

Plant community ecology

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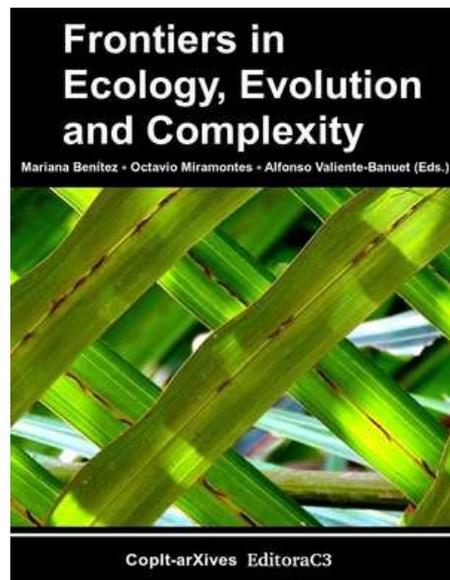
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Plant community ecology

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1 Abstract

As long as human activities have continued to disturb Earth's climate, biota, and entire ecosystems at unprecedented rates, the science of ecology needs to provide realistic knowledge. We propose that this knowledge can only be provided under a community ecology approach. In this essay we propose a conceptual framework for plant community ecology considering both historical biogeographical processes and biotic interactions, and discuss the ways in which these two components evolve in mutual response to each other. Given the overwhelming complexity of multiple ecological processes we need to understand general patterns governing the assembly of communities to be able to face the sixth major extinction in the history of life and to transit towards sustainable practices in ecosystems.

2 Resumen

En tanto continúen las actividades humanas que están perturbando el clima global, a la biota y a ecosistemas completos a tasas sin precedente, la ciencia de la ecología debe proveer conocimiento realista. Nosotros proponemos que este conocimiento solo puede ser provisto bajo un enfoque de la ecología de comunidades. En este ensayo proponemos un enfoque conceptual para la ecología de comunidades de plantas considerando tanto procesos de biogeografía histórica como de interacciones bióticas, discutiendo la forma cómo ambos componentes evolucionan como respuesta de su interrelación. Dada la abrumadora complejidad de múltiples procesos ecológicos necesitamos entender de manera integral los procesos que gobiernan la organización de las comunidades para ser capaces de encarar la sexta mayor extinción de especies en la historia de la vida y poder transitar a prácticas sustentables en los ecosistemas.

3 Introduction

The vast number of species inhabiting the Earth are not randomly distributed, but are distributed differentially in ecosystems across different geographical areas. The central issue of community ecology is to determine those processes that determine that composition of species within a particular geographical area. A community is comprised of the entirety of the biotic elements in an ecosystem: an interactive assemblage of species occurring together within a particular geographical area, a set of species whose ecological function and dynamics are in some way interdependent [1]. In an ecological context, interdependence means that life is supported by life, in such a way that ecological interrelationships among species are central to the maintenance of species in communities. However, the mechanisms explaining which species form a community do not only depend on the biotic interactions but also on the historical events through the geological time (speciation, extinction, and immigration); this provides the source of species that eventually make up the community (i.e., the regional species pool). Consequently, a community is a subset of species from the regional species pool that are able to colonize an area and interact among them, a topic named “community assembly rules” [2]. Thus, although community ecology embraces the study of the mechanisms of biotic interactions that support life, it also depends upon the historical biogeographical processes that have molded regional species pools over geological time.

The overwhelming complexity of understanding multiple ecological processes occurring at different temporal scales has led ecologists to approach community assembly rules by breaking this complexity into small bits of research. However, although this approach has proven to be efficient in answering a few specific questions, in order to understand the general patterns governing the assembly of communities it is required to consider other conceptual framework and methodologies which consider the complexity of these processes. Firstly, ecologists have traditionally only emphasized local short-term ecological processes, ignoring evolutionary processes that can help to explain the patterns found in current communities. Secondly, when biotic interactions have been acknowledge in community ecology, the approach has been to study specific ecological interactions focusing on small subsets of species, isolating them from the rest of co-occurring ecological processes within their community context. The aim of this essay is to propose a conceptual framework and methodologies to analyze plant communities integrating both the historical and ecological processes, and to discuss the ways in which these two temporal components may evolve in mutual response to each other. To do this, we first discuss our personal view on the main methodological limitations of the historical background of community ecology; these have traditionally looked for explanations to diversity patterns as arising exclusively from the individual behavior of species or their subsets usually taken out of context. Then, we discuss a conceptual framework that highlights the relevance of considering large levels of temporal and spatial scales to understand the regional species pool. We show how the biogeographic properties of the regional species pool,

linked with systematic biology, geology, and paleontology has led to the development of phylogeny-based approaches which have provided challenging results suggesting extremely fruitful hypotheses on the regional causes of species diversity [3], as well as the ecology underlying phylogenetic community structure [4]. Lastly, we integrate a series of examples for each topic trying to illustrate the ideas. In doing this, we hope to spark the interest of many students in the study of communities.

4 Historical background

The histories of ecology and biogeography are indissolubly tied as they emerged at the same time with overlapping explanations for species richness patterns from local to global scales. For example, Alexander von Humboldt is often credited with the first ideas about the influence of climate on plant distribution and the foundations of ecology and biogeography. Although true, the credit comes also initially from Carl Ludwig Willdenow [5], who recognized the dominant role of climate in governing plant geography and vegetation zonation [6], thus opening the emergence of ecology to explain biogeographical patterns. However, the emphasis on local, short-term ecological processes by ecologists on one hand and on historical long-term evolutionary processes by biogeographers on the other provoked an early separation of ecology and biogeography. This divergence was noticed by one of the earliest biogeographers, the Swiss botanist Alphonse De Candolle, as one of the main obstacles for the development of biogeography as well as of ecology [7]. Despite the recognition that local diversity patterns are affected by biogeographic, historical and evolutionary processes [8, 9], community ecologists disconnected rapidly from the historical aspects of natural systems and tried to understand communities just in terms of the individual properties of species in communities. For example, the most accepted idea on community organization assumed that communities are the result of the confluence of species adapted to a specific environment [10], and the outcome of competitive exclusion [11]. This axiomatic-like paradigm originated from Darwin's ideas connecting natural selection with the universal density-dependent Malthusian population theory [12]. Thus, competition was thought to affect the numerical processes in both populations and communities. Therefore, the species composition of a given area is determined by the physiological tolerances of species to the specific environment, and then by the omnipotent role of competition to finally determine the specific composition of communities [11].

Philosophically, Gleason's view about communities can be traced back to the seventeenth century philosophy of René Descartes's *Discours* in which phenomena are the consequences of the confluence of the individual atomistic bits, each with its own intrinsic properties, determining the behavior of the system as a whole [13]. From this perspective, parts of a whole (e.g., species) are ontologically prior, and thus lines of causality run from part to whole, and therefore the whole (e.g. community) is defined by the sum of its parts.

Cartesian reductionism therefore denies the possibility of emergent properties as a consequence of the interaction between the parts [13]. Actually, parts do acquire new properties by being together imparting new properties to the whole, but the true magnitude of said properties at the community level can only emerge when processes that drive diversity are analyzed under a complete framework without isolating the processes to a few levels. However, in practice and probably as a way to simplify the problem, biotic interactions have traditionally been analyzed as isolated pairwise interactions, an approach that also has been highly influenced by Lotka [14] and Volterra [15] models, in which biotic interactions are considered in pairs of species. Although successful in determining specific interaction mechanisms, such a reductionist approach has limited the search for emergent properties at the community level, being at the same time one of the main impediments to the development of community ecology. However, the development and the use of methodological tools by ecologists -such as complex networks theory- represent a great step for the analysis of complete sets of species and the search for emergent properties in communities.

5 The framework

Proper understanding of a community should be viewed as a contingent structure in reciprocal interaction with its own parts (i.e., species and their interactions at different trophic levels) and with the regional species pool of which it is a part [13]. Traditionally, a community has been considered to be a subset of species from the biogeographic region after the species have passed through an environmental filter (Figure 1a). However, biotic interactions may be also the responsible for the maintenance (Figure 1b) or the local extinction (Figure 1c) of some of those species. Once the regional species pool has been reduced to the community composition, as mentioned above, to study community ecology ecologists commonly have isolated interactions from the complex community context. For example, plants interact with other plants, pollinators, herbivores, etc, (Figure 1d), but this traditional approach has forgotten the unseen majority, namely soil microbes [16] (Figure 1e). Thus, ecological linkages between aboveground and belowground biota have acquired a growing recognition since the past decade [17], although both have traditionally been considered in isolation from one another. Numerous studies prove plant-mediated linkages between aboveground and belowground biota ([17], and references therein). For example, while herbivores may affect the function of soil communities, in turn soil microorganisms can change the morphology and chemical composition of plant tissues, altering the fecundity and activities of aboveground herbivores [18]. Moreover, the presence of belowground mutualists such as arbuscular mycorrhizal fungi in the roots increase pollinator visitation and seed set of plants [19]. In short, the microbes that live belowground directly and indirectly influence the productivity, diversity, and composition of plant communities.

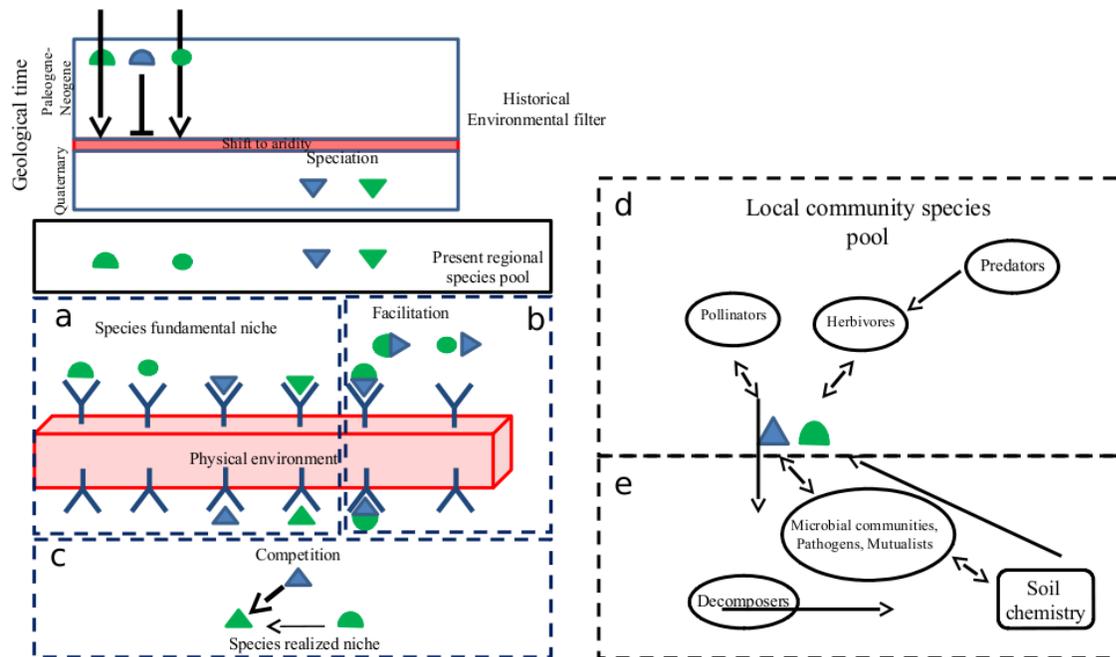


Figure 1: The regional species pool is originated from a mixture of different lineages or species (triangles, circles and semicircles) that originated in different geological times and have survived (\leftarrow) or become extinct (\dashv) in different historical environmental filters such as the shift to a more arid environment which occurred from the Paleogene/Neogene to the Quaternary. Paleogene/-Neogene species (circles and semicircles) evolved under an environment different from current conditions and might not be by perfectly adapted to the current physical environment (species fundamental niche, a). However, some Paleogene/Neogene species can remain in present communities thanks to the buffered conditions provided by recent evolved drought tolerant species (Quaternary) (triangles) that recreated the Paleogene/Neogene environmental conditions (facilitation, b). Afterwards, the regional species pool is reduced to the local community species pool due to ecological processes such as competition that can lead some species to local extinction (e.g green triangle) (competition, c). The width of the arrows indicates the strength of competition of one species on another. In addition to competition, multiple ecological interactions, both above (d) and below ground (e) also act synergistically to define the local community species pool. For example, plants interact with other plants, pollinators, herbivores, and also with soil microbes. However, ecological linkages between aboveground and below ground biota have been traditionally considered in isolation from one another.

6 Regional species pool and ecological connections

In community ecology, the composition of local communities depends on the regional species pool, which in turn is determined by large-scale biogeographical processes [3]. However, to understand global patterns of biodiversity, it is necessary to know the ecological processes that have eliminated species from communities or allowed them to persist through time [20] (Figure 1b). Current plant communities are the product of historical sorting processes and, therefore, they include mixtures of floristic elements that evolved during different geological times. Thanks to paleoecological reconstructions of paleofloras using leaf characters [21] we know that many of those species evolved under different environmental conditions and inhabit plant communities different from those in which they originated [22]. The notion that interdependent processes among plant species have been insignificant over evolutionary time frames has been central to the Gleason's ideas, assuming that plant communities do not possess stable properties determined by plant-plant interactions. However, the idea that communities are constituted by adapted species to a specific environment [10] has lost terrain by showing that present-day species inhabit environments different to those where they originated, and that facilitative ecological interactions among plant species have been a crucial component of historical and sorting processes that allowed species to survive under dramatic changes of global climate [20]. Particularly, one of the most important floristic sorting periods worldwide to affect modern plant communities occurred during the shift from the wet Paleogene/Neogene periods to the unusually dry Quaternary, when most global deserts developed [20]. During this transition a wave of new plant species emerged, presumably in response to the new climate. In contrast, many Paleogene/Neogene species that have been tracked through the fossil record in different environments remained relatively abundant despite the development of a much more unfavourable climate for species adapted to moist conditions [20]. However, these old species remained thanks to the buffered conditions provided by recent evolved drought tolerant species (Quaternary) that recreated the Paleogene/Neogene environmental conditions [20]. Regeneration niches and recruitment life histories strategies of taxa belonging to old lineages match with the environment in which these taxa evolved and consequently nowadays, after an environmental shift to arid conditions, positive biotic interactions are crucial for the maintenance of old lineages, constituting a key aspect to understand the maintenance of local and regional species pools. In other words, niche conservatism (i.e., related lineages tend to have similar niche requirements) offers a mechanism to explain large and local-scale species-richness patterns, thus reconciling ecological and evolutionary perspectives. In our framework, positive local ecological processes have acted by expanding the fundamental niche of species allowing old lineages to be part of communities quite different from those where those species evolved (Figure 1b).

At present megadiverse areas of the world such as Mexico are inhabited by very old lineages under conditions that are quite different from those where species originated, and

therefore it is possible that similar processes have occurred worldwide affecting regional species pools. This fact emphasizes the importance of paleobotanical and paleoecological research. For example, biogeographical and paleobotanical evidence of megadiverse areas of tropical America such as in the Neotropics [23], including different parts of Mexico [24, 25] that harbor higher number of plant species than other continental areas with similar ecological conditions, indicate that most of the taxa evolved during the last 65 Ma of the Cenozoic era and have persisted through evolutionary time [24, 26, 27]. In particular, the Paleogene/Neogene transition constitutes a paramount to understand the evolution and mixing of taxa to explain the causes of megadiversity patterns in these areas [20, 24, 28]. For example, the fossil plant record has already shown that forests and savannas covered areas of the present subtropical and tropical deserts well into the Eocene, and that tropical forest, woodland and thorn forest covered the modern tropical deserts into the Middle and late Neogene [22, 29].

7 Niche conservatism and phylogenetic community structure

Species that evolved within a similar environment are expected to possess similar traits that might have provided them with fitness advantages in said environment. Traditionally, in an attempt to search for patterns in the species composition and dynamics of communities, species have been treated as equivalent units, with independent functional traits. However, as many species traits are evolutionarily conserved, it can be expected for lineages originated during different geological times, and environments, which now coexist in communities composed of a mixture of lineages, to present different traits. Thus, closely related species, or lineages originated in a given environment, will tend to be more similar regarding their ecology and life-history strategies shaped by species traits [30, 31], and so to have similar requirements to survive and reproduce (i.e., niche conservatism).

The ecology and life-history strategies of a species can determine two main processes that have been traditionally thought to structure ecological communities: competition and habitat filtering (e.g., [32, 33]). Ecological similarity can result in more severe competition between closely related species than between distantly related species, as the former will share similar requirements and ways of exploiting the resources. However, it is also a general pattern that species inhabiting extreme habitat share similar traits, such as many desert plant communities which are dominated by spiny or succulent plant species, most of them taxonomically related (e.g. cacti).

The phylogenetic structure of a community can provide insight to the ecological processes that are taking place in that community. Many classical topics in community ecology have been enriched with the consideration of the phylogenetic relationships among species in the community compared to the regional pool. For example, regarding species diversity, it is essential to understand why similar habitats in different regions have different numbers of species. One potential explanation is that different regions are occupied by

different clades (e.g. [34, 35]), which in turn can differ in their potential for diversification (e.g., [36, 37]). The availability of phylogenies, along with methods for the construction of supertrees, now allows community structure to be assessed phylogenetically. As an example, Phylomatic is a tool for attaching members of a list of taxa to a “master” phylogeny of the angiosperm, using the internal node names of the megatree [38]. Afterwards the resulting phylogeny can be used as an input in available software for the analyses of phylogenetic community structure such as PHYLOCOM [39] or several packages in R.

In the past few decades, a new conceptual framework has been developed in which phylogenetic information from co-occurring species is used as an indicator of two main assembly processes (competition and habitat filtering) [4]. This framework has provided a set of methods aimed at testing the structure of communities. Multiple metrics, null models and statistical testing have been developed that quantify the distribution of taxa in a community relative to the regional species pool [40]. A broadly used metric that quantifies the distribution of taxa in a sample relative to a regional pool is the Net Relatedness Index (NRI). This is a standardized measure of the mean pairwise phylogenetic distance of taxa in a sample (MPD), relative to the MPD of a similar sample selected randomly from the regional pool. The Nearest Taxon Index (NTI) is also a standardized measure of the phylogenetic distance to the nearest taxon for each taxon in the sample. In general terms, the objective of calculating these metrics is to detect patterns (e.g., clustering, overdispersion) from which it is possible to infer community processes (e.g., filtering, competition). Both NRI and NTI increase with increasing clustering and become negative with overdispersion. Clustering or overdispersion can be studied either on species traits (phenotypic clustering or overdispersion) or on the phylogenetic relationships of species (phylogenetic clustering or overdispersion) [41].

Phenotype-based methods aim to infer the assembly process from the distribution of species traits in the communities relative to the distribution of traits in the available species pool. Phenotypic clustering arises when co-occurring species are more similar (phenotypically) than expected from the distribution of traits in the regional species pool, whereas phenotypic overdispersion refers to co-occurring species which are less similar (phenotypically) than expected in the same species pool. In general, when environmental filtering is the main assembly process, species in the community tend to share the trait values which enable them to tolerate that environmental filter, leading to phenotypic clustering. However, when competition is the main assembly process, phenotypically similar species tend to exclude each other, leading to phenotypic overdispersion [32]. In addition, phenotypic information can be combined with co-occurrence or environmental information to test whether similar phenotypes co-occur in environments. For example, Verdú & Pausas [42], use the matrix correlation method to show that plant species sharing the same post-fire germination trait tend to co-occur (phenotypic clustering) in fire-prone communities.

However, there are several difficulties to completely characterize the phenotype of all the species in a community. The feasibility of measuring certain traits, or the selection of

certain traits considered ecologically relevant, can influence the community patterns studied. Phylogenetic relatedness -given that phenotypes are likely to be conserved because of common ancestry- can be considered a proxy for the species similarity considering every phylogenetically conserved functional trait and not only the traits that are easy to measure or intuitively relevant. In addition, phenotypic and phylogenetic information can be combined to differentiate between environmental filtering and competitive exclusion [4]. For example, the implications of a phylogenetic clustering in a community structured by an environmental filter depend on whether the trait evolved in a conserved or convergent way. If the traits that confer tolerance to the environmental filter are phylogenetically conserved, the coexisting species will be both phylogenetically and phenotypically clustered. However, if distantly related species have more similar trait values than expected by chance (trait convergence), the coexisting species will be phenotypically clustered but phylogenetically overdispersed.

When traits are phylogenetically conserved, the implications of phylogenetic clustering or overdispersion in community structure can be understood in the same way as the implications of phenotypic clustering or overdispersion. Phylogenetic clustering implies that closely related species co-occur more often than expected according to a null model, while phylogenetic overdispersion indicates that closely related species co-occur less often than expected. Based on coexistence theory, when species compete for the same limiting resource, all but one species will be driven to extinction. Accordingly species can coexist by inhabiting different niches that partition the available resources (i.e phylogenetic overdispersion), and competitive exclusion will prevent coexistence of similar species [43]. More recently it has been reported other ecological processes, such as facilitation, complementary to competition which can also result in phylogenetic overdispersion.

8 The role of plant-plant interactions in structuring communities

Positive and negative interactions act simultaneously, and the balance between them ultimately determines coexistence. For example, positive interactions like plant facilitation can turn into negative interactions (competition along the ontogeny of a plant), and this can influence the phylogenetic community structure of the community [44]. Plant-plant facilitation is a key process structuring plant communities in semi-arid environments. In some plant communities, more than 90% of the species recruit successfully only beneath the canopies of nurse plants and therefore are maintained via facilitation [45, 46]. Facilitation, as well as competition, is an ecological process influenced by the phylogeny of the species involved. Within a community, approaches using null models have been used to test for the effects of the balance between facilitation and competition on the phylogenetic structure of the community. Valiente-Banuet and Verdú [44] characterized the facilitated-nurse pairwise interaction present in three different communities. They dis-

tinguished between the interactions in which the nurse and the seedlings of facilitated species persisted when facilitated become adults (remaining interactions; facilitation), and those interactions in which the facilitated species outcompete the nurse later in time (lost interactions; competition), and calculated the mean phylogenetic distance between the nurse and the facilitated species in those two types of interactions. They compared these values with the frequency distribution of the phylogenetic distance between a nurse and a facilitated species chosen randomly from the species pool in the community (null model). The mean phylogenetic distance between the nurse and the facilitated species was significantly lower and higher in the lost and remaining interactions respectively than expected by chance. This result shows that facilitation occurs among distantly related species, and only interactions above a threshold of phylogenetic distance remain later in time, potentially driving coexistence patterns and phylogenetic overdispersion in the community influenced by plant facilitation. In addition, the regeneration niche (i.e., if a species can regenerate in the open or only beneath another plant (facilitated) has been shown to be phylogenetically conserved [46], so that closely related species tend to be either nurse or facilitated species. In order to test for a phylogenetic signal in a trait, one may assess whether related species are more similar than expected by chance, based on the minimum number of evolutionary steps required to obtain the observed distribution of the traits in the phylogeny. The minimum number of evolutionary steps observed is compared with a null model, in which the taxa are reshuffled across the tips of the phylogeny several times and the distribution of the minimum steps required in each time is estimated.

9 From pair-wise interactions to community approaches: ecological networks

There is evidence, at different spatial and temporal scales, that plant facilitation is a species-specific process (i.e., non-random), and that nurse species tend to facilitate distantly related facilitated species. An interesting approach used to explore non-random patterns in multiple species interactions is network analyses. Bipartite ecological networks provide a framework to assess a wide variety of ecological processes in which nodes (species) of two different guilds (parties) are connected by links (interactions) between (but not within) guilds [47]. Historically, these networks have been described and analyzed by graph theory, and allow testing for non-random patterns in the interactions between two guilds. A few interesting characteristics, among many others, than can be extracted from a network are, for example, the species degree (i.e., the number of different species a certain species interacts with, distinguishing between generalist and specialist species), the nestedness (i.e., a pattern of interaction in which specialists interact with species that form perfect subsets of the species with which generalists interact, avoiding specialist-specialist interactions) or the modularity (i.e., a tendency of certain species (a module) to interact more between themselves than with species from other modules) [48].

One interesting contribution from complex networks is the recognition that several mutualistic networks, despite differences in the nature of their nodes, exhibit similar characteristics, such as nestedness. This has implications for the robustness of the system to the loss of species and the maintenance of biodiversity [47]. In the case of facilitation, although most of the knowledge is based on isolated pairwise species interactions, a network approach provides the potential to test for non-random patterns of associations between nurse and facilitated species in

complex ecological communities. The networks between nurse and facilitated species have been shown to behave as a mutualistic network, presenting a nested structure in which a few generalist nurses facilitate a large number of species while the rest of nurses facilitate only a subset of them [49].

10 Multiple ecological processes acting synergistically

Although the structure of plant facilitation networks indicates that nurse-facilitated interactions are specific and non-random, it is still unknown which mechanisms could be underlying the fact that facilitation is more prone to occur between distantly related species. It has been argued that multiple ecological relevant traits are phylogenetically conserved, and these traits will ultimately condition with which species (pollinators, dispersers, mutualistic fungi pathogens, predators) a particular plant can interact. It has been shown across the entire tree of life that closely related species tend to interact with similar species [50]. Thus, facilitation between distantly related species could imply that they provide different microbes to the rhizosphere. This will be beneficial in the case of pathogens, as avoiding plants that share similar pathogens could be a driver of coexistence, or also, in the case of positive interactions, increasing the richness or diversity of mutualists could be beneficial due to functional complementarity of the mutualistic species. Plant-arbuscular mycorrhizal fungi (AMF) symbiosis is one of the oldest positive associations on earth and the majority of plant species interact with AMF in all kinds of environments [51]. The richness and the phylogenetic diversity of AMF have been shown to increase plant biomass and promote plant coexistence [52–54]. Accordingly, the specificity in plant facilitation associations could be influenced by the AMF with which each plant species interacts, and provides to the common rhizosphere. Firstly, for plant-AMF interactions to condition plant-plant interactions, it has to be proven that plant-AMF interactions are non-random, so that different plant species can interact with different AMF. As mentioned before, one approach to test for non-random interactions within the whole community is network analyses. Montesinos-Navarro et al. [55] proved using network analyses that plant-AMF network show a non-random pattern of associations, presented a modular pattern. This means that there are certain plant and AMF that tend to interact more between them than with plants or AMF in other modules. Later on, using dissimilarity index they characterized the community of AMF with which each plant species tend to interact, and showed

that the plant-plant associations that are more frequent in the community occur between pairs of plant species that have a more dissimilar community of AMF associated to their roots [56]. These approaches represent examples of how multiple and connected ecological processes can be understood by considering simultaneously the communities of several interacting guilds.

Finally, these multi-guild interactions occur within very limited local space. Plant facilitation generates a cluster distribution of plants (and associated species with which they interact) throughout space, resulting in discrete vegetation patches. This spatial distribution of ecological interactions in space leads the way to the consideration of multiple patches as a meta-community and allows applying analytical techniques to explore phylogenetic community structure developed for approaching multi-guild interactions in meta-communities frameworks [57].

11 Implications on biodiversity maintenance and sustainable development

As long as human activities have continued to disturb Earth's climate, biota, and entire ecosystems at unprecedented rates, the science of ecology has been subjected to considerable criticism, because of its incapacity to fill the gap between ecological theory and management/conservation practices [58]. One of the main tasks of this big challenge for community ecology is to determine the way in which plant communities are assembled [59], as well as what the effects of species overexploitation, habitat disturbance and biotic invasions on this assemblage will be. Particularly relevant will be to predict how ecological communities will respond to different rates of species loss and to determine the existence of a threshold for ecosystem collapse. The loss of biological diversity is one of the most pronounced changes to global environment which is able to impact biomass production and ecosystem services [60]. Of course, the design of management policies before humans continue disturbance practices is at the center of any discussion.

Given the interdependence among species in ecological communities, the loss of species can trigger a cascade of secondary extinctions with potentially dramatic effects on the functioning and stability of ecosystems upon which a growing human population depends [61, 62]. All species are embedded in networks of ecological interactions and the understanding of the robustness of these interaction networks to species loss is essential to forecast the effects of populations' decline and species extinctions [63]. Network theory has been a useful tool for simulating co-extinction cascades following the removal of particular species [64], but these simulations have typically been performed as part of theoretical scenarios, as opposed to realistic human-driven realistic scenarios [58]. Recently, multiple networks approaches have been proposed for agroecosystems [63] showing that interdependent networks do not strongly covary in their robustness and then the manage-

ment or restoration practices benefiting one functional group will not inevitably benefit others.

A recent new approach has been used to assess co-extinction cascades into a realistic scenario by combining multiple ecological networks (facilitation, pollination, and seed dispersal networks) in central México (Los Reyes Metzontla, Puebla) in a Popoloca town whose subsistence economy is sustained by ceramic pottery production and agave extraction for mezcal production. Pottery production demands large volumes of wood for fuel for firing ceramics, thus impacting plant nurses and facilitated species. These human effects in one network (facilitation), may, through feedback loops, impact concomitant (pollination and dispersal) networks of interactions to produce co-extinction cascades leading to ecosystem collapse [58]. This study documents that ecosystems can be more vulnerable than they seem, when most of the species depends on others for their maintenance and how the system can reach a critical threshold of rapid and unexpected change.

Also given the high degree of habitat destruction, ecological restoration will necessarily be a key process for the conservation of biodiversity, which can benefit from the knowledge acquired among disciplines such as community ecology and evolutionary ecology [65]. As we have shown here, biotic interactions assembling plant communities can be positive (facilitation) and negative (competition) and operate simultaneously. The balance between these facilitative interactions and subsequent competition is one of the mechanisms triggering succession, thus providing a good scenario for ecological restoration. Despite the ubiquity of plant facilitation for ecological restoration of disturbed ecosystems, this interaction was not considered for restoration until very recently [66]. Such a gap is consistent with the traditional view that competition is the omnipresent force shaping ecological communities [67]. In contrast to competition-focused afforestation techniques, in which seedlings are planted after eliminating the pre-existing vegetation, restoration based on facilitation, consists of planting the plants spatially associated with other plants, which provides them with a favorable microhabitat [68]. In fact, nurse-based restoration experiments have been increasingly performed in different types of ecosystems worldwide, with varying success (see [69], for a review). Similarly, nurse-assisted planting may promote more rapid natural succession in disturbed habitats in tropical areas [70].

Through considering restoration studies worldwide and by means of a Bayesian meta-analysis of nurse-based restoration experiments, the importance of phylogenetic relatedness and life-form disparity in the survival, growth and density of facilitated plants was tested [65]. This study found that the more similar the life forms of neighboring plants are, the greater the positive effect of phylogenetic distance is on survival and density. This result suggests that other characteristics beyond life form are also contained in the phylogeny, and the larger the phylogenetic distance, the less is the niche overlap, and therefore the less intense is the competition.

12 Concluding remarks

Human alteration of the global environment is triggering ecologists to fill the gap between ecological theory and management and conservation practices, at a point where realistic knowledge is urgently needed. We propose that this approach can only be achieved under the community ecology framework in which all the processes maintaining biodiversity are linked as we have tried to exemplify here. Only until we modify our theoretical and methodological approaches will we be able to face the present sixth major extinction event in the history of life, transiting towards sustainable practices in ecosystems.

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