


## Emerging Voices in Botany

# Contextualizing the ecology of plant–plant interactions and constructive networks

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### Abstract

Botanical concepts have traditionally viewed the environment as a static box containing plants. In this box, plants compete with one another and act as passive resource consumers subjected to the environment in a top-down manner. This entails that plants have only negative effects on other plants and have no influence on the environment. By contrast, there is increasing evidence that plants have positive, bottom-up engineering effects and diversity effects on other plants and on the environment. Here, to overcome limitations of top-down environmental control, antagonistic-only, and pairwise interactions, I propose the concept of constructive networks. Constructive networks unify niche construction and network theory recognizing that (i) plants have manifold ecological functions and impacts on their neighbors, and (ii) the environment shapes and is shaped by diverse organisms, primarily plants. Constructive networks integrate both plant–environment and plant–plant interactions in a relational context. It is addressed how plants influence the environment and support or inhibit other plant species by physically, biochemically, and ecologically shaping environmental conditions. Constructive networks acknowledge the fact that diverse plants change and create novel environmental conditions as well as co-produce, share, and transform resources, thereby influencing biological communities and the environment in constructive ways. Different interaction types are considered simultaneously in constructive networks. Yet, the understanding of constructive networks is mainly limited by identifying plant links. This barrier may be overcome by applying complexity theory and statistical mechanics to comparative data and experimental field botany. Considering multiple interaction types and feedbacks between plants and the environment may improve our understanding of mechanisms responsible for biodiversity maintenance and help us to better anticipate the response of plant systems to global change.

**Key words:** biodiversity, community ecology, ecological networks, plant facilitation, species interactions

## Introduction

For centuries, scientists deduced properties of natural systems and hence inferred all their possible past and future states by breaking them up in basic units and meticulously measuring every and each part in isolation. This reductionist approach works well with unanimated bodies, but poses serious limits at the time of understanding living systems (Prigogine and Stengers, 1979).

The common feature of living systems is that they involve many ‘components’ that interact with each other and with their environment in a nonlinear way, and are consequently organized in an integrated, emergent ensemble (Ulanowicz, 2018). Hence, each component influences the others and it is also influenced by them. By reducing organisms, plant communities or ecosystems into single isolated genes, cells, individuals or populations we modify their functionality and restrict our inference of their interactive nature (Kauffman, 2019). As a consequence, plant systems cannot be fully understood by analyzing parts of them in isolation.

With the main goal of studying the relationships underlying biological systems, ecology has developed as the science of “how organisms interact with each other and with their environment” (Bersier, 2007; Levin, 2009). Focusing upon system mechanisms, mass and energy exchanges, and species interactions, ecology emphasizes relationships and processes over objects. This way, plant ecology can overcome limitations posed by biological reductionism and address the complexity of plant systems.

Ecological thinking in botany can be traced back to the ancient philosopher Theophrastus (371 BC–287 BC), who classified plants according to their reproduction, locality, size and practical uses in his *Historia Plantarum*. But the scientific field of plant ecology emerged from its biogeographic origins during the 19th century thanks to the work of the naturalist Alexander von Humboldt (1769–1859), who first studied how form and function of plants are affected by physical conditions, and provided the first description of global vegetation distribution according to climate (von Humboldt and Bonpland, 1805). Since then, plant ecology has grown from describing patterns of species and communities to inferring processes driving species diversity and diversification, towards the studies of species–environment relationships and the role of plant interactions for the functioning and stability of global ecosystems.

It is well recognized that the history of biodiversity is fundamentally a history of species interactions (Thompson, 1999; Bascompte and Jordano, 2014). In this sense, biodiversity is more than a list of genes or species. Solid evidence indicates that positive interactions are widespread in nature as mutualism and facilitation are increasingly recognized to be fundamental processes in the ecology and evolution of plants (Stachowicz, 2001; Callaway et al., 2002; Bruno et al., 2003; Callaway, 2007; Bascompte and Jordano, 2014; Cavieres et al., 2014; Losapio et al., 2021b). Despite recent advances in analyzing networks of interactions involving plant species (Levine et al., 2017; Alcántara et al., 2019; Losapio et al., 2021b), we are still far from understanding plant–plant networks and their role in maintaining biodiversity and regulating ecosystem functioning.

## The problem of analogies from animal studies

The idea of nature and life as a competitive race dates back to the late eighteenth century, and it is widespread not only in natural sciences but it is also embedded in many areas of social sciences

and arts. This idea is illustrated well by the painting *The struggle for existence* (1879) (Figure 1) which depicts the typical human view of a nature ‘red in tooth and claw’. This painting shows the degree to which culture and sciences have been dominated by antagonistic-oriented paradigms for centuries.

Such a strong focus on animal antagonistic interactions is exemplified by the emphasis on predation over herbivory (Figure 2a) and parasitism over mutualism (Figure 2b): during the last thirty years (from 1992 to 2022), studies on predation or parasitism have been published three to four times more than studies on herbivory or mutualism. If we consider that plants constitute 95% of terrestrial biomass (Bar-On et al., 2018), then this disproportionate focus on animal antagonistic interactions is especially striking. Given the central role attributed to competition and predation between animals, it is not surprising that theoretical and experimental studies in botany and plant ecology have been centered around antagonistic interactions between plants (Bronstein, 2009). Indeed, studies on plant competition are published ten times (!) more than those on plant facilitation (Figure 2c).

Despite half a century of research on competitive interactions and more than 33 thousand papers published on plant competition over the last thirty years, it is not clear how different species coexist in natural communities (Verhoef and Morin, 2010; Saavedra et al., 2017) nor how plant diversity supports ecosystem functioning (Wright et al., 2017). Most likely, the majority of these papers just assumed competition as a default explanation. Major focus on predation and competition left out of the picture fundamental biological phenomena such as mutualism in plant–animal interactions and facilitation in plant–plant interactions.

Unfortunately, the study of interactions between plant species have developed around theories and models formalized for antagonistic interactions between animals, an approach that poses serious limitations in understanding the ecology and evolution of plants. There are four fundamentals of plant biology that invalidates zoocentric analogies, assumptions, theories, and explanations. These four intrinsic properties of plants make them interconnected and interdependent on each other and coupled to their environment.

First, zoocentric models of predator–prey or consumer–resource interactions assumes plants as consumers. On the contrary, plants are the producers. Plants do not (only) consume nutrients, but first and foremost they produce organic matter by converting solar energy. In natural communities, i.e. not in agricultural settings where biomass is exported from the system, matter (i.e., resources and nutrients) is recycled within the ecosystem through plant biogeochemical paths, species interactions (e.g., herbivory) and environmental disturbance (e.g., fire) (Keddy, 2017). Notably, thanks to microorganism mutualistic partners hosted in their roots, plants do increase soil resources via transforming mineral compounds into organic nutrients (Tedersoo et al., 2020). Most importantly, while predation and herbivory are phenomenologically similar, animal preys cannot benefit from predation, whereas many plants may benefit from herbivory, such as in the case of compensatory growth (Archibald et al., 2019).

Second, the concept of individual in plants is remarkably different from the animal kingdom as plants are not individualistic but modular organisms (Keddy, 2017). What is an individual plant? How do we deal with clonal plants for which the concept of ‘individual’ is much more blurred? Is an individual a ramet or a genet? The notorious example of quaking aspen (*Populus tremuloides*) clonal colony of an ‘individual’ constituting a hundred-acres forest

Fig. 1: The struggle for existence, George Bouverie Goddard 1879 (1832–1886), National Museums Liverpool. Photo credit: Walker Art Gallery.

Fig. 2: Number of papers published from 1992 to 2022 as indexed on Web of Science (data retrieved on December 16 2022) focusing on animal and antagonistic interactions over plant and positive interactions. Search terms (title and abstract) were herbivory, predation, mutualism, parasitism, plant competition, and plant facilitation.

is emblematic of the difficulties associated with defining and identifying individual identity in the plant kingdom. Annual plants are the exception as their life cycle and individual fitness component are comparable to those of animals (Levine et al., 2017), but annual plants are poorly representative of global flora and biomes, making them unsuited to broader generalization and deeper understanding. For these reasons, zoocentric models based on individual fitness have a limited validity when applied to plant diversity and plant communities.

Third, plants have no consciousness nor cognition. Plants do not deliberately, intentionally make arbitrary decisions to facilitate other plants. Although plants form communities, communicate and actively respond to cues and their changing environment, they do not have social behaviour, they do not have intentions to coexist in the same community nor consciously chose their mating partners (Mescher and Pearse, 2016). Nevertheless, teleology, anthropomorphism, the figurative and metaphoric character of language and our semantic interpretations (Mescher and Pearse, 2016; Varella, 2018) embedded in animal–plant analogies may create biases, misunderstanding and misinterpretation in plant science.

Finally, the view of plants as sessile, unanimated organisms brought along a series of limitations. One of those is the prominent emphasis on deterministic top-down control of the environment on plants. Accordingly, plant species and ecological communities are analysed as a typological construct, assemblages of populations or species that share common adaptations and differentiate niches in response to levels of competition (Callaway, 2007; Saavedra et al., 2017). But this view of niches and the environment as an ‘abiotic’ static box leaves a lot to desire because it falls short in explaining the fact that organisms can actively modify their environment by creating new and destroying former biophysical conditions (Lewontin, 1983). As a matter of fact, organisms are not just passively influenced by abiotic factors, but rather they can ‘act’ upon their surroundings and change the environment (Chase and Leibold, 2003).

These four fundamental differences may explain why zoocentric ecologists and evolutionary biologists refuse the expectation that species interaction outcomes and stability are flipped in plant communities: while competition among animals increases when resources are scarce, plant competition increases with increasing resources, such as in agricultural systems (Keddy, 2017; Schöb et al., 2018), whereas plant facilitation prevails in harsh and poor-resource environments (Callaway et al., 2002).

### Plant–plant interactions beyond competition

For as much as the environment influences plants, in turn plants can modify their surrounding environment by creating new habitats and destroying former ones. This way, plants ultimately influence the dynamic of evolutionary and ecological processes in fundamental ways (Kéfi et al., 2012). The implications of these

facts are two-fold. First, plant species are not only top-down selected by the environment, but can rather bottom-up influence and change environmental conditions (Jones et al., 1994; Ellison et al., 2005; Schöb et al., 2012; Losapio et al., 2023). Second, plants may create the environmental conditions that allow other species to thrive, i.e., facilitate other plants (Bruno et al., 2003; Callaway, 2007; McIntire and Fajardo, 2014).

Plant facilitation is the positive interaction between two or more plant species in which a plant benefit from another one which may or may not benefit from it (Bertness and Callaway, 1994; Callaway, 2007). Facilitation occurs if the overall improvement of the environment results in a positive net outcome for at least one plant species. There is facilitation when plants or different species are experiencing greater dispersal success, recruitment, growth, survival, reproduction, and fitness in the presence of neighbors than in their absence (see (Callaway, 2007)). Consequently, the difference between mutualism and facilitation is that in mutualism both partners benefit from the interactions, whereas in facilitation the benefits interest at least one partner while the other one may not necessarily benefit. For example, annual herbs in arid ecosystems establish, recruit and survive more often, make better photosynthesis and produce more seeds beneath the canopy of shrubs than in shrub absence (Pugnaire, 2010). In turn, the effects for the shrub may range from negative to positive, including neutral, depending on the ecological process considered and the climate (Schöb et al., 2014; Losapio et al., 2021a). Hence, facilitation has been usually seen as commensalism (Callaway, 2007), but it may cover the whole spectrum from mutualism to parasitism (Schöb et al., 2014).

Across different systems, from alpine to deserts and kelp forests, facilitation mechanisms by plants are mainly due to modification of local environmental conditions (Bruno et al., 2003; Callaway, 2007; McIntire and Fajardo, 2014) and the construction of novel niche space (Schöb et al., 2012) in a way that it benefits other species. This facilitation process includes the following mechanisms (for a complete discussion, see (Callaway, 2007; McIntire and Fajardo, 2014)): (i) creation of habitat structural features and sheltering such as providing grow substrate or physical protection against herbivores, (ii) increase of resource availability such as improving soil organic matter, providing nutrients, increasing soil moisture or attracting pollinators, and (iii) decrease of stress and disturbance such as lower UV radiation and vapor pressure deficit, lower pathogen incidence, soil stabilization, decrease of temperature extremes.

As opposed to mutualism, facilitation between two plant species involves both direct effects (e.g. physical presence as well as the effects of plant activity on the environment) and indirect interactions (e.g. involvement of species from different trophic levels such as pollinators, herbivores, or microorganisms) (Callaway, 2007). Regardless of the outcome, mechanism-specific benefits and costs of plant interactions may concur at the same time between two plants (Losapio et al., 2019). This is the case, for instance,

when facilitation for recruitment and vegetative growth goes along with competition for pollination or seed dispersal (Ghazoul, 2006; Rumeu et al., 2019; Losapio et al., 2021a). A final difference between facilitation and mutualism lies in the research approach they received in the last two decades. While mutualistic interactions have undergone the “network revolution”, plant facilitation has been analyzed by looking at pairwise interactions as the study of facilitative interactions has hardly considered ecological networks (Losapio et al., 2019).

### Ecological networks involving plant facilitation

Since the end of the twentieth century, many systems including the human brain, food webs, financial markets and electrical grids among others have been described as networks (Cohen and Havlin, 2010). These networks, mathematically modeled as graphs, are defined by nodes that are connected through links. The generality and flexibility of such mathematical tool allowed scientists from multiple fields to reveal universal patterns and processes across diverse systems (Newman et al., 2006). The study of food webs, implemented by analyzing the network of ‘who eats whom’, greatly improved our understanding of the complexity and stability of trophic interactions among species, providing important insight into the persistence and dynamic of natural ecosystems. For instance, now we can know better predict and anticipate the impact of global change on food webs (Cohen and Havlin, 2010) and manage ecosystems accordingly. Certainly, network thinking is by no means new to ecology (Bascompte and Jordano, 2014). Darwin was among the first recognizing the importance of ecological networks when he described natural communities as a ‘tangled bank of complex species interactions’ (Bersier, 2007). Thanks to the recent confluence of ecological and network sciences, a number of new opportunities approaching plants from a complex systems perspective are now open.

Likewise, research on mutualistic networks involving plant–pollinator interactions and seed dispersal discovered ecological and evolutionary processes maintaining biodiversity at the community level (Bascompte and Jordano, 2014). Plant and pollinator communities are composed by heterogeneous interactions differentiated along a gradient of specialization–generalization. The majority of species are specialists that interact with only few other species, while the minority is composed of generalist species. Understanding this particular arrangement of network-level interactions is important for the maintenance of biodiversity given that the particular structure of ecological networks has important implications for biodiversity dynamics, particularly for the stable coexistence of species and the robustness of ecosystems (Bascompte and Jordano, 2014).

Yet, networks of interactions within plant communities have been less explored in comparison to other ecological systems. On one hand, theoretical models of perfectly intransitive competitive networks showed that coexistence via intransitive competition (e.g. species A outcompetes species B, B outcompetes C, and C in turn outcompetes A) is a stabilizing niche mechanism that might favor species diversity (Grilli et al., 2017). On the other hand, empirical models of community-level facilitation showed recurrent patterns underlying the structure of plant networks between facilitator and facilitated species (Verdú and Valiente-Banuet, 2008; Saiz et al., 2018; Alcántara et al., 2019; Losapio et al., 2019). These plant facilitation networks can either be organized in a nested way around

a core of overlapping interactions, or in a modular way with independent groups of species. Either ways, plant facilitation networks showed high resistance to environmental change drivers related to stress (Losapio et al., 2019). This resistance to external perturbations can decrease local co-extinctions, thus sustaining biodiversity. Looking at different interaction types, it turned out that biodiversity increases with increasing the prevalence of network motifs that include both facilitation and competition among plants (Losapio et al., 2021b).

Despite these recent advances, we are still far from building comprehensive and robust networks of interactions among plant species, which also hinders our ability of unveiling factors responsible for predicting community structure and dynamics.

### Constructive networks

On top of limitations arising from zoocentric models, there are two additional issues with understanding plant–plant interactions at the network level. First, with increasing plant diversity, it becomes difficult to experimentally and computationally assess all possible combinations of species interactions. For instance, a community of only 10 plant species would require parametrizing all intraspecific ( $n = 10$ ), two-species ( $n = 45$ ), three-species ( $n = 120$ ), four-species ( $n = 210$ ), and so on combination of possible interactions, which is practically unfeasible.

Second, we cannot always see plant–plant interactions with our naked eyes or under a microscope. It is much easier to look at ‘who eats whom’ or ‘who is visited by whom’ than ‘who facilitates whom’ simply because the latter is most of the time not visible to us. Furthermore, plant–plant interaction mechanisms and the constructive effects of plants on the environment hardly emerge in controlled greenhouse conditions.

All together, identifying all possible facilitative or competitive interactions in a diverse community is not as straightforward because experimental manipulation is often unfeasible. Hence, the study of plant networks is limited primarily by the identification of plant network links. To overcome those limitations, I propose the concept and implementation of constructive networks.

The ‘ability’ of plants to change the structure of habitats, modulate resources available to other species, and influence the physical, chemical, and biological conditions of the environment developed into the concepts of nurse plants, keystone plants, ecosystem engineers (Jones et al., 1994), and foundation species (Ellison et al., 2005) (see also (Lewontin, 1983; McIntire and Fajardo, 2014)). The formalization of these concepts further developed into the frameworks of integrated community (Lortie et al., 2004), niche construction theory (Odling-Smee et al., 1996) and contemporary niche theory (Chase and Leibold, 2003).

Constructive networks build on and unify niche construction and complex network theories. Constructive networks are ensembles of different relationships and interaction types including plant–plant and species–environment interactions. They recognize that plants have manifold ecological functions and the environment shapes and is shaped by diverse organisms, primarily plants. Constructive networks integrate both plant–environment and plant–plant interactions, addressing the way in which plants influence the environment, other plants, and the interactions between the environment and other species. In a relational context, constructive networks consider that plants support or inhibit other plant species by physically (e.g., mosses living on tree bark), biochemically (e.g., fixing soil nitrogen), and ecologically (e.g., reducing heat



Fig. 3: **(Top)** Idealized ecosystem representing different plant species, some of them acting as foundation species (Ash tree, a), keystone species (Kangaroo grass, b), or nurse plants (*Ephedra*, c). Microhabitats are characterized by plant communities creating different soils and microclimate conditions. Some plant species live only in association to foundation or keystone species, such as Lily (d) or Flax (e). Species such as Barreloclover (f) grow worst with Ash tree but better with Kangaroo grass, while other like Lavander (g) are not particularly influenced by neighbors. Finally, plant species like Stiff brome (h) and Hairy bittercress (i) are facilitated by nurse plant *Ephedra*. **(Bottom)** Workflow prototype for implementing constructive networks with Markov networks. Comparative data of plant communities across microhabitats is the input matrix. Results of Markov networks will provide  $\alpha$  and  $\beta$  parameters, indicating plant–microhabitat and plant–plant associations, respectively. Different environmental factors such as soil and microclimate variables can be also used for addressing plant–environment interactions. Using  $\alpha$  associations, one can build plant–microhabitat networks. Here, plants are depicted as green nodes, microhabitats or environmental factors as pink nodes, and associations as pink links. Then, one can build plant–plant associations networks using  $\beta$  parameters in Markov networks. Those putative interactions shall be further confirmed empirically with additional and independent data on ecological mechanisms of plant–plant interactions, including facilitation or competition for recruitment, growth and reproduction. Hence, one can create plant–plant networks with plant species (green nodes) and their species-specific interactions (red links).

and drought stress) shaping environmental conditions, species–environment or plant–plant interactions. In constructive networks, diverse plants change and create novel environmental conditions as well as co-produce, transform, and share resources, thereby influencing the environment in constructive ways.

Associations between plants species (i.e., significantly higher or lower co-occurrence frequency than expected by chance) can be used as a proxy of plant facilitation links under certain circumstances. For instance, when facilitation mechanisms are known, such as in the well-studied cases of nurse plants in high-alpine and arid environments (Verdú and Valiente-Banuet, 2008; Burns and Zotz, 2010; Saiz et al., 2017), plant associations provide a reliable signal for inferring plant network links (Alcántara et al., 2019; Losapio et al., 2019). But plant facilitation goes beyond nurse plant systems and conspicuous vegetation patterns (Liancourt and Dolezal, 2021).

Provided that co-occurrence is considered at the adequate spatial scale and multiple factors are taken into account, inferred statistical associations between plants from co-occurrence data may provide a signal for putative plant interaction links (Losapio et al., 2021b). Then, putative interactions shall be further confirmed empirically with additional and independent data on plant recruitment, growth, survival, reproduction, and fitness (Figure 3). Notably, this way one can also distinguish between the long-term ecological outcome of plant interactions (e.g., spatial displacement or spatial aggregation) from the plethora of underlying mechanisms (e.g., increase in water uptake or decrease in pollination).

Currently, the best way forward to resolving the question of how to infer plant–plant interactions from associations and build plant networks is given by statistical physics. I propose here to adapt a novel analytical model of Markov networks (Harris, 2016). With Markov networks it is possible to make inference about the association matrix from co-occurrence data on the basis of conditional relationships among species (Azae et al., 2010). In its canonical definition, a Markov network defines the relative probability of observing a pool of species  $y$  as

$$p(\vec{y}; \alpha, \beta) \propto \exp \left( \sum_i \alpha_i y_i + \sum_{i,j} \beta_{ij} y_i y_j \right)$$

where  $\alpha_i$  is the direct effect of environmental factors on each species  $i$ , and  $\beta$  is the relative probability that target species  $i$  and neighboring species  $j$  will co-occur, conditioned by species-specific

environmental/microhabitat effects and after controlling for the other species in the network (Figure 3).

When a plant species  $i$  is particularly associated to a microhabitat or an environmental factor, then  $\alpha_i > 0$ , while  $\alpha_i < 0$  if a plant species does not thrive in a microhabitat or is negatively affected by an environmental factor. Similarly,  $\beta_{ij} < 0$  if two plant species  $i$  and  $j$  are negatively associated with each other, otherwise  $\beta > 0$  if two plant species are positively associated. The model can be generalized to any plant community with different plant species, microhabitats and environmental factors. Model coefficients  $\alpha_i$  and  $\beta_{ij}$  would be better estimated from abundance data rather than presence/absence by parametrizing the Markov network model using poisson or negative binomial distributions.

Those inferred parameters, which once more are statistical associations among plant species and are only putative of interaction outcome, shall be further compared to null models and can be used as links in constructive networks. A constructive network would contain first of all those two matrices (Figure 3): the first one with species–environment relationships  $\alpha_i$ , the second one with species–species associations  $\beta_{ij}$ . The two matrices can be collated into a single multilayer network (Figure 4). This way, species can have different links in terms of link types, such as species–environment relationships  $\alpha_i$  and species–species associations  $\beta_{ij}$ , and with varying strength and directionality, i.e., positive and negative links. As species–species associations are correlative and symmetric, i.e.,  $\beta_{ij} = \beta_{ji}$ , between two plant species there would be just one link.

Yet, plant co-occurrence may just provide a putative outcome or an indication of interactions, so statistical associations between plant species must be interpreted as hypotheses about the outcome of species interactions (Blanchet et al., 2020). One of the main advantages of using Markov network for inference of species interactions as compared to e.g. Gaussian Graphical Models (which makes us of partial correlation coefficients) include the possibility of (i) distinguishing between species–environment and species–species relationships, and (ii) addressing non-linear dependencies between species and the environment.

Identifying and proving plant–plant interactions would require experimental manipulation by validating experimentally or through additional, independent evidence those inferred associations. For instance, those putative interactions can be further confirmed empirically with additional experiments on ecological mechanisms involving recruitment, stress amelioration, pollination attractiveness, or herbivory protection. Those new independent

Fig. 4: **a)** A small Markov network of one nurse plant species ('Nurse') and two other plant species ('Sub 1' and 'Sub 2'). Arrows indicate positive ('+', blue) and negative ('-', red) associations, which point from the nurse to the subordinate for the  $\alpha_i$  interaction coefficient, and point between subordinates in case of  $\beta_{ij}$  interaction coefficient. Arrow size indicates association strength. **b)** A constructive network with different plant species and link types where nurse plants facilitate the occurrence of two plant species (Sub 2 and Sub 1), while exclude a third species (Sub 3) which thrives in open microhabitats. Meanwhile, putative competition is occurring among two "subordinate" plant species. Line thickness is proportional to link weights.

Fig. 5: Example of plant systems where different plant species act as ecosystem engineers (left: *Hormathophylla spinosa* in high-alpine ecosystem) or nurse plants (right: *Retama sphaerocarpa* in Mediterranean woodlands). Neighboring plant species were either removed or added as experimental treatments to address the effects and mechanisms of plant facilitation and interference in plant–pollinator networks.

data shall be part of the ensemble of constructive networks. At the end, we would have a much smaller set of potential interactions to be proved as compared to screening and testing all possible interactions. This represents a feasible option for building more robust species interaction networks.

In the specific case of nurse plant system facilitation (Figure 4a), this Markov network model shall be adapted considering the microhabitat conditions created by nurse plants in conjunction with open areas (i.e., where nurse plants do not grow) as two distinct microhabitats, i.e., the microhabitat/environment in the previous equation. In the resulting constructive network (Figure 4b), nurse plants, "subordinate" species and open microhabitats are the nodes, the nurse– and open–subordinate interactions and subordinate–subordinate interactions are the links estimated by  $\alpha_i$  and  $\beta_{ij}$  coefficients, respectively. Then, model parameters  $\alpha_i$  and  $\beta_{ij}$  can be verified empirically by manipulating plant occurrence in different microhabitats or plant density in replacement series and then by looking at plant performance and outcomes.

Finally, to understand how plant species influence and are influenced by the environment, plant communities can be coupled to environmental factors by means of dynamic models (Kéfi et al., 2012; Levine et al., 2017; Saavedra et al., 2017; Losapio et al., 2021b). A system of differential equations can be used to describe species–environment interactions including plant community dynamics and environment state variables. The community dynamics of  $S$  plant species, i.e., changes in abundance/cover  $N_i$  of plant species  $i$  over time  $t$ , in response to environmental conditions  $k$  can be described using inferred Markov network parameters as

$$\frac{dN_i}{dt} = N_i \left( r_i + \sum_{j=1}^S B_{ij} N_j \right) + f(A_i, k) N_i$$

where  $f(A_i, k)$  is the function describing the rescaled effect  $\alpha_i$  of environmental factor  $k$  on plant species  $i$ , and  $B_{ij}$  is the rescaled effect of plant species  $j$  on  $i$ .

The dynamics of the environment  $E$  representing changes in the environmental factors  $k$  can be described as

$$\frac{dE_k}{dt} = f(K) + f(\gamma_{ki}) N_i$$

where  $f(K)$  is the function describing the state of global environmental conditions  $K$  at local environmental scale, and  $f(\gamma_{ki})$  is the function describing the effects  $\gamma_{ki}$  of plant species on the environment. In this general form, one can parametrize  $\gamma_{ki}$  the various ways in which plant species influence the environment by altering energy, water, carbon and nutrient fluxes.

## Conclusions

In agreement with niche construction and complex network theories, I propose the notion of constructive networks. Constructive networks integrate fundamental biological processes with first principles of plant ecology. The unique properties of plants that make them producers of oxygen, organic matter, and resources locate them at the core of mass, energy, and information flows. Beyond their topological position within ecological networks, plants modify environmental conditions in ways that influence the same network at higher levels. Multiple mechanisms are known by which plants interact with each other, but many still remain to be uncovered. Our improving knowledge of plant engineering and diversity effects provides just one iconic example by which plants construct environments where other species can thrive. Yet, we shall broaden and deepen our understanding of the multiple ways plant change the environment bottom-up and influence directly or indirectly multiple species and diverse communities. Moving beyond models for animal competition and top-down environmental control should proceed along with developing analytical approaches and experiments. Understanding plant–plant networks requires overcoming limitations of identifying plant links by integrating complexity theories with comparative data, statistical modelling, and experimental field botany. Constructive networks can help us to identify the role of plant network features and ecological processes contributing to biodiversity maintenance and ecosystem functioning, and to anticipate the response of plant systems to global change.

## Data availability

Data reporting number of papers published in different fields (Fig. 2) can be found as supplementary material.

## Code availability

Not applicable.

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Fig. 1:

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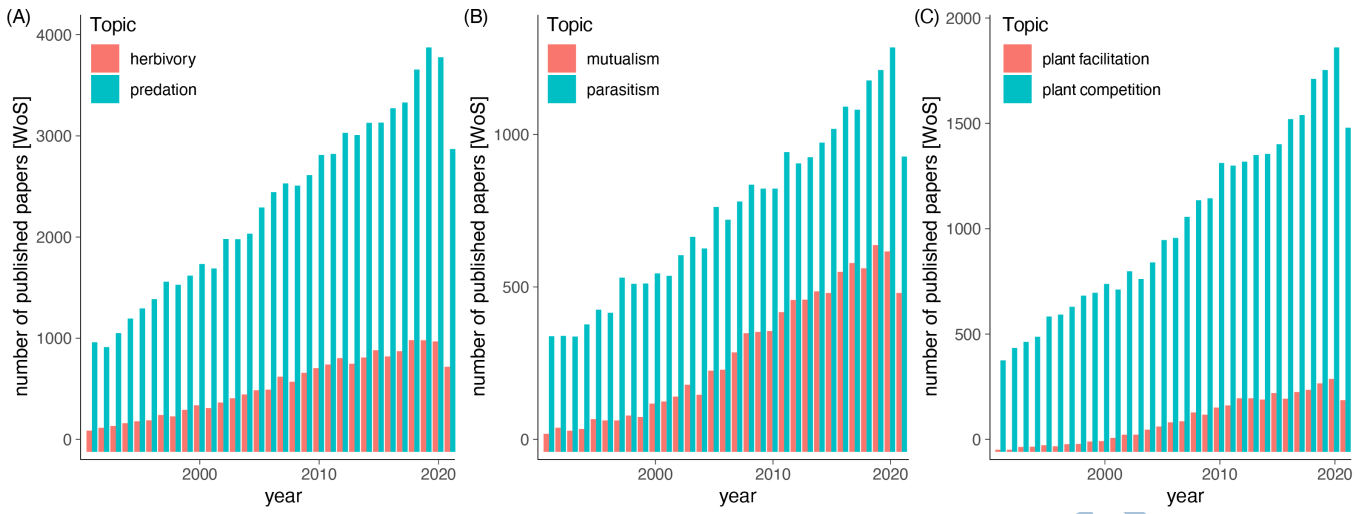


Fig. 2:

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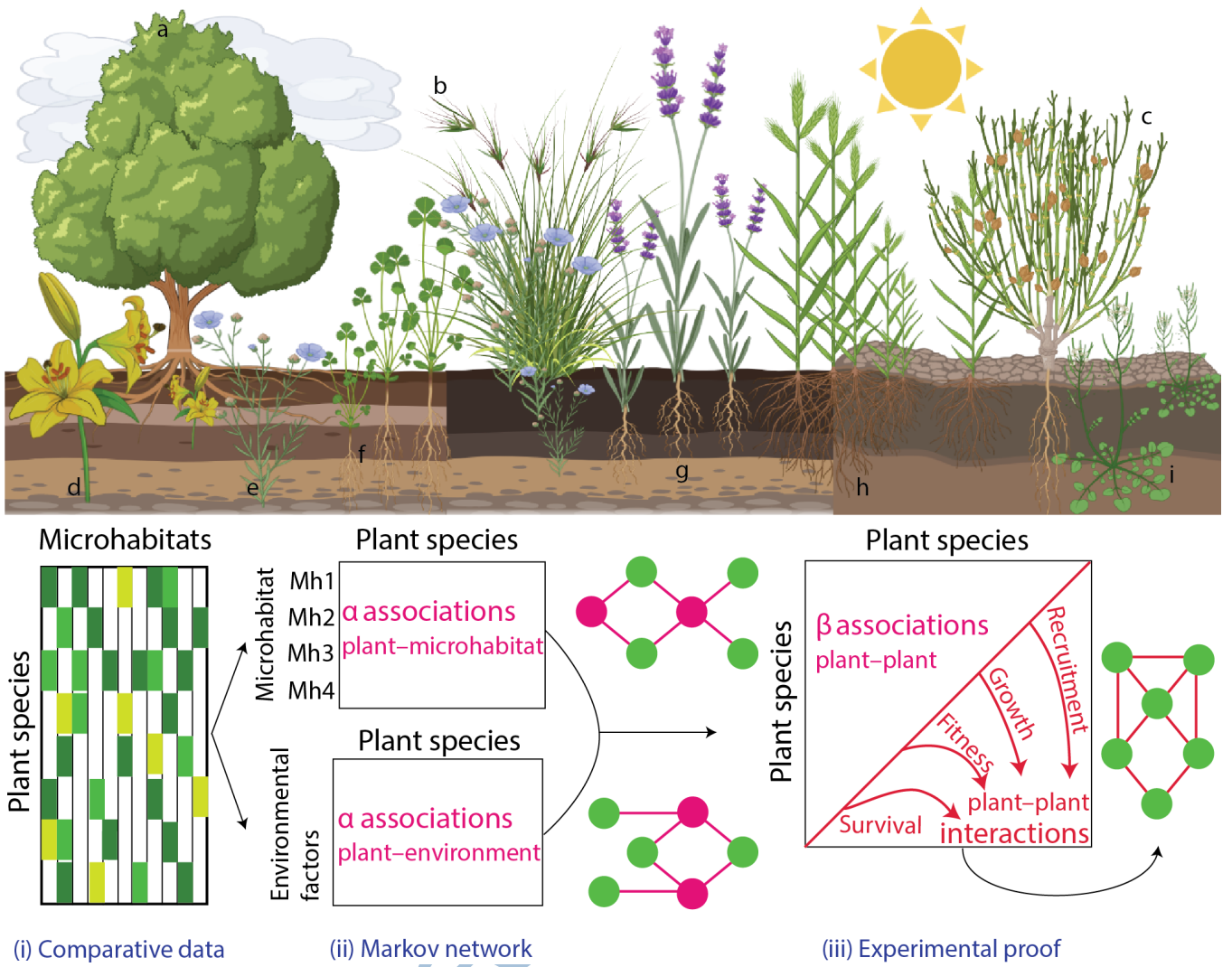


Fig. 3:

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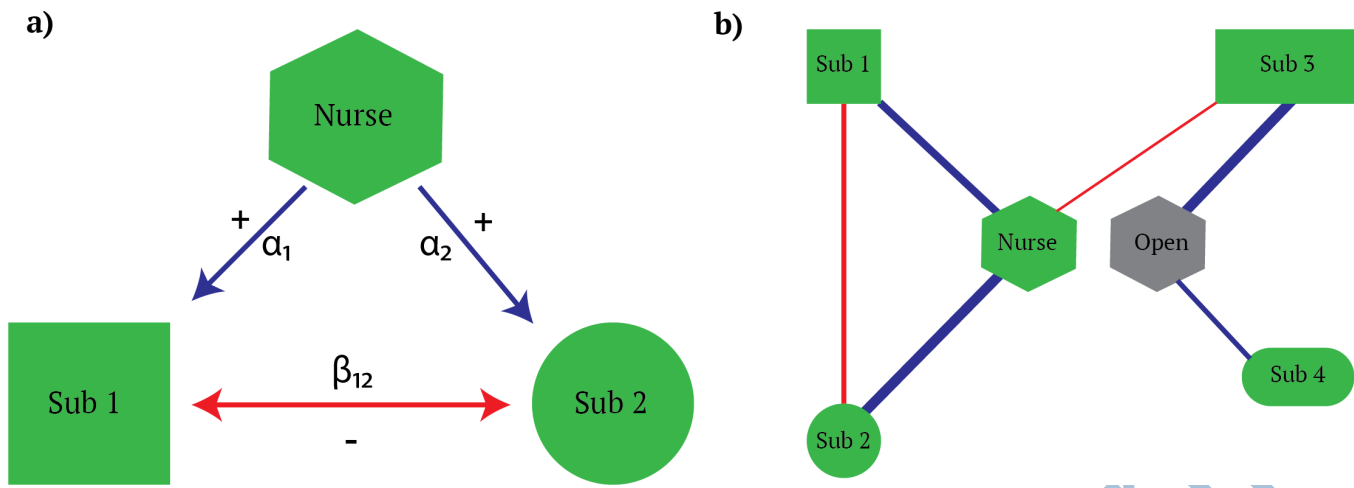


Fig. 4:

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Fig. 5:

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