RESEARCH ARTICLE

Plant functional traits involved in the assembly of canopy–recruit interactions

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Abstract

Questions: The assembly of plant communities depends strongly on mechanisms that determine the recruitment of different plant species. Studying recruitment using a trait-based approach may help in the search for general or dominant mechanisms involved in this process. Here, we try to disentangle what traits of saplings and established (canopy) plants can be considered as functional for recruitment, and whether the complementarity of these functional traits may be a driver of the plant community assembly.

Location: Regional. Two pine–oak forest communities in Sierra Sur de Jaén and one in Sierra de Segura, southeast of the Iberian peninsula.

Methods: In each forest community, we established three 50 m × 50 m plots, where we identified the saplings of each species recruiting under the canopy of each species or in open interspaces. The study focuses on 37 woody species. Measures of 18 traits were conducted for 30 saplings and 10 adults of each species.

Results: Seed mass and the ratio height:basal diameter of saplings were positively associated with species abundance in the sapling bank under vegetation, while abundance in the sapling bank in open interspaces was only related to the type of mycorrhizal association. On the other hand, some traits of adult plants (leaf mass per unit area [LMA], seed dispersal mechanism, leaf habit and branch density) favour the recruitment of other species in their close proximity. However, we found only circumstantial evidence of canopy/recruit trait complementarity affecting recruitment.

Conclusions: Our results suggest that the assembly of canopy–recruit interactions is primarily driven by the filtering effect of canopy species on recruitment, through traits that affect both seed arrival and soil properties. Species abundance in the sapling bank was related to resource acquisition traits. We did not find any clear evidence supporting that trait complementarity is involved in the interaction between canopy and recruit species.

KEYWORDS
canopy service, functional traits, mediterranean forests, plant community assembly, plant recruitment, recruitment networks, sapling bank, trait-based approach, woody plants

1 | INTRODUCTION

The assembly of local plant communities is influenced by the composition of the regional species pool and its interaction with local biotic and abiotic filters (Kraft and Ackerly, 2014; Kraft et al., 2015). In the hierarchy framework, after abiotic filters sieve the regional plant species pool, biotic filters acquire more importance by interacting with the resultant plant species (Luzuriaga et al., 2012). Here, several biotic factors, such as plant–plant interaction, herbivorous insects, pathogens or mycorrhizal fungi, have been considered as drivers of community assembly at local scales (Janzen, 1970; Connell, 1971; Bagchi et al., 2014; Montesinos-Navarro et al., 2016). In fact, plant–plant interactions, both positive and negative, are considered one of the main drivers in community assembly (Callaway and Walker, 1997). Negative plant–plant interactions (competition) may determine the exclusion of a species from a local assembly, even if this species is able to tolerate the local abiotic conditions (Zenni and Nuñez, 2013). On the other hand, positive plant–plant interactions (facilitation), may allow the persistence of a given species in a local community, even if the general abiotic environment is not favourable (Valiente-Banuet et al., 2006). Plant–plant interactions are particularly strong and asymmetric between established adult individuals and young plants recruiting in their close proximity (Grubb, 1977). The study of plant–plant interactions that occur during the recruitment stages can provide insight into the persistence of species in local communities (Valiente-Banuet et al., 2006; Poorter et al., 2008; Alcántara and Rey, 2012; Umaña et al., 2017), and thus, in the role of plant–plant interactions on community assembly and dynamics.

Recruitment is a key ecosystem function as it is fundamental for the dynamics of plant communities. Recruitment networks depict the structure of interactions between established plants and the plants recruiting beneath them in a local community, which we call canopy and recruit species, respectively (Alcántara et al., 2019). The analysis of recruitment networks provides insights on how plant–plant interactions affect species persistence in local plant communities (Alcántara and Rey, 2012; Alcántara et al., 2017). If we are to develop generalizations about the traits that determine the outcome of plant–plant interactions, we must consider explicitly the difference between the effect that a species has on others and the response of the same species to the presence of others (Goldberg, 1990; Goldberg and Landa, 1991). To this end, we can explore the matrix corresponding to the recruitment network. This matrix has canopy species in columns and recruit species in rows, and the cells of the matrix contain the frequency of saplings of the recruit species found under individuals of the canopy species (Alcántara et al., 2019). The recruitment matrix provides a description of the sapling bank of the community: the abundance of juvenile individuals of each species and their spatial association with adult plants of any species. From this matrix, we can obtain three descriptors of the sapling bank: canopy service, participation in the sapling bank and pairwise recruitment efficiency.

The canopy service provided by a given species can be measured as the density of saplings of any species that recruit under adult individuals of the species (i.e. the column sum in the recruitment matrix); it informs about whether adult plants of a species enhance or depress sapling recruitment under their canopy (Alcántara et al., 2018), thus reinforcing, weakening or biasing the sapling bank of the whole community. Certain plant species may play a key role in the community by allowing the recruitment of many other plant species. For example, Verdú and Valiente-Banuet (2008) found that *Mimosa luisana* facilitates the recruitment of 92.3% of the species in arid communities from Mexico. The participation in the sapling bank is defined by the abundance of saplings of a species in the sapling bank of the community (i.e. the row sum in the recruitment matrix); it informs on the suitability of the biotic and abiotic local environment for the recruitment of a species, and its prospects for persistence. For instance, recruitment collapse associated with climate change threatens the persistence of Ponderosa pine during this century (Petrie et al., 2017). Both canopy service and sapling bank summarize the outcome of multiple pairwise canopy–recruit interactions in which a given species is involved. To better understand how these two aspects emerge, we need to explore also how these pairwise interactions are assembled. To this end, we define pairwise recruitment efficiency as the density of one species recruiting under another (i.e. the cell elements of the recruitment matrix). Pairwise recruitment efficiency reflects the effects of the canopy species on the participation of the recruit species in the sapling bank. These effects may be driven by different ecological mechanisms, such as competition, facilitation, propagule filtering, growth strategies or shared pathogens and herbivores (Goldberg, 1990; Westoby et al., 1996; Coomes and Grubb, 2000; Callaway, 2007; Pounden et al., 2008; Poorter et al., 2009).

The factors that drive pairwise interactions in ecological systems, such as plant–pollinator, predator–prey or plant–dispersal agent, are receiving much attention. For example, the interaction between plants and hummingbirds can be driven by corolla length and bill length (Maglianesi et al., 2014), by beak length and fruit length in the case of seed dispersal by birds (Dehling et al., 2014), and by the relative sizes of predator and prey in food webs (Cohen et al., 1993). These studies are proving the utility of the functional traits approach to understand the assembly of complex ecological networks. Although plant–plant interactions have a high degree of pairwise specificity (Landero and Valiente-Banuet, 2010; Alcántara et al., 2018), the factors that promote this specificity are largely unknown. Some studies have suggested that mechanisms related to plant phylogeny and stochastic processes are involved (Valiente-Banuet et al., 2006; Alcántara et al., 2015 and Alcántara et al., 2019), but to improve our understanding of how recruitment networks are assembled, we need to move from these general factors to specific traits or mechanisms.

Functional traits may help understanding the relationship between ecological processes and community dynamics (Adler et al., 2013; Cadotte et al., 2015; Funk et al., 2017). Plant recruitment is the outcome of multiple processes, such as seed dispersal, seed germination, establishment, and survival in the face of pathogens, herbivores or competition. The success in each of these processes

may be driven by different functional traits (Larson and Funk, 2016). For example, traits related to saplings' shade tolerance (e.g. high specific leaf area [SLA], slow growth rate; Janse-Ten Klooster et al., 2007) provide advantages under strong asymmetric competition for light against large neighbours, and large seed size favours germination and establishment under dry conditions (Leishman and Westoby, 1994). Therefore, the choice of plant traits must be consistent with the environmental conditions and studied processes (Weiss and Ray, 2019). As a fundamental step towards identifying general or dominant mechanisms of plant community assembly and dynamics, we need to identify functional traits related to recruitment at the community level. In this study, we evaluated the functionality of 21 traits of adult plants and 16 traits of saplings in the three different aspects of the recruitment network. More specifically, we address the following questions: (a) what traits of adult plants determine the strength of the canopy service; (b) what traits of recruit species determine their participation in the sapling bank; and (c) is there any complementarity between traits of canopy and recruit plants that explain the efficiency of the pairwise interactions?

2 | METHODS

2.1 | Study areas and plant sampling design

This work was conducted in two protected areas of the southeastern Iberian peninsula, Sierra Sur de Jaén and Sierra de Segura, where we studied three communities: a pine forest of Sierra Sur de Jaén (PFJ, hereafter), a mixed pine–oak forest of Sierra de Jaén (MFJ, hereafter) and a mixed pine–oak forest of Sierra de Segura (MFS, hereafter). In these communities, rainfall is concentrated during spring and autumn, reaching mean annual values of 611.67 mm at MFS, and 535.39 mm at PFJ and MFJ. The coldest month is January, especially at MFS, where the mean temperature approaches 6°C, whereas at PFJ and MFJ mean temperature exceeds 10°C. Summer season in these ecosystems is characterized by long periods of drought and high temperatures. All the communities occur in calcareous areas but the soil is more developed at MFS. Species richness is higher at MFJ (Appendix S1).

In each community, we stablished three 50 m × 50 m plots where we registered every sapling, and identified its canopy plant or whether it was recruiting in open interspaces (i.e. far from other plants). See Alcántara et al. (2019) for full details of the sampling protocol. Additionally, we also recorded the cover (crown projection on the ground) of adults as a surrogate for potential seed production of each species in each plot. Similarly, we estimated the cover of each species between 0 m and 1.5 m from ground level (where recruitment takes place) as a surrogate for the amount of space most strongly influenced by established individuals of each canopy species. This sampling allows us to measure (a) pairwise recruitment efficiency as the frequency of saplings of each species growing under adults of different canopy species or in open interspaces. From these

data, we can obtain: (b) the canopy service provided by each species measured as the summed frequency of saplings growing under a specific adult species; and (c) the participation of each species to the structure of the sapling bank recruiting directly under the vegetation or in open interspaces, measured respectively as the summed frequency of saplings of each species growing in the close proximity of established individuals of any other species or in open interspaces.

2.2 | Traits sampling design

Within each community, we chose the species occurring in at least two of the three plots. For each species, 30 saplings (15 located underneath canopy plants, and 15 located in open interspaces) and 10 adults were chosen distanced at least 10 m along 100 m long parallel transects distributed in the surroundings of the three plots of each community. Since environmental conditions and soil properties are similar at PFJ and MFJ, we assumed that traits do not differ within species in these two communities (Zhao et al., 2020).

The traits were divided into categories: plant structural traits, leaf traits, mutualism-related traits and seed mass. Plant structural traits included height, EBD (equivalent basal diameter), ratio height:EBD, basal area, canopy area, canopy volume and branch density for canopy plants. In the case of saplings, we only consider height:EBD as structural trait since sapling height and EBD can vary widely between individuals of the same species but different age, while their ratio is more stable. Leaf traits included LFW (leaf fresh weight), LL (leaf length), LA (leaf area), LDMC (leaf dry matter content), SLA (specific leaf area) and LMA (leaf mass per unit area, inverse of SLA), LWC (leaf water content), LN (leaf nitrogen), and leaf habit (evergreen vs deciduous), for both adults and saplings. In mutualism-related traits we included seed dispersal mechanism (fleshy vs dry-fruited), and mycorrhizal association (arbuscular, AM, vs ectomycorrhizal, ECM). Most traits were measured following the procedures of Cornelissen et al. (2003) and are described in detail in the Supporting Information (Appendix S2). Structural and leaf traits are available at TRY-DB (Kattge et al., 2020).

2.3 | Data analyses

2.3.1 | Preliminary analyses

Firstly, we tested whether traits of saplings and adults differed significantly among species, and whether traits differed between saplings recruited under adults or in open interspaces (open, hereafter). Only traits that varied significantly between species were retained for further analyses (Appendix S3). Secondly, we explored by means of Principal Components Analysis (PCA) the correlations between plant structural traits and between leaf traits. From each PCA, we retained the components with eigenvalues larger than 1. From each of these components, we retained the variable with higher correlation (see Appendix S4 for the PCA results). This allows filtering

out highly correlated traits, retaining a set of independent potential functional traits for further analyses.

2.3.2 | Determining functional traits explaining the sapling bank and the canopy service

To test trait effects on participation in the sapling bank (both under vegetation cover or in the open), and on canopy service, we fitted separately for each trait a generalized linear model with negative binomial distribution function. We use the Community Assembly by Trait Selection (CATS) analytic approach as proposed by Warton et al. (2015). The model included as dependent variable the frequency (i.e. number of saplings) of each species in the sapling bank or the frequency of saplings integrating the canopy service of each species. As explanatory variables, we included the trait, community and cover. In the analyses of the sapling bank, cover was entered as the cover of adult canopies, as an estimate of the potential abundance of seed sources. In the analyses of canopy service, cover was entered as the cover of each adult species at ground level, as an estimate of the space available for canopy–recruit interactions. We also included the cover × site interaction to control for variation in cover effect across sites. Adding the trait × site interaction in this model did not improve the Akaike Information Criterion (AIC), so we present results of the model for each trait without this interaction. Note that canopy plants refer to adults of each species, but they are not necessarily in the canopy layer (i.e. shrub species).

2.3.3 | Determining functional traits explaining pairwise recruitment efficiency

To test for trait effects on pairwise recruitment efficiency, we fitted a generalized linear mixed model using, as fixed effects, species cover and the functional traits identified in the previous analyses: branch density, seed dispersal mechanism, LMA and leaf habit for canopy service, and ratio height:EBD and seed mass for sapling bank under vegetation cover. As random effects we included the identity of canopy and recruit species to control for autocorrelation between interactions involving the same canopy or recruit species. We also included all the trait interactions between sapling bank functional traits and canopy service functional traits to explore trait complementarity between saplings and adults. Note however, that the interaction between branch density of canopy plants and seed mass of recruits was removed due to model convergence problems. The model was fitted using a zero-inflated negative binomial distribution (the model fitted with Poisson; Poisson with zero inflation or negative binomial had higher AIC). The zero inflation term included the cover of the canopy and recruit species. The model was fitted separately for each community (PFJ, MFJ and MFS). Only the interspecific interactions were included in the analyses because the ecological mechanisms driving conspecific interactions are likely different from those driving interspecific interactions (such as Janzen–Connell effects; Janzen, 1970; Connell, 1971).

All the statistical analyses were conducted in the R environment version 3.6.1 using the R *markdown* package version 1.15 (R Core Team, 2016). PCAs were developed by using the *factoextra* R package, version 1.0.7 (Kassambara and Mundt, 2017). The generalized linear mixed models were fitted by means of the *glmmTMB* R package version 1.0.1 (Brooks et al., 2017). Predictions of the models were evaluated with the *emmeans* R package version 1.4.6 (Lenth et al., 2018). All graphics were done with *ggplot2* R package version 3.3.0 (Wickham, 2011).

3 | RESULTS

3.1 | Preliminary analyses

All traits differed among species, both for adults and for saplings (Appendix S3). None of the 11 sapling traits measured varied between microhabitats (under vegetation vs open) in Sierra de Jaén and only four varied in Sierra de Segura. In Sierra de Segura, sapling LMA differed significantly between microhabitats, while EBD, ratio height:EBD and LN also varied between microhabitats but this variation depended on the species. In general, these results indicate that plasticity associated with recruitment in these two microhabitats is much lower than the magnitude of variation between species. Following the results of PCAs of adult plant structural traits, we retained for subsequent analyses: height, height:EBD and branch density. In the case of leaf traits, we retained LA, LMA and LN; and in the case of sapling traits, LA, LMA and LN (Appendix S4). We also included in the subsequent analyses seed mass and dichotomous traits: leaf habit, seed dispersal mechanism and mycorrhizal association.

3.2 | Determining functional traits in relation to participation in the sapling bank and canopy service

Branch density, LMA, seed dispersal mechanism and leaf habit had a significant effect on the frequency of saplings under adult plants of different species, and we therefore considered these as canopy service functional traits (Table 1). Branch density was negatively correlated with canopy service, while LMA was positively correlated (Figure 1). Dry fruitiness and evergreen leaves improved the canopy service (Figure 1). Canopy service was scarcely affected by site effect, and was positively related with canopy species cover (Table 1).

Height:EBD and seed mass had significant effects on the number of saplings of each species recruited under vegetation cover and were therefore considered as sapling bank functional traits (Table 1). Height:EBD was negatively related to species abundance in the sapling bank, whereas seed mass was positively related (Figure 2). Finally, only mycorrhizal association was functional in relation to the sapling bank in the open (Table 1). The sapling bank of ECM species

TABLE 1 Results of models exploring whether traits are functional for canopy service and for participation in the sapling bank (under adults and in open)

Model		Estimated trait effect	Wald χ^2			
Dependent variable	Trait tested		Trait	Site	Cover	Site × Cover
Canopy service	Height	0.054	2.72	3.57	15.01*	2.30
	Height:EBD	0.818	1.06	4.03	17.69*	2.15
	Branch density*	−0.002*	4.67*	3.76	15.14*	1.78
	LA	−0.013	1.98	4.18	17.82*	3.01
	LMA*	6.405*	6.14*	0.13	19.53*	2.94
	LN	−0.035	2.11	0.13	16.77*	2.53
	Seed dispersal mechanism*	−0.561*	5.66*	4.14	15.48*	3.11
	Leaf habit*	0.792*	9.71*	6.14*	21.22*	3.15
	Mycorrhizal association	0.444	2.17	4.05	12.73*	2.38
Sapling bank under vegetation cover	Height:EBD*	−1.457*	6.96*	1.24	19.39*	11.75*
	LA	0.012	0.26	0.80	21.61*	14.17*
	LMA	−15.820	1.69	0.70	24.12*	16.92*
	LN	0.009	0.02	0.85	18.36*	13.03*
	Seed dispersal mechanism	0.217	0.52	0.62	21.69*	14.55*
	Leaf habit	−0.217	0.41	0.94	22.49*	14.38*
	Mycorrhizal association	0.605	2.42	2.05	12.16*	9.64*
	Seed mass*	9.1×10^{-5}*	7.16*	1.80	23.82*	13.79*
Sapling bank in open	Height:EBD	−0.553	1.64	2.02	19.86*	17.49*
	LA	0.002	0.007	1.31	19.51*	20.85*
	LMA	−10.580	1.01	1.92	21.11*	23.17*
	LN	0.008	0.02	1.06	18.53*	19.87*
	Seed dispersal mechanism	−0.539	2.74	1.92	16.83*	17.47*
	Leaf habit	0.287	0.54	1.76	18.10*	18.97*
	Mycorrhizal association*	1.137*	7.08*	3.85	9.44*	11.65*
	Seed mass	2.01×10^{-5}	0.28	0.94	20.46*	21.11*

Note: Models were fitted separately for each trait. For each trait we provide its estimated effect according to the fitted model and its significance evaluated by means of a Wald chi-square test. Significant effects ($p < 0.05$) are indicated by *. Since we dealt with categorical traits, the values shown in the table correspond to "fleshy-fruited," "evergreen leaves" and "ectomycorrhizal association (ECM)" for seed dispersal mechanisms, leaf habit and mycorrhizal association, respectively. EBD, equivalent basal diameter; LA, leaf area; LMA, leaf mass per unit area; LN, leaf nitrogen.

in the open was more abundant (mean ± *SE*: 0.35 ± 0.004 saplings/m²) than that of AM species (mean ± *SE*: 0.11 ± 0.003 saplings/m²). Both under vegetation cover and in the open the sapling bank was affected by the interaction between recruit species cover and site.

3.3 | Determining functional in relation to pairwise recruitment efficiency

Our results showed that pairwise recruitment efficiency did not depend on the complementarity between the traits of saplings and adults in Sierra Sur de Jaén. In Sierra de Segura, the interaction of sapling seed mass with LMA and seed dispersal mechanism of canopy plants was significant. Saplings of species with small seed mass were significantly more abundant under species of canopy plants with low LMA (Table 2). On the other hand, species with larger seed

mass had higher recruitment under fleshy-fruited canopy plant species, but seed mass had no effect under dry-fruited plants (Table 2).

4 | DISCUSSION

We have found that the assembly of the sapling bank is driven by traits of the saplings and traits of the adult plants. Branch density, LMA, seed dispersal mechanism and leaf habit of adult plants are related to their canopy service, acting as functional traits that modulate the abundance of saplings under the cover of different plant species. On the other hand, the ratio height:EBD and seed mass were related to variation between species in their participation in the sapling bank under the cover of vegetation. In the open, only mycorrhizal association can be considered as functional in relation to sapling recruitment. These results suggest that the recruitment
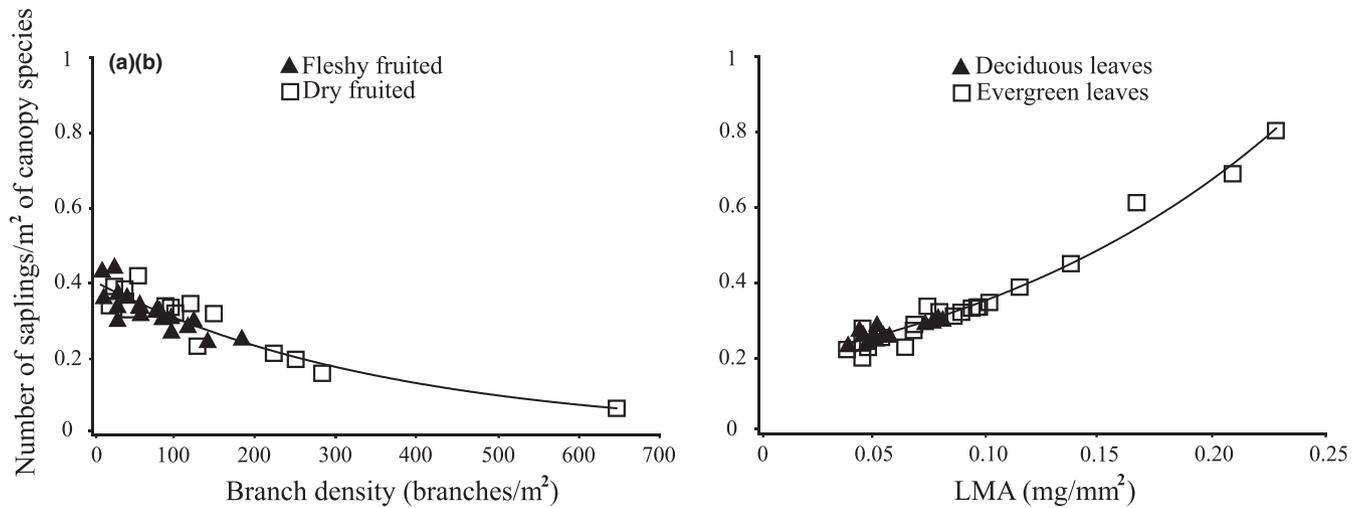
FIGURE 1 Predictions of the relationship between the canopy service and traits of the canopy plants. Only traits considered as functional for the canopy service are represented. (a) Branch density and seed dispersal mechanisms. (b) Leaf mass per unit area (LMA) and leaf habit. The *y*-axis represents the model-predicted estimates of recruitment density (saplings/m^2 of canopy species) under each canopy species assuming the mean cover of species in the mixed pine-oak forest community of Sierra de Jaén (112.52 m^2)
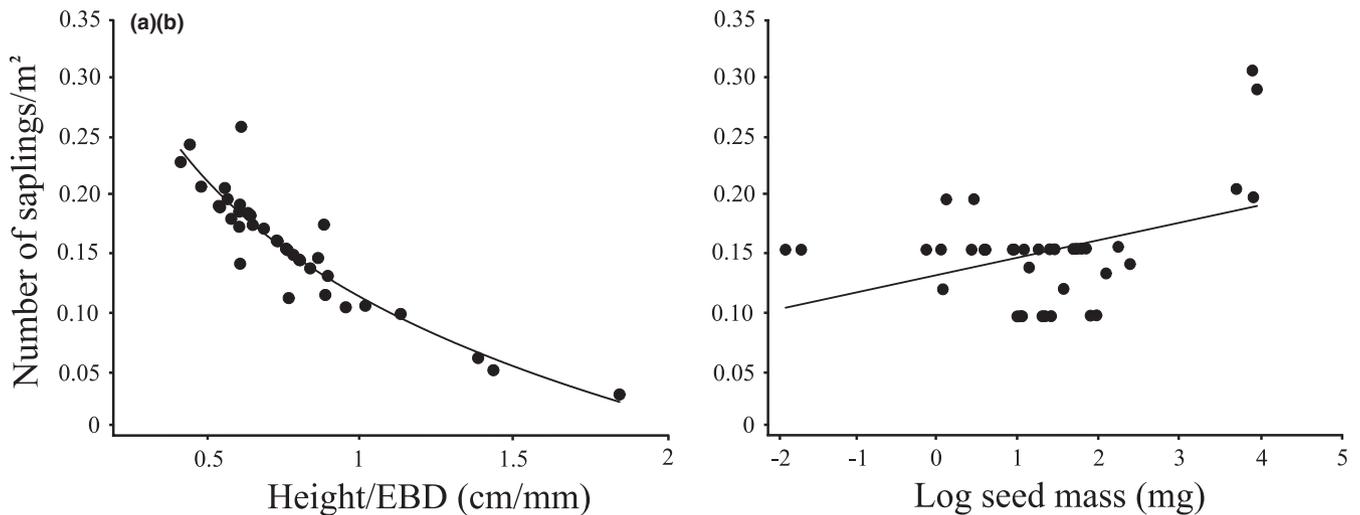

FIGURE 2 Predictions of the relationship between abundance in the sapling bank under vegetation cover and traits of saplings that showed significance under vegetation cover: height/equivalent basal diameter (EBD) (a) and seed mass (b). These traits were considered as functional for the sapling bank and were included in subsequent analyses. The *y*-axis represents the model-predicted estimates of recruitment efficiency (saplings/m^2 of recruit species) assuming the mean cover of species in the mixed pine–oak forest community of Sierra de Jaén community (344.30 m^2)

environment in the open is less heterogeneous than under the cover of different plant species, where this heterogeneity might be dealt with through the participation of a more diverse set of functional traits. Finally, none of the canopy–recruit trait interactions analysed was related to pairwise recruitment efficiency in two of the three communities studied, and only two out of seven interactions were significant in one of the communities. This inconsistency between communities regarding the influence of trait complementarity suggests that the pairwise specificity of canopy–recruit interactions is not driven by trait complementarity between the interacting species.

4.1 | Traits of adult plants functional in relation to canopy service

Canopy service reflects the effect of each species on the formation of the sapling bank of the whole community. Different species modify the microhabitat in their close proximity in ways that can be beneficial or detrimental for recruitment (van de Voorde et al., 2011; Aponte et al., 2013). Our results show that species with evergreen leaves, that produce dry fruits, have low branch density or high LMA provide a better canopy service.

TABLE 2 Results of generalized linear mixed models testing whether functional traits explain the pairwise recruitment efficiency at each site

Model predictors	PFJ				MFJ				MFS			
Traits (Canopy, Sapling and Canopy × Sapling)	Estimate	SE	Z-value	p-value	Estimate	SE	Z-value	p-value	Estimate	SE	Z-value	p-value
Canopy LMA	-1.840	13.710	-0.134	0.893	9.565	8.184	1.169	0.243	4.141	10.730	0.386	0.700
Canopy branch density	3.4×10^{-5}	0.011	0.031	0.975	0.003	0.005	0.651	0.515	-0.002	0.006	-0.300	0.764
Canopy leaf habit	-0.903	1.503	-0.601	0.548	0.967	0.766	1.262	0.207	1.188	1.012	1.175	0.240
Canopy seed dispersal mechanism	-1.950	1.194	-1.633	0.103	-0.834	0.724	-1.152	0.249	-0.539	0.899	-0.599	0.549
Sapling height:EBD*	-7.528	2.822	-2.668	0.008*	0.442	1.147	0.385	0.700	0.122	1.610	0.076	0.940
Sapling seed mass	8.8×10^{-5}	1.2×10^{-4}	0.730	0.466	-6.1×10^{-5}	1.2×10^{-4}	-0.509	0.611	-1.3×10^{-4}	1.7×10^{-4}	-0.799	0.424
Cover of canopy plants*	9.5×10^{-5}	1.6×10^{-4}	0.610	0.542	0.001	3.2×10^{-4}	2.961	0.003*	0.001	3.2×10^{-4}	2.158	0.031*
Cover of seed producers*	0.001	0.001	1.581	0.114	0.005	0.001	3.861	$1.1 \times 10^{-4*}$	0.005	0.001	3.993	$6.5 \times 10^{-5*}$
LMA : height:EBD	12.380	15.610	0.794	0.427	-10.370	7.088	-1.463	0.143	4.822	8.235	0.586	0.558
LMA : seed mass*	-9.9×10^{-5}	0.001	-0.176	0.860	4.2×10^{-4}	4.8×10^{-4}	0.887	0.375	0.002	0.001	2.414	0.016*
Branch density : height:EBD	-0.014	0.014	-0.968	0.333	-0.010	0.007	-1.327	0.185	-0.011	0.008	-1.367	0.172
Leaf habit : height:EBD	2.557	1.849	1.383	0.167	-0.269	0.681	-0.395	0.693	-1.034	0.885	-1.169	0.243
Leaf habit : seed mass	-3.6×10^{-5}	8.3×10^{-5}	-0.444	0.657	-2.4×10^{-5}	7.3×10^{-5}	-0.322	0.747	-1.1×10^{-4}	9.6×10^{-5}	-1.086	0.277
Seed dispersal mechanism : height:EBD	2.865	1.497	1.914	0.056	0.329	0.649	0.506	0.613	0.736	0.838	0.877	0.380
Seed dispersal mechanism : seed mass*	4.3×10^{-5}	6.9×10^{-5}	0.636	0.525	2.8×10^{-5}	7.0×10^{-5}	0.396	0.692	2.3×10^{-4}	1.0×10^{-4}	2.156	0.031*
Zero-inflation terms												
Cover of canopy plants*	-0.182	0.072	-2.521	0.012*	-0.007	0.006	-1.191	0.234	-0.039	0.067	-0.572	0.568
Cover of seed producers	0.001	0.003	0.189	0.850	-0.006	0.003	-1.787	0.074	-0.031	0.042	-0.740	0.460

Note: The model includes functional traits for sapling bank, functional traits for canopy service, and their two-way interactions as estimates of trait complementarity between saplings and canopy plants (see *Methods*). The model was fitted using a zero-inflated negative binomial distribution. As zero-inflation terms we used the cover of the canopy and recruit species. The identities of the recruit and canopy plants were used as random blocking effects. Significance is evaluated by means of Z-tests and is indicated by * ($p < 0.05$). Since we dealt with categorical traits, the values shown in the table correspond to "fleshy-fruited" and "evergreen leaves" for seed dispersal mechanisms and leaf habit, respectively. EBD, equivalent basal diameter; LMA, leaf mass per unit area.

High branch density may affect recruitment by acting as a physical barrier repelling the arrival of seeds. For instance, in plants with very high branch density, like *Thymus* spp., winged and plumed seeds (e.g. *Acer* spp. or *Pinus* spp.) or large seeds dropped by birds (e.g. *Crataegus* spp. or *Prunus spinosa*) may collide with the branches and fall around the canopy but not beneath it (Pounden et al., 2008). On the other hand, species with low branch density, like *Acer monspessulanum* or *Pistacia terebinthus*, do not easily repel wind-dispersed seeds and may provide perches favouring the foraging activity of frugivorous birds, enhancing the deposition of seeds under their canopy (McClanahan and Wolfe, 1987; Zapata et al., 2014). On the other hand, branch density may also affect the canopy service through modulating the light availability. High branch density may project a strong shadow that prevents the recruitment of species with higher light requirements (Wright, 2002; Rüger et al., 2009).

A significant, but moderate contribution to the canopy service was associated with the seed dispersal mechanisms of the canopy plants. Although it could be expected that the foraging activity of birds should increase the canopy service under fleshy-fruited plants, we obtained the opposite result. Plants bearing fleshy fruits provided slightly worse canopy service than those producing dry fruits. This was unexpected because fleshy-fruited plants are known to induce the nucleation of seeds from other bird-dispersed species (Verdú and García-Fayos, 1996; García et al., 2000). However, it is possible that post-dispersal processes (e.g. seed predation, seedling mortality) are stronger under fleshy-fruited species, maybe as a consequence of the attraction of rodents and ungulates looking for fallen fleshy fruits that accumulate on the ground under the trees, or due to the propagation of generalist fungal pathogens associated with a high density of rotting fruits on the ground.

Regarding leaf traits of the adult plants, we observed an enhanced canopy service under species with high LMA and evergreen leaves. Indeed, some authors have found higher LMA in evergreen than in deciduous plants (Poorter et al., 2009). High LMA impacts negatively on litter decomposition rates (Xiong and Nilsson, 1999; Garnier et al., 2004), and this may have indirect effects on soil properties that affect recruitment. For example, species with a high LMA, like *Pinus halepensis* or *Quercus ilex*, have low decomposition rates, providing the soil with a thicker layer of litter (Kazakou et al., 2009) and high soil moisture that may enhance the persistence of saplings in the dry season of the Mediterranean climate. However, oppositely to our results, studies focusing on the dynamics of herbaceous communities have found that the litter accumulation associated with high LMA depressed both recruitment and species richness under canopy cover (Carson and Peterson, 1990; Xiong et al., 2003), so it seems likely that the relationship between LMA and the canopy service may depend on the life form of saplings. In turn, deciduous leaf habit may impose strong seasonality on the soil nutrient use, since deciduous plants need to grow new leaves to replace the shedded ones, demanding a high amount of nutrients during the early growing season that would not be available for the saplings. Oppositely, evergreen woody plants might not impose this strong seasonality, leaving nutrients more available during the growing season for

saplings recruited underneath evergreen than under deciduous adult plants (Aerts, 1990; Lal et al., 2001).

Although the summer drought is considered the most important climatic stress in Mediterranean vegetation, Mediterranean mountains also experience periods of freezing temperatures and snowfall which impact plant recruitment (Ramírez et al., 2006). Better canopy service by evergreen than by deciduous plants cannot be related to amelioration of summer drought stress because both evergreen and deciduous species provide shelter in summer. However, the evergreen leaf habit may also enhance canopy service by providing shelter to seedlings and saplings against cold-related climatic incidences such as frosts or snowfalls.

4.2 | Traits of saplings functional in relation to the participation in the sapling bank

The participation of species in the sapling bank reflects the general suitability of the habitat for recruitment. As a key demographic stage, a high sapling abundance is expected to indicate a high probability of persistence of a species in the community. Our results show that height:EBD ratio, seed mass and mycorrhizal association play a role in explaining the participation of species in the sapling bank.

Slow growth is a conservative strategy for the use of resources, which provides a greater chance to persist in early life stages (Welden et al., 1991; Lucas et al., 2013). This strategy is related to species' shade tolerance (Bazzaz, 1979), so slow-growing species may dominate the sapling bank under vegetation, increasing their chances to exploit newly created vacant spaces (Zobel and Antos, 1991; Sakai, 1995). It is well known that shade tolerance plays an important role in the recruitment niche of species and it is related to several traits of the saplings, such as ratio height:EBD or SLA (Bazzaz, 1979; Pacala et al., 1994; Silvertown, 2004; Rüger et al., 2009). Our results support this relationship. Under vegetation cover, where less light is available, species with a low height:EBD ratio (i.e. slow growth; Pacala et al., 1994) achieved higher recruitment. In this way, slow-growing species such as *Quercus ilex* or *Pinus nigra* showed a more abundant sapling bank than fast-growing species such as *Ulex parviflorus* or *Genista cinerea*. Moreover, this relationship did not occur in the open, where light is not limiting.

Saplings of species with larger seeds tended to be more abundant under vegetation cover. Larger seed mass provides multiple advantages to the seeds and seedlings, like enhanced germination and escape from seed predators, higher tolerance to herbivores and faster access to below- and above-ground resources (Westoby et al., 1996). However, this effect was absent in the open. Thus, the benefit of seed mass does not seem to be related to tolerance of the harsher ground conditions that occur in the open (e.g. lower soil water residence time, extreme summer and winter temperatures, photoinhibition), but rather, to the diverse biotic interactions that plants have to address while recruiting under vegetation cover. On the other hand, the structure of the sapling bank in the open was exclusively explained by the mycorrhizal association. This

may reflect the importance of the symbiosis under more stressful conditions like those occurring in the open in Mediterranean systems (Morte et al., 2000; Zhang et al., 2010; Armada et al., 2015). Saplings associated with ECM fungi were more abundant than those associated with AM fungi. Both symbioses improve nutrient and water acquisition, especially under water shortage, something typical in Mediterranean systems (Caravaca et al., 2004; Lehto and Zwiazek, 2011; Birhane et al., 2012). Despite both associations improving plant performance, ECM fungi have much better dispersal abilities than AM fungi (Egan et al., 2014; Horton, 2017), so places far from established plants (i.e. open interspaces) are more likely to contain ECM than AM propagules. Some ECM fungi can even form a persistent propagule bank in the soil, favouring the establishment of early-successional plant species (Ashkannejhad and Horton, 2006).

4.3 | No evidence of functional trait complementary between adults and saplings in relation to the pairwise recruitment efficiency

The efficiency of canopy–recruit interactions in our study's communities is pairwise specific (Alcántara et al., 2018), as has been found in other studies of plant–plant interactions (Castillo-Landero and Valiente-Banuet, 2010; Lan et al., 2012). However, the present results suggest that this specificity is not based on complementary functional traits. In other ecological systems, like plant–pollinators or plant–seed dispersers, the complementarity between the traits of both organisms plays a key role in the stability of the systems, showing a straight link to the success of the process (Herrera, 1984; Pichler et al., 2020). Unlike these interactions, it seems that the structure of plant recruitment networks is not mediated by the complementarity of traits between the interacting species at local scales. Kunstler et al. (2016) found similar results, determining a weak effect of trait dissimilarity on the strength of competition. We found only two significant trait interactions out of the seven tested, and these only in one of the three studied communities. This lack of consistency suggests that these two trait interactions might be either spurious or the result of idiosyncratic species composition in particular communities. It is possible that the outcome of each pairwise canopy–recruit interaction depends on particular details of the life history of the species, like the particularities of the mutualistic and antagonistic species shared by the interacting plants.

5 | CONCLUSIONS

Functional traits in the sapling bank seem to be related to resource acquisition (height:EBD, seed mass and type of mycorrhizal association), as could be expected at early stages of plant life. Taken together, there was a larger number of functional traits involved in the canopy service than in the participation in the sapling bank.

This suggests that the assembly of canopy–recruit interactions is primarily driven by the canopy species' effect on recruitment, rather than by how different species respond to the recruitment environment. Similar results have been found in the context of competition between annual plants (Goldberg and Landa, 1991; Liancourt et al., 2009). Our results also agree with studies of plant–soil feedbacks, showing that different species modify the soil environment differently affecting recruitment and the assembly of communities (Mangan et al., 2010; Kadowaki et al., 2018; Crawford et al., 2019). However, our results also suggest that in natural conditions, canopy species may filter recruitment not only through plant–soil feedbacks, but also by conditioning the accumulation of seeds under their canopy, since traits related to seed interception and seed dispersal mechanisms were also associated with the canopy service.

The diversity of functional traits related to the canopy service opens the possibility for recruitment niche partitioning between recruit species. Each canopy trait may represent a different recruitment niche axis, so combinations of the four functional traits for canopy service can provide a multitude of potential recruitment niches to support the coexistence of diverse forest species.

DATA AVAILABILITY STATEMENT
Trait-based data that support the findings of the study are available upon request in the TRY Plant Trait Database at (Kattge et al., 2020). All data on interaction frequencies by canopy–recruit pair are available at the Dryad Digital Repository at https://doi.org/10.5061/dryad.bh8n5j8 (see Alcántara et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. List of species.

Appendix S3. Trait measures.

Appendix S2. Traits differing between species.

Appendix S4. Principal Components Analysis of leaf traits of saplings.