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Key concepts and a world-wide look at plant recruitment networks

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†Our dear colleague Michel Faife-Cabrera passed away before the completion of this study.

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ABSTRACT

Plant–plant interactions are major determinants of the dynamics of terrestrial ecosystems. There is a long tradition in the study of these interactions, their mechanisms and their consequences using experimental, observational and theoretical approaches. Empirical studies overwhelmingly focus at the level of species pairs or small sets of species. Although empirical data on these interactions at the community level are scarce, such studies have gained pace in the last decade. Studying plant–plant interactions at the community level requires knowledge of which species interact with which others, so an ecological networks approach must be incorporated into the basic toolbox of plant community ecology. The concept of recruitment networks (RNs) provides an integrative framework and new insights for many topics in the field of plant community ecology. RNs synthesise the set of canopy–recruit interactions in a local plant assemblage. Canopy–recruit interactions describe which ("canopy") species allow the recruitment of other species in their vicinity and how. Here we critically review basic concepts of ecological network theory as they apply to RNs. We use RecruitNet, a recently published worldwide data set of canopy–recruit interactions, to describe RN patterns emerging at the interaction, species, and community levels, and relate them to different abiotic gradients. Our results show that RNs can be sampled with high accuracy. The studies included in RecruitNet show a very high mean network completeness (95%), indicating that undetected canopy–recruit pairs must be few and occur very infrequently. Across 351,064 canopy–recruit pairs analysed, the effect of the interaction on recruitment was neutral in an average of 69% of the interactions per community, but the remaining interactions were positive (i.e. facilitative) five times more often than negative (i.e. competitive), and positive interactions had twice the strength of negative ones. Moreover, the frequency and strength of facilitation increases along a climatic aridity gradient worldwide, so the demography of plant communities is increasingly strongly dependent on facilitation as aridity increases. At network level, species can be ascribed to four functional types depending on their position in the network: core, satellite, strict transients and disturbance-dependent transients. This functional structure can allow a rough estimation of which species are more likely to persist. In RecruitNet communities, this functional structure most often departs from random null model expectation and could allow on average the persistence of 77% of the species in a local community. The functional structure of RNs also varies along the aridity gradient, but differently in shrubland than in forest communities. This variation suggests an increase in the probability of species persistence with aridity in forests, while such probability remains roughly constant along the gradient in shrublands. The different functional structure of RNs between forests and shrublands could contribute to explaining their co-occurrence as alternative stable states of the vegetation under the same climatic conditions. This review is not exhaustive of all the topics that can be addressed using the framework of RNs, but instead aims to present some of the interesting insights that it can bring to the field of plant community ecology.

Key words: canopy service, ecological networks, facilitation, interaction strength, plant–plant interactions, recruitment niche, replacement networks, sapling bank, stress gradient hypothesis, strongly connected components.

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I. INTRODUCTION

The concept of community has always included the idea that species (more properly, populations) must interact with each other to be considered part of an ecological community. As interactions between species are one of the main drivers of community dynamics, their study is fundamental to understand how and why communities change (Brooker *et al.*, 2009). Addressing such interactions is a long-lasting target of community ecology and is becoming more critical under the need to preserve and recover natural communities disturbed by the many drivers of global change.

Plant community ecology has developed together with the theoretical and experimental study of plant–plant interactions (Schaffer & Leigh, 1976; Bazzaz, 1990). However, the empirical description of plant communities has traditionally treated species as ecologically independent entities. Accordingly, plant communities have been commonly described in terms of lists of species (i.e. floristic composition), counts of species richness (or other diversity indices) and their relative abundances (e.g. rank-abundance curves), disregarding explicit consideration of the interactive nature of the community (Kent, 2012). With the aim of providing a more complete understanding of the structure and dynamics of natural plant communities, recent efforts are developing new approaches to the observational study of plant–plant interactions that can provide information simultaneously for large numbers of interacting species within a local community (Losapio, Montesinos-Navarro & Saiz, 2019b).

The last decades have witnessed the development of important conceptual and analytical advances in the study of ecological communities under the scope of complex ecological networks [Pascual & Dunne, 2006; Bascompte & Jordano, 2014; Poisot, Stouffer & Kéfi, 2016; see Delmas *et al.* (2019) and Blüthgen & Staab (2024), for recent reviews on the analysis of ecological networks]. Such advances are now entering the field of plant community ecology (Lortie *et al.*, 2004; Losapio *et al.*, 2019b; Kinlock, 2021), but plant–plant interactions remain one of the least studied interactions from the ecological networks perspective. For example, the recent review by Xing & Faile (2021) included only one meta-analytic study of plant–plant interactions (Naranjo *et al.*, 2019), which focused on commensalistic epiphyte–phorophyte networks, one of the least common types of plant–plant interactions [only 8–10% of vascular plants are epiphytes and predominantly inhabit the humid tropics (Benzing, 2008; Zotz *et al.*, 2021)]. The incorporation of the ecological networks perspective into plant community ecology is fundamental since ecological network studies are moving towards the integration of multiple types of interactions to continue their task of embracing increasingly realistic levels of complexity (Pilosof *et al.*, 2017). However, this task will lack a fundamental component if plant–plant interaction networks are not included.

One reason for the scarce inclusion of the network approach in plant community ecology is the difficulty of

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identifying plant–plant interactions in the field, for a sufficiently large number of species, without manipulative experiments (Freckleton & Watkinson, 2001). Possibly the most accurate non-manipulative methods used to infer plant–plant interactions and their role on community dynamics are those that use long-term monitoring and stem-mapping of large plots (e.g. Ledo, Condés & Montes, 2011), although such methods are not amenable to addressing problems that require rapid data collection (e.g. in time-limited survey campaigns or to assist in vegetation management plans) or the sampling of a large number of sites. In recent years, several approaches have been used to address these limitations. Co-occurrence networks (Delalandre & Montesinos-Navarro, 2018; Saiz *et al.*, 2018; Calatayud *et al.*, 2020; Losapio *et al.*, 2021) used spatial associations in species abundance to hypothesise the existence of negative and positive interactions between pairs of species. As an alternative approach, recruitment networks (RNs; Alcántara *et al.*, 2019a) divide plant life cycles operatively into two phases: the recruitment phase that covers from seed dispersal to the pre-reproductive stage of the individual plant, and the established phase that includes the maturity and senescence stages. Recruitment interactions occur when an established individual (generically a "canopy plant") influences the success of individual plants recruiting in its proximity (in general terms, "canopy–recruit interactions"). The RNs approach infers that the interaction has positive (or negative) demographic effects on the recruiting species population when recruitment is higher (or lower) in close proximity to individuals of the canopy species than in spaces away from established plants (generically, "Open" spaces).

In this review we focus on the RN approach. RNs are easily incorporated into a variety of models of plant community dynamics through the concept of plant-by-plant replacement. Regardless of the factors considered, most theories on the dynamics and stability of plant communities are based on this concept. It is simple: when a plant dies, one or more individuals of the same or different species, take its place in a relentless process of death and replacement (Buffon, 1742, cited in Egerton, 2015; Horn, 1975; Connell & Slatyer, 1977; Grubb, 1977; Tilman, 1994; Pacala *et al.*, 1998; Hubbell, 2001; Snyder & Chesson, 2003; Allesina & Levine, 2011; Myster, 2012; Alcántara, Rey & Manzaneda, 2015; Miller & Allesina, 2021). In RNs, we assume that when a plant dies, it will be replaced by those that recruit close to it. This recruitment and replacement mechanism can be seen as a unifying principle of plant community dynamics (Grubb, 1977; Myster, 2012).

Knowledge on how canopy plants drive recruitment is key given the fundamental importance of recruitment for plant population and community dynamics. Indeed, the strongest filter to individual plant survival, and hence the narrowest bottleneck in demography, takes place during the recruitment phase. Numerous studies have found that the probability that a seed becomes an established juvenile plant is most often $<10^{-3}$ per cohort (Rey & Alcántara, 2000; Gulias *et al.*, 2004; Gómez-Aparicio, 2008; Terborgh *et al.*, 2014, Quintero *et al.*, 2024). Ultimately, changes in plant species composition resulting from local facilitative and competitive effects on recruitment may propagate through the ecosystem (Navarro-Cano, Goberna & Verdú, 2021b), modulating the functions performed by multiple taxa intimately associated with the plants, like the soil microbiota (Navarro-Cano *et al.*, 2019), pollinators (Losapio *et al.*, 2019a), seed dispersers (Carlo, 2005), and herbivores (Barbosa *et al.*, 2009).

Given the large body of theoretical and empirical work on plant–plant competition and plant community dynamics, it is surprising that we still lack a clear view of the structure of plant–plant interaction networks (Soliveres *et al.*, 2015; Alcántara, Pulgar & Rey, 2017; Saiz *et al.*, 2018; Calatayud *et al.*, 2020; Sánchez-Martín, Verdú & Montesinos-Navarro, 2023, Bimler *et al.*, 2024). Nevertheless, theoretical studies clearly demonstrate that the structure of plant–plant competitive networks has profound impacts on community stability (Allesina & Levine, 2011; Barabás, Michalska-Smith & Allesina, 2016). Unfortunately, the structure of competition networks has been determined in just a handful of experimental studies conducted with no more than 10 species, most often short-lived herbs (Kinlock, 2019). Thus, we know virtually nothing about the structure of such networks in nature, so most theoretical studies simply assume that all species within a local assemblage compete with each other. This does not take into account that, at the population level, facilitation can overcome competition (Olsen *et al.*, 2016) or that some pairs of species may not actually compete in the field due to different factors (e.g. seed dispersal limitation can decrease substantially the chances that individuals of rare species meet each other; Alcántara *et al.*, 2018). Our knowledge of the structure of facilitation networks has not advanced since the pioneering study of Verdú & Valiente-Banuet (2008) on empirical facilitation networks, with their study more often cited than repeated (Alcántara *et al.*, 2019a).

In an effort to overcome this knowledge gap, we have recently compiled a worldwide database (RecruitNet; Verdú *et al.*, 2023) of 143 plant–plant RNs describing the frequency of 118,411 unique canopy–recruit pairs involving 3318 vascular plant species from all biogeographic realms apart from Antarctica. This data set allows us to undertake a basic analysis of RN properties and to explore their global patterns of variation. By aggregating the information on canopy–recruit pairs, RNs allow describing patterns and exploring their generating processes and mechanisms at different levels, including interactions (links), species (nodes) and the whole local community (network). For example, at the link level one can explore which interactions enhance or depress recruitment (Alcántara *et al.*, 2018), at the node level it is possible to explore which species are recruiting under a given canopy species (i.e. the "canopy service" provided by the canopy species) (Verdú & Valiente-Banuet, 2008) or which canopy species allow the recruitment of a given recruit (i.e. the recruit's "recruitment niche") (Valiente-Banuet *et al.*, 2006), and at the network level one can explore the existence of patterns in the association of multiple species (Alcántara & Rey, 2012).

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Beyond the quantitative and qualitative aspects that can be described at link, node and network levels, RNs also inform about dynamics and stability properties of the plant community (Verdú & Valiente-Banuet, 2008; Alcántara & Rey, 2012; Alcántara *et al.*, 2015) and the ecological consequences of interactions (Valiente-Banuet & Verdú, 2013; Fodor, Haruta & Dorog, 2018). Most of these properties can be related to network descriptors such as connectance (May, 1973; Poisot & Gravel, 2014), nestedness (Bastolla *et al.*, 2009; Fortuna *et al.*, 2010), modularity (Gilarranz *et al.*, 2017), or strongly connected components (SCCs) (May & Leonard, 1975; Laird & Schamp, 2009; Alcántara *et al.*, 2017). Therefore, RNs provide a framework that allows integrating multiple levels of enquiry in the study of plant community ecology. For example, research lines using this framework can explore the intimate mechanisms driving canopy–recruit interactions [e.g. microclimate modifications, shared pathogens (Perea *et al.*, 2020, 2021b; Pérez-Navarro *et al.*, 2024)] and the functional traits involved (Navarro-Cano *et al.*, 2021a; Perea, Garrido & Alcántara, 2021a), scale them up to assess their relative contribution to the outcome of canopy–recruit interactions (Montesinos-Navarro, Valiente-Banuet & Verdú, 2019; Pajares-Murgó *et al.*, 2024a), and scale them up again to assess the final effect of these intimate interactions on the assembly and dynamics of the local plant community (Garrido *et al.*, 2023; Pajares-Murgó *et al.*, 2024b).

Here we review basic concepts of ecological network theory as they apply to RNs, and use the RecruitNet database (Verdú *et al.*, 2023) to describe the global patterns emerging at link, node and network levels. Our objective is to provide basic guidance for the study of RNs and show the insights that it can yield in the field of plant community ecology. This review does not intend to be exhaustive of how all the existing network descriptors apply to RNs, since the number of such descriptors is very large, highly redundant, and constantly growing. There is ample room for future studies on RNs to apply other (or new) network descriptors and to explore their implications for the structure, stability and dynamics of plant communities.

II. RECRUITMENT NETWORKS AS GRAPHS

(1) Nodes and their roles: unipartite and bipartite graphs

The description of ecological networks relies heavily on concepts from graph theory [see Delmas *et al.* (2019) for a review], so a minimum familiarity with some basic concepts will help in translating graph properties into ecological concepts (Fig. 1). Graphs contain two sets of elements: nodes and links (also called vertices and edges). Nodes in RNs represent different species, or more precisely, the populations of different species present in the studied local community. In addition, RNs incorporate a node representing open spaces. The size of a network equals the number of nodes it contains (N) which in RNs is the number of species plus one (for the Open node). RN studies often focus on particular subsets of species, usually corresponding to the most frequent life habits in the community (e.g. including all woody plants, only trees or shrubs and herbs), so care must be taken on the scope of species included when comparing the size of RNs.

A fundamental property of RNs is that they are "unipartite graphs" (or "one-mode" networks) since there is a single set of nodes that can play two roles: each species can act as both canopy and recruit. This is similar to food webs, where each species can be both the consumer and the resource. Moreover, this makes them different to other types of ecological networks that are "bipartite graphs" (or "two-mode" networks) with two non-overlapping sets of species, each playing a different role, as in plant–pollinator or host–parasite networks. In any event, due to the dual nature of nodes, RNs could be interpreted as bipartite graphs, with a set of canopy and a set of recruit species. This approach has been taken in studies of facilitation networks (Verdú & Valiente-Banuet, 2008), with canopy species playing the role of nurse plants (note that nurse species are canopy plants that have a positive effect on recruitment), and where the set of nurse species does not totally overlap with the set of recruited species (i.e. many recruit species may not act as nurses for other plants). There is no strong *a priori* reason to prefer the uni- or bi-partite approach in the analysis of RNs, so using one or the other should be decided depending on the research questions addressed and the type of community studied. For questions related to the relative abundances of species and the stability or dynamics of plant communities, the unipartite approach will be preferred most often because it is more directly related to theoretical models (Alcántara *et al.*, 2015). However, the bipartite approach would be frequently preferred when addressing questions that involve intrinsically different sets of species [e.g. the effect of nurse shrubs on the recruitment of herbs in desert or ecotone communities (Losapio *et al.*, 2018; Marcilio-Silva *et al.*, 2015)]. Unless otherwise stated, hereafter we will focus on the unipartite description of RNs.

(2) Links as interactions

Links carry the most important information in networks since they represent the very nature of interactions (e.g. flow of a resource, provision of a service). The outcome of canopy–recruit interactions not only depends on the direct interaction between two plants (e.g. through competition for light and nutrients) but also on the abiotic microenvironment (which may be modified by the canopy plant) and a variable number of interactions with third species that are to some extent specialists on the canopy and/or recruit species (e.g. mycorrhizal fungi, seed dispersers, seed predators, herbivores, and pathogens). All this complexity introduces a level of uncertainty in the outcome of the interaction between a given recruiting individual and its canopy plant. Thus, in the context of community ecology, the outcome of canopy–recruit interactions must be considered at the population

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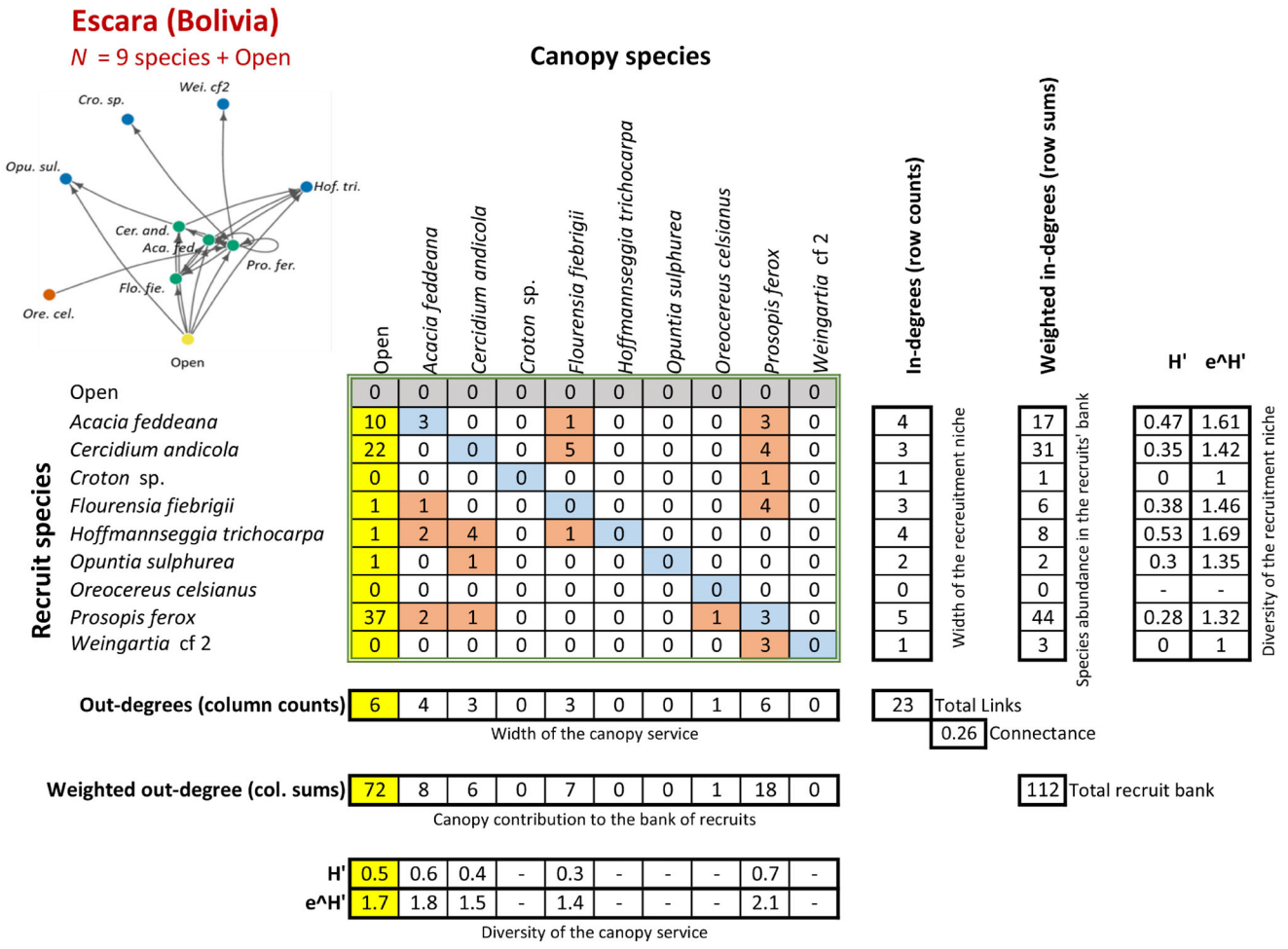

Fig. 1. Example of basic analysis of the recruitment network of a mountain semi-desert community (Escara, Bolivia). The recruitment matrix contains the frequency of canopy–recruit interactions, with the canopy species represented in columns and the recruit species in rows. The first row (grey) and column (yellow) correspond to the node Open that represents recruitment far from other plants. The main diagonal (blue) contains the frequency of intraspecific recruitment. The graph representation of the recruitment has one node for each species (plus Open) and the arrows point from the canopy to the recruit species (species names are indicated with the first three letters of the genus and species). Node colours indicate their functional roles (as explained in Section V.3): yellow for the Open node, green for core species, blue for satellite species and orange for transient species. Values resulting from aggregating cell values along rows or columns inform, respectively, on properties of the "recruitment bank" and "canopy service" of each species. For example, the counts of non-zero cells along rows or columns indicate the in- and out-degree of each species, forming the width of the recruitment niche and canopy service. Similarly, the sums along rows and columns provide the species abundance in, and the canopy contribution to, the recruitment bank. Finally, Shannon diversity (H') and the effective number of partners ($e^{H'}$) can be measured from row and column entries. Data from RecruitNet (Verdú *et al.*, 2023).

level, rather than at the individual level. Indeed, according to Abrams (1987), two species interact, directly or indirectly, if the presence of one of them in the community has an effect on the population dynamics of the second. To the extent that recruitment is a key process in plant population dynamics and that the probability or rate of recruitment is affected by the presence and identity of canopy species, we can consider that the local populations of the canopy and recruiting species interact. Given the complexity of processes involved in recruitment, the net effect of the interaction can be expected to vary depending on the particular pair of interacting species and the ecological context in which the interaction may take place (see Section III.2).

In RNs, a link from species j to species i indicates that species i recruits under (or in close proximity to, or in the microhabitat conditioned by) established individuals of canopy species j. In the case of node Open, a link from it to a given species i indicates that individuals of this species can recruit away from established plants. Consequently, RNs belong to the class of so-called "directed networks",

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like food webs, pollen transfer networks or the Internet. Accordingly, links in RNs are depicted as arrows pointing from the canopy to the recruit species (Fig. 1). Note that links in RNs are unidirectional since species *i* may recruit under *j* but the opposite does not necessarily occur. When two species recruit under each other, there are two arrows between them, each pointing in one direction. Interestingly, it is possible that a species recruits under the influence of conspecifics, so RNs can contain "self-loops" that can be very important in the context of density-dependent dynamics, like in Lotka–Volterra competition or Janzen–Connell models.

(3) Adjacency matrix and link weights

The analysis of networks is based on their adjacency matrices (Fig. 1). The adjacency matrix of RNs (hereafter, the recruitment matrix) shows canopy species as columns and recruit species as rows, with cells indicating some property of the links. Exactly the same species (and Open) appear as rows and columns, and in the same order. Figure 1 shows the node Open in the first column of the matrix, with entries corresponding to species able to recruit away from established plants. Accordingly, the first row also represents the node Open; it has all its entries as zeroes, meaning that when a plant dies, it is replaced by a new plant, not by Open. The cells in the community matrix of models of community dynamics (Novak *et al.*, 2016) have a correspondence with the links of the RN and their weight or strength. Ideally, the weight of the interaction should be a measure of the strength of the effect of one species on the demographics of the other, in units defined by some theoretical model, so that the network could be used directly to study the theoretical community dynamics. Although such measures can be estimated through experimentation, this approach is not usually feasible, so alternative, observational surrogates are frequently employed (Vázquez, Morris & Jordano, 2005).

In its most simple definition, links indicate the existence of an interaction between the nodes that they connect; this would be a binary (or "unweighted" or "qualitative") network, with a corresponding recruitment matrix filled with ones or zeroes to indicate the pairs of species that interact. A more informative weight in RNs is the frequency of recruitment (f_{ij}), which indicates how often the recruits of species *i* are found under the canopy species *j*. Other possible weights, which can be estimated directly through surveys or derived from f_{ij}, are the density of recruitment (by calculating the frequency of recruitment of species *i* per unit area of canopy species *j*), the efficiency of recruitment (by calculating the frequency of recruitment per unit area of canopy species and per unit cover of the recruited species), the consistency of the interaction (as the probability that the interaction between *i* and *j* occurs relative to the number of plots where adults of both species co-occur) or the incidence of the interaction (proportion of plots where the interaction was detected).

III. PAIRWISE CANOPY–RECRUIT INTERACTIONS (LINK LEVEL)

(1) Completeness of the sampled recruitment networks: link coverage

Regardless of the weight chosen, a fundamental preliminary step in RN analysis is determining the extent to which the whole set of canopy–recruit interactions present in the community has been recorded. Link coverage can be assessed using the procedure proposed by Chao *et al.* (2014) to determine the completeness of the estimated species richness in field surveys (implemented in the R package *iNEXT*; Hsieh, Ma & Chao, 2016). In RNs, link coverage measures the probability that the next pair of canopy–recruit individuals detected in a survey belongs to a pair of species that has already been recorded. With coverage values close to 1, the canopy–recruit pairs that remain to be found will be those that occur at very low frequency in the community, so their contribution to most network properties is likely to be very small. Link coverage in the RecruitNet database averaged 0.95, ranging between 0.60 and 1.00, with most studies (86.71%) reaching a coverage above 0.90 (Verdú *et al.*, 2023). This indicates that the occurrence and frequency of most interactions in empirical RNs are well approximated in most studies. Moreover, Pulgar, Alcántara & Rey (2017) showed that estimates of connectance and the functional structure of the networks (see Section V.4) are robust to sampling effort.

(2) Interaction sign and strength: positive, neutral and negative effects of canopy species on recruitment

The measures of link weight in Section II.3 (presence/absence, frequency, density, efficiency, consistency and incidence of the interaction) provide the information necessary to describe the RN. However, these magnitudes do not suffice to describe the effect (sign and strength) of canopy–recruit interactions. For example, a species may have a high density of recruitment under a given canopy species but an even higher density in Open, so the canopy species would actually be limiting, although not preventing, its recruitment. The sign of canopy–recruit interactions can be explored by testing whether the observed abundance of recruitment of species *i* under canopy species *j* is higher or lower than in Open relative to what could be expected from the cover of species *j* and Open (Verdú & Valiente-Banuet, 2008). Note that even a canopy species with a significantly negative effect on a recruit species can nevertheless have a net positive contribution to the recruit bank of the latter if it allows the recruitment of a few individuals. What the negative effect means is that the recruit species could have a higher recruitment in the local community if the canopy species were substituted by Open, not that the presence of the canopy species would totally prevent its recruitment. In this case, the

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canopy species exerts a competitive effect on the recruit species by depressing its recruitment.

In turn, the strength of canopy–recruit interactions can be measured by comparing the recruitment of species i under canopy species j or in Open interspaces relative to some reference value (see for example Díaz-Sierra *et al.*, 2017). Different indices of plant–plant interaction strength use different reference values, and this confers on them different properties that must be considered for each particular purpose (see Table S1 and Fig. S1 in online Supporting Information, Appendix S1). In the context of RNs, we will use the index of Neighbour Suitability (N_s) proposed by Mingo (2014):

$$N_S = \frac{r_{ij} - r_{io}}{r_i^*}$$

where r_{ij} and r_{io} are, respectively, the recruitment density of species i under canopy species j and in Open, and r_i* is the maximum recruitment density achieved by species i in any canopy species or in Open within the local assemblage. This index ranges between −1 and 1, with the sign indicating whether the canopy species j decreases or increases the recruitment of species i relative to the recruitment it achieves in Open, and the magnitude indicating how large the differential effect is of the canopy species j relative to the maximum recruitment observed by species i in the local assemblage under study. In Fig. 1, if we had used recruitment density as the weight in the matrix, N_s would be the difference between the entry of one cell and the entry in column Open of the same row, divided by the maximum entry in the row.

To test whether a canopy species affects the recruitment of a given recruit species, we use a chi-squared goodness of fit test assessing whether the frequency of recruits of species i associated with individuals of canopy species j or recruiting in Open departs from the frequencies expected from the relative cover of canopy and Open in a given local assemblage (see Appendix S2). Those interactions in which the number of recruits under canopy were significantly higher or lower than expected by the canopy cover were labelled, respectively, as "positive" or "negative", and non-significant interactions were labelled as "neutral". Once the interactions of each study site were classified, we used paired t-tests addressing the hypothesis that the mean frequency and absolute strength does not differ between positive and negative interactions in a local community. Finally, estimates of mean interaction strength and their comparison among different factor levels were obtained by fitting Bayesian models that included the factors as fixed effect (or the intercept only, when estimating the global mean) and the identity of the recruit and canopy species and the study site as random factors (see Appendix S3 and Figs S2 and S3 for further details).

After discarding 911 local canopy–recruit pairs due to lack of power to run the chi-squared test, the RecruitNet contains four times more interactions with negative than with positive sign (281,653 *versus* 69,411). However, 99.04% of the pairs with negative sign and 74.27% of those with positive sign did not differ from the neutral expectation, so the majority of pairwise interactions can be considered neutral. The median percentage of neutral interactions per community was 75.53% (mean: 69.62%; quartile range: 52.83%–85.26%; hereafter, ranges are provided for the 25% and 75% quartiles of the observed distribution). Among non-neutral interactions, positive interactions prevailed over negative ones (respectively: median = 19.75%, quartile range: 9.77%–36.65% *versus* median = 0.99%, quartile range: 0.00%–5.83%; paired t-test: $t = 8.08$, df = 90, $P < 0.001$; only localities with at least 10 testable interactions were included). Furthermore, positive interactions within each community were twice stronger than negative ones (absolute values of N_s: mean = 0.56, quartile range: 0.42–0.70 *versus* mean = 0.24, quartile range: 0.04–0.36; paired t-test of absolute values = 10.12; df = 59, $P < 0.001$). Therefore, the net outcome of canopy–recruit interactions on recruitment is more frequently positive, and positive outcomes tend to be stronger than negative ones. Indeed, the global mean N_s was 0.13 (sample size = 350,097 pairs; 95% credible interval: 0.06–0.21; $P(H_0: N_s = 0) < 0.006$; see Table S2).

These results contrast with findings of meta-analyses of plant–plant interaction studies conducted in the field, which suggest that competition occurs more frequently than facilitation in plant communities worldwide (Yang *et al.*, 2022). This discrepancy could be the result of using different methodologies. On the one hand, Yang *et al.* (2022) did not take into account the statistical significance of interactions when classifying them into positive or negative (i.e. they did not consider the possible existence of neutral interactions). They found a larger number of interactions with negative than with positive sign. This trend was also present in the RecruitNet data set, which contains four times more interactions with negative than with positive sign. However, considering only the statistically significant interactions, this pattern is reversed and canopy–recruit pairs with positive sign turn out to be six times more frequent than those with negative sign (17,780 *versus* 2660, respectively). On the other hand, Yang *et al.*, (2022) measured interaction strength using the commutative symmetry intensity index $\mathrm{NInt_C}$, an interaction intensity index, while we used N_s, an interaction importance index. This difference is relevant since importance indices relativise interaction strength to the maximum performance of the recruit plant within the set of environmental conditions of the studied local community (i.e. across canopy species and Open) (see Appendix S1 for further details). When we applied $\mathrm{NInt_C}$ to the RecruitNet data set, the global mean interaction strength was $\mathrm{NInt_C} = -0.225$ (95% credible interval: −0.323, −0.131; effective samples = 1031, $P(H_0: \mathrm{NInt_C} = 0) < 0.001$) which clearly contrasts with the positive value obtained above with N_s. This difference could be the consequence of the absence of recruitment in a large proportion of canopy–recruit pairs, since $\mathrm{NInt_C}$ takes its minimum value (−1) when species lack recruitment under a canopy plant, regardless of how much they recruit in Open or in other canopy species in the locality, what results in a strongly biased distribution of interaction strength values (Fig. S1).

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On more ecological grounds, reviews of plant–plant interactions including diverse life forms suggest that competition is stronger in herbs or grasses than in woody species (Gómez-Aparicio, 2009; He, Bertness & Altieri, 2013). Thus, the high proportion of woody species in the RecruitNet data set (75.7%) may contribute to the mean positive effect of canopy plants on recruitment that we found. However, we found that herbs are as good nurses as woody plants (mean N_s, respectively: 0.16, 95% CI: 0.06–0.29 *versus* 0.17, 95% CI: 0.07–0.30; Tables 1 and S3). Still, most herb species in the RecruitNet data set are long-lived perennials (e.g. tussock grasses and megaforbs) so more studies of RNs in communities dominated by short-lived herbs (e.g. temperate grasslands, ruderal communities) are needed.

The predominance of positive over negative interactions in the RecruitNet database also could be enhanced by a sampling bias towards arid habitats where facilitation is dominant (López *et al.*, 2016; Rey *et al.*, 2016), a trend that is tested in Section III.3. Also, it should be noted that experimental studies of plant–plant interactions tend to detect more competition and less facilitation than observational studies (Kinlock, 2019; Yang *et al.*, 2022). The simplicity of experiments between pairs of species isolated from the rest of the community and from other organisms co-occurring in the ecosystem is obviously designed to enhance the detection of competition for resources. However, this precludes determining whether, in natural settings, competition is blurred or counteracted by abiotic factors or by the effects of third species (Bairey, Kelsic & Kishony, 2016; Daniel *et al.*, 2024).

Yet another possible factor contributing to the predominance of positive over negative interactions could be the existence of stronger intra- than interspecific competition (Adler *et al.*, 2018). Since in any community we can test N intraspecific canopy–recruit interactions but up to N^2–N interspecific ones, the global average is more likely to be similar to the outcome of interspecific interactions. In the context of plant community dynamics, differences in sign or strength between intra- and interspecific interactions are very relevant because stability should be greatly enhanced when species limit their own recruitment more strongly than the recruitment of other species (Janzen, 1970; Connell, 1971; Chesson, 2000; Barabás *et al.*, 2016). Moreover, the mechanisms involved in intra- and interspecific interactions are quite different. For example, recruitment under conspecifics can be negatively affected by the presence of specialist pathogens or herbivores, which are much less likely to affect recruitment under heterospecific individuals (Fricke, Tewksbury & Rogers, 2014; Yamazaki, Iwamoto & Seiwa, 2009). However, in our analysis of the RecruitNet data, intraspecific interactions affecting recruitment were more positive ($N_s = 0.24$; 95% CI: 0.13 to 0.35) than interspecific interactions ($N_s = 0.10$; 95% CI: −0.02 to 0.21) (see Table S3). Although it remains to be explored whether this pattern may change with the environment or with plant ontogeny (Miriti, 2006; Le Roux, Shaw & Chown, 2013; Navarro-Cano *et al.*, 2016), this result challenges the theoretical expectations that species should exert stronger control on conspecifics. Indeed, facilitation between conspecifics has also been reported and several mechanisms described, including sharing of mycorrhizal symbionts, and abiotic stress reduction (Fajardo & McIntire, 2011; Montesinos-Navarro *et al.*, 2019; Zhang & Tielbörger, 2019). Similarly, Yang *et al.* (2022) found that the sign of interactions does not differ between intra- and interspecific interactions. If control of conspecific recruitment is not necessarily stronger than the control of heterospecifics, other mechanisms may be driving the stability of the community. One such mechanism is the intransitivity of interactions, which we will address in Section V.3.

(3) Gradients in interaction strength and sign

Since the net outcome of canopy–recruit interactions depends on the contribution of multiple biotic and abiotic factors, environmental gradients of variation in this outcome can be difficult to predict. Possibly the best-known gradients of variation in this outcome are related to successional changes after disturbance (Connell & Slatyer, 1977) and to geographic variation in environmental stress (Bertness & Callaway, 1994).

The net outcome of plant–plant interactions is expected to change during succession, with positive interactions being more frequent or stronger early after disturbance, and

Table 1. Results of a Bayesian model estimating the mean of interaction strength (neighbour suitability, N_s) of intra- and interspecific interactions and in interactions involving woody or herb species.

Parameter	Posterior mean	Lower 95% CI	Upper 95% CI	Effective samples	*p*MCMC
Intercept	0.047	−0.060	0.168	1000	0.358
Type (T): Intraspecific	0.114	0.090	0.136	1000	<0.001
Life habit of canopy (LHC): Woody	0.022	0.007	0.037	1000	<0.001
Life habit of recruit (LHR): Woody	0.085	0.031	0.135	1000	0.002
T: Intraspecific × LHC: Woody	−0.026	−0.158	0.091	1000	0.686
T: Intraspecific × LHR: Woody	0.074	−0.066	0.187	1000	0.270
LHC: Woody × LHR: Woody	−0.004	−0.013	0.007	1102	0.504

The value of *p*MCMC indicates twice the posterior probability that the estimate is negative or positive (whichever probability is smallest). See Appendix S3 for further details.

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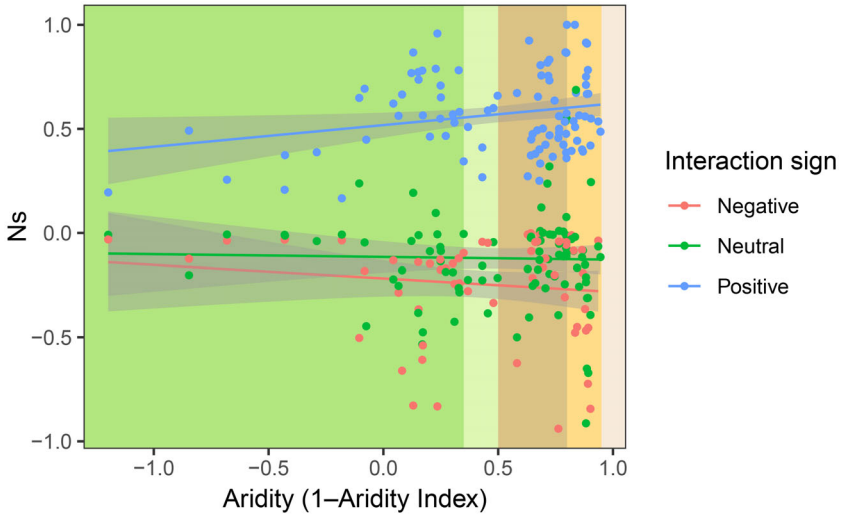

Fig. 2. Relationships between aridity (measured as 1 – Aridity Index) and the mean strength of positive, negative and neutral canopy–recruit interactions measured as the Neighbour suitability index (*Ns*) in each local community. Background shading indicates the climate of the community: humid (<0.35), dry subhumid (0.35–0.50), semiarid (0.50–0.80), arid (0.80–0.95) and desert (>0.95). Aridity Index values were obtained from Zomer *et al.* (2022).

becoming negative as vegetation recovers (Yin *et al.*, 2022). The RecruitNet database includes qualitative information on the successional stage of the sampled communities. A Bayesian model testing the hypothesis that N_s varies between successional stages (Table S4) indicates that mean N_s was not different from zero in the three successional stages (posterior means: 0.10, −0.01 and 0.14 in early, mid and late stages, respectively), without evidence for differences among them. This observation contrasts with the trend found by Yin *et al.* (2022) in a long-term study of old field succession. In fact, there is experimental evidence that several mechanisms may be acting simultaneously in plant succession and that species replacement through the succession will depend on the identity of the pioneer as well as the benefactor species (Armesto & Pickett, 1986; Paterno, Siqueira-Filho & Ganade, 2016). Nevertheless, differences in the factors that unleashed the succession can have important implications for canopy–recruit interactions. For example, we would expect domestic ungulates to have a differential impact on recruiting species depending on their characteristics and on the canopy species' palatability, and strong winds or crown fire should have a greater impact on adult plants than on the recruitment bank, while the opposite is expected in habitats prone to flooding or surface fire. Thus, successional stage and disturbance type may interact to determine the strength of canopy–recruit interactions.

The most studied driver of variation in the sign and strength of plant–plant interactions is the stress caused by aridity (Berdugo *et al.*, 2022). According to the stress gradient hypothesis (SGH; Bertness & Callaway, 1994), facilitative (positive) interactions should increase along a stress gradient while competitive (negative) ones should decrease. The present study allows testing this hypothesis at the global scale with possibly the widest aridity gradient ever studied (1–Aridity Index range: −1.2 to 0.95) and involving the widest set of species (3318 vascular plants) and ecosystem types used to date (48 ecoregions of the world, representing 10 of the 14 types of terrestrial biomes defined in Olson *et al.*, 2001). Note that the aridity index in its original scale (i.e. as developed for climate studies; Zomer, Xu & Trabucco, 2022) takes larger values for less arid places, so in ecological studies its scale is frequently reversed to 1 – Aridity Index for clarity of interpretation. Our results agree with those of He *et al.* (2013) and strongly support the SGH since the strength of positive canopy–recruit interactions increased with aridity while that of negative and neutral interactions scarcely changed (Fig. 2, Table 2). Moreover, positive interactions were stronger (in absolute value) than negative interactions throughout the gradient. This result clearly shows that facilitation of recruitment by established plants is strong in most plant communities, not only in arid ones. Nevertheless, the greater variability in the interaction

Table 2. Results of Generalized Linear Mixed Model testing the relationship between aridity and the within-community mean strength of positive, negative and neutral interactions.

Parameter	Estimate ± SE	$\mathcal{Z}$	$P(>\|\mathcal{Z}\|)$
Intercept	−0.217 ± 0.038	−5.781	<0.0001
Aridity	−0.061 ± 0.061	−1.009	0.313
Sign neutral	0.102 ± 0.051	1.993	0.046
Sign positive	0.737 ± 0.051	14.425	<0.0001
Aridity × Sign neutral	0.047 ± 0.081	0.576	0.564
Aridity × Sign positive	0.159 ± 0.081	1.963	0.050

The model included the study site as a random (block) effect. The model was fitted with a Gaussian distribution and identity link-function using the R package *glmmTMB* (Brooks *et al.*, 2017).

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strength values in the most arid zones compared to relatively less arid zones indicates the necessity to take other factors into account (Michalet, 2007; Maestre *et al.*, 2009). It is possible that the pattern of variation does not monotonically increase with stress, as our analyses assume, but that it reaches a peak close to the extreme (Michalet *et al.*, 2014). In this case, the mixture of gradients with different peaks could cause higher dispersion at the extreme of the gradient. Increasing uncertainty in environmental conditions, such as more stochasticity in precipitation and greater diurnal temperature ranges, or the interaction between climatic and edaphic aridity will also be worth exploring to understand this pattern better.

IV. RECRUITMENT NICHE AND CANOPY SERVICE: IN- AND OUT-DEGREES

Directed networks allow dissecting the effects of interactions in two aspects: the effect of a given species on the others and the effect of multiple species on a given one. In RNs, the "canopy service" describes how canopy plants modulate the abundance and composition of recruiting species, while the "recruitment niche" describes how the recruitment of a given species is modulated by the presence of other plants (Fig. 1). The description and interpretation of these aspects depend on the type of interaction weights. Using an unweighted network, we can estimate the width of the canopy service as the number of species that recruit under a given canopy species (its "out-degree" in graph terminology, also known as "vulnerability" of the resource in some ecological networks), or the width of the recruitment niche as the number of species under which it recruits (its "in-degree", also known as "generality" of the consumer in some ecological networks). When the network is weighted by the frequency of interactions, we can estimate the weighted degree (simple sum of interaction weights). The "weighted out-degree" indicates the total number of recruits of any species found under a given canopy species, which can be interpreted as the canopy species' contribution to the bank of recruits in the community. In turn, the "weighted in-degree" indicates the total number of recruits of a given species, which describes its abundance in the recruits' bank of the community.

Another common use of the degrees and derived metrics is exploring the level of specialisation of the interactions among species (Blüthgen *et al.*, 2008). The width of the recruitment niche and canopy service can be weighted by interaction strength to provide a more nuanced measure of generalisation or specialisation of the recruitment niche and service.

There is ample evidence that certain plant species can provide a particularly positive canopy service (i.e. are good nurses) [e.g. Gómez-Aparicio *et al.*, 2004; Navarro-Cano, Verdú & Goberna, 2018; see Filazzola & Lortie (2014) for a review of nursing mechanisms]. Moreover, Perea *et al.* (2021a) showed that plant functional traits contribute to structuring the canopy service and recruitment bank in Mediterranean mixed forests from southern Spain. Understanding the configuration of the canopy service and recruitment niche of species can provide new insights for multiple ecological research lines. For example, the width and composition of the canopy service can inform questions related to the functional redundancy of canopy species (if canopy services of different species overlap extensively) or help in the identification of keystone species when one or a few of them provide canopy service to a wide subset of species with narrow or highly specialised recruitment niches. It could also be possible to compare the composition of recruitment niches between species to determine their overlap and assess whether closely related species show more similar niches or, more generally, whether the structure of recruitment niches in a community shows a phylogenetic signal. These and other questions are worth addressing, but for brevity we do not consider them further here. Instead, we present an initial analysis of the frequency of species providing a positive, neutral and negative canopy service or having recruit banks that receive positive, neutral or negative effects from the established plants.

We used the chi-squared tests described in Section III.2 to assess: (*i*) whether the canopy service provided by a species had an overall positive, negative or neutral effect on recruitment, by comparing the total number of recruits (of any species) under the canopy species against the number in Open; and (*ii*) whether the recruit bank of a species was positively, negatively or not affected by the cover of canopy plants, by comparing its total number of recruits under canopy plants against the number in Open. The majority of canopy species within a community (median = 54.41%, quartile range: 28.57%–80.91%) provided a net positive canopy service while only a small percentage (median = 0%, quartile range: 0%–17.42%) depressed recruitment. The median percentage of species with a neutral canopy service was 31.25% (quartile range: 12.70%–50.00%). This suggests that a large proportion of canopy species in plant communities can be considered as nurse species that, through direct or indirect mechanisms, facilitate the recruitment of others. On the other hand, very few species seem actively to prevent recruitment in their vicinity. These can be suspected to release some allelopathic substances or attract generalist antagonists. In turn, around half of the recruit species within a community showed a neutral association with canopy plants (median = 52.17%, quartile range: 36.18%–73.62%), so their observed (realised) recruitment niche was likely the result of stochastic processes (e.g. random seed dispersal) or a balanced (neutralising) outcome of positive and negative interactions. Among the remaining species, most of them (median = 34.37%, quartile range: 12.50%–55.00%) benefitted from canopy plants and much fewer (median = 1.59%, quartile range: 0%–13.48%) were adversely affected by canopies. These results are clearly in line with our previous analysis at the link level (Section III.2) and challenge the prevailing view that competition is the dominant force driving the dynamics of plant communities. Competition may dominate other

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aspects of the plant's demography (vegetative growth, fecundity, adult mortality), but recruitment appears to be dominated by facilitative canopy–recruit interactions.

V. INTERACTIONS IN THE LOCAL COMMUNITY (NETWORK LEVEL)

Some network-level descriptors are summary properties of nodes and/or edges (e.g. connectance, degree distribution) while others are properties of network structure (like nestedness or modularity), since their values depend on which nodes are connected with which others (i.e. two networks with the same number of nodes and edges can have a totally different structure). We can consider another type of network-level structural descriptor: those that inform explicitly about some aspects of system functioning. This is the case, for example of network diameter, mean path and loop length or SCCs, which inform about the lengths of the routes that resources or services can follow and whether these can be recycled in one or different parts of the network.

To describe the structure of RNs, we explore connectance, degree distributions, nestedness and modularity (Delmas *et al.*, 2019): connectance describes the proportion of interactions observed relative to the maximum potential number of interactions in the system; degree distributions describe the frequency distribution of nodes with different degrees; nestedness refers to the tendency of specialist species (i.e. those interacting with few species) to interact with generalists; and modularity defines groups of species that interact more among themselves than with others. In addition, to explore the relationship between structure and stability in RNs, we use the qualitative approach to species persistence (a measure of system stability) based on the analysis of SCCs proposed by Alcántara & Rey (2012). Since variation in sampling intensity among studies can bias network descriptors, affecting their relationships with environmental gradients (Brimacombe *et al.*, 2022), we restricted our analyses to those RNs with a link coverage of at least 0.9 (mean coverage ± S.D.: 0.97 ± 0.03, $N = 124$). Based on the results in Section III.3, here we explore the effect of aridity on network properties. In addition, we explore whether and how RNs vary between forests and shrublands (other types of formations in the database were grasslands, savannas and mangroves, but there were less than six cases of each, so we could not include them in this analysis).

(1) Connectance

Connectance (C) is probably the most frequently used network property. It is a measure of complexity and is linked to the stability of the ecological system (May, 1973; Allesina & Tang, 2012). Moreover, many network properties vary depending on C (Fortuna *et al.*, 2010; Poisot & Gravel, 2014). Its exact calculation depends on the type of network. For example, in general unipartite directed networks with L links and N nodes, $C = L/N^2$, while in bipartite networks $C = L/(N_i N_j)$ (where N_i and N_j are the number of nodes of each type). In RNs we use $C = L/N(N–1)$ since, by definition, the node Open does not "recruit" under plants but plants can recruit in open spaces.

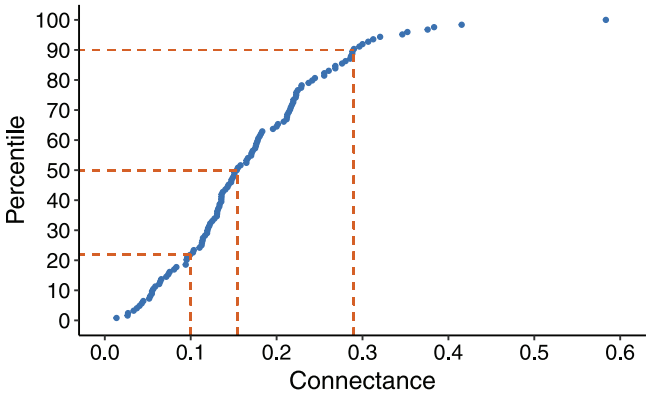

Fig. 3. Cumulative frequency of connectance (C) in recruitment networks (RNs) of the RecruitNet database. The dashed lines indicate the 22%, 50% and 90% percentiles. Observed C values range from a minimum of 0.014 to a maximum of 0.583.

Connectance in RNs is low (mean 0.175), with 90% of the networks showing values below 0.3 (Fig. 3). This means that in the majority of studied communities less than one in three possible canopy–recruit interactions occur, and in many cases (22% of RNs) they are less than one in ten. Connectance did not vary with aridity and was almost double in forests and grasslands (mean ± SE: 0.245 ± 0.017 and 0.210 ± 0.122, respectively) than in shrublands (0.135 ± 0.009) (Table 3). The reason for this difference among habitats is not clear. It might be that shrub species tend to deliver a negative canopy service more often than trees or grasses. For example, Tüfekcioğlu & Tavşanoğlu (2022) show that closed shrublands contain fewer saplings compared to pine forests and open shrublands in the Eastern Mediterranean Basin. Interestingly, however, in a meta-analysis of experiments of facilitative interactions in restoration, Gómez-Aparicio (2009) found that shrubs are usually the life form with the largest facilitative effect on the planted saplings (compared with

Table 3. Test of the effect of habitat (forest, shrubland, grassland) and aridity on connectance.

Effect	Type III Wald Chi-square	df	P
Habitat	22.895	2	<0.0001
Aridity	2.693	1	0.101
Habitat × Aridity	1.732	2	0.421

Results of Generalized Linear Model assuming that connectance follows a beta distribution. Moran's I test for distance-based autocorrelation was not significant ($P = 0.18$). Model fitted with the R package glmmTMB (Brooks *et al.*, 2017) and residuals checked with package DHARMa (Hartig, 2022).

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herbs, grasses and trees). If shrubs appear here to have a low canopy service, this must be related largely to negative effects during the dispersal phase (e.g. limited seed arrival and high seed predation under shrubs), since the microhabitat they generate is usually quite good for seedling emergence and survival. Accordingly, Perea *et al.* (2021b) found that canopy plants with high branch density (like many small shrubs in the genera *Thymus* or *Ulex*) tend to depress recruitment, possibly by repelling seed arrival or by impeding sapling growth through their entangled canopy.

(2) Assembly rules: degree distributions and network-generating models

The degree of a given species does not convey much information on its own, so it should be compared with the degree of the rest of the species in the community. Studies of ecological networks often investigate whether the frequency distribution of degrees (or simply, degree distribution) can be approximated by different types of statistical distributions because these have different implications regarding network structure and its assembly rules. In the context of networks, assembly rules describe the processes by which new nodes or links enter into a network. For example, assuming equal seed production and dispersal ability across recruiting species, and equally abundant canopy species, if new recruits establish at random among the available canopy species, the resulting network will show a Poisson degree distribution, but if new recruits establish preferentially under particular canopy species (e.g. those that are better nurse plants), the network will show a degree distribution that follows a power law (Delmas *et al.*, 2019). This is an interesting research avenue that deserves the attention of future studies of RNs. Unfortunately, accurate statistical analyses testing whether the degree distribution of a network fits better to some probability distribution require hundreds or thousands of species representing a wide range of degrees (Clauset, Shalizi & Newman, 2009), so they can only be used in particularly species-rich communities. Figure 4 shows the fit of the largest network in the RecruitNet database (Wanang, from Papua New Guinea, with 557 species). The network fitted better to the truncated power law (Appendix S4, Table S5), however there are clear discrepancies between the observed frequency of species with high degree and the frequencies expected under this distribution. Exploring these departures can be informative, since they may suggest limitations in the width of recruitment niches and canopy service. In any case, this sample size limitation currently prevents the search for general patterns of degree distributions in RNs.

A currently more tractable research avenue to infer assembly rules for RNs would be to propose generating models based on the ecology of recruitment (i.e. ecological rules that determine which species recruits under whom), and test their ability in reproducing networks with the same properties as empirical RNs. For example, Alcántara, Garrido & Rey (2019b) fitted models of f_{ij} as a function of canopy and recruit species cover and the phylogenetic distance between

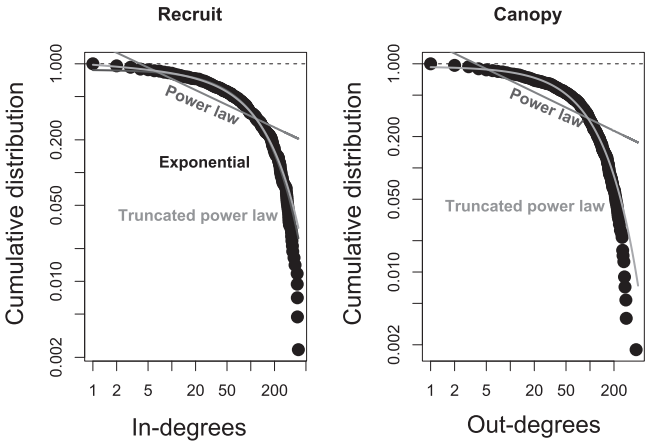

Fig. 4. Fit of the in- and out-degree distributions of the largest network in the RecruitNet database (Wanang, from Papua New Guinea, with 557 species) to the exponential, power law and truncated power law distributions (the exponential distribution could not be fitted to the out-degrees). Statistical tests of fit are provided in Appendix S4. According to Akaike Information Criteria, the best fit was achieved with the truncated power law, but note that, nevertheless, this distribution overestimates the frequency of species with very large degrees.

them. The fitted models were used to predict new networks and obtain several network descriptors. Their analysis showed that the networks constructed from models incorporating phylogenetic distances in addition to species cover were the best to reproduce network properties. Phylogenetic distance is a surrogate for generic species differences, but we still need to discern whether these generic differences are explained, for example, by particular functional traits of canopy and recruit species (Valiente-Banuet *et al.*, 2006; Butterfield & Briggs 2011; Navarro-Cano *et al.*, 2021a) or by their shared interactions with other organisms (Montesinos-Navarro *et al.*, 2012; Garrido *et al.*, 2023; Pajares-Murgó *et al.*, 2024a).

(3) Nestedness and modularity

A wide recruitment niche should enhance the persistence of a species by guaranteeing that it easily finds some suitable canopy species for recruitment. On the other hand, a wide canopy service identifies species with a high contribution to the maintenance of species diversity in the community. Thus, understanding how recruitment niches and canopy services are simultaneously arranged in a network can provide insight on species persistence and species richness.

(a) *Nestedness*

A network is perfectly nested if the interactions of a given node are a subset of the interactions of all nodes with larger degree. In a perfectly nested RN, (*i*) the recruitment niche of a species is a subset of the recruitment niche of all species

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with wider niches, and simultaneously, and (*ii*) a canopy species provides recruitment space for a subset of the species that recruit under species that provide a wider canopy service. Although nestedness is one of the most used descriptors of ecological networks, its causes and consequences remain unclear (Mariani *et al.*, 2019; Blüthgen & Staab, 2024). Recent studies suggest that nestedness should be interpreted as a by-product of heterogeneous degree distributions and not as a pattern emerging directly from some ecological process (Payrató-Borrás, Hernández & Moreno, 2019). Our results in RNs point in this direction. Only one in 123 studied RNs showed higher NODFc (nestedness metric based on overlap and decreasing fill; Almeida-Neto *et al.*, 2008) than expected from the fixed-fixed null model where the number of interactions per species are kept at the observed values (i.e. the degree distributions are preserved). It is possible that the fixed-fixed null model underestimates the number of nested networks (Ulrich & Gotelli, 2007), but it should perform satisfactorily in combination with NODF, given the high completeness of the studied networks (Bruno *et al.*, 2020). Therefore, our results clearly suggest that nestedness in RNs is not likely the result of any deterministic ecological process. Moreover, the effects of nestedness on network stability can also depend on degree distribution. For example, although RNs are robust to extinction cascades, this occurs mostly when the probability of extinction depends inversely on species degree (i.e. when the sequence of extinctions starts with the most specialised species) (Burgos *et al.*, 2007; Verdú & Valiente-Banuet, 2008), so degree distribution is actually the main contributor to robustness. Furthermore, theoretical analyses indicate that the resilience of nested networks would actually be due to their heterogeneity in degree distributions (Feng & Takemoto, 2014).

(*b*) *Modularity*

Modularity is a measure of the extent to which networks are formed by loosely interconnected subgroups (frequently called modules or compartments) of internally densely connected nodes. Compartments can be caused by the spatial or temporal separation of groups of species in a heterogeneous environment (e.g. co-evolved lineages of plants and pollinators; Olesen *et al.*, 2007). The existence of compartmentalisation in ecological networks can have important implications for the assembly and functioning of ecological communities, but as in the case of nestedness, the relationships of modularity with the functional properties of the systems that the networks represent are not generalisable. For example, theoretically, modularity in food webs can have positive effects on system functioning by reducing competition (Rezende *et al.*, 2009) or by restraining the spread of disturbances (Stouffer & Bascompte, 2011), but the analysis of empirical networks conducted by Thébault & Fontaine (2010) found that modularity was not related to persistence (defined as the proportion of species persisting in equilibrium according to a given model of community dynamics) and was weakly related to resilience in trophic networks, and was related negatively with persistence in mutualistic networks. Besides these contrasting findings, the best way of detecting modularity is still an open question. Measuring modularity consists of performing a recursive search where nodes are partitioned into modules and then some index of modularity is calculated and updated until the index reaches a maximum (e.g. Newman, 2006). The resulting number of modules, the nodes forming each module and the final modularity value depend on the algorithm used in the search, the number of iterations and the index that is maximised. Moreover, as for nestedness, the significance of the estimated value can vary strongly depending on the null model used.

To explore the existence of modularity in RNs we used two algorithms: walktrap (from the R package *iGraph*; Csárdy & Nepusz, 2006) and simulated annealing (in *Netcarto*; Doulcier & Stoufer, 2023), again using the fixed-fixed null model. The estimates of modularity using both methods were correlated ($r = 0.56$; $N = 130$; $P < 0.001$). We found evidence for modularity being higher than expected from the null model in 25 out of 112 RNs using the walktrap algorithm and only in 13 out of 121 using simulated annealing. Both algorithms agreed in only six networks. Thus, we found clear evidence for modularity in less than 5.36% of all RNs. Taken together, these results show how different methods provide different results in the analysis of modularity.

Given that we did not find strong support for the general existence of nestedness or modularity in RNs, we did not conduct analyses exploring the drivers of these properties, their variation along environmental gradients or their relationships with persistence.

(4) Functional structure and species persistence

The analysis of the functional structure in directed networks is based on a qualitative approach to infer species' persistence according to their position in the network (Alcántara & Rey, 2012; Alcántara *et al.*, 2017). This approach can be applied to systems described by unipartite directed networks (like RNs, competition networks or food webs) where interactions represent the flow of some resource or the provision of some service from the provider to the receiver. Replacement dynamics in plant communities can be modelled as the interchange of space, or the resources it contains, from the canopy plant to the recruit plants (Alcántara *et al.*, 2015). Hence, RNs describe the structure of the basic process that drives the dynamics of the community.

Alcántara & Rey (2012) derived a qualitative way to infer potential species persistence from their position in the RN based on a combination of non-negative matrix theory and graph theory. Basically, directed unipartite graphs can be unambiguously dissected into SCCs (Fig. 5). SCCs are the largest possible subgroups of nodes connected so that all the nodes in a subgroup can be reached from all others following the directions of the links. SCCs can have any size, from a single node (a trivial SCC) to the whole network. Accordingly, a network of N nodes can contain between 1 and N SCCs. Non-trivial SCCs represent intransitive relationships between

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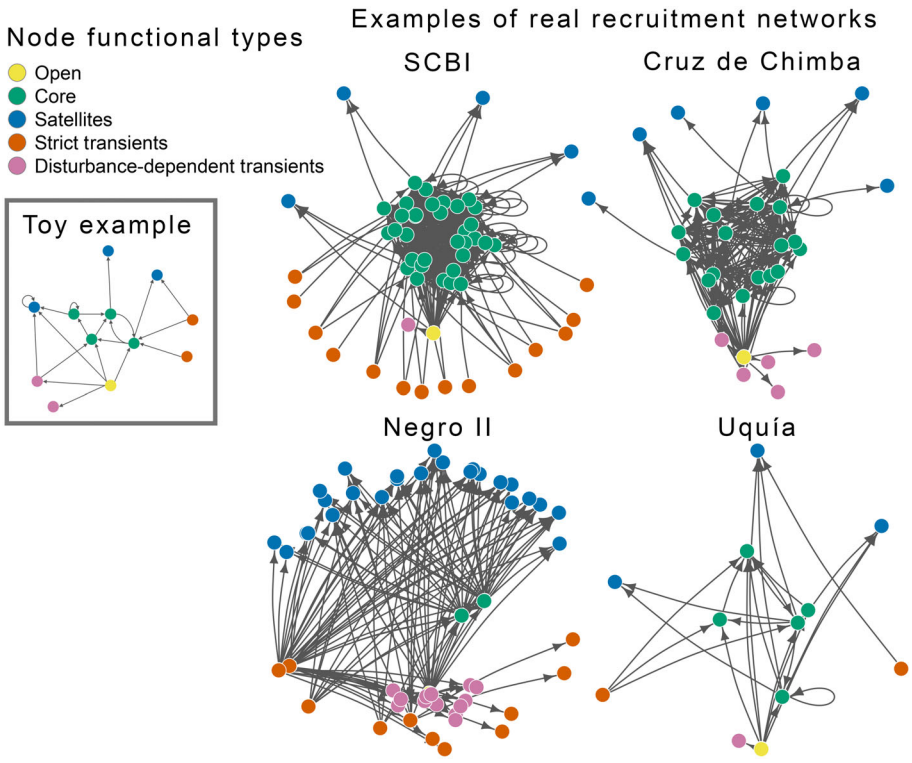

Fig. 5. Functional topology of recruitment networks (RNs). Nodes represent species (except the Open node) and arrows point from the canopy to the recruit species. The toy example (inset panel) illustrates the types of functional roles of the nodes defined by the relationships between the strongly connected components (SCCs). In this toy example there are nine SCCs; only one of them (the core) is non-trivial since it is formed by four nodes, and the rest are trivial (i.e. formed by a single node each). There are two trivial SCCs corresponding to disturbance-dependent transients (they only receive arrows from Open node), two trivial SCCs corresponding to strict transient species (they do not receive any arrows) and three trivial SCCs corresponding to satellite species (they do not send any arrows). The examples of real RNs correspond to: SCBI which represents the typical RN of forests in humid regions (eastern mixed deciduous forest for North America), Cruz de Chimba which represents the RN of dryland forests (mediterranean pine-oak forest), Negro II representing a shrubland from humid regions (Andean alpine dwarf shrubland) and Uquía, which is a shrubland from drylands (Andean mountain desert).

the species. In RNs we can use the term "intransitive recruitment" to describe cases such as this: species A recruits under B, B recruits under C, and C recruits under A. Intransitivity is a network-level property that can explain species coexistence (Laird & Schamp, 2009, Alcántara *et al.*, 2017). Basically, replacement dynamics can be interpreted as the interchange of space between the populations of different plant species forming the local community. Thus, space "flows" between species under replacement dynamics, just like carbon or energy is interchanged between species or compartments in ecosystem models. The local population of a species can persist if the amount of space it receives (by its recruits replacing dead plants or growing in Open interspaces), compensates for the amount it loses due to death. Intransitive replacement implies a cycle in the interchange of space. Within a cycle, in the absence of disturbances, the flow eventually stabilises at a level where all species compensate exactly for their losses and can coexist stably at equilibrium. Besides, since the dynamics take place within a local community, the amount of space is limited, so the abundance of species in a cycle cannot go to infinity.

In the case of RNs, we can define five types of SCCs which play different functional roles. The "core" of the network is the largest non-trivial SCC. All species in the core must recruit, at least in the vicinity of another core species, and allow the recruitment of at least another core species. "Satellites" are non-core, trivial or non-trivial SCCs that can be reached from some core species, following the direction of the arrows. Most often, satellites are trivial SCCs integrated by a species that recruits in the vicinity of some core species but that does not show recruitment of any species in its vicinity. Thus, satellites either prevent the arrival of seeds under their canopy (e.g. small shrubs with dense branching; Perea *et al.*, 2021b) or suppress germination or seedling survival (e.g. by releasing allelopathic compounds; Thorpe *et al.*, 2009). Those SCCs that cannot be reached in the network from some core species are "transients". The node representing open space is considered transient under the assumption that, in the absence of disturbance, plants will eventually occupy all the space suitable for recruitment. Most often, transient species are trivial SCCs. We can distinguish two types of transients: "disturbance-dependent

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transients" are those that can only be reached from the Open node (i.e. species that only recruit away from established plants; for example, shade-intolerant species), while "strict transients" are those that cannot be reached from any other node (i.e. those that do not recruit in the studied local assemblage; for example, long-lived pioneer species in late successional stages; Rüger *et al.*, 2023).

Assuming that the dynamics of the system is linear and time-invariant (LTI dynamics), like in Markov models (Horn, 1975; Siles *et al.*, 2008), the set of species persisting in equilibrium can be determined as follows: all the nodes in the core SCC and those reachable from them (satellites) will persist (in the sense that their abundance would never become exactly zero), and the rest (transients) will eventually become extinct. This means that the presence of a large group of species recruiting intransitively (the core) can improve the probability of persistence of other species that recruit transitively with it (the satellites) (Alcántara *et al.*, 2017). To determine which species will persist, one can either find which species form the core and which are satellites or, more simply, one can count the number of non-zero values in the dominant eigenvector of the binary adjacency matrix of the RN (although this does not indicate if a species is core or satellite). When the dynamics are non-linear, these methods cannot be guaranteed to hold, but simulations have shown that the probability of persistence is higher and the time to extinction is longer for core and satellite than for transient species (Alcántara *et al.*, 2017). The sum of core and satellite species is a qualitative approximation for the number of species that can potentially persist. Alternatively, the proportion of transient species in the network (1–persistence), can be interpreted as the "extinction debt" of the community (Hanski & Ovaskainen, 2002; Kuussaari *et al.*, 2009), and represents the minimum proportion of species that would become extinct under the current environmental conditions once plants occupy all the space suitable for recruitment in the locality. Disturbance-dependent transients could persist if there are recurrent disturbances of sufficient spatial extent and short return time.

On average, the core of a local community involved 46.66% of its species (range: 3.92%–87.50%), there were 30.15% satellite species (range: 0.00%–91.30%), 11.00% strict transients (range: 0.00%–54.17%) and 12.18% disturbance-dependent species (range: 0.00%–70.59%). An average of 76.82% of the species would persist (range: 29.41%–100%). Although the assembly of canopy–recruit interactions in a local community shows the signal of the action of some deterministic processes, the precise outcome of the process of recruitment (i.e. how many recruits of a given species will finally be recruited under a given canopy species) is difficult to predict because it is subject to many stochastic factors. Therefore, we must contrast the observed functional structure of RNs against a null random model to assess whether it could be the realisation of a stochastic process. As in the analyses of nestedness and modularity, we used the fixed-fixed null model to this end. At first glance, one would expect that randomly assembled RNs should show any of the endless complex graph structures possible. However, in connected directed graphs assembled randomly, most nodes soon coalesce into a large (so called "giant") SCC as the mean degree increases, while the other nodes tend to remain as trivial SCCs (Karp, 1990). This is the type of structure we found, since almost all RNs (97.33%) had a single non-trivial SCC. The proportion of core and disturbance-dependent transient species did not differ from the null model expectation in, respectively, 86.88% and 100.00% of the RNs. However, 72.13% of the RNs had more satellite species and 63.93% had fewer strict transients than expected from the null model. The proportion of persistent species was higher than expected from the null model in 68.85% of the networks and lower in 21.31%.

Unlike what we found for nestedness and modularity, the functional structure of most RNs cannot simply be a consequence of heterogeneous degree distributions because it departs in some aspects from the fixed-fixed null model. Our results suggest that stochastic factors during recruitment contribute more importantly in shaping the number of both core and disturbance-dependent transient species. Conversely, the frequency of satellite and strict transient species departs from the null model, suggesting the action of deterministic factors driving their pairwise canopy–recruit interactions. Therefore, the high persistence inferred for most RNs would be the combined outcome of stochastic factors favouring a large core and deterministic factors increasing the frequency of satellite species and decreasing that of strict transients. Interestingly, while some studies suggest that plant–plant competitive interactions are seldom assembled intransitively (Godoy *et al.*, 2017; but see Bimler *et al.*, 2024), our results show that canopy–recruit interactions in the vast majority of plant communities studied contain a subset of species that recruit intransitively (a non-trivial core). If replacement dynamics is a good approximation to the real dynamics of plant communities, our results suggest that intransitive recruitment can be a widespread mechanism stabilising species coexistence.

(5) Exploring environmental gradients in the functional structure

Networks for which a core cannot be assumed (i.e. those with only trivial SCCs) were excluded from analyses because their SCCs cannot be classified into functional types. The final subset used in the study of environmental gradients included 94 networks. The functional structure of RNs is highly variable among communities, as indicated by the wide range of values in the proportion of the different functional elements. To explore how the different components of the functional structure vary along environmental gradients it is necessary to account for the intrinsic correlation between them (e.g. a network with a larger proportion of species in the core will necessarily have a lower proportion of other elements). This type of data requires compositional analysis. According to van den Boogaart & Tolosana-Delgado (2013), when the composition is based on a small total number of counts (number of species per RN in our case), the correct analysis

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should be based on the multivariate counts rather than on their transformation into proportions. Thus, we fitted multivariate models using a model-based approach to the analysis of multivariate abundance data (Warton, 2011), as implemented in the function "manyglm" of the R package *mvabund* (Wang *et al.*, 2012). The model included as dependent variables the number of core, satellite, disturbance-dependent and strict transient species in each RN, assuming they follow a negative binomial distribution. The independent variables were the type of vegetation (forest *versus* shrubland), aridity (1 – Aridity Index) and their interaction. To account for the different size of the RNs, we incorporated the logarithm of the number of nodes as an offset variable, which allows interpreting the results in terms of proportion of species of each functional type. To test the significance of effects we used the "score" option. Finally, we assumed an unstructured correlation matrix since the number of dependent variables ($N = 4$) was much smaller than the number of cases ($N = 98$).

The multivariate test (Table 4A) suggests that the functional structure varies with aridity, but the details of this variation depend on the habitat. To assess how the frequency of each functional role varied, we must carry out univariate tests (Table 4B, Fig. 6). The proportion of core species was higher in forests than in shrublands. It did not vary consistently with aridity in forests but increased sharply in shrublands so that the proportion became similar in both habitats when aridity reached its maximum. The proportion of satellite species was similar in forests and shrublands at the arid extreme of the gradient. However, as the climate becomes less arid, this proportion varies in opposite directions in each habitat, decreasing in forests and increasing in shrublands. The proportion of disturbance-dependent transients did not vary with aridity in shrublands but increased in forests. Finally, the proportion of strict transients did not vary with aridity in shrublands but decreased in forests, being more common in forests from humid climates.

The large proportion of core species and low proportion of satellite ones in forests could be related to the general amelioration of the microclimate provided by the tree canopies, which may enhance recruitment in general, so most plant species can easily recruit under most other plant species (Liancourt & Dolezal, 2021). In these conditions, species that would otherwise play the role of satellite can easily become core species. However, the proportion of core species increases in shrublands with increasing aridity at the expense of satellite species. Shrublands in humid environments can be very closed, so competition for light and water could be strongly limiting recruitment, resulting in an increased abundance of satellite species. However, as aridity increases, the shrublands become more open, and recruits rely more strongly on facilitation (Bertness & Callaway, 1994; see Section V.4), favouring the formation of larger cores. The results of Tüfekcioğlu & Tavşanoğlu (2022) point to the importance of shrub cover for recruitment, since they found twice as many seedlings in open shrublands than in closed shrublands of a Mediterranean ecosystem.

The abundance of strict transients in humid forests is remarkable. Species that appear in RNs as strict transients are typically those represented in the community by very few adult plants and that lack recruits in the locality. This may correspond to the life-history strategy of long-lived pioneer (LLP) species, whose populations persist due to their early arrival in tree-fall gaps, rapid growth and long lifespan, but that fail to recruit in the closed vegetation. LLP species can be dominant in many tropical forests (Rüger *et al.*, 2023), but it is not clear why fewer species would show this strategy as aridity increases. It seems that LLP strategy is associated with lower drought tolerance (Guillemot *et al.*, 2022), so they would become more scarce as aridity increases.

In general, the configuration of RNs favours the persistence of most species since, on average, the sum of core and satellite species represents 76.81% of species in a given

Table 4. Results of compositional analysis testing the variation in the number of core, satellite, disturbance-dependent transient and strict transient species with aridity and habitat type (forest *versus* shrubland). (A) Multivariate test of effects. (B) Univariate tests for each effect and the whole model, indicating Score values and associated *P* values in parentheses.

A

Effect	Score	*P*
Habitat (*H*)	74.40	<0.001
Aridity (*A*)	23.55	<0.001
H × A	28.47	<0.001

B

Functional role	*H*	*A*	*H* × *A*	Model	R^2
Core	15.132 (0.001)	0.051 (0.838)	11.001 (0.001)	18.757 (0.001)	0.19
Sat	48.746 (0.001)	11.454 (0.001)	24.564 (0.001)	27.384 (0.001)	0.42
ddTrans	1.878 (0.179)	3.790 (0.092)	4.362 (0.039)	4.266 (0.196)	0.03
StrTrans	3.528 (0.094)	12.816 (0.001)	6.056 (0.020)	25.582 (0.001)	0.29

Functional roles are indicated as Core, Sat (satellite), ddTrans (disturbance-dependent transients) and strTrans (strictly transient). The column R^2 indicates the variance in the observed frequencies explained by the model predicted values.

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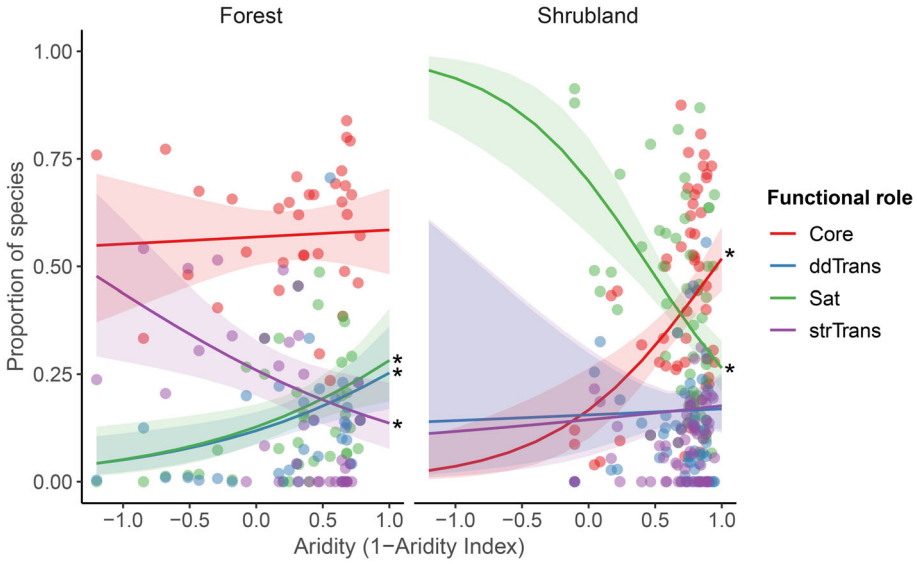

Fig. 6. Variation of the components of the functional structure with habitat (forest *versus* shrubland) and aridity. Lines are univariate fits to the data, with shadings indicating their 95% confidence interval. Functional roles are indicated as Core, Sat (satellite), ddTrans (disturbance-dependent transients) and strTrans (strictly transient). Functional roles whose relative frequency varied significantly with aridity are indicated with an asterisk.

community. This agrees with what could be expected in natural communities. If the species pool in natural plant communities has been filtered by the environment, we should find that most species should be able to persist. However, persistence increases with aridity in forests while it remains roughly constant in shrublands. In forests, most species form the core independently of the level of aridity, while the proportion of satellite species increases with aridity at the same pace as the disturbance-dependent species, but the proportion of strict transients decreases. Therefore, total persistence in forests increases with aridity due mainly to the strong filter that drought imposes on strict transient species. In the case of shrublands, the gradient of aridity induces a turnover between core and satellite species while both types of transients vary little, resulting in a roughly constant average persistence. Nevertheless, although the functional structure of RNs in shrublands would allow the potential persistence of most species, their configuration in humid climates is based on a very small core. This implies that the stability of the community may rely on just a few species. For example, the RN from Negro II (Fig. 5) has just 2 core species and 25 satellites. Any disturbance that affects these core species will have a strong impact on the community, transforming many satellites into strict transients, thus increasing the risk of extinction of many species.

Our results also suggest that shrublands in humid climates should be less stable than forests because these form a species-rich, more stable, core in these climates. Indeed, shrublands in temperate humid regions are most often the result of disturbance, and they typically revert to forests once disturbance ceases and succession advances. However, forests and shrublands can be considered also as alternative stable states under different disturbance regimes related, for example, to fire frequency, the abundance of large herbivores or changes in aridity (Baudena *et al.*, 2020; Pausas & Bond, 2020). It is possible that these disturbance regimes could be responsible for the contrasting differences in RN functional structure between forests and shrublands that experience similar levels of aridity, and that this reorganisation of the RNs could explain the different stability of these alternative states. This is a very interesting possibility that deserves theoretical analysis.

VI. FUTURE RESEARCH ON THE ECOLOGY OF RECRUITMENT NETWORKS

For brevity, we have deliberately obviated in this review the evolutionary aspects of canopy–recruit interactions, like the evolution of plant functional traits or the coevolution between plants and other organisms that mediate the interaction. Research on these aspects clearly deserves the attention of future studies. Focusing on ecological aspects of RNs, future studies should proceed in two main directions: (*i*) determining causal relationships between RN properties and plant community structure and dynamics; and (*ii*) determining the biotic and abiotic factors that drive the assembly of RNs.

(1) Causal relationships between RN properties and plant community structure and dynamics

For this objective, it is necessary to discern whether the structure of RNs provides valid predictions about species

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abundance, persistence or propensity to extinction in real communities, and informs on the stability and dynamic properties of the community. This requires a combination of theoretical and empirical studies (both experimental and observational) explicitly designed for this purpose. Integrating extensive empirical data in modelling and theoretical studies is fundamental for the advance of community ecology (Agrawal *et al.*, 2007). The network approach provides a direct way to feed complex mathematical models with data easily obtained from field studies to explore the potential consequences of changes in species or interactions for community dynamics and stability in realistic scenarios (Staniczenko *et al.*, 2017). As we showed in Section V.3, under linear dynamics, it is possible to obtain a qualitative approach to potential species persistence (Alcántara & Rey, 2012). In a more complex model, Alcántara *et al.* (2015) used data from RNs to explore how network structure modulates the response of a forest community to disturbance. This model requires information on vegetative growth rates of adults and recruits and death rates of adult plants, that can be inferred from allometric relationships between plant size and these rates across multiple species. The models proposed by Eppinga *et al.* (2018) or Miller & Allesina (2021) can also accommodate RN data and have an intermediate level of complexity, so they are likely amenable for exploring the dynamic and stability properties of multiple RNs.

Experimental validation of RN predictions should be possible using communities of short-lived herbs. One possible approach could start with a plant–soil feedback experiment (Brinkman *et al.*, 2010) where soil conditioned by each species is used to cultivate plants of all other species, so the frequency or probability of replacement of one species by another can be estimated to build the recruitment matrix. In a second step, using this matrix in a model of community dynamics, one can predict which species or subsets of them should be able to coexist (Pajares-Murgó *et al.*, 2024b). Finally, in a third step, it should be possible experimentally to cultivate different subsets of species to assess whether their persistence is properly predicted by the model.

Experimental approaches are more difficult in the case of communities dominated by long-lived plants. In such communities, the RN can be determined using standard observational methods (Alcántara *et al.*, 2019a), and predictions would be derived from theoretical models and validated with observational data. For example, it should be possible to assess whether species predicted to be excluded occur less often (are rare) in the community, or whether the subsets of species predicted to coexist actually do co-occur at a local scale more frequently than those predicted to be unstable.

(2) Understanding the factors driving RN structure

The other important direction in which RN studies can progress is in understanding the factors driving RN structure. Since the outcome of canopy–recruit interactions is influenced by interactions between plants and multiple organisms (e.g. mycorrhizal fungi, pathogens, seed dispersers, seed predators, herbivores), and by the abiotic environment (e.g. soil and climate), changes in both the biotic and abiotic environment can affect RN structure, with derived consequences for the structure and dynamics of the plant community. The role of biotic factors can be dissected experimentally through the controlled addition or removal of organisms. For example, plant–soil feedback experiments can explore the role of different components of the soil community on recruitment (Klironomos, 2002; Perea *et al.*, 2023). Field experiments can use seed addition and exclusion treatments to assess the role of seed dispersal limitation, fungi, granivores or herbivores on canopy–recruit interactions (Rey, Ramírez & Sánchez-Lafuente, 2006; Aicher, Larios & Suding, 2011; Luo, He & Yu, 2013). A third way to explore the role of different organisms on RNs is a multilayer approach. Observational studies can be used to build RNs and networks of interactions between the same plant species and different organisms. For example, Garrido *et al.* (2023) connected the RN to the plant–AMF (arbuscular mycorrhizal fungi) network in two forests from southern Spain and found that the frequency of canopy–recruit interactions was higher between plant species that associated with more similar communities of AMF, and that canopy service and abundance in the recruit bank varied with the number of AMF associated with each plant species.

The role of abiotic factors on canopy–recruit interactions can be also assessed experimentally by manipulating factors such as light, water and nutrient availability or temperature, but plant responses to these factors can be frequently mediated by their interactions with other organisms. For example, water and nutrient acquisition can be modulated by mycorrhizal fungi and mutualistic bacteria. Thus, rather than isolating the effect of an abiotic factor on canopy–recruit interactions, experiments should aim at understanding how abiotic factors interact with other organisms to affect canopy–recruit interactions (Verwijmeren *et al.*, 2019). Observational approaches can also be used, as we have shown here in the case of aridity. Besides exploring general gradients of variation in canopy–recruit interactions, it will be interesting to explore how individual canopy–recruit pairs, or different aspects of the canopy service, recruitment niche and recruiting bank of particular species, vary along such gradients. For example, it should be possible to fit functions of variation in the frequency or efficiency of the interactions with aridity to predict the response of canopy–recruit interactions and RNs to the aridity levels projected by climate change models.

VII. CONCLUSIONS

(1) The observational study of most types of ecological networks (e.g. plant–pollinators, plant–seed dispersers, host–parasite, predator–prey) requires a very high sampling effort to obtain a robust estimate of the network. This is not the case for RNs, especially in the case of woody plants, since recruits

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can be monitored and quantified at any time and are more easily surveyed than elusive interacting animals. Accordingly, analysis of link coverage in the RecruitNet database shows that reaching values above 0.9 is often possible, so the properties of the network can be estimated very accurately.

(2) The frequency of canopy–recruit interactions is a basic aspect of plant community demography. Our results based on this population-level parameter contrast with findings in classic studies that measure the effect of the interaction on individual fitness (usually plant growth or reproductive output). While these studies tend to find a prevalence of competitive outcomes in plant–plant interactions, our results show that, at the population level, canopy–recruit interactions are driven primarily by stochastic (neutral) processes, and when there is a deterministic (non-random) effect of the canopy species on recruitment, the probability of this effect being positive is five times higher than being negative. Moreover, positive canopy–recruit interactions are stronger than negative ones. These results challenge the prevailing view of competition as the dominant force structuring plant communities. Although competition may dominate other aspects of plant demography (such as growth and fecundity), our results strongly suggest that facilitation is critical for recruitment in natural plant communities.

(3) The sign of plant–plant interactions during recruitment is known to become more positive as aridity increases (the stress gradient hypothesis). Studies to date have focused on altitudinal gradients or particular vegetation types. Our results show that this aridity gradient exists worldwide across different types of vegetation, from tropical to temperate forests, and from desert to alpine shrublands. Thus, the demography of plant communities is increasingly dependent on facilitation as aridity increases, a trend that deserves attention under ongoing climate change, particularly in climatic regions where plant species lack traits to recruit under arid conditions.

(4) Unlike most other ecological interaction networks, the pattern of nestedness or modularity in RNs does not differ from the expectation based on a null model. The null model that we used (with fixed row and column sums) could be considered too stringent, but it guarantees that the simulated networks have exactly the same in- and out-degree distribution as the observed networks. Thus our results agree with studies showing that, in RNs, these network properties could be a by-product of processes that give rise to heterogeneous degree distributions. For example, preferential linkage, whereby certain canopy species provide much better canopy service, could explain the similarity observed in the degree distribution of the largest networks of the RecruitNet database to the distribution expected according to power law.

(5) The analysis of the functional structure of RNs provides a first, rough, qualitative, approach to species persistence. A more detailed approach should make use of fully parameterised theoretical models. Assuming that replacement dynamics is a good approximation to the dynamics of real plant communities (as most theoretical studies do), our results suggest that the functional structure of RNs can allow the coexistence of most plant species. This structure is not the simple result of stochastic processes of assembly of canopy–recruit interactions and, in most of the studied communities, contains a subset of species that recruit intransitively. Thus, our results suggest that intransitive recruitment can be a widespread mechanism stabilising species coexistence in plant communities.

(6) The functional structure of RNs varies with aridity, but the pattern of variation is not the same in forests and shrublands. Interestingly, variation of RN structure with aridity in shrublands has a buffering effect on persistence, which remains largely constant along the gradient. However, forest RNs change in a way that increases potential persistence as aridity increases. The different structure of RNs between forests and shrublands could contribute to explain their co-occurrence as alternative stable states of the vegetation under the same climatic conditions.

(7) In this study we have tried to show how the concept of RNs can provide an integrative framework for a large part of the field of plant community ecology. The present review is not exhaustive regarding the many topics that RNs could help address on plant community structure and dynamics. Moreover, we have applied a few basic analytical tools available in the field of network ecology, so there is plenty of room for further analyses. Our objective here has been to explore some of the simplest but interesting among these topics. We have only scratched the surface of possibilities of the RN approach, and yet we have shown that it provides insights on many aspects of plant community ecology that currently proceed independently: from the ecological underpinnings of canopy–recruit interactions to the functional roles of species on community dynamics or the empirical evaluation of mathematical arguments that explain species coexistence.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Choice of interaction strength index.
Fig. S1. Frequency distribution of $NInt_A$ and $NInt_C$ in the RecruitNet database ($N = 350{,}095$ canopy–recruit pairs).
Table S1. Indices that can be used to measure interaction strength in studies of plant–plant interactions.
Appendix S2. Relationship between interaction strength indices and chi-squared statistic.
Appendix S3. Analyses of variation in interaction strength (N_s).
Fig. S2. Frequency distribution of N_s index in the RecruitNet database ($N = 350{,}097$ canopy–recruit pairs for which N_s could be estimated).
Fig. S3. Trace plot and posterior distribution for the intercept term, which is the global mean N_s after controlling for variation among species (canopy and recruit species) and among study sites through a Bayesian model: 0.126.
Table S2. Results of a Bayesian model estimating the global mean of interaction strength (N_s).
Table S3. Estimated means for significant effects found in the analysis of Table 1.
Table S4. Results of Bayesian model testing for variation of N_s along successional stages.
Appendix S4. Testing the fit of degree distribution.
Table S5. Fit of degree distributions to the Wanang recruitment network.

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