The evolutionary stability of antagonistic plant facilitation across environmental gradients

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Data accessibility statement: All the computational code with model implementation are available at https://github.com/gandreguetto/antagonistic-facilitation.

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Abstract

Plant interactions, understood as the net effect of an individual on the fitness of a neighbor, vary in strength and can shift from negative interference to positive facilitation as the environmental conditions change in time and space. However, the biophysical mechanisms underlying these changes are not well understood. Additionally, evolutionary theory questions the stability of antagonistic facilitation. Using a mechanistic model for belowground resource competition between individual plants, we find that, under stress conditions, antagonistic facilitation is evolutionarily stable even when both interacting plants compete for resources. This supports the theory of ecosystem engineers in primary succession and nurse plants in the stress gradient hypothesis. Furthermore, we find that the proportion of the limiting resource that spontaneously becomes available to any plant is the key environmental parameter determining the evolutionary stability of facilitation. This represents a challenge and a potential confusion factor for empirical studies.

1. Introduction

Antagonistic facilitation is the interaction in which one individual increases the fitness of a second individual, which, in return, reduces the fitness of its benefactor, for example via competition for a common resource. Antagonistic facilitation is frequent in nature, from microbial (West *et al.* 2006; Foster 2010; Tarnita 2017) to plant communities (Brooker *et al.* 2008; Schöb *et al.* 2014; Soliveres *et al.* 2015), and it contributes to the increase and maintenance of local biodiversity and ecosystem services (Schöb *et al.* 2012; Bulleri *et al.* 2016, 2018; Cavieres *et al.* 2016; Wright *et al.* 2017; Losapio *et al.* 2021a).

Antagonistic facilitation is often associated with ecosystem engineers, i.e., individuals that modify their local environment creating habitats that are more conducive for life in the long term (Hastings *et al.* 2007; Gore *et al.* 2009; Cordero *et al.* 2012; Schöb *et al.* 2014; Estrela *et al.* 2018; Losapio *et al.* 2021b). Yet, its evolution and stability pose an evolutionary dilemma, which made antagonistic facilitation subject of intense research over the last decades (Nowak 2006). To resolve this question, many theoretical studies have incorporated different mechanisms, such as a population spatial structure or individual reputations, into game-theoretical frameworks (Nowak 2006). More recently, experiments in microbes have both tested these model predictions and found alternative mechanisms that stabilize antagonistic facilitation (Rainey & Rainey 2003; Drescher *et al.* 2014). At larger scales, however, antagonistic facilitation remains poorly understood.

In plant communities, ecosystem engineers are usually shrubs that colonize inhospitable habitats such as sand dunes, volcanic eruptions, deglaciation lands, or unstable stony grounds during the process of primary succession (Mori *et al.* 2017; Bai *et al.* 2018; Karadimou *et al.* 2018; Kjær *et al.* 2018). To grow in such conditions, plant ecosystem engineers need to evolve specific traits that allow them to colonize hostile environments where most plants cannot survive (Verdú *et al.* 2021). Once the ecosystem engineer has established, opportunistic individuals that were unable to colonize the landscape by themselves can establish and proliferate (Crain & Bertness 2006). As a result, ecosystem engineers and opportunistic plants interact via antagonistic facilitation. The former acts as a nurse plant, and the latter profits from the nursing effect of the ecosystem engineer but also competes with its benefactor for shared resources. A few theoretical studies have investigated how this association is sustained in the long term, suggesting that antagonistic facilitation is

evolutionarily unstable and thus dissolves through the course of evolution (Brooker *et al.* 2008; Bronstein 2009) or that it stabilizes only if facilitator plants cluster and engage locally in mutualistic interactions (Kéfi *et al.* 2008).

The mechanisms by which a nurse plant can facilitate the success of neighbors and promote primary succession are diverse, and soil amelioration is a major one (Pugnaire *et al.* 2004; Lozano *et al.* 2017; Koffel *et al.* 2018). For example, the root exudation of organic acids, chemical signals, and enzymes can have several positive effects on soil quality for roots. It can dissolve unavailable soil nutrients such as phosphorus (P), iron (Fe), or potassium (K), avoid toxic effects of hypoxia or an excess of aluminum (Al), and allow the establishment of symbiotic relations with nitrogen (N)-fixing microorganisms (Jones 1998; Dakora & Phillips 2002; Hinsinger *et al.* 2011). Because N and P are essential resources for plants and are typically sparse in soils, plants that can boost the availability of these macronutrients have received considerable attention (Lambers *et al.* 2008). Plants adapted to grow in P-deficient soils can develop expensive structures, known as cluster roots, that allow them to release P that has been sorbed to soil particles and make it available for locally foraging roots (Raven *et al.* 2018; Britto Costa *et al.* 2021). Some plants growing in N-limited soils can also develop root nodules, establishing mutualistic relations with N-fixing microorganisms that trade N for photosynthates (Sprent 1989; van Velzen *et al.* 2019). Moreover, some plants can increase soil moisture by having root systems with specific characteristics. For example, plants with roots able to break superficial soil compaction can increase local water infiltration to the soil (Montaña 1992; Bromley *et al.* 1997), and plants with deep tap roots reaching the water table can increase water availability in superficial soil layers by hydraulic lift (Caldwell & Richards 1989; Zapater *et al.* 2011; Prieto *et al.* 2012).

In all these situations, plant ecosystem engineers have specific root traits that allow them to locally ameliorate soil conditions at a cost to themselves, creating islands of fertility where opportunistic plants can potentially grow.

We investigate the shifts in plant interactions across environmental gradients and the evolutionary stability of antagonistic facilitation using soil-ameliorating ecosystem engineers as case study. We hypothesize that, contrary to general belief, antagonistic facilitation might be evolutionarily stable if facilitator plants find net rewards in bearing the soil ameliorating trait despite the collateral attraction of opportunistic plants. This situation is possible if the self-benefits of the trait overweight the costs of competition with the opportunistic neighbors. We test this hypothesis theoretically, using a modeling framework for belowground resource competition that describes resource dynamics explicitly. Our model results can encapsulate processes happening within the life span of an individual, the evolution of species, and the geological time (**Fig. 1**). Accounting for the phenotypically plastic root distribution of plants, the evolution of the ecosystem engineer trait, and the long-term improvement of the soil over the course of succession, we investigate under which conditions antagonistic facilitation may be beneficial for both interacting plants and hence evolutionarily stable.

2. Materials and Methods

2.1 Model formulation

We extend the spatially explicit model for resource competition introduced in Cabal *et al.*, 2020 to account for facilitation (Cabal *et al.* 2021). The model assumes a series of processes governing the dynamics of a soil resource W and provides the net resource gain for

each plant due to the balance between how much resource it uptakes at a soil location and the cost of exploiting it. To investigate the evolution of plant antagonistic facilitation, we consider two types of plants. Plant ecosystem engineers can enhance soil resource availability by evolving a resource mining trait ϕ. This trait bears a cost that is added to the cost of building and maintaining the root system. Opportunistic plants cannot develop the resource mining trait.

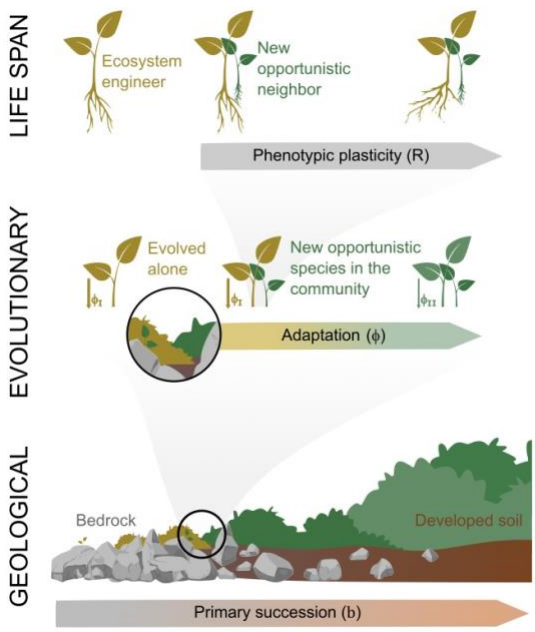

Figure 1: The different temporal scales at which we assessed the emergence of facilitative interactions, including the plastic response of plant root distribution R at the life span time scale, the adaptive response of the ecosystem engineers' facilitator trait ϕ at the evolutionary time scale, and the change in the fraction of soil resource that is spontaneously available over succession b at the geological time scale.

Resource dynamics. We model resource dynamics in each soil point as a combination of three processes: input at rate I, abiotic decay at rate δ, and resource uptake by the fine roots R at a per capita rate α (see **Table 1** for a summary of the environmental parameters and their dimensions). Lastly, we model the resource input assuming positive feedback between

resource availability and mining intensity. In soils lacking engineer plants roots, the fraction of available resource is equal to b ($0 \leq b \leq 1$) and it increases with engineer root density R_E due to the mining trait. We model this positive feedback assuming that I saturates at high mining intensity ϕR_E,

$$I(\phi, R_E) = \omega \frac{b + \phi R_E}{1 + \phi R_E} \tag{1}$$

Putting all these terms together, the resource concentration changes at each soil location according to

$$\frac{\partial W(\ell, t)}{\partial t} = I(\phi, R_E) - \alpha R W - \delta W \tag{2}$$

where we have dropped the dependence on space and time from the terms on the right of Eq. (2) and ℓ is the spatial coordinate of the soil location measured from the the insertion point of the focal plant's stem to the soil surface.

Net resource gain. At each soil location the net resource gain of an individual plant, j, at time t is the balance between the resource uptake and the associated cost,

$$G_j(\ell, t) = \left[WUE\, \alpha\, W(\ell, t) - C_j(\ell, \phi)\right] R_j(\ell) \tag{3}$$

where R is the fine root density (units of fine root biomass per unit of soil volume), C is the cost of producing and maintaining such root density, and WUE is the resource use efficiency that represents the conversion factor from harvested resource to new root biomass. Because the cost function depends on the distance between the soil patch and the plant insertion point to the soil surface, the model is spatially explicit. We account for three contributions to the cost function: the cost of producing and maintaining fine roots that absorb resources from the soil c_r, the cost of building and maintaining transportation roots that connect the fine roots to

the plant stem c_t (Cabal *et al.* 2020), and the cost per unit density of fine roots associated to a unit increase in the resource-mining trait c_e,

$$C_j(\ell, \phi) = c_r + c_t\, \ell^2 + c_e\, \phi \tag{4}$$

For opportunistic plants, $\phi = 0$ and the cost function in Eq. (4) has only two contributions (see **Table 2** for a summary of the plant parameters).

2.2 Model characteristic timescales.

We parameterize and analyze the model at three nested timescales. From shorter to longer, these timescales are: (i) the lifespan of a plant individual in which the spatial distribution of fine root biomass changes, (ii) the evolutionary timescale in which species evolve, including the resource-mining trait, and adapt to the environment, and (iii) the geological scale at which the environment matures driving successional changes in the community and we expect environmental parameters to vary (**Fig. 1**). Changes occurring in each of these timescales involve changes at shorter scales according to the new conditions found in every scenario. For example, as the resource-mining trait changes in evolutionary time to adapt to fixed environmental conditions, the spatial distribution of roots will also change according to the new level of resources mined by the plant.

(i) Changes in the spatial distribution of fine root biomass at the individual lifespan timescale. The spatial distribution of fine root biomass, $R(\ell)$, is a plastic trait tuned by a single plant over the course of its life span. Because the resource dynamics is much faster than root growth, we can assume that the resource concentration is in quasi-equilibrium in each step of plant growth and write a closed expression for the net resource gain of each plant at a given soil location (see SM for a full derivation),

$$G_j(\ell) = \left[\frac{WUE\ \alpha_j\ I(\phi, R_E)}{\delta + \sum_{i=1}^{n} \alpha_i\ R_i(\ell)} - C(\ell, \phi)\right] R_j(\ell) \tag{5}$$

Where R_E is the total root biomass of engineer plants at location ℓ. To optimize G in a given environmental scenario, we look for combinations of root density profiles and resource mining intensity that optimize the net resource gain in Eq. (5).

(ii) Changes in the resource-mining trait at the evolutionary time scale. The resource mining trait is normally assumed to remain constant over the lifespan of an individual, even if in some cases plants can tune it (Barron *et al.* 2011). Therefore, we consider that the resource-mining trait ϕ is fixed by evolution and its value does not vary spatially or in time for a given plant. Resource mining may evolve in ecosystem engineer plants when they are alone (ϕ_I) or, following a primary colonization by opportunistic plants, when they interact with opportunistic plants (ϕ_{II}) (see Supplementary Material for a detailed explanation on how we calculate these values). Modeling a community considering several individual opportunistic and engineer plants in interaction with one another would make the model mathematically intractable and require many arbitrary choices about community size and spatial structure. Instead, to get a general competitive background for the evolution of ϕ_{II}, we modeled the opportunistic individual as a spreading plant that grows vegetatively covering the soil surface (de Kroons & Hutchings 1995). These spreading opportunistic plants distribute their stem everywhere in the soil surface, like a stolon or a rhizome, so their roots grow across the canopy area of the ecosystem engineer at no horizontal space-related costs. Mathematically, this growth strategy implies removing the costs associated with transportation roots, $c_t = 0$. We consider this assumption to be a more realistic and tractable

representation of the average background community to which ecosystem engineers may have adapted.

(iii) Environmental changes in soil quality at the geological time scale. Three parameters determine soil resource dynamics: ω, b, and δ. Among them, the proportion of existing resource that becomes available spontaneously without plant mining b, may be key to understanding the mechanisms that mediate facilitation. Indeed, an engineer plant cannot increase the total amount of physical resource available in a soil location, but only the amount of such resource available to roots. It is also reasonable to assume that b is the main environmental parameter increasing over primary succession. For example, if water is the limiting resource and we consider two locations at different successional stages where precipitation is identical, the amount of rainwater that becomes available to plants will depend on water absorption rates and holding capacity of soils. While most water will quickly runoff in immature soils, more water will become available to plants as the substrate particle size decreases and the organic matter content increases in more developed soils. This increase in water availability is represented in our model by a larger b. In another example, rocks contain a lot of mineral nutrients that are not available to plant roots except for a small fraction that may dissolve in the rock interface. In more developed soils, however, most of these mineral nutrients incorporated into soil necromass and available to plants. These two examples illustrate how the environmental parameter b embodies the changes happening in soils over primary succession and how more mature soils offer a larger fraction of resources to roots relative to the resources physically present. Therefore, we mimicked a geological time scale varying the parameter b for fixed values of the other environmental parameters ω and δ.

Table 1: Parameter description and values (if not indicated otherwise) for the environmental resource dynamics.

Parameter (Environment)	Symbol	Units	Value
Potential resource input	ω	$ml.day^{-1}$	5
Proportion of ω abiotically available	b	-	0.05
Resource abiotic decay rate	δ	day^{-1}	0.1

Table 2: Parameter description and values for the plant functional traits in spreading opportunistic plants (SPR), normal opportunistic plants (NOP), and ecosystem engineer plants (EEP).

Parameter (Functional traits)	Symbol	Units	SOP	NOP	EEP
Uptake rate per unit fine root weight	α	$ml.mg^{-1}.day^{-1}$	10	10	10
Resource use efficiency	WUE	$ml.mg^{-1}$	1	1	1
Cost of fine roots	c_r	$ml.cm^3.mg^{-1}.day^{-1}$	5	5	5
Cost of transportation roots	c_t	$ml.cm^3.mg^{-1}.day^{-1}$	0	0.2	0.2
Cost of facilitation trait	c_e	$ml.cm^3.mg^{-1}.day^{-1}$	0	0	1.25
Resource-mining trait	ϕ	$ml.mg^{-1}.day^{-1}$	0	0	ϕ_I, ϕ_{II}

2.3 Two-step model analysis

We conducted a two-stage computational analysis. First, we parameterized the model to mimic conditions representing a specific moment in successional and evolutionary time. Then, we studied plant-plant interactions simulating experiments at the life span timescale using the previously parameterized scenarios.

Model parameterization. To mimic natual conditions in which engineer plants might have evolved the resource mining trait, we allow ϕ to evolve either assuming that soil-engineer plants grow alone, ϕ_I, or competing with spreading opportunistic plants, ϕ_{II}. We obtain these values of ϕ for a range of environmental stresses, from $b = 0$ (high stress) to $b = 1$ (low stress). This first analysis yields evolutionary stable values of the resource mining trait

for an ecosystem engineer plant at a given successional stage that adapted growing alone or surrounded by opportunistic plants.

Model experiments. Then, we take individual plants from the above parameterized conditions (i.e., using the values ϕ_I or ϕ_{II} expected to evolve at a given b) and simulate experiments with such plants at the scale of their life span. We perform two classes of independent experiments, a first type in which we grow the engineer or the opportunistic plant alone, and a second type in which we grow an opportunistic-engineer pair of interacting plants separated by a distance d. In this second setup, we assumed that both plants shared the same insertion point to the soil ($d = 0$) to maximize the strength and effects of the interaction. For each set of experiments, we obtained the root biomass distribution $R(\ell)$ and calculated the plant-level resource gain associated to such root distribution, $\mathcal{G}$, integrating G [Eq. (5)] in space. Finally, using the results from both sets of experiments, we estimated the net interaction between the two plants by comparing the plant-level net resource gain of solitary and paired individuals. Following a similar procedure, we also calculated the total root biomass of plants, $\mathfrak{R}$, by integrating the local $R(\ell)$ values across space and estimated the difference in root proliferation by comparing the values for solitary and paired plants.

To measure both the net interaction outcome in pairwise experiments, and to which extent the opportunistic plant changes its root biomass in the presence of the nurse plant, we calculated coefficients based on normalized ratios N (Dohn *et al.* 2013):

$$N_X = \frac{X_{interact} - X_{solo}}{X_{interact} + X_{solo}} \tag{6}$$

Where X takes value $\mathfrak{R}$ or $\mathcal{G}$ depending on whether we measure changes in root production or the net interaction outcome. $X_{interact}$ is the value obtained for $\mathfrak{R}$ or $\mathcal{G}$ when the opportunistic

plant grows close to nurse plant and X_{solo} is the value obtained for solitary plants. N can vary from -1 to 1. For the net interaction outcome, $N_{\mathcal{G}} = -1$ indicates that the plant cannot coexist with the neighbor (competitive exclusion); $-1 < N_{\mathcal{G}} < 0$ indicates net interference; $N_{\mathcal{G}} = 0$ no effect; $0 < N_{\mathcal{G}} < 1$, net facilitation; and $N_{\mathcal{G}} = 1$ indicates that the plant cannot exist without the neighbor (obligatory facilitation). For root biomass measurements, $N_{\mathfrak{R}} < 0$ indicates root underproliferation and $N_{\mathfrak{R}} > 0$, overproliferation with respect to a solo plant.

3. Results

3.1 Opportunistic plants do not survive alone and engineer plants evolve in very stressful habitats.

Only engineer plants with a mining intensity above a given threshold can colonize and survive in stressful habitats, represented by values of b below a critical threshold $b_{c\text{-}o}$. Plants investing in resource mining below this threshold, including opportunistic ones, cannot survive because their root production and maintenance cost outweigh resource uptake (**Fig. 2**). The optimal resource mining intensity for solitary soil engineer plants is a finite value ϕ_I that depends on the environmental stress. Values greater than ϕ_I are suboptimal because the costs of increasing the mining capacity outweigh the revenue per unit increase. Indeed, at very high values of ϕ the plant-level net resource gain and the optimal root biomass become zero. The cost of producing roots with such level of mining ability exceed the amount of resource that such roots can mine and uptake, and the plant cannot establish. The optimal value of the resource mining trait for solitary individuals, however, does not coincide with the value of ϕ at which root biomass is maximal for these plants. Values of ϕ lower than ϕ_I

result in more roots, but with lower marginal gain (**Fig. 2a**). Lastly, we find that the presence of spreading opportunistic plants triggers a post-colonization evolutionary drift on the resource mining trait. This shift in the resource mining trait, from ϕ_I to a lower value ϕ_{II} (**Fig. 3a**), is caused by the changes in the resource dynamics prompted by the colonization of opportunistic individuals.

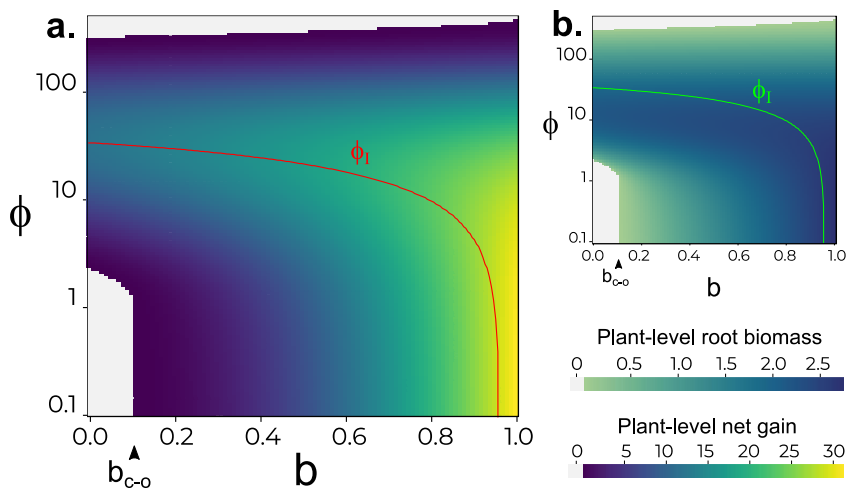

Figure 2: (a)Plant-level net gain and (b) fine root biomass as a function of ϕ (log-scaled axis) and b for a soil engineer plant growing solo. Lines in both panels represent the value of the mining trait that evolves at different successional times, ϕ_I. The point $b_{c\text{-}o}$ is the stress threshold below which opportunistic plants cannot survive (light gray region).

3.2 Shifts from antagonistic facilitation to mutual interference as environmental stress decreases.

Antagonistic facilitation is evolutionary stable in stressful habitats, represented by low values of b, regardless of whether engineer plants evolved resource mining in the presence of opportunistic neighbors (ϕ_{II}) or solitary (ϕ_I) (green shaded region in **Fig. 3b**). This evolutionary stability allows opportunistic plants to survive at the shelter of engineer plants in environments where they would not survive on their own, i.e., where $b < b_{c\text{-}o}$. Moreover, at values of b higher than $b_{c\text{-}o}$ but still low, opportunistic individuals growing close to a soil engineer exhibit higher plant-level net gain than solitary ones. Engineer plants have

a strong positive effect on opportunistic neighbors before they evolve to adapt to its presence (ϕ_I). The evolutionary drift on the resource mining trait from ϕ_I to a lower value ϕ_{II} increases the engineer's net gain and decreases the opportunistic plant's net gain when they interact. However, engineer plants benefit from a non-zero ϕ_{II} value, which also benefits their competitors and allows their survival in highly stressed environments, $b < b_{c\text{-}o}$. These results show that antagonistic facilitation is evolutionary stable in our model, and that engineer plants have a positive effect on opportunistic individuals (facilitation) for any b below a critical shifting point b_s (**Fig. 3b**). We calculate this shifting point using only ϕ_{II} because ϕ evolves much faster than soil successional change and we expect the transition from ϕ_I to ϕ_{II} to be abrupt at the geological scale. Above b_s, the net gain of an opportunistic plant is higher when it grows alone than near an engineer plant. Therefore, the strength of exploitative competition exceeds the positive effect of the engineer's mining trait on the opportunistic plant and the interaction becomes mutual interference.

The amount of resource that engineer plants can mine becomes progressively lower as b increases and more resource is spontaneously available for plants, which also results in smaller net gain differences between solitary engineer and opportunistic plants. We define the critical b for engineer plants $b_{c\text{-}e} < 1$ as the maximum value of b at which resource mining is evolutionarily stable and hence engineer plants can persist. Our results show that above $b_{c\text{-}e}$ the optimal value of the evolved mining trait is $\phi_{II} = 0$, suggesting that engineer plants would evolve to lose the resource mining trait and become opportunistic (**Fig. 3**). In other words, ecosystem engineers cannot persist in very mild environments, and they might lose the

mining trait to not be outcompeted, or specialize in resource-poor patches in the case of heterogeneous ecosystems.

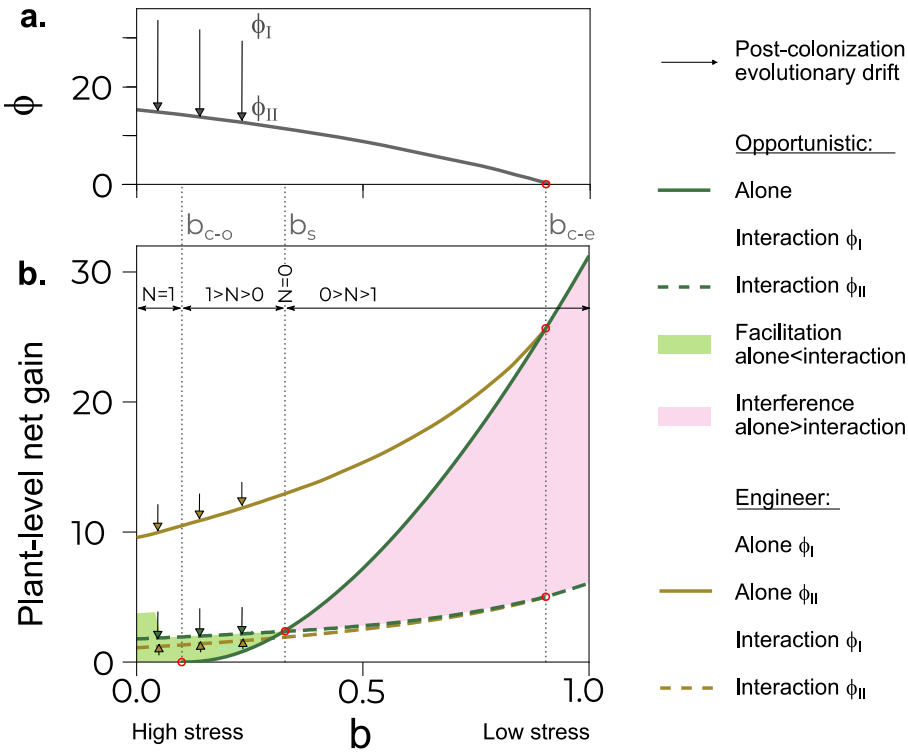

Figure 3: (a) Mining trait ϕ_I in an evolutionary equilibrium resulting from the model parameterization step of the analysis across an environmental gradient defined by *b*. (b) Plant-level net resource gain as a function of *b* for plants growing alone and engineer-opportunistic pairs. Different lines show different evolutionary equilibria as indicated in the legend: ϕ_I (only shown for low-*b* scenarios where engineer plants may have evolved alone) and ϕ_{II}.

3.3 The effects of different environmental parameters on plant interaction and root proliferation

Finally, we evaluate the effects of the three environmental parameters, *b*, δ, and ω on the biotic interaction. We have seen that, for fixed values of δ and ω, ϕ_{II} decreases progressively as *b* increases, until $\phi_{II} = 0$ at low stress levels represented by $b = b_{c\text{-}e}$. When the stress is caused by δ or ω, however, ϕ_{II} changes abruptly from 0, at high levels of δ- and ω-stress, to a positive value when stress levels go below a threshold (**Fig. 4a, b**).

The Dohn's coefficient for the plant-level net gain $N_{\mathcal{G}}$ shows that the interaction transitions gradually from facilitation at low levels of b (high b-stress) toward higher levels of b. Indeed, above $b_{c\text{-}e}$ the engineer loses the mining trait and hence the result is two opportunistic plants competing exploitatively. For the other environmental parameters, however, $N_{\mathcal{G}}$ shows that plants cannot survive at very high levels of δ-stress and ω-stress (**Fig 4c, d**). At lower stresses, there is an environmental threshold (solid green lines in **Fig. 4c, d**) below which pairs of plants can survive but engineers do not evolve a positive value in their mining trait. For that range of environmental values, defined by moderately high levels of δ-stress and ω-stress pairs of exploitative plants compete similarly to what we observe for $b \geq b_{c\text{-}e}$. At even lower δ- and ω-stress, we find a second threshold where engineer plants acquire their positive mining trait in an abrupt shift (dashed red lines in **Fig. 4c, d**). After passing that second threshold the net interaction, measured by $N_{\mathcal{G}}$, depends strongly on b, but it barely changes with δ and ω. Only for a very narrow range of intermediate values of b, the interaction changes slightly as a function of the other parameters, namely from facilitation to competition as δ-stress decreases, but from competition to facilitation as ω-stress decreases. We observe that the fraction of resource that is available without the intervention of mining b, rather than the potential resource input ω or the physical decay rate of the resource δ, accounts for most of the variation in the sign and the strength of the biotic interaction. This justifies choosing b as the main environmental parameter in our study but also has important consequences in the interpretation of ecological theory.

The analysis of root production using the Dohn's coefficient for root biomass N_R shows that transition from facilitation to competition (**solid golden line in Fig. 4e, f**) does not coincide with transition from opportunistic plants root overproliferation to

underproliferation (**solid blue line in Fig 4e, f**). This result allows for three possible interaction outcomes. First, when there is antagonistic facilitation the opportunistic plant always overproliferates roots (F-Ov). Second, plants might interact via mutual interference, but the opportunistic plant still overproliferate roots as compared to growing alone (I-Ov). This overproliferation is the result of the tragedy of the commons in root competition (Cabal 2022). Finally, plants might interfere with each other and underproliferate roots (I-Und). The latter two interaction outcomes can happen for positive values of ϕ_{II} (active mining of the engineer) or for $\phi_{II} = 0$ (both plants compete equally).

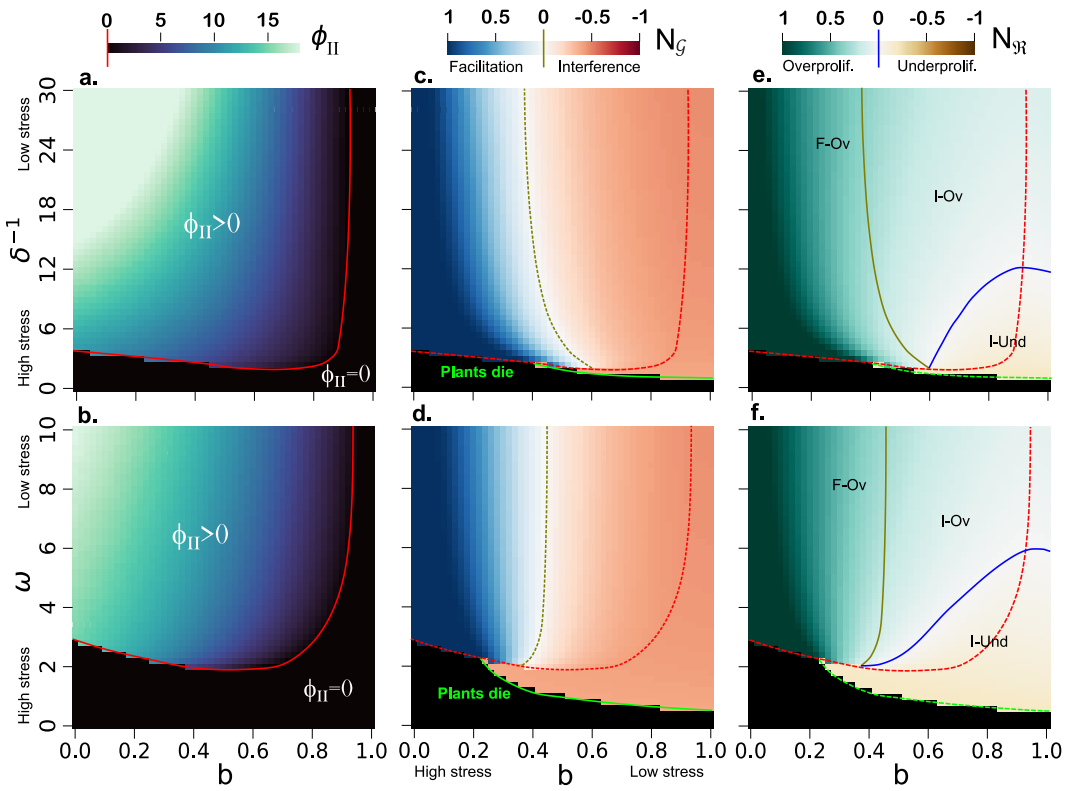

Figure 4: Changes in the resource-mining trait ϕ_{II} (a, b); the Dohn's interaction coefficient for the plant-level net resource gain $N_{\mathcal{G}}$ (c, d); and for root biomass $N_{\mathfrak{R}}$ of the opportunistic plant in interaction with an engineer individual (e, f). We measure each of these changes at different values of the three environmental parameters b, ω and δ. The cases F-Ov, I-Ov and I-Und are describe in the main text.

4. Discussion

4.1 Successional changes in plant biotic interactions

The amount of resource available to plants without the intervention of root mining is the leading force driving the change in plant interactions over successional time. Only ecosystem engineers can colonize highly stressed ecosystems, representing the initial stages of succession ($b < b_{c\text{-}o}$) at which opportunistic plants cannot survive on their own. Nevertheless, after engineers colonize the system, opportunistic plants can establish an obligatory interaction with their benefactors and invade the ecosystem growing at the shelter of their root crown. Previous work has suggested that nurse plants may lose their mining trait over the course of evolution in the presence of opportunistic neighbors that benefit from it at no cost (Walker & Chapin III 1987; Koffel *et al.* 2018; Song *et al.* 2019). Our results, however, suggest that antagonistic facilitation is evolutionarily stable at high environmental stresses because nurse plants benefit from bearing the mining trait despite the presence of opportunistic plants. For environmental stresses higher than a critical value b_s, the engineer plant has an overall positive effect on the opportunistic because the benefits of mining overcome resource competition. In environments milder than b_s, resource competition becomes the dominant force and the net interaction between the soil-engineer and the opportunistic plant transitions from antagonistic facilitation to mutual interference. Finally, for $b > b_{c\text{-}e}$, representing low environmental stress like, for example, in well-developed soils, most of the resource becomes spontaneously available to the plants and all plants evolve an opportunistic strategy.

4.2 Consequences for the stress gradient hypothesis

Some ecosystems, such as deserts, Mediterranean shrublands, or tropical savannas, are more stressful and resource-poor than others, such as temperate or tropical forests, even when successionally mature. The stress gradient hypothesis (SGH) predicts that facilitation must dominate in more stressful habitats while interference must prevail in mild conditions (Bronstein 2009). Because meta-analyses of studies reporting facilitation over stress gradients did not find consistent support for this theory, several authors suggested that stress could be classified as resource-stress and non-resource-stress, and only the former leads to SGH predictions (Bertness & Callaway 1994; He *et al.* 2013). Our model further dissects resource-stress into three parameters; the total input of resource ω (e.g., levels of precipitation), the fraction of such resource that becomes available to plants spontaneously b (e.g., how much of the rainwater infiltrates in bare soil and becomes available to roots without the intervention of ecosystem engineers), and the rate of physical resource decay δ (e.g., how fast the infiltrated water leaves the soil due to evaporation or percolation). Our results support the SGH for resource stress if the stress is caused by b, but the other environmental parameters did not impact the net interaction significantly. We show that b is main driver of shifts in plant biotic interactions across resource stress gradients. Moderate changes in b would dominate and mask the effects on plant biotic interactions of changes in any of the other environmental parameters.

The humped-back SGH, an alternative theory to study plant facilitation and biotic interactions, suggests that plant facilitation maximizes at moderate, rather than highest, levels of stress (Maestre *et al.* 2005, 2009). Our results support humped-back SGH when extreme stress is caused by δ or ω. We observe an abrupt strategy shift in engineer plants that lose

their mining trait when δ or ω drive increases in environmental stress. At a narrow range of intermediate values of *b*, this shift can cause a sudden transition from interference between two opportunistic plants to facilitation where one plant becomes the nurse plant, followed by a gradual loss of the net facilitation.

Teasing apart the contributions of all three parameters to resource dynamics will allow researchers to elaborate more mechanistic descriptions of the resource stress and therefore develop more comprehensive theories regarding the importance of facilitation across a stress gradient.

4.3. Consequences for empirical studies

Our results have clear consequences for the interpretation of empirical studies addressing interaction shifts across environmental gradients. We have identified two major sources of potential confusion based on our model. First is the fact that *b* is the main environmental driver of shifts in plant interactions. This parameter, which could represent, for example, water infiltration:runoff ratio, is much harder to determine empirically than the other two environmental parameters ω or δ (e.g., rainfall or soil drying rates). Many empirical studies assess the changes in plant interaction across environmental gradients using the latter two variables, and our model suggests that this may not be the right approach. Second, many studies consider that an increase in plant biomass when plants interact indicates facilitation because they assume that plant biomass is a good proxy for plant fitness (Younginger *et al.* 2017). Our results suggest that plant biomass is a misleading fitness surrogate, despite we find that facilitated plants always overproliferate roots, because plants might also overproliferate roots due to a tragedy of the commons (Gersani *et al.* 2001; Cabal *et al.* 2020; Cabal 2022).

5. Conclusions

Antagonistic facilitation enables more diverse plant communities in stressful environments at the initial stages of primary succession and may accelerate the development of mature soils. It also may promote plant biodiversity in harsh habitats, such as deserts or Mediterranean shrublands, where nurse plants facilitate the survival of other species that depend on them. To mechanistically understand how the plant-plant interaction shifts across resource-stress gradients, it is fundamental to distinguish the biophysical parameters underpinning soil resource availability. We have proved that the main parameter explaining shifts in plant-plant interactions across resource-stress gradients is the proportion of the existing resource that becomes available to roots spontaneously (such as the proportion of rainfall that infiltrates in soil instead of running-off when the resource is water). The amount or resource input (such as rainfall when the resource is water) or the physical decay (such as loses of soil water through evaporation or percolation) play a secondary role. Accounting for this level of mechanistic detail in mathematical models for plant interactions and measuring these parameters in field studies is key to better understand the fundamental drivers of plant-plant interactions.

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