nature ecology & evolution

Article

https://doi.org/10.1038/s41559-025-02766-9

Indirect reciprocal facilitation promotes species coexistence in plant communities worldwide

Received: 12 September 2024

Accepted: 20 May 2025

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Plant–plant facilitation is key to supporting species persistence within communities. However, as beneficiary species mature and compete with their benefactors, competition appears to dominate, suggesting that facilitation has a limited role in long-term community structuring. Here, we propose that facilitation can consistently enhance diversity when it occurs reciprocally between interacting species. Leveraging spatial associations between recruits and canopy species to infer recruiting interactions, we analyse a global dataset of 96 plant community recruitment networks, encompassing 2,403 non-transient populations across 23 countries. We show that ~90% of facilitation events were reciprocated, primarily mediated by intermediary species that transmit benefits through indirect facilitation loops, ultimately returning these benefits to the original benefactors. We find stronger positive effects within longer facilitation loops coupled with fewer negative interactions, which are essential conditions for benefactors to receive increased returns and, consequently, for the long-term persistence of indirect reciprocal facilitation. A positive empirical relationship between indirect reciprocity and species richness, substantiated by numerical simulations, indicates that these conditions also foster species coexistence. Our findings highlight the underappreciated role of indirect reciprocal facilitation in maintaining biodiversity.

The concept of ‘struggle for existence’ has profoundly influenced research in ecology and evolution hitherto. As such, our understanding of species coexistence remains deeply entrenched in the foundational perspective that views competitive exclusion within resource-limited environments as the primary mechanism structuring biodiversity[1]. However, the empirical prevalence of species-rich communities has consistently challenged the expectations of this winners-take-all paradigm, giving rise to a notable contradiction known as the diversity paradox[2]. If ecological success relies on efficient resource exploitation, leading to the exclusion of weak competitors, what accounts for the widespread occurrence of species-rich communities?

Among the mechanisms that have been proposed to reconcile this contradiction, facilitation emerges as a widely recognized assembly process which fosters the local persistence of species that might otherwise be excluded from the communities[3–6]. Facilitative interactions are particularly numerous and well-documented in plant communities, especially those governing recruitment dynamics between benefactors (referred to as nurses) and beneficiary species (facilitated seedlings or saplings). However, nurse–recruit interactions can eventually shift to competition as beneficiary recruits mature and compete for resources with their nurse benefactors[7], thus supporting the prevailing notion that facilitation entails a strong fitness cost for benefactors[8].

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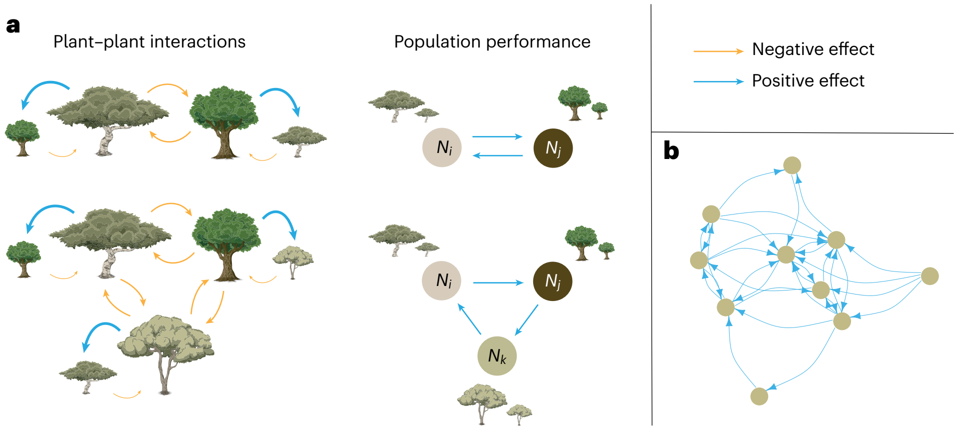

Fig. 1 | Conceptual model for direct and indirect reciprocal facilitation. **a**, The top-left scheme depicts two nurse plants of distinct species (represented by larger icons) alongside one recruiting individual of either species (smaller icons). While plants of either species can negatively impact each other through competition (orange arrows, with their width representing the intensity of the effect), these negative effects can be offset by a stronger positive influence from nurse plants on the recruits of competing species (blue arrows), thereby enhancing their recruitment rate. These individual interactions collectively generate a direct reciprocal positive effect between populations N_i and N_j (top-right scheme), which promotes species coexistence in the community. The bottom schemes depict a similar scenario, but in this case the benefit of nursing the recruits of the competing species returns indirectly through a third intermediary species. **b**, A real facilitation network within a Mediterranean oak forest in Spain, where each circle represents a population of a different species (based on data from the present study). For enhanced visualization, negative effects were omitted.

Consequently, facilitative interactions are deemed to play a minor role in the long-term structuring of communities relative to competition[9–11]. However, facilitation could act as a stable strategy governing the assembly of communities and enhancing diversity when broadening our perspective to the benefit obtained by the recruits of nurse plants. In this context, the fitness cost incurred by nurse individuals of a species in facilitating recruits from another species can be offset if the recruits from the former are, in turn, facilitated by the mature beneficiaries of the latter. This reciprocal benefit can manifest through direct pairwise interactions, or as an integral component of multispecies cascades featuring loops of indirect facilitations—in accordance with the notion that 'the friend of my friend is my friend' (Fig. 1). It is important to note that while facilitation is a well-established mechanism in ecological succession[12], reciprocal facilitation can operate independently of the successional context. Successional processes typically involve unidirectional facilitation, where early-successional species benefit late-successional ones as communities progress through stages[13]. In contrast, reciprocal facilitation enables immediate, circular interactions among species within established communities[14].

Here, we evaluated the prevalence of reciprocal facilitative interactions using a global dataset comprising 96 woody plant recruitment networks in 23 countries across five continents, including 1,626 species[15]. Each network represents a community wherein the species significantly facilitating the recruitment of others, known as 'nurses', were identified, and the corresponding number of recruits was quantified. We inferred nurse–recruit interactions on the basis of patterns of recruit abundance beneath and outside the canopy, following a widely used approach[16–19]. The use of this approach to infer these interactions is supported by three key factors. First, canopy individuals can modify the microhabitat beneath them, creating distinct microclimatic conditions compared to the surrounding environment[20,21] that influence recruit establishment[22–24]. Canopy plants modify not only the microclimate beneath them but also shape the soil and structural microenvironments, influencing plant recruitment through plant–soil feedbacks[25–27], providing perches to seed-dispersing birds[28] and protecting recruits against large herbivores[29]. Second, because adult plants typically establish before recruits grow beneath their canopy[20], and because interactions between them are generally asymmetric, causal relationships are expected to be directional, with canopy cover influencing recruit abundance rather than the reverse. Finally, these asymmetries suggest that the presence of heterospecific recruits under the canopy has little effect on recruit abundance through indirect interactions with nurse–recruit dynamics. Although recruitment is a key stage in the plant life cycle, we emphasize that the spatial associations inferred between adult and recruit individuals are not direct indicators of long-term outcomes of species interactions. Rather, our focus is on detecting patterns of reciprocal facilitation during recruitment, which we argue can play a central role in sustaining biodiversity and shaping community structure over time—even if facilitative interactions eventually shift to competition as beneficiaries mature (Fig. 1).

Results and discussion

We found that the vast majority of non-transient populations (that is, inclusive of both adults and recruit individuals within a given local community; $n = 2,403$) significantly facilitated at least one distinct species and recruited under the canopy of at least one other species, thus playing a dual role as benefactors and beneficiaries (Fig. 2a). Remarkably, >90% of these populations experienced reciprocal benefits (Fig. 2a). Moreover, this pattern is reflected at the interaction level, with 86.7% of all facilitation events reciprocated (bootstrapped 95% confidence interval (CI) 61.26–93.24%). A facilitation event can be reciprocated through multiple loops within the network, involving different numbers of intermediary species (with a minimum of zero if the facilitation event is directly reciprocated; Supplementary Fig. 1). However, shorter loops should arguably reduce the potential for disruptions or delays in the reciprocity process, thereby increasing its reliability and predictability. Taking this into account, we focused on the shortest available loop and found that indirectly reciprocated facilitation events (those where the shortest loop involved at least one intermediary species) were more prevalent (72.9%, bootstrapped 95% CI 43.7–79.6%) compared to those directly reciprocated (13.9% [11.4–22.5%]). The number of intermediary species encompassed along the shortest loops was low, with either one (46.8 % [36.8–60.3]) or two (40.8% [30.4–43.1]) species in most cases (Fig. 2b). Finally, most of the communities featured at least one reciprocal facilitation event (58.3% [49.9–68.7%]), and the average proportion of these events relative to the total number of facilitation events within these communities—degree of reciprocity—was rather high (mean 51.1% [43.9–57.8%], Fig. 2c). Overall, these findings demonstrate the widespread occurrence of reciprocal facilitation, particularly its indirect form, across plant populations and communities.

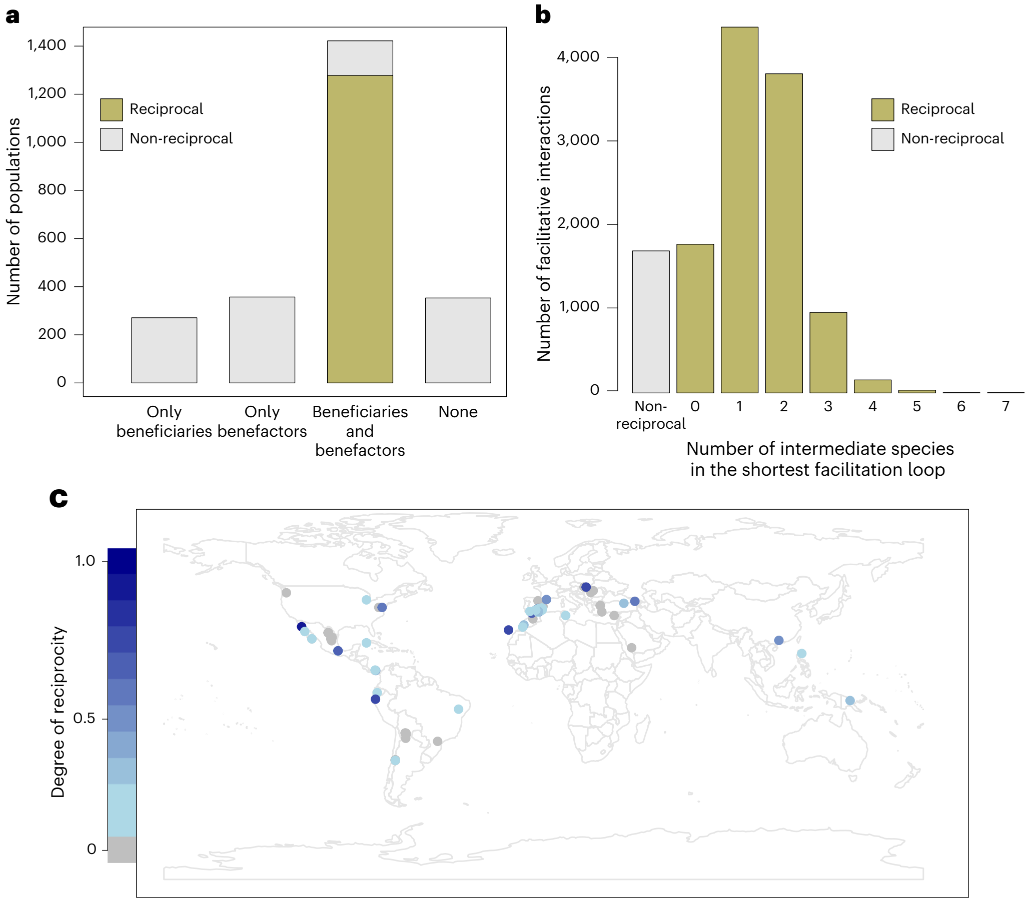

Fig. 2 | Reciprocal facilitation is a prevalent characteristic of plant populations and communities. a, Most populations in the dataset acted as both benefactors and beneficiaries, and the majority of them experienced reciprocal benefits. **b**, Most reciprocal facilitation events involved only one or two intermediary species when considering the shortest available loop reciprocating them within the networks. **c**, Reciprocal facilitation was also frequent at the community level, with most communities showing a large proportion of reciprocal facilitation events relative to the total number of facilitation events within them (degree of reciprocity).

The high prevalence of indirect reciprocal facilitative interactions within plant communities poses a challenge to explain their long-term persistence. We envision two conditions for this type of interaction to assemble and become evolutionarily stable through the enhancement of the benefit returned to the benefactors. First, the strength of recruiting interactions within indirect reciprocal facilitation loops should be strong enough to ensure the transmission of the benefits derived from the act of nursing. Should benefactor populations receive only minimal benefits from their beneficiaries (either directly or indirectly), they would experience selective pressures to discontinue the 'chain of favours' and thus evade the fitness cost associated with acting as nurses. Given the arguably increased likelihood of benefit-transmission disruptions within longer facilitation loops, we anticipate a positive correlation between the average number of species serving as intermediaries in reciprocating benefits and the average strength of positive recruiting interactions. Second, in line with the theory of reciprocal altruism[30], greater returned benefits should lead to reduced selective pressure for benefactor populations to act as strong competitors within facilitation loops. If benefactors were to outcompete intermediary species responsible for transmitting facilitation benefits within a facilitation loop, they would ultimately receive fewer or no benefits from acting as nurses. Therefore, we anticipate a reduction in negative interactions within facilitation loops, so that interferences in the transmission of benefits become mitigated.

Consistent with our expectations, we found a strong positive correlation between the average number of species serving as intermediaries in reciprocating benefits and the average strength of positive recruiting interactions ($R^2 = 0.32$, $P < 0.001$; Fig. 3a). Additionally, the empirical probability of benefactors engaged in indirect facilitation loops to exhibit negative recruiting interactions with other species within the same loop was significantly lower than expected by chance ($V = 51{,}795$, $P < 0.001$; Fig. 3b), further supporting the requisite essential for the stability of indirect reciprocal facilitative interactions: the enhancement of the benefit returned to the benefactors. These findings would explain the high prevalence of indirect reciprocal facilitation within the communities, suggesting that the structure of facilitation networks is not merely transitory. Instead, they might have been reinforced over time due to genuine selective pressures guiding individuals towards strengthening facilitative interactions and avoiding competition[30].

The underlying mechanisms sustaining reciprocal facilitation in recruitment networks should align with those fostering species diversity. In this way, reduced negative interactions and strengthened facilitation are likely to lead to low rates of local extinction within communities, thus allowing the persistence of a higher number of species than expected under the competitive exclusion principle[31,32]. Supporting this notion, the degree of indirect reciprocity was a good predictor of species richness ($R^2 = 0.72$, $P < 0.001$; Fig. 4a). This effect remains consistent regardless of other potential predictors, including sampling extent (total sampled area) and methodology, current and past climates and network connectance (Supplementary Appendix 2). Moreover, it holds true even after accounting for the greater likelihood of having more reciprocal facilitations in species-rich communities by

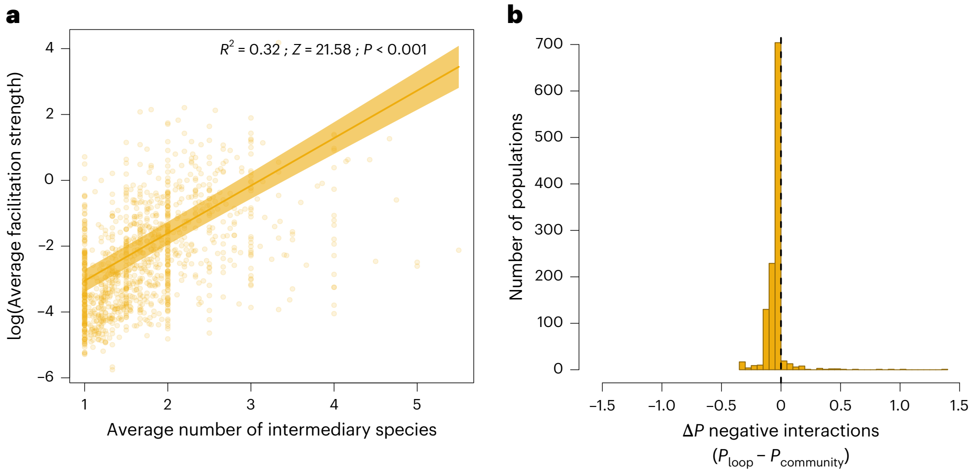

Fig. 3 | Reciprocal facilitative recruiting interactions are stronger in longer facilitation loops, where negative interactions are unlikely to occur. a, The relationship between (i) the average number of intermediary species involved in the shortest loops that indirectly reciprocate each facilitation event initiated by a benefactor species (one loop per event) and (ii) the average strength of the positive recruiting interactions closing the loops (log-transformed), where the said benefactor species acts as beneficiary. The strength of each recruiting interaction was computed using the NII as it is described in Methods. The shaded area around the trend line represents the 95% CI of the predictions (see also Extended Data Fig. 1). **b**, The difference between the empirical probability of observing negative recruiting interactions within indirect facilitation loops (P^{loop}) and the empirical probability of observing such interactions in the corresponding communities ($P^{community}$). Probabilities were arcsine-transformed solely for graphical presentation.

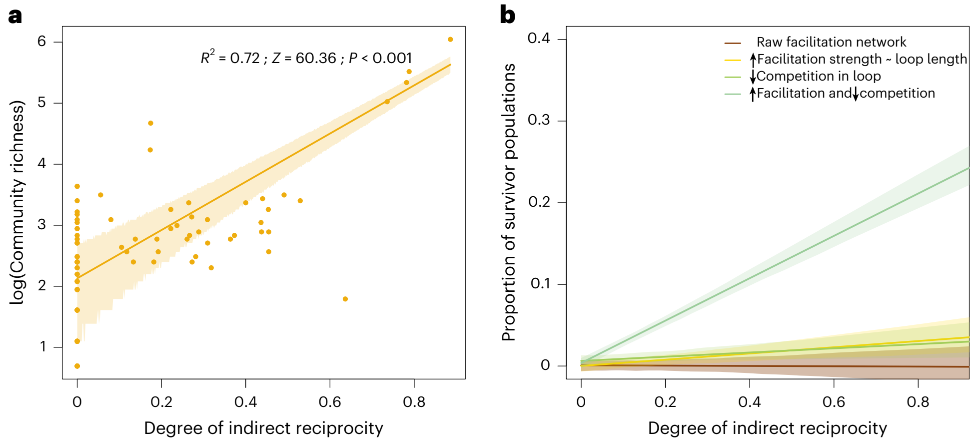

Fig. 4 | The degree of indirect reciprocity as a predictor of biodiversity. a, Relationship between the degree of indirect reciprocity and species richness (log-transformed) in the communities. The shaded area around the trend line indicates 95% bootstrapped CIs for the predictions. The relationship was assessed with a generalized linear model, assuming a Poisson error family and a log link function. The goodness-of-fit of the model was evaluated using the pseudo-R^2 by McFadden. **b**, This relationship is supported in multispecies generalized Lotka–Volterra models, contingent upon the fulfilment of the two conditions for the stability of indirect reciprocal facilitative interactions: (i) stronger facilitative effects within longer facilitation loops and (ii) a lower probability of negative effects on intermediary species within facilitation loops. The panel depicts the relationship between the simulated survival fraction of species (response variable) and the observed degree of indirect reciprocity in interaction with four distinct simulated scenarios (explanatory variables), while accounting for community identity as a random effect. The shaded areas around the trend lines indicate 95% CIs for the predictions. The inset legend maps trend lines to simulation scenarios: raw facilitation network (scenario 1), increased facilitation strength ~ loop length (scenario 2), decreased competition in loop (scenario 3) and increased facilitation and descreased competition (scenario 4) (Methods; Supplementary Appendix 8 gives robustness analyses of parameter selection).

mere chance (Supplementary Appendix 2) or when considering the biome of each community (Supplementary Appendix 3).

To conclusively validate the role of indirect reciprocal facilitative interactions in community assembly and biodiversity maintenance would require direct observations of how these interactions affect species performance, which is unfeasible in natural, globally distributed, species-rich plant communities. Hence, we used dynamic simulations based on the observed facilitation networks to provide additional evidence on how the underlying mechanisms contributing to the prevalence of indirect reciprocal facilitative interactions enhance species coexistence under a generalized competitive scenario. Our simulations predicted an increase in population survival rate (and consequently, an increase in species richness) with the degree of indirect reciprocity in the communities, reflecting the pattern observed in real-world communities. However, this positive relationship is only attained when facilitation is more heavily returned in longer loops or under a sustained lower probability of competitive interactions within facilitation loops (Fig. 4b). Furthermore, the combination of both processes yielded the strongest reciprocity–survival relationship. In sum, simulations show that the two conditions conducive to the enhancement of the benefit returned to the benefactors through indirect reciprocal facilitations synergistically promote species diversity at the community level, thus forging a crucial connection between the evolution of indirect mutualism and the maintenance of biodiversity[30].

Our approach leverages recruit counts beneath adult canopies and in open gaps to gain insights into recruitment dynamics. However, some significant effects may still be attributable to shared microenvironmental preferences between adults and recruits, interactions among recruits or statistical artifacts resulting from multiple comparisons, rather than representing genuine canopy-driven effects on recruitment. Thus, we tested the robustness of our findings by reanalyzing the data, randomly removing 5%, 10%, 20% and up to 30% of significant nurse–recruit associations per community, assuming that these were driven by factors unrelated to the true canopy effects. Our results remained consistent both qualitatively and quantitatively, even under stringent and unlikely assumptions (Supplementary Appendix 4), demonstrating that the reported findings on reciprocal facilitation are robust to detection uncertainties and reinforcing the validity of our conclusions. Nonetheless, we acknowledge that experimental assessments remain the only definitive way to unequivocally determine nurse–recruit interactions. Moreover, future research could also explore how facilitation-related traits—such as root system, leaf economic spectrum, canopy shape and seed and fruit characteristics—evolve to shape nurse–recruit reciprocal interactions[33], whether these interactions are modulated by species diversity under the canopy[34], and if they are generalizable to other non-woody plant communities and across different trophic levels.

Over the past century, ecologists have grappled with comprehending the prevalence of species-rich communities within a conceptual framework anchored in the competitive exclusion principle[35,36], and most proposals aimed at resolving the ensuing diversity paradox stem from this competition-centric perspective[37,38]. Our research on plant recruitment interactions suggests that the emergence of facilitative synergies among potential competitors should also be considered. The findings support the idea that competition is not necessarily the primary force governing species coexistence[37,39–41], suggesting that reciprocal facilitative interactions could be a widespread mechanism underlying long-term community structure.

Methods

Recruitment data

We compiled our dataset from RecruitNet, a global database of plant recruitment networks spanning temperate and tropical biomes[15]. Details can be found in the supplementary material of ref. 15, with a comprehensive explanation of the sampling methods provided by ref. 42. Each network in the database delineates a community wherein the canopy species under which another species recruits is identified. The plots used to delineate the communities (median $N = 8.5$; bootstrapped 95% CI 4–16) were established in locations selected for their homogeneity in macroenvironmental conditions, ensuring consistency and minimizing the potential influence of external factors on co-occurrence patterns between canopy species and recruits. Plot sizes (median 500 m^2; bootstrapped 95% CI 258.04–600 m^2) were adjusted according to the specific characteristics of each community to accurately capture recruitment dynamics. Sampling was conducted following one of the three protocols described previously[15]. Although these protocols differ procedurally, they ultimately yield the same type of information: the exact number of recruits of each species growing beneath each canopy species and in open gaps, along with the cover of canopy species and the proportion of open gaps. Recruits were defined as young, non-reproductive individuals that are typically less than one-fourth the size of a fully grown adult of the species[42], and canopy individuals (nurses) were those more directly conditioning the microenvironment of the recruits (see ref. 15 and references therein for further methodological details).

The total number of adult and recruit individuals of a species observed in a community constitutes a population. We focused on populations of woody plant species because, while herbaceous plants are often facilitated by woody species, they are unlikely to substantially influence the recruitment of woody plants due to structural limitations (herbaceous plants rarely have a canopy that modifies the macroclimate). Moreover, we focused on non-transient populations that include both adults and recruits, as they form the stable core of the communities (median plant cover 99% and percentage of recruits 98%). Transient populations, comprising only adult or recruit individuals but not both, cannot simultaneously act as benefactors and beneficiaries within their communities, yet they still count towards species richness. Nevertheless, species richness based solely on non-transient populations was highly correlated with species richness that included both transient and non-transient populations (Pearson $r = 0.99$). Moreover, our results remained highly consistent even when both herbaceous and transient populations were included in the analyses (Supplementary Appendix 5).

Our final dataset comprised 96 woody plant recruitment networks in 23 countries across five continents, including 2,403 non-transient populations from 1,626 species. Facilitative interactions, particularly those related to recruitment, are typically reported from arid and semi-arid environments[43]. Accordingly, our dataset included a greater representation of communities from Mediterranean regions (42), along with 18 from dry deserts, 20 from temperate areas and 16 from tropical latitudes. Nevertheless, our results remained consistent even after accounting for the uneven representation of biomes (Supplementary Appendix 3).

Inference of positive or negative canopy effects on recruits

We used chi-square goodness-of-fit tests to evaluate the impact of canopy species (nurses) on recruiting species, differentiating between positive and negative effects. Specifically, we tested whether the observed number of recruits of species j growing under the canopy of i and in open gaps deviated from the expected frequencies, given the canopy cover of i and the proportion of open gaps within each community[19]. A higher-than-expected number of recruits of j growing under the canopy of i indicated a positive impact of i on j (canopy-enhanced recruitment, namely a facilitation event) and, conversely, a lower-than-expected number of under-canopy recruits was interpreted as evidence of negative effects (canopy-suppressed recruitment). All P values were computed using Monte Carlo simulations ($n = 2{,}000$ replicates) and statistical significance was assessed at a 5% nominal alpha.

Facilitation network construction and measures of reciprocity

To measure reciprocal facilitation, we constructed a weighted, unipartite and directed network of significant positive recruiting interactions per community. In these networks, species in each community are depicted as nodes and the links (arrows) represent facilitation events, indicating which species (benefactors, origin of the arrows) enhances the recruitment of another (beneficiaries, arrowheads). We characterized reciprocal facilitation within each network across three distinct levels of biological organization: interactions, populations and communities. At the interaction level, we used the breadth-first search algorithm from the igraph R package[44] to determine the minimum number of intermediary species required for a facilitation event, initiated by a benefactor species i, to be reciprocated. The minimum number of intermediary species is zero if species j recruits under the canopy of i and vice versa, in which case both facilitation events are directly reciprocated (as in top-right diagram of Fig. 1a). However, if one or more intermediary species k are required to reciprocate a facilitation event initiated by benefactor i, so that i facilitates j, j facilitates k_1, k_1 facilitates k_m and k_m closes the loop facilitating i (with m being the total number of intermediary species in the loop), the facilitation event from i to j is indirectly reciprocated (as in bottom-right diagram of Fig. 1a).

To characterize reciprocal facilitation at the population level, we computed the number of populations engaged in at least one reciprocal facilitation event. At the community level, we calculated the degree of reciprocity by determining the percentage of reciprocal facilitation events relative to all facilitation events within the communities. Additionally, we calculated the degree of indirect reciprocity by determining the percentage of indirectly reciprocated facilitation events relative to all facilitation events.

Strength of facilitative interactions and number of intermediary species

We tested the hypothesis that facilitation events are more strongly returned as the number of intermediary species encompassed along the shortest available loops reciprocating them increases. For this, we first developed an index (nursing intensity index, NII) to quantify the strength of significant positive recruiting interactions (facilitation events):

$$\mathrm{NII}_{ij} = \frac{R_{ji}}{C_i} - \frac{R_{j\text{-open}}}{C_{\text{open}}}$$

where R_{ji} is the fraction of recruits of species *j* under the canopy of *i*, C_i is the canopy cover of *i*, $R_{j\text{-open}}$ is the fraction of recruits of *j* growing in open gaps and C_{open} is the proportion of open gaps in the community. High values occur when most recruits of species *j* grow under the cover of a scarce canopy species *i* and fewer recruits of *j* grow in prevalent open gaps. Conversely, the index yields low values when recruits of *j* predominantly grow in limited open gaps and the canopy cover of species *i* is high.

We fitted a generalized linear mixed model with a Gamma error family and a log link function, relating (1) the average number of intermediary species encompassed along the shortest loops indirectly reciprocating the facilitation events provided by species *j* (fixed effect; Supplementary Fig. 1) and (2) the average strength of the positive recruiting interactions closing the loops, where said species *j* acted as beneficiary (response variable). Thus, directly reciprocated facilitation events (those involving no intermediary species in the shortest loop returning the benefit) were excluded from this analysis. Nonetheless, including directly reciprocated facilitation events provided very similar results (Extended Data Fig. 1). Since some species occurred in multiple communities, both the identity of the species and the communities in which they occur were included as random factors. The model was fitted using the glmmTMB R package[45] and a marginal R^2 was computed as outlined previously[46] and implemented in the MuMIn R package[47]. To verify the robustness of the results obtained from this model in the presence of outliers, we identified extreme values as those below the 5th percentile or above the 95th percentile in a simulated distribution ($n = 1{,}000$) generated from the model fitted to the full dataset using the DHARMa R package[48]. After excluding these values, the analysis yielded consistent results (Supplementary Appendix 6).

Negative recruiting interactions within indirect facilitation loops

We tested the hypothesis that benefactor species exhibit a reduced tendency to interact negatively with recruiting individuals of the intermediary species encompassed along the shortest loops indirectly reciprocating the facilitation events initiated by said benefactor species. To assess this, we tested whether the empirical probability of observing such negative interactions was lower than the empirical probability of observing negative recruiting interactions between any pair of species in the community. The probability of a negative interaction from benefactor *i* to intermediary species *k* in facilitation loop *l* was calculated as:

$$P_i^l = \frac{l_k^{\text{neg}}}{N_k}$$

where l_k^{neg} is the number of significant negative interactions from benefactor *i* to any intermediary species *k* in loop *l* and N_k is the number of intermediary species *k* in loop *l*. Note that P_i^l is not computable for facilitation events involving no intermediary species in the shortest loop returning the benefit (when $N_k = 0$). Therefore, directly reciprocated facilitation events were excluded from this analysis. Then, we estimated the probability of a negative recruiting interaction between any pair of species in the community *k* as:

$$P_k^{\text{community}} = \frac{l_{\text{neg}}}{N \times (N-1) - l_{\text{pos}}}$$

where l_{neg} is the number of significant negative recruiting interactions in community *k*, *N* is the number of species in the community and l_{pos} is the number of significant positive recruiting interactions in the community. We subtracted the number of positive interactions in the denominator because positive and negative interactions are inferred from the same statistical test (chi-square goodness-of-fit) and therefore it is impossible for a species to simultaneously establish a positive and a negative link towards the same species. Nevertheless, the results remain unchanged even without subtracting the number of positive interactions (Supplementary Appendix 7). We then computed the average P_i^l for each benefactor species examined in the community and compared it with $P_k^{\text{community}}$ using a paired Wilcoxon test under the alternative hypothesis that the averaged P_i^l was lower than $P_k^{\text{community}}$.

Numerical simulations

We used a phenomenological model of community dynamics to elucidate how reciprocal facilitation contributes to maintaining biodiversity amidst competitive interactions. Our approach involved a system of ordinary differential equations derived from a multispecies generalization of the Lotka–Volterra model as previously described[6]. Through simulations, we examined how the abundance N_i of each species *i* within a community, consisting of *S* species, is influenced by the presence of any other species *j*:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i r_i \left(1 + \sum_{j}^{S} \alpha_{ij} N_j\right)$$

where r_i represents the intrinsic growth rate of species *i* and α_{ij} is the net influence of species *j* on the abundance of *i*. This net influence was calculated by subtracting the competitive effect of species *j* on species *i* ($\alpha_{ij}^{\text{competition}}$) from the facilitative effect ($\alpha_{ij}^{\text{facilitation}}$), so that $\alpha_{ij} = \alpha_{ij}^{\text{facilitation}} - \alpha_{ij}^{\text{competition}}$. Therefore, if $\alpha_{ij} < 0$, species *j* exerts a negative net influence on the abundance of species *i*. Conversely, if $\alpha_{ij} > 0$, species *j* exerts a positive net influence on the abundance of species *i*. At the beginning of the simulations, the population size *N* for all species in the community was set to 1.

We parametrized a specific model for each of the 96 communities surveyed in the study. To do so, we first developed a square matrix with simulated pairwise facilitative effects per community *k*, where $\alpha_{ij}^{\text{facilitation}} \neq 0$ only if species *j* significantly facilitated species *i* in the real-world community *k* and $\alpha_{ij}^{\text{facilitation}} = 0$ otherwise. Similarly, we created a square matrix with simulated pairwise competitive effects, assuming a default setting of generalized competition where any species can exert a negative effect on the growth of any other species ($\alpha_{ij}^{\text{competition}} \neq 0$ with a 0.95 probability). Thereby, a net influence matrix was derived by subtracting the $\alpha_{ij}^{\text{competition}}$ matrix from the $\alpha_{ij}^{\text{facilitation}}$ matrix. We set intrinsic growth rates r_i by sampling from a uniform distribution spanning the lower to the upper bounds of the 95% CI around the geometric mean (0.85, s.d. = 10.79) of the empirical distribution of intrinsic growth rates (one empirical distribution for the entire set of communities analysed). This distribution was estimated as the ratio of recruits of species *i* growing in open gaps within community *k* to the total cover of open gaps in *k*. By modifying the entries in the $\alpha_{ij}^{\text{facilitation}}$ and $\alpha_{ij}^{\text{competition}}$ matrices, we created four different scenarios as follows.

Scenario 1—raw topology of facilitative interaction networks

To evaluate whether the unweighted topology of observed facilitative interaction networks alone explain the positive relationship between indirect reciprocal facilitation (degree of indirect reciprocity) and species richness in the communities, we randomly assigned $\alpha_{ij}^{\text{facilitation}}$ scores across the facilitative links observed in the real communities. These scores were sampled from a uniform distribution spanning the lower to the upper bounds of the 95% CI around the geometric mean (0.04, s.d. = 4.56) of the empirical distribution of NII values (one empirical distribution for the entire set of communities analysed). On the other hand, $\alpha_{ij}^{\text{competition}}$ scores were sampled from the same distribution of NII values whenever the species were set to exert a negative effect on the growth of other species (0.95 probability) and otherwise $\alpha_{ij}^{\text{competition}} = 0$.

Scenario 2—stronger facilitative effects within longer facilitation loops

In this scenario, the strength of the facilitative effect of species *j* on species *i* increased linearly with the number of intermediary species encompassed along the shortest facilitation loop including both species in community *k* (S_{loop}), where species *j* closes the loop by returning the benefit to species *i*:

$$\alpha_{ij}^{\text{facilitation}} = \mu^{\text{facilitation}} + \beta S_{\text{loop}}$$

where $\mu^{\text{facilitation}}$ represents the geometric mean of the empirical distribution of NII values and β is the slope of the linear relationship between $\alpha_{ij}^{\text{facilitation}}$ and S_{loop}, sampled from a normal distribution with a mean of 0.075 and a standard deviation of 0.05, truncated between 0 and infinity. The sampled β values, centred on 0.075, yielded facilitation coefficients within the observed range. For example, in the longest facilitation loop observed ($S_{\text{loop}} = 7$), the expected average $\alpha_{ij}^{\text{facilitation}}$ is 0.56, which falls within the empirical distribution of NII values (with the 95th percentile at 0.69). Nonetheless, centring β values on different means produced consistent results (Supplementary Appendix 8). Note that $S_{\text{loop}} = 0$ if species *j* directly benefits from species *i* in the facilitation network. The $\alpha_{ij}^{\text{competition}}$ matrix was configured as in scenario 1.

Scenario 3—decreased probability for intermediary species to be negatively impacted

In this scenario, the probability of species *j* exerting a negative effect on the growth of species *i* within community *k* was contingent upon whether species *i* served as an intermediary species in any of the shortest facilitation loops reciprocating the facilitation events initiated by species *j*. If this condition was met, the probability that $\alpha_{ij}^{\text{competition}} \neq 0$ was adjusted from the default setting of 0.95 to 0.38 (that is, decreased by a factor of 2.5). Alternative reductions of this probability produced consistent results (Supplementary Appendix 8). The $\alpha_{ij}^{\text{competition}}$ scores were sampled as described in scenario 1 regardless of this adjustment and the $\alpha_{ij}^{\text{facilitation}}$ matrix was configured as in scenario 1.

Scenario 4—stronger facilitative effects within longer facilitation loops and decreased probability for intermediary species to be negatively impacted

In this scenario, $\alpha_{ij}^{\text{facilitation}}$ and $\alpha_{ij}^{\text{competition}}$ matrices were configured as in scenarios 2 and 3, respectively. This set-up enabled us to incorporate into the model the two mechanisms that we hypothesized as crucial for stabilizing indirect reciprocal facilitative interactions.

We generated 25 net influence matrices per scenario and community ($n = 25$ replicates × 4 scenarios × 96 communities = 9,600). We ran all simulations for 100 model time steps and computed the survival fraction of species (excluding the superior competitor) at the conclusion of each replicate. Species whose population size *N* was <1 at the end of a replicate were considered extinct. For the numerical integration, we used Hindmarsh's solver[49]. To assess the impact of reciprocal facilitation on biodiversity maintenance, we fitted a linear mixed model using the survival fraction of species in each community as the response variable, with the degree of indirect reciprocity in interaction with scenario type as explanatory variables and community as a random variable.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The raw database that supports the findings of this study is described in the data paper 'RecruitNet: a global database of plant recruitment networks'[15], published in *Ecology*, and the complete dataset is available via Zenodo at https://doi.org/10.5281/zenodo.6567608 (ref. 50). The data supporting the results of this study are available via Figshare at https://doi.org/10.6084/m9.figshare.28322822.v1 (ref. 51). Source data are provided with this paper.

Code availability

The code used to generate all reported results is available via Figshare at https://doi.org/10.6084/m9.figshare.28322822.v1 (ref. 51).

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Acknowledgements

This research was supported by the project PID2022-138776NA-I00 (Spanish Ministry of Science and Innovation), granted to R.M.-V.; and the projects PID2020-114851GA-I00 (Spanish Ministry of Science and Innovation) and RARABUN 2022/00156/001 (Comunidad de Madrid Government), granted to J.C. R.M.-V. and J.C. were supported by the Ramón y Cajal programme (RYC2023-044256-I and RYC2021-034013-I), funded by the Spanish Ministry of Science and Innovation.

Author contributions

R.M.-V. and J.C. conceived the ideas. J.C. conducted the analyses with assistance from E.A. R.M.-V. and J.C. drafted the figures, while R.M.-V. led the writing with inputs from J.C. M.V., J.M.A., J.L.G. and A.M.-N. provided an accurate understanding of the dataset and valuable feedback on the research. All authors read and commented on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-025-02766-9.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-025-02766-9.

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Peer review information *Nature Ecology & Evolution* thanks the anonymous reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

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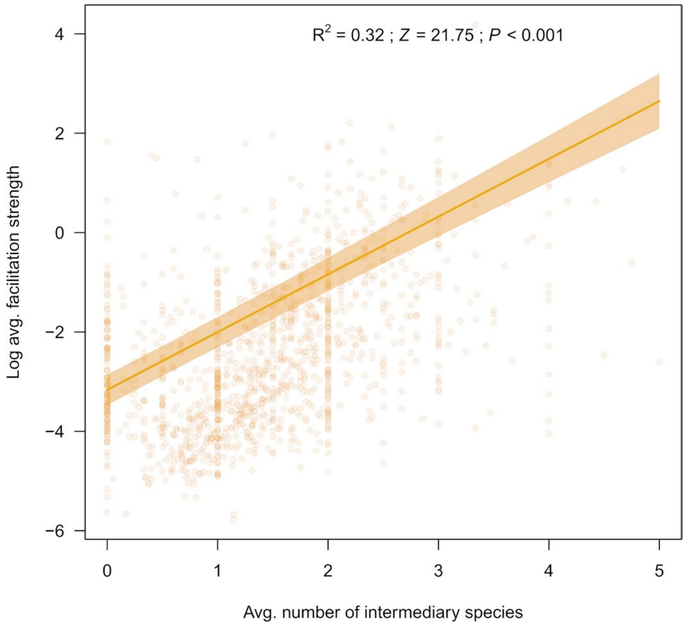

Extended Data Fig. 1 | Relationship between the average number of intermediary species encompassed along the shortest loops directly or indirectly reciprocating the facilitation events initiated by a benefactor species and the average strength of the positive recruiting interactions closing the loops (log-transformed), where said benefactor species acts as beneficiary. The strength of each recruiting interaction was computed using the Nursing Intensity Index (NII) as it is described in the methods. The shaded area around the trend line represents the 95% confidence interval of the predictions.