicate that initial conditions are important drivers for late stages in ecological succession [34].
Figure 1: Schematic representation of ecological succession dynamics of a forest ecosystem. The changes in relative abundances indicates the shifts in the structures of biological communities. Facilitation dominates early stages while competition becomes the dominant interaction between species at late stages. Modified from Lucas Martin Frey 2011 (Creative Commons Attribution 3.0.).

Box 2: Biological Invasion

The colonization of new areas by organisms is a fundamental aspect of ecology. Colonization contributes to the formation and maintenance of ecosystems, being crucial for the dynamics of natural communities. For human-made systems, such as plantations, biological invasions can negatively affect the ecological balance and food production. Recent estimates place the annual cost of losses due to biological invasions around US$ 27 billion, reaching a stunning mark of US$ 1.3 trillion over the course of 47 years [35]. This outrageous sum and the dire consequences to food security highlight the necessity to understand how biological invasions happens and what influences them.

In broader terms, the successful colonization depends on the species’ ability to surpass the ecological filters of the target region. Filters are the collection of environmental and ecological aspects that in someway suppress or restrict the survival of organisms in a given habitat. They can represent harsh conditions like dryness, temperature, presence of predators, etc. Strong ecological filters hinder the development of species so much that only a handful of specialized species can flourish. These species tend to take part in facilitation processes with others in order to counterbalance the stress imposed by the environment. In contrast, weak filters provide natural shelters and foster a far more diverse, but less specialized, biological community characterized by ample competition between species. The amplitudes of these competitions constitute yet another ecological filter, a dynamical one, with a stronger dependence on the current state of the ecosystem.

In the context of colonization, dynamical filters are known as ecological priority effects and they can influence the organization of biological communities [36]. For instance, early colonizers can monopolize resources and maintain their dominant status even against superior competitors due to their shear abundance (founder effect), inverting the usual species exclusion. These effects must be taken into account by restoration and conservation efforts, especially those that aim to preserve or reintroduce native species to target locations.

2. Models of population dynamics
The question of human population growth has been one of vital importance since the dawn of civilisation. Regular censuses allowed to keep track of the evolution and the compilation of their data were a precious aid in the formulation of modelling-based descriptions of the dynamics. Given the reproductive mechanisms, it is clear that an initial population, if left unchecked, will grow in a geometric way. Malthus [37] was the first in addressing the question in a rigorous way, pointing out that the population growth cannot be indefinitely sustained, given that the resources do not increase with the same rate. The geometric growth to which Malthus refers to is what in modern parlance we call an exponential increase, governed by the equation

\[ \frac{dN}{dt} = \lambda N \]  

where \( N \) is the population. The solution of (1) is simply \( N = N_0 e^{\lambda t} \).

The fact that the scarcity of resources can curb the exponential growth of the population, was incorporated in a mathematical formulation proposed by Verhulst [38]. The equation, known today under the moniker of logistic, has the form

\[ \frac{dN}{dt} = \lambda \left( N - \frac{N^2}{K} \right), \]  

with solution

\[ N = \frac{N_0 K}{N_0 + (K - N_0)e^{-\lambda t}}. \]  

The \( N^2 \) term, which is essential for halting the exponential growth, is what we would call a self-interaction term, encoding the interspecies competition for resources. When \( t \to \infty \) the population tends to the value \( K \), which is often referred to as the carrying capacity of the environment, corresponding to the maximal value of the population that can be sustained. We shall not pursue the discussion of the Verhulst equation, often criticised for its extreme simplicity, but we shall present, as an aside, the work of Morisita [39], who addressed the question of the form of the logistic equation when one considers that the population grows by spurts occurring at regular time intervals. Morisita obtained the recursion relation

\[ N_{t+\tau} - N_t = \mu \left( N_t - \frac{N_t N_{t+\tau}}{K} \right), \]  

where \( \tau \) is the time step and \( \mu = e^{\lambda \tau} - 1 \). It turns out that (4) is satisfied by (3) when the latter is sampled over the grid points \( t_0 + n\tau \). In the next section we shall return on the Morisita approach, with further comments.

The situation becomes more interesting when one considers two interdependent species. The classical situation is the one known as a predator-prey one, where one species (the predator) depends on the other (the prey) for its subsistence. The simplest mathematical formulation of such a situation is that proposed by Lotka [40] and, independently, by Volterra [6]. The proposed model uses the chemical principle of mass action. Namely, the interaction between the populations is represented by the product of their biomass densities. The system thus assumes the form

\[ \frac{dn}{dt} = \lambda n - anp \]  

\[ \frac{dp}{dt} = bnp - \mu p. \]  

One remarks that the predator \( p \) cannot survive in the absence of prey, while the population of the latter, in the absence of predator, grows unchecked. In this respect it would have been more natural
to introduce a slightly modified system where the population of the prey is governed by a logistic equation

\[
\frac{dn}{dt} = \lambda n \left( 1 - \frac{n}{k} \right) - anp
\]

(6a)

\[
\frac{dp}{dt} = bnp - \mu p.
\]

(6b)

A major contribution to the theory of predator-prey systems was the introduction of what Salomon [41] called the functional response. He argued that, since a predator can handle only a finite number of prey per unit time, the death rate of the prey, the \(-anp\) in (6a), must depend non-linearly on the prey density, i.e. \(-a(n)p\). Holling [42] proposed an explicit realisation of these ideas by introducing, what is known today as, the disk equation. According to him a suitable expression for \(a(n)\) is

\[
a(n) = \frac{fn}{n + \kappa},
\]

(7)

which happens to be identical to the Michaelis-Menten [43] equation for enzyme kinetics. Combining all these features one of the authors (BG) introduced in [44] the predator-prey model

\[
\frac{dn}{dt} = \lambda n \left( 1 - \frac{n}{k} \right) - ap \frac{n}{1 + \sigma n}
\]

(8a)

\[
\frac{dp}{dt} = bnp \frac{n}{1 + \rho n} - \mu p.
\]

(8b)

Having discussed the classic population dynamics models, we turn now to the ones pertaining directly to the theme of this paper. While we shall be interested in species which are in direct competition for resources we shall eschew the case where upon species acts like a resource for the other. A successful model describing the situation of competition through reproductive interference is the one due to Kuno. In [45] he proposed a model involving two competing species which we can rewrite by reorganising the terms with respect to the original formulation (for reasons that will become clearer later) as

\[
x' = a \left( \frac{x}{x + \alpha y} - fx \right) x - \lambda x
\]

(9a)

\[
y' = b \left( \frac{y}{y + \beta x} - gy \right) y - \mu y.
\]

(9b)

where \(x\) and \(y\) are the biomass densities of the two species and the prime indicates a derivation with respect to time. Here, the interference between the species affects the birth rate of each as a diluting effect. Kuno presents, in parallel to this model, a Lotka-Volterra one where the two species compete for a common resource

\[
x' = c (1 - fx) x - \alpha xy
\]

(10a)

\[
y' = d (1 - gy) y - \beta yx.
\]

(10b)

Note that (10) does not describe a predator-prey system, the interaction term being noxious to both species, each of which would have survived and grown to capacity in the absence of the other. We shall return to the Kuno model in the next section.

3. Building a model for competing and cooperating species

Before considering the case of two competing species, we shall revisit the case of a single species investigating possible extensions of the simple logistic equation. Our approach will be, in some remote sense, inspired by the work of Aubier who introduced a density dependent mortality term in a model
aiming at describing an asymmetric competition between two species. Here we shall ignore the two-
species case focusing on the density dependent mortality effect on a single species. The corresponding
equation has the form

\[ x' = ax \left( 1 - \frac{x}{k} \right) - \lambda \frac{x}{1 + \sigma x} \]  

(11)

We now try to bring (11) as close as possible to the form of Kuno equation. We obtain

\[ x' = ax \left( \frac{cx + d}{1 + \sigma x} - \frac{x}{k} \right) - \lambda x \]  

(12)

Note that when all coefficients in (11) are positive, the \( c \) in (12) is negative. This is a specific feature
of the model of Aubier and need not concern us further. The conclusion we can draw from (12) is that
an extension of the logistic model is possible where the term controlling the capacity is a homographic
function of the density. This leads thus to the following expression, obtained after the appropriate
scaling of the \( x \) variable

\[ x' = ax \left( \frac{x + \beta}{x + \gamma} - x \right) - \lambda x \]  

(13)

We claim that the solution of (13) behaves exactly like the solution of the logistic equation. Clearly
when \( \beta = \gamma \) (13) is just a way of rewriting (2), but the overall behaviour is the same even when \( \beta, \gamma \)
are unrelated. Before proceeding to a numerical simulation of (13) in order to confirm our claim we
must produce a discrete analogue thereof. For this we shall use the method one of the authors (BG)
developed in [46]. It is a method directly inspired from the works of Mickens [47]. The best way to
describe this discretisation procedure is by using the catchy phrase published in [48]: ‘if all quantities
are positive, no minus sign should appear anywhere’. In the present situation we deal indeed with
quantities that are by principle positive, being biomass densities and thus the prescription just cited
can apply. The way to implement this is through the appropriate staggering of the variables. In order
to show how the method works we shall revisited the approach of Morisita. We start from the logistic
equation

\[ x' = \lambda x - \mu x^2, \]  

(14)

introduce a forward difference for the derivative and rewrite the \( x^2 \) as \( x_n x_{n+1} \) instead of \( x_n^2 \). We have thus (\( \delta \) being the discretisation step):

\[ \frac{x_{n+1} - x_n}{\delta} = \lambda x_n - \mu x_n x_{n+1}. \]  

(15)

This leads to the mapping

\[ x_{n+1} = x_n \frac{1 + \lambda \delta}{1 + \mu \delta x_n} \]  

(16)

which is precisely the one we obtain from the recursion of Morisita, upon solving for \( N_{t+\tau} \). We turn
now to (13) and again introduce a forward difference for the derivative and obtain:

\[ \frac{x_{n+1} - x_n}{\delta} = ax_n \frac{x_n + \beta}{x_n + \gamma} - ax_n x_{n+1} - \lambda x_{n+1} \]  

(17)

leading to the mapping

\[ x_{n+1} = x_n \frac{1 + a \delta \frac{x_n + \beta}{x_n + \gamma}}{1 + \lambda \delta + a \delta x_n}, \]  

(18)

which can be used to integrate (13).
Figure 2. Evolution of the biomass $x$ versus time for model (13). Parameters: $x(0) = 10^{-3}$, $a = 2.0$, $\beta = 0.2$, $\gamma = 0.1$, $\lambda = 10^{-3}$

Figure 2 shows such a simulation and the resemblance to the solution of the logistic is uncanny. Note that the asymptotic value of $x$, which plays the role of the ecological capacity, is obtained in a complicated way from the parameters of the model. However, and this is an important feature of our discretisation approach, the fixed points and their stability conditions are exactly the same in the continuous and the discrete system.

Having set the model for a single species we turn now to the case where two species are present. The difference of our approach and that of Kuno is that we assume that the two species may not only compete but also cooperate. At this point a remark is in order. The terms ‘cooperation’ and ‘competition’ are used rather loosely. In the present context cooperation should better be understood as ‘facilitation’ whereupon a species profits from the presence of the other. In the same spirit competition is to be understood as ‘hindrance’, one species preventing the other to realise its full potential. Having clarified the real meaning of the terms we shall be using throughout the paper, we can proceed to the construction of our model.

Starting from the equations (9) where only competition is present we extend equation (13) introducing a capacity involving also cooperation terms leading to the system

\[ x' = a \left( \frac{x + f_{xy}y}{x + h_{xy}y} - x \right) x - \lambda x \]  
\[ y' = b \left( \frac{y + f_{yx}x}{y + h_{yx}x} - y \right) y - \mu y. \]

where the terms $f_{xy}y$ (respectively $h_{xy}y$) quantifies how much the growth of species $x$ is facilitated (resp. hindered) by the presence of species $y$. Clearly the case of pure, Kuno-like, competition can be obtained from (19) by putting $f_{xy} = f_{yx} = 0$. A pure cooperation situation would correspond to $h_{xy} = h_{yx} = 0$.

Before proceeding further it is interesting to study the fixed points of (19) as well as their stability properties. Three distinct situations do exist: both fixed points are 0, one fixed point is 0 while the other is finite and finally both fixed points can be finite. The stability of the fixed points $(0,0)$ leads to the consideration of the system

\[ \xi' = \Lambda \xi - \lambda \xi \]  
\[ \psi' = M \psi - \mu \psi \]
where $\Lambda$ and $M$ are the limits of the expressions $a(x + f_{xy}y)/(x + h_{xy}y)$ and $b(y + f_{yx}x)/(y + h_{yx}x)$ when $x \to 0$ and $y \to 0$. However the values of $\Lambda$ and $M$ depend on the precise way $x$ and $y$ tend to 0 and thus it is not easy to give a criterion for the attraction to the point $(0,0)$. However it is clear that when the parameters $\lambda$ and $\mu$ are large enough the solution of (19) is attracted to $(0,0)$.

Figure 3 shows such an example.

We turn now to the case where at least one of the fixed points is not zero. The fixed points are given by the equations

\begin{align*}
    x_*(ax_*^2 + ah_{xy}x_*y_* + (\lambda - a)x_* + (h_{xy}\lambda - af_{xy})y_*) &= 0 \quad (21a) \\
    y_*(by_*^2 + bh_{yx}x_*y_* + (\mu - b)y_* + (h_{yx}\mu - bf_{yx})x_*) &= 0 \quad (21b)
\end{align*}

When one of the fixed points, say $y_*$, is zero the other one is given by $x_* = 1 - \lambda/a$. The characteristic equation has two roots, one which is by construction negative $\omega_1 = -ax_*$, and one $\omega_2 = \mu - bf_{yx}/h_{yx}$ which can be made to take a negative value (meaning that the fixed point is attractive) with the appropriate choice of the parameters. Assuming that both $x_*$ and $y_*$ are non-zero one must solve (21) leading, upon elimination, to a cubic equation for of them. In order to bypass this difficulty we shall use the trick, already introduced in [48], solving for two of the parameters which enter linearly (here $\lambda$ and $\mu$), which is tantamount to considering $x_*$ and $y_*$ as new parameters. Once we do this the characteristic equation can be written in a most compact way

\begin{align*}
    \omega^2(x_* + h_{xy}y_*)^2(y_* + h_{yx}x_*)^2 + \omega \left( ax_*(y_* + h_{yx}x_*)^2((x_* + h_{xy}y_*)^2 + y_*(f_{xy} - h_{xy})) + by_*(x_* + h_{xy}y_*)^2((y_* + h_{yx}x_*)^2 + x_*(f_{yx} - h_{yx})) \right) + abx_*y_* \left( (f_{xy} - h_{xy})y_*(y_* + h_{yx}x_*)^2 + (f_{yx} - h_{yx})x_*(x_* + h_{xy}y_*)^2 + (x_* + h_{xy}y_*)^2(y_* + h_{yx}x_*)^2 \right) &= 0. \quad (22)
\end{align*}

Given this complicated expression, it is not possible to perform the stability analysis in full generality. However if one fixes the values of the parameters of the problem, checking the stability of the fixed points becomes elementary.

Extending the model to more than two species is straightforward but an important choice is in order. It is clear that the possibility of every species to interact (either in competition or in cooperation) with all the other species should be present in the model. This means that one must extend the capacity function but this can be done in different ways. Let us illustrate this in the case of three interacting species, $x$, $y$, $z$. Focusing on the capacity of species $x$, two possibilities exist, an “additive” one.
or a “multiplicative” one

\[
\frac{x + f_{xy}y + f_{xz}z}{x + h_{xy}y + h_{xz}z},
\]

Extending this to a higher number of species does not present any difficulty, but one must make a choice between an additive or multiplicative interaction for every new species.

Constructing discrete analogues of equations, like (19), involving two species, or in fact any higher number of species, is elementary if one follows the prescription introduced for the single species equation (21): one discretises the \(x^2\) term as \(x_n x_{n+1}\) and staggers the \(-\lambda x\) term, obtaining \(-\lambda x_{n+1}\). This guarantees the positivity of the solution of the system, once one starts with positive initial conditions and positive coefficients.

4. Results

In this section we are going to present results obtained through simulations based on our model (19). We shall start by considering two species. In order to be able to refer to each of them in a simple way we shall call them A and B.

The first results we are going to present are meant to highlight the effect of competition among species. In the first simulation we focus on a case where species B is not influenced by A but presents a hindrance to the latter.

![Figure 4. Evolution of the abundance of the two species A and B versus time, with only B-towards-A hindrance. For species A (black line), \(x(0) = 8.0 \times 10^{-4}\), \(a = 3.0\), \(f_{xy} = 0.0\), \(h_{xy} = 1.0\), \(\lambda = 0.5\) and for species B (red line), \(y(0) = 1.0 \times 10^{-3}\), \(b = 1.0\), \(f_{yx} = 0.0\), \(h_{yx} = 0.0\), \(\mu = 0.5\).](image)

The result of this competition, (shown in Figure 4), is that species A grows during a certain time but starts declining when B initiates its growth, and, ultimately, disappears. The scenario illustrates the principle of species exclusion [9].

Next we show a few more example of the effect of competition among species.
Figure 5. Evolution of the abundance of the two species A and B versus time, with B-towards-A and A-towards-B hindrance. For species A (black line), \( x(0) = 1.0 \times 10^{-2}, a = 3.0, f_{xy} = 0.0, h_{xy} = 0.5, \lambda = 0.1 \) and for species B (red line), \( y(0) = 7.0 \times 10^{-3}, b = 1.0, f_{yx} = 0.0, h_{yx} = 0.1, \mu = 0.1 \).

Figure 5 depicts a situation similar to that of 4 albeit one where there exist a mutual, but rather mild, competition between the two species. Species A has now the time to reach a temporary equilibrium, but the growth of species B disturbs it pushing the population of species A towards a new, lower, fixed point. In this case, both species can coexist at the cost of reduced fitness.

Another interesting effect, resulting from competition between species is the one known as the ‘founder’ effect also known as priority effect [36], in which new invasions depend on the order of previous colonization.

Figure 6. Evolution of the abundance of the two species A and B versus time. For species A (black line), \( a = 15.4, f_{xy} = 0.0, h_{xy} = 1.0, \lambda = 1.0 \) and for species B (red line), \( y(0) = 1.0 \times 10^{-2}, b = 2.0, f_{yx} = 0.0, h_{yx} = 1.0, \mu = 1.0 \). The species A is introduced at time \( t = 10 \) with an exponential function \( x(t) = 0.11(1 - \exp(-0.6(t - 10)/500)) \).

In Figure 6 we present a simulation of this effect: species B being well entrenched hinders the growth of A, through competition, and forces it to disappearance, paying the price with only a temporary decrease of its population. However it must be pointed out that by fine tuning the amount of competition between the two species we can have a situation similar to the one present in Figure 4, whereupon species A does not totally disappear but reaches some finite equilibrium.
The final competition-induced example of evolution is the one we call the ‘tornado effect’, see Figure 7. The two species coexist but A is more abundant than B. Then due to an extreme event (hence the tornado moniker) the population of A is decimated. During the time where the headcount of A is low species B profits in order to increase its population. However this respite is temporary, and once the population of A starts growing the population of B diminishes reverting to the previous equilibrium. It is interesting to point out here that if by chance species B was the one to be more abundant before the devastation the subsequent evolution would have been the same i.e. species A would temporarily grow only to revert to the previous equilibrium after a short lapse of time. The restoration towards the previous steady state is in agreement with empirical data observed in natural forests after the passage of hurricanes [49] (see Appendix A).

We now turn to the case where cooperation is present among the species. Figure 8 shows what happens in such a case. Species A becomes well established and reaches a first equilibrium point. Species B grows out of a smaller initial population and thus needs some time in order to reach a substantial
headcount, it facilitates the growth of A pushing it to a higher equilibrium point. It is interesting at this point to wonder what would remain of the founder effect were species to exhibit some degree of cooperation.

Figure 9. Evolution of the abundance of the two species A and B versus time, with competition and cooperation, in the context of the founder effect. For species A (black line), $a = 3.0$, $f_{xy} = 0.1$, $h_{xy} = 1.5$, $\lambda = 0.1$ and for species B (red line) $y(0) = 1.0 \times 10^{-4}$, $b = 1.0$, $f_{yx} = 2.5$, $h_{yx} = 0.0$, $\mu = 0.1$. Species A is introduced at time $t = 10$ with an exponential function $x(t) = 0.11(1 - \exp(-0.6(t - 10)/500))$.

In Figure 9 we present the results of a simulation where the late arriving species A can persist indefinitely thanks to a, loosely adjusted, rate of cooperation with the already entrenched B. It is remarkable that the appearance of species A facilitates the growth of B pushing it to a higher headcount.

In fact, depending on the amount of cooperation between the two species, the late appearing A can grow up to an equilibrium point surpassing that of B. Notably, this result describes the arrival of rare and specialized species in mature ecosystems such as mature soils communities [50] or above ground species in primary tropical forests [51]. These species can only explore specific niches which are created and maintained by the continuous ecological activity of other species. Hence, the establishment of these rare groups depends strictly on the presence of a previously established community providing the necessary supporting conditions.

The final example involving two species is somewhat special in the sense that our two different species could be two specimens of the same one. It is well known that the interactions between different species but also between one specimen of one species with its neighbour can be modulated by the external stress. It has been shown that these interactions should shift from negative (competition) to positive (facilitation) across gradients of increasing external stress. This effect has been called the stress gradient hypothesis. To measure the interactions, researchers usually perform neighbour removal experiments, that consist in removing the neighbours around a target plant. After some time of growth of the target plant, its biomass is measured and compared to the biomass when the neighbours are left intact. If the biomass without neighbours is lower than with intact neighbours, this means that there was facilitation between the target plant and its neighbours. A biomass without neighbours larger than with intact neighbours signals competition. For example, in [52], nurse trees create a favorable environment in a very arid region, shedding the sun light and keeping the moisture of the soil. The authors showed that the outcome of the interactions between understory species is competition at the center of the canopy, where the stress is low, and switch to facilitation at the border of the canopy where the stress is higher.

We model the neighbour removal experiments by running the simulations with two species that represent two groups of the same species (in that case they have the same growth and death rates)
or different species. Then the neighbours are removed and their concentration is set to zero. The neighbours are called here species A and the target plant is called species B.

![Figure 10](image1.png)

**Figure 10.** Evolution of the abundance of the two species, A and B versus time, with competition. For species A (black line), $x(0) = 1.0 \times 10^{-3}$, $a = 1.0$, $f_{xy} = 0.0$, $h_{xy} = 0.1$, $\lambda = 0.1$ and for species B (red line), $y(0) = 1.5 \times 10^{-3}$, $b = 1.0$, $f_{yx} = 0.0$, $h_{yx} = 0.3$, $\mu = 0.1$. The abundance of species A, $x$, is set to zero at time $t = 30$.

With pure competition between the two groups, the target species (B) starts to grow when the neighbours (A) are removed (Figure 10).

![Figure 11](image2.png)

**Figure 11.** Evolution of the abundance of the two species, A (full line) and B (dashed line) versus time, with facilitation. For species A (black line), $x(0) = 1.0 \times 10^{-2}$, $a = 3.0$, $f_{xy} = 0.1$, $h_{xy} = 0.0$, $\lambda = 0.1$ and for species B (red line), $y(0) = 1.0 \times 10^{-2}$, $b = 1.0$, $f_{yx} = 0.5$, $h_{yx} = 0.0$, $\mu = 0.1$. The abundance of species A, $x$, is set to zero at time $t = 30$.

With pure facilitation, the abundance of the target species decreases and a new equilibrium is reached, lower than the one before the removal (Figure 11).

We turn now to the consideration of three species and their interactions. The simulations were performed using the ‘additive’ assumption for the capacity function. While the ‘multiplicative’ one has the advantage of introducing pairwise interactions it has also a major drawback: when two species happen to vanish the corresponding factor in the capacity function becomes indeterminate. The additive ansatz is not plagued by this and, as a matter of fact, it does simplify calculations. Since
we are going to work with three species we denote them as A, B and C. We keep the same notations for the facilitation and hindrance parameters as for two species. The death rates of species A, B and C are respectively $\lambda$, $\mu$ and $\eta$. We do not intend to present a complete exploration of the parameter space and the possible consequences. We shall rather present a selection of results which highlight the richness of the interactions.

In Figure 12 we show an evolution which is reminiscent of the famous Tilman drawing. In this classic example, Tilman shows the successional process involving grass and non-grass species in old fields in a more competitive than facilitating case.

Figures 12 and 13. Evolution of the abundance of three species versus time. For species A (black line), $x(0) = 1.0 \times 10^{-2}$, $a = 3.0$, $\lambda = 0.1$, $f_{xy} = 0.0$, $f_{xz} = 0.5$, $h_{xy} = 3.0$, $h_{xz} = 0.0$. For species B (red line), $y(0) = 1.0 \times 10^{-3}$, $b = 1.0$, $\mu = 0.1$, $f_{yx} = 1.0$, $f_{yz} = 0.0$, $h_{yx} = 0.5$, $h_{yz} = 0.0$. For species C (blue line), $z(0) = 0.8$, $c = 2.0$, $\eta = 1.0$, $f_{zy} = 0.0$, $f_{zx} = 0.0$, $h_{zy} = 2.0$, $h_{zx} = 2.0$.

In Figure 12 we show an evolution which is reminiscent of the famous Tilman drawing. In this classic example, Tilman shows the successional process involving grass and non-grass species in old fields in a more competitive than facilitating case.

Figure 13 shows an evolution of three species where the first two have a mutual facilitation and evolve in a pattern similar to that of Figure 8. However when, much later, the third species, C, arrives hindering the growth of species A but facilitating that of B, the equilibria do change and the relative abundances are reshuffled.
An interesting situation is presented in Figure 14. Here species C starts growing but its competition with A pushes it to near extinction. However, the late arrival of species B, which is in mutual cooperation with the other two not only revives species C but it also pushes A to a higher equilibrium.

In the figures above we presented situations where two of species disappeared in the long run (Figure 12) and two where all three species survived (Figures 13 and 14). It goes without saying that a situation where only one of the three species arrives in the long run is equally possible.

5. Discussion

5.1 The interaction compass in a single model

The presence of mutable interactions in plants explained by the stress gradient hypothesis underscores the necessity to include positive, negative, and neutral interactions in biological systems [1]. Our model captures the various types of ecological interaction (mutualism, neutralism, pure competition, etc) depending on the values (or intervals) of the parameters \(f_{xy}, f_{yx}\) and \(h_{xy}, h_{yx}\) in (19a) and (19b).

The first pair quantifies facilitation while the second one corresponds to hindrances between the two species. The mathematical structure of (19), together with the generalization for more species, ensures the dynamics remains regular at any time instant. In practice, this means that populations never diverge, even for simultaneous cooperation. Note that we do not impose explicit resource dynamics, which is often used to limit the exponential growth in mutualist partner species. This simplification allow us to explain the complex patterns that emerge from species interaction alone without prior knowledge about the organisms’ physiology or the details of the spatial distribution of resources, extraction, exchange, spatial diffusion and movement patterns of individuals or subgroups when applicable.

As a result of this compact formulation, the plasticity of ecological interactions is attributed to the dependence of \(\{f_{xy}, f_{yx}, h_{xy}, h_{yx}\}\) on external stress factors. The interaction is positive, negative, or neutral depending on the sign of the difference between facilitation and hindrance parameters, \(f_{xy} - h_{xy}\). The case \(f_{xy} = h_{xy} = 0\) bring us to the familiar scenario of independent species but the situation is less intuitive for other values. In particular, the interspecific competition is higher than...
the intraspecific with $f_{xy} = h_{xy} > 1$ but the facilitation term compensates and produces a null effect in the end. In Figures 10 and 11, we simulate experiments in which the plants surrounding a target species are completely removed from the environment at $t = t_0$. The discontinuity of the growth of the target species is proportional to $(h_{xy} - f_{xy})$. In Figure 10 (Figure 11), the discontinuity is positive (negative) in agreement with the competition (cooperation) driven process. The removal of smaller amounts of neighbours (instead of all of them) corresponds to discontinuities with different amplitudes. If the fraction of removed individuals can be estimated, then one can compute the coefficients $f_{xy}$ and $h_{xy}$ under the assumption that stress factors remain constant.

5.2 Asymmetric facilitation improves survival and invasion odds

We do not claim our model is the only one to describe the full range of interactions in ecology. On the contrary, there exists a plethora of models that produce the same effect as discussed in the previous sections. Here, the population maximum for each species is dynamically adjusted to reflect the influences of other elements of the community. It expands the foundations put forth by Kuno by considering the positive role of facilitators in addition to the negative impact of competitors. The results in Figures 4 and 5 reinforce this message in which coexistence occurs between competitive species as long as the intraspecific competition is larger than the interspecific one, i.e. $h_{xy} < 1$ and $h_{yx} < 1$, as reported in [45], and in agreement with the Chesson’s coexistence theory [17].

In the context of a pure competitive scenario, the equilibrium densities sit at unitary values after species exclusion, or values lower than one which reflects the sub-optimal growth under competitive coexistence. In the case of species exclusion, the fittest species tend to dominate and exclude the other. The exception for this rule occurs when the less fit species B excludes the other due to a stronger competitive barrier for the invader (priority effect) which we depict in Figure 6. The most notable consequences of the ecological priority effect can be appreciated in the wake of large disturbances or during the colonization of new regions. In both cases, the effect can lead ecosystems with similar biological background into distinct successional routes and thus different community structures.

A remarkable phenomenon takes place when the facilitation is asymmetric. In Figure 7, a species with higher fitness (B) invades an environment with another population already entrenched. Instead of triggering the priority effect and thus species exclusion (see Figure 6), the species with lower fitness (A) but higher initial headcount keeps its dominance and, simultaneously, limits the growth of B. The inversion is only possible because the asymmetric facilitation pushes up the sub-optimal species A which in turn increases the growth pressure on the invader B. This symbiosis loosely resembles the husbandry of species B by A in a cooperative-competitive process.

Conversely, the successful invasion of A into a region with a stable population of species B depends, crucially, on biological processes that mirror facilitation (see Figure 8). This happens because the stability of the population B, as an initial condition, reduces the window of opportunity for species A to invade since it is less apt. The facilitation in this context balances the negative effects of the competition and, for large enough values of facilitation, A can overthrow the more adapted species B reversing the core idea behind species exclusion.

5.3 Applications to conservation efforts

The loss of biodiversity has been acknowledged as a global and widespread issue that directly or indirectly affects human livelihood and health. It has also been linked to the reduced exploration of ecosystems and, thus, the elimination of niches which creates a downward spiral tendency that only accelerates the exclusion of species. Yet, ecological conservation faces a tremendous number of challenges. The most pressing ones take place at global scales such as climate changes and habitat degradation. At local scales, subtle effects surface ranging from biological invasions by aggressive competitors to changes in interspecies interaction induced by varying environmental stress (anthropogenic
or not). A question of practical interest therefore arises on how these effects impact the ecological succession at typical time scales pertinent to recovery efforts.

To answer that question, it is convenient first to revisit the famous experiments put forth by Tilman in the late 80s [22]. In short, the experiments describe the various stages of the ecological succession observed in old fields in Cedar Creek Natural History Area (CCNHA), Minnesota. Old fields comprise the collection of abandoned agricultural areas sorted according to their abandonment date, where each area corresponds to a certain stage of the succession. Data on plant diversity, biomass, and abundance span more than 80 years and remains to date one of the most iconic representations of plant succession. The experiments conducted at CCNHA have served to identify the environmental constraints and the basic mechanisms associated with plant interactions in order to build the foundations of a modern predictive ecological theory.

In the early stages, the successional structure at CCNHA depicts the alternate dominance between short-lived agricultural weeds and perennial grass with notable differences in the trait distribution for colonization, resource capture, and biomass distribution. For the three more common and representative species, the plant succession occurs between the *Agrostis scabra*, followed by *Agropyron repens*, and finally by the superior competitor *Schizachyrium scoparium*. The former displays enhanced colonization traits with improved seed production and dispersal. As a result, *Agrostis* tends to be the early colonizer, later displaced by *Agropyron*, which allocates more biomass to the quick formation of roots and specialized root tissue (rhizome) to increase nitrogen capture. *Schizachyrium* lacks the competitive ability to be an early colonizer or compete with the fast growing *Agrostis*. However, once *Agropyron* becomes dominant, *Schizachyrium* profits from its lower nitrogen requirements to persist in the habitat to become the dominant species. In Figure 12, the generalization of our model with three competing species recovers the general aspects of the data presented by Tilman.

At early stages of plant succession, the general trend mirrors the exclusion of species. However, a growing body of work suggests that maximum biodiversity takes place at mid-succession stages, as reported for boreal forests [53]. The strong resource competition experienced by fast growing colonizers is replaced, in part, by a mixture of hindrance and facilitation between shade-tolerant species, leading to the creation of new niches and the efficient partition of existing ones. While this can be complicated in competition-driven models, it is only a matter of parameter adjustment in our model. In fact, it is easy to tune the parameters for three species in order to produce periods with reduced growth, resembling the plateau-like curves generally associated with plant succession. Similar to the case of two species, facilitation parameters favor species coexistence and they can even invert the final community structure depending on their relative amplitude compared to hindrance ones. Figure 13 exhibits a case in which a sub-optimal species become the dominant in a given environment by profiting from the growth of an invader. Note that if one is not aware of the presence of the invader, one would (incorrectly) conclude that the subdominant species somehow evolved or improved its competitive abilities in a very short timeframe.

The biodiversity of a given region is also linked to the presence of foundation species, functional groups of habit-forming species that mold the ecosystem [24]. Their decline often precedes the passage towards a new stage of the ecological succession, which can be either an advancement or a regression. The latter can occur by natural means (natural fires and similar events) or by degradation of the habitat. In the first case, the population of foundation species experiences a reduction but rebounds later (see Figure 8), while in the second case the foundation species become less efficient competitors. For mature ecosystems, the regression to previous successional stages implies a loss in biodiversity which might take years to decades to recover from. Therefore, foundation species are generally accepted as the primary targets for conservation efforts.

However, the restoration of degraded habitats still remains a challenge and often requires long-term commitment and resources. In the short-term, another burdensome task concerns the restoration of ill-adapted organisms in degraded conditions: the target species for conservation actions might
disappear due to the pressure of competitors more adapted to the current conditions. Thus, it is reasonable to look for mechanisms that mitigate the abundance loss of foundation species if one hopes to maintain the correct functioning of the system. A pathway to reverse the decline consists of actions which re-introduce or stimulate the growth of supporting species. Figure 14 depicts the facilitation-driven mechanism to preserve the foundation species. The introduction of the supporting species compensates the reduced competitiveness of the target ones and reverses the population exclusion. Because the supporting species are also successful invaders, they thrive in the degraded habitat and can maintain themselves without external help. In practice, the early introduction of supporting species just accelerate the return to the target stage of the ecological succession. Without them, the return interval would be increased by the waiting time necessary for the system to meet the required conditions for the successful invasions of foundation species, in agreement with the emergence of facilitating processes in mid-succession stages [53].

6. Conclusion

In this paper, we have proposed a new model that extends the Kuno model to address multispecies population dynamics focusing on the facilitation and cooperative regime. Our extension implicitly includes the stress gradient hypothesis, i.e. facilitation parameters. It allows the model to address non-trivial transients, such as biological invasion, ecological succession, Tilman drawings etc. Also, it naturally avoids divergences always presenting finite asymptotic behaviors, i.e., the species carrying capacity is an emergent quantity. Other than allowing robust behaviors, the model also allows fine tuning, which can be an effective mechanism in the recuperation of ecological systems. The main issue we want to stress is the richness of transient behavior, with support of ecological examples. The long time behavior can be analytically inferred by stability analysis. Although we have not performed an exhaustive study in the parameter space, which we have kept to the minimum dimensions, we are able to retrieve several known ecological regimes. Nevertheless, a more systematic analysis of the parameter space could reveal other interesting regimes especially when the number of species is increased.

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**APPENDIX A**

The example explores long-term data of vegetation succession and recovery after perturbations in a permanent parcel maintained by Woods [49], at Dukes Research Natural Area (DNA), Michigan, USA. The original data represent the diameter at breast height (DBH) of wood stems discriminated by plant species in several plots, totaling 20 ha. The data regard a chronosequence of 19 years, from 1989 to 2007, as previous samples were taken at very large intervals. The region is periodically affected by winds, with a strong event in 2002, highlighting the relevance of this database to understand recovering processes.

We explored the DNA data as a single site, summing the respective DBH of species by year. Of the 32 species observed in the region (one is unknown), 24 were observed at least once since 1989.
The dimension of the dataset is reduced by grouping species as follows. We consider the population DBH over time as only variable and group species by their relative variation over time. This sorting scheme eliminates the necessity of ad hoc information about individual species as per usual in the formal functional analysis.

More specifically, we employed the Principal Component Analysis (PCA) based on covariances of species DBH. The PCA indicated at least 4 relevant dimensions to explain the data dispersion (eigenvalues larger than 1) following Kaiser criterion. Next, we calculate the dissimilarity matrix based on Euclidean distances in species coordinates. The hierarchical clustering (Ward method) is subsequently used and produces two groups (Figure A1), which are for our purposes considered as distinct functional groups.

Note that our sorting approach creates competing groups in a simpler manner compared to traditional trait-driven approaches, which often require in-depth knowledge about the pertinent species involved. This is only possible because we only intend to group species based on their relative dominance. Hence, we denote “Group 1” the group formed by dominant species; and “Group 2” the species that grow when the density of Group 1 decreases. Next, we compute the total DBH per group as it provides a quantitative functional response, allowing us to investigate the interactions between both groups in terms of population dynamics.

Figure A2 depicts the DBH for each group over time. Species in Group 1 are periodically disturbed by strong winds, an external factor that negatively affects their DBH. The decrease of the dominant group triggers a brief spurt of growth by species in Group 2, suggesting a competitive context. Shortly after the disturbances, the population returns to the original levels, suggesting that the secondary succession follows similar trajectories in the region.

Figure A.1: Hierarchical spectral clustering based on species DBH in a chronosequence. The dashed line represents the cutoff distance linkage to create two groups. The classification does not rely on species traits.
Figure A.2: Successional dynamics in Dukes Research Natural Area, Michigan, USA. The curves represent the DBH of tree species after grouping. (left) Raw DBH values for Group 1 and Group 2 per year. (right) Normalized values.