A conceptual model for linking traits to plant community assembly using experiments and simulations

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Abstract

1. We review the underlying principles of plant community assembly and build a conceptual model into which we map experiments and simulation approaches.

2. In this model, environmental filtering selects individuals from a species pool based on non-independent traits bounded by trade-offs. The feedback of communities on environmental factors mimics plant-plant interactions, producing fine-scale heterogeneity and spatial/temporal nesting among factors, which affect trait diversity in the communities.

3. Synthetic community experiments focus on the effects of a target species mixture on ecosystem functioning, and weeding non-target species usually halts the assembly process. Experiments on natural communities involve manipulating established assembly processes in pre-existing communities through species removal or addition, altering resources, conditions, or disturbances.

4. Stochastic, individual-based models can simulate plant metacommunities, either based on ecophysiological mechanisms or statistical approaches to predict the successful establishment of individual plants based on their traits and local conditions and implicitly model plant interactions through the feedback of the community on the environment.

5. *Synthesis*. Experiments and simulation models are promising tools for studying plant community assembly, yet further exploration is needed on the coordination between functional traits during environmental filtering, the feedback from the existing community on environmental factors, and nested environmental factors creating fine-scale heterogeneity.

Keywords: Biodiversity experiments, Biotic filtering, Community assembly, Community simulation, Environmental filtering, Plant-plant interactions, Traits

Introduction

Ecologists have long been searching for links between plant traits and environmental factors that may explain how plants assemble in communities (Grime, 1979; Keddy, 1992; Pillar & Orlóci, 1993; Raunkiaer, 1934; Warming, 1909). However, revealing the assembly processes that generate observed trait patterns is not straightforward (e.g. Münkemüller et al., 2020). While we often examine trait-environment relations by integrating traits at the community level and examining patterns (Bruelheide et al., 2018; de Bello, 2021; Pillar et al., 2009), the assembly process selects individuals with sets of non-independent, *coordinated traits* whose relations may be restricted by trade-offs (Díaz et al., 2016; Joswig et al., 2022). Consequently, the filtering effects of environmental and biological factors on a functional trait perspective are often blurred (Anderegg, 2023). Furthermore, in community assembly processes, some traits may become more limiting than others depending on the filtering strength of the factors upon each trait (Pillar et al., 2021). Additionally, ecologists often differentiate between abiotic factors (such as temperature, precipitation, and soil properties) and biotic ones represented by plant-plant interactions (e.g. Bennett & Pärtel, 2017). The effects of abiotic and biotic factors can be distinguished by the convergence and divergence patterns generated at the community level and by examining shifts in trait-based dissimilarities from the species pool to within communities (Bennett & Pärtel, 2017; de Bello et al., 2012). However, environmental factors may change during the community assembly process, not only by external drivers but also due to *feedback* from the existing community (HilleRisLambers et al., 2012). Moreover, environmental factors may be spatially and temporally structured at different scales (Grime, 2002), so their effects are often *nested* and influence community assembly processes at a finer resolution than the grain size of the studied community units.

In this review/synthesis, we examine concepts, look into the literature for evidence and build a conceptual model (Figure 1) to tackle these issues by using a range of experiments and simulation models in the search for causal links between traits and community assembly. In a broad sense, we consider a community assembly experiment any experiment involving the manipulation of community components and/or environmental factors used to explore their effects on the community assembly processes. Experiments designed for other aims might also be used for this purpose, such as the well-known biodiversity-ecosystem functioning experiments, that manipulate species diversity and/or composition to examine species loss effects on ecosystem functioning (Bruelheide et al., 2014; Schmid et al., 2017). These experiments may also manipulate environmental factors (e.g. climatic conditions, resources, disturbances) for evaluating how species are locally selected. Here we focus on those experiments considering plant traits. By manipulating species diversity, community composition, and/or environmental factors that might alter the community composition, we can assess how species (and their traits) relate to each other, affecting the community assembly and ecosystem functions. Such an experimental setting, therefore also allows for exploring spatially nested ecological filters.

Plant community assembly is often studied by analysing patterns in community data from both experimental and non-experimental setups. However, while these patterns can suggest assembly processes, the conclusions are rather weak since other implicit processes could also produce similar patterns (Botta-Dukát & Czúcz, 2016). To gain a better understanding of assembly processes, researchers can use community simulation models that integrate information on functional traits in a species pool and their relations with environmental factors and ecosystem effects (e.g. Pillar et al., 2021; Scheiter et al., 2013). Such models can simulate communities and explore assembly processes that normally cannot be accessed through experiments or observational data due to limitations in spatial and temporal resolution or study extent. By comparing the patterns observed in simulated communities with expected patterns based on proposed processes, researchers can empirically verify their hypotheses. However, simulation results depend on the assumptions and parameters chosen by the researcher, and therefore it is essential to carefully review and define how community assembly can be related to traits through simulations.

In this paper, we discuss the underlying concepts of a general causal model and the potential and limitations of ecological experiments for studying plant community assembly. Specifically, we focus on experiments in which communities are assessed with regard to their dynamics and functioning after being assembled from scratch by sowing species mixtures, or being (re)assembled by removing or adding target species or manipulating environmental factors in natural communities. We also discuss the possibilities for integrating such conceptual and experimental approaches with predictive computational models that simulate community assembly based on rules representing the proposed processes. This is a non-exhaustive review where for both types of studies, experiments and computational models, we focus only on studies that specifically deal with functional traits.

A conceptual model for community assembly

Plant community assembly is a process that takes place in local communities and involves a species pool. In Figure 1, we present a conceptual causal model that we advocate for the study of plant community assembly and ecosystem functioning. Accordingly, species co-occur in communities that are arbitrarily defined at a given spatial/temporal scale. The set of communities composes a metacommunity (Leibold et al., 2004) represented by matrix **C**. Environmental factors (matrix **E**) filter species and this process is mediated by the traits of each species individuals (matrix **T**). The idea of a hierarchy of factors is appealing, represented by decreasing grain sizes of **E**, starting with regional climate and moving to local disturbances, microclimate and soil conditions acting as serial filters. These filters select those species from the species pool that will establish successfully at a community site (HilleRisLambers et al., 2012; Keddy, 1992). However, the fate of an individual plant is determined by all these factors acting simultaneously, independently or interacting with each other in their local selection effects on individuals, given the individuals' trait values (Belyea & Lancaster, 1999). Furthermore, considering the number of communities is sufficiently large, the regional species pool is defined by the set of species occurring in the metacommunity, while the habitat- or site-specific species pool (Bennett & Pärtel, 2021; Zobel, 2016) is defined by the species in the regional species pool that, due to their traits

(Bennett & Pärtel, 2017), can potentially occur under the given local environmental conditions in a community site.

It is worth remembering that the selected units in the filtering process (Figure 1a) are individual organisms with sets of traits that cannot be separated physically in response to different factors (Violle et al., 2007). While traits vary mostly between species, some traits may have high intraspecific variability (Siefert et al., 2015) that is relevant for community assembly (Carmona et al., 2019; Davrinche & Haider, 2021; Kraft et al., 2014; Pérez-Ramos et al., 2019). Additionally, the traits are not independent of each other, and the multivariate trait space of the regional species pool is not completely filled by the possible combinations of trait values (Díaz et al., 2016; Joswig et al., 2022) due to trade-offs related to ecological and phylogenetic constraints in the evolution of plants (Moles & Westoby, 2006; Wright et al., 2004). As a result, the selection process is mediated by a set of coordinated trait values within the same organism rather than single traits. Grime (1974, 1977) introduced the concept of whole-plant strategies to relate traits with environmental factors (i.e. the CSR model), which may be helpful for understanding community assembly when placed in the context of trade-offs (Pierce et al., 2013).

The community level functional descriptor **Q** in Figure 1a is defined through trait-based analysis. This approach integrates the taxonomic composition (a matrix **C** of species by sites) with the corresponding traits (a species by traits matrix **T**) and scales them to the community level (matrix **Q**). As **T** is carried by the filtered species in **C**, which define **Q** by computation, it is incorrect to attribute a causal link between these matrices (Grace et al., 2022). For simplicity, **Q** is represented as **Q**~**TC** (or **TC**~**Q**). Depending on the analytical approach, **Q** may be a matrix of sites described by community-weighted mean (CWM) traits or some measure of functional diversity (de Bello, 2021). Alternatively, **Q** may be a composition matrix of sites described by species after fuzzy-weighting (Pillar's smoothing, Pillar et al., 2009), which is analogous to the Beals transformation (De Cáceres & Legendre, 2008). However, instead of co-occurrence probabilities, fuzzy-weighting is based on the trait (or phylogenetic, Duarte et al., 2016) similarities between the species in the regional species pool. That is, a species not currently present has a probability of belonging to a local community given the similarities of this species to the ones that are present in the local community (Pillar et al., 2009; Pillar & Duarte, 2010).

Besides environmental filtering, species interactions – such as competition and facilitation – are also considered important processes in community assembly (Chesson, 2000; Diamond, 1975; Götzenberger et al., 2012; HilleRisLambers et al., 2012). Most of the research regarding the assembly process has been focused on competitive interactions between species, suggesting interspecific competition leads to nonrandom co-occurrence patterns (Diamond, 1975). The competitive effect refers to the ability of a species to suppress the growth of neighbouring plants mainly through the depletion of resources, while the competitive response refers to the ability of a species to tolerate resource levels that have been reduced due to competition (Goldberg, 1990; Goldberg & Werner, 1983). The relevance of positive interactions in community assembly is also well documented (Bertness & Callaway, 1994; Michalet, 2007; Zhang et al., 2022). Facilitation has been proposed as an important process for community assembly, in which a species modifies resources or conditions with a positive effect on the performance of its neighbours (Callaway & Walker, 1997; Michalet & Pugnaire, 2016). The relative strength of facilitative–competitive outcomes have been demonstrated along environmental gradients in different ecosystems (Bertness & Callaway, 1994; He et al., 2013). Furthermore, these interactions drive priority effects in plant community assembly (Fukami et al., 2005; Roscher et al., 2014; Stuble et al., 2017).

Nevertheless, in the end plant-plant interactions are mostly mediated by environmental filtering, since biotic interactions are mediated by the effect or the response of the interacting species on resources and/or conditions (Schöb et al., 2017). Functionally translating this concept (Figure 1a), the plant traits integrated at the community level in **Q** (e.g. community-weighted mean, functional diversity, fuzzy-weighted composition) may indirectly affect **E** (e.g. light and nutrient availability, microclimate, disturbances by herbivory and fire) through ecosystem functions or processes in **F** (e.g. productivity, and processes enhancing palatability or flammability). Though testing causal models with feedback is complex and requires advanced techniques (Grace, 2006; Shipley, 2000), such feedback paths have an impact on the community assembly process and should not be ignored. What may be interpreted as a plant-plant interaction may actually be mediated by the feedback (HilleRisLambers et al., 2012) from the existing community on resources and conditions, the "interaction milieu" *sensu* McGill et al. (2006), or by disturbance (e.g. Adler et al., 2001; Grime, 2006), which consequently create fine-scale heterogeneity. In this case, the specificity of plant-plant interactions may be driven by the plant traits in their ecosystem effects and community assembly responses (Schöb et al., 2017), which can be affected by phenotypic plasticity (Pérez-Ramos et al., 2019). Additionally, the environmental heterogeneity created in this process is often nested (Figure 1b), as some environmental factors may be modified at a finer scale than others and remain unmeasured at a finer grain than the observed community units (Pillar et al., 2021; Vellend, 2016). This idea carries important consequences for the simulation and understanding of community assembly, as the relevant process that selects the species in the end is environmental filtering, which occurs at a very fine spatial/temporal scale (Price et al., 2014). Further, as demonstrated in Pillar (2023), when there is interaction between factors in the environmental filtering process based on species traits, the expected trait values at the community level will exhibit a divergence pattern. This occurs because the selection effect driven by one factor is modulated by another factor, resulting in a pattern of beta trait divergence associated with either factor. Since the underlying ecological factors are often spatially nested, beta diversity between communities described at a finer grain size may be observed as alpha diversity within communities at coarser grains. Furthermore, in nature, feedback-driven factors are often hidden and difficult to measure. These hidden factors, although interacting with measurable ones, can generate trait divergence patterns.

Many experiments that investigate functional aspects of plant community assembly, especially those that assess feedback processes (e.g. plant-soil feedback), indicate that the assembly process affected by biotic filters can actually be translated as a shift in abiotic conditions/resources at a very fine scale (Helsen et al., 2016; Teixeira et al., 2020). The same idea is theoretically demonstrated by Adler et al. (2013). Therefore, in the context of plant-plant interactions, we question the biotic-abiotic duality as two separate abstractions and suggest that they are not separable; it is only a matter of considering or not the intermediate processes. For example, in the case of competing plants, they deplete resources which subsequently become scarcer for one another. Nurse plants, on the other hand, benefit nearby plants through various mechanisms such as reducing abiotic stress, improving soil moisture and nutrients, and offering protection against herbivores (see e.g. Filazzola & Lortie, 2014). Palatable plants may draw grazers to a feeding spot where the feedback of plant composition on animal behaviour leads to the formation of grazing lawns interspersed by vegetation patches dominated by taller unpalatable plants (Caram et al., 2023; Fischer et al., 2019). Moreover, allelopathic plants release chemical substances that might affect the growth of neighbouring plants (Hierro & Callaway, 2021). This idea is illustrated in Figure 1, where we intentionally do not place a direct connection of species composition to itself (**C**->**C**). Therefore, in this conceptual model, all biotic community assembly processes occur through the environment, i.e. **Q**->**F**->**E**->(**TC**~**Q**). In Figure 1b, the thick arrow on the small **E** represents the fine-scale effects of the community on assembly feedback. While thinner arrows pointing to the bigger **E**s represent the decreasing importance of feedback effects on environmental conditions at coarser scales.

The idea of tracing the feedback path **Q**->**F**->**E**->(**TC**~**Q**) to understand plant-plant interactions is appealing. However, measuring the environmental factors that undergo modifications during this process can be challenging, especially at the spatial and temporal resolutions in which changes occur in the plant communities. Nonetheless, Pillar et al. (2021) demonstrated that even when hidden, the environmental factors involved in community assembly can be inferred, as they leave "ghost marks" in the way plants assemble according to their traits, which is reflected in **Q**. The higher the match between the fuzzy-weighted composition in **Q** and the Beals transformed species composition matrix (De Cáceres & Legendre, 2008), derived from species co-occurrence probabilities, the better the traits considered in fuzzy-weighting reflect co-occurrence, i.e., the way species have assembled in the communities (Pillar et al., 2021). Furthermore, with an appropriate sampling design, this analysis could be done at different community unit scales (analogously as suggested by Münkemüller et al., 2020). Once the most relevant traits in community assembly are identified, the underlying environmental factors can be inferred if their relations with the traits are known. For example, specific leaf area is recognized as a trait that responds to nutrient supply. Among these factors, those that portray fine-scale variations within communities are more likely the ones influenced by the community feedback. Therefore, we emphasise the importance of considering this feedback path when designing experiments and simulation models to explore community assembly.

How experiments help understanding community assembly

In general, we can find different types of experiments depending on the initial conditions of the target community. These may be synthetic community experiments established from scratch, or natural community experiments in which the communities are manipulated by removals, additions or by changing resources and conditions. However, some studies have a combined experimental approach (e.g. addition experiments in synthetic communities).

Synthetic community experiments

Synthetic community experiments are a classic type of biodiversity experiment (e.g. Tilman et al., 2001). However, as we will demonstrate in this section, the utility of synthetic community experiments in addressing questions about community assembly is limited unless the process of community assembly is not hindered by the removal of non-target species. In these experiments, the composition of the species mixtures is defined a priori and then sowed or planted in the field or in pots. To explore the effects of community functional structure on ecosystem processes and community assembly, functional trait information can be integrated with species' taxonomic identity, allowing a posteriori analysis (e.g. Roscher et al., 2014) of the experiment’s results.

A further deployment of the synthetic community experiments is the trait-based biodiversity experiment, where the design of the synthetic communities considers not only species' taxonomic identity but also their functional traits. The communities' composition is then defined based on the species traits, aiming for a range of variation in trait composition and diversity (Dias et al., 2013). Scherer-Lorenzen et al. (2007) assembled synthetic forest communities based on traits linked to resource acquisition. Ebeling et al. (2014) did a similar experiment in grassland, which allowed for the isolation of the effect of trait composition and diversity on soil processes (Steinauer et al., 2017) and stability (Fischer et al., 2016). Other studies have adopted similar approaches, such as Galland et al. (2019) and Karimi et al. (2022), who sowed species mixtures presenting independent levels of functional diversity and phylogenetic diversity, and Pichon et al. (2022) who sowed mixtures with different species richness and characterised by slow- or fast-growing species, combined with treatments of N enrichment and pathogen removal. However, studies such as Fukami et al. (2005) and Veen et al. (2018) may have potential confounding effects of species identities, due to the small number of combinations of species for each mixture with a specified functional and phylogenetic diversity.

In synthetic community experiments, the process of community assembly takes place over the further development of the communities by means of newly colonising species and changes in abundance or extinction of target species. However, this development is usually not the focus of the study, and there is an effort to remove non-target species in the community to keep only the target ones. This can be challenging, as maintaining the intended composition may not be possible due to extinctions (see Weisser et al. (2017) and Karimi et al. (2022)). In this respect, Grime (2002) argues that “we should not merely review the traits of the plant species in a plant community in order to predict their effects on ecosystem functioning: we should also use them to understand how they were admitted to the vegetation in the first place”. Thus, synthetic community biodiversity experiments help understanding biodiversity effects on ecosystem functioning, but they are not usually used for exploring intrinsic assembly processes, which are mostly halted by artificially removing non-target species. A side-effect of this is the risk of a confounding effect of the disturbance caused by the removal of non-target species. If some mixtures are less resistant to the colonisation of non-target species, they may also suffer a stronger effect of disturbance. Placing this approach in Figure 1a, its focus is on the **Q**->**F** link, assuming unrealistically that **TC~ Q** does not vary during the experiment**.** Furthermore, most studies with synthetic communities ignore the "natural" state of community development, as the intended parameters of the communities, not the realised ones, are often used as predictors.

Yet, we find a few studies based on synthetic community experiments that have evaluated the effects of mixtures of planted species and their traits on different aspects of community assembly, i.e. implicitly following the feedback paths in the conceptual model of Figure 1. Among them, we mention Roscher et al. (2009, 2013, 2014, 2016), who assessed non-weeded plots of the Jena experiment to explore questions related to colonisation and invasion. Galland et al. (2019) assessed the resistance of resident communities to the natural colonisation by species that were not included in mixtures manipulated with different levels of functional diversity and phylogenetic diversity. However, Galland et al. (2019) did not consider this process from the perspective of the resident communities, i.e. how they changed upon the colonisation of new species and in what direction. Interestingly, Pichon et al. (2022) tested hypotheses about the effects of N enrichment and pathogen removal on sowed species mixtures presenting contrasting growth strategies, with a focus on changes in relative species abundances and intraspecific trait variation. Similarly, Karimi et al. (2022) were interested in the temporal dynamics of the communities composed of sowed species mixtures with varying functional diversity and phylogenetic diversity. Nonetheless, since the experimental approaches adopted by Pichon et al. (2022) and Karimi et al. (2022) included the removal of non-target species, it is not possible to disentangle the effects, on community assembly, of the initial functional composition or diversity from those caused by the removal of non-target species followed by the establishment of new ones before the next weeding.

Natural community experiments

In contrast with synthetic community experiments, natural community experiments start from pre-existing natural communities, where the previous assembly processes are preserved. Placed within the context of Figure 1, the species composition (**C**) and resulting traits at the community level (**Q**) can be manipulated by removing or adding target components. This manipulation is achieved through the use of biodiversity removal experiments and biodiversity addition experiments, respectively. **C** and **Q** can also be manipulated by altering either the resources, environmental conditions, disturbances or trophic interactions to which the communities are subject. The goal is to manipulate community feedback on ecosystem functions and environmental factors, which in turn affect community assembly – the feedback paths described in Figure 1.

Removal experiments are based on the removal of target species, or functional groups, from natural communities (Díaz et al., 2003). We mention the experiment of Mason et al. (2011), which tested the hypothesis that niche overlap in terms of functional traits among the remaining species would decrease with the removal of the dominant species, with consequences on community assembly. Also, the grassland experiment of Joner et al. (2011) tested the hypothesis that the removal of dominant species of the same functional group (only graminoids or only forbs) would reduce functional redundancy and thus the opportunities for species compensation within functional groups in terms of cover (confirmed) and biomass production (not confirmed).

Along the same line, the experiment performed by Herben et al. (2013) evaluated the response of the remaining community to plant functional group removal. This study did not support the hypothesis that replacement groups are necessary to maintain biomass production. However, Herben et al. (2013) found differences between groups composed primarily of grasses and groups composed of dicots, suggesting the importance of species differences in the regeneration niche as one of the key traits in the functioning of communities. A similar approach of removing entire functional groups was adopted by Helsen et al. (2016), which suggested the persistence of priority effects in community assembly, as the target species recovered a few years after removal. Lyu et al. (2017) manipulated natural grassland communities by creating plots with different species richness from one to eight, with different species identity combinations, plus the controls with no removal. The focus was on the original intended composition, not on the community assembly process taking place after the removals. Plant traits, though measured, were not considered in the selection of the species.

Removal experiments are important tools applied for the study of plant invasions. They can be used to test for biotic resistance to invasion by manipulating certain components of the resident community (e.g. through functional group removal), which is important for predicting alien species establishment (e.g. Byun et al., 2013; Carr et al., 2019; Park et al., 2022; Puritty et al., 2018). The removal of invasive alien species in local communities has been useful to studying the processes of invasion and community reassembly (e.g. Fried et al., 2019; Guido et al., 2021; Guido & Pillar, 2017).

Although removal experiments are an interesting approach for gaining insight into the community assembly process, there are methodological limitations that should be considered. Díaz et al. (2003) suggested that the removal effect might be the result of at least three components: (i) the loss of certain traits, which is the focus of most studies, (ii) the response of the remaining plants, depending on which plants occupy the released resources, and (iii) the disturbance effect itself, which involves non-target changes in resource supply. However, most studies did not consider an appropriate treatment control to disentangle these effects, leading to ambiguous interpretations (Guido & Pillar, 2015). To avoid this, it is necessary to include a removal control to distinguish the effects of biomass removal disturbance from the local species extinction effect. This can be done, for example, by removing an equivalent amount of biomass without altering trait community composition (Guido & Pillar, 2015).

Biodiversity addition experiments involve sowing (i.e. seed-addition) or planting species into an established community to evaluate the effect of the added components on the assembly process. In most cases, the established community is naturally assembled, and target components are introduced. However, a few studies combined species addition in synthetic community experiments (e.g. Fargione & Tilman, 2005; Roscher et al., 2009, 2014). Addition experiments aim to manipulate propagule supply by adding new species' propagules or seedlings to a local community. The added species may belong to the regional species pool or be alien species (e.g. Bennett & Pärtel, 2017, 2021; Breitschwerdt et al., 2015; Kempel et al., 2013; Oster & Eriksson, 2012). The success and abundance of the added species, as well as the dynamics of the resident community after the addition (e.g. an increase/decrease in diversity, or displacement of certain groups), are affected by the similarities between the resident community and the added species in terms of traits (Houseman & Gross, 2011).

If a species can successfully establish in the community only when it is experimentally added, then its absence in the local community may be due to dispersal limitation (Houseman & Gross, 2011; Kandlikar et al., 2022). However, if an added species fails to establish despite overcoming propagule limitation, the species trait values may be unsuitable under the prevailing environmental or biotic filtering. This is related to the trait similarities between the added species and the resident community (Bennett & Pärtel, 2017; Breitschwerdt et al., 2015). To evaluate addition experiments in grassland, Bennet & Pärtel (2017, 2021) analysed the composition of species pools from the regional to the site-specific pool and to the local communities to predict the probabilities of a given species to be part of the site-specific pool and to successfully establish in a local (resident) community. For such modelling, they used as predictors the measured trait dissimilarity of each species from each site-specific species pool (or from each local community), and as responses the presence/absence of the species in the site-specific species pool (or in the local community). This multi-scale model of community assembly was useful for predicting species establishment but performed poorly for predicting biotic interactions (Bennett & Pärtel, 2021). However, the traits of the species composition observed in a resident community may modify the local environment in a way that prevents certain species from establishing, even if they belong to the site-specific species pool. Therefore, we suggest that the understanding of the failure or success of added species establishment may benefit from the consideration of the feedback path shown in Figure 1.

Community assembly studies often use experiments to manipulate environmental factors and assess the selecting effect of the environment on species based on their traits. These experiments typically involve in situ manipulation of resources (such as nutrient addition, rain manipulation, and shading), conditions (such as using open top chambers to control temperature), and disturbance by trophic interactions (such as grazing) or by fire, mostly in natural communities. Another common approach is the turf/monolith-transplant, which involves relocating the entire community to a new environment (e.g. Debouk et al., 2015).

While most of these experiments do not control the processes at the level of metacommunity (i.e. available propagules from the surrounding communities), they offer the advantage of being established in natural communities. By altering environmental factors, researchers can evaluate the effects of these changes, or the cessation of a disturbance regime (e.g. grazing) on community assembly through species re-sorting.

Environmental manipulation can also be combined with other approaches, such as removal experiments (as shown in Mason et al., 2011). Such integration can enhance our understanding of succession dynamics from degraded to target conditions in restoration and provide insights for improving community recovery, thus bridging the gap between theory and practice (e.g. Funk et al., 2008; Navarro-Cano et al., 2019; Temperon & Hobbs, 2004).

One promising yet rare experimental approach is manipulating environmental heterogeneity. For example, Price et al. (2014) conducted a mesocosm experiment to test the effects of soil fertility and heterogeneity on synthetic grassland communities. Through changes in traits related to resource acquisition and competitive ability, they found that soil heterogeneity significantly affected the community-weighted mean (CWM) and niche overlap of co-occurring species. This indicates that the fine-scale distribution of resources in the soil plays an important role in community assembly. Additionally, as shown in Figure 1, heterogeneity may also be created in the process of community assembly. Furthermore, experimental manipulations of environmental factors could be employed to examine hypotheses regarding potential feedback loops illustrated in Figure 1. For instance, a finely tuned, localized addition of nitrogen fertilizer in an experiment could be employed to obscure or mimic the feedback loop generated by the introduction of legumes into the plant communities. Similarly, introducing experimental changes in light exposure or shading could obscure or replicate a feedback loop created by taller plants influencing the availability of light to shorter plants. A good example of this type of experiment is found in Craine & Orians (2004).

Community assembly simulation models: a quest for a synthesis

The simulation of community assembly involves proposing causal links between traits and community assembly to guide the simulation process, which will hopefully generate expected patterns in the simulated data. Model validation can be based on the correspondence between the expected and the observed patterns in simulated data. Model validation can also be based on the correspondence between simulated and experimental/observational data, which is a test for the model assumptions. Despite simplifying assumptions, simulation models allow testing hypotheses about how plant traits, environmental factors, species interactions, and metacommunity-level factors such as dispersal limitation influence community composition and diversity. Here we focus on niche models that consider plant selection (filtering) processes involving at least plant traits in a species pool and environmental factors. We focus our discussion on stochastic individual-based models that predict community assembly. Additionally, we highlight models that address the community assembly processes indicated in the conceptual model of Figure 1.

Process-based models, such as the dynamic global vegetation models (DGVMs), can simulate the establishment of individuals in plant communities based on ecophysiological processes that link traits or plant functional traits (PFTs) to environmental conditions (e.g. Blanco et al., 2014; Scheiter & Higgins, 2009; Smith et al., 2001). Regarding the simulation of community assembly, these models implicitly model plant interactions by considering the impact of each individual on the available resources, which, in turn, affects the fitness of other individuals in the community, in line with the conceptual causal model depicted in Figure 1. Such a feedback approach is advantageous compared to the use of Lotka-Volterra competition coefficients, which are difficult to obtain (Scheiter et al., 2013; Shipley et al., 2006) and, more importantly, are not linked to the actual resources the plants are competing for. Furthermore, spatially explicit process-based models (e.g. Blanco et al., 2014) can consider the effects of dispersal limitation at the metacommunity level. However, early DGVMs were limited by the very small number of PFTs and by fixed trait values that were often tuned during the model calibration process (Scheiter et al., 2013). Such poor functional diversity does not allow for the study of realistic community assembly processes. In this regard, Scheiter et al. (2013) proposed a flexible trait-based approach for the development of process-based models with a large number of plant types presenting different trait value combinations, which can be filtered by factors considered in the community assembly process. Similarly, Metcalfe et al. (2020) developed a process-based simulation model of annual plant communities, which generated data with emergent diversity patterns that were not explicitly anticipated in the model design. This approach helps closing the gap between process-based models and community assembly.

Some community assembly models do not include explicit processes of plant establishment by adopting a statistical approach for predicting the successful establishment of an individual plant given its traits and the local conditions. Among these, the community assembly via trait selection (CATS) model uses as input a matrix of species by traits, and for each site a vector of expected community-weighted mean (CWM) values for the traits. The expected CWMs can be found empirically by fitting regression models of observed CWM on environmental factors (Keddy & Laughlin, 2021; Strahan et al., 2018). In the CATS model, the predicted vector of relative species abundances for each site is then obtained by solving a system of linear constraint equations that (a) the species proportions add to unity and (b) maximise Shannon entropy in the community, and (c) the predicted CWM is closest to the expected CWM. The CATS model has been extended by incorporating a fourth constraint (d) that the relative species abundances must also satisfy a specified prior that can be set to reflect dispersal limitation (Shipley et al., 2012; Sonnier et al., 2010). At a first glance, the maximum entropy restriction seems arbitrary (Keddy & Laughlin, 2021), but the solution with maximum entropy reveals the most likely species composition among the many solutions that would meet conditions (a) and (c) (Shipley et al., 2006). The CATS model is purely driven by environmental filtering and ignores interactions (and the feedback path we propose in Figure 1). Yet, it has been successfully applied for predicting plant communities across environmental gradients (see Keddy & Laughlin, 2021 for a review), though the predictive power declines with species richness (Laughlin & Laughlin, 2013; Sonnier et al., 2010). Keddy & Laughlin (2021) suggest that the maximum entropy solution also pushes towards increased trait divergence and against dominance by few species, thus predicting a species composition that is closer to natural communities. However, no predictions can be made about which factors would drive such trait divergence.

Here we focus our attention on the stochastic, individual-based models described by Botta-Dukát & Czúcz (2016) and Pillar et al. (2021), which also adopt a statistical approach for linking traits to environmental factors. These simulation models, with some limitations, can help deciphering the links between plant traits and community assembly according to the conceptual model of Figure 1. Botta-Dukát & Czúcz (2016) used a simple simulation model to test the ability of functional diversity indices to detect trait convergence/divergence patterns generated by community assembly. The model input includes a species pool described by traits related to resource use that have a specified correlation structure; a set of sites along an environmental gradient defining optimal (expected) trait values; environmental filtering parameters that specify the tolerance of each species, given the deviation between its trait values and the expected optimal site-specific trait values; and competition parameters for each trait and pair of species. The trait deviations from the optimal and the competitive pressure that are given by trait differences between species determine the individual survival probability at each site. Therefore, the model of Botta-Dukát & Czúcz (2016) adopts an a priori approach to species interactions, rather than the feedback loop through environmental factors we present in Figure 1. Dispersal limitation is not considered.

In line with the conceptual model shown in Figure 1, Pillar et al. (2021) (see also Pillar 2023) described a spatially explicit metacommunity simulation model to explore the effects of the trait correlation structure in the species pool, the number of traits, and the strength of interaction effects of environmental factors on community assembly. The input for the metacommunity simulation model includes a species pool, and the corresponding traits and propagule dispersal parameters. The sites are mapped on the geographical space and described by environmental factors, which may be spatially nested. Seeds arrive at a site with a dispersal probability predicted by the distance from source sites with the same species in the metacommunity, which is applied to a dispersal function with parameters set for each species.

The niche basis of the simulation model described in Pillar et al. (2021) (see also Pillar, 2023) lies in a specified pool of species with observed trait values, and a trait space with sites described by expected traits values. The expected trait values are based on imputed or empirically determined linear function parameters (slopes) linking each trait to the one or more environmental factors taken independently or interacting. In this trait space, once propagules arrive, the probability that individuals of a species will recruit and survive at the site will depend on (i) how critical is the trait for the species' fitness, and (ii) how close the species is, in trait space, to the expected optimal trait value at the site. Survival also includes a species-specific density-dependent mortality probability. The process of colonisation and death of individuals is repeated many times and for all sites until saturation. In this process, the feedback of the communities on the environmental factors can be considered (Pillar, 2023). This model has been successfully used to assess the effect of hidden factors in the perception of relevant traits in community assembly (Pillar et al., 2021). Additionally, by simulating spatially nested, including feedback-driven factors, trait divergence was generated at the beta or alpha dimensions, depending on the scale of the community units, which mimics observed patterns in nature (Pillar, 2023). This provides empirical evidence that patterns appearing as plant-to-plant interactions actually emerge through environmental filtering driven by the feedback path proposed in our conceptual model (Figure 1).

In the context of community assembly modelling, the species pool can either be a real one (e.g. Metcalfe et al., 2020), where trait patterns may reflect well-known trade-offs that limit the realized trait space (e.g. as described by Díaz et al., 2016), or it can be simulated based on a known trait correlation structure to represent these trade-offs (e.g. as in Dantas de Paula et al., 2021). The role of these trade-offs in community assembly can be assessed in simulation models by examining different levels of trait collinearity and strengths of the filtering factors. As demonstrated in Pillar et al. (2021), one trait may be more limiting than another depending on the strength of the factor effects, but this suppression effect is only present if these traits are independent each other at the individual level, i.e., are not bound by the same trade-off.

Conclusions

Our synthesis of concepts and methodological approaches indicates that plant community experiments and simulation models are useful tools for studying community assembly and understanding the underlying processes that generate observed patterns. However, we have identified limitations that hinder a deeper understanding of the links between environmental factors, plant traits, species assembly, and ecosystem functions. We highlight three aspects that, if explored more deeply, could open new avenues in community assembly studies: i) coordination between functional traits, so that environmental filtering selects individuals from a species pool based on non-independent traits bounded by trade-offs; ii) feedback from the existing community, which can modify environmental factors during the assembly process and generate iii) nested environmental variation, which may exhibit distinct spatial and temporal structured at different scales, further producing fine-scale heterogeneity and trait divergence. To address these gaps and guide future studies, we advocate a conceptual model that explicitly indicates the causal links connecting community assembly processes (see Figure 1).

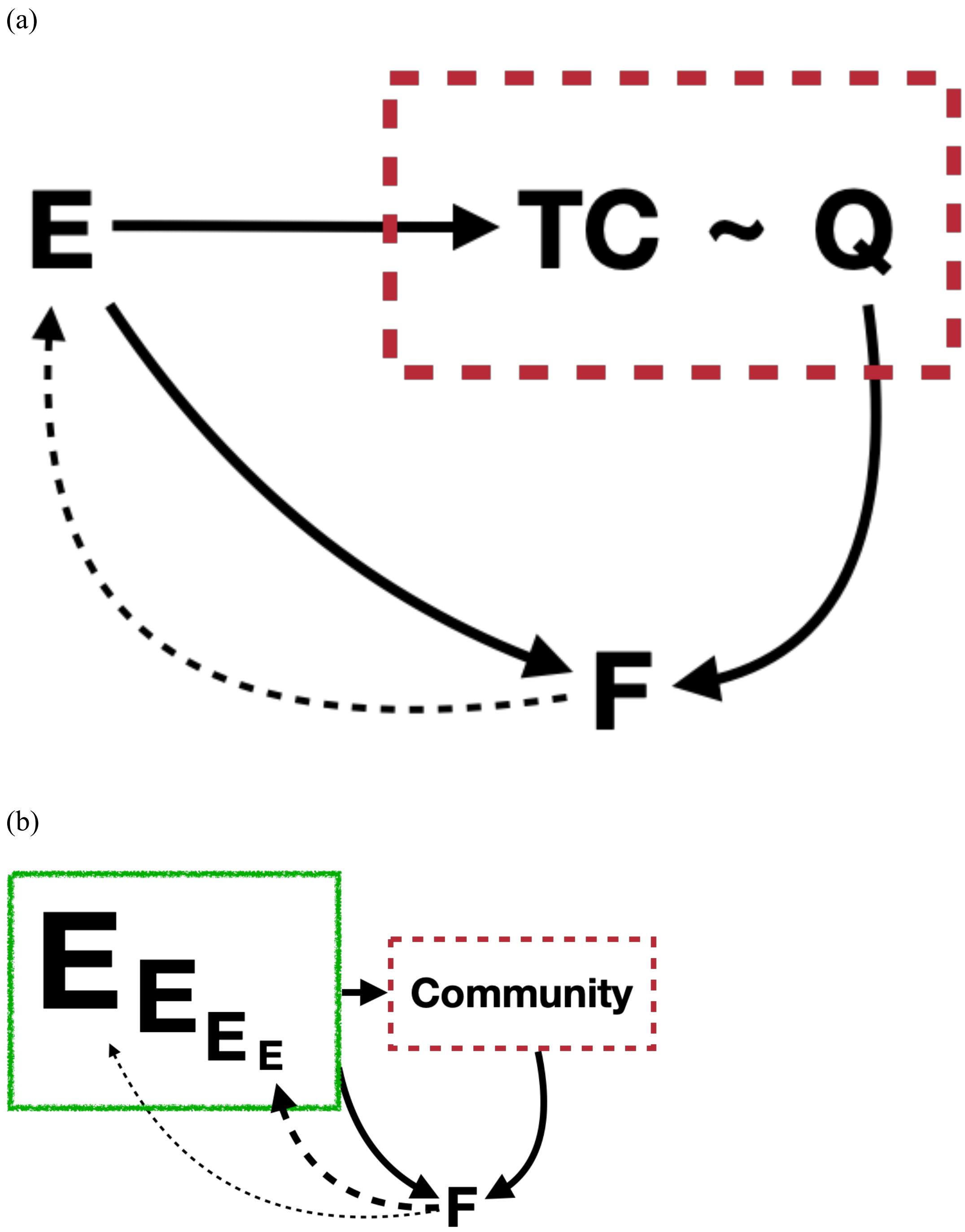

FIGURE **1**. A conceptual causal model that explains community assembly and ecosystem functioning. In (a), each node in the model is represented by a matrix. The communities (**C**) defined at a given spatial/temporal scale consist of individuals, belonging to a species pool, that have been filtered by one or more environmental factors (**E**) mediated by one or more traits of the individuals (**T**). The set of communities in **C** forms a metacommunity where propagule dispersal occurs. Since the traits and the species cannot be separated, matrices **T** and **C** are represented as a block matrix **TC** of species by traits and by communities. **Q** expresses traits integrated at the community level (e.g. community-weighted means, functional diversity, fuzzy-weighted species composition), and is computed using the species abundances in **C** and their corresponding traits in **T**, which are represented within the box. The plant communities in **Q** may provide feedback on **E** via ecosystem processes or functions (**F**), indicated by the dashed arrow. As highlighted in (b), the feedback effect depends on the scale of the spatial/temporal variation of the environmental factors in **E**, with stronger effects at finer grains and decreasing effects in coarse grains. Environmental factors in **E** are resources (e.g. light, nutrients, water), conditions (e.g. temperature), disturbances (e.g. herbivory, fire), which are affected by ecosystem functions or processes defined by **F** (e.g. productivity, decomposition, enhanced palatability of flammability). It is important to note that plant-plant interactions are mediated by such feedback, as changes in **E** can influence the community assembly process. Additionally, ecosystem functions (**F**) can be affected directly by environmental factors in (**E**).

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Authors' contributions

V.D.P. proposed and designed the study in collaboration with all other authors. All authors (V.D.P., A.G., D.H., F.M.F.) contributed equally to the literature search, screening, and idea development presented in this paper. V.D.P drafted the initial version, and all authors made significant contributions to the writing process and approved the final version for publication.

Data Availability Statement

No data was analysed.

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