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The ecology of plant interactions:
A giant with feet of clay

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Abstract

1. Ecologists use the net biotic interactions among plants as a major factor to predict other ecosystem features, such as species diversity, community structure, or plant atmospheric carbon uptake. By adopting this approach, ecologists have built a giant body of theory founded on observational evidence. However, growing evidence points out that this may not be the right approach.

2. The literature addressing the biophysical mechanisms underlying the plant interactions is much scarcer. A rising number of scientists claim the need for a mechanistic understanding of plant interactions due to the limitations that a phenomenological approach raises both in empirical and theoretical studies. Scattered studies have recently taken such a mechanistic approach, but we still lack a general theoretical framework to study mechanistically plant interactions.

3. In this review, we first recapitulate the elementary units of plant interactions, i.e., all the known biophysical processes affected by the presence of an influencing plant and the possible phenotypic responses of plants influenced by those processes. Second, we discuss how a net interaction between two plants emerges from the simultaneous effect of these elementary units. Third, we touch upon the spatial and temporal variability of the net interaction and discuss the links between this variability and the underlying biophysical processes.

4. We conclude by discussing how to integrate these processes into a mechanistic framework for plant interactions that must necessarily focus on the individual scale and explicitly incorporate the spatial structure of the community and environmental factors: the plant interaction models (PIM). A PIM incorporates a pair or few plants interacting with their physical environment so that the biotic interaction is not imposed but emerges from the model. This type of model can provide concise, mechanistic hypotheses to be tested empirically.

5. This review calls for a paradigm shift in the ecology of plant interactions, from the classic species interaction study towards a more mechanistic individual-level approach. It also presents a comprehensive foundation for studying the mechanisms underpinning the net interaction between two plants.

Keywords: Biotic interactions; Ecological modeling; Plant facilitation; Plant community ecology; Spatial ecology; Theoretical ecology**.**

Introduction

Biotic interactions are fundamental ecological predictors used to estimate many ecological features of plant communities. For example, plant-animal interactions shape plant communities in several ways: herbivory promotes plant biodiversity (Janzen, 1970) and limits plant productivity (Polis, 1999), and pollination prevents plant species extinction (Goulson, Nicholls, Botías, & Rotheray, 2015). However, biotic interactions are more intense between phylogenetically related taxa (Violle, Nemergut, Pu, & Jiang, 2011) and the interactions among plants (hereafter plant interactions) are of particular relevance because plants compete intensively with each other for the same resources.

Based on assumptions about the nature of net interactions among plants, theoretical ecologists explain ecosystem structure and dynamics, from the landscape to the global scale. 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, Serra-Diaz, Syphard, & Regan, 2016). Plant interactions also shape the diversity and distribution of land plants globally (Bulleri, Bruno, Silliman, & Stachowicz, 2016; Tirado & Pugnaire, 2005) and their persistence under climate change conditions (Fernando Valladares, Bastias, Godoy, Granda, & Escudero, 2015). Moreover, spatial models for vegetation dynamics in semiarid drylands predict the existence of sudden, hard-to-revert desertification events (Rietkerk et al., 2002). The importance of all these predictions is indisputable.

Pushed by these overarching theories, empirical ecologists have focused on measuring net interactions among plants. For example, theoretical studies on biodiversity maintenance state that more intense intraspecific interference 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 (Adler et al., 2018; Lamanna et al., 2017). Also, an alternative theory states that facilitation by nurse plants promotes coexistence, expands species' niches, and ultimately leads to higher biodiversity in stressful habitats (Bulleri et al., 2016; Callaway, 1995). Several empirical studies have tried to validate such predictions by reporting positive net interactions among plants (Santiago Soliveres & Maestre, 2014). Similarly, theory predicts that vegetation patchiness in drylands could indicate imminent desertification transitions driven by facilitation (Kéfi et al., 2007). These results motivated empirical studies relating vegetation cover and patch size distributions to the provision of ecosystem functionality (Berdugo, Kéfi, Soliveres, & Maestre, 2017). All these three types of studies provide phenomenological support for their respective ecological theory.

While the relevance of these theories is beyond argument, an increasing number of scientists yearn for a more nuanced understanding of the processes that lay the foundation for plant net interactions. Theories that rely on assumed net interactions among plants risk misleading the mechanisms behind their predictions. For instance, a recent study found that the environmental variation *per se* is not a key driver of species functional trait expression in the context of facilitation, indicating the need of assessing more context-specific mechanisms to understanding positive net interactions (van der Merwe, Greve, Olivier, & le Roux, 2020). In another example, models for vegetation pattern formation reproduce the same family of patterns observed in drylands around the world (Borgogno, D'Odorico, Laio, & Ridolfi, 2009) regardless of whether net interactions among plants are assumed to be purely competitive (Martínez-García, Calabrese, Hernández-García, & López, 2013, 2014) or a combination of facilitation and interference functioning at different scales (Rietkerk et al., 2002). Hence mechanisms creating these patterns remain unknown (Martínez-García & López, 2018). Additionally, recent research claims that observational studies reporting net interactions in nature may not be free from methodological and statistical biases (Rinella, Strong, & Vermeire, 2020), and eliminating biases from these data is tricky without more information about the mechanisms underpinning the interactions (Detto, Visser, Wright, & Pacala, 2019). Consequently, a rising number of empiricists and statisticians claim for studies that tackle the biotic interactions among plants mechanistically.

What is mechanistic and phenomenological will depend on each specific research question and approach. The pairwise interactions between organisms of a biological community result from two net interactions going in opposite directions –from one individual to another– which, in turn, integrate several trophic and non-trophic interaction forces (Callaway and Walker 1997). Here, we consider these interaction forces as the primary mechanisms determining plant interactions, whereas we consider phenomenological to observe or assume the overall biological effect of a focal plant on its neighbors (the net interaction) without any further consideration. Shedding light on the mechanisms that underpin the net interactions is an essential pending task for plant interaction ecologists. This task will require a conceptual shift in plant community ecology, from a species interaction approach to a purely individualistic one. Most studies that tackle the plant interactions measure the net interaction between individuals and then classify them by species to make conclusions at the species level. While these studies are empirically measuring individuals, they are conceptually focusing on plant populations of different species: By using the species as a main statistical factor, these studies lose track of the interaction mechanisms. Investigating the plant interactions at finer biological scales (**Figure 1**) in further detail is necessary to cement our understanding of many fundamental ecological principles.

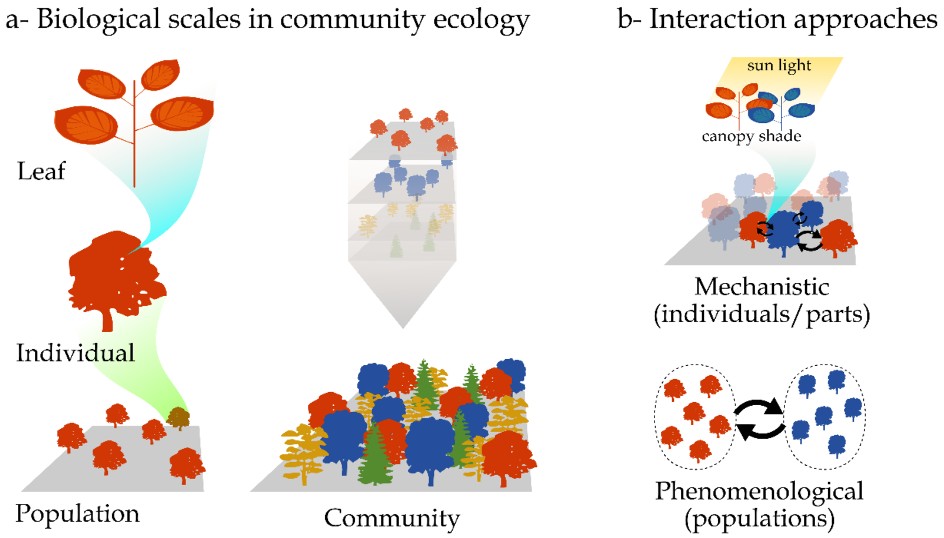

Figure 1: *Schematic of* ***a****- the different biological scales of plant communities that are of interest for ecologists and* ***b****- some examples of how the biotic interactions among plants can be conceptually approached from each of the different scales shown in* ***a****.*

In this review, we aim at establishing a framework to study mechanistically plant net interactions, based on the three fundamental features of the interacting plants that shape such interaction: the distance between individual plants, their functional traits, and the environmental conditions in which the interaction takes place (**Figure 2**). To that end, we first recapitulate the fundamental biophysical processes by which plants can interact with each other. Second, we address plant phenotypical responses to these interaction forces from a game-theoretical perspective. Third, we analyze how interaction forces and plant strategies may integrate into a directional net interaction, i.e., the overall biological effect of one plant on another. Fourth, we tackle the effects of the distance between the pair of interacting plants on the interaction forces and the net interaction. Fifth, we discuss how net interactions may change in space and time and how that relates to the fundamental mechanisms underlying plant interactions. Sixth, we assess the pros and cons of alternative conceptual approaches to plant interactions from the lenses of existing models. Seventh, based on all of the above, we propose developing plant interaction models (PIMs): models based on biophysical and ecophysiological processes in which the net interaction between a pair of individual plants in space emerges from a detailed description of their underlying interaction forces. We hope this review will foster a paradigm shift in the plant interaction ecology, from the currently dominant phenomenological approach towards a more mechanistic approach to plant interactions, necessary to build the theory from the ground up.

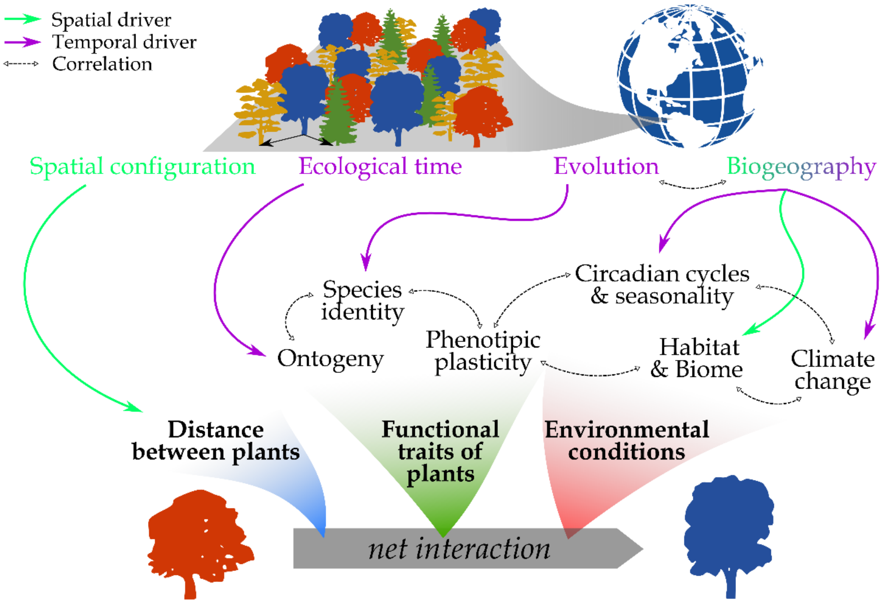

Figure 2: *Schematic of the main spatial and temporal drivers of the net interaction, mediated mechanistically by the distance between two individual plants, their functional traits, and the environmental conditions in which the interaction takes place.*

Box 1: Glossary

Lexical arbitrariness leads to confusion in the biotic interaction literature. An established definition of the existing terms referring to biotic interaction levels and mechanisms would make literature clearer and more comprehensible (Trinder et al. 2013). A paradigmatic example illustrating this confusion is the word competition, which is used interchangeably to refer to different things. In community-level biotic interaction charts, competition refers to the negative pairwise interaction (-/-), as opposed to, for instance, mutualism (+/+) (e.g., in Godsoe et al. 2017). In some fields, such as plant positive interactions research, it is common to use competition to refer to a negative net interaction instead of facilitation (Filazzola and Lortie 2014). Finally, in an ecophysiology context, competition is the fight among individuals for a specific resource (Grime 1973), regardless of whether the net interactive effect is positive or negative, hence being an interaction force. The Merriam Webster dictionary goes in this same direction and defines competition as the "active demand by two or more organisms or kinds of organisms for some environmental resource in short supply." This problem similarly affects other related terms (West et al. 2007). To avoid confusion within this text, and hopefully to contribute a more precise use of the words across sub-disciplines, we propose the following glossary of biotic interaction terms.

Biophysical process		A local modification of the physical (or chemical) environment that is a direct or indirect result of the presence of a plant.
Primary (biophysical) process		A biophysical process by which a plant directly modifies its direct physical surroundings.
Interaction force		A biophysical process by which a plant affects the environment in a way that impacts the fitness of any neighbor plant.
	Competition	(sensu Grime, 1973) Trophic interaction force; plants compete for each quantum of light, molecule of water, or ion nutrient.
Net interaction		The net outcome of all the interaction forces, giving the net biological effect of a plant on the fitness of a neighboring plant.
	Facilitation	(sensu Callaway, 1995) Positive directional net interaction.

	Interference	(sensu Harper, 1961) Negative directional net interaction.
Pairwise interaction	The complete (bidirectional) biotic interaction between two plants.	
Plant Interaction Model (PIM)	Family of models that focus on a detailed description of the biophysical processes and plant phenotypic responses letting the net interaction emerge. They must be individual-based, incorporate the spatial structure of the community, and explicitly account for environmental factors.	

1- The biophysical processes underpinning plant interactions

To develop a mechanistic understanding of plant net interactions, we first need to know the several, somewhat independent, biophysical processes underneath it. In the context of plant interactions, we can classify biophysical processes as primary processes (the direct effects of the influencing plants in their immediate surrounding), interaction forces (the biophysical changes resulting from the influencing plant that directly affect the influenced plant, i.e., the proximal cause of the interaction), and intermediary processes (any biophysical process mediating between a primary process and an interaction force).

The main primary processes of plant interactions are the effects of a plant canopy casting shade (Fernando Valladares, Laanisto, Niinemets, & Zavala, 2016), baffling wind (Leonard & Croft, 2006), intercepting rainfall (Muzylo et al., 2009), and transpiring water (Flerchinger, Reba, Link, & Marks, 2015); the effects of both plant canopies and root systems producing litter (Xiong & Nilsson, 1999); and the effects of root systems absorbing soil water (Lambers, Chapin III, & Pons, 2008b), exuding plant water (Prieto, Armas, & Pugnaire, 2012), absorbing mineral nutrients (Lambers, Chapin III, & Pons, 2008a), altering soil physical structure (Angers & Caron, 1998), and exuding metabolites (Bertin, Yang, & Weston, 2003). These primary processes ultimately affect, sometimes antagonistically, several interaction forces, as it is, for example, the case of shade in hot, semiarid habitats (**Figure 3**).

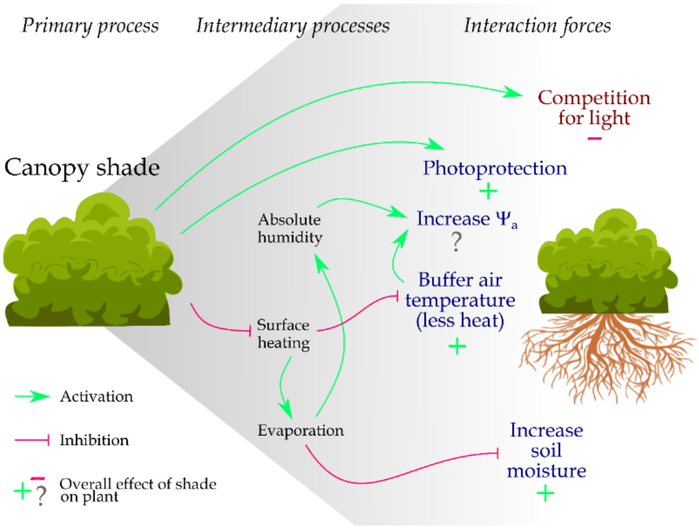

Figure 3: *Schematic example of how a primary process, canopy shade, affects various interaction forces in hot semiarid and arid systems.*

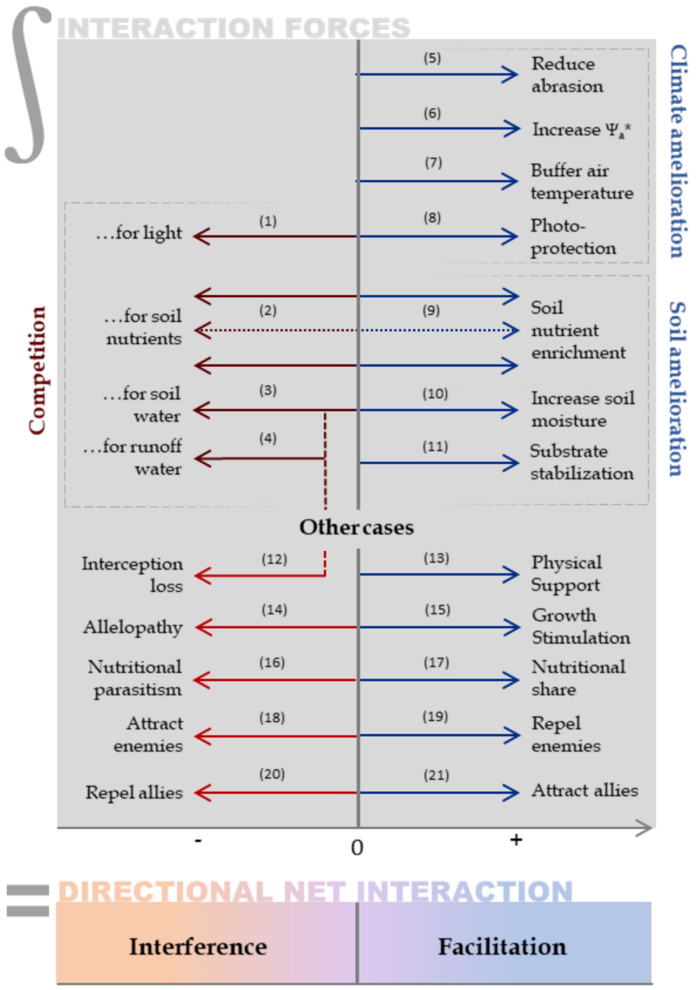

Figure 4: *List of positive and negative existing interaction forces leading to a net interaction. Mathematical symbols on the left of the boxes indicate that the integration of*

*all interaction forces determines the value of a single net interaction. Several arrows for soil nutrient forces represent the fact that there are different nutrients involved (N, P, K, etc.). Numbers next to the arrows refer to the interaction force in the text (Supplementary Material). *Atmospheric water potential.*

A comprehensive literature review on plant interactions allowed us to identify twenty-one types of interaction forces potentially relevant to understanding every single net interaction mechanistically (**Figure 4**). In the supplementary material (**SM: A review of plant interaction mechanisms**), we provide a full summary of the literature review explaining each of these interaction forces, with references to studies addressing each of them.

2- The phenotypic response of plants to interactions

Plants can sense their surrounding habitat (McNickle, St. Clair, & Cahill, 2009) and show plastic phenotypical responses to the presence of neighbors (Abakumova, Zobel, Lepik, & Semchenko, 2016; Turcotte & Levine, 2016). To develop a mechanistic approach to plant interactions, understanding how the influenced plant responds phenotypically to the interaction forces is crucial. After reviewing the interaction forces in the previous section, we now discuss observed plant phenotypical responses.

Game theory, originally developed to study the interaction among rational decision-makers, became a powerful tool to investigate evolutionary questions towards the end of the XX century (Maynard Smith, 1982). More recently, it has become a very successful framework to study plant phenotypical responses to biotic interactions in an evolutionary context (Mcnickle & Dybzinski, 2013). In times of classical optimality (Parker & Maynard Smith, 1990), game theory revolutionized the field of evolutionary ecology because it demonstrated that non-optimal traits might evolve when the net reward of a resource-allocation strategy –that is, the difference between the reproductive benefits of such strategy and the costs of adopting it– are evaluated in the presence of interacting individuals.

Game theory thus broadened the concept of optimality, allowing researchers to define different types of optimal strategies. An individual optimal refers to the strategy maximizing the net reward for an individual growing without neighbors. A collective optimal is the strategy maximizing the overall net reward for a whole population of individuals (hereafter, cooperation). Finally, an evolutionarily stable strategy (ESS) is the strategy that maximizes the net reward for an individual that selfishly interacts with other individuals of the population, and that cannot be invaded by any other better strategy. While game theory provides methods to solve for collective optimization (e.g., Pareto-optimality, see Pulliam et al. 1982), it often assumes that individual responses to biotic interaction forces evolved by natural selection follow an ESS. Two particularly well-known plant competitive interactions serve as examples of how traits evolved under un ESS are different from optimality: The arms race in competition for light and the tragedy of the commons in competition for soil resources.

To study competition for light from a game-theoretical perspective, we can think of a plant as a photosynthetic crown placed on top of a woody trunk. The crown area determines plants' potential to intercept light and, therefore, its yield. The individual optimal strategy for plants is to invest all their resources into maximizing a flat photosynthetic crown area at the ground level. (**Figure 5a**). However, in interaction with neighbor plants, competition for light becomes asymmetric because taller individuals get most of it and shaded individuals almost none. Therefore, a plant may benefit from first growing the trunk to be taller than its neighbors and, after that, grow its crown. Nevertheless, suppose all individuals in the community follow this behavior. In that case, following the ESS, they escalate in the production of increasingly taller trunks and end up engaging in an ecological arms race that makes them invest most of their resources into conflict without getting any significant benefit from it (Dybzinski, Farrior, Wolf, Reich, & Pacala, 2011; Falster & Westoby, 2003) (**Figure 5b**). Indeed, trees invest about 80% of their biomass in growing robust columns of wood on top of which they place their leaf canopy (Poorter et al., 2015). Finally, if plants pursue a collective optimal, they would have the same crown area exposed to sunlight but at the ground level (**Figure 5c**), thereby intercepting the same light at a much lower cost. In that case, all the energy gathered from sunlight could be invested in reproduction.

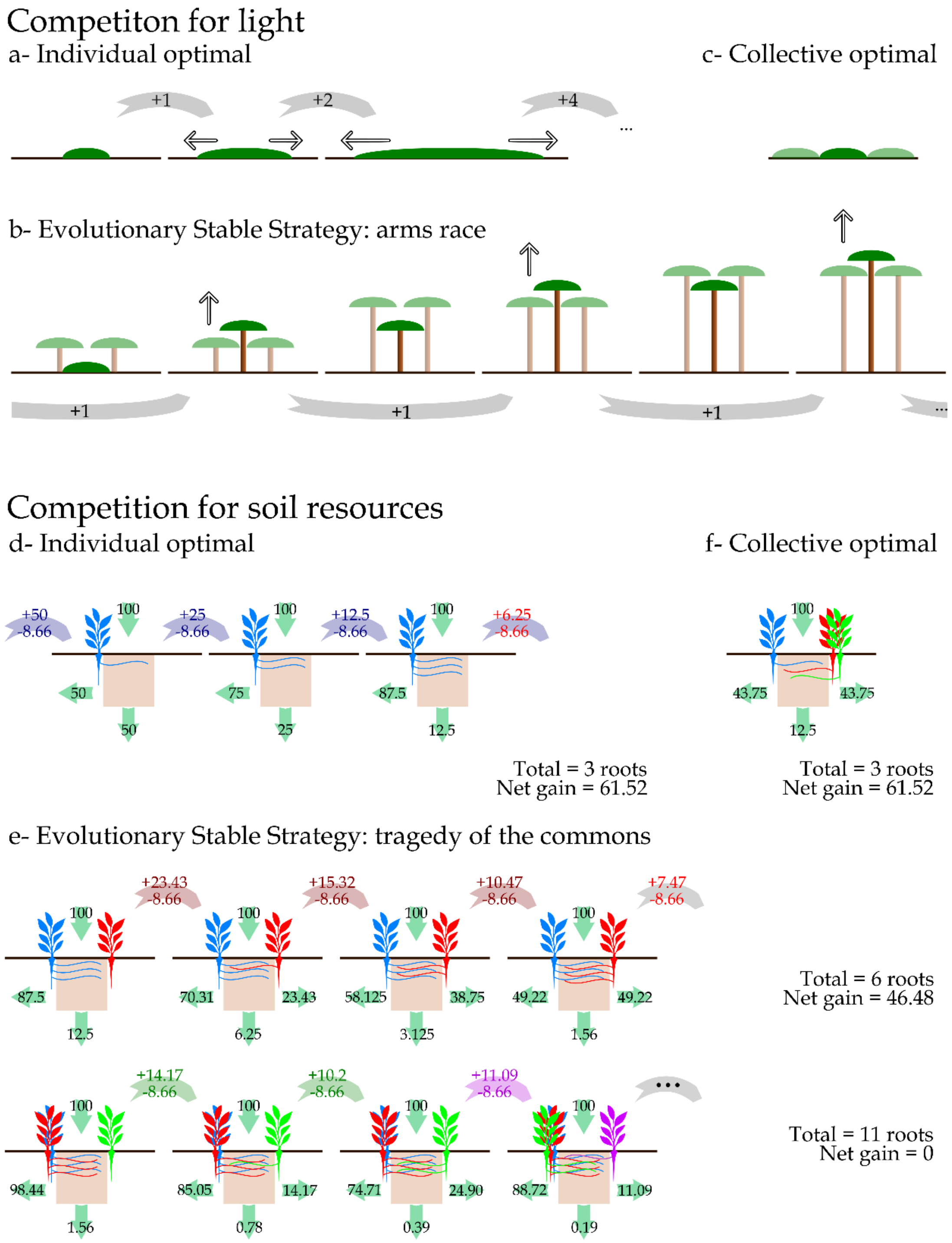

Figure 5: *Simplified examples illustrating the tragedy of the commons as a result of evolutionarily stable strategies in plant competition for light and soil resources. In competition for light* ***a-*** *a plant with initial crown size unity intercepts one unit of sunlight and allocates this energy in growing out, thus doubling its crown area and solar interception. In the next growth step, the plant will invest the energy obtained from two units of sunlight into horizontal growth, and so on.* ***b-*** *In an ESS, neighbors tend to overgrow the plant getting the benefit of asymmetric competition; hence the focal plant*

will invest one unit of energy in growing up rather than out, reaching the canopy without increasing its light interception area. This is different from the ***c****- collective optimum in which plant crowns are territorial, but plants do not invest in growing trunks either. In competition for soil resources,* ***d****- a plant will decide whether to grow a root in a patch of soil where 100 units of a resource are available depending on the marginal gain. In the case in which each root costs 8.66 units of resource, the first root uptakes 50 units, and each extra root increase the uptake by 50% (2 roots uptake 75 units, 3 roots 87.5, 4 roots 93.75, and so on), the plant will stop with two roots as the marginal benefit of adding a fourth root is negative (93.75 - 87.5 - 8.66 = -2.41). One can calculate that* ***e****- the ESS predicts other plants will find a marginal benefit of growing a fourth and more extra roots, as they will be stealing nutrients from other plants' roots. However,* ***f****- the collective optimum is attained, like the individual optimum, when there are no more than 3 roots in the patch, with which the plant community can maximize the net collective gain at a value of 61.52 (= 87.5 - 3 * 8.66).*

Game-theoretical studies of competition for soil resources have predicted that plants may engage in a tragedy of the commons (Gersani et al., 2001; Zea-Cabrera, Iwasa, Levin, & Rodríguez-Iturbe, 2006). The tragedy of the commons is a situation in a shared-resource system in which the collective action of a group of individuals acting independently from each other and pursuing their own self-interest leads to the depletion of the shared resource (Hardin 1968). To illustrate how a tragedy of the commons emerges due to competition for soil resources, we can consider a scenario in which a plant can exploit a patch of soil that contains 100 units of a resource. In this patch, the plant grows roots with a cost of 8.66 units of resource per root, and each new root increases total foraging by half the amount of remaining resource in the patch. The first root would uptake 50 resource units, the second root would increase the total uptake by 25 units, the third one by 12.5, and so on.

For a single plant, this increase in uptake is the marginal gain obtained from each consecutive root. Moreover, the form it grows implies that the allocation of new roots reduces the average resource uptake of pre-existing roots (hereafter, new roots "steal" resources from pre-existing roots). For example, if the plant allocates two roots, the uptake per root is (50+25)/2 = 37.5, and the second root has stolen from the first one 37.5-

25=12.5 units of the resource. In the hypothetical situation described above, and for an individual optimal, the plant will not grow more than three roots because the marginal benefit of a fourth root is lower than its allocation cost (6.25<8.66) (**Figure 5d**). However, if a second plant accesses the same patch inhabited by the three-root plant, the new plant's marginal benefit upon allocating its first root –which coincides with the average uptake per root in the soil patch– is (50+25+12.5+6.25)/4=23.43. Notice that the second plant's marginal benefit allocating its first root is much larger than that of the first plant allocating a fourth root, which is 6.25. This difference arises because the new plant steals resources from its neighbor rather than from its own pre-existing roots. Iterating this calculation, one can see that for an ESS, the second plant still benefits from allocating a second and a third root in the same patch, and this whole process repeats if a third individual colonizes the patch, then a fourth, and so on (**Figure 5e**). The number of roots exploiting the soil patch increases with the number of plants that colonize it, which reduces the average resource uptake per root and ultimately leads to less efficient foraging. This exploitative process continues until the cost of allocating a root equals the average uptake per root, which is at 11 roots in our example. As plants increasingly deplete the resource in the patch, the net gain for the community, i.e., the sum of the net rewards of all coexisting plants, tends to zero. Empirical studies evidencing increased root allocation of plants in response to the presence of neighbors support this theoretical prediction (Maina et al. 2002, O'Brien et al. 2005, but see Semchenko et al. 2007). In our example, the collective optimal, which pursues the maximization of the net gain, is attained with three roots, regardless of how many plants these roots belong to (**Figure 5f**).

In their review, Mcnickle and Dybzinski (2013) address cases, beyond competition for light and soil resources, in which plants may inefficiently allocate resources following an ESS, such as the arms races in attracting allies or repelling enemies. As in the examples addressed before, the allocation of resources to plant defenses against enemies must not be seen as an individual optimization. The strategy of the neighbors also must be considered because neighbors can deflect enemies to the focal plant by overinvesting in their own defense. Plants will overinvest resources into defenses to deflect herbivores and parasites to neighbors, but neighbors adopting the same ESS leads to allocating energy into non-effective defense. Similarly, low plant investment in attracting allies can limit their availability if the local environment does not attract them, yet neighbors investing too much in attracting allies can increase competition for them by decreasing the rate at which they visit the focal plant. Individuals whose investment in attracting pollinators or seed-disperser animals is higher than the individual optimal will evolve as an ESS. However, in a plant community in which all individuals follow that strategy, such investment will not return a net benefit to the plants. While necessary to capture the relevant ecological responses of plants to interaction forces, Mcnickle and Dybzinski (2013) conclude that the game theoretical approach is still not widespread in the plant community ecology literature.

3- Scaling up to the net interaction

The different interaction forces and the phenotypical responses of plants scale up, leading to net interactions. However, our understanding of this unifying process is very poor (Filazzola & Lortie, 2014). A first step towards linking net interactions to the underpinning mechanisms is to precisely define what a net interaction is. In general, the net interaction is the net effect a neighbor has on the fitness of the focal plant, i.e., on the success of the focal plant at passing its genes to the next generation (Hamilton, 1964). While simple to state from a theoretical perspective, evaluating an individual plant's fitness is almost impossible empirically. Hence, researchers need to resort to indicators that can be measured in the field, such as the biomass allocated into reproduction, hereafter fecundity. The fitness-fecundity relation depends on many factors such as differences between pollen or ovules (Primack & Hyesoon Kang, 1989), seed number to seed size ratio (Geritz, Van Der Meijden, & Metz, 1999), or diminishing returns of increased seed sets (Campbell, Brody, Price, Waser, & Aldridge, 2017). However, fecundity is generally considered a good indicator of fitness. Net interactions are often assessed by comparing plant fecundity in the presence and (all else equal) in the absence of a neighbor of interest (**Figure 6**, red arrow).

Proxies such as dry biomass or growth rates tend to correlate well with fecundity in plants and are often used as surrogates (Younginger, Sirová, Cruzan, & Ballhorn, 2017). Indexes to calculate the net interaction based on this type of observations exist (Armas, Ordiales, & Pugnaire, 2004). However, a recent study has shown that the direction of the observed net interaction among plants may depend on the fecundity surrogate (somatic biomass, seed germination, or plant survival). Therefore, empirical observations of net interactions must be interpreted with caution (Lozano, Armas, Hortal, Casanoves, & Pugnaire, 2017).

From a mechanistic perspective, this is a non-surprising finding as biophysical processes may affect these measures differentially: For instance, attracting allies **(21)**see Figure 1 such as pollinators, will increase the focal plant's seed yield, but it seems unlikely that it would affect its somatic biomass; arms race during the competition for light **(1)** should increase the allocation into somatic biomass at the expense of reproductive allocation, and similarly; increase soil moisture **(10)** will enhance plant somatic growth, but it is unclear whether its relation to reproductive yield is linear. All in all, two main questions need to be addressed in order to dive into the mechanisms underpinning plant net interactions.

The first question is, how can we make a connection between biophysical processes and the observed net interaction? This question remains open, and few studies have tried to address the complexity of this problem. For instance, Valladares et al. (2016) reviewed how the net interaction results from integrating several biophysical processes focusing on a primary process: canopy shade. Canopy shade is an interesting example because it is linked to diverse biophysical processes of different nature (light, water, and thermic stresses) that affect antagonistic interaction forces (see **Figure 3**). Shading is a ubiquitous competitive mechanism **(1)** that generates plant stress because it limits sunlight energy. However, shade can also activate positive interaction forces by reducing water stress **(6)** **(10),** heat stress **(7)**, and trough photoprotection **(8),** avoiding the direct negative effect of an excess of light causing photoinhibition of photosynthesis (Kothari, Montgomery, & Cavender-Bares, 2020). Focusing on a primary process is particularly interesting for empirical researchers because primary biophysical processes, like shade, can be artificially manipulated in experimental setups keeping all the other variables under control (De Castanho & Prado, 2014).

A different way to tackle the integrative study of the interaction mechanisms is from a resource-based perspective. For instance, Butterfield et al. (2016) simulated water flows in soils and plants in order to test whether facilitation interactions could emerge and, if so, under which conditions. Of course, water-related interaction forces are not imposed in their model, but they emerge from the abiotic and biotic water movements. A resource-based theoretical approach requires modeling the fluxes of a given resource in the habitat of the focal plant with and without the interacting neighbor, and the difference in environmental stress between both conditions provides a mechanistic explanation to the difference in fitness that the focal plant experiences (**Figure 6**, water flows and blue arrow). Focusing on a specific resource is advantageous for modelers because they can simulate the flow of a resource through the physical compartments of the ecosystem.

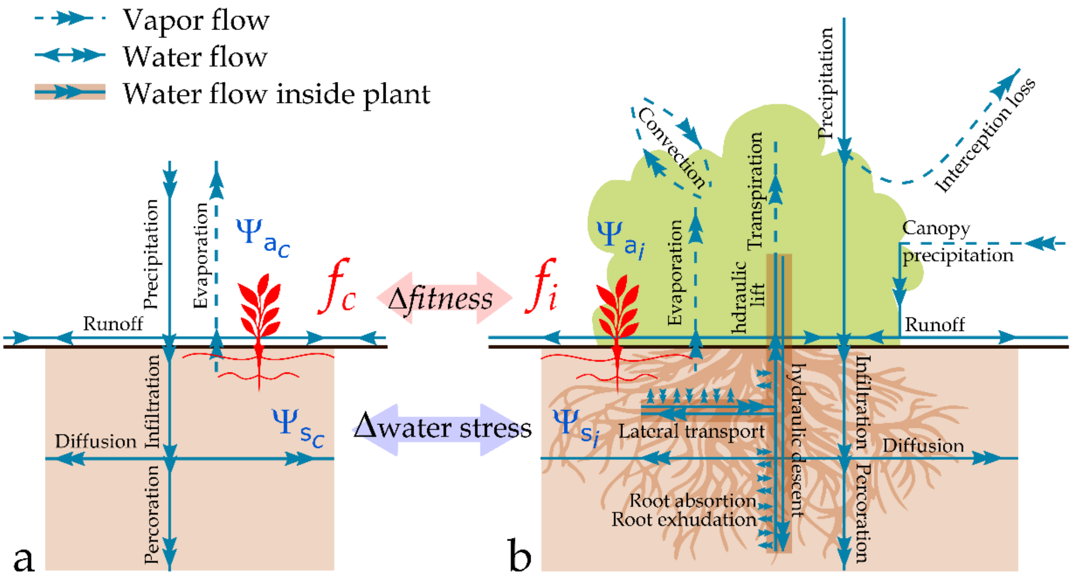

Figure 6: *Schematic of two approaches to the net interactions. Phenomenological studies observe the effect of a neighbor (shrubby plant) on a focal plant (red plant) by measuring a fitness surrogate of the focal plant when growing* ***a****- alone (control, f_c), or* ***b****- in the presence of that neighbor all else equal (interacting, f_i). Alternatively, an integrative mechanistic study relies on comparing the control and the interacting physical environment of the focal plant. A possible approach to the mechanistic study would be to focus on a resource and consider how the neighbor alters the resource dynamics. In the figure, the resource is water, and modeling water fluxes* ***a****- with and* ***b****- without the shrubby plant allows to compare the water stress to which the red plant is exposed through predictions of soil water potentials (Ψ_s) and atmospheric water potentials (Ψ_a).*

The second question is, how do plants respond phenotypically to several interaction forces entangled with each other in highly nonlinear ways (Meron, 2015)? Ecologists have long been interested in the study of plant strategies to cope with resource co-limitation. For instance, Bloom et al. (1985) developed the optimal foraging hypothesis, stating that plants will adapt their phenotype so that all essential resources are equally limiting. More recently, and using evolutionary game theory, McNickle et al. (2016)

modeled biomass allocation to leaves, stem, and roots. They noticed that, although classic-optimality models predict that plants should allocate all their resources into reproduction after reaching a threshold size (Bazzaz, Chiariello, Coley, & Pitelka, 1987), observations from forests show that adult trees invest less than 10% to reproduction (Luyssaert et al., 2007). Calculating the aboveground and belowground ESS regarding biomass allocation into leaves, stems, and roots, they predicted that plants forage inefficiently, over-allocating resources into roots, stems, and leaves, at the expense of their lifetime fecundity. The model, in which allometries emerge naturally from allocation strategies rather than being imposed, successfully predicted the physiognomy of vegetation across different biomes. For example, it correctly predicted that plants with less stem than roots or leaves were more abundant in habitats corresponding to shrubland biomes, while plants investing most to stems and engaging in an arms race dominated wet tropical climates.

4- The effect of the distance between plants on interactions

While the ecological processes are highly scale-dependent, only recently ecologists have become aware of the importance of this scale dependence (McGill, 2010). The zone of influence of a plant, defined as the space circumscribing all other individuals that interact with the focal plant, is a concept developed in the late sixties (Opie 1968), underscoring, for the first time, the importance of spatial configuration in plant community ecology. The introduction of this concept fostered the development of statistical methods to infer the range and sign of net interactions between plants from spatial point patterns, starting with the Ripley's K index (Ripley, 1978). Statistical spatial correlations can be used as a proxy to many ecological processes (McIntire & Fajardo, 2009), providing an alternative approach to empirically reporting net interactions from observing fitness differences. For instance, clumped vegetation patterns must be observed when there is facilitation (Haase et al. 1996), but over-dispersed patterns emerge under interference when competition is asymmetric (Stoll & Bergius, 2005). For a comprehensive review of spatial correlation techniques and the ecological importance of patterns and scale, see Dray et al. (2012) and Chave (2013), respectively. Here, we focus on the scarcer literature studying the mechanisms underpinning the change in the net interaction with increasing distance between two plants.

Generally, all interaction forces in **Figure 4** must vary in intensity with the distance from an influencing plant. Probably, the first interaction force that was explicitly suggested to vary with the distance between two plants is the effect of a plant attracting enemies **(18)** to another plant, as stated by the Janzen-Connell hypothesis (Connell, 1971; Janzen, 1970). Like in the Janzen-Connell hypothesis, many other interaction forces will progressively lose strength with increasing distance to the plant center. However, the change in intensity of each interaction force with space is, at least to a certain extent, independent of changes of other interaction forces. Therefore, to fully understand how a net interaction changes with increasing distance between interacting plants, the scaling-up of interaction forces to net interactions needs to be calculated independently at each distance from the influenced plant.

A few examples of scale-dependent feedbacks (SDFs, switches in the sign of net interaction with inter-individual distance) exist. The first proposed SDF states that facilitation may dominate when plants are close to each other, but there is interference when they are farther away in semiarid open-canopy vegetation (Bromley, Brouwer, Barker, Gaze, & Valentin, 1997). This particular type of SDF has been primarily used in models of semiarid vegetation to investigate the formation of large-scale spatial patterns (Hillerislambers, Rietkerk, van den Bosch, Prins, & Kroon, 2001) and to assess the risk of these ecosystems to suffer catastrophic, irreversible desertification events (Rietkerk, Dekker, De Ruiter, & Van De Koppel, 2004). However, this SDF is too simplistic from a mechanistic perspective, because it only accounts for two spatially-complementary interaction forces: Competition for runoff water **(3)** dominates in bare soils far from the plant because plants increase soil infiltration and hence moisture **(10)** under their canopy (**Figure 7a**). An alternative example is the work by Trautz et al. (2017), who studied two independent, antagonistic water-mediated interaction forces: Competition for soil water **(3)** had a stronger (negative) effect on water stress near the plant, while, by transpiring water that is dispersed by wind, plants increased atmospheric water potential **(6)** farther away (**Figure 7b**). This study shows that, when investigating different water-related biophysical processes, one could find opposing SDF depending on the interaction forces considered. However, what net interaction would result from integrating all the water-related biophysical processes shown in **Figure 6** is still unclear.

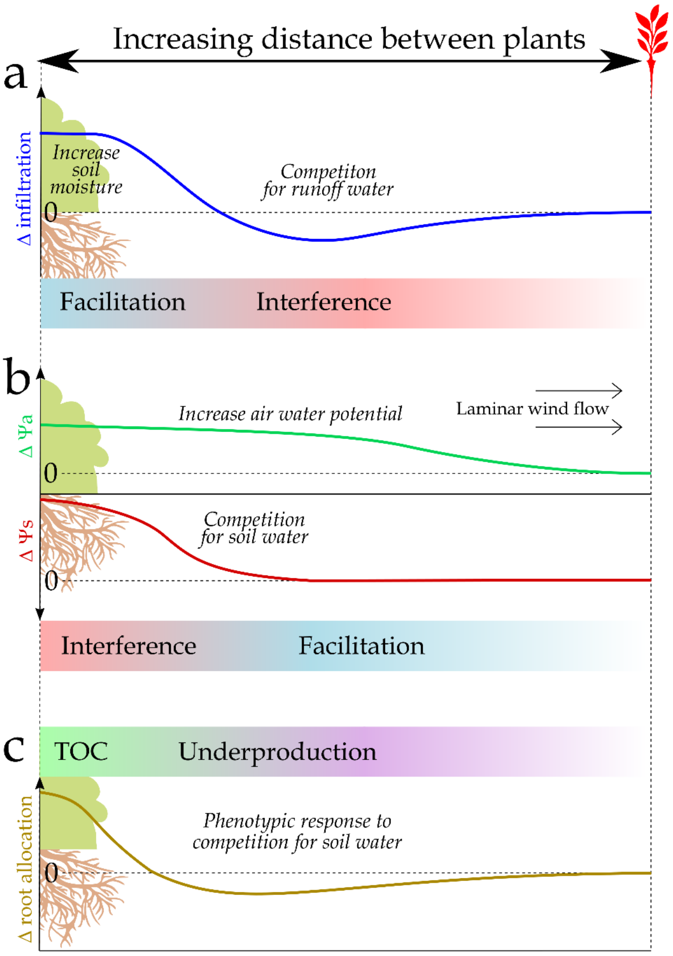

Figure 7: *Schematic of how the distance between plants is an essential driver of certain interaction mechanisms.* ***a****- The classic SDF showing how short-range facilitation and long-range interference may emerge by plants altering the soil infiltration capacity.* ***b****- An alternative SDF showing how short-range interference and long-range facilitation may emerge from combining competition for soil water and increased atmospheric water potential.* ***c****- The space-dependent phenotypic response of plants to competition for soil resources according to the theory of the exploitative segregation of plant roots.*

The phenotypic responses of plants to interaction forces also change with the distance between individuals. Because most game-theoretical models investigating plant behavioral responses are not spatially-explicit, this question remains largely unexplored. However, the recently published theory of the exploitative segregation of plant roots predicts that plants over-proliferate roots and engage in a tragedy of the commons when growing in a crowded community, but under-invest in their roots when neighbors are farther apart (**Figure 7c**) (Cabal, Martínez-García, De Castro, Valladares, & Pacala, 2020). Both over- and under- investments in root systems are explained by a single spatial EES, resulting from the changing balance between local root over-proliferation nearby a plant's stem and local underproliferation farther away in the direction of the competitor. This novel theory reconciles seemingly opposing previous findings in root foraging literature: root territoriality (Schenk, Callaway, & Mahall, 1999), which intuitively led to assume under-investment into roots, studies that do report this underinvestment (Chen et al., 2015), and the tragedy of the commons (Gersani et al., 2001). It also highlights the importance of incorporating spatial processes in game-theoretical models aiming to investigate plant interactions.

5- A dynamic view of the net interaction

The biophysical processes and the plant phenotypic responses to interaction forces vary with time and space. This variability might be due to changes in the distance between interacting plants, their functional traits, and environmental factors. To mechanistically explain the net interaction between two plants at a given location and moment, researchers need to account for the dynamism of these drivers. In the previous section, we reviewed the case of the distance between plants. Next, we discuss how spatiotemporal changes in environmental conditions and plant functional traits modify net interactions.

Firstly, environmental quality is a major driver of changes in net interactions. Grime (1973) found, for the first time, that competition can become more intense with increasing environmental quality. Later, facilitation among plants started to interest community ecologists (Hunter & Aarssen, 1988), leading to the stress gradient hypothesis (SGH). The SGH states that positive interaction forces may dominate with increasing environmental stress, allowing the emergence of facilitation (Bertness & Shumway, 1993). It mostly predicts that interference or facilitation dominance is robust to spatial variation in habitat conditions (Maestre, Valladares, & Reynolds, 2005). However, temporal heterogeneity may produce switches in the sign of net interaction at the scale of days (Wright, Schnitzer, & Reich, 2015), seasons (Breshears, Nyhan, Heil, & Wilcox, 1998; Kikvidze, Khetsuriani, Kikodze, & Callaway, 2006), and even between years (del Río, Schütze, & Pretzsch, 2014; F. Valladares & Pearcy, 2002). A variation of the SGH, the so-called hump-shaped SGH, suggests that, while facilitation may emerge under increasing stress in mild environments, the net interaction may switch back to interference under extreme stress conditions (Holmgren & Scheffer, 2010). This collapse of facilitation has been found in water-limited habitats (Maestre, Bautista, & Cortina, 2003), cold climates (Koyama & Tsuyuzaki, 2013), and along gradients of grazing intensity (Michalet, Le Bagousse-Pinguet, Maalouf, & Lortie, 2014). Nevertheless, facilitation has been measured in one of the most inhospitable land surfaces on earth: Antarctica (Molina-Montenegro et al., 2013).

From a mechanistic point of view, environmental conditions modify the biophysical processes that underpin plant interactions. While many studies report changes in net interactions across stress conditions, very few studies accurately report the biophysical processes responsible for those changes. We have argued that, by modeling the biophysical processes related to a specific resource, we could explain mechanistically the difference in fitness that a plant experiences in the presence of a neighbor (see **Figure 6**). Indeed, the model we used as an example to illustrate this (Butterfield et al., 2016) incorporates environmental variation. By running their simulation under different environmental conditions, the authors could compare water stress changes in the presence or absence of a shrubby neighbor in different habitat conditions. They concluded that the effect of shrub cover altering water stress conditions was different under changing precipitation regimes. For instance, they found that the positive effect of shrubs on shallow soil water decays with a decrease in precipitation, giving support to a hump-shaped SGH. Also, Anthelme et al. (2012) evaluated the effect of nurse plants along an altitude gradient empirically. They observed interference in low altitudes but facilitation at higher stress conditions. They then measured the interaction forces involved and identified soil nutrient enrichment **(9)** and an increase in soil water **(10)** as the main drivers of the shift in net interaction. The data they gathered represents an example of a first step towards the mechanistic understanding of shifts in net interaction across environmental gradients.

Secondly, 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 (Fichtner et al., 2017; Kunstler et al., 2016). Plant functional traits have an evident genetic background that is species-specific (Pereira & Des Marais, 2020). Consequently, 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, Michalet, & Callaway, 2001) or the influencing (Pugnaire, Armas, & Valladares, 2004) individuals.

However, functional traits are far from being solely restricted to species identity (Cadotte, Carscadden, & Mirotchnick, 2011). Functional traits vary substantially with ontogeny, plant size being a paradigmatic example of that change. For instance, the functional traits of a tree seedling look more like herbaceous plants than to adult individuals of its species (Niklas et al., 2007). Some studies have reported shifts in the net interaction with increasing size of the influencing plants (Miriti, 2006), of the influenced plant (Álvarez-Yépiz, Búrquez, & Dovčiak, 2014; S. Soliveres, de Soto, Maestre, & Olano, 2010), and when both plants grow together (Schiffers & Tielbörger, 2006) within species pairs. Nevertheless, plants also 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 this environmentally-induced phenotypic plasticity that ultimately has a strong effect on plant net interactions (McGill, Enquist, Weiher, & Westoby, 2006; Fernando Valladares, Gianoli, & Gómez, 2007). From a mechanistic approach, the functional traits of the influencing plant modify the biophysical processes underpinning plant interactions. For instance, shorter plants will have a smaller zone of influence (Casper, Schenk, & Jackson, 2003), plants with higher specific root length may compete for soil resources more efficiently (Erktan, McCormack, & Roumet, 2018), plants with deeper roots can increase shallow soil water trough hydraulic lift (Walter, 1971), or plants with a higher leaf-area index will produce a more intense shade (Jordan, 1969). The treatment of functional traits variation needs to be careful, as discerning the phenotypic plasticity of a plant in response to abiotic environmental change or in response to a biotic interaction is an arduous task.

Predicting major ecologic features is a paramount goal of environmental sciences to fight against the current anthropogenic global crisis. It requires understanding global-scale spatial and temporal vegetation responses to climate change, mediated at least partially by plant interactions (Scheiner et al., 2011). Our current understanding of plant ecophysiology presumably provides tools to start approaching a theoretical treatment of this problem, but its complexity, as depicted through this review, is enormous. Some studies have tackled multi-level effects phenomenologically. For instance, Wright et al. (2014) showed how both biotic (ontogeny) and abiotic (circadian cycles and seasons) temporal factors together drive complex, continuous changes in the net interaction between two plants. Le Roux, Shaw, & Chown, (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 both the direct abiotic effect of environmental stress and plasticity in the phenotypic response of influencing plants to that stress drive in combination spatial changes in the net interaction. Metz and Tielbörger (2016) considered the environmental spatiotemporal variation altogether, reporting facilitation only in certain locations and at specific times at which stressful environmental conditions arise. However, we are still far from a mechanistic framework that, based on biophysical processes, would allow us to predict how net interactions vary in time and space with the distance between plants, the functional traits of the plants, and the environmental conditions in which the interaction takes place.

6- Conceptual approaches to plant interactions

There are several conceptual approaches to study plant interactions, and models incorporating the plant interactions to make predictions of major ecosystem features provide us with a good overview of existing theoretical approaches to plant interactions. We can classify existing models into three families: population, individual-based, and plant-continuum models, each of them showing different pros and cons (**Table 1**). This section reviews these families of models and their main characteristics to get a more in-depth insight into the differences between the alternative possible conceptual approaches to plant interactions.

Following a chronological order, the first approach to study populations of interacting agents dates back to the logistic equation for intraspecific competition (Verhulst, 1845). Later work by Lotka, Volterra, and others extended this model to systems with more than one species and other ecological interactions, specially prey-predator (Lotka, 1920, 1924; Volterra, 1926). At least two factors explain the great success of this family of demographic models during the last century. First, they provide good fits to empirical observations. Notably remarkable are the data from the Hudson's Bay Company on fluctuations of lynxes and hares in Canada that confirmed predictions of prey-predator models (Hewitt, 1921) and the experiments by Gause et al. (1934) to test intraspecific competition in populations of paramecia. Second, because demographic models focus on the species identity of the interacting agents and are mathematically tractable

(Wangersky, 1978), they allowed researchers to identify simple rules that allow coexistence between antagonistic species (Hardin, 1960).

Approach	**Analytical tractability***	**Spatial processes**	**Biophysical processes**	**Population size**	**Trait variability**	**Game theory**	**Foundational paper and recent literature review for each approach**
Population	✓	✗	~	✓	✗	✗	(Lotka, 1924), (Jeltsch, Moloney, Schurr, Köchy, & Schwager, 2008)
Individual	✗	✓	✓	✓	✓	✓	(Botkin, Janak, & Wallis, 1972), (Shugart et al., 2018)
Continuum	✓	✓	~	✗	✗	✗	(Lefever & Lejeune, 1997), (Meron et al., 2019)

Table 1: *The three classic modeling approaches to plant biotic interactions (from different biological scales): classic demographic models (population), individual-based models (individual), plant-continuum models (foraging organs).* ✗ *cannot incorporate,* ~ *can poorly incorporate,* ✓ *can accurately incorporate. *Analytical tractability correlates with increasing computational limits when simulating large populations or spatial scales.*

The first limitation of this population-level approach is that plants are sessile organisms that interact only with their neighbors. The concerns for the low suitability of these models to plant communities was probably first raised by Fagerström (1988), who highlighted that sessile organisms must only compete with close neighbors and supported the use of spatially explicit approaches. Interactions in both Verhulst and 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, provided that their trajectories intersect by chance (Hutchinson and Waser 2007, O'Dwyer 2020). In addition to this theoretical limitation, plant demographic empirical studies are generally labor-intensive. They require large sample sizes, long-term, long-range data sets, and large arrays of variables (Ehrlén, Morris, von Euler, & Dahlgren, 2016). The analysis of demographic-level data to assess biotic interaction 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). Moreover, 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). All in all, this approach cannot incorporate all the mechanistic complexity underpinning plant interactions (see **Figure 1**). Two alternative modeling approaches were developed during the last decades of the XXth century: The individual-based approach and the biomass-based continuum approach (Klausmeier, 1999; Lefever & Lejeune, 1997).

Individual-based models (IBM) are, generally, computer simulations of individuals interacting in a spatial environment composed of independent grid cells of the size of the crown of an adult plant. The first vegetation dynamics IBM of this kind is probably *jabowa* (Botkin et al. 1972), and this approach has received considerable attention since. Various modeling advances have been developed, such as *foret* (Shugart, and West 1980), which incorporated dependence between the cells in the grid, and *sortie* (Pacala et al. 1996), which was the first fully spatially-explicit IBM. Among the hindrances of this type of models, two are the most remarkable. First, the smallest spatial scale is that of the individual. Second, they are mathematically less tractable than models based on ordinary differential equations (Meron et al., 2019), but tools to treat them analytically also exist (Iwasa, 2010; Matsuda, Ogita, Sasaki, & Sato, 1992).

The other alternative to well-mixed demographic-level models is the plant-continuum approach, based on partial differential equations (PDEs) for the evolution in time and space of vegetation biomass density (Holmes, Lewis, Banks, & Veit, 1994). These models have contributed crucially to our qualitative understanding of vegetation spatial pattern formation in drylands and have helped to hypothesize how those patterns may anticipate desertification transitions (Bonachela et al., 2015; Fernandez-Oto, Tzuk, & Meron, 2019; Meron, 2018; Rietkerk et al., 2002). Earlier models in this family were kernel-based models encapsulating every feedback between plants and their environment in the sign of the net interaction among plants (Lefever & Lejeune, 1997). More recent ecohydrological models describe scale-dependent feedbacks between water and vegetation explicitly (**Figure 6a**) (Klausmeier, 1999; Rietkerk et al., 2002). Albeit more mechanistic, the latter tend to focus on a small set of interactions that are hypothesized to play a critical role in the question under study. This simplification provides an analytically tractable mathematical description of the system that explains large-scale processes that involve many individuals. However, by discarding many other processes, they do not provide good quantitative predictions (Meron et al. 2019).

Plant-continuum models lose track of discrete individuals, which is an important limitation because many events in nature are discrete and poorly approximated by a continuous description. For example, PDEs cannot track population sizes, nor can they account for discrete individual's life events properly. For instance, when an individual dies, a large amount of vegetation biomass disappears, while plant-continuum models only produce continuous decays of biomass density. Other limitations associated to losing track of the individual plants appear both in population and continuum approaches because they substitute plant individuals by higher biological-scale variables –namely population size or biomass respectively–, which are commonly associated with a species. Through this review, we have shown that net interactions depend largely on factors unrelated to the taxonomic identity of the interacting plants. One example is the distance between individual plants, which may be responsible for switching the sign of the interaction between any pair of individuals. Another example is the ontogeny, making tree seedlings interact with other plants more like an herbaceous plant than like adult trees of its own species. Only an individual conceptual approach to plant interactions can accurately represent the diversity and spatial complexity depicted by plant functional traits (Zakharova, Meyer, & Seifan, 2019). The game-theoretical response of plants to interactions is a paradigmatic example of that, showing that only when individual plants are considered, inefficient foraging of a shared resource can be predicted according to an ESS (Rankin, Bargum, & Kokko, 2007). How could phenomena like these be modeled without incorporating individual plants in space explicitly?

7- A framework to study the mechanisms under net interactions

We propose a new approach to understand plant interactions mechanistically. This approach may help to cement –or, in some cases, challenge– plant ecological theories. We propose developing plant-interaction models (PIM), a new family of models that focus on yielding predictions of plant interactions from the underpinning biophysical mechanisms. A PIM focuses on pairs or very small groups of plant individuals in explicit space, and incorporates a detailed description of their biophysical environment. By modeling the biophysical processes occurring between the plants and their shared physical environment, and their phenotypical response to this processes from a game theory perspective, biotic interactions should emerge in the PIM. By comparing the overall success of plants modeled with and without neighbors (see example in **Figure 6**), the model results can be used to assess the emerging net interaction sign and intensity.

Some preliminary examples of PIMs already exist (Butterfield et al., 2016; Cabal et al., 2020), but a comprehensive understanding requires accounting for more complex situations. The development of PIM can feed plant community ecologists with concrete mechanistic hypotheses that can be tested empirically. For instance, researchers may be able to better understand plant facilitation by investigating the conditions in which it emerges and which positive interaction forces are the main drivers in different scenarios. Thereby, PIMs may produce mechanistic rules to understand the stress gradient hypothesis –which are the environmental drivers of facilitation emerging+ in space and time–, biodiversity patterns –what intraspecific and interspecific functional traits combinations can promote species coexistence–, and scale-dependent feedbacks –how does the sign of net interaction switches with the inter-plant distance– just to name a few examples.

Conclusions

Plant interactions are often assumed to be the net effect of a neighbor on a focal individual. A simple, phenomenological approach to plant interactions can build or validate ecological principles without fundamentally understanding the underpinning mechanisms. We have shown that net interactions rely on several biophysical processes and involve counterintuitive dynamical responses of plants based on game theory. Hence, our review calls for a mechanistic understanding that cements relevant predictions on biodiversity patterns, climate change scenarios, or ecosystem dynamics. We highlight that an individual-level approach is necessary to study plant interactions mechanistically and integrating biophysical processes, short-scale spatial structure, plant phenotypic plasticity, and game theory. The development of individual-based models incorporating biophysical processes and plants' ESS in which net interactions emerge are necessary to advance our mechanistic knowledge of plant interactions. This line proposes a new conceptual approach to study plant interactions from a mechanistic perspective: the plant interaction models (PIM). The PIMs can integrate the biophysical processes and the evolutionarily stable strategies (ESS) of plants in relation to the spatial configuration of the sessile community, the functional traits of the plants, and the environmental conditions. Empirical studies reporting the mechanisms underpinning the plant interactions among individuals, controlling for –but not focused on– the species identity of the interacting individuals, may also significantly enrich our knowledge of this field. Only by incorporating the high complexity of mechanisms underpinning net interactions from an individual-level approach will the plant interaction ecology firmly stand on its own two feet.

References

Abakumova, M., Zobel, K., Lepik, A., & Semchenko, M. (2016). Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytologist*, *211*(2), 455–463. doi: 10.1111/nph.13935

Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, A., … Veblen, K. E. (2018). Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters*, *21*(9), 1319–1329. doi: 10.1111/ele.13098

Álvarez-Yépiz, J. C., Búrquez, A., & Dovčiak, M. (2014). Ontogenetic shifts in plant-plant interactions in a rare cycad within angiosperm communities. *Oecologia*, *175*(2), 725–735. doi: 10.1007/s00442-014-2929-3

Anderegg, L. D. L., Loy, X., Markham, I. P., Elmer, C. M., Hovenden, M. J., Ris Lambers, J. H., & Mayfield, M. M. (2021). Aridity drives coordinated trait shifts but not decreased trait variance across the geographic range of eight Australian trees. *New Phytologist*, *229*(3), 1375–1387. doi: 10.1111/nph.16795

Angers, D. A., & Caron, J. (1998). Plant-induced changes in soil structure: Processes and feedbacks. *Biogeochemistry*, *42*, 55–72. doi: 10.1007/978-94-017-2691-7_3

Anthelme, F., Buendia, B., Mazoyer, C., & Dangles, O. (2012). Unexpected mechanisms sustain the stress gradient hypothesis in a tropical alpine environment. *Journal of Vegetation Science*, *23*(1), 62–72. doi: 10.1111/j.1654-1103.2011.01333.x

Armas, C., Ordiales, R., & Pugnaire, F. I. (2004). Measuring plant interactions: A new comparative index. *Ecology*, *85*(10), 2682–2686. doi: 10.1890/03-0650

Bazzaz, F. A., Chiariello, N. R., Coley, P. D., & Pitelka, L. F. (1987). Allocating Resources to Reproduction and Defense. *BioScience*, *37*(1), 58–67. doi: 10.2307/1310178

Bella, I. E. (1971). A New Competition Model for Individual Trees. *Forest Science*, *17*(3), 364–372. doi: 10.1093/forestscience/17.3.364

Berdugo, M., Kéfi, S., Soliveres, S., & Maestre, F. T. (2017). Plant spatial patterns identify alternative ecosystem multifunctionality states in global drylands. *Nature Ecology and Evolution*, *1*(3), 1–7. doi: 10.1038/s41559-016-0003

Bertin, C., Yang, X., & Weston, L. A. (2003). The role of root exudates and allelochemicals in the rhizosphere. *Plant and Soil*, *256*, 67–83. doi: 10.1023/A:1026290508166

Bertness, M. D. ., & Shumway, S. W. . (1993). Competition and Facilitation in Marsh Plants. *The American Naturalist*, *142*(4), 718–724. doi: 10.1086/285567

Bloom, A. J., Chapin, F. S., & Mooney, H. A. (1985). Resource Limitation in Plants-An Economic Analogy. *Annual Review of Ecology and Systematics*, *16*, 363–392. doi: 10.1146/annurev.es.16.110185.002051

Bonachela, J. A., Pringle, R. M., Sheffer, E., Coverdale, T. C., Guyton, J. A., Caylor, K. K., … Tarnita, C. E. (2015). Termite mounds can increase the robustness of dryland ecosystems to climatic change. *Science*, *347*(6222), 651–655. doi: 10.1080/19443994.2014.939496

Bonanomi, G., Stinca, A., Chirico, G. B., Ciaschetti, G., Saracino, A., & Incerti, G. (2016). Cushion plant morphology controls biogenic capability and facilitation effects of Silene acaulis along an elevation gradient. *Functional Ecology*, *30*(7), 1216–1226. doi: 10.1111/1365-2435.12596

Borgogno, F., D'Odorico, P., Laio, F., & Ridolfi, L. (2009). Mathematical models of vegetation pattern formation in ecohydrology. *Reviews of Geophysics*, *47*, 1–36. doi: 10.1029/2007RG000256

Botkin, D. B., Janak, J. F., & Wallis, J. R. (1972). *Some Ecological Consequences of a*

Computer Model of Forest Growth. *60*(3), 849–872. doi: 10.2307/2258570

Breshears, D. D., Nyhan, J. W., Heil, C. E., & Wilcox, B. P. (1998). Effects of Woody Plants on Microclimate in a Semiarid Woodland: Soil Temperature and Evaporation in Canopy and Intercanopy Patches. *International Journal of Plant Sciences*, *159*(6), 1010–1017. doi: 10.1086/314083

Bromley, J., Brouwer, J., Barker, A. P., Gaze, S. R., & Valentin, C. (1997). The role of surface water redistribution in an area of patterned vegetation in a semi-arid environment, south-west Niger. *Journal of Hydrology*, *198*, 1–29. doi: 10.1016/S0022-1694(96)03322-7

Brooker, R. W. (2006). Plant-plant interactions and environmental change. *New Phytologist*, *171*(2), 271–284. doi: 10.1111/j.1469-8137.2006.01752.x

Bulleri, F., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. (2016). Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology*, *30*(1), 70–78. doi: 10.1111/1365-2435.12528

Butterfield, B. J., Bradford, J. B., Armas, C., Prieto, I., & Pugnaire, F. I. (2016). Does the stress-gradient hypothesis hold water? Disentangling spatial and temporal variation in plant effects on soil moisture in dryland systems. *Functional Ecology*, *30*(1), 10–19. doi: 10.1111/1365-2435.12592

Cabal, C., Martínez-García, R., De Castro, A., Valladares, F., & Pacala, S. W. (2020). The Exploitative Segregation of Plant Roots. *Science*, *370*(6521), 1197–1199. doi: 10.1126/science.aba9877

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*(5), 1079–1087. doi: 10.1111/j.1365-2664.2011.02048.x

Callaway, R. M. (1995). Positive Interactions among Plants. *The Botanical Review*, *61*(4), 306–349. doi: 10.1080/19312458.2016.1150444

Campbell, D. R., Brody, A. K., Price, M. V., Waser, N. M., & Aldridge, G. (2017). Is plant fitness proportional to seed set? An experiment and a spatial model. *American Naturalist*, *190*(6), 818–827. doi: 10.1086/694116

Casper, B. B., Schenk, H. J., & Jackson, R. B. (2003). DEFINING A PLANT'S

BELOWGROUND ZONE OF INFLUENCE\rdoi:10.1890/02-0287. *Ecology*, *84*(9), 2313–2321. Retrieved from http://www.esajournals.org/doi/abs/10.1890/02-0287

Chave, J. (2013). The problem of pattern and scale in ecology: What have we learned in 20 years? *Ecology Letters*, *16*(s1), 4–16. doi: 10.1111/ele.12048

Chen, B. J. W., During, H. J., Vermeulen, P. J., de Kroon, H., Poorter, H., & Anten, N. P. R. (2015). Corrections for rooting volume and plant size reveal negative effects of neighbour presence on root allocation in pea. *Functional Ecology*, *29*(11), 1383–1391. doi: 10.1111/1365-2435.12450

Chesson, P. L. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, *31*(2000), 343–366. doi: 10.1146/annurev.ecolsys.31.1.343

Choler, P., Michalet, R., & Callaway, R. M. (2001). Facilitation and Competition on Gradients in Alpine Plant Communities. *Ecology*, *82*(12), 3295–3308. doi: 10.1890/0012-9658(2001)082[3295:FACOGI]2.0.CO;2

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. Den Boer & G. R. Gradwell. (Eds.), *Dynamics of Population* (pp. 298–312). Wageningen: Pudoc.

De Castanho, C. T., & Prado, P. I. (2014). Benefit of shading by nurse plant does not change along a stress gradient in a coastal dune. *PLoS ONE*, *9*(8), 1–9. doi: 10.1371/journal.pone.0105082

del Río, M., Schütze, G., & Pretzsch, H. (2014). Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biology*, *16*(1), 166–176. doi: 10.1111/plb.12029

Detto, M., Visser, M. D., Wright, S. J., & Pacala, S. W. (2019). Bias in the detection of negative density dependence in plant communities. *Ecology Letters*, *22*(11), 1923–1939. doi: 10.1111/ele.13372

Dray, S., Pélissier, R., Couteron, P., Fortin, M. J., Legendre, P., Peres-Neto, P. R., … Wagner, H. H. (2012). Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, *82*(3), 257–275. doi: 10.1890/11-1183.1

Dybzinski, R., Farrior, C., Wolf, A., Reich, P. B., & Pacala, S. W. (2011). Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: An analytically tractable, individual-based model and quantitative comparisons to data. In *American Naturalist* (Vol. 177). doi: 10.1086/657992

Ehrlén, J., Morris, W. F., von Euler, T., & Dahlgren, J. P. (2016). Advancing environmentally explicit structured population models of plants. *Journal of Ecology*, *104*(2), 292–305. doi: 10.1111/1365-2745.12523

Erktan, A., McCormack, M. L., & Roumet, C. (2018). Frontiers in root ecology: recent advances and future challenges. *Plant and Soil*, *424*(1–2), 1–9. doi: 10.1007/s11104-018-3618-5

Fagerström, T. (1988). Lotteries in communities of sessile organisms. *Trends in Ecology and Evolution*, *3*(11), 303–306. doi: 10.1016/0169-5347(88)90106-1

Falster, D. S., & Westoby, M. (2003). Plant height and evolutionary games. *Trends in Ecology and Evolution*, *18*(7), 337–342. doi: 10.1016/S0169-5347(03)00061-2

Fernandez-Oto, C., Tzuk, O., & Meron, E. (2019). Front Instabilities Can Reverse Desertification. *Physical Review Letters*, *122*, 048101. doi: 10.1103/PhysRevLett.122.048101

Fichtner, A., Härdtle, W., Li, Y., Bruelheide, H., Kunz, M., & von Oheimb, G. (2017). From competition to facilitation: how tree species respond to neighbourhood diversity. *Ecology Letters*, *20*(7), 892–900. doi: 10.1111/ele.12786

Filazzola, A., & Lortie, C. J. (2014). A systematic review and conceptual framework for the mechanistic pathways of nurse plants. *Global Ecology and Biogeography*, *23*(12), 1335–1345. doi: 10.1111/geb.12202

Flerchinger, G. N., Reba, M. L., Link, T. E., & Marks, D. (2015). Modeling temperature and humidity profiles within forest canopies. *Agricultural and Forest Meteorology*, *213*, 251–262. doi: 10.1016/j.agrformet.2015.07.007

Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(14), 3725–3734. doi:

10.1073/pnas.1519911113

Gause, G. F., Nastukova, O. K., & Alpatov, W. W. (1934). The Influence of Biologically Conditioned Media on the Growth of a Mixed Population of Paramecium caudatum and P. aureliax. *Journal of Animal Ecology*, *3*(2), 222–230. doi: 10.2307/1145

Geritz, S. A. H., Van Der Meijden, E., & Metz, J. A. J. (1999). Evolutionary dynamics of seed size and seedling competitive ability. *Theoretical Population Biology*, *55*(3), 324–343. doi: 10.1006/tpbi.1998.1409

Gersani, M., Brown, J. S., Brien, E. E. O., Maina, G. M., Journal, S., Aug, N., … Abramsky, Z. (2001). Tragedy of the Commons as a Result of Root Competition. *Journal of Ecology*, *89*(4), 660–669. doi: 10.1046/j.0022-0477.2001.00609.x

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*. doi: 10.1126/science.1255957

Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, *242*(5396), 344–347. doi: 10.1038/242344a0

Haase, P., Pugnaire, F. I., Clark, S. C., & Incoll, L. D. (1996). Spatial patterns in a two-tiered semi-arid shrubland in southeastern Spain. *Journal of Vegetation Science*, *7*(4), 527–534. doi: 10.2307/3236301

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*(1), 1–16. doi: 10.1016/0022-5193(64)90038-4

Hardin, G. (1960). The competitive exclusion principle. *Science*, *131*(3409), 1292–1297. doi: 10.1126/science.131.3409.1292

Hardin, G. (1968). The Tragedy of Commons. *Science*, *162*(3859), 1243–1248. doi: 10.1126/science.162.3859.1243

Harper, J. L. (1961). Approaches to the study of plant competition. *Symposia of the Society for Experimental Biology*, *15*, 1–39.

Hewitt, C. G. (1921). The periodic fluctuations of our fur-bearing animals. In *The conservation of the wild life of Canada* (pp. 213–234). New York: Charles

Scribner's Sons.

Hillerislambers, R., Rietkerk, M., van den Bosch, F., Prins, H. H. T., & Kroon, H. De. (2001). Vegetation Pattern Formation in Semi-Arid Grazing Systems. *Ecology*, *82*(1), 50–61. doi: 10.1890/0012-9658(2001)082[0050:VPFISA]2.0.CO;2

Holmes, E. . E. ., Lewis, M. . A. ., Banks, J. . E., & Veit, R. . R. . (1994). Partial Differential Equations in Ecology : Spatial Interactions and Population Dynamics. *Ecology*, *75*(1), 17–29. doi: 10.2307/1939378

Holmgren, M., & Scheffer, M. (2010). Strong facilitation in mild environments: The stress gradient hypothesis revisited. *Journal of Ecology*, *98*(6), 1269–1275. doi: 10.1111/j.1365-2745.2010.01709.x

Hunter, A. F., & Aarssen, L. W. (1988). Plants helping plants. *BioScience*, *38*(1), 34–40. doi: 10.2307/1310644

Hutchinson, J. M. C., & Waser, P. M. (2007). Use , misuse and extensions of "ideal gas" models of animal encounter. *Biological Reviews*, *82*(23), 335–359. doi: 10.1111/j.1469-185X.2007.00014.x

Iwasa, Y. (2010). Lattice Models and Pair Approximation in Ecology. In U. Dieckmann, R. Law, & J. A. J. Metz (Eds.), *The Geometry of Ecological Interactions* (pp. 227–251). Cambridge: Cambridge University Press. doi: 10.1017/cbo9780511525537.016

Janzen, D. H. (1970). Herbivores and the Number of Tree Species in Tropical Forests. *The American Naturalist*, *104*(940), 501–528. doi: 10.1086/282687

Jeltsch, F., Moloney, K. A., Schurr, F. M., Köchy, M., & Schwager, M. (2008). The state of plant population modelling in light of environmental change. *Perspectives in Plant Ecology, Evolution and Systematics*, *9*(3–4), 171–189. doi: 10.1016/j.ppees.2007.11.004

Jordan, C. F. (1969). Derivation of Leaf-Area Index from Quality of Light on the Forest Floor. *Ecology*, *50*(4), 663–666. doi: 10.2307/1936256

Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., & De Ruiter, P. C. (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, *449*(7159), 213–217. doi:

10.1038/nature06111

Kikvidze, Z., Khetsuriani, L., Kikodze, D., & Callaway, R. M. (2006). Seasonal shifts in competition and facilitation in subalpine plant communities of the central Caucasus. *Journal of Vegetation Science*, *17*(1), 77–82. doi: 10.1111/j.1654-1103.2006.tb02425.x

Klausmeier, C. A. (1999). Regular and Irregular Patterns in Semiarid Vegetation. *Science*, *284*(5421), 1826–1828. doi: 10.1126/science.284.5421.1826

Kothari, S., Montgomery, R., & Cavender-Bares, J. (2020). Physiological responses to light explain competition and facilitation in a tree diversity experiment. *BioRxiv*. doi: 10.1101/845701

Koyama, A., & Tsuyuzaki, S. (2013). Facilitation by tussock-forming species on seedling establishment collapses in an extreme drought year in a post-mined Sphagnum peatland. *Journal of Vegetation Science*, *24*(3), 473–483. doi: 10.1111/j.1654-1103.2012.01474.x

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., … Westoby, M. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, *529*(7585), 204–207. doi: 10.1038/nature16476

Lamanna, J. A., Mangan, S. A., Alonso, A., Bourg, N. A., Brockelman, W. Y., Bunyavejchewin, S., … Memiaghe, H. R. (2017). Plant diversity increases with the strength of negative density dependence at the global scale. *Science*, *356*, 1389–1392.

Lambers, H., Chapin III, F. S., & Pons, T. L. (2008a). Mineral nutrition. In H. Lambers, F. S. Chapin III, & T. L. Pons (Eds.), *Plant Physiological Ecology* (Second, pp. 255–320). New York, US: Springer. doi: 10.1007/978-0-387-78341-3_6

Lambers, H., Chapin III, F. S., & Pons, T. L. (2008b). Plant water relations. In H. Lambers, F. S. Chapin III, & T. L. Pons (Eds.), *Plant Physiological Ecology* (Second, pp. 163–223). New York, US: Springer. doi: 10.1007/978-0-387-78341-3_3

Le Roux, P. C., Shaw, J. D., & Chown, S. L. (2013). Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New*

Phytologist, *200*(1), 241–250. doi: 10.1111/nph.12349

Lefever, R., & Lejeune, O. (1997). On the origin of tiger bush. *Bulletin of Mathematical Biology*, *59*(2), 263–294. doi: 10.1007/BF02462004

Leonard, L. A., & Croft, A. L. (2006). The effect of standing biomass on flow velocity and turbulence in Spartina alterniflora canopies. *Estuarine, Coastal and Shelf Science*, *69*(3–4), 325–336. doi: 10.1016/j.ecss.2006.05.004

Lotka, A. J. (1920). Analytical Note on Certain Rhythmic Relations in Organic Systems. *Proc. Natl. Acad. Sci. USA*, *6*, 410–415.

Lotka, A. J. (1924). Elements of physical biology. In *Williams and Wilkins*. Baltimore: Williams and Wilkins.

Lozano, Y. M., Armas, C., Hortal, S., Casanoves, F., & Pugnaire, F. I. (2017). Disentangling above- and below-ground facilitation drivers in arid environments: the role of soil microorganisms, soil properties and microhabitat. *New Phytologist*, *216*(4), 1236–1246. doi: 10.1111/nph.14499

Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., … Janssens, I. A. (2007). CO2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, *13*, 2509– 2537. doi: 10.1111/j.1365-2486.2007.01439.x

Maestre, F. T., Bautista, S., & Cortina, J. (2003). Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology*, *84*(12), 3186–3197. doi: 10.1890/02-0635

Maestre, F. T., Valladares, F., & Reynolds, J. F. (2005). Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, *93*(4), 748–757. doi: 10.1111/j.1365-2745.2005.01017.x

Maina, G. G., Brown, J. S., & Gersani, M. (2002). Intra-Plant versus Inter-Plant Root Competition in Beans : Avoidance , Resource Matching or Tragedy of the Commons. *Plant Ecology*, *160*(2), 235–247. doi: 10.1023/A:1015822003011

Martínez-García, R., Calabrese, J. M., Hernández-García, E., & López, C. (2013). Vegetation pattern formation in semiarid systems without facilitative mechanisms.

Geophysical Research Letters, *40*, 6143–6147.

Martínez-García, R., Calabrese, J. M., Hernández-García, E., & López, C. (2014). Minimal mechanisms for vegetation patterns in semiarid regions. *Philosophical Transactions of the Royal Society A*, *372*(2027), 20140068. doi: 10.1098/rsta.2014.0068

Martínez-García, R., & López, C. (2018). From scale-dependent feedbacks to long-range competition alone: a short review on pattern-forming mechanisms in arid ecosystems. *ArXiv*, 1801.01399.

Matsuda, H., Ogita, N., Sasaki, A., & Sato, K. (1992). Statistical Mechanics of Population: The Lattice Lotka-Volterra Model. *Progress of Theoretical Physics*, *88*(6), 1035–1049. doi: 10.1143/ptp/88.6.1035

Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge: Cambridge University Press. doi: 10.2277/0521288843

McGill, B. J. (2010). Matters of scale. *Science*. doi: 10.1126/science.1188528

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, *21*(4), 178–185. doi: 10.1016/j.tree.2006.02.002

McIntire, E. J. B., & Fajardo, A. (2009). Beyond description: The active and effective way to infer processes from spatial patterns. *Ecology*, *90*(1), 46–56. doi: 10.1890/07-2096.1

Mcnickle, G. G., & Dybzinski, R. (2013). Game theory and plant ecology. *Ecology Letters*, *16*(4), 545–555. doi: 10.1111/ele.12071

McNickle, G. G., Gonzalez-Meler, M. A., Lynch, D. J., Baltzer, J. L., & Brown, J. S. (2016). The world's biomes and primary production as a triple tragedy of the commons foraging game played among plants. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1842), 1–9. doi: 10.1098/rspb.2016.1993

McNickle, G. G., St. Clair, C. C., & Cahill, J. F. (2009). Focusing the metaphor: plant root foraging behaviour. *Trends in Ecology and Evolution*, *24*(8), 419–426. doi: 10.1016/j.tree.2009.03.004

Meron, E. (2015). *Nonlinear Physics of Ecosystems*. CRC Press.

Meron, E. (2018). From Patterns to Function in Living Systems: Dryland Ecosystems as a Case Study. *Annu. Rev. Condens. Matter Phys*, *9*(November 2017), 79–103. doi: 10.1146/annurev-conmatphys

Meron, E., Bennett, J. J. R., Fernandez-Oto, C., Tzuk, O., Zelnik, Y. R., & Grafi, G. (2019). Continuum Modeling of Discrete Plant Communities: Why Does It Work and Why Is It Advantageous? *Mathematics*, *7*(10), 987. doi: 10.3390/math7100987

Metz, J., & Tielbörger, K. (2016). Spatial and temporal aridity gradients provide poor proxies for plant-plant interactions under climate change: A large-scale experiment. *Functional Ecology*, *30*(1), 20–29. doi: 10.1111/1365-2435.12599

Michalet, R., Le Bagousse-Pinguet, Y., Maalouf, J. P., & Lortie, C. J. (2014). Two alternatives to the stress-gradient hypothesis at the edge of life: The collapse of facilitation and the switch from facilitation to competition. *Journal of Vegetation Science*, *25*(2), 609–613. doi: 10.1111/jvs.12123

Miriti, M. N. (2006). Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology*, *94*(5), 973–979. doi: 10.1111/j.1365-2745.2006.01138.x

Molina-Montenegro, M. A., Ricote-Martínez, N., Muñoz-Ramírez, C., Gómez-González, S., Torres-Díaz, C., Salgado-Luarte, C., & Gianoli, E. (2013). Positive interactions between the lichen Usnea antarctica (Parmeliaceae) and the native flora in Maritime Antarctica. *Journal of Vegetation Science*, *24*(3), 463–472. doi: 10.1111/j.1654-1103.2012.01480.x

Muzylo, A., Llorens, P., Valente, F., Keizer, J. J., Domingo, F., & Gash, J. H. C. (2009). A review of rainfall interception modelling. *Journal of Hydrology*, *370*(1–4), 191–206. doi: 10.1016/j.jhydrol.2009.02.058

Niklas, K. J., Cobb, E. D., Niinemets, Ü., Reich, P. B., Sellin, A., Shipley, B., & Wright, I. J. (2007). "Diminishing returns" in the scaling of functional leaf traits across and within species groups. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(21), 8891–8896. doi: 10.1073/pnas.0701135104

O'Brien, E. E., Gersani, M., & Brown, J. S. (2005). Root proliferation and seed yield in response to spatial heterogeneity of below-ground competition. *New Phytologist*, *168*(2), 401–412. doi: 10.1111/j.1469-8137.2005.01520.x

O'Dwyer, J. P. (2020). Beyond an ecological ideal gas law. *Nature Ecology and Evolution*, *4*, 14–15. doi: 10.1038/s41559-019-1066-0

Opie, J. (1968). Predictability of Individual Tree Growth Using Various Definitions of Competing Basal Area. *Forest Science*, *14*(3), 314–323. doi: 10.1093/forestscience/14.3.314

Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. J. A., Kobe, R. K., & Ribbens, E. (1996). Forest Models Defined by Field Measurements : Estimation , Error Analysis and Dynamics. *Ecological Monographs*, *66*(1), 1–43. doi: 10.2307/2963479

Parker, G. A., & Maynard Smith, J. (1990). Optimality theory in evolutionary biology. *Nature*, *348*, 27–33. doi: 10.1038/348027a0

Pereira, C. G., & Des Marais, D. L. (2020). The genetic basis of plant functional traits and the evolution of plant-environment interactions. *International Journal of Plant Sciences*, *181*(1), 56–74. doi: 10.1086/706190

Polis, G. A. (1999). Why Are Parts of the World Green? Multiple Factors Control Productivity and the Distribution of Biomass Author. *Oikos*, *86*(1), 3–15. doi: 10.2307/3546565

Poorter, H., Jagodzinski, A. M., Ruiz-Peinado, R., Kuyah, S., Luo, Y., Oleksyn, J., … Sack, L. (2015). How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist*, *208*, 736–749. doi: 10.1111/nph.13571

Prieto, I., Armas, C., & Pugnaire, F. I. (2012). Water release through plant roots: New insights into its consequences at the plant and ecosystem level. *New Phytologist*, *193*(4), 830–841. doi: 10.1111/j.1469-8137.2011.04039.x

Primack, R. B., & Hyesoon Kang. (1989). Measuring fitness and natural selection in wild plant populations. *Annual Review of Ecology and Systematics. Vol. 20*, *20*, 367–396. doi: 10.1146/annurev.es.20.110189.002055

Pugnaire, F. I., Armas, C., & Valladares, F. (2004). Soil as a mediator in plant-plant interactions in a semi-arid community. *Journal of Vegetation Science*, *15*(1), 85–92. doi: 10.1111/j.1654-1103.2004.tb02240.x

Pulliam, H. R., Pyke, G. H., & Caraco, T. (1982). The scanning behavior of juncos: A game-theoretical approach. *Journal of Theoretical Biology*, *95*(1), 89–103. doi: 10.1016/0022-5193(82)90289-2

Rankin, D. J., Bargum, K., & Kokko, H. (2007). The tragedy of the commons in evolutionary biology. *Trends in Ecology and Evolution*, *22*(12), 643–651. doi: 10.1016/j.tree.2007.07.009

Rietkerk, Boerlijst, van Langevelde, HilleRisLambers, van de Koppel, Kumar, … de Roos. (2002). Self-Organization of Vegetation in Arid Ecosystems. *The American Naturalist*, *160*(4), 524. doi: 10.2307/3079239

Rietkerk, M., Dekker, S. C., De Ruiter, P. C., & Van De Koppel, J. (2004). Self-organized patchiness and catastrophic shifts in ecosystems. *Science*. doi: 10.1126/science.1101867

Rinella, M. J., Strong, D. J., & Vermeire, L. T. (2020). Omitted variable bias in studies of plant interactions. *Ecology*, *0*(0), 1–7. doi: 10.1002/ecy.3020

Ripley, B. D. (1978). Spectral Analysis and the Analysis of Pattern in Plant Communities. *Journal of Ecology*, *66*(3), 965–981. doi: 10.2307/2259308

Scheiner, S. M., Chiarucci, A., Fox, G. A., Helmus, M. R., McGlinn, D. J., & Willing, M. R. (2011). The underpinnings of the relationship of species richness with space and time. *Ecological Monographs*, *81*(2), 195–213. doi: 10.1890/10-1426.1

Schenk, H. J., Callaway, R. M., & Mahall, B. E. (1999). Spatial Root Segregation: Are Plants Territorial? *Advances in Ecological Research*, *28*, 145–180. doi: 10.1016/S0065-2504(08)60032-X

Schiffers, K., & Tielbörger, K. (2006). Ontogenetic shifts in interactions among annual plants. *Journal of Ecology*, *94*(2), 336–341. doi: 10.1111/j.1365-2745.2006.01097.x

Semchenko, M., Hutchings, M. J., & John, E. A. (2007). Challenging the tragedy of the commons in root competition: Confounding effects of neighbour presence and substrate volume. *Journal of Ecology*, *95*(2), 252–260. doi: 10.1111/j.1365-2745.2007.01210.x

Shugart, H. H., & West, D. C. (1980). Forest Succession Models. *BioScience*, *30*(5), 308–313. doi: 10.2307/1307854

Shugart, H. H., Wang, B., Fischer, R., Ma, J., Fang, J., Yan, X., … Armstrong, A. H. (2018). Gap models and their individual-based relatives in the assessment of the consequences of global change. *Environmental Research Letters*, *13*(033001). doi: 10.1088/1748-9326/aaaacc

Soliveres, S., de Soto, L., Maestre, F. T., & Olano, J. M. (2010). Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. *Perspectives in Plant Ecology, Evolution and Systematics*, *12*(3), 227–234. doi: 10.1016/j.ppees.2010.02.003

Soliveres, Santiago, & Maestre, F. T. (2014). Plant-plant interactions, environmental gradients and plant diversity: A global synthesis of community-level studies. *Perspectives in Plant Ecology, Evolution and Systematics*, *16*(4), 154–163. doi: 10.1016/j.ppees.2014.04.001

Stoll, P., & Bergius, E. (2005). Pattern and process: Competition causes regular spacing of individuals within plant populations. *Journal of Ecology*, *93*(2), 395–403. doi: 10.1111/j.0022-0477.2005.00989.x

Tirado, R., & Pugnaire, F. I. (2005). Community structure and positive interactions in constraining environments. *Oikos*, *11*(3), 437–444. doi: 10.1111/j.1600-0706.2005.14094.x

Trautz, A. C., Illangasekare, T. H., & Rodriguez-Iturbe, I. (2017). Role of co-occurring competition and facilitation in plant spacing hydrodynamics in water-limited environments. *Proceedings of the National Academy of Sciences*, *114*(35), 9379–9384. doi: 10.1073/pnas.1706046114

Turcotte, M. M., & Levine, J. M. (2016). Phenotypic Plasticity and Species Coexistence. *Trends in Ecology and Evolution*, *31*(10), 803–813. doi: 10.1016/j.tree.2016.07.013

Valladares, F., & Pearcy, R. W. (2002). Drought can be more critical in the shade than in the sun: A field study of carbon gain and photo-inhibition in a Californian shrub during a dry El Niño year. *Plant, Cell and Environment*, *25*(6), 749–759. doi: 10.1046/j.1365-3040.2002.00856.x

Valladares, Fernando, Bastias, C. C., Godoy, O., Granda, E., & Escudero, A. (2015). Species coexistence in a changing world. *Frontiers in Plant Science*, *6*(866), 1–16. doi: 10.3389/fpls.2015.00866

Valladares, Fernando, Gianoli, E., & Gómez, J. M. (2007). Ecological limits to plant phenotypic plasticity. *New Phytologist*, *176*(4), 749–763. doi: 10.1111/j.1469-8137.2007.02275.x

Valladares, Fernando, Laanisto, L., Niinemets, Ü., & Zavala, M. A. (2016). Shedding light on shade: ecological perspectives of understorey plant life. *Plant Ecology and Diversity*, *9*(3), 237–251. doi: 10.1080/17550874.2016.1210262

van der Merwe, S., Greve, M., Olivier, B., & le Roux, P. C. (2020). Testing the role of functional trait expression in plant–plant facilitation. *Functional Ecology*, *35*(1), 255–265. doi: 10.1111/1365-2435.13681

Verhulst, P.-F. (1845). Recherches mathématiques sur la loi d'accroissement de la population. *Mémoires de l'Académie Royale Des Sciences, Des Lettres et Des Beaux-Arts de Belgique*, *18*, 1–42.

Violle, C., Nemergut, D. R., Pu, Z., & Jiang, L. (2011). Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, *14*(8), 782–787. doi: 10.1111/j.1461-0248.2011.01644.x

Volterra, V. (1926). Variazioni e fluttuazioni del numero d’individui in specie animali conviventi. *Memorie Della R. Accademia Dei Lincei*. doi: 10.1093/icesjms/3.1.3

Walter, H. (1971). Introduction. In J. H. Burnett (Ed.), *Ecology of Tropical and Subtropical Vegetation* (pp. 1–70). Edimburgh: Oliver & Boyd.

Wangersky, P. J. (1978). Lotka-Volterra Population Models. *Annual Review of Ecology and Systematics*, *9*, 189–218. doi: 10.1146/annurev.es.09.110178.001201

Wright, A., Schnitzer, S. A., & Reich, P. B. (2014). Living close to your neighbors: The importance of both competition and facilitation in plant communities. *Ecology*, *95*(8), 2213–2223. doi: 10.1890/13-1855.1

Wright, A., Schnitzer, S. A., & Reich, P. B. (2015). Daily environmental conditions determine the competition-facilitation balance for plant water status. *Journal of Ecology*, *103*(3), 648–656. doi: 10.1111/1365-2745.12397

Xiong, S., & Nilsson, C. (1999). The effects of plant litter on vegetation: A meta-analysis. *Journal of Ecology*, *87*(6), 984–994. doi: 10.1046/j.1365-2745.1999.00414.x

Younginger, B. S., Sirová, D., Cruzan, M. B., & Ballhorn, D. J. (2017). Is Biomass a Reliable Estimate of Plant Fitness? *Applications in Plant Sciences*, *5*(2), 1–8. doi: 10.3732/apps.1600094

Zakharova, L., Meyer, K. M., & Seifan, M. (2019). Trait-based modelling in ecology: A review of two decades of research. *Ecological Modelling*, *407*(January), 108703. doi: 10.1016/j.ecolmodel.2019.05.008

Zea-Cabrera, E., Iwasa, Y., Levin, S., & Rodríguez-Iturbe, I. (2006). Tragedy of the commons in plant water use. *Water Resources Research*, *42*(SUPPL.), 1–12. doi: 10.1029/2005WR004514