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The Ecology of Plant Interactions: A Giant with Feet of Clay

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Abstract

Ecologists use the net biotic interactions among plants to predict fundamental ecosystem features. Following this approach, ecologists have built a giant body of theory founded on observational evidence. However, due to the limitations that a phenomenological approach raises both in empirical and theoretical studies, an increasing number of scientists claim the need for a mechanistic understanding of plant interaction outcomes, and a few studies have taken such a mechanistic approach. In this synthesis, we propose a modeling framework to study the plant interaction mechanistically. We first establish a conceptual ground to frame plant-plant interactions, and then, we propose to formalize this research line theoretically developing a family of individual-based, spatially-explicit models in which biotic interactions are an emergent property mediated by the interaction between plants' functional traits and the environment. These models allow researchers to evaluate the strength and sign of biotic interactions under different environmental scenarios and thus constitute a powerful tool to investigate the mechanisms underlying facilitation, species coexistence, or the formation of vegetation spatial patterns.

Keywords: Plant-plant interactions; Stress gradient hypothesis; Functional trait ecology; Inter-plant distance; Individual-based models; Consumer-resource models

> “*Vegetation, in its broader aspects, is composed of a number of plant individuals. The development and maintenance of vegetation is therefore merely the resultant of the development and maintenance of the component individuals, and is favored, modified, retarded, or inhibited by all causes which influence the component plants. According to this view, the phenomena of vegetation depend completely upon the phenomena of the individual.*
>
> (Gleason 1917)

> “*Here, competition is defined as the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space. This choice of words allows competition to be defined in relation to its mechanism rather than its effects.*
>
> (Grime 1977)

1. Introduction

Fighting against the current anthropogenic environmental crisis (Steffen et al. 2018) requires understanding global-scale spatial and temporal vegetation responses to climate change, mediated, at least partially, by plant interactions (Scheiner et al. 2011). Plant theoretical ecologists explain ecosystem structure and dynamics based on biotic interactions. For example, net interactions allow to forecast climate-change scenarios (Brooker 2006) and explain the efficacy of plant communities at up-taking atmospheric carbon, thereby buffering climate change (Franklin et al. 2016). Plant interactions shape the diversity and distribution of land plants globally (Tirado and Pugnaire 2005, Bulleri et al. 2016) and their persistence under climate change conditions (Valladares et al. 2015). Spatial models for vegetation dynamics in semiarid drylands predict the existence of sudden, hard-to-revert desertification events (Rietkerk et al. 2002) and how changes in the spatial distribution of plants might help avoiding them (Rietkerk et al. 2021)

Empiricists have focused on validating ecological theories measuring net interactions among plants. Theory states that more intense intraspecific relative to interspecific interference stabilizes species coexistence (Chesson 2000) –species coexistence being axiomatic to species diversity. Moved by these results, many empirical studies compare intraspecific with interspecific net interactions to explain biodiversity variability across biomes (Lamanna et al. 2017, Adler et al. 2018). An alternative theory states that facilitation by nurse plants promotes coexistence, expands species' niches, and ultimately leads to higher biodiversity in stressful habitats (Callaway 1995, Bulleri et al. 2016). Several empirical studies have tried to validate such predictions by reporting positive net interactions among plants (Soliveres and Maestre 2014). Models predict that vegetation patchiness in drylands could indicate imminent desertification transitions driven by facilitation (Kéfi et al. 2007). These predictions motivated empirical studies relating vegetation cover and patch size distributions to the provision of ecosystem functionality (Berdugo et al. 2017).

Nevertheless, both modeling and empirical studies have recently evidenced the weaknesses of this phenomenological approach. For example, models for vegetation pattern formation reproduce the same family of patterns observed in drylands worldwide (Borgogno et al. 2009) regardless of whether net interactions among plants are assumed to be purely competitive (Martínez-García et al. 2013, 2014) or a combination of facilitation and interference acting at different scales (Rietkerk et al. 2002). Mechanisms creating these patterns remain unknown, even though the dynamics of recovery of the ecosystem function strongly depends on them (Martinez-Garcia et al. 2021). On the other hand, empirical studies based on the observation of net interactions are the subject of unavoidable biases. Plant demographic studies are generally labor-intensive, as they require large sample sizes, long-term, long-range data sets, and large arrays of variables (Ehrlén et al. 2016). The analysis of these demographic data to assess biotic interactions may be prone to strong statistical biases in detecting negative density-dependences, which questions a large body of literature explaining plant species biodiversity across biomes (Detto et al. 2019). Most studies on species coexistence are observational, which makes it challenging to control neighbor variability and leads to omitted variable biases in the estimated effects of neighbors on targeted plants (Rinella et al. 2020). A mechanistic study of plant interactions has gained prominence over the last two decades (Michalet and Pugnaire 2016). However, unveiling the mechanisms that underpin plant interactions is a pending task for ecologists.

We hence argue that the ecology of plant interactions is a giant with feet of clay. We call it ‘a giant’ because it supports many relevant scientific theories. Nevertheless, it has ‘feet of clay’ because it stands on weak foundations, and an increasing number of scientists yearn for a more nuanced understanding of plant interaction mechanisms. Here, we aim to establish a modeling framework to study plant net interactions that relies on a detailed mathematical description of its underpinning biophysical processes. To this end, we first set a common ground by defining what a mechanistic approach is, and why a mechanistic study of plant interaction outcomes must prevail in the context of various ecological questions. We discuss the spatial and temporal dynamics of the interactions, stressing the inaccuracy of accepting a static picture of the net interaction among two plants. We then present a spatially-explicit, individual-level modeling framework to study plant interactions based on their functional traits and the biophysical environment. We discuss how such models can improve our mechanistic understanding of phenomena such as plant facilitation, species coexistence, or self-organized vegetation spatial patterns.

2. The mechanistic study of plant interactions

Biotic interactions happen at various biological scales, from the pairwise interactions among plant populations, i.e. the reciprocal effects of two populations on each other's demographic dynamics, to the net effect that an individual plant has on the fitness of a neighbor, and to the biophysical and ecophysiological processes underlying this net interaction between individuals. A definition of what is 'mechanistic' and 'phenomenological' depends largely on each specific research question and approach, and in the context of plant interactions the biological scale of study is decisive. Here, we use the adjective 'phenomenological' to refer to studies of plant interactions based on the net interactions (**Fig 1 a** and **b**). We thus consider that models assuming net interactions and observational studies reporting net interactions are phenomenological.

The 'mechanistic' approach to plant interactions has received increasing attention over the last decades. However, we still lack a consensual definition of what we consider 'mechanistic' in the field of plant interactions. For instance, some researchers have used this word to refer to demographic processes, such as the dispersal or growth rates of the interacting populations (Jeltsch et al. 2008). In niche theory, 'mechanistic' refers to the species' niche overlap and their relative fitness differences (Letten et al. 2017, Godwin et al. 2020). However, a classic approach to the 'mechanistic' understanding of the interaction between plants requires investigating how plants alter their abiotic environment, and how this environmental change ultimately affects other plants (Grime 1977, Tilman 1980).

The mechanistic approach to competition for shared resources conceived as an emergent property of consumer-resource dynamics raised in the second half of the twentieth century. The first studies that considered explicitly changes in the abundance of a specific resource as the mechanism leading to plant interactions go back to 1960*s* (Grime 1963, Grime and Jeffrey 1965). Later theoretical formalizations of such approach, in the context of the competitive exclusion dilemma (Hardin 1960, Hutchinson 1961, Macarthur and Levins 1967, Grime 1973), gave rise to the development of consumer-resource models of competing populations (MacArthur 1970, Tilman 1976, 1977) based on Lotka-Volterra equations (Lotka 1920, 1924, Volterra 1926). Those models were later adapted to study plant species coexistence in habitats that are heterogeneous in space or time (Tilman 1988, Tilman and Pacala 1993, Downing and Tilman 1994). Many publications have followed this mechanistic school to study competition for a shared resource in plant communities to our days (Chesson 1994, 2000, Adler et al. 2007, Harpole and Tilman 2007, HilleRisLambers et al. 2012, Kleinhesselink and Adler 2015, Letten et al. 2017, Germain et al. 2021).

The mechanistic approach that we endorse in this article is not conceptually different from that already defended a few decades ago by pioneer ecologists like Grime or Tilman. Our goal here is to extend it to include more diverse mechanisms of plant interaction and thus make it suitable to investigate questions in plant ecology other than species coexistence. Indeed, while the most influential mechanistic research on plant interactions published between the 60's and the 80's were focused on resource competition, by the end of that period a few studies started to highlight the importance of positive interactions among plants (Hunter and Aarssen 1988, Bertness and Callaway 1994, Callaway 1995), and of negative non-trophic interaction forces such as allelopathy (Whittaker and Feeny 1971, Rice 1984, Mahall and Callaway 1991). These studies added a layer of complexity to the study of plant interactions, as they suggested that the net effect of a plant on a neighbor's fitness is far from being limited to competition for trophic resources. Instead, it is an emergent property resulting from several trophic and non-trophic interaction forces acting together, which can fall in any point of the facilitation-interference[1] gradient (Callaway and Walker 1997, Schenk 2006, Wright et al. 2014). For instance, a plant can modify the water available for another plant through many biophysical mechanisms, including but not limited to soil water uptake by roots (**Fig 1 c**). This broader view to plant interactions concerned the species coexistence study (Mcintire and Fajardo 2014, Bulleri et al. 2016), but it went beyond such debate and gave rise to new major ecological theories, such as the stress gradient hypothesis (Maestre et al. 2009) and the self-organized formation of vegetation spatial patterns (Borgogno et al. 2009).

This approach is complex and challenging, because it requires accounting for many physicochemical pathways involving several resources. To sort such diversity of mechanisms, we conducted an exhaustive literature review on the biophysical mechanisms underlying the plant interactions (**Supplementary Material**) and classified them as 'primary processes,' 'intermediary processes,' and 'interaction forces'. The primary processes are the direct effects of influencing plants on their immediate surroundings; the intermediary processes are biophysical processes mediating between a primary process and an interaction force; the interactions forces are the biophysical changes resulting from the influencing plant that affect the influenced plant directly. The interaction forces are especially important because they are the proximal cause of the interaction (**Fig 1 d**). By balancing the effects of all interaction forces, we can link the interaction mechanisms to the phenomenological net interaction (**Fig 1, grey arrow**).

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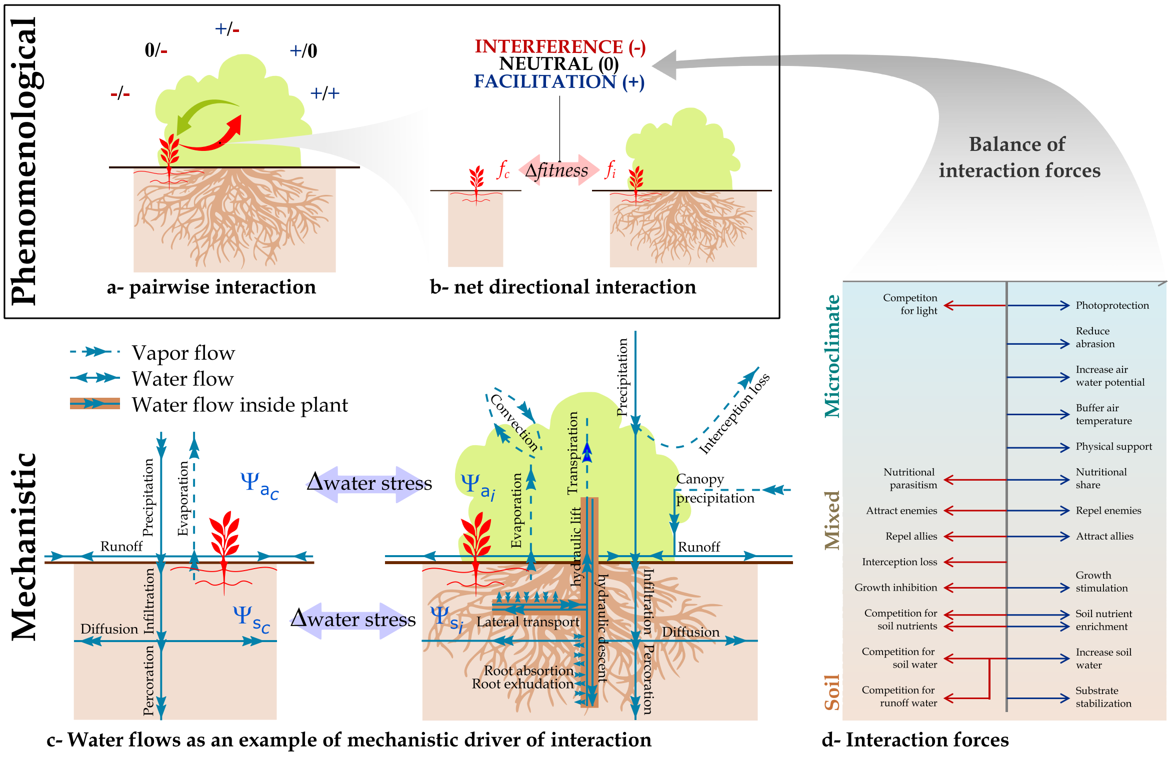
[1] Through this review, we use "interference" to refer to the net negative effect of a plant on a neighbor (or a species on another) to accentuate its difference with competition (for resources).



a- pairwise interaction

b- net directional interaction

c- Water flows as an example of mechanistic driver of interaction

d- Interaction forces

Figure 1: The different scales to study interactions can be phenomenological, such as **a-** the pairwise interaction (bidirectional interaction between a pair of plants) or **b-** the net interaction (the fitness difference for a focal plant [red] when interacting with an influencing plant [shrub] compared to when free from the interaction). They can also be mechanistic, as is the case of **c-** the differences in water stress experienced by a focal plant [red] in the presence and absence of an influencing plant [shrub]. While many biophysical mechanisms underpin the net interaction, the ultimate causes of the interaction are the **d-** interaction forces (see **SM**). Δ stands for a difference. Ψ stands for the water potential. Sub-indexes stand for air (*a*), soil (*s*), control plants without neighbor (*c*), and interacting plant (*i*).

3. The dynamic nature of interactions

Researchers can determine empirically, or assume theoretically, the net interaction among a given pair of plants at a specific location and moment. However, this only provides a static and phenomenological picture of the interaction. Plant interactions vary in space and time, changing their strength and switching their sign. This variability might be due to changes in the distance between the interacting plants, in their functional traits, and in the environmental factors (**Fig 2**). As we will argue in this section, this variability is crucial but still poorly understood, and ecological theories accounting for this variability must describe the plant interaction mechanistically.

First, the interaction between a pair of plants will depend largely on the distance between the plants. The Janzen-Connell hypothesis (Janzen 1970, Connell 1971) suggested, for the first time, that plant interaction strength decreases gradually as the distance between two plants increases. More recently, ecologists became interested in identifying scale-dependent feedbacks, i.e., switches in net interaction sign with inter-plant distance. Some studies have reported scale-dependent feedbacks in which facilitation dominates close to the influencing plant and interference when plants are farther apart, because plants increase water infiltration locally and reduce the water that can infiltrate in their surroundings (Bromley et al. 1997). In contrast, other studies have found that plants must interfere with a very close neighbor but facilitate if it is farther when both the environmental stress in open areas and the competition for resources near the neighbor are elevated, because facilitation may emerge at intermediate distances. This may happen when competition for light is excessive in intense shade but shade ameliorates the thermic and hydric environment for plants (Eränen and Kozlov 2007), or when competition for water is high but transpiring plants decrease the air water stress to neighbors (Trautz et al. 2017). The coexistence of these opposing scale-dependent-feedback hypotheses, and the lack of an explanation of the contexts in which they may occur, illustrates both how little we know about the variability of interactions with inter-plant distances and how important this distance can be at shaping the interaction outcome. Additionally, it has been investigated how the foraging strategy of competing plants changes with interplant distance, affecting their inversion into foraging organs and hence their phenotype. Plants can shift from a root overproliferation to a root underproliferation strategy as the interplant distance increases (Cabal et al. 2020).

Second, the functional traits of the two interacting plants are a major driver of changes in net interactions. Global-scale studies relate the intensity and the sign of the net interaction between plants to their functional traits (Kunstler et al. 2016, Fichtner et al. 2017). Plant functional traits have an evident genetic background that is species-specific (Pereira and Des Marais 2020). Interaction studies report co-occurring cases of interference and facilitation where shifts in net interaction depend only on the species identity of the influenced (Choler et al. 2001) or the influencing individual (Pugnaire et al. 2004). However, functional traits are not restricted to species identity (Cadotte et al. 2011). They vary substantially with ontogeny, and plant size is a paradigmatic example of that change. Some studies have reported shifts in the net interaction with increasing size of the influencing plants (Miriti 2006), of the influenced plant (Soliveres et al. 2010, Álvarez-Yépiz et al. 2014), and when both plants grow together within species pairs (Schiffers and Tielbörger 2006). Moreover, some plants show a much greater intraspecific than interspecific functional trait diversity across large environmental gradients (Anderegg et al. 2021). Modern functional ecology underscores the need to account for the environmentally induced phenotypic plasticity that strongly affects plant net interactions (McGill et al. 2006, Valladares et al. 2007). The mechanistic link between functional traits and plant net interactions is, however, far from well understood (van der Merwe et al. 2020).

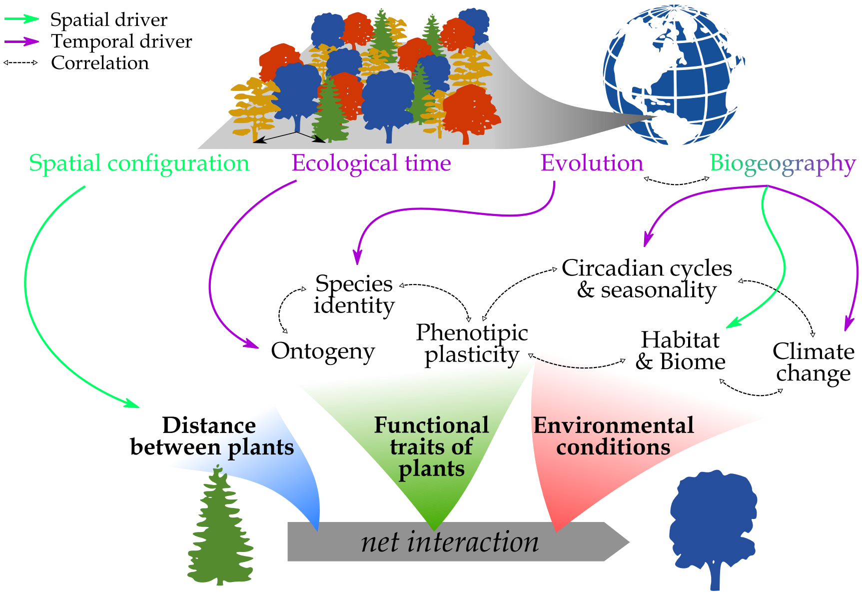


Figure 2: Schematic of the main spatial and temporal drivers of the net interaction, mediated mechanistically by the distance between two individual plants, their functional traits, and the environmental conditions in which the interaction occurs.

Third, environmental quality is a major driver of changes in net interactions. Grime (1973) found, for the first time, that competition could become more intense with increasing environmental quality. Later, community ecologists became interested in positive interaction effects among plants (Hunter and Aarssen 1988) and developed the stress gradient hypothesis, according to which positive interaction forces may dominate when the environmental stress gets more intense (Bertness and Callaway 1994). This theory predicts that spatial variability in habitat conditions modifies the dominance of interference or facilitation, with mild stress conditions maximizing facilitation (Michalet et al. 2006, Holmgren and Scheffer 2010). Temporal heterogeneity may also drive switches in the sign of net interactions due to changes in environmental stress between years (Valladares and Pearcy 2002, del Río et al. 2014), seasons (Breshears et al. 1998, Kikvidze et al. 2006), and even at the scale of days (Wright et al. 2015). While the stress gradient hypothesis has fostered the scientific interest in facilitation, the biophysical mechanisms explaining how plant interactions respond to environmental changes remain largely understudied (Soliveres et al. 2015).

A few studies have investigated the dynamics of plant net interactions in time and space when all three variability factors act together. Wright et al. (2014) showed how biotic (ontogeny) and abiotic (circadian cycles and seasons) temporal factors jointly drive continuous changes in the net interaction between two plants. Le Roux et al. (2013) studied the temporal shifts in plant interactions with ontogeny across two spatial environmental gradients, altitude, and wind exposure. Bonanomi et al. (2016) provided an example of how the direct abiotic effect of environmental stress combined with plasticity in the phenotypic response of influencing plants to that stress drive spatial changes in the net interaction. Rietkerk et al. (2002) investigated the biotic interaction across environmental gradients accounting for the inter-plant distance. Metz and Tielbörger (2016) considered the environmental spatiotemporal variation in plant net interactions, finding facilitation only where and when stressful environmental conditions arise. Despite these results, we are still far from understanding how net interactions vary in time and space altogether and as a consequence of the distance between plants, the functional traits of the plants, and the environmental conditions. To address this problem, ecologists need to seek a mechanistic study of the plant biotic interactions based in the biophysical processes underlying such dynamism.

3. Introducing the SIFTED models

Mathematical models are a valuable tool to formalize theories in ecology and evolutionary biology (Otto and Day 2007). We define *SIFTED* models (Spatilly-explicit Individual-based Functional Traits and Environment Driven models) as models that investigate plant biotic interactions departing from a description of their underlying biophysical and ecophysiological processes. Based on the dynamic nature of interactions reviewed herein and on what we have learned from existing ecophysiological models, we consider that SIFTED models need to account for four fundamental features of plant communities (**Fig 3**):

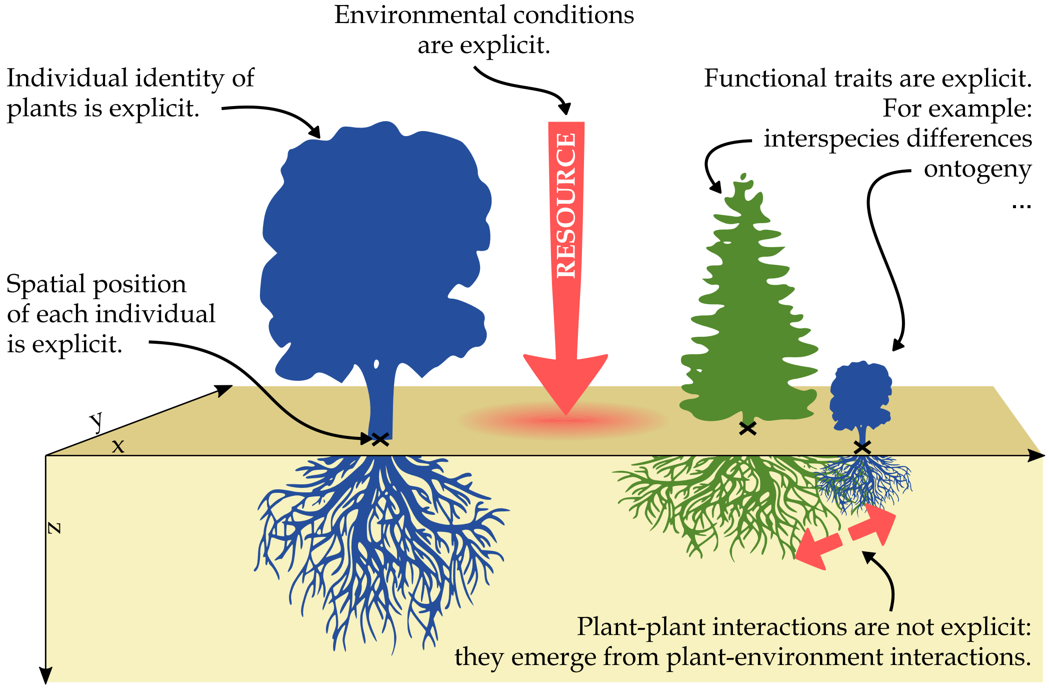


Figure 3: Main features of a SIFTED model.

(i) **Discrete individuals** (*sensu* groups of plant organs physiologically connected by sap flow). Many natural phenomena are discrete and poorly approximated by a continuous description. The study of plant behavior as an evolutionary game is a paradigmatic example of this, as plants are self-aware organisms that may engage in suboptimal strategies when competing with others (Rankin et al. 2007, Mcnickle and Dybzinski 2013).

(ii) **The spatial location of the plants**. Plants are sessile organisms that interact only with their neighbors. As we reviewed in section 3, there are several situations in which the spatial location of plants, and more specifically the distance between interacting plants, is crucial to predict the net interaction outcome.

(iii) **Plant functional traits**. Functional traits determine how a plant will interact with the environment. Plants of different species usually differ in functional traits, but plants from the same species can also be quite different from each other (Ahrens et al. 2021, Anderegg et al. 2021). For example, the age of the plant and the biotic and abiotic environment that plants experience will trigger changes in their functional traits within a species through phenotypic plasticity. SIFTED models need to account for such an intraspecific functional trait variation.

(iv) **Environmental conditions**. SIFTED models must describe physical flows of matter and energy within the community explicitly. One of the main characteristics of a SIFTED model is plant interactions are not an assumption of the model, but an emergent property based on the interaction between the plants and the environmental conditions, usually represented by resources.

SIFTED models are a particular class of individual based models (IBM) (Railsback and Grimm 2019), a modeling approach developed by theoretical ecologists departing from cellular automata (Neumann 1966, Botkin et al. 1972) that has applications in many other disciplines (De Marchi and Page 2014). IBMs were first simulations of individuals growing in independent grid cells of the size of the crown of an adult plant. Later, they became increasingly complex, incorporating ingredients such as dependence between grid cells (Shugart, and West 1980) and full explicit space (Pacala et al. 1996), and tools to treat them analytically were developed (Strigul et al. 2008, Iwasa 2010). Despite this theoretical progress, the main limitation of IBMs remains on their high computational demands and low mathematical tractability, especially when researchers target large systems and long temporal scales such as in earth system models (Shugart et al. 2018). This limitation also applies for SIFTED models. However, SIFTED models developed for small systems and short time scales can be extremely useful to investigate specific ecological questions. For instance, SIFTED models have successfully predicted the root foraging behavior of pairs of competing plants (Novoplansky and Cohen 1997, O'Brien et al. 2007, Cabal et al. 2020) and simulated relatively small tiles of forest in which a few individual trees compete for light (Strigul et al. 2008, Kolobov and Frisman 2016, Eloy et al. 2017).

4. SIFTED models and facilitation research

Facilitation is a widely recognized plant net interaction outcome with extensive empirical support (Brooker et al. 2008, Soliveres and Maestre 2014, Michalet and Pugnaire 2016). However, our theoretical understanding of the mechanisms underlying the emergence of facilitative relationships among plants—which must be competing for resources—is still poor. In this scenario, SIFTED models can predict the necessary conditions for facilitation to occur. For instance, canopy shade is a primary process affecting diverse biophysical mechanisms. It is responsible for competition for light and buffers plant thermal and hydric stress (Kothari et al. 2021) (**Fig SM1**). Therefore, changing canopy shade intensity or its effect under different abiotic conditions can drive switches in the net interaction sign (Valladares et al. 2016). Zavala and Bravo De La Parra (2005) developed a SIFTED model that coupled light penetration through the canopy and water flows with a size-structured forest simulator to explore competition-to-facilitation shifts in diverse light and hydric environments. In a second example, the stress gradient hypothesis states that facilitation interactions may emerge as we move towards drier conditions in a water availability gradient (Maestre et al. 2009), but there is little we know about why this is so. Butterfield et al. (2016) developed a SIFTED model simulating water flows in soils and plants across gradients of increasing precipitation to test the conditions in which facilitation emerges. Their simulations demonstrated that the positive effects of plants on soil moisture decreased with increasing aridity. However, they found that the positive effects of shrub cover are maximum at mid-points of the aridity gradient in extreme years. Their SIFTED model hence showed that the stress-gradient hypothesis is true for specific aridity gradients.

5. SIFTED Models and species coexistence

Understanding how species that share the same resources coexist is a long-standing goal of ecological theory. Initially, researchers tackled this problem from a demographic approach, i.e., based on "species interaction" models where assumed interactions among populations of different species lead to exclusion or coexistence. This approach dates back to the logistic equation for intraspecific competition (Verhulst 1845), later extended to systems with more than one species (Lotka 1920, 1924, Volterra 1926). At least two factors explain the great success of demographic models during the last century. First, they provided very good fits to contemporary empirical observations (Hewitt 1921, Gause et al. 1934). Second, they are mathematically tractable (Wangersky 1978), allowing researchers to identify simple rules that enable coexistence between antagonistic species (Chesson 2000, Hubbell 2001). Modern studies have tended to adopt an approach based on functional groups rather than species (McGill et al. 2006, Jeltsch et al. 2008, Zakharova et al. 2019). These models, however, still describe population dynamics (now defined in terms of functional groups) and do not account for how such functional traits relate to the mechanisms acting at the level of individual plants.

The first concerns about the low suitability of a demographic approach to study interactions in plant communities were probably raised by Fagerström (1988), who highlighted that sessile organisms must only interact with close neighbors. Interactions in Lotka-Volterra equations rely on the so-called law of mass action, which assumes that individuals occupy the entire population range uniformly and are equally likely to interact with each other (Hutchinson and Waser 2007, O'Dwyer 2020), an assumption that breaks when individuals do not occupy the entire population range uniformly (Martinez-Garcia et al. 2020). A nouvelle vague of plant coexistence studies points to the direction of plant phenotypic plasticity as the right approach to understand how interacting plants share habitats and resources accounting for the local processes happening at the scale of individual plants (Turcotte and Levine 2016, Levine et al. 2017). Following this approach, many researchers have undertaken a mechanistic study of species coexistence, based on the intraspecific functional trait variation of phenotypically plastic individuals responding to the local environmental conditions (Godwin et al. 2020, Bakker et al. 2021, Escudero et al. 2021, Fajardo and Velázquez 2021, Kinlock and Munch 2021).

From a theoretical point of view, SIFTED models represent a starting point to work in that direction. For instance, Cipriotti et al. (2012, 2014) developed a spatially-explicit individual-based model to study the coexistence between several species of shrubs and grasses in a steppe. They accounted for the vertical distribution of the roots of the two plant groups as a trait and incorporated water dynamics as an environmental driver of the interactions among the individuals. While uncertainty in model parameters is one major limitation of SIFTED models, the authors developed an inverse pattern-oriented approach that allowed them to control for this problem. They identified the main bottom-up drivers of coexistence in their study site, concluding that facilitation may be unnecessary for diverse plants to cluster around large shrubs and that grass-shrub community dynamics is driven by a complex network of plant interactions that changes in space and time. More recently, Pękalski and Wang (2021) developed a SIFTED model to investigate whether two species might coexist via competitor–colonizer interactions, confirming that intense intraspecific interference may be a leading force to coexistence.

6. SIFTED models and vegetation spatial patterns

Self-organized formation of spatial patterns, which emerge because plant interactions are dependent on the inter-plant distance, have received a lot of attention from modelers (Rietkerk et al. 2004, Borgogno et al. 2009, Meron et al. 2019). We could classify most of these existing models as “continuum vegetation models” because they describe the dynamics of the aboveground spatial distribution of vegetation density defined as a continuous variable. Ecologists adopted such approach based on Turing’s seminal work to describe animal coat pattern formation (Turing 1952). Earlier continuum vegetation models encapsulate the net interaction among plants in a single kernel function (Lefever and Lejeune 1997), but soon after models incorporated scale-dependent feedbacks between water and vegetation explicitly (Klausmeier 1999). Modern formalisms account for a detailed description of the ecohydrological dynamics, including belowground processes (Inderjit et al. 2021) and the plants functional traits (Bera et al. 2021). While this state-of-the-art family of models gather most necessary features of SIFTED models, they do not account for the individual identity of plants and hence do not describe some of the mechanisms underlying vegetation growth.

While describing vegetation coverage as a continuous field is a convenient simplification in some scenarios (Meron et al. 2019), there are several reasons why SIFTED models can significantly improve our mechanistic understanding of self-organized vegetation spatial patterns. SIFTED models can incorporate demographic processes, the resource foraging behavior of plants in three-dimensional space, and biomass allocation strategies of plants. For instance, 100 kg of plant mass will not behave the same way if representing a single large tree or one hundred one-kilogram saplings, both covering the same surface of land. From a demographic point of view, the tree may die in a single discrete stressful event;

however, if there were 100 saplings, we would expect some to die yet others could survive a disturbance. In addition, the tree will reproduce and represent a source of propagules, whereas the saplings are not in their reproductive stage. Indeed, due to this biomass allocation into reproductive tissues, older trees will progressively slow down their vegetative growth whereas 100 saplings would invest all of their resources into growth (Iwasa and Cohen 1989, Pugliese and Kozlowski 1990). Finally, the way plants forage resources in the patch of land will differ significantly between both scenarios because the intensity of inter-individual competition is different. Game theory predicts that competing plants may engage in a tragedy of the commons, inefficiently growing foraging organs such as their roots (Gersani et al. 2001, Rankin et al. 2007, Cabal et al. 2020). Evolutionary game-theory models also predict changes in the amount of resources plants allocate belowground or aboveground (McNickle et al. 2016, Kim et al. 2021), which has clear implications in the resulting vegetation patterns that we observe from aerial photograph.

Vincenot et al. (2016, 2017) developed a SIFTED model to study vegetation pattern formation, including gaps, labyrinths, spots and rings, based in water availability or autotoxicity processes. Their results confirmed the prevailing theory on self-organized vegetation patterning, but also revealed the importance of individual-based processes neglected by reaction-diffusion, density-based models. For instance, they highlighted the importance of plant age, architectural growth constraints, and reproductive maturity as drivers of aggregated patterns of vegetation under water limitation. Moreover, because individual-based dynamics couple dispersal to reproduction, their approach provides a more realistic framework to investigate the impact of seasonal variability on spatial patterns. Seasonal rainfall can also be incorporated in continuum models (Bonachela et al. 2015, Veldhuis et al. 2021), but because they incorporate dispersal and reproduction as independent processes, vegetation patches will continue to expand even during extremely arid periods that do not allow for vegetation growth. Finally, although there are continuum models that account for demographic stochasticity (Martínez-García et al. 2013), they do so at the cost of losing mathematical tractability, which is one of the strengthens of a density-based description. Vincenot et al. (2016, 2017) SIFTED approach allows for a more direct treatment of stochastic demographic events, crucial to recover less regular, more realistic pattern shapes. The results yielded by their individual-based approach also presents other advantages, such as allowing to track the age and biomass distribution of the plants in the community.

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