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Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology

Official Journal of the Societa Botanica Italiana

ISSN: 1126-3504 (Print) 1724-5575 (Online) Journal homepage: www.tandfonline.com/journals/tplb20

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To cite this article: Elena Constantinou, Alicia Montesinos-Navarro, Dimitrios Sarris & Ioannis N. Vogiatzakis (2025) Facilitation network in phryganic plant communities: evidence from a Mediterranean island, Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology, 159:3, 596-605, DOI: 10.1080/11263504.2025.2489992

To link to this article: https://doi.org/10.1080/11263504.2025.2489992

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PLANT BIOSYSTEMS - AN INTERNATIONAL JOURNAL DEALING WITH ALL ASPECTS OF PLANT BIOLOGY
2025, VOL. 159, NO. 3, 596–605
https://doi.org/10.1080/11263504.2025.2489992

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Facilitation network in phryganic plant communities: evidence from a Mediterranean island

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ABSTRACT

Plant to plant interactions are key drivers of community structure and assembly. We investigate the effect of facilitation on phryganic plant community structure, focusing on plant crown size, and whether the identified facilitative interactions related to community architecture are common in arid environments. We analysed the spatial patterns of 11 species in an arid area in Cyprus. A matrix was created to illustrate the associations between recruited and canopy species, which were found to be more positive than expected by chance, based on the Chi-square test. The corresponding indices of nestedness and connectance were calculated. The associations between recruited and canopy species were found to be positive, exhibiting a high nested structure ($p<0.001$) with a 26% connectance in a non-random nested pattern. The presence of facilitative interactions was confirmed by the almost double number of recruits under the canopies of facilitators versus open ground. *Ziziphus lotus*, demonstrated the highest facilitation capacity (ca. 1.4 times higher than expected; covering ca. 57% of the area occupied by the nurses). *Thymbra capitata* and *Noaea mucronata* followed. The high degree of regularity in the assembly of plants within the community suggests that a facilitator's network is fundamental for maintaining plant diversity in phryganic communities.

ARTICLE HISTORY
Received 26 July 2024
Accepted 3 April 2025

KEYWORDS
Desertification; drylands; ecosystem engineer; *Ziziphus lotus*; facilitation interactions

Introduction

During the last decades, plant to plant interactions have been found to act as key drivers of community structure and assembly (McIntire and Fajardo 2014), influencing biodiversity, ecological functions, and services (Valiente-Banuet et al. 2015). Facilitation is an interaction in which one species benefits, while the other is not detrimentally affected (Aslan et al. 2015), and is particularly important for plant community structure under stress: aridity, grazing, direct light, and high temperatures (Pugnaire and Luque 2001; Bruno et al. 2003; Tirado and Pugnaire 2005; Callaway 2007). Facilitation has been extensively studied as part of a system of protected and protective plants (termed nurse plants) considered favorable to young plants' survival (Sosa and Fleming 2002; Valiente-Banuet et al. 2002; Padilla and Pugnaire 2006; Holland and Molina-Freaner 2013). A nurse plant can be a herb, a shrub, or a tree species. When physical stress and consumer pressure are relatively low, competitive interactions among plants may be the most prominent. However, as abiotic stress or consumer pressure increases, the role of nurse plants as facilitators becomes more crucial in plant communities. Nurse plants provide shelter with their canopies, helping to buffer the extremes of the abiotic environment and reduce the impact of herbivory (Pugnaire and Luque 2001). Although the nurse plant effect was extensively studied in desert areas and areas around the Mediterranean basin (Gómez-Aparicio et al. 2004), the phenomenon can span from tropical to Subantarctic latitudes (Gómez-Aparicio et al. 2004; Cavieres and Badano 2009). In this context, the nurse species can be seen as the founder species (Dayton 1972; Gómez-Aparicio et al. 2004; Lortie 2017).

In the last decades, ecological networks have been incorporated into the study of plant to plant facilitative interactions contributing to a deeper understanding of the organization and functioning of plant communities (Verdú and Valiente-Banuet 2008; Verdú et al. 2023). In this approach, the network represents the organization of the interactions between nurse plant species and the facilitated plant species that tend to recruit under their canopy. Ecological networks are composed of nodes (i.e. species) and links (i.e. the presence or absence of the tendency to recruit associated with any given nurse plant species), therefore they can be represented by a qualitative presence or absence binary matrix (0/1). Moreover, the recruitment frequency of one species under any given nurse plant species can be used as a proxy for plant interaction strength, using a quantitative matrix to characterize the ecological network (Alcántara et al. 2019). Ecological networks show several topological properties that recurrently appear in many mutualistic interactions and have

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Published online 16 Apr 2025

been widely explored since this pattern was described (Bascompte and Jordano 2007). Nestedness is a particular ecological pattern widely reported for both metacommunities and networks of interacting species (Almeida-Neto et al. 2008). Nestedness describes the pattern where the species present at species poor sites form proper subsets of the species in species richer sites (Patterson and Atmar 1986). It is a property of assemblages, not of individual species (Wright et al. 1997). It has been interpreted as a measure of biogeographic order in the distribution of species (Fleishman et al. 2007). The presence of strong nestedness can suggest coupled gradients of site environmental characteristics and species traits (Ulrich et al. 2009). Connectance is the fraction of pairs of nurses and facilitated plant species that directly interact (Verdú and Valiente-Banuet 2008). It indicates the proportion of recruitment interactions relative to the maximum possible in the assemblage.

Plant to plant interactions can be assessed using different types of networks depending on the ecological process of interest. Facilitation networks (FNs) are networks that only consider the plant associations that occur more frequently than those expected by chance (Alcántara et al. 2019). In vegetation communities driven by facilitation, FNs display a nested pattern, similar to that described in other positive ecological interactions such as pollination, seed dispersal, or mycorrhizal symbiosis. This structure has been reported to enhance community robustness, reducing the risk of coextinctions due to the potential loss of interacting species (Bascompte and Jordano 2007; Verdú and Valiente-Banuet 2008; Montesinos-Navarro et al. 2012).

Phryganic plant communities (spiny heath; phrygana) are characterized by cushion forming, thermo Mediterranean summer deciduous, thorny, and sclerophyllous plants, found across the Mediterranean (EUNIS, 2019). Phrygana is often of secondary origin and could result from abandoned cultivated fields, postfire regeneration stages of woodland, and rangeland vegetation. The long list of anthropogenic pressures and threats that created the mosaic structure of this ecosystem includes intensive grazing, transportation, and service corridors, urbanization, residential, and commercial development, and fires (Tsiourlis et al. 2007).

The mature phase of phryganic plant communities of Cyprus is dominated by *Ziziphus lotus* (L.) Lam., a deciduous phreatophytic shrub that reaches up to 3 m in height. *Z. lotus* is native to the Mediterranean region and is considered an ecosystem engineering species (Constantinou et al. 2021; 2023). Shallow rooted Mediterranean shrubs, long-lived perennial herbs, and herbaceous species are often aggregated around *Z. lotus* forming islands of vegetation (Figure 1b). Despite the hints that this system can be governed by facilitative interactions among plants, the architecture of its network of interactions, and its potential vulnerability based on its network properties have not been previously assessed.

The spatial distribution of this type of vegetation, within the habitat, has elicited various interpretations of their community dynamics (Pérez-Latorre et al. 2010). Shrubs could potentially create a microenvironment that (1) reduces the effect of dry and hot external environmental conditions, (2) provides refuge and food for reptiles, rodents, and birds, among other groups, and (3) drives favorable nursing processes for several plant species (Fuentes et al. 1986; Badano et al. 2005). Thus, enhances complex ecological interactions among multiple species simultaneously (Verdú and Valiente-Banuet 2008).

This paper aims to improve our poor understanding of the facilitation dynamics within phryganic communities. As facilitation structures plant communities in arid and stressful environments, we hypothesized that: (1) this process will also contribute to the structure of a phryganic community; (2) shrubs and subshrubs with larger crowns will provide a more

Figure 1. (a) Location of the natura site of Alykos potamos—Agios Sozomenos in Cyprus and (b) caption of the study area in the Middle of march 2019 (photo Constantinou E).

efficient canopy service (Anthelme and Dangles 2012), and (3) the architecture of the facilitative interactions in phryganic communities will resemble that of other arid environments, showing low connectance (<30%) and a nested pattern (Verdú and Valiente-Banuet, 2008).

Materials and methods

Study area

The field study was carried out in March and April 2019 in a 0.135 km^2 experimental site of an arid phryganic plant community with *Ziziphus lotus* within the Natura site of Alykos potamos—Agios Sozomenos (35°03′33′′ N, 33°25′23′′ E; Figure 1) in the island of Cyprus. The soil of the study area is sandy with low organic content in the upper 10 cm and no statistically significant differences in depth throughout the study area (Constantinou et al. 2023). The site hosts important biodiversity and is part of the European Natura 2000 network (CY2000002). Its climate is arid (annual rainfall <400mm; P/ETo < 0.2; P = precipitation; ETo = reference evapotranspiration) with hot, dry summers from May to the middle of October and mild winters from November to March (IACO 2007). The average annual rainfall is 386 mm, and the mean annual temperature is 18.32 °C (Cyprus Department of Environment 2007). The site's vegetation is formed by woody perennial shrubs such as *Ziziphus lotus* (L.) Lam., *Rhamnus oleoides* subsp. *graecus* (Boiss. & Reut.) Holmboe, and *Crataegus azarolus* var. *aronia* L.; woody perennial subshrubs such as *Noaea mucronate* (Forssk.) Asch. & Schweinf., *Thymbra capitata* (L.) Cav., *Sarcopoterium spinosum* (L.) Spach, *Phagnalon rupestre* (L.) DC., *Teucrium micropodioides* Rouy, and *Helianthemum obtusifolium* Dunal; the woody perennial liana *Asparagus stipularis* Forssk. and the annual forb *Anthemis tricolor* Boiss. (Cyprus Department of Environment 2007). Three out of the eleven plant species found in the area are endemic to Cyprus i.e. *Anthemis tricolor*, *Helianthemum obtusifolium*, and *Teucrium micropodioides*.

Sampling design

We sampled using the line-intercept method, along thirty line transects, 50 m in length each. The line transects were placed throughout the study site at least 20 m apart, avoiding any rock outcrops (Figure 2). Along each line transect, we identified woody species and long lived herbs intercepted by the line and recorded each species' intercept distance. For each line transect, we recorded: the number and intercept distance of canopies per species, the number and intercept distance of open ground, and the number of recruits per species under each canopy and in open ground. The cover was calculated by adding all intercept distances, per species and open ground, and expressing this total as a percentage (%) of the line length. Each transect was regarded as one sample unit, so thirty transects were measured to conduct stable statistical analyses of data.

As a "canopy" species, we defined fully developed adult woody perennial plants or longlived herbs (Alcántara et al. 2019). A detailed list of all the species that acted as canopies in transects, their growth form, the average diameter of each species crown, and the percentage of the transect they cover are listed in Table 1. As a "recruit", we defined young woody perennial plants, or longlived herbs, that did not reach their reproductive stage as not having set a negligible number of flowers or fruits compared to the crop produced by a fully grown adult of the same species (Alcántara et al. 2019; Verdú et al. 2023). Suppressed adult individuals of the species and vegetative sprouts were not counted as recruits and in case of doubt, the recruits were ignored. Plant-plant interactions based on the co-occurrence of adults were excluded because

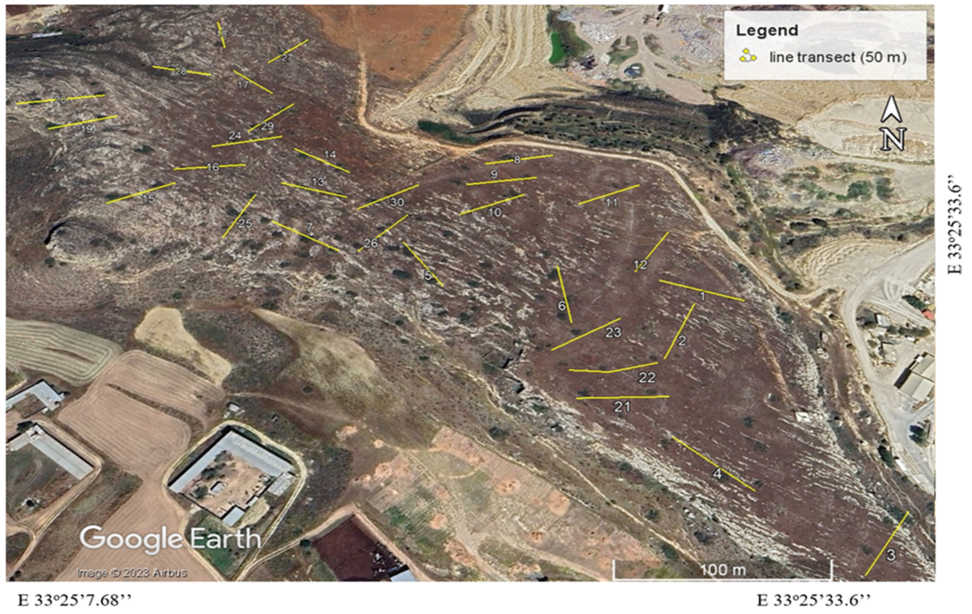

Figure 2. Aerial photo of the study area, with the location of the thirty line transects (yellow lines). For each line transect, we recorded: the number and intercept distance of canopies per species, the number and intercept distance of open ground, and the number of recruits per species under each canopy and in open ground.

of the impossibility of discerning between the canopy and the recruited species (Verdú et al. 2023). A detailed list of all the species identified as recruits can be found in Table 3.

Statistical analysis

To determine whether facilitation contributes to the structure of the phryganic community, the number of recruits was used as an indicator of the strength of facilitation interactions. We compared the distribution of recruits among all the canopies and open ground with the random distribution expected by chance (i.e. compared to the expected number of recruits under canopies, and in the open ground if their presence were determined solely by the percentage of the lines intercepted by canopies versus open ground, in total). To determine whether shrubs and subshrubs with larger crowns will provide a more efficient canopy service, we compared the distribution of recruits among each canopy species with the random distribution expected by chance (i.e. based on the percentage of the lines intercepted by each canopy). A chi square goodness of fit test was used after verifying the assumptions that the sample was sufficient and randomly drawn from the population and that each category contained more than 20 coexisting observations (Table 3). A *P* value less than 0.05 indicated statistical significance. A species was considered as a facilitator when the total number of recruits under its canopies was greater than that expected by chance. A species was considered as being favored by facilitation when the number of recruits under canopy plants was greater than that expected by chance. Statistical analysis was carried out using the IBM SPSS program v. 25.0.

To determine whether the architecture of the facilitative interactions in phryganic communities resembles that of other arid environments, showing low connectance (<30%) and a nested pattern, the facilitation interactions in the community were depicted as a network. The quantitative matrix (0/1 matrix; 0: not statistically significant or no cooccurrences; 1: statistically significant cooccurrences) contained only the associations between recruits and canopy species (i.e. nurses) proven to be higher than expected by chance according to the Chi square test. Thus, the network was formed by two sets of nodes (i.e. nurses and the recruited plant species) linked by interactions between any species pair. Using this matrix, we calculated the network's nestedness and connectance. To measure nestedness per se we chose the Nestedness metric based on Overlap and Decreasing Fill (NODF) (Almeida-Neto et al. 2008), using the opensource application for nestedness analysis NeD (Strona et al. 2014). The value of NODF increases with nestedness up to 100 for perfectly nested matrices. To assess the significance of NODF we used two null models (EE and CE) provided by the NeD software. The randomization algorithms of the null models followed the following rules: (1) EE (equiprobable row totals, equiprobable column totals) which maintains the total number of species occurrences in the matrix, but allows both row and column totals to vary freely; (2) CE, probability of a cell aij shows the average of the probabilities of occupancy of its row and column and is calculated by the equation: $CE = \left(Pi / Col + \mathrm{Pj} / R \right) \div 2$, in which *Pi* is the number of presences in row *i*, *Pj* is the number of presences in the column *j*, *Col* is the number of columns and *R* is the number of rows. The value of *P* was estimated using both the null models.

Connectance (C) was calculated by the equation $C = L / (S^2 - S)$ in which *L* is the total number of interactions observed in the assemblage and *S* is the number of species observed in the assemblage (Pulgar et al. 2017).

Table 1. A detailed list of all the species that acted as canopies in the line transects.

Canopy species	Growth form	Average diameter and standard error of the crown (m)	Percentage of the transect covered (%)
Ziziphus lotus	Shrub	4.5 ± 0.27	21%
Noaea mucronata	Subshrub	0.35 ± 0.01	11%
Thymbra capitata	Subshrub	0.3 ± 0.01	6%
Asparagus stipularis	Liana	0.4 ± 0.23	<1%
Rhamnus oleoides subsp. *graecus*	Shrub	1.8 ± 0.21	<1%
Sarcopoterium spinosum	Shrub	0.7 ± 0.04	<1%

Each species' growth form, the average diameter of the crown, and the percentage of the transect they cover.

Results

The plant community is structured by facilitation

Our results showed that overall the observed number of recruits under canopies was more than double the expected number (914 versus 386, respectively). The observed number of recruits in the open ground was 160, and the expected number was 688 (ca. four times less than expected) (x^2 (1, $N = 1074$) = 1128.7, $p < 0.0001$) (Table 2; Figures 3 and 4).

Shrubs and subshrubs with larger crowns provide a more efficient canopy service

From the species effectively acting as nurse plants, *Z. lotus* showed a significantly greater density of recruits under its canopy (i.e. nurse) compared to the density of recruits under the other nurses in total (x^2 (1, $N = 914$) = 226.535, $p < 0.0001$). The observed number of recruits under *Z. lotus* was 746 while the expected number was 521 (ca. 1.4 times higher than expected) (Figure 5). *Thymbra capitata* and *Noaea*

Table 2. Descriptive statistics of the study community.

No. species	No. nurse species	No. species recruiting under nurses	No. recruits under nurse plants	No. recruits in open ground	Percentage (%) of the lines intercepted by nurse plants	Percentage (%) of the lines with open ground	x^2	*P*
11	6	9	914	160	37	63	1128.7*	< 0.0001

*The tare x^2 test is significant since the observed number of recruits (all species pooled) under nurses is higher than expected by chance (i.e. based on the total percentage of all the lines intercepted by nurses versus open ground).

mucronata showed a smaller canopy service since the observed number of recruits under *Thymbra capitata* was 75 while the expected number was 148 (approx. 2 times less than expected; x^2 (1, $N=914$) = 41.314, $p<0.0001$) and the observed number of recruits under *Noaea mucronata* was 41 while the expected number was 269 (approx. 6.6 times less than expected; x^2 (1, $N=914$) = 273.331, $p<0.0001$) (Figure 5).

Due to the small number of individuals observed under *Asparagus stipularis, Sarcopoterium spinosum,* and *Rhamnus oleoides* subsp. graecus it was not possible to conduct this statistical analysis for them. All species recorded with at least one recruit under its canopy, linked with their recruited species, are presented in Figure 4. *Crataegus azarolus* var. *aronia*, *Helianthemum obtusifolium*, *Phagnalon rupestre*, and *Teucrium micropodioides* were never observed as canopy species, *Ziziphus lotus* was never observed as a recruit, and *Anthemis tricolor* was only observed in open ground never acting as a canopy species. The number of recruits per canopy species and in open ground are presented in Table 3.

Species facilitated by nurses

Asparagus stipularis, *Phagnalon rupestre, Noaea mucronata*, and *Sarcopoterium spinosum* showed a significantly higher number of recruits under nurses (approximately 2.6, 2.7, 2, and 2.6 times more recruits were found under a nurse than expected, respectively) at $p<0.0001$ (Figure 6). However, the recruits of *Thymbra capitata* were randomly distributed at $p=0.496$ (Figure 6).

Recruits of *Asparagus stipularis*, *Phagnalon rupestre, Noaea mucronata*, and *Thymbra capitata* showed a statistically higher dependency on *Z. lotus* as their nurse plant than on other nurse plants in the community (approximately 1.6, 1.7, 1.6, and 1.5 times more recruits were found under *Z. lotus* than expected, respectively) (Figure 7).

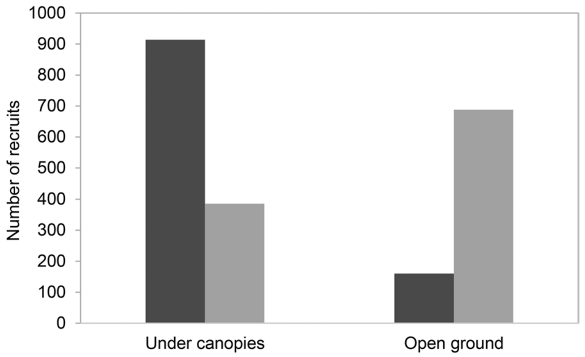

Figure 3. The observed number of recruits (dark grey) vs. the expected number (light grey), under canopies and open ground, respectively. The boxes' range represents the recruits' numbers at $p<0.0001$.

Due to the small number of individuals observed, statistical analysis for the species: *Anthemis tricolor, Rhamnus oleoides* subsp. *graecus*, *Crataegus azarolus* var. *aronia*, *Helianthemum obtusifolium,* and *Teucrium micropodioides* were not possible. The numbers of all plants recorded as recruits under nurses and in open ground are presented in Table 3.

Network nestedness analysis

NODF analysis confirmed that species interactions were significantly more nested than would be expected by chance ($\mathrm{NODF}_{\mathrm{Total}}$ = 87.09, $p<0.001$). The nestedness contribution of recruits ($\mathrm{NODF}_{\mathrm{Row}}$) was smaller than the nestedness contribution of canopies ($\mathrm{NODF}_{\mathrm{Column}}$) (Table 4). The nestedness observed in the network was significantly larger than that expected by both null models ($\mathrm{NODF}_{\mathrm{Total}}$ (EE)= 53.068; $\mathrm{NODF}_{\mathrm{Total}}$ (CE)= 53.37) (Table 4). The community was characterized by a low connectance ($C=0.26$), all the interactions between canopies and their recruited plants are shown in Figure 4.

Discussion

Plant communities characterized by a network like structure have been observed in various ecosystems, such as the creosote bush scrub communities in North American desert (Verdú and Valiente-Banuet 2011), the forest communities and anthropogenic micro deserts of high salinity in south eastern Spain (Alcántara and Rey 2012; Navarro-Cano et al. 2021) or the alpine and tropical alpine plant communities (Anthelme and Dangles 2012; Losapio et al. 2019; Pescador et al. 2020). The semi arid phryganic plant community with *Ziziphus lotus* (0.135 km^2) is similarly structured by facilitation. About twice as many recruited plants were encountered under the canopies of facilitators versus open ground (Figure 3). The architecture of the facilitative interactions in the phryganic community resembles that of other arid environments and is characterized by a non-random, nested pattern. In particular, the community exhibited high NODF values, significantly different ($p<0.001$) relative to the simulated values created by two null models (Table 4) and a low connectance value (26% of the potential links). Out of the eleven woody species and long lived herbs found in this low species richness community, ten were part of the facilitation network which may be one of the reasons behind its high nestedness.

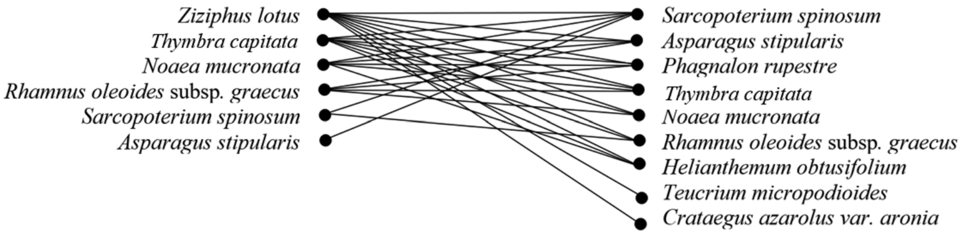

Figure 4. Facilitation network of the community, showing the interactions between nurses (left) and their recruited species (right). Note that *anthemis tricolor* is not present in the network since it was only found in open ground.

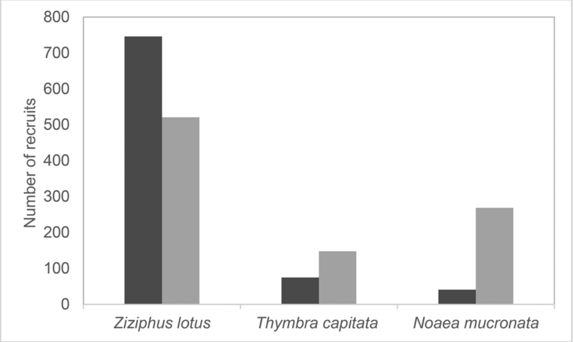

Figure 5. The observed number of recruits (dark grey) vs the expected number of recruits (light grey) under *Ziziphus lotus*, *Thymbra capitata,* and *Noaea mucronata*. The boxes' range represents the recruits' numbers at $p < 0.0001$.

The high nestedness is a characteristic of communities with low species richness (Pescador et al. 2020), in which the meta-community follows a dynamic process with a dominant species (i.e. a nurse plant such as *Z. lotus*) and the rest of the species arranged in sequential order according to ecological factors (Ulrich et al. 2009). These results indicate a high degree of regularity in the assembly of plant species within the community, suggesting that a facilitator's network is fundamental for maintaining plant diversity in such phryganic communities.

Although nestedness studies in a post community context are conducted on large spatial scales, spatial community scale studies can help us identify biotic interactions that play a dominant role in the construction of a plant community (Burns 2007). These biotic drivers were evidenced by the presence of significant interactions among specific species in our phryganic community reflected in the low connectance between facilitators and their facilitated plant species. A similar network was described for Mediterranean alpine grasslands (plant–patch network nestedness) by Pescador et al. (2020).

Shrubs and subshrubs with larger crowns provided a more efficient canopy service. *Z. lotus*, an established facilitator in the community, also characterized as an ecosystem engineer (Constantinou et al. 2021; 2023), was the species with the largest crown in diameter (Table 1; Figure 5). It demonstrated the highest facilitation capacity (ca. 1.4 times higher than expected) followed by facilitators with smaller in diameter crowns such as *Thymbra capitata* and *Noaea mucronata* (Table 1 and Figure 5). The facilitator's size is expected to increase the frequency of facilitative interactions (Callaway and Walker 1997; Anthelme and Dangles 2012). The increased ability of *Z. lotus* to facilitate plants under its canopy compared to the other facilitating species in the community with smaller crowns can be related to its capacity to efficiently concentrate resources under its foliage (Connor and McCoy 2001; Constantinou et al. 2021). Microclimate and moisture availability most likely become more favorable for plant establishment under the large and dense *Z. lotus* crowns, since high levels of solar radiation and soil evaporative forcing in drylands, can become limiting for germination and sapling establishment (Príncipe et al. 2019).

Biotic interactions can play a dominant role in structuring a plant community (Olesen and Jordano 2002; Verdú and

Table 3. The percentage (%) of the line intercepted by each nurse species and open ground and the number of recruits per species, respectively.

	Number of recruits per species									
Canopy species and open ground (% of the line intercepted by the canopy species)	*Asparagus stipularis*	*Noaea mucronata*	*Phagnalon rupestre*	*Thymbra capitata*	*Sarcopoterium spinosum*	*Helianthemum obtusifolium*	*Teucrium micropodioides*	*Rhamnus oleoides* subsp. *graecus*	*Crataegus azarolus* var. *aronia*	*Anthemis tricolor*
Ziziphus lotus (~21%)	347	174	125	47	23	2	15	10	2	
Noaea mucronata (~11%)	8		27	2	2	2				
Thymbra capitata (~6%)	15	23	29	**2**	1	2		3		
Asparagus stipularis (<1%)					1					
Rhamnus oleoides subsp. *graecus* (<1%)	2	2	1	1						
Sarcopoterium spinosum (~1%)					**42**			2		
Open ground (~63%)	24	86	23	80	2	8	20	9		2

Interspecific interactions are in bold.

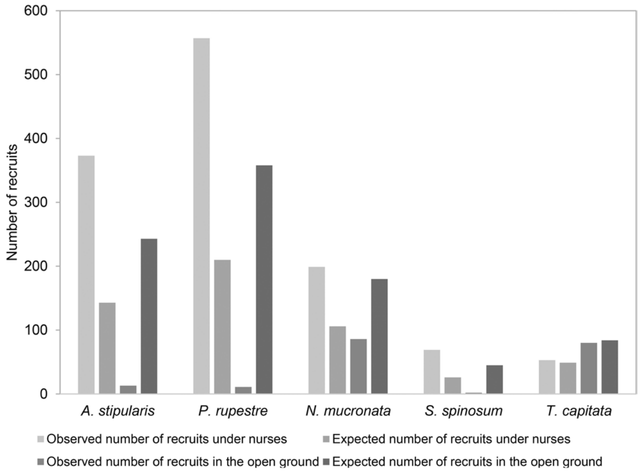

Figure 6. The observed number of recruits vs the expected number of recruits under nurses and in open ground for *Asparagus stipularis*, *Phagnalon rupestre*, *Noaea mucronata*, *Sarcopoterium spinosum* ($p < 0.0001$), and *Thymbra capitata* ($p = 0.496$).

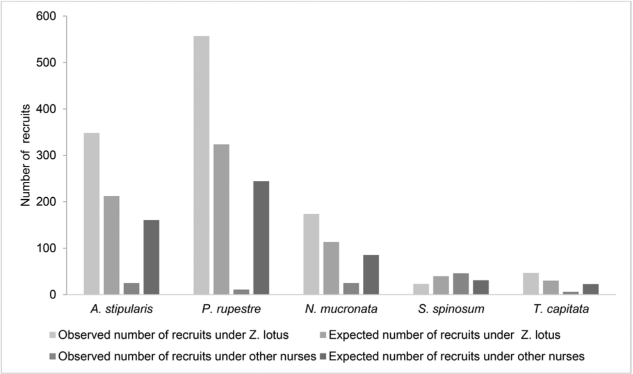

Figure 7. The observed number of recruits vs the expected number of recruits under *Z. lotus* and other canopies for *Asparagus stipularis*, *Phagnalon rupestre*, *Noaea mucronata*, *Sarcopoterium spinosum* and *Thymbra capitata* ($p < 0.0001$).

Table 4. NODF measure of nestedness.

	Total	Column (canopies)	Row (recruits)
NODF	87.09	86.57	88.33
NODF (EE)	53.068	54.176	52.61
NODF (CE)	53.37	56.03	52.26

NODFTotal: total matrix nestedness; NODFColum: nestedness among all columns (canopies); NODFRow: nestedness among all rows (recruits); NODF(EE): nestedness of null model EE (equiprobable row totals, equiprobable column totals) which maintains the total number of species occurrences in the matrix, but allows both row and column totals to vary freely; NODF(CE): nestedness of null model where the probability of a cell *aij* showing a presence is ($Pi/Col + Pj/R$)÷2, in which *Pi* is the number of presences in row *i*, *Pj* is the number of presences in the column *j*, *Col* is the number of columns and *R* is the number of rows.

Valiente-Banuet 2008). Following the theory of mutualistic networks (Bastolla et al. 2009), the observed nested patterns may be driven by positive associations among the facilitators and their recruits. This can promote the patched distribution observed, as the product of subsets of a common species pool, rather than plant spatial patterns defined by chance (Fortuna et al. 2010). By defining the extent of each species' recruits under facilitators within the community we discovered that *Asparagus stipularis*, *Phagnalon rupestre*, *Noaea mucronata*, and *Sarcopoterium spinosum* had almost a three times higher number of recruits under nurse plants than expected by chance (Figure 6). This dependence proved to be higher towards *Z. lotus*, the species with the largest crown in diameter, regarding *Asparagus stipularis*, *Phagnalon rupestre*, and *Noaea mucronata* (approximately two times more recruits were found under *Z. lotus*) (Figure 7). *Sarcopoterium spinosum* was mostly facilitated by adult plants of its species (Figure 7). This could be due to a process of autofacilitation, or seep trap or limited dispersal. Out of the ten perennial species present at the site, *Ziziphus lotus* was the only species that did not display any dependence on nurses for its regeneration (Table 3). Furthermore, *Thymbra capitata* although present as a recruit under nurses, mainly under *Z. lotus* (Figure 7), did now show any statistically significant dependence on them (Figure 6).

The plant community's resistance to the loss of species is highly related to the structure of plant to plant interaction networks (Verdú and Valiente-Banuet 2011; Alcántara and Rey 2012; Pulgar et al. 2017). Thus, the high nestedness and low connectance in the phryganic community detected herein suggest robustness to species loss and structure breakdown (Verdú and Valiente-Banuet 2008). Then again, the robustness of the community's structure may be threatened if extinction affects the most connected species (Verdú and Valiente-Banuet 2008). In our case, the most connected nurse species were found to be *Z. lotus*, *T. capitata*, and *N. mucronata*. Thus, removing or reducing their populations could have detrimental effects on the regeneration of many other species within the community (Table 3; Dunne 2006; Valiente-Banuet and Verdú 2013). Since benefactor species are key for conservation efforts in communities governed by facilitation (Altieri et al. 2007) *Z. lotus*, *T. capitata*, and *N. mucronata* should be the keystones of any conservation attempt to protect the community's biodiversity and preserve the ecosystem services it provides.

Among the three nurse species, *Z. lotus* was found to be both the most connected and the most abundant nurse species (ca. 57% of the area occupied by the nurses corresponds to the ground covered by *Z. lotus*). Therefore, prioritizing its conservation may provide the community with resistance to climate change or other anthropogenic related pressures. Note that the facilitation properties of *Z. lotus* have so far been documented for an area that exceeds up to 5 meters outside its crown. *T. capitata* has been found with significantly increased densities and soil moisture availability within this zone, most likely because of the hydraulic lifting properties of *Z. lotus* (Constantinou et al. 2023). The significant effect that *Z. lotus* has been found to exercise on thyme populations provides additional support to the hierarchy suggested above in terms of conservation prioritization. However, we demonstrate here for the first time that the crown of *Z. lotus*, despite having a profound role in the regeneration of most plants in the community, does not appear to positively influence *T. capitata*. Our results suggest that *T. capitata* is most likely a light-demanding species that cannot cope efficiently with the light stress conditions created within *Z. lotus* crown nor under other nurses (Figure 6).

Most plant to plant interaction networks studied in other arid environments report connectance below 30% (Alcántara et al. 2019). The connectance we recorded in the community reached 26%. Neutral or positive interspecific interactions were more frequent while intraspecific interactions, although present, were much less frequent (Table 3). The frequency of canopy–recruit interactions is positively related to the abundance of the interacting species (Verdú and Valiente-Banuet, 2011; Marcilio-Silva et al. 2015; Alcántara et al. 2018). Our results revealed that the canopy recruit interactions are not only explained by the species abundance suggesting that there can be other ecological processes beyond species abundance that shape these species-specific interactions (Figure 3, 5–7). Alcántara et al. (2018) suggested that an important proportion of potential interactions is impeded for ecological reasons. In addition, the frequency of any individual canopy–recruit interaction results from the balance between multiple positive and negative interactions, which can be determined by multiple factors. Nonetheless, water availability is the most limiting factor for plant productivity in dryland ecosystems (Sarris et al. 2011; Dorman et al. 2015; Griffin-Nolan et al. 2018).

This priority habitat is listed in European habitat types as East Mediterranean phrygana (formations with lower *Z. lotus* shrubs) and Mediterranean arborescent scrubs with *Z. lotus* (European Red List of Habitats 2016; Mendoza-Fernández et al. 2019). These plant communities can be found in the Iberian Southeast, Cyprus, Sicily, and surrounding islands under a xerophytic thermo Mediterranean bioclimate. However, *Z. lotus* natural distribution range covers the entire North Africa, Asia Minor, and countries of the Middle East. Furthermore, Ziziphus forms the type of vegetation that can produce the maximum biomass to the existing climate (Mendoza-Fernández et al. 2019) making its conservation/restoration valuable for boosting ecosystem productivity and combating desertification phenomena (Constantinou et al. 2023). This study is the very first attempt to evaluate the presence and structure of ecological networks in plant communities of Cyprus, providing much needed knowledge about the interactions forming phryganic communities, particularly under the influence of an ecosystem engineer species. Since the study focused exclusively on the recruitment stage, the possibility that facilitation might shift to competition when facilitated plants grow up cannot be disregarded (Tielborger and Kadmon 2000). Although there is increasing evidence of the permanence of the nature of the interactions between functionally different species exists (Navarro-Cano et al. 2019), a further evaluation of phryganic communities is needed to establish knowledge regarding species interactions in their adult form (Sortibrán et al. 2014, 2019; Montesinos-Navarro et al. 2016a, 2016b, 2017). A further investigation of the nurse plant traits, beyond the diameter of their crown, will allow us to better understand how biodiversity in the phryganic communities is shaped and how to apply this knowledge to restore species (Navarro-Cano et al. 2021) and ecosystem functions (Montoya et al. 2012; Navarro-Cano et al. 2018).

Disclosure statement

The authors report no potential conflict of interest.

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