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FACILITATION INTERACTIONS IN DRYLAND ECOSYSTEMS OF CYPRUS, BASED ON *ZIZIPHUS LOTUS*

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Summary

Drylands cover ca. 40% of the Earth's land surface. Positive interactions between nurse plants and their facilitated species are highly present in these habitats, where water availability is the key limiting factor for plant productivity. Plant communities characterized by a network-like structure have been observed in various ecosystems. However, it is unknown if facilitation governs the structure of phryganic plant communities, which adult species are effective as facilitators, and which species are more dependent on facilitation. To answer this, we assessed the percentage of young plants under the canopy of adult species compared to open ground and the presence of a nested pattern, in a 0.136 km^2 experimental site. Phryganic plant communities with *Ziziphus lotus*, in Cyprus, are characterized by a non-random, nested pattern exhibiting high NODF values ($p<0.001$). *Ziziphus lotus*, *Thymus capitatus*, and *Noaea mucronata* are the main facilitators in the community. *Asparagus stipularis*, *Phagnalon rupestre*, *Noaea mucronata*, and *Sarcopoterium spinosum* proved to be highly dependent on nurses. For such ecosystems to retain productivity and biodiversity, would be valuable to identify/promote keystone plant species that (i) have developed strategies to more efficiently utilize moisture resources not easily accessible and (ii) improve moisture conditions for neighboring plants. The very deep-rooted *Ziziphus lotus,* considered an ecosystem engineer, is one such example. However, it is not known which biotic traits: (a) canopy interception of moisture/rainfall, (b) hydraulic redistribution of deep ground moisture by roots, or non-biotic factors: (c) soil's volume, and (d) organic matter content, *Z. lotus* activates/modulates to play such a role. We, thus, selected dryland ecosystems where the plant dominates and measured for potential effects on the less deep-rooted *Thymbra capitata*. For assessing impacts on ecosystem productivity, we measured the spatial aggregation of ca. 3600 *T. capitata* plants. As a proxy for soil moisture availability (SMA) and its spatial variability, we conducted a seven-year-long study using thymes' nighttime rehydration. Sampling extended up to 15m away from *Z. lotus.* The density of *T. capitata* plants growing up to 5m around *Z. lotus* vs. thymes growing 10–15m away was found significantly increased (2.5 to 4.5 times), while their stem/leaf moisture was ca. 10% higher at predawn compared to nightfall during the dry season. This suggests that ecosystem productivity is driven by a greater SMA around *Z. lotus* permitting more thyme daytime transpiration, in contrast to thymes growing further away. The phenomenon appeared only under dry topsoil (during the dry season; becoming stronger during dry climatic years). Nor did

morning dew/rainfall interception from the canopy or soil depth/organic matter show significant effects, leaving only the hydraulic lift (HL) properties of *Z. lotus* as the most likely driver for SMA. Density and stem moisture for thymes growing near *Z. lotus* do not seem to be significantly affected by topography. Thus, the deep-rooting properties and HL potential of *Z. lotus* may be the key to enabling it to boost ecosystem productivity. Knowing species interactions and the traits that form them will allow us to better understand how biodiversity in the phryganic communities is shaped. This way we will be able to apply this knowledge to restore species and ecosystem functions.

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List of Acronyms

CDE Cyprus Department of Environment

DOC dissolvable organic carbon

EUNIS European Nature Information System

FNs Facilitation Networks

HD Hydraulic Diameter

HL Hydraulic Lift

HR hydraulic redistribution

IDM De Martonne Aridity Index

IQR interquartile range

MC moisture content

MCD Moisture Content Difference index

MTEs Mediterranean-Type Ecosystems

NODF Nestedness metric based on Overlap and Decreasing Fill

RNs Recruitment Networks

SE Standard Error

SGH Stress-Gradient Hypothesis

SLA Specific Leaf Area

SMA Soil Moisture Availability

TOC Total Organic Carbon

VWC Volumetric Water Content

WD Wood Density

Chapter 1

Introduction

1.1 Background

Plant–plant interactions play a key role in regulating the composition of communities and ecosystems (Brooker, 2006). They demonstrate impacts that spread across all ecosystems by affecting resource availability and habitat structure. Facilitative interactions, in particular, are very important to promote plant species survival under environmental conditions that would otherwise be too stressful for them (Choler et al., 2001; Cavieres et al., 2002), and thus effectively influencing their realized niche (Bruno et al., 2003). Many studies that have successfully incorporated multiple species interactions, including facilitation, have clearly demonstrated that community assembly cannot be adequately understood when viewed simply as a sum of pairwise species interactions (Bertness et al., 2006; van de Koppel et al., 2006). One way of illustrating the complexity resulting from multiple interactions in plant communities is to conceive plant communities as ecological networks in which species interact with others associated with one or more other species (Valiente-Banuet, 2008). The extinction of these ecological interactions is an important component of biodiversity loss that goes along with or may even precede species extinctions (Janzen, 1974; Tylianakis et al., 2008; Aizen, Sabatino & Tylianakis, 2012). The main anthropogenic drivers of the extinction of ecological interactions and species are currently the fast-paced rates of habitat loss and fragmentation, and large-scale disturbances (e.g., biological invasions and habitat degradation) (Valiente-Banuet et al., 2015). Thus, the study of plant-to-plant interactions is a major although often neglected component of biodiversity that needs to be addressed in order to assess ecosystem health and define critical indicators providing early diagnosis of environmental problems (Tylianakis et al., 2010; Aizen, Sabatino & Tylianakis, 2012; Dirzo et al., 2014; Valiente-Banuet et al., 2015). Through this knowledge, we will in turn improve our ability to understand, predict and even reduce environmental change's impacts on ecosystems. The identification of facilitators or nurse plants, plants that positively affect and enhance the growth as well as survival rates of seedlings and plants under them (Egerton et al., 2000; Tewksbury and Lloyd, 2001; Pugnaire et al., 1996a, b; Holzapfel and Mahall, 1999) is an important step towards the conservation and effective restoration of plant communities and ecosystems. Understanding the formation of positive interaction networks, such as facilitation networks, within communities is also a necessary tool for the realization of this goal. Positive interaction networks provide information regarding the effects of the interaction on a population (demographic) level enabling ecologists to link interaction networks with the analysis of plant community dynamics (Verdú and Valiente-Banuet, 2008; Levine, Bascompte, Adler, & Allesina, 2017).

Phryganic communities are the most common and resilient communities in the Mediterranean region (Tsiourlis, Konstantinidis, and Xofis, 2007; European Red List of Habitats, 2016). They have been shaped by anthropogenic pressures for hundreds of years adapted to the the region's conditions. Due to the socio-economic changes of the last 50 years (Moatti & Thiébault, 2016), there is an increasing trend in their quality and quantity. As a result, they are a "least concerned" habitat (according to the European Red List of Habitats 2016) since they have an extensive distribution in the Eastern Mediterranean and there has not been any recorded decline to their extent or quality. At the same time, they are the biotic communities whose species seem to be the least affected by climate change (Harrison et al., 2006). Nevertheless, prognoses of species range losses across the Mediterranean cannot be taken as precise forecasts. In fact, prognoses could be really underestimating the risks given the uncertainties in climate change scenarios, and the effect of important disturbances such as land use change, fires, and their synergistic effects (Morán-Ordóñez et al., 2019, IPBES, 2019). Phryganic communities, as part of dryland biodiversity, offer significant global economic value, providing biodiversity products and ecosystem services (Balzan et al., 2020). Many cultivated plants originate from the drylands, thus providing an important genetic reservoir as climate change creates a demand for new adaptations and results in the extinction of wild breeds. Also, services such as cultural identity and spirituality are central to dryland cultures and can be integral to the protection of dryland ecosystems since there has been an observable correlation between land degradation and cultural degradation in drylands demonstrating their interconnectedness (Davies et al., 2012).

This demonstrates the importance of sustaining plant communities in the driest parts of the Mediterranean region and the need to study and protect them from ever-increasing anthropogenic pressures.

The physiology and adaptations of the plants shaping these ecosystems as well as their composition are well-documented (Margaris and Vokou, 1982; Galmés et al., 2011; EUNIS, 2019). The importance of dominant perennial plants' facilitating effect and the consequent formation of "fertile islands" is also well documented (He et al., 2013; Gómez-Aparicio et al., 2005; Pugnaire et al., 2011; Navarro-Cano et al., 2015; Pinna et al., 2021). However, there is a gap in our knowledge regarding the identification of the facilitative interactions that play a dominant role in the construction of phryganic plant communities and regulate their pesistence and composition. In particular, the identification of key facilitators and species that depend heavily on facilitation is important for assessing the resilience of the plant community to extinction (Verdú and Valiente-Banuet, 2008; Alcántara and Rey, 2012; Pulgar et al., 2017).

1.2 Mediterranean-Type Shrublands

The Mediterranean basin has probably played the most fundamental role in the historical evolution of humankind through the development of numerous civilizations (Di Castri and Mooney, 1973). Today's human-made Mediterranean landscapes are the result of the transformation and shaping of primitive ecosystems by these civilizations. Agriculture and animal husbandry by the old Mediterranean civilizations, dated earlier than 10 000 BP in the eastern Mediterranean and around 8000 BP in Greece and the western Mediterranean, reshaped natural forests into more diversified landscapes, creating in many regions land use models whose aim was to achieve sustainable long-term ecosystem management (Joffre et al., 2007). The long-term management of Mediterranean ecosystems has not always resulted in a decrease in biodiversity but on the contrary has been beneficial for many of its components (Davis and Richardson, 1995).

In addition to the Mediterranean basin, Mediterranean-type ecosystems (MTEs) are found in four other world regions: California, southwestern and southern Australia, central Chile, and southern Africa. Despite their large geographical separation, these ecosystems show strong similarities not only in terms of their climatic trends but also in terms of vegetation structure and general patterns of land use and landscape appearance. The availability of water, along with the lack of nutrients in the soil, are the main environmental factors that exert the strongest control over the productivity of plants affecting the nature and distribution of vegetation in the Mediterranean Basin. Therefore, the 400 mm isohyet of the mean annual rainfall (P) is used to distinguish the EU-Mediterranean zone (P>400 mm) from the steppe-Mediterranean zone (P <400 mm) (Joffre and Rambal, 2002). Zones receiving less than 100 mm of annual rainfall are considered deserts and they are excluded from the Mediterranean climate area. Based on these criteria the Mediterranean ecosystems occupy a total area of about 2.76 Mkm^2 corresponding to 2.3% of the Earth's surface. The largest region is around the Mediterranean Basin with 1.68 Mkm^2 (60% of the total Mediterranean climate area), followed by 0.28, 0.61, 0.13, and 0.06 Mkm^2 for California, Australia, Chile, and South Africa, respectively.

There is an enormous literature addressing the strong similarities between the floras of MTEs throughout the world (Di Castri and Mooney, 1973; Di Castri et al., 1981; Davis and Richardson, 1995). The Mediterranean floras of the northern hemisphere (the Mediterranean Basin and California) contain elements from two broad categories, Palaeo- and Neo-Mediterranean. The floras of the Mediterranean Basin and California have their common origin in the fact that Europe and North America were in contact until the late Cretaceous and began to break apart 160 million years ago. Therefore, many genera of woody plants associated with the Arcto-Tertiary flora are common to the Mediterranean region and California, having a major contribution to the vegetation of both regions (Di Castri and Mooney, 1973). The main representatives of the woody plants associated with the Arcto-Tertiary flora in the Mediterranean Basin include genera such as *Acer*, *Aesculus*, *Alnus*, *Arbutus*, *Cercis*, *Clematis*, *Crataegus*, *Cupressus*, *Fraxinus*, *Juniperus*, *Lonicera*, *Pinus*, *Platanus*, *Populus*, *Prunus*, *Quercus*, *Rhamnus*, *Rosa*, *Rubus*, *Smilax*, *Styrax*, *Viburnum*, and *Vitis*. The 'NeoMediterranean' genera representing taxa that appeared after the establishment of a Mediterranean-type climate in the Mediterranean Basin include genera such *Amelanchier*, *Cistus*, *Clematis*, *Halimium*, and *Helianthemum*. There is also a strong presence of genera that seem to have been associated with semiarid fringes of the tropics in Eurasia including genera such as *Ceratonia*, *Chamaerops*, *Cotinus*, *Laurus*, *Myrtus*, *Olea*, *Paliurus*, and *Phillyrea*. About 10% of the genera and more than 40% of the species in each of the northern Mediterranean areas are endemic (MedECC, 2020).

As indicated by the genera found in the Mediterranean Basin (Table 1.1), and in the other four MTEs regions alike, evergreen species are more abundant than deciduous ones and the vegetation formations are characterized by the dominance of trees and woody shrubs with small, sclerophyllous leaves. Nevertheless, while the woody shrub sclerophyllous growth form is the dominant element, it never represents the majority of the total flora. The main vegetation formations are called by different names in different MTEs regions (i.e., 'garrigue' or 'maquis' in France depending on the nature of the soil substrate (calcareous or siliceous), 'chaparral' in California, 'heath' and 'mallee' in Australia, 'matorral' in Chile and 'fynbos' in South Africa). This list is not exhaustive and other colloquial names may apply elsewhere for short to tall shrublands or woodlands. These formations are similar in their aspect and have provided the ideal testing ground for the theory of ecological convergence from evolutionary, morphological, and physiological points of view (Di Castri and Mooney, 1973). The importance of sclerophyllous evergreen plants has been interpreted as an adaptation to the unique environmental conditions associated with the Mediterranean climate. The possible functional role of sclerophylly has been interpreted in different ways: adaptation to drought, adaptation to nutrient deficiency in soils, and/or adaptation to herbivory.

Quézel (1981), distinguished the vegetation types of the Mediterranean region as arborescent matorral, maquis and garigue, and phrygana (Table 1.2). The vegetation was considered in terms of its general physiognomy and its response to some major biogeographical and ecological factors, and not in terms of its overall phytosociological interpretation. In literature, the Mediterranean basin ecosystems are divided into two geographical areas, the western and the eastern Mediterranean ecosystems (Di Castri et al., 1981; European Red List of Habitats, 2016).

Table 1. 1 Principal plant families and genera found in the Mediterranean Basin (Quézel, 1981)

Family	**Names of genera**
Fabaceae (Leguminosae)	*Adenocarpus, Anthyllis, Astragalus, Calicotome, Ceratonia, Coronilla, Cytisus, Cytisopsis, Dorycnium, Ebenus, Genista, Gonocytisus, Retama, Spartium, Ulex*
Lamiaceae	*Lavandula, Phlomis, Prasium, Rosmarinus, Salvia, Satureja (*incl. *Micromeria), Sideritis, Teucrium, Thymus, Thymbra*
Cistaceae	*Cistus, Fumana, Helianthemum, Halimium, Tuberaria*
Gymnospermae	*Pinus, Juniperus, Cupressus, Tetraclinis, Ephedra*
Asteraceae (Compositae)	*Centaurea, Artemisia, Phagnalon, Stahaelina*
Oleaceae	*Fontanesia, Jasminum, Olea, Phillyrea*
Ericaceae	*Erica, Calluna, Arbutus*
Liliaceae	*Asparagus, Ruscus, Smilax*
Rhamnaceae	*Rhamnus, Paliurus, Ziziphus*
Anacardiaceae	*Pistacia, Rhus*
Caprifoliaceae	*Viburnum, Lonicera*
Rosaceae	*Sarcopoterium, Prunus*
Thymelaeaceae	*Thymalaea, Daphne*
Aceraceae	*Acer*
Apiaceae	*Bupleurum*
Arecaceae	*Chamaerops*
Periplocaceae	*Periploca*
Boraginaceae	*Lithospermum*
Celastraceae	*Maytenus*
Cyperaceae	*Carex*
Euphorbiaceae	*Euphorbia*
Fagaceae	*Quercus*
Globulariaceae	*Globularia*
Hypericaceae	*Hypericum*
Lauraceae	*Laurus*
Linaceae	*Linum*
Myrtaceae	*Myrtus*
Polygalaceae	*Polygala*
Santalaceae	*Osyris*
Styracaceae	*Styrax*

Table 1. 2 The vegetation types of the Mediterranean region (Quézel, 1981)

Vegetation type	Definition
Matorral	By matorral, one means the formation of woody plants, whose aerial parts are not differentiated into trunk and leaves because they are much ramified from the base and are of shrubby habit, either upright or prostrate owing to the wind
Maquis	A dense mostly evergreen shrub community 1-3 m high characteristic of the Mediterranean region
Garrigue	A community of low scattered often spiny and aromatic shrubs of the Mediterranean region
Phrygana	A Greek term denoting low shrub developed over dry stony soil in the Mediterranean region. In general, is an equivalent term to garrigue which is used in the West Mediterranean.

1.2.1 Ecosystems of the Mediterranean Basin

In the western Mediterranean, the vegetation structure reaches its highest level of complexity (Quézel, 1981). In this region, arborescent matorral, both on calcareous and non-calcareous substrates, represent pre- or post-forest formations with a more or less dense arborescent cover and an evergreen shrub stratum. The structure of these communities is a priori hybrid since forest species, various species of the arid and semi-arid zones, and species characteristic of the maquis and garrigue coexist (Quézel, 1981; European Red List of Habitats, 2016). Regarding the presence of maquis and garrigue, there is no distinction between the two landscape types (calcareous and non-calcareous substrates) since they have a complete range of intermediate types. They represent the vegetation structure of the evergreen shrublands of the western Mediterranean Basin. Maquis and garrigue on non-calcareous substrates are very common and have great floristic richness (Quézel, 1981; Guarino et al., 2020). They are present in Spain, the south of Portugal, the Provence, on the North African coast, and in the east of Algeria and seem to belong to the class Cisto-Lavanduletea, which includes groups of evergreen nanophanerophytes and calcifugous chamaephytes. Phrygana, as heathing formations of mainly thorny, summer deciduous with a cushion habit chamaephytes, occupies only a small area in the western Mediterranean, in semi-arid north Africa, the calcareous coast of Provence, and Sardinia (European Red List of Habitats, 2016). The formations are included in the class Crithmo – Limoniatalia (Quézel, 1981).

In the eastern Mediterranean, two very distinct biogeographical areas are distinguished by Di Castri et al. (1981). One occurs on the Dalmatian coast, as far as the south of Epirus including parts of the Adriatic coast of Italy, and the other for the rest of the Basin. In the eastern Mediterranean area, there are many similarities between the floristic composition of the arborescent matorral on calcareous and non-calcareous substrates. On calcareous soils, the communities are formed by *Olea* and *Pistacia lentiscus*, sometimes with *Ceratonia*, by sclerophyllous and semi-deciduous oaks and Mediterranean conifers (European Red List of Habitats, 2016). Most of the species along with many phanerophytes and or nano phanerophytes occur on non-calcareous substrates as well. There is no distinction in classes between the maquis and garrigue on calcareous and non-calcareous substrates. In general, certain types of high maquis and arborescent matorral belong to Quercetea ilicis, and the lower formations belong to Cisto-Micromerietea. Particularly in Greece, western Anatolia, and Lebanon associations relating to the Cisto- Micromerietea and Cisto- Micromerietalia do occur but are rather poor floristically. In Greece and Anatolia, there are sporadic appearances of maquis with *Erica arborea* along with shrubby *Quercus ilex*. A special type of maquis and garrigue appear in southern Anatolia formed by *Pinus brutia* associated with *Quercus microphylla*. In Greece and Anatolia, maquis dominated by *Arbutus andrachne* associated with *Q. coccifera* (or *Quercus ilex*) appears on calcareous and marl substrates. The garrigue communities of the region belong to the Cistion orientale and are of numerous distinct groupings characterized by their richness in representatives of the genera *Phlomis*, *Salvia,* and *Sideritis*. In the eastern Mediterranean area, phrygana occupies an important place. They are present in Greece and the Aegean islands, the Anatolian coast, and the Middle East.

1.2.2 Mediterranean Phrygana

The term phrygana was first mentioned by Theophrastus, a Greek philosopher (371 – 287 BC), as follows: «... φρύγανον δε το από ρίζης πολυστέλεχες και πολύκλαδον, οίον και γάμβρη και πήγανον .... » (which means «... phryganon is the one that rises from the root with many stems and many branches; for instance, thymbra and peganum .... ») (Margaris, 1976). The term phrygana in the current sense was introduced, according to Margaris (1976), by Heldreich in 1877 and represents a formation in which the sub-shrubby plants, Theophrastus called phrygana, prevail. Much later we can find the term "phrygana" described as "perennial chamaephytes" by Kavvádas (1956). In the Greek literature, the term «διάπλαση Φρυγάνων», which is Greek for "Phrygana formations", has prevailed and according to Gkaniátsas (1967) is defined as a physiognomically well-shaped type of vegetation, composed of predominantly xeromorphous shrubs with scarce grasses as well as of geophytes". Phryganic ecosystems develop at the xerothermal edge of Mediterranean climate areas (Margaris, 1980; Margaris and Vokou, 1982; Papanastásis, 1984). The characteristic of phryganic ecosystems is that they are dominated by semi-shrubs, i.e., woody plants, with a height of less than one meter which are generally deciduous during the dry seasons and may be divided into various associations belonging mainly to the Cisto-Micromerietea (Quézel, 1981). Among the ground-covering shrubs, there are many gaps with herbaceous vegetation. In other words, phrygana is: "open woody plant communities with semi-shrubs as the main structural component and herbaceous vegetation as the secondary" (Papanastásis, 1984). Herbaceous vegetation is an important structural component of phryganic ecosystems, though its size and composition are not constant, but are influenced by many factors, among which are the specific climatic conditions and soil environment of the area, fire, and herbivores, especially livestock. It also seems that as we move from the warmest to the coldest part of the zone there is an increase in perennial herbaceous species at the expense of annuals (Papanastásis, 1984).

According to EUNIS habitat classification (2012 amended 2019), phrygana formations in the western part of the Mediterranean (or Western Mediterranean spiny heath) are rare and confined to rocky cliff tops, from southern Portugal to the Balearic and Tyrrhenian islands. Their further succession is limited by the shallow rocky soils on the steep slopes, the constant winds, the salt spray, and threats such as recreation and tourist infrastructure. Western Mediterranean phrygana total estimated area in Europe, based on the territorial data provided, is 241 Km^2 from which 19 Km^2 in Corsica and mainland France, 146 Km^2 in Sardinia and Sicily, 71 Km^2 in Malta, 4.3 Km^2 in Portugal and 6.4 Km^2 in the Balearic Islands and mainland Spain (European Red List of Habitats, 2016) (Fig. 1.1).

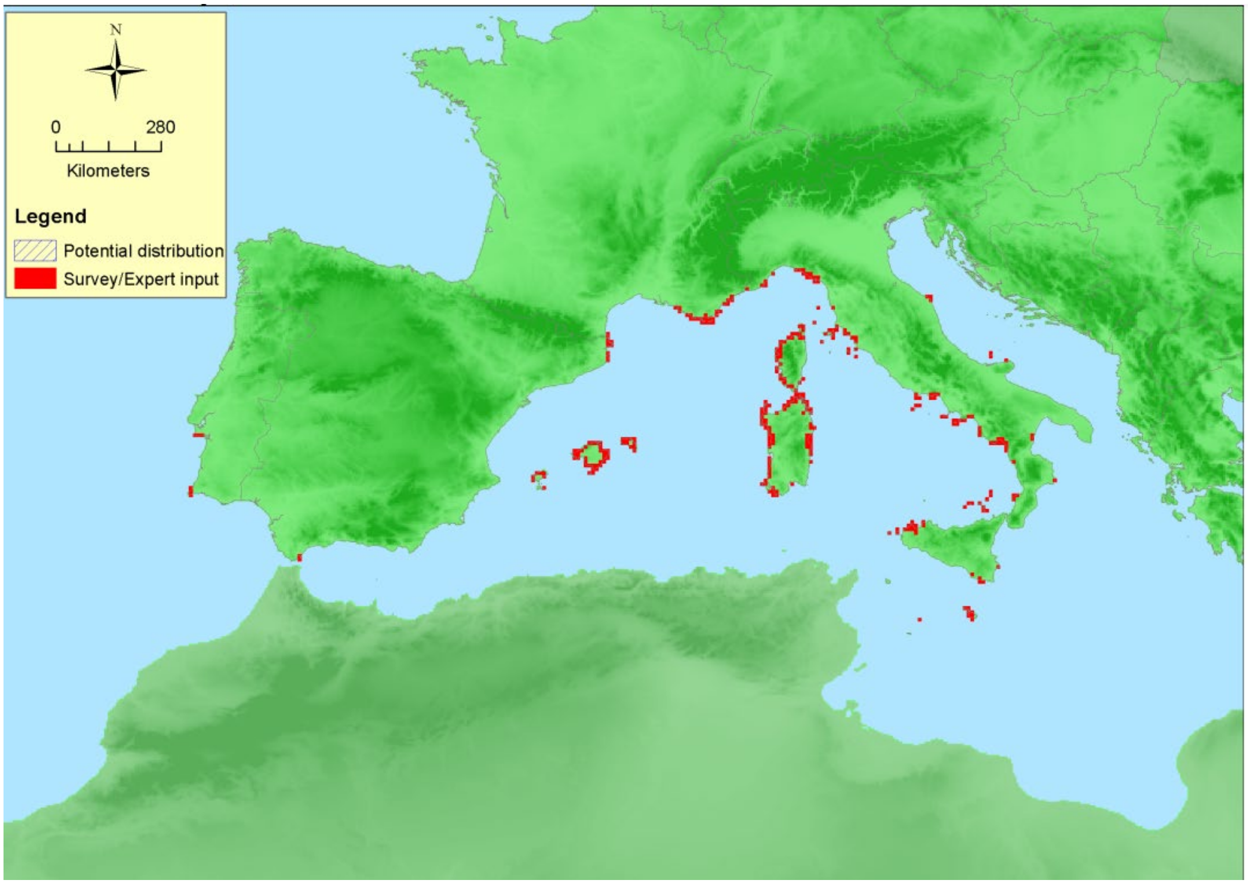


Figure 1. 1 Western Mediterranean Phrygana distribution map.The map likely provides the complete distribution of the habitat, with maybe some data gaps in Sicily and the southern Italian Peninsula (Source European Red List of Habitats - 2016).

In EUNIS habitat classification (2012 amended 2019), East Mediterranean phrygana (or Eastern Mediterranean spiny heath) is described as a habitat of low, thorny hemispherical shrubs and mat formers, widespread at low and middle altitudes in the eastern Mediterranean and Anatolian regions (Fig. 1.2). East Mediterranean phrygana is one of the most species-rich habitats of the Mediterranean basin and occurs naturally on dry sites with shallow soils. Only in Greece, phryganic communities cover more than ten million acres (Margaris, 1976; Papanastásis, 1984) and can be found in Crete and the Aegean islands all the way to Epirus and Macedonia, which represent the cold boundaries of their distribution in Greece. The East Mediterranean phrygana total estimated area in Europe, based on the territorial data provided (European Red List of Habitats 2016), is 8186 Km^2 from which 7910 Km^2 is in Crete, East Aegean islands, and Greece (mainland and other islands), 192 Km^2 is in Cyprus, 16.4 Km^2 is in Italy mainland and Sicily, and 1 Km^2 is in Malta. In other parts of its distribution, phrygana communities are of secondary origin as the result of a retrogressive succession of destroyed forests (Carlström, 1987) or evergreen sclerophyllous vegetation such as maquis or in other cases, different phrygana communities form stages of post-fire succession. On ex-arable land, after abandonment, phrygana communities of different predominating species, depending on the crop, can act as pioneers of ecosystems of progressive succession until their final stage "climax" (Dáphis, 1986). In Greece, phryganic ecosystem suffers from rainfall scarcity and uneven distribution and intensive grazing. Where the pressure of grazing is less, vegetation grows and some of the plants lose their characteristic hemispherical form. In these areas, the vegetation becomes higher and denser and is often mistakenly referred to as "maquis" vegetation, when only the height of the plants is taken into account (Carlström, 1987).

Human action has eliminated the original variability of the phrygana communities related to climatic factors, particularly in continental Greece; as a result, most of the phrygana communities in this part of the country are the result of human impact (Barbero and Quézel, 1989), being in most cases stages of human-made degradation of the original Mediterranean forest (European Red List of Habitats, 2016). Grazing at moderate intensity is one of the drivers that contribute to the preservation of favorable conservation status of the habitat structure, but intensive grazing contributes to the deterioration of its structure (Kachler et al.). Today the most important pressures faced by phrygana, beyond intensive grazing, are the creation and expansion of transport and service corridors as well as urbanization, residential and commercial development, recreation, and tourist infrastructure (European Red List of Habitats, 2016).

The phryganic formations of Greece, depending on the prevailing species, could be classified into seven main types (Margaris, 1976). The predominant species of the phryganic formations are *Sarcopoterium spinosum*, *Corydothymus capitatus* (=*Thymus capitatus*), *Satureja thybra*, *Genista acanthoclada*, *Anthylis hermaniae*, *Euphorbia acanthothamnos*, and *Phlomis fruticose* and their spread is directly related to the amount of their dynamic evapotranspiration. Debazec et Mavrommatis (1969), as cited by Papanastásis (1976), classify phrygana as the following types: *Phlomis fruticosa*, *Poterium spinosum* (=*Sarcopoterium spinosum*), *Corydothymus capitatus* (=*Thymus capitatus*), *Ballota acetabulosa*, and *Cistus* sp.

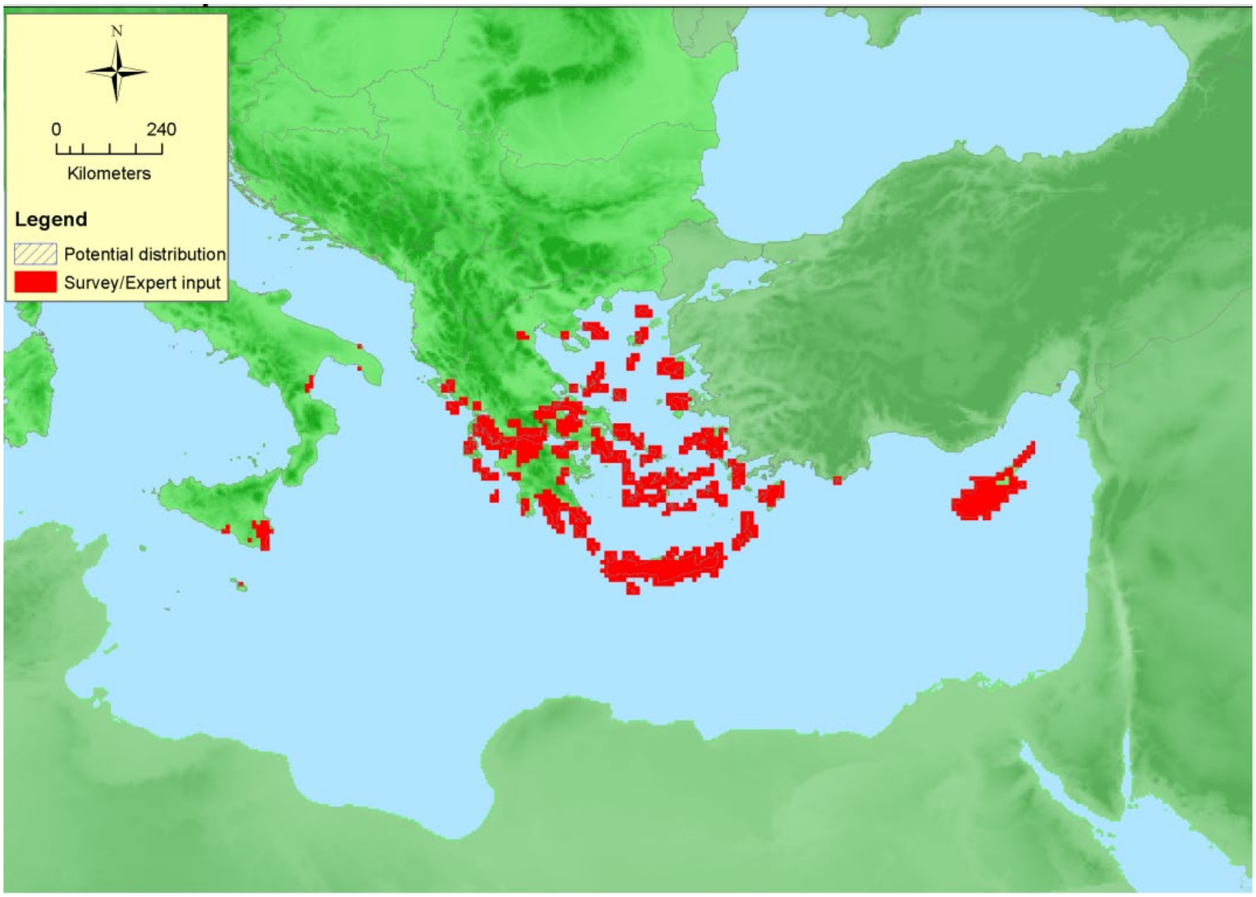


Figure 1. 2 Eastern Mediterranean Phrygana distribution map. The map likely provides the complete distribution of the habitat in Greece, Italy, and Cyprus, but some occurrences in southern Albania are possible and the distribution in Bulgaria is missing (Source: European Red List of Habitats, 2016).

1.3 Cyprian phrygana

Cyprian phrygana is the cushion-forming thermo-Mediterranean summer-deciduous, often thorny, sclerophyllous formations of Cyprus covering an area of 192 Km^2 (Fig. 1.3). They are mostly characteristic of the central plains, on sandy and loamy soils at thermo and meso-Mediterranean altitudinal levels of 0-800 m a.s.l. Their affinities are Irano-Turanian and they have a semi-steppic batha appearance. Phryganic communities in Cyprus are formed by *Sarcopoterium spinosum*, *Thymus capitatus* (*Coridothymus capitatus*), *Lithodora hispidula* (*Lithospermum hispidulum*), *Onosma fruticosum*, and *Galium suberosum* (EUNIS habitat classification, 2012 amended 2019). This habitat can be of a primary origin, have a climax character, or is often the result of a retrogressive succession of evergreen sclerophyllous vegetation.

The habitat type *Sarcopoterium spinosum* phrygana (EUNIS habitat classification, 2012 amended 2019) of low, thorny formations of hemispherical shrubs of the coastal thermo-Mediterranean zone can be found in 39 Natura 2000 sites in Cyprus. As stated by the Conservation status (2013-2018) of habitats (Habitats Directive, Article 17) their conservation status in Cyprus is poor. The most characteristic plant representatives of this habitat are *Thymbra capitata* (syn., *Thymus capitatus*), *Sarcopoterium spinosum*, *Phagnalon rupestre* ssp. *rupestre*, *Noaea mucronata, Echium angustifolium*, and many herbaceous species and scattered *Ziziphus lotus* and *Crataegus azarolus* shrubs growing among phrygana. Especially in Ethniko Dasiko Parko Rizoelias (Natura 2000 site CY6000006), the phryganic community, which is the dominant natural vegetation, is probably a remnant of old *Ziziphus lotus* scrub formation (EUNIS habitat classification: Arborescent matorrals with *Ziziphus lotus*). This community consists mainly of *Thymus capitatus*, *Phagnalon rupestre*, *Asphodelus aestivus*, *Allium cupani*, *Stipa barbata*, *Atractylis canselata*, *Onobrychis venosa*, *Helianthemum obtusifolium*, *Asparagus stipularis*, *Echium angustifolium*, *Carlina involucrata* and very scattered individuals of *Ziziphus lotus* (Cyprus Department of Environment - NATURA 2000 - Standard data form, 2017).

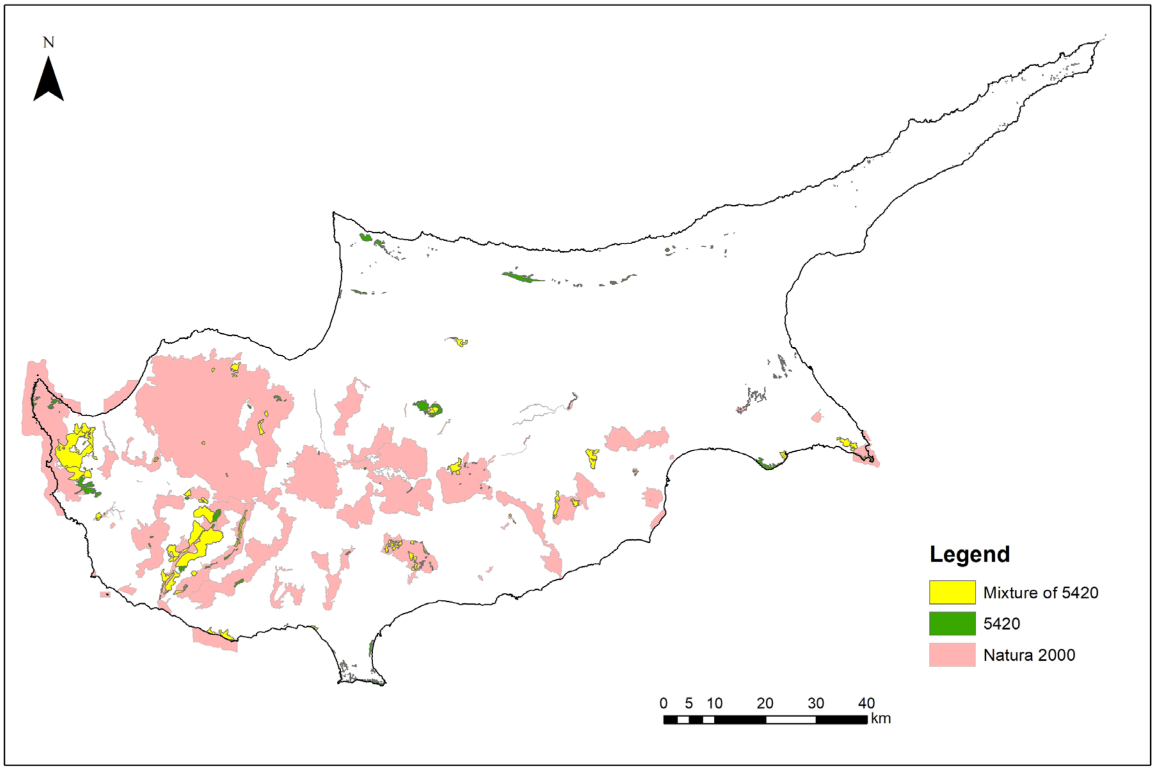


Figure 1. 3 Distribution of *Sarcopoterium spinosum* - Phrygana (Habitat type 5420) in Natura 2000 sites on the island of Cyprus.

1.3.1 *Ziziphus lotus*

Ziziphus lotus (L.) Lam. (Rhamnaceae) is a perennial, often winter-deciduous, arborescent cushion-like shrub, 50-250 cm tall that is a native shrub of North Africa, the Middle East, and southern Europe (Sánchez-Gómez, Carrión, Hernández, & Guerra, 2003) as a dominant plant of the groundwater-dependent ecosystems in European drylands (Guirado et al., 2018) (Fig. 1.4). *Ziziphus lotus* is a phreatophyte species which develops deep roots of up to 60 m (Le Houérou, 2006) to reach the water table, and has been recently identified as a facultative phreatophyte with anisohydric behavior (Torres-García et al., 2021a). The deep root system and modular growth make *Ziziphus lotus* a drought-avoiding species, whereas the anisohydric behavior and leaf phenology are more related to its drought-tolerance strategies (Torres-García et al., 2021a). Besides this, *Z. lotus* is the engineer species of an ecosystem (Constantinou et. al, 2021) of conservation concern in Europe (92/43/EEC Habitats Directive).

Figure 1. 4 Distribution of "Priority Habitat 5220*—Arborescent Shrub with Ziziphus" in Europe and the records of *Z. lotus* contained in the Global Biodiversity Information Facility in North Africa and the Middle East (Guirado et al., 2018).

The shrub's canopy is structured by a thorny complex of shoots and branches, as the result of a repeated growth pattern of the modular units each growing season (Torres-García et al., 2021b; Houma et al., 2022). As described by Torres-García et al. (2021b), the modular units, consisting of short and long shoots, exhibit differentiation and heterophylly that may promote the investment of resources in specific functions throughout the growing season, either for growth or reproduction. Short shoots have short internodes covered by non-photosynthetic leaves (cataphylls) that protect the apical and lateral meristems. These apical meristems become long shoots that produce spiny lateral branches or plagiotropic branches. The lateral meristems develop one to six deciduous flowering branches, in charge of the reproductive functions, during wetter conditions at the beginning of the growing season (Jafri, 1977). Long shoots are dedicated to the vegetative growth and space colonization of the plant, particularly during drier and warmer years. Their nodes carry one leaf each with two curved stipular spines of equal size at both sides and two basipetal meristems at the leaf axil. Late flowers or new short shoots are produced by the proximal meristems repeating the pattern and creating new modular units in the following growing season. The distal meristem becomes a plagiotropic branch with two dimorphic stipular spines at its base that after the first growing season, along with the long shoots remain in the shrub as lignified non-leaved branches. This growth pattern and architecture are present regardless of the plant's age (Torres-García et al., 2021b).

The presence of *Ziziphus lotus* in arid regions is ensured by its phreatophytic behavior and thus its ability to use the existing groundwater. The effects of climate change on the amount of groundwater could call into question its ability to survive in the future. The decline in groundwater caused by the reduction of precipitation and the increase in the atmospheric evaporative demand, due to high temperatures, could threaten the survival of the species and the groundwater-dependent ecosystems it inhabits in the Mediterranean Basin. This is one of the reasons the Mediterranean arborescent scrubs with *Ziziphus lotus* have been coded as a priority habitat 5220* (arborescent matorral with *Ziziphus*). They have been included in the Habitats Directive of the European Commission since 1992 (Habitats Council Directive 92/43/EEC, 1992), which lists Europe's most endangered and vulnerable habitats. These plant communities are present in the Iberian Southeast, Cyprus, Sicily, and surrounding islands, corresponding to communities characterized by several strata of shrubs, bushes, and herbaceous species, dominated by shrubs up to 3 m high, thorny, and impenetrable, which are often aggregated forming islands of vegetation (Mendoza-Fernández, 2019).

1.4 Research aims

The aims of this thesis are to:

1. evaluate whether phryganic plant communities form a facilitation interaction network with a nested pattern that matches the properties described for other positive ecological interaction networks.
2. assess the potential role of *Ziziphus lotus* as an eco-engineer at the habitat level.
3. provide conclusive evidence of *Z. lotus*'s role as an ecosystem engineer in improving ecosystem productivity and provide insight into its functioning as a drylands' ecosystem engineer plant.

1.5 Research questions

1. Are phryganic plant communities structured by facilitation? And if so, does the structure of their interaction network match the properties described for other positive ecological interaction networks? As evidence for a facilitation structured community, we expect higher recruitment of young plants under the canopy of the same or other species compared to open ground. Also, we expect the facilitation network to show a nested pattern, as reported in other plant communities driven by facilitation and by other positive interactions.
2. Are some adult species more effective as facilitators (nurse plants) than others? A higher frequency of positive co-occurrence of plant species under the canopy of an adult individual compared to other adult species, would be evidence for a more effective nurse plant.
3. Are some recruited species more dependent on facilitation than others? If a recruited species is more dependent on facilitation, we expect that it will show a more positive co-occurrence under a nurse's canopy compared to its existence in open ground.
4. Can *Z. lotus* positively influence the density of *T. capitata* and if so, is this influence based on *T. capitata* proximity to *Z. lotus*?
5. Is there conclusive evidence to support that *Z. lotus* may indeed improve ecosystem productivity?
6. What are the key traits that permit *Z. lotus* to act as an ecosystem engineer?

1.6 Thesis structure

The thesis of the structure is summarized below (see also Figure 1.5).

Chapter 2: *Facilitation in mainstream ecological theory*. Nurse plants act as facilitators that positively affect and enhance the growth and survival of other plants, while plants that act as ecosystem engineers can alter population, community, and ecosystem characteristics. Shrubs play an important role as both facilitators and engineers of ecosystems, especially in stressful environments. Their facilitating action is governed by various functional mechanisms, the presence and effectiveness of which is affected by stress factors. Ecological networks are tools that help us understand these effects of facilitation on plant communities.

Chapter 3: *Facilitation and recruitment networks in a phryganic plant community in Cyprus*. We investigate whether a phryganic plant community is structured by facilitation, which species are more effective as adult facilitators, and which are more dependent on facilitation. A non-random nested pattern, exhibiting a high nested structure was identified. The presence of species-specific interactions was reflected by the high connectance between cluster facilitators and their facilitated plant species, confirmed by ca. double number of recruits under the canopies of facilitators versus open ground. *Ziziphus lotus* demonstrated the highest facilitation capacity) and was independent from nurses, followed by *Thymus capitatus* and *Noaea mucronata*. *Ziziphus lotus* facilitated *Asparagus stipularis*, *Phagnalon rupestre* and *Noaea mucronata*. *Thymus capitatus* was found statistically independfrom from nurses, while *Sarcopoterium spinosum* was found to be autofacilitated.

Chapter 4: *The possible role of Ziziphus lotus as an ecosystem engineer in semiarid landscapes.* An investigation of *Ziziphus lotus* role as an ecosystem engineer. *T. capitata* significantly increases in density and significally improves its night-time rehydration in mid-summer when growing up to 5m around *Z. lotus* compared to thymes growing 10–15m away. Topography does not affects the density or stem moisture for thymes growing near *Z. lotus*. Consequently, *Z. lotus* may have the properties to be classified as an ecosystem engineer and the potential to boost productivity in arid and semiarid ecosystems.

Chapter 5: *How can ecosystem engineer plants boost productivity in east Mediterranean drylands.* An investigation of biotic traits and non-biotic factors that *Ziziphus lotus* activates/modulates to improve moisture conditions for neighboring plants. The research included canopy interception of moisture/rainfall, hydraulic redistribution of deep ground moisture by roots, soil's volume, and organic matter content. Results confirmed the statistically significant increase in the density of *T. capitata* plants up to 5 m around Z. lotus The increase in *T. capitata* stem/leaf moisture during dawn compared to evening during the dry season, suggests that ecosystem productivity is driven by a greater soil moisture availability around *Z. lotus*. A greater soil moisture availability permits improves thyme daytime transpiration, in contrast to thymes growing further away. The phenomenon appeared only during the dry season and becomes stronger during dry climatic years. Morning dew, rainfall interception from the canopy, soil depth and organic matter did not show significant effects. Thus, the hydraulic lift properties of *Z. lotus* are most likely the driver for the improved soil moisture availability.

Chapter 6: Phryganic communities are governed by facilitation, exhibiting an ecological network's highly nested structure and specific characteristics. *Ziziphus lotus*, a dominant plant in arid and semiarid environments, is proved to act not only as a facilitator in the community but also has the properties of an ecosystem engineer boosting productivity.

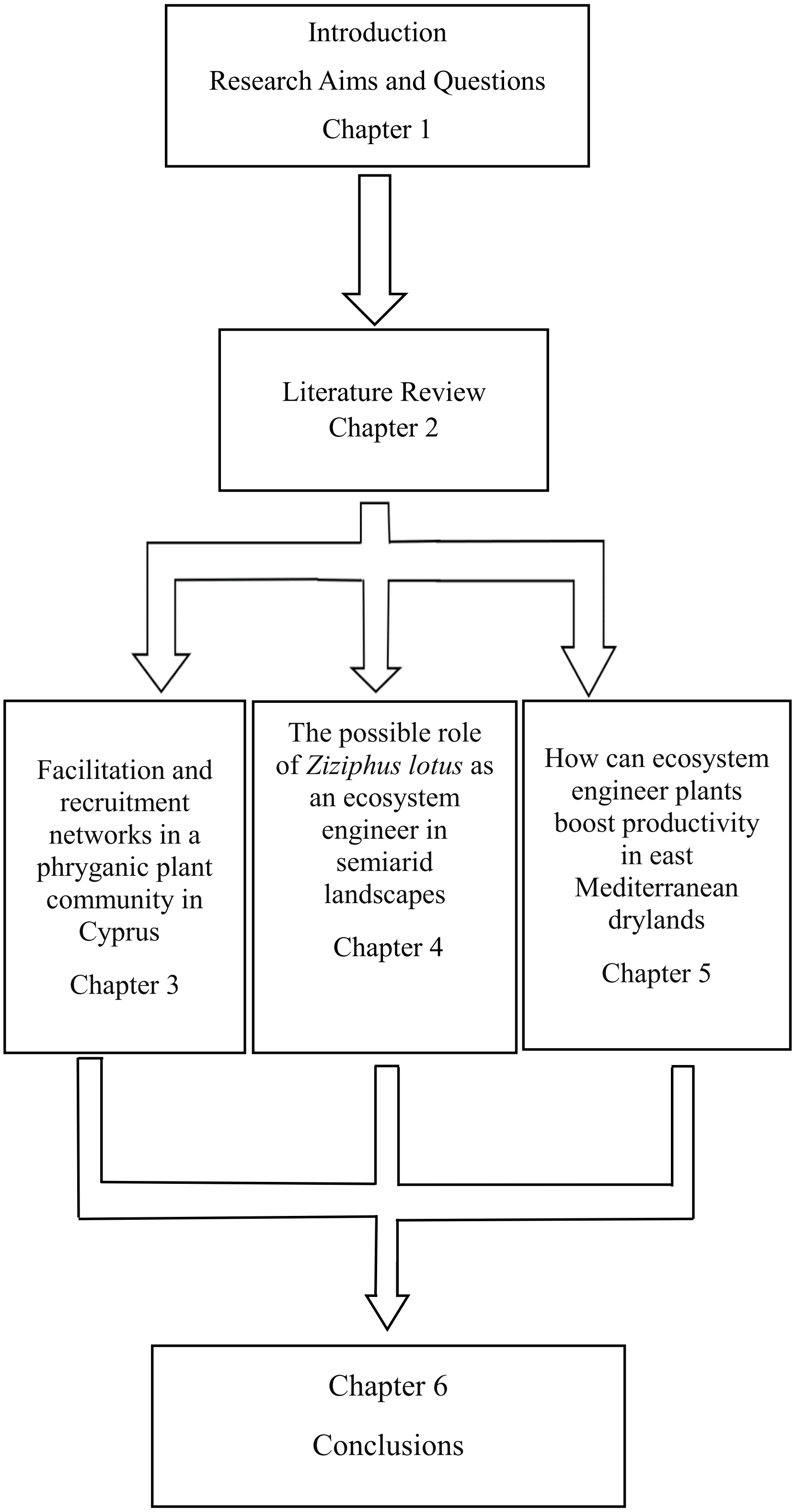


Figure 1. 5 Flow chart diagram illustrating thesis structure.

Chapter 2

Literature Review

2.1 Introduction

Facilitative or positive interactions are universal, and they lie at the root of many different evolutionary phenomena as old as the origin of eukaryotic cells to the radiation of flowering plants and the thriving of coral reefs (Boucher, 1985). Facilitation occurs when two living organisms coexist and at least one of them benefits while the other is not harmed (Bruno et al., 2003). Whereas mutualism often involves the physical intermingling of two species throughout much of their life history, in facilitation simply the presence of a species may modify its local environment and thus facilitate others. For example, by simply casting their shade, trees may alter light and moisture on the forest floor leading to the presence of a new group of living organisms, while corals form reefs increasing habitat complexity and thereby providing habitat for countless other species. In conclusion, positive interactions can arise when one organism makes the nearby surrounding environment more favorable for another either directly (by reducing thermal, water, or nutrient stress through nutritional symbioses or shading) or indirectly (by removing competitors or predators) and may encompass tightly coevolved, mutually obligate relationships as well as much looser, facultative interactions (Bruno et al., 2003).

The study of species interactions is one of the most fundamental issues in ecology, necessary to develop a predictive understanding of the response of the community and ecosystem to accelerated environmental change (Tylianakis et al., 2008; Harmon et al., 2009; Harley, 2011; Valiente-Banuet, 2015). Recognition of the importance of positive species interactions has challenged many basic ecological paradigms and predictions based solely on negative species interactions (Mulder et al., 2001; Bruno et al., 2003). Positive species interactions can govern the stability, productivity, energy flux, and diversity of ecosystems (Mulder, et al. 2001;

Cardinale et al., 2002; Kleinhesselink et al., 2014; Losapio et al., 2021). In contrast with negative species interactions that can drive species extinctions (Sax & Gaines, 2008) and diversity loss (Hautier et al., 2009), positive interactions maintain diversity in harsh environments where species often rely on each other to persist (Padilla and Pugnaire, 2006; Cavieres & Badano, 2009).

2.2 Facilitation in plants

The spatial arrangement of plants in a community, its structure, and dynamics are shaped by the various interactions between individuals of different species in that community (Tirado and Pugnaire, 2005; Padilla and Pugnaire, 2006; see also Figure 2.1). Facilitation occurs when one plant species, frequently referred to as a "nurse" plant or "canopy" plant improves the survival or growth of another, frequently referred to as a "target" species or "recruit" species, by expanding its realized niche (Soliveres et al., 2011), by ameliorating abiotic conditions (Jankju, 2013) or improving resource availability (Zou et al., 2005). Facilitation provides important heterogeneity in the regeneration niches necessary to maintain species richness in semiarid communities (Valiente-Banuet et al., 2006). In natural communities, species may interact with each other both negatively and positively (Menge & Sutherland, 1987; Tilman, 1988; Bertness & Callaway, 1994; Callaway et al., 2002). The net balance of these positive and negative effects among plants characterizes the interaction either as competition or facilitation (Callaway and Walker, 1997; Holmgren et al., 1997). Competition characterizes a community governed by negative effects between neighboring plants, due to limited resources or allelopathy. Alternatively, when plants improve the survival, reproduction, growth, or fitness of their neighboring species, therefore exercise a positive influence, the interaction results in facilitation (Callaway, 2007). In facilitation, an adult plant creates a beneficial micro-environment for its neighboring seedlings with presumably little effect on the adult plant, although authors have described a facultative mutualism phenomenon in the same relationships (Pugnaire et al., 1996a, b; Moro et al., 1997; Gibson et al., 1998). In certain stressful environments, many studies have shown the dominance of positive rather than negative interactions (Callaway et al., 2002; Bruno et al., 2003; Brooker et al., 2008; Odadi et al., 2011). Processes resulting in positive interactions are commonly reported in arid, semiarid, and alpine ecosystems (Valiente-Banuet and Verdu, 2007; Gómez-Aparicio, 2009; Soliveres and Maestre, 2014; Cavieres et al., 2016). Competition, on the other hand, seems to predominate under milder conditions (Bertness & Callaway, 1994; Maestre et al., 2009; Rey et al., 2016).

At the beginning of the 20th century, Shreve (1910, 1917) described seedlings' establishment in arid environments as a rare and sporadic event, mainly a result of high temperatures and low moisture regimes. By the end of the century, the seedling establishment of many species was described to be more frequent under canopies of adult plants of the same or another species

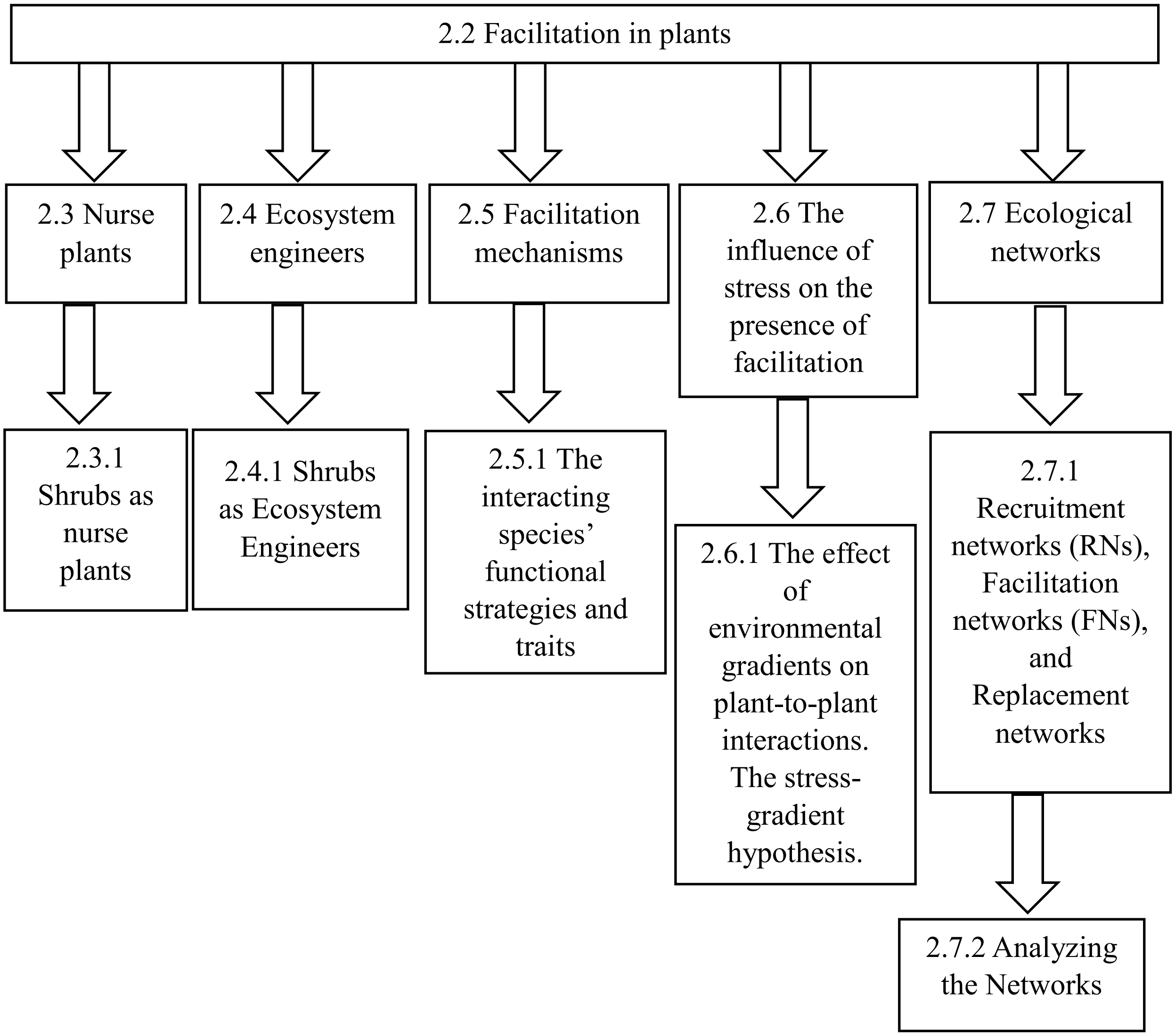


Figure 2. 1 Flow chart diagram illustrating the structure of Chapter 2.

which provides a less stressful micro-environment, as a response to these harsh conditions (Fllner & Shmida, 1981). Although competition has been the most studied ecological interaction in the past, by the begging of the 21st century facilitation received increasing attention (Flores and Jurado, 2003). Several theoretical models and experiments demonstrated its importance to plant diversity in terms of functional traits diversity (Spasojevic and Suding, 2012; Schöb et al., 2013, Madrigal-González et al., 2020), taxonomic richness (Cavieres et al., 2002, 2014; Cavieres and Badano, 2009; Sklenář, 2009) as well as phylogenetic diversity (Bruno et al., 2003; Valiente-Banuet and Verdú, 2007; Butterfield et al., 2013; Pistón et al., 2015; Vega-Álvarez et al., 2019). At the same time, the importance of facilitation in promoting various ecosystem functions was demonstrated through its ability to connect phylogenetically and functionally diverse communities (Navarro-Cano et al. 2014; 2016). Facilitative interactions operate to regulate plant success and community composition through various mechanisms. These mechanisms include the classic nurse plant effects, the buffering of the substrate and air temperature (Tewksbury & Lloyd, 2001), the enhancement of soil moisture and nutrient content, and the protection against drought and browsing (Brooker et al., 2007). Facilitation extends its effect through the attraction of pollinators (González-Varo, Arroyo & Aparicio, 2009; González-Varo et al., 2010), the capacity for resource-sharing through common mycorrhizal networks (Montesinos-Navarro et al., 2016a), and the positive impact on soil nitrogen availability (Montesinos-Navarro et al. 2017).

The need to include facilitation into mainstream ecological theory and the suggestion that this process will 'challenge some of our most cherished paradigms' was introduced in the early 20th century by Bruno et al. (2003). They revised the ecological theory to include the positive density-dependence at high population densities, inclusion of facilitation in the diversity–invasibility paradigm and the role of dominant species in regulating local diversity. Thus, they predicted the potential expansion of the formerly realized niche by facilitation and proposed a revision of the theory. Three years later, Michalet et al. (2006) tried to place consideration of facilitation as one of the central theories of plant community ecology and suggested a revision of the universal adaptive strategy theory of Grime's model (1973) to incorporate facilitative interactions in plant communities.

2.3 Nurse plants

Since plants in early life stages are highly vulnerable to environmental stress, the likelihood of plant establishment and survival to the adult stage in high-stress environments may increase with the presence of nurse plants (Escudero et al., 2005; Flores and Jurado, 2003). Nurse species perform important roles in structuring plant communities at a global scale (Table 2.1). The presence of key nurse species in the communities is reflected by the accumulation of plant species that form species-rich areas (Soliveres et al., 2011), whereas the presence of highly competitive or allelopathic plants would be reflected in a decrease in plant diversity in the area (Arroyo et al., 2015). The first recorded examples of close spatial association between plants that are more beneficial than harmful on seedlings are known with the term "nurse plant syndrome" (Niering et al., 1963).

Table 2. 1 Types of environments where nurse plants were documented.

Type of environment	**Indicative literature**
Arid and semi-arid environments	Holzapfel and Mahall, 1999; Flores and Jurado, 2003; Gómez-Aparicio et. al, 2004; Landero & Valiente-Banuet, 2010; Poulos, Rayburn, & Schupp, 2014; Paterno et al., 2016; Woods & Miriti, 2016
Semi-arid gypsum plant communities	Foronda et al., 2019
Mediterranean climate shrubland	Fuentes et al. 1984; Holmgren, et al. 2012
Mountain ranges in dry environments	Schöb, Armas, Guler, Prieto, & Pugnaire, 2013
Salt marshes	Bertness and Hacker, 1994; Bertness and Callaway, 1994
Mangroves	Lewis, 2005; Lewis and Gilmore, 2007; McKee et al., 2007
Alpine habitats	Cavieres et al., 2006

Plant life stages (e.g., seed, seedling, juvenile, pre-reproductive adult, reproductive adult, and senescent adult) may affect the outcome of interactions between plant species (Callaway and Walker, 1997). Although the balance of competition and facilitation could shift among the various life stages of the beneficiary and the benefactor, the beneficiary species' seedlings' survival is found to be higher when they are spatially associated with nurse plants. The strength of facilitative interactions may depend on the age of the benefactor (Kellman and Kading, 1992), suggesting that the positive effects of benefactors are stronger when beneficiaries are young and small. The benefactors' densities are also an influencing factor (Walker, 1994), high densities may resist intrusion, facilitating the settlement and growth of other species. Thereby these contrasting effects of neighbor density, or other life stage characteristics, may vary with abiotic stress.

The "nurse plant syndrome" or "nurse-protégé" interactions (Cody, 1993) are common across diverse environments (Table 2.1) but are most frequently reported in arid and semi-arid ecosystems (Flores and Jurado, 2003). This suggests that aridity may be an important factor in this interaction. Due to the large number of taxa involved, already recorded since the beginning of the 20th century (147 nurse species in 40 families and 429 facilitated species in 84 families), the nurse-protégé interaction seems to lie outside phylogenetic constraints (Flores and Jurado, 2003). The nurse effects, however, might vary from positive to negative depending on the target species that establishes under the nurse crown, a process referred to as species-specific interaction outcome (Callaway, 1998; Callaway & Walker, 1997). Species-specific interaction outcomes, found in a wide range of ecosystems, pointed them as a strong factor modulating seedling regeneration in plant communities (Paterno et al., 2016). In high-diversity ecosystems where multiple pairs of nurse and target species can interact, though, predicting the outcome of nurse-target interactions can be difficult. Nurse plants may show a positive effect on one target's survival but a negative or neutral effect on its growth (Gómez-Aparicio, 2009; Paterno et al., 2016), thus making the interaction predictions even more complex. Recognizing the need to identify each nurse's traits that could influence the target's performance, some authors have pointed out that nurse-target interaction outcomes could be predicted based on nurse species' ecological strategies (Schöb et al., 2013; Soliveres, Smit, & Maestre, 2015). Nurses from different successional stages can alter the conditions and the available resources for the same target species (Diaz & Cabido, 2001). The interaction outcomes might also depend on how nurse strategies combine with different target needs. For instance, when targets are more prone to water stress, they are more likely to be facilitated by nurses that maintain water in the system, for example, by performing hydraulic lift or presenting high water use efficiency (Holmgren, et al. 2012; Paterno et al., 2016; Woods & Miriti, 2016).

2.3.1 Shrubs as nurse plants

The major role of the facilitation of shrubs, particularly in stressful environments, has been mentioned in several studies that recognize the importance of beneficial interactions in the dynamics of plant communities (Gómez-Aparicio et al., 2004; Cushman et al., 2010; Kleinhesselink et al., 2014; Macek et al., 2016; Foronda et al., 2019). Experiments showed that shrubs acting as nurse plants, especially in Mediterranean environments, is not a local or sporadic phenomenon restricted to a few species' assemblages and environmental conditions, but a more widespread phenomenon (Gómez-Aparicio et al., 2004).

In semi-arid ecosystems, the beneficial plant-to-plant associations that determine the pattern and structure of plant communities were described as fertility islands (Pugnaire et al., 1996a), vegetation clumps (Eccles et al., 1999), and plant cushions (Cavieres et al., 2006), where each partner benefits from greater resource availability. This interaction between species suggests that the mutual benefit of the connection is best characterized as facultative mutualism (Pugnaire et al., 1996a; Gómez-Aparicio et. al, 2004). The nurse shrubs strongly improve their own environment by various mechanisms (Table 2.2), facilitating the growth of other plant species underneath their canopy, and obtaining benefits from the sheltering plants underneath. Facilitated plants demonstrate greater specific leaf area, greater leaf and shoot mass, more flowers, and a higher nitrogen concentration in leaf tissue than isolated plants, suggesting increased availability of resources. At the same time, the nurse plants themselves have higher total biomass, higher total nitrogen, and higher shoot water potential at midday than shrubs of the same species which do not act as nurse plants (Pugnaire et al., 1996a).

In the Mediterranean semi-arid and arid areas, drought intensity seems to directly affect the type of interactions between neighboring plants. Along with aridity gradients, the form of association between the close plants and nurse shrubs shifts from negative to positive (Gómez-Aparicio et. al, 2004). At the arid end of the gradient, strong positive interactions lead to the improvement in above-ground productivity, richness, seedling density, and seed bank density of the annual plant community, as well as the productiveness of annual plant populations under nurse shrubs

(Holzapfel et al., 2006; Prieto et al., 2011). However, these effects are not present at the lower wet end, suggesting that positive interactions become less significant with increasing rainfall, thus shifting the interaction balances at the community level in large geographical gradients.

Table 2. 2 Facilitation mechanisms by shrubs.

Facilitation mechanisms	**Related literature**
Physical differences between shrub canopies and open areas	Valiente-Banuet and Verdu, 2007
Canopy accumulation of fine, windblown material enhancing seed germination	Wallace & Romney, 1980
Reduction of solar radiation and temperature	McAuliffe, 1988; Valiente-Banuet & Ezcurra, 1991
Provision of higher soil nutrient levels by the accumulation of organic debris or nitrogen fixation	Tiedemann & Klemmedson, 1973; Lajtha & Schlesinger, 1986; Bonanomi et al., 2011; Brooker et al., 2008; Maestre et al., 2010
Provision of shelter under their canopy, shading and higher soil, and air humidity	Sosa and Fleming, 2002; Valiente-Banuet et al., 2002; Padilla and Pugnaire, 2006; Holland and Mollina-Freaner, 2013
Reduced plant transpiration and improved water status	Soriano and Sala, 1986; Franco and Nobel, 1989; Pugnaire et al., 1996a, b; Valladares and Pearcy, 2002
Lower consumer pressure / associational resistance	Verwijmeren et al., 2019; Hay, 1986

In arid environments, the role of positive interactions in structuring plant communities and increasing biological diversity is very crucial (Tewksbury and Lloyd, 2001). Long-lived desert shrubs play an important role in building plant communities and promoting biodiversity. The role of facilitation in extreme environments is emphasized by the positive effects of adult plant canopies of different sizes has on plant richness and abundance in communities of xeric habitats. In semi-arid ecosystems, the associational resistance between drought and grazing provided by shrubs maybe the most important mechanism resulting in positive plant–plant interactions (Louthan et al., 2014; Perea and Gil, 2014; Tálamo et al., 2015).

On the contrary, in mesic sites, adult plant canopies have very little effect on perennials and a negative effect on richness, suggesting predominantly competitive effects in less stressful environments. Overall, adult plant canopies increase biological diversity where abiotic stress is high but do not increase diversity in more mesic areas. In the subalpine forest environments, nurse plants enhance tree-seedling establishment by ameliorating the interactive effects of temperature and light (Egerton et al., 2000). Shading by nurse plants can ameliorate tree-seedling stress at low temperatures, and thus help facilitate regeneration by nurse plants in frost-prone environments. Over winter, sheltered seedlings as less photo-inhibited, have higher photosynthetic CO_2 assimilation rates, lose less leaf area, and maintain a higher leaf-area ratio than exposed seedlings. These differences are consistent with greater growth for sheltered than exposed seedlings by the end of winter. Facilitation by shrubs was found to have a significant effect both in sunny conditions and in shady conditions (Gómez-Aparicio et. al, 2004). Regarding the importance of facilitating the survival of seedlings, in arid high-altitude zones, there has been a widely documented spatial correlation between nurse shrubs and nurse cushion plants with other plant species in both higher (Soliveres & Maestre, 2014) and lower elevations (Gómez-Aparicio et. al, 2004; Cavieres et al., 2006). This result suggests that nurse plants play a critical role in structuring plant communities, regardless of altitude, and that climatic changes could be very relevant to the persistence of plant communities (Gauquelin et al., 2018).

2.4 Ecosystem engineers

Organisms that directly or indirectly modulate resource availability to other species by causing physical state changes in biotic or abiotic materials, are characterized as ecosystem engineers (Jones et al. 1994, 1997). The non-trophic impacts of such taxa, which can potentially be found in all ecosystems (Jones et al., 1994), can alter population, community, and ecosystem characteristics through the creation, modification, or maintenance of habitats in the environment (Wright & Jones, 2004). However, as stress increases, the microenvironment produced by the engineering species stays relatively constant. Thus, the relative effect of the engineer is greater in an otherwise stressful environment (Bertness and Callaway, 1994; Badano and Cavieres, 2006; Maestre et al., 2009). These activities of ecosystem engineers lead to considerable spatial heterogeneity, creating distinct mosaics of engineered and unmodified patches throughout landscapes (Badano et al., 2005; Wright et al., 2006; Shachak et al., 2008). Ecosystem engineers are a taxonomically diverse group, with representatives including vertebrates, invertebrates, algae, nonvascular plants, and higher plants (especially woody species). Plants which act as ecosystem engineers support the ecological network and facilitate biodiversity maintenance influencing various aspects and mechanisms (Table 2.3). These positive effects can provide benefits to associated plant species by facilitating their establishment, growth, survival, and reproduction increasing plant diversity at the community level (McIntire and Fajardo, 2014; Schöb et al., 2014; Losapio et al., 2018). However, ecosystem engineering is a much more important factor in shaping and preserving certain ecosystems than others (Jones et al., 1997). Thus, the itentification of ecosystem engineers is not only fundamentally interesting but also has a meaningful and practical value in conservation and management.

Table 2. 3 Beneficial action of ecosystem engineers.

Ecosystem engineers' effects	**Indicative articles**
Ameliorate environmental conditions, decrease stress and disturbance, and ultimately support the ecological network	Cavieres et al., 2014; Losapio et al., 2018; Thomsen et al., 2018; Ellison, 2019
Increase habitat complexity	Jones et al., 1994; Stachowicz, 2001; Ellison et al., 2005
Create new habitat space	Hutchinson, 1978; Odling-Smee et al., 2003; Schöb et al., 2012
Facilitate biodiversity maintenance	Wright et al., 2006; He et al., 2013; Bulleri et al., 2018
Increase plant diversity at the community level	Armas et al., 2011; Cavieres et al., 2014; Kikvidze et al., 2015
Mitigate the disturbances from herbivory	Cushman et al., 2011
Mitigate the disturbances from intense sunlight	Valiente-Banuet and Ezcurra, 1991
Mitigate the disturbances from wind	Carlsson and Callaghan, 1991
Increasing the availability of soil resources	Schlesinger et al., 1990; Pugnaire et al., 1996; Shumway, 2000; Cushman et al., 2010

Jones et al. (1997) identified six factors that scale the impact of engineers on habitat formation. These factors include:

(1) the lifetime per capita activity of the individual engineering organisms,

(2) their population density,

(3) the local and regional spatial distribution of the population,

(4) the length of time the population has been at a site,

(5) the type and formation rate of the constructs, artifacts, or impacts, and whether these are durable in the absence of the engineers.

The measurement of the first five factors is relatively easy for many physical engineering species. The sixth factor refers to the number and types of resources that are directly or indirectly controlled, the ways these resources are controlled, and the number of other organisms that depend on these resources. However, a full understanding of the impact of an ecosystem engineer on the formation of an ecosystem is not fully possible without the investigation of the sixth factor despite the difficulty it entails. It is also important to realize that engineers and "keystone species" are not synonymous. Many engineers have small, difficult-to-detect effects; only some have dramatic effects, but where they do, understanding how the engineers modify and modulate resource flows for other species, and create and maintain entire habitats, are among the most significant and poorly researched questions in ecology (Jones et al., 1997).

When determining the ecological strategies of plant ecosystem engineers, it is important to consider that nurses from different successive stages could have different impacts on the same target species, a process that could partly explain the interaction results for specific species (Fagundes et al., 2018). Studies showed that pioneer nurses in semiarid systems have a higher tolerance to environmental stresses such as light intensity and drought (Kitao et al., 2000), which affects the conditions and resources provided to their neighbors (Diaz & Cabido, 2001). Pioneer nurses, acting as ecosystem engineers in an arid environment deplete resources slower than late-successional nurses by having stress-tolerant features such as high wood density, and small size, which would allow them to establish in harsh or degraded areas (Grime, 1977). At the same time, pioneer nurses exhibit features related to high relative growth rates, such as low wood density and large size, which would guarantee rapid colonization in open gaps (Kazakou et al., 2006).

2.4.1 Shrubs as Ecosystem Engineers

Shrubs are dominant features of many landscapes throughout the world and can play key roles as ecosystem engineers by altering the physical environment beneath their canopies as well as the characteristics of plant populations, communities, and ecosystems (Hunter & Aarssen, 1988; Callaway, 1995; Scholes & Archer, 1997; Wright et al., 2006; Shachak et al., 2008). By sheltering their associated species, shrub ecosystem engineers increase species richness in their local ecosystems (Ballantyne & Pickering, 2015; Cáceres et al., 2015; Chen et al., 2019). Even though sometimes species richness can be significantly higher in surrounding areas than under shrubs, ecosystem engineering shrubs can harbor exclusive species, accounting for a significant percentage of the local species richness (De Villiers et al., 2001). Ecosystem engineering shrubs often have a distinct understory species associated with them, representing a source of beta diversity (Valiente-Banuet and Verdu, 2007; Cavieres and Badano, 2009; Butterfield et al., 2013). This increase in beta diversity tends to be more pronounced in more stressful environments (Badano and Cavieres, 2006; Cavieres and Badano, 2009; Armas et al., 2011).

Shrub species acting as ecosystem engineers, modify the microenvironment, by different effects and variations magnitudes along the environmental stress gradients offering suitable micro-sites for less tolerant species and leading to increases in species diversity (Chen et al., 2019). In arid environments, shrubs modify the microhabitat under their crown inducing lower soil temperatures, higher soil moisture contents, reduced evaporative demands, and improved soil organic matter contents (Aguiar and Sala, 1994; Franco-Pizanã et al., 1996; Holmgren et al., 1997; Pariente, 2002). In addition, the shrub canopy causes a radiation balance that results in a narrower temperature range under the crown of the bush than in open areas while more extreme maximum and minimum temperatures can be recorded in the environment outside the shrub influence (Cáceres et al., 2015). At the ecosystem level, more plant litter is accumulated in areas beneath shrubs, and this is associated with soil under shrub species having higher pools of ammonium and nitrate and the fact that the rates of nitrate mineralization are faster beneath the canopy compared to open ground (Cushman et al., 2010). Apart from ameliorating soil nutrient and water stresses and reducing temperature fluctuations, shrubs can engineer the local ecosystem by changing particle size distribution, increasing soil organic matter, and reducing local wind speeds (Kleinhesselink et al., 2014). The strong effects of shrubs on wind and organic matter strengthen the importance of shrubs in creating spatial heterogeneity in soil (Schlesinger et al., 1990; Alpert and Mooney, 1996; Pugnaire et al., 1996; Shumway, 2000). The increase in organic matter under shrubs, especially when they are growing on young soils (Malagón, 1982) clearly suggests another effect of their ecosystem engineering, in which the shrub's necromass production contributes to generating resource islands (Pérez, 1992; Anthelme et al., 2012; Ramírez et al., 2015). The increase in the organic matter could in turn be linked to an increase in the soil's water and nutrient-holding capacity (Körner, 2003). Shrubs could also increase soil water through increased fog interception and decreased evaporative demands under the canopy, as has been documented in semi-arid environments (Callaway, 1995; Callaway and Pugnaire, 2007).

2.5 Facilitation mechanisms

The functional mechanisms governing facilitation between plants have been explored through detailed studies since the beginning of the 21st century (Brooker et al., 2008). The benefits for facilitated plants come from mechanisms that achieve one or more of the following benefits:

- temperature regulation (e.g., cooler temperature on hot days and protection from mild frosts),
- greater water availability (e.g., the roots of facilitating plants lift water from deeper into topsoil making it available to the facilitated plant, higher rates of water filtration and fewer losses from evaporation),
- an increase of nutrients in the soil; protection against grazing or encroachment; natural support; less soil compaction and less soil erosion (Flores and Jurado, 2003). Thus, the effect of facilitating plants on conspecific facilitated plants decreases fast with distance from the trunk (Comita et al., 2014; Swamy et al., 2011).

The importance of abiotic (microhabitat amelioration) and biotic (herbivory protection) mechanisms of facilitation in plant communities was tested by Gómez-Aparicio et al. (2008) in the Mediterranean mountain forests. Strong summer drought is the main characteristic of these systems, a fact that has a strong negative effect on the regeneration of tree and shrub species because it causes great losses in seedlings and saplings during the early stages of their establishment (Rey & Alcántara, 2000; García, 2001; Traveset et al., 2003; Castro et al., 2004).

Shrub canopies turned out to create a distinctive but crucial, micro-environment for saplings' survival in critical seasons, micro-environment. In mid-summer, shrubs provide moderate shade increasing young woody neighboring plants' survival and reducing photo-inhibition without reducing carbon gain significantly (Valladares et al., 2005; Gómez-Aparicio et al., 2006). Specifically, Gómez-Aparicio et al. (2008) revealed a mean daily air and soil temperature reduction of almost 10 ºC under shrubs, resulting in a vapor pressure deficit and thus an atmospheric evapotranspiration demand reduction by 50% and a photosynthetic photon flux density decreased of 70%. During drought and high mean air temperatures, leaf overheating is an important stress factor that suppresses transpiration (Larcher, 2003), thus this daily air reduction produced by shrubs reduces this risk. Moreover, the reduction of vapor pressure deficit under shrubs improves the water status of saplings (Holmgren et al., 1997; Domingo et al., 1999). Shrubs, as facilitators, also ameliorate negative temperatures in winter and reduce the risk of frost damage to tissues (Kikvidze & Nakhutsrishvili, 1998; Núñez et al., 1999). Although facilitation by shrubs due to microclimatic amelioration has been reported mainly during the dry and hot Mediterranean summer (Callaway, 1992; Rousset & Lepart, 1999; Castro et al., 2004), protection by shrubs in winter can be even more important at higher altitudes where plants are exposed to double abiotic stress involving both drought and frosts (Terradas, 2001). Litter accumulation under shrubs can reduce freeze-thaw cycles in the soil resulting in heaving of the soil surface and thus diminishing the mortality of seedlings due to uprooting and/or fracture (Gill & Marks, 1991; Gobbi & Schlichter, 1998). The relative importance of protection against herbivory as facilitation mechanisms varies strongly depending on herbivore pressure and the characteristics of the interacting plant species (Valiente-Banuet & Ezcurra, 1991; Callaway et al., 1996; Baraza et al., 2006).

2.5.1 The interacting species' functional strategies and traits

Facilitation strength is frequently described as being species-specific or depending on the identity of the interacting species combination (Landero and Valiente, 2010; Michalet et al., 2015; Paterno et al., 2016; Fagundes et al., 2018). Although speculative, there has been a suggestion that communities have relied on facilitation by maintaining their nurse species since ancient times (Valiente-Banuet and Verdu, 2007). However, to advance our understanding of such positive interactions, and gain theoretical generality, one needs to abandon the taxonomic perspective and adopt a more functional approach (Soliveres et al., 2015; Paterno et al., 2016).

Functional strategies define how plants use the available resources (Grime, 1977) and consequently how they affect the environmental conditions and resources of their neighbors (Violle et al., 2009). Adult plants with conservative strategies for obtaining resources such as low specific leaf area (SLA), high wood density (WD), and low hydraulic diameter (HD) will likely have a low resource depletion rate (Grime, 1977; Reich, 2014; Roussel et al., 2009; Diaz et al., 2016), leaving more resources available for target species that develop under their crown. On the other hand, it is expected that adult plants with demanding acquired strategies (high SLA, low WD, high HD) will have higher rates of resource depletion and, as a result, reduce the resources available for the target plants. However, potential facilitator traits alone are not enough to predict facilitation effects since plants with both types of resource acquisition strategies have been reported as feasible facilitators (Maestre et al., 2009; Graff and Aguiar, 2017).

Although there is no consensus that these broad functional groups can explain the multitude of species-specific interactions found in the literature (Gómez-Aparício, 2009; Fagundes et al., 2018), facilitation target plants' stress tolerance has often been considered a key mechanism for predicting facilitation. Stress-sensitive target plants tend to have a higher potential to be facilitated while stress-tolerant plants might not rely on facilitation for survival and growth (Liancourt et al., 2005; Rolhauser and Puchet, 2016). Adult facilitators' traits have been thought or found to be more important than target traits in determining interaction outcomes (Callaway, 2007; Gómez-Aparicio, 2009). However, a global synthesis performed by He, Bertness, and Altieri (2013) reveals that both target and adult neighbor traits are important.

The interacting species' life forms and their life history stage, particularly neighbors, largely influenced the interaction outcome (Gómez-Aparicio, 2009). Young trees are beneficiaries of facilitation, because they are late-successional and often intolerant to stress (Gómez-Aparicio, 2009), and thus more dependent on the amelioration of environmental stress by their neighbors, while adult trees are often benefactors due to the large above-ground size that shades, retains water and nutrients and protects beneficiaries from herbivory (Callaway & Walker, 1997; Callaway, 2007). Shrubs in their adult form have great facilitative effects, especially on trees, while herbs have strong negative effects, especially on other types of herbs (Gómez-Aparicio, 2009). Adult plant canopy size also mediates positive interactions, with larger canopies supporting larger perennials in both xeric and mesic sites (Tewksbury and Lloyd, 2001). Grasses on the other hand, always act as strong competitors likely due to their fibrous roots and large root-to-shoot ratios (Caldwell & Richards, 1986; Gómez-Aparicio, 2009). In relation to life history, most juvenile plants, as more vulnerable to environmental stress, are thus more likely than adult plants to be the beneficiaries in a facilitation interaction (Callaway & Walker, 1997; Miriti, 2006). On the contrary, annual juveniles act as strong competitors to their adult neighbors than perennials, especially in low-stress conditions (Gómez-Aparicio, 2009). Plants' origins are another factor that influences the interaction outcome; studies revealed that exotic plants exhibit competitive behaviors towards their neighbors while native plants exhibit neutral to facilitative interactions, which is consistent with the invasion ecology hypotheses (Levine et al., 2003; Vila & Weiner, 2004).

However, it should be noted that the outcome of plant interactions is the product of the traits of both target and adult neighbor species and the stress conditions of their specific habitats. Under certain conditions grasses have been identified as facilitators (Bertness & Ewanchuk, 2002; Van Uytvancket al., 2008), shrubs and trees as competitors (Dullinger et al., 2005), and exotics as facilitators (Yang et al., 2009). The key difference is high stress since highly competitive species have decreased competitive or neutral effects at high stress, whereas less competitive species have strong facilitative effects (He, Bertness, and Altieri, 2013).

2.6 The influence of stress on the presence of facilitation

Although many of the studies on facilitation have focused on cold or arid climates and ecosystems, the strong effects of facilitation are not necessarily restricted to traditionally considered stressful environments. Empirical studies have found facilitation to be essential for seedlings establishment in both moister and warmer ecosystems (Pugnaire and Luque, 2001;

Ganade & Brown, 2002; Pages & Michalet, 2003; Holmgren & Scheffer, 2010), although, when measured as growth plant interactions were found to be less competitive and more facilitative in cold and arid climates than in moderate and Mediterranean climates. Mediterranean shrubs, semiarid steppes, marshes, tropical sub-humid forests, arid shrubland, arid rangelands, and semiarid abandoned fields are some of the ecosystems in which the phenomenon of facilitation has been observed and studied (Padilla and Pugnaire, 2006). Overall, species present in each ecosystem are adapted to those local conditions (Holmgren & Scheffer, 2010), thus, any increase in the environmental stress will lead to deviations from their evolved optima, in which case, the facilitative interactions with neighbors are expected to increase (Choler et al., 2001; Wang et al., 2008). However, the importance of facilitation on community assembly seems to disappear under extreme drought stress (Zhang et al., 2022).

2.6.1 The effect of environmental gradients on plant-to-plant interactions. The stress-gradient hypothesis.

According to the stress-gradient hypothesis (SGH), as suggested by Bertness and Callaway (1994), facilitation in communities increases and competition decreases with increasing abiotic and/or biotic stress. Despite the numerous field experiments and intense discussions over the last decades, ecologists still cannot agree on the generality of the SGH (Maestre et al., 2005; Brooker, 2006; Lortie & Callaway, 2006; Callaway, 2007). Differences in the type of stresses (e.g., physical, resource, grazing), species characteristics (e.g., origins, life histories, functional traits), and ecosystem types have been suggested to prevent the presence of a widely applicable model of how species interactions may shift with increasing stress (Lortie & Callaway, 2006; Maestre et al., 2009).

It is generally accepted that facilitation increases with increasing physical stresses, like salinity in coastal marshes (Bertness & Hacker, 1994; Bertness & Ewanchuk, 2002) and cold in alpine grasslands (Callaway et al., 2002; Badano et al., 2007). The examination of the relative importance of competitive and facilitating interactions along elevation and topographic gradients in alpine environments was made by Choler et al. (2001). Through their research, it became clear that facilitation increases with an increase in altitude or exposure and is particularly strong for species that are at their highest elevation or normal limit. Therefore, facilitation may promote the expansion of niches in such severe environments. This argument was supported by a multi-site examination of the relationship between environmental severity and plant-plant interactions in arctic-alpine environments by Callaway et al. (2002). They observed a generalized transition from competition to facilitation as the average community interaction as the altitude increases and demonstrated the relationship between the dominant type of interaction and environmental severity on a large scale. In contrast, mixed data on the application of SGH have been reported in studies on water/rainfall gradients in arid and semi-arid ecosystems (Tielbörger & Kadmon, 2000; Maestre & Cortina, 2004; Armas & Pugnaire, 2005; Holzapfel et al., 2006). Maestre and Cortina (2004) investigated the form of the interactions between plants at the extremes of the gradient. The study revealed that competitive interactions dominated at both extremes of the gradient, thus they suggest that a shift from facilitation to competition under high abiotic stress conditions is likely to occur when the levels of the most limiting resource are so low that the benefits provided by the facilitator cannot overcome its own resource uptake. The temporal environmental variation between competition and facilitation was studied by Tielbörger and Kadmon (2000) in desert plants. Their study revealed a relationship between the form of the effects desert bushes had on annuals and the amount of annual rainfall. Increased precipitation changed the effect of bushes from negative to neutral or from neutral to positive depending on the species. Many others have questioned the generality of SGH, suggesting that it may not apply to gradients in resources, such as water and nutrients (Maestre et al. 2005, 2009; Michalet, 2007) and that at high levels of resource limitations, resource consumption, and competition dominate plant relationships (Maestre et al. 2009). The two previous widely cited studies which found no increase in positive interactions with stress in arid ecosystems (i.e., Maestre & Cortina, 2004; Maestre et al., 2005), under stricter re-analyses of their data showed increasing facilitation and decreasing competition with stress (Lortie & Callaway, 2006; Callaway, 2007). However, it has also been argued that biotic stress (such as herbivory) may lead to patterns of species interactions along stress gradients differing from abiotic factors (Smit et al., 2008). In addition, studies from grazed ecosystems showed that facilitation intensity increases from low to high grazing pressure but decreased again when very high grazing pressure occurs (Smit et al., 2007; Graff and Aguiar, 2011; Saiz and Alados, 2012). This is due to the fact that at very high grazing pressure nurse plants themselves get damaged by grazing or trampling (Michalet et al., 2014), or because herbivores started searching more intensively for resources, effectively removing the protective effects of the nurse plant

(Soliveres et al., 2011). Thus, adding consumer pressure to drought stress may possibly act as an accelerator in the waning of positive interactions at the extreme end of an aridity gradient (Verwijmeren et al., 2013). Recent meta-analyses have examined the generality of the SGH in arid ecosystems but the global generality of the SGH remains to be tested by synthesizing the studies that have accumulated over the last decades (He, Bertness, and Altieri, 2013).

The form of species interactions along stress gradients might also be affected by the interacting species traits (Lortie & Callaway, 2006; Castanho et al., 2012). In a review, Maestre et al. (2009) consider it necessary to incorporate species' tolerance to stress and their competitive ability to have a more improved version of SGH. Empirical studies also tested whether plant growth form, life history stage, and origins can affect the way species interactions change along stress gradients. Many of these traits including growth form (Cornelissen et al., 2003; Violle et al., 2007), life history, stress tolerance, competitive ability, and origins (native vs. exotic) were found to influence the outcome of plant interactions. Studies that investigated these possible effects of traits have demonstrated the ability of shrubs to have more facilitative effects while herbs and exotic species often have strong negative effects (Gómez-Aparicio, 2009; Vilà & Weiner, 2004). Juvenile plants are more likely to start their life cycle as beneficiaries but may turn out to be competitors with age (Tewksbury & Lloyd, 2001; Sthultz et al., 2007). Moreover, stress-tolerant species are more likely to be benefactors, while stress-intolerant species are often beneficiaries (Liancourt et al., 2005; He et al., 2012).

2.7 Ecological networks

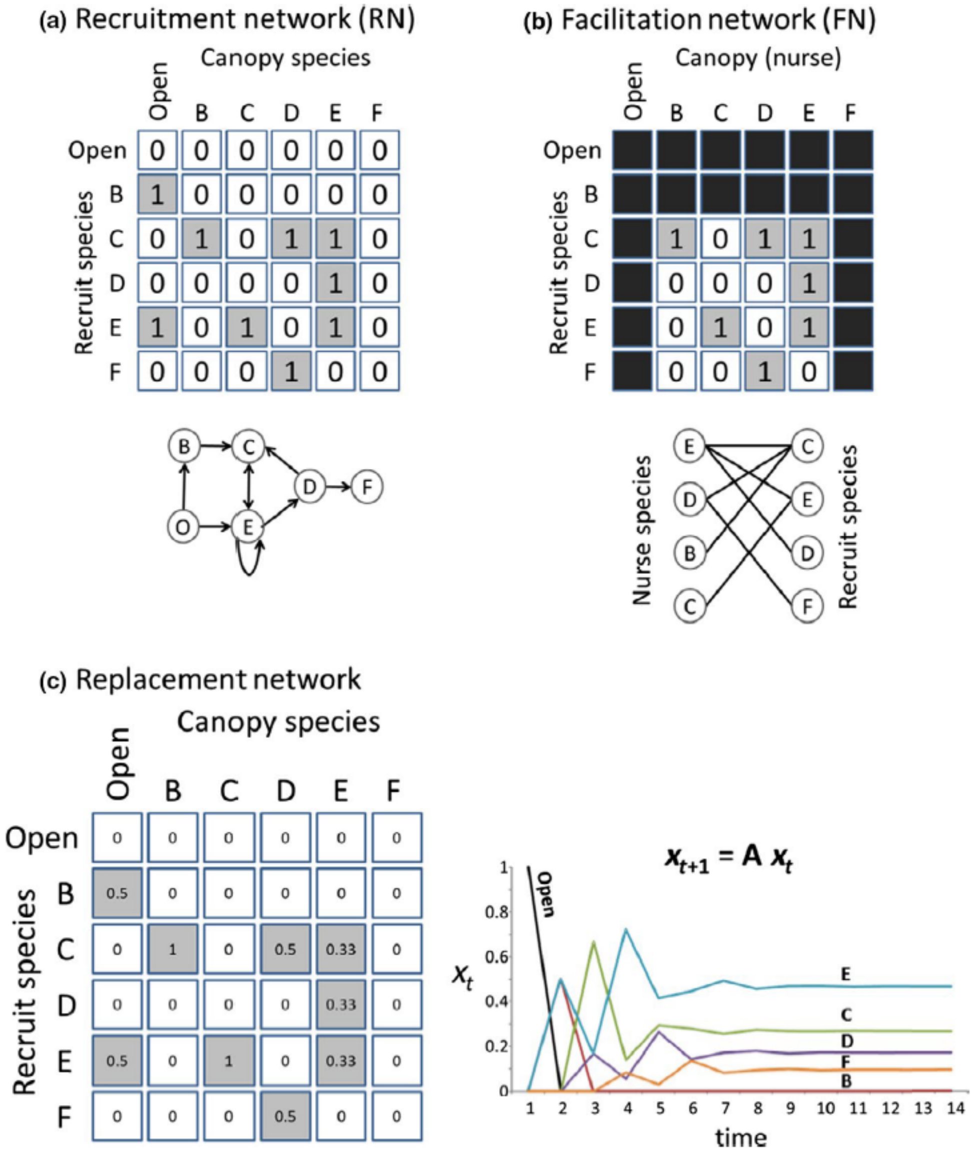
All evidence emphasizes the importance of facilitation inclusion in the mainstream ecological theory (Bruno et al., 2003; Tirado and Pugnaire, 2005). Nevertheless, in order to fully understand the effects of facilitation on biodiversity maintenance, ecologists need to uncover properties that may emerge when many species grow together; therefore, the study of pairwise interactions proves to be inadequate (Levins and Lewontin, 1985). The determination of mechanisms that drive species composition and maintenance of species diversity in plant community assemblages is nowadays central to ecology, but still, there is limited knowledge of the complex characteristics in multispecies systems in which each species interacts with others.

Many studies that have successfully incorporated multiple species interactions including facilitation have clearly demonstrated that community assembly cannot be understood as the sum of pairwise species interactions (Bertness et al., 2006; van de Koppel et al., 2006). These studies have challenged the traditional view of multiple benefactor species as being redundant in the assembly of the community (Bruno and Bertness, 2001) and demonstrated that multiple benefactors may act synergistically and set off a facilitating cascade (Altieri et al., 2007, Verdú and Valiente-Banuet, 2008).

One means of illustrating the complexity resulting from multiple interactions in plant communities is to conceive them as ecological networks in which species interact with others associated with one or more other species (Valiente-Banuet, 2008). The biological complex networks theory has been used as a tool to explain how species interact in different plant–animal, animal–animal, or plant–plant systems (Bascompte & Jordano, 2007). A particular interest in environmentally mediated positive, non-trophic interactions (i.e., facilitation) that occur between independent plants has been resurgent since the begging of the century (Bruno et al., 2003, Brooker et al., 2008). A facilitative network is constituted by benefactor (nurse) species interacting with beneficiary (facilitated) species. In synthesis, facilitation among plants can scale up to a full network, supporting ecosystem functioning both directly via microhabitat amelioration and indirectly via diversity effects. In this context, Verdú and Valiente-Banuet (2008) pioneered the analysis of plant facilitative interactions as ecological networks, FNs (facilitation networks), at the community level. A facilitation network describes all plant–plant facilitative interactions, at the scale of the whole community, which are approached as a network of interactions between nurse plants and facilitated plants recruiting under their canopy. Within almost two decades since the work of Verdú & Valiente-Banuet (2008), several studies on networks described recruitment interactions occurring in plant communities (Fodor, Haruta, & Dorog, 2018; Marcilio-Silva et al., 2015; Pulgar, Alcántara, & Rey, 2017; Verdú & Valiente-Banuet, 2011).

2.7.1 Recruitment networks (RNs), Facilitation networks (FNs), and Replacement networks

Recruitment networks (RNs), Facilitation networks (FNs), and Replacement networks are different representations of the interactions between established plants (canopy or nurse plants) and plants recruiting beneath them (Fig 2.1). In all three types of network analysis, a matrix construction is essential. Besides their distinctive differences, in all matrixes, the nodes represent populations of different species, and their links indicate the qualitative (binary presence/absence) or quantitative magnitude of the effect of the population of one species on the population of the other. Their common aim is to understand the organization and functioning of plant communities (excluding small herbaceous species) by using the frequency of recruitment of one species under another as a surrogate for interaction strength; and since they explore community-level questions, they consider all the possible pairwise interactions between as many species as possible within a given local community (Alcántara et al., 2019). For the construction of the presence/absence matrix, the terms "recruit" and "canopy" are widely used. A "recruit" is defined as a less than 1-year-old plant, that has not reached the reproductive stage or has signs of having set a negligible number of flowers or fruits compared to the crop produced by a fully-grown adult of the species (Alcántara et al., 2019). The size of a recruit is highly dependent on the life history and growth rate of the species, but in general, the size of a recruit should be much smaller than a quarter of a fully grown adult of the species excluding vegetative sprouts. A canopy plant's ability to affect a recruit depends on the recruit's distance (*d*) from the canopy's trunk (Comita et al., 2014; Swamy et al., 2011), by the density of the canopy plants a few meters around the recruit (Condit, Hubbell, & Foster, 1994; Queenborough et al., 2007) and the impact of any underground and aboveground dimensions of the canopy. In the Mediterranean pine–oak forests Alcántara et al. (2019) used $d = 0.5$ m, but it is suggested that distance can be adjusted to each species based on previous knowledge. This distance should be short enough that the roots of the new recruit are in contact with the roots of the canopy plant.



(a) Recruitment network (RN)

	Open	B	C	D	E	F
Open	0	0	0	0	0	0
B	1	0	0	0	0	0
C	0	1	0	1	1	0
D	0	0	0	0	1	0
E	1	0	1	0	1	0
F	0	0	0	1	0	0

(b) Facilitation network (FN)

	Open	B	C	D	E	F
Open	■	■	■	■	■	■
B	■	■	■	■	■	■
C	■	1	0	1	1	■
D	■	0	0	0	1	■
E	■	0	1	0	1	■
F	■	0	0	1	0	■

(c) Replacement network

	Open	B	C	D	E	F
Open	0	0	0	0	0	0
B	0.5	0	0	0	0	0
C	0	1	0	0.5	0.33	0
D	0	0	0	0	0.33	0
E	0.5	0	1	0	0.33	0
F	0	0	0	0.5	0	0

Figure 2. 2 Comparison of matrix and graph formation for (a) Recruitment networks (RNs), (b) Facilitation networks (FNs), and (c) Replacement networks. The three networks are different representations of the interactions between established plants (canopy or nurse plants) and plants recruiting beneath them. (a) An RNs matrix contains information on the recruitment interactions between all possible pairs of species, and between recruiting species and open interspaces. Interacting species and open interspaces are represented by their own node. Every species potentially participates as a canopy and as a recruit, so the network is unipartite. As RNs are directed networks, in the graph representation, the interactions are indicated as arrows pointing from the canopy to the recruited species. (b) FNs focus on the subset of species whose recruitment is facilitated by some of the canopy species (black cells in the matrix are those present in the RN but not in the FN). FNs are bipartite networks with a group of species playing the role of nurses and another group with the role of recruits, which is why the group of nurses does not include as a node either open ground or those species under which no other plant was found recruiting since (some species may occur in both groups) and those that recruit only in open ground. Thus, FNs are subnetworks of RNs. (c) Replacement networks are functions of RNs whereas the entries of the RN are transformed into transition probabilities so that the matrix can be incorporated into a simple Markov model of community dynamics (Alcántara et al., 2019).

Recruitment networks (RNs) contain information on the recruitment interactions between all possible pairs of species, and between recruiting species and open interspaces that are represented by their own node. Every species potentially participates as a canopy and as a recruit, so the network is unipartite (Alcántara et al., 2019). Two species interact if one of them has an effect on the population dynamics of the second (Abrams, 1987). Thus, the presence of saplings of the recruit species under individuals of the canopy species is an indication that the canopy species is making a positive contribution to the sapling bank of the recruit population, even if individual saplings experience competition from the canopy plant (e.g., achieving lower growth rates). Facilitation networks (FNs) focus on the subset of species whose recruitment is facilitated by some of the canopy species. FNs are bipartite networks, with a group of species playing the role of nurses and another group with the role of recruits; some species can occur in both groups, but this is not a necessary condition. The group of nurses does not include open ground as a node, nor those species under which no other plant was found recruiting. Similarly, FNs exclude from the group of recruit species those that recruit only in open ground, like pioneer and shade-intolerant plants (Alcántara et al., 2019). Thus, FNs are subnetworks of RNs. Replacement networks are functions of RNs, since RNs also contain valuable information on the functional role that each species plays in community dynamics and coexistence using models of replacement dynamics. The concept of replacement network derives from the concept of replacement dynamics used in most theoretical models of plant community dynamics (when a plant dies, another of the same or different species takes its place). To build a replacement network one can transform recruitment frequencies to replacement probabilities for use in Markov Chain models (Horn, 1976; Siles et al., 2008) or to recruitment densities for use in compartmental models (Alcántara, Rey, & Manzaneda, 2015).

2.7.2 Analyzing the Networks

There are very important differences between a network structure obtained focusing on the canopy–recruit interactions and the one obtained using “classic” co-occurrence methods even when referring to the same species community (Delalandre & Montesinos-Navarro, 2018; Freilich et al., 2018). The different properties among positive interaction networks and “classic” co-occurrence networks are not merely semantic but have important implications for the descriptive study of the networks and for their use in theoretical models of community dynamics. Plant-to-plant interactions in classic co-occurrence networks are implied after the existence of statistically significant spatial covariation in the abundance (or presence) of two mainly adult plant species across samples (Saiz, Alados, & Pueyo, 2014; Saiz, Gómez-Gardeñes, Borda, & Maestre, 2018). That is consequently the reason behind the symmetric, signed (positively or negatively), and undirected interaction matrices of the cooccurrence networks, since if species A spatially covaries (positively or negatively) with species B, then B necessarily "interacts" in the same way with A. However, in RNs the existence of an interaction does not depend on the existence and power of statistical tests, only on the observation that recruitment there exists of one species under the other exists. Thus, two species can covary negatively in space; nevertheless, one may recruit under the other. In this way, interaction matrices from RNs are not necessarily symmetric, since the recruitment of species A under B does not necessarily imply that B recruits under A and RNs matrixes do not have an associated sign, since they have only zero entries, for no recruits observed, or positive entries when recruits are observed under a canopy. The first studies depicting plant RNs (Verdú & Valiente-Banuet, 2008; Verdú et al., 2010) focused on the importance of the facilitative effect of nurse plants on the recruitment of other plants in drought-prone environments; thence the term FNs. However, the concept can be generalized to include any recruitment interaction, not only those involving facilitation. Thus, a recruitment network can be defined as a network depicting the interactions between established (canopy) plants and plants recruiting beneath them. In this context, the term "canopy plant" instead of "nurse plant" can be used because the first does not assume any positive or negative effect of the established plant on the recruiting one.

The complex nature of plant–plant facilitation offers many possibilities to build different types of facilitation networks (FNs) besides networks of recruitment interactions. For example, links instead of recruitment interactions could represent, the effect of shared pollinators on plant reproduction (Moeller, 2004) or the effect of shared mutualistic fungi on plant nutrition (Montesinos- Navarro, Verdú, Querejeta, & Valiente-Banuet, 2017). Despite the importance of the other aspects of facilitation, in increasing our knowledge of the mechanisms of facilitation and the way facilitation combines within a broader context of higher-order interactions (Levine, Bascompte, Adler, & Allesina, 2017) focusing on recruitment interactions for building a facilitation network has its own important advantages. Recruitment interaction networks provide information regarding the effects of the interaction on a population (demographic) level enabling us to connect interaction networks with the analysis of the plant community dynamics. At the same time recruitment interaction networks are the integrated outcome at the population level of all the above multiple interactions (pollination, seed dispersal, seed predation, pathogen, and herbivore attack) and their sapling banks contain several cohorts, thus their structure is less influenced by particularly good or bad years for the interactions such as years of extreme weather conditions or by population cycles of certain species (e.g., masting events, pest outbreaks) (Alcántara et al., 2019).

Inferences about the community and the possible interaction properties of its plants can be obtained by analyzing RNs (Poisot, Stouffer, & Kéfi, 2016). Connectance, as the ratio of the realized number of interactions to the maximum potential number of interactions that could occur in the network, could lead to several assumptions about the relations formed by the plants in the community. Most RNs studied to date show connectance below 30% which implies that more than 70% of the potential interactions in a local community are unobserved interactions. The frequency of canopy–recruit interactions can either be positively related to the abundance of the interacting species (Verdú and Valiente-Banuet, 2011; Marcilio-Silva et al., 2015; Alcántara, Pulgar, Trøjelsgaard, Garrido, and Rey, 2018) or indicate that an important part of the potential interactions is impeded for some ecological reason (Alcántara et al., 2018). In the first case, these are “neutral - forbidden” interactions as defined by Canard et al. (2012) while in the second case, they are “forbidden links” as defined by Olesen et al. (2011). Among the realized interactions, interspecific interactions have more frequently neutral or enhancing effects on recruitment, while intraspecific interactions have more frequently depressing effects although intraspecific enhancing effects can also be found. The abundance and ratio of these types of interactions in a community are linked to its stability. Networks containing many weak and few strong interactions are proved to be more stable (McCann, Hastings, & Huxel, 1998; Wootton & Stouffer, 2016), while the coexistence of species that differ in fitness requires stronger intra- than interspecific limitation of population growth (Chesson, 2000). In RNs analyzed by Verdú and Valiente-Banuet (2011) and Alcántara, Garrido, and Rey (2019) there was evidence suggesting that the second property may be acting in those communities, creating a community compensatory trend whereby more abundant species had lower rates of recruitment than rarer ones (Comita et al., 2007; Connell, Tracey, & Webb, 1984; Soliveres et al., 2015). The structure of RNs could lead to plant communities with high resistance to species loss and allow the long-term coexistence of many species. However, this is highly linked to the degree of the connectance of the species present in the community. When a species disappears from a community its interactions disappear too, this can affect other species and may unleash a cascade of secondary extinctions. Research suggests that the structure of RNs can make plant communities very resistant to the removal of species (Verdú and Valiente-Banuet, 2008; Alcántara and Rey, 2012; Pulgar et al., 2017), but the extinction of a few highly connected species could be fatal for all the other species connected to it (Valiente-Banuet & Verdú, 2013). Most RNs contain a core of highly interconnected species which is formed by a set of species interacting intransitively among them (Alcántara et al., 2017). Under replacement dynamics, this core would allow the long-term coexistence not only of the group of species involved but also of their satellite species, thus having a major effect on species richness and community stability depending on their presence or disappearance from the community.

There can be multiple factors determining the frequency of individual canopy–recruit positive interactions (i.e., the abundance of the interacting species, seed dispersal vectors, seed predators, herbivores, pathogens, mycorrhizal fungi, symbiotic bacteria, competitors, and pure chance). Verdú and Valiente-Banuet (2008, 2011) and Alcántara et al. (2018) found that the frequency of canopy–recruit positive interactions increase with the phylogenetic distance between species. This phylogenetic pattern could be justified when closely related species are functionally similar so that competitive exclusion could take place, or if third interactants, such as pathogens, affected closely related species more strongly. On the contrary, distantly related species might function differently and compete less strongly or even help each other through complementary effects (Montesinos-Navarro et al., 2017). However, this is not a rule for all communities. For example, Marcilio-Silva et al. (2015) found that the best model explaining an observed facilitation network in subtropical Brazilian forest–grassland included species abundance but not phylogeny. These could be some of the reasons why the outcome of canopy–recruit interactions can be depressing, neutral, or enhancing for recruitment since it results from the balance between multiple positive and negative interactions. Overall, plant facilitation networks tend to be structured following a significant phenotypic pattern, where functionally similar species tend to recruit under functionally similar nurses, as shown by Navarro-Cano et al. (2021). This pattern continuously participates in the community's formation as time passes and the recruited species go into an adult stage, as it is the result of interactions being mediated by the traits of both benefactors and beneficiaries instead of randomness (Bastazini et al., 2017). Even after seedling growth, most initial facilitation interactions are maintained over time, evidence of this phenomenon is the preservation of 80% of interactions in communities in southeastern Spain (Navarro-Cano et al., 2021) and 53% of interactions in Mexican desert communities (Valiente-Banuet and Verdú, 2008) both communities strongly shaped by facilitation. Phenotypic characterizations have shown differences in the traits of nurses and facilitated species in different biomes and that these traits are strongly dependent on the environmental context (Butterfield and Callaway, 2013; Navarro-Cano et al., 2021). For example, facilitated species from North American deserts are taller, have larger seeds, and invest more in roots than nurses (Butterfield and Briggs, 2011). Inn Mediterranean-type ecosystems though, facilitated plants are animal-dispersed, evergreen, long-rooted, resprouting species with large leaves while nurses have the opposite trait states (Valiente-Banuet et al., 2006). On the contrary, nurses in extremely stressful mine tailings studied by Navarro-Cano et al. (2021) tended to have CAM/C4 metabolism, the ability to resprout, were taller, with longer leaves, and larger roots than facilitated species.

The structure of a network is the outcome of a balance between competition and facilitation and as such requires further information than a simple categorization of nurses and facilitated plants. Since facilitation is an interaction among specific species and therefore a suitable nurse for some species can be a strong competitor for others (Callaway, 2007), it is important to study the phenotypes of both nurses and facilitated plants to understand the ways in which they fit together. This will allow us to understand the effect of facilitation interactions. Many studies have hypothesized and supported the presence of an important phenotypic signal underlying the presence of facilitation. To prove this presence many studies used phylogenetics as a proxy of phenotypic distances between nurses and facilitated plants (Alcántara et al., 2018, 2019; Marcilio-Silva et al., 2015; Valiente-Banuet and Verdú, 2008; Verdú et al., 2010) and others used actual phenotypic characteristics (Schöb et al., 2018; Navarro-Cano et al., 2019; Navarro-Cano et al., 2021). A network of facilitation interactions between nurses and seedlings is expected to display a phenotypic signal if nurse species with similar traits provide similar microhabitats and seedlings of species resembling their traits require similar microhabitats to recruit (Verdú et al., 2010). Studying three different nurse species Schöb et al. (2018) supported this expectation, showing that differences in the effect traits significantly explained the differences in the response traits of their facilitated plants. Experimental evidence provided by Navarro-Cano et al. (2019) concluded that the probability of germination of seeds from different species sown under different nurses increases with the trait distance between the nurse and the facilitated species. Navarro-Cano et al. (2021) suggested that trait matching via exploitation barriers was the most relevant linkage rule explaining their under-study facilitation network because trait values of nurses and facilitated plants tended to separate rather than overlap. In a facilitation network trait matching via exploitation barriers occurs when a trait limits the interaction to those species whose traits are below a barrier value (Santamaría and Rodríguez-Gironés, 2007). Root depth was found to act as such a barrier trait with deep-rooted nurses blocking deep-rooted species to access their facilitative effect, although some root-shallowed nurses facilitating deep-rooted species may also be present. The results of Navarro-Cano et al. (2021) confirmed the presence of important phenotypic signals since they proved that nurses with similar phenotypes tend to facilitate species that are also similar in their phenotypes while being phenotypically distant from their benefactors. Seed size and root length are traits that together with height and leaf traits become relevant for nurses to interact with their facilitated plants. Trait differences may result not only in reduced competition but also in increased benefits derived from complementarity (i.e., hydraulic lift from deep to shallow-rooted species; Zou et al., 2005), ultimately promoting facilitation (Montesinos-Navarro et al., 2017).

Chapter 3

Facilitation and recruitment networks in a phryganic plant community in Cyprus[1]

3.1 Introduction

Communities' structure, especially under stress, is driven by positive species interactions such as facilitation (Callaway, 2007; Bruno et al., 2003; Tirado and Pugnaire, 2005). During the last decades, plant-to-plant interactions are considered key components of biodiversity, ecological functions, and services (Valiente-Banuet et al., 2015) as well as key drivers of community structure and assembly (McIntire and Fajardo, 2014).

Facilitation is an interaction in which one species benefit, while the other is not detrimentally affected (Aslan et al., 2015). In plant communities, 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 Mollina-Freaner, 2013). Facilitation is demonstrated mostly under stressful conditions: aridity, grazing, direct light, and high temperatures (Pugnaire and Luque, 2001) where the nurse plant can be an herb, a shrub, or a tree species. Nurse plants' canopy provides shelter and improves soil, air humidity, and favorable temperatures. However, facilitation can be size-dependent. As soon as the beneficiary plants have overgrown their

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[1] Constantinou, E., Montesinos-Navarro, A., Sarris, D., Vogiatzakis, I.N. (submitted) Facilitation and recruitment dynamics within a phryganic community dominated by an ecosystem engineer plant. *Journal of Vegetation Science*

benefactors (Soliveres et al., 2010), competition might replace facilitation, mostly in closely related taxa (Valiente-Banuet and Verdú, 2008). Although the nurse plant effect was extensively studied in desert areas and areas around the Mediterranean basin (Gómez-Aparicio et al., 2004), the phenomenon is expected to be expressed in other climatic conditions as well, spanning from tropical to sub-Antarctic 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 et al., 2018).

According to the European Red List of Habitats (EUNIS, 2019), the Cyprian phrygana are cushion-forming thermo-Mediterranean summer-deciduous, often thorny, sclerophyllous formations of the island of Cyprus. They are mostly characteristic of the island's central plains, having a semisteppic batha appearance. Cyprian phrygana as a subset of the East Mediterranean phrygana is an outpost of the continental formations of thorny burnet (*Sarcopoterium*) bathas units to *Lithospermum hispidulum* bathas, with Irano-Turanian affinities (Litav and Orshan, 1971; Zohary, 1973). Depending on their location, these communities can be formed by *Sarcopoterium spinosum*, *Thymbra capitata* (syn. *Thymus capitatus*), *Asphodelus aestivus*, *Fumana thymifolia*, *Helianthemum obtusifolium*, *Onosma fruticosa*, *Phagnalon rupestre* ssp. *rupestre*, *Noaea mucronata,* and *Teucrium micropodioides* (Cyprus Department of Environment, 2007). The habitat of the spiny heath (phrygana) of the Eastern Mediterranean in general, is distributed in dry sites with shallow sandy and loamy soils and may be of primary origin (natural vegetation) or have a climax character especially in Cyprus and the Aegean islands, as well as in the coastal zones of Anatolia, Syria, and Lebanon. It is often of secondary origin and could be the result of a retrogressive succession of evergreen sclerophyllous vegetation, post-fire regeneration stages of woodland and rangeland vegetation, and abandoned cultivated fields.

The European Environmental Agency reported the current habitat area to be 192 Km^2 in 2019, equivalent to 4.9% of the total natural vegetation of the island (43.8% are high forests and the rest 51.3% other lower vegetation such as maquis and garique). Cyprian phrygana faces various pressures and threats. The conservation status of the habitat is classified as poor and changes in management and policy are needed to bring it back to favorable status, although there is still no risk of extinction in the near future. Human activities have eliminated the initial variability of phrygana communities which were originally shaped by purely climatic factors and as a result, most of the phrygana communities in many parts of the country are the result of human impact (Trabaud, 1982). In fact, phryganic ecosystems are in most cases stages of anthropogenic degradation of the original Mediterranean forests. The long list of anthropogenic pressures and threats that created the mosaic structure of the ecosystem (Tsiourlis et al, 2007) includes intensive grazing, transportation and service corridors, urbanization, residential and commercial development, and fires.

Ziziphus lotus, a small deciduous tree in the buckthorn family *Rhamnaceae*, is native to the Mediterranean region and listed in European habitat types such as East Mediterranean phrygana (formations with lower *Ziziphus lotus* shrubs) and Mediterranean arborescent scrubs with *Ziziphus lotus*, a priority habitat according to the European Habitats Directive (European Red List of Habitats, 2016; Mendoza-Fernández et al., 2019). These plant communities are recognized in the Iberian Southeast, Cyprus, Sicily, and surrounding islands. The largest patches of these communities are distributed under a xerophytic Thermo-Mediterranean bioclimate and correspond to the mature phase or climax of the climatophilous and edapho-xero-psammophilous vegetation series (Valle and Lorite, 2005; European Red List of Habitats, 2016). In Cyprus, representative communities of this habitat type cover an area of approximately 113 ha distributed in 11 Natura 2000 sites (CDE, 2007). The habitat used to be abundant mostly along the island's Mesaoria plain and central hill zone, but due to strong anthropogenic pressure, the habitat’s species are now found in isolated clusters, usually at the boundaries of cultivated fields. This habitat forms the type of vegetation that can produce the maximum biomass in relation to the existing climate (Mendoza-Fernández et al., 2019).

The climatological factors that control this type of vegetation include the absence of frost, mild annual average temperatures, high temperatures, absence of precipitation during the dry season, and high solar radiation throughout the year (Tirado, 2009). In Cyprus, the communities are dominated by the phreatophyte *Z. lotus*, which reaches up to 3 m in height, shallow-rooted Mediterranean shrubs, long-lived perennial herbs, and herbaceous species which are often aggregated around *Z. lotus* forming islands of vegetation (Fig. 3.1b).

In addition, this impressive, from a landscape point of view, hemispherical cluster vegetation, which is common in the Mediterranean, has triggered various interpretations of the dynamics of the community (Pérez-Latorre et al., 2010). These clusters can potentially create a microenvironment inside them that reduces the effect of dry and hot external environmental conditions, provide refuge and food for reptiles, rodents, and birds, among other groups, as well as favorable nursing processes for several plant species (Fuentes et al., 1986; Badano et al., 2005). These clusters of vegetation can enhance complex ecological interactions among multiple species simultaneously, which can conform to ecological networks with intrinsic properties.

In this context, Verdú and Valiente-Banuet (2008) pioneered the analysis of plant facilitative interactions as ecological networks at the community level. At the scale of the whole community, plant–plant facilitative interactions can be approached as a network of interactions between nurse plants and facilitated plants recruited under their canopy. Plant ecological networks are aimed at understanding the organization and functioning of plant communities. The populations of different species are represented by their nodes, while the qualitative (binary presence/absence) or quantitative magnitude of the effect each species' population has on another species' population is indicated by their links. The strength of every interaction is determined using the frequency of recruitment of one species under another as a proxy for a fitness component.

Plant-plant interactions can be assessed using different types of networks depending on the ecological process of interest. Recruitment networks (RNs) are networks depicting which plant species recruit under others, while facilitation networks (FNs) are subnetworks of these RNs that only consider the associations that are more likely to occur 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, and this structure has been reported to provide a community with the robustness to cope with any potential loss of interacting species (Verdú and Valiente-Banuet, 2008; Montesinos-Navarro et al., 2012; Bascompte and Jordano, 2007).

This study addresses the following questions:

1. Can phryganic plant communities be structured by facilitation? And if so, does the structure of their interaction network match the properties described for other positive ecological interaction networks? If the community is structured by facilitation, we expect higher recruitment of young plants under the canopy of the same or other species compared to open ground. Also, we expect the facilitation network to show a nested pattern, as reported in other plant communities driven by facilitation and by other positive interactions.
2. Are some adult species more effective as facilitators (nurse plants) than others? If an adult individual of a given species would act as a more effective nurse plant than other species perform, we expect that it will show a more positive co-occurrence of plant species under its canopy than the rest.
3. Are some recruited species more dependent on facilitation than others? If a recruited species is more dependent on facilitation, we expect that it will show a more positive co-occurrence under a nurse's canopy compared to its presence in open ground.

3.2 Materials and methods

The field study was carried out in March and April 2019 in a 0.136 km^2 experimental site of an arid phryganic plant community with *Ziziphus lotus* within the Natura site of Alykos potamos – Agios Sozomenos (35º03΄33΄΄ N, 33º25΄23΄΄ E; Fig.1) in the island of Cyprus. The soil within the experimental area is sandy with poor organic content at the top 10 cm and is of Calcaric Regosols. The site hosts important biodiversity elements and is part of the European Natura 2000 network (CY2000002). Its climate is arid (annual rainfall <400mm; P/ETo<0.2) with hot, dry summers from May to mid-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 ºC. (Department of Meteorology, 2020). The vegetation of the site is dominated by small shrubs such as *Ziziphus lotus*, *Noaea mucronata*, *Phagnalon rupestre*, *Thymus capitatus*, *Asparagus stipularis*, *Teucrium micropodioides*, *Helianthemum obtusifolium*, *Sarcopoterium spinosum*, *Rhamnus oleoides* subsp. *graecus* and *Crataegus azarolu* (Cyprus Department of Environment, 2007). Seven endemic plants to Cyprus can be found in the area: *Anthemis tricolor, Carlina involucrata* ssp. *Cyprica, Helianthemum obtusifolium, Onopordum cyprium, Onosma fruticose, Ophrys kotschyi,* and *Teucrium micropodioides.*

Figure 3. 1 (a) Location of the Natura site of Alykos potamos – Agios Sozomenos in Cyprus and (b) caption of the study area in mid-March 2019 (Photo Constantinou E).

3.2.1 Sampling design

Thirty plots were randomly distributed throughout the study site (Fig. 3.2). Our sampling effort curve (Fig. 3) indicates that stable estimates can be obtained with this sampling effort, which covered 0.126 km^2. Each plot had an area of 500 m^2 and dimensions of 10 m by 50 m. We sampled using the line-intercept method along a line of 50 m placed lengthwise in the middle of each plot, recording the presence of woody species and long-lived perennial herbs.

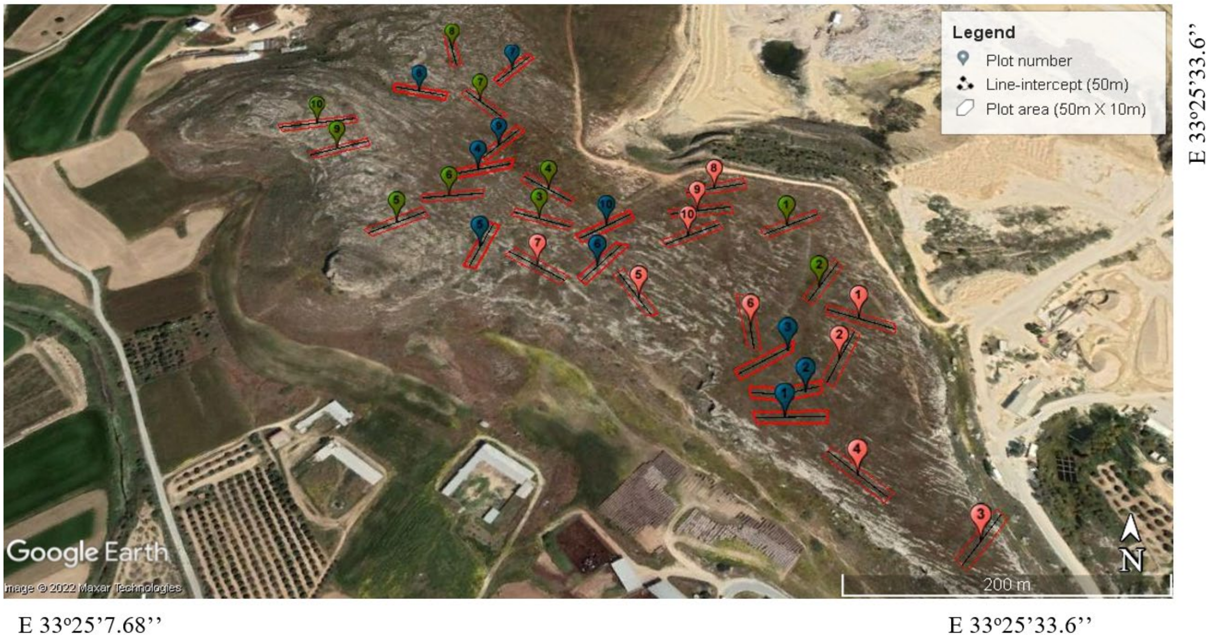

Figure 3. 2 Aerial photo of the study area, with the location of the thirty randomly distributed plotswithin which the number of the canopy and recruited plants were measured along the line intercepts.

As a "canopy" species, we defined any fully developed adult woody plant or long-lived perennial herb (Alcántara et al., 2019). On the other hand, a "recruit" is a less than one year-old plant, which did not reach the reproductive stage or had signs of 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). In general, the size of a recruit was less than a quarter of the size of a fully developed adult of the species. The process of recruitment is driven by mechanisms that take place on the forest floor (post-dispersal seed predation, germination, mycorrhizal associations, soil pathogens, herbivores, soil nutrients, and microclimatic amelioration by plants). To identify the canopy with an effect on each recruit, we considered that the direct effects of a canopy plant on the recruiting plant depend primarily on plant parts located within a few centimeters belowground (where recruit roots grow) and less than 1.5 m above ground. Only free-standing recruits were considered, vegetative sprouts were not counted as recruits and in case of doubt, the recruit was ignored.

The entire ground surface along each line intercept was systematically "scanned" searching for recruiting plants so that each canopy species was sampled proportionally to its abundance. For each plot, we recorded: the number and length of canopies per species, the number and length of open ground, and the number of recruits per species under each canopy and in open ground. The percentage of the line intercept that was covered by each canopy species or open gap was then calculated for every plot.

The community was found to be formed by 11 different species of woody plants or long-lived perennial herbs. We identified six species acting as canopy plants, namely: *Ziziphus lotus, Noaea mucronata, Thymus capitatus*, *Asparagus stipularis, Rhamnus oleoides* subsp. *graecus,* and *Sarcopoterium spinosum*. Ten species were identified acting as recruits, namely: *Anthemis tricolor*, *Asparagus stipularis*, *Crataegus azarolus* var. *aronia*, *Helianthemum obtusifolium*, *Noaea mucronata, Phagnalon rupestre*, *Rhamnus oleoides* subsp. *graecus*, *Sarcopoterium spinosum*, *Teucrium micropodioides,* and *Thymus capitatus.*

3.3 Statistical analysis

A rarefaction curve was used to assess the sampling effort efficiency, following the methods proposed by Chao et al. (2014), using the PAST software (Hammer et al., 2001). For the accumulation curve, the independent variable was the number of plots, and the dependent variable was the number of accumulated species with 95% confidence intervals.

A Chi-square test of goodness-of-fit was performed to test for significant positive or negative associations among the plant species of the community. A species was considered as being facilitated when the percentage of individuals recruited under adult plants of other species was greater than that expected by chance based on the percentage of adult plants cover vs. open space. Individual x^2 tests were conducted only for those species with at least 20 positive co-occurrences with other plant species (Table 3.3), in order to estimate each species' dependence on facilitation and nursery effect in the community. To do so, we repeated the analysis considering firstly each species observed as a recruit, to assess their dependence on facilitation, and secondly, each species acting as the canopy of any recruit, to assess their nursery effect. Statistical analysis was carried out using the IBM SPSS program v. 25.0.

Facilitation interactions in the community were depicted as a network consisting of two sets of nodes (canopies and recruited plant species) linked by interactions between any species pair. We constructed a matrix containing the associations between a recruit and a canopy species proven to be more positive than expected by chance according to the Chi-square test (0/1 matrix) to calculate the number of species interactions (nestedness) as well as the network's connectance.

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), and has been interpreted as a measure of biogeographic order in the distribution of species (Atmar and Patterson, 1993; in Fleishman et al., 2007). In meta-communities, the presence of strong nestedness is a clear indication of 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) and indicates the proportion of recruitment interactions relative to the maximum possible in the assemblage. 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).

To measure nestedness per se we chose the Nestedness metric based on Overlap and Decreasing Fill (NODF) (Almeida-Neto et al., 2008) which improves on previous estimates by calculating nestedness independently among rows and columns. Values of NODF increase with nestedness, perfectly nested matrices have values of 100, and we calculated this using the open-source application for nestedness analysis NeD (Stroma et al., 2014). 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 show the average of the probabilities of occupancy of its row and column and is calculated by the equation: [(Pi/C) + (Pj/R)]/2, in which Pi is the number of presences in row I, Pj is the number of presences in the column j, C is the number of columns and R is the number of rows. The value of *P* was estimated using both the null models.

3.4 Results

The rarefaction curve for the species sampled reached an asymptote (Fig. 3.3), indicating that the sampling effort was large enough to fully capture the composition of species assemblages.

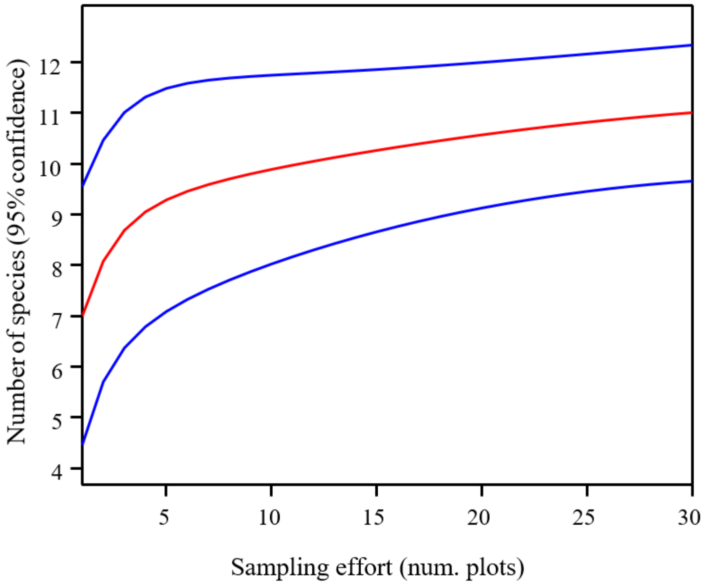

Figure 3. 3 The species accumulation curve for species diversity data (red line), was obtained following methods proposed by Chao et al. (2014). For the accumulation curve, the independent variable is the number of plots, and the dependent variable is the number of accumulated species. Confidence intervals (±95% confidence intervals) are presented in blue lines.

3.4.1 Network nestedness analysis

NODF analysis confirmed that species interactions were significantly more nested than would be expected by chance ($NODF_{Total}$=87.09, *P*=<0.001). Nestedness contribution of recruits ($NODF_{Row}$) was smaller than the nestedness contribution of canopies ($NODF_{Column}$) (Table 3.1). The nestedness observed in the network was significantly larger than that expected by both null models ($NODF_{Total}$ (EE)= 53.068; $NODF_{Total}$ (CE)= 53.37) (Table 3.1). The community was also characterized by a relatively high connectance (C=0.26), all the interactions between canopies and their recruited plants are shown in Figure 3.5.

Table 3. 1 NODF measure of nestedness.

	Total	Column	Row
NODF	87.09	86.57	88.33
NODF (EE)	53.068	54.176	52.61
NODF (CE)	53.37	56.03	52.26
P	<0.001	<0.001	<0.001

$NODF_{Total}$: total matrix nestedness; $NODF_{Colum}$: nestedness among all columns (canopies); $NODF_{Row}$: 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 a_{ij} showing a presence is $[(P_i/C) + (P_j/R)]/2$, in which P_i is the number of presences in row i, P_j is the number of presences in the column j, C is the number of columns and R is the number of rows.

3.4.2 Plant community is structured by facilitation.

Our results showed that overall, the observed number of recruitments under canopies was more than double the expected number (914 versus 386 respectively), while 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, $p < 0.0001$, Cohen's ω = 1.03) (Table 3.2; Fig. 3.4).

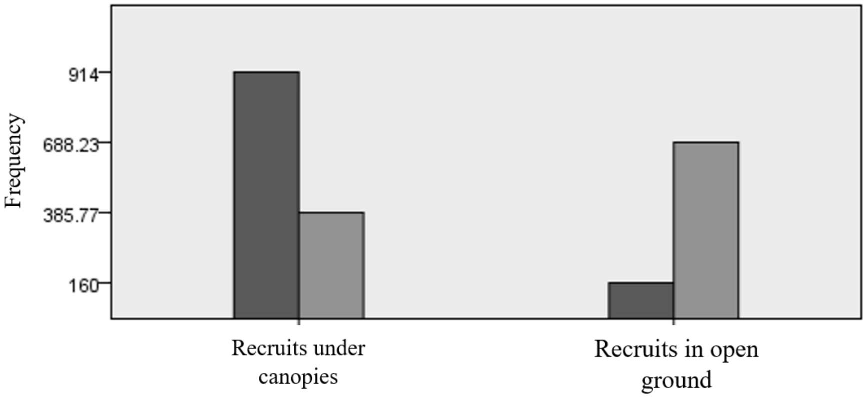

Figure 3. 4 The observed frequencies of recruits (dark grey) vs. the expected frequencies (light grey) under a canopy and in open ground respectively. The boxes' range represents the recruits' frequencies at $p < 0.0001$.

Table 3. 2 Descriptive statistics of the study community

No. species	No. nurse species	Species facilitated[a] (%)	No. individuals beneath nurse plants	No. individuals in open space	Total nurse plant cover (%)	Open ground cover (%)	x^2	*P*
11	6	40	914	160	37	63	1128.7	< 0.0001

Note: The tare x^2 test is significant if the observed number of individuals (all species pooled) recruiting under nurses is higher than expected by the proportion of area occupied by plant cover. [a] A species was considered to be facilitated when the percentage of individuals recruited under nurses was greater than expected by the percentage of the nurses cover in the community concerning open space. Individual x^2 tests were conducted only for the dominant species.

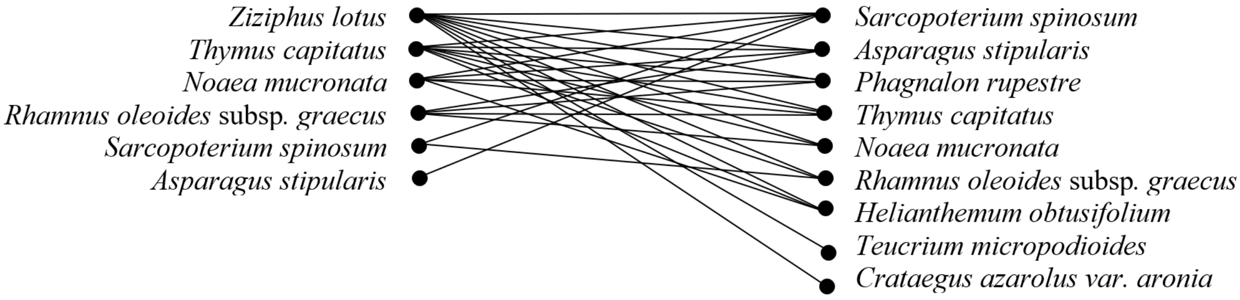

Figure 3. 5 Facilitation network of the community, showing the interactions between nurses (left) and their recruited species (right).

From the species effectively acting as nurse plants, *Z. lotus* showed a significantly greater capacity to harbor recruits under its canopy (i.e., nurse) compared to the capacity of the other canopy plants (X^2 (1, *N* = 914) = 226.535, $p < 0.0001$, Cohen's ω = 0.5). The observed number of recruitments under *Z. lotus* was 746 while the expected number based on its percentage of the cover was 521 (ca. 1.4 times higher than expected) (Fig. 3.6a). At the same time, the observed number of recruits under other canopies was 168, while the expected number based on the percentage of cover of the rest of the species was 393 (ca. 2.3 times less than expected). *Noaea mucronata* and *Thymus capitatus* were shown to have less capacity to nurse than the other canopy plants in total since the observed number of recruits under *Noaea mucronata* was 41 while the expected number was 269 (approx. 6.6 times less than expected) (Fig. 3.6b) and the observed number of recruits under *Thymus capitatus* was 75 while the expected number was 148 (approx. 2 times less than expected) (Fig. 3.6c). At the same time, in the case of *Noaea mucronata,* the observed number of recruits under other canopies was 873 while the expected number was 645 (X^2 (1, N = 914) = 273.331, $p < 0.0001$, Cohen's ω = 0.55) and 839 over 766 for *Thymus capitatus* (X^2 (1, N = 914) = 41.314, $p < 0.0001$, Cohen's ω = 0.21). Consequently, the null hypothesis that recruits occur with specified probabilities (percentage of the transect) under *Noaea mucronata* or *Thymus capitatus* Vs other canopies was rejected.

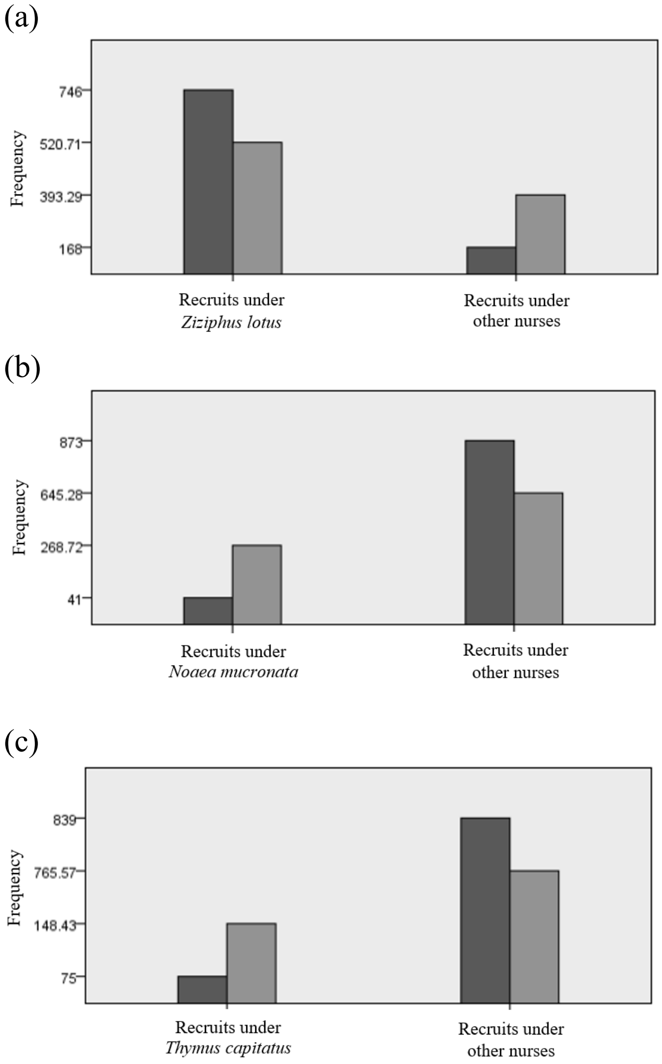

Figure 3. 6 The observed frequencies of recruits (dark grey) vs. the expected frequencies of recruits (light grey) under *Z. lotus* (a), *Noaea mucronata* (b), *Thymus capitatus* (c), and other canopiesrespectively. The boxes' range represents the recruits' frequencies at $p < 0.0001$.

Z. lotus showed greater nurse capacity compared to *Thymus capitatus* or *Noaea mucronata*. The observed number of recruits under *Thymus capitatus* was 75 while the expected number was 182 (approx. 2.4 times less than expected) (Fig. 3.7a) while the observed number of recruits under *Ziziphus lotus* was 746 while the expected number was 639. When comparing *Ziziphus lotus* to *Noaea mucronata*, the observed number of recruits under *Noaea mucronata* was 41 while the expected number was 268 (approx. 6.5 times less than expected) (Fig. 3.7b) and the observed number of recruits under *Ziziphus lotus* was 746 while the expected number was 519. Therefore, the null hypothesis that recruits occur with specified probabilities (percentage of the transect) under *Thymus capitatus* or *Noaea mucronata* Vs *Ziziphus lotus* was rejected (X^2 (1, N = 821) = 81.136, $p < 0.0001$, Cohen's ω = 0.31 and X^2 (1, N = 787) = 292,308, $p < 0.0001$, Cohen's ω = 0.61 respectively).

Comparing *Thymus capitatus* Vs *Noaea mucronata* ability as canopies, the observed number of recruits under *Thymus capitatus* was 75 while the expected number was 41 (approx. 2 times more than expected) and the observed number of recruits under *Noaea mucronata* was 41 while the expected number was 75 (Fig. 3.7c). Thus, the null hypothesis that recruits occur with specified probabilities (percentage of the transect) under *Thymus capitatus* Vs *Noaea mucronata* was rejected (X^2 (1, N = 116) = 41.341, $p < 0.0001$, Cohen's ω = 0.6).

Due to the small number of individuals observed as nurses' statistical analysis of *Asparagus stipularis, Sarcopoterium spinosum,* and *Rhamnus oleoides subsp. graecus,* which also acted as canopy plants, was not possible. All species recorded as nurses linked with their recruited species are presented in Figure 3.5. *Crataegus azarolus var. aronia*, *Helianthemum obtusifolium*, *Phagnalon rupestre*, and *Teucrium micropodioides* were never observed as canopy plants, and *Ziziphus lotus* was never observed as a recruit. The number of recruits per nurse species is presented in Table 3.3.

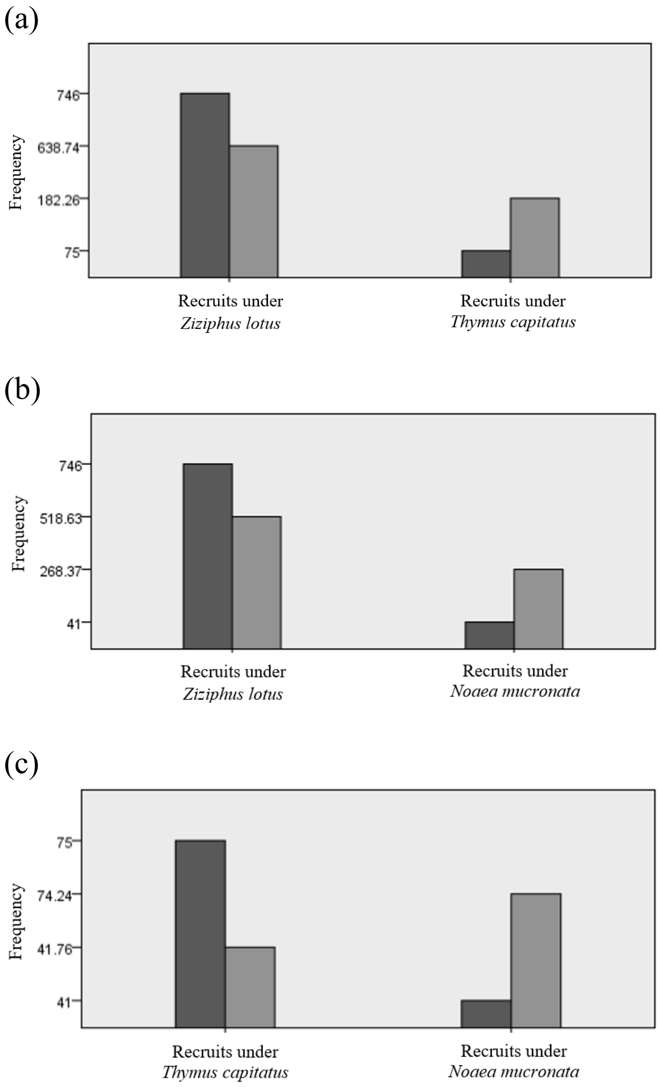

Figure 3. 7 The observed frequencies of recruits (dark grey) Vs the hypothesized frequencies of recruits (light grey) under *Z. lotus* and *Thymus capitatus* (a), *Z. lotus* and *Noaea mucronata* (b), and *Thymus capitatus* and *Noaea mucronata* (c). The boxes' range represents the recruits' frequencies at $p < 0.0001$.

Table 3. 3 Recruited species and the number of plants per species under the canopy plant species. Interspecific interactions are in bold.

Nurse species	Recruited species and Number of recruits								
	Asparagus stipularis	*Crataegus azarolus.*	*Helianthemum obtusifolium*	*Noaea mucronata*	*Phagnalon rupestre*	*Rhamnus oleoides*	*Sarcopoterium spinosum*	*Teucrium micropodioides*	*Thymus capitatus*
Asparagus stipularis							1		
Noaea mucronata	8		2		27		2		2
Rhamnus oleoides subsp. graecus	2			2	1				1
Sarcopoterium spinosum						2	**42**		
Ziziphus lotus	347	2	2	174	125	10	23	15	47
Thymus capitatus	15		2	23	29	3	1		**2**

3.4.3 Species dependence on facilitation

Asparagus stipularis, *Phagnalon rupestre, Noaea mucronata*, and *Sarcopoterium spinosum* showed to be highly dependent on nurses (approximately 2.6, 2.7, 2, and 2.6 times more recruits were found under a nurse than expected respectively) (Fig. 3.8a, b, c, and d). The observed number of recruits under nurses versus the expected number as well as the observed number of recruits in the open ground versus the expected are shown in Table 3.4.

Table 3. 4 The observed number of recruits under nurses versus open ground and their expected numbers are based on the percentage of cover of each environment respectively.

Recruited species	The observed number of recruits under nurses	Expected number of recruits under nurses	The observed number of recruits in the open ground	Expected number of recruits in the open ground
Asparagus stipularis	373	143	13	243
Phagnalon rupestre	557	210	11	358
Noaea mucronata	199	106	86	180
Sarcopoterium spinosum	69	26	2	45

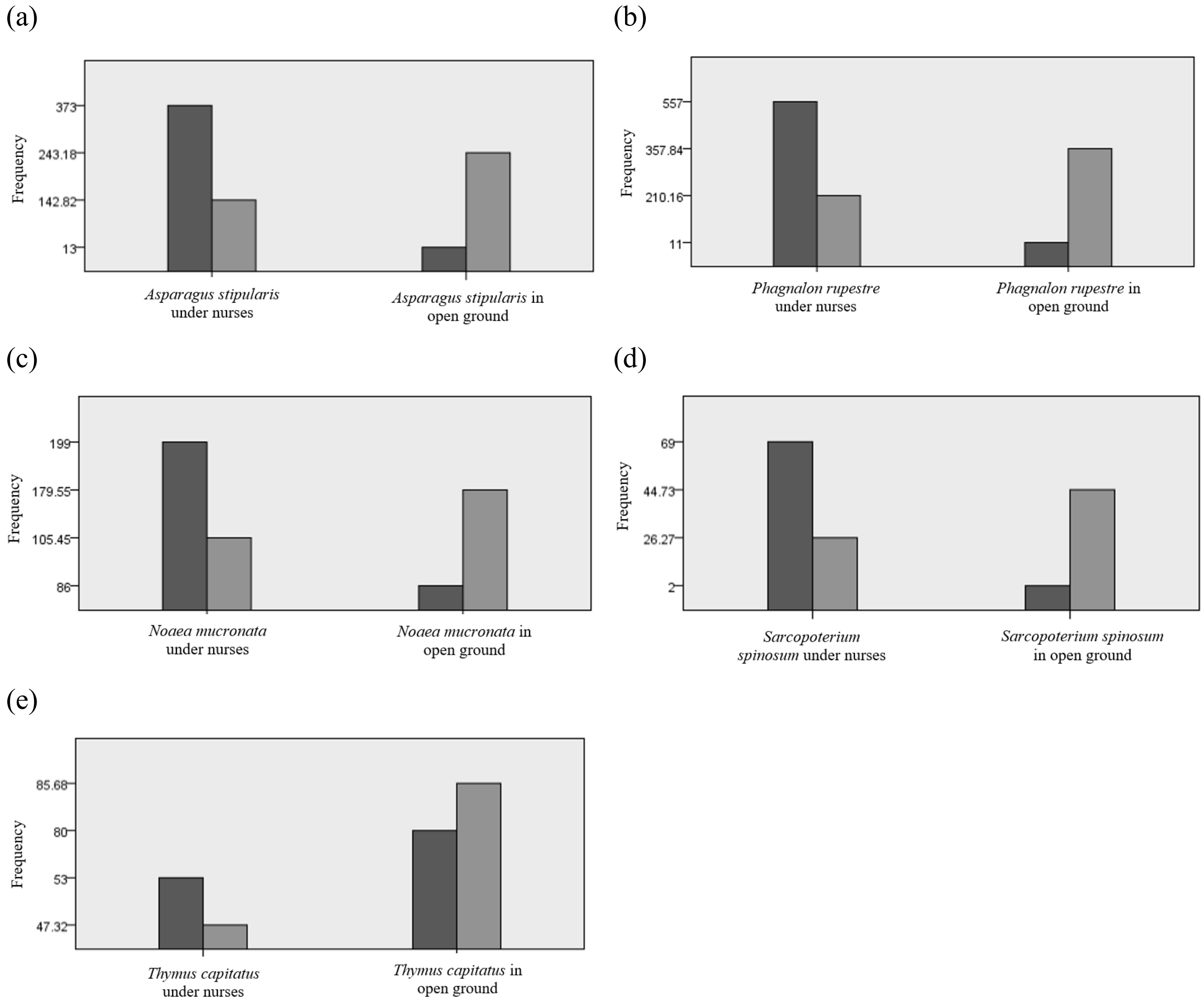

Figure 3. 8 The observed frequencies of recruits (dark grey) Vs the expected frequencies (light grey) of recruits under a nurse and in open ground for *Asparagus stipularis* (a), *Phagnalon rupestre* (b), *Noaea mucronatamucronata* (c), *Sarcopoterium spinosum* (d) and *Thymus capitatus* (e) at $p < 0.0001$ for (a), (b), (c), (d) and $p = 0.496$ for (e).

The recruits of *Asparagus stipularis*, *Phagnalon rupestre*, *Noaea mucronata*, and *Sarcopoterium spinosum* showed a significantly positive association with nurses compared to open ground (X^2 (1, $N = 386$) = 588.851, $p < 0.0001$, Cohen's ω = 1.24; X^2 (1, $N = 568$) = 908.590, $p < 0.0001$, Cohen's ω = 1.26 and X^2 (1, $N = 285$) = 131.735, $p < 0.0001$, Cohen's ω = 0.68, and X^2 (1, $N = 71$) = 110.323, $p < 0.0001$, Cohen's ω = 1.25 respectively).

However, the recruits of *Thymus capitatus* were randomly distributed, without a significant association with nurses or open ground (X^2 (1, N = 133) = 0.463, p = 0.496, Cohen's ω = 0.06). The observed number of *Thymus capitatus* recruits under nurses was 53 while the expected number was 49. The observed number of *Thymus capitatus* recruits in the open ground was 80 while the expected number was 84 (Fig. 3.8d). *Asparagus stipularis*, *Phagnalon rupestre, Noaea mucronata*, and *Thymus capitatus* 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) (Fig. 9a, b, and c). Thus the null hypothesis that *Asparagus stipularis*, *Phagnalon rupestre*, *Noaea mucronata,* or *Thymus capitatus* recruits occur with specified probabilities (percentage of the transect) under *Z. lotus* Vs other canopies was rejected (X^2 (1, N = 373) = 200.5, p < 0.0001, Cohen's ω = 0.73; X^2 (1, N =568) = 390.764, p < 0.0001, Cohen's ω = 0.83, X^2 (1, N = 199) = 75.217, p < 0.0001, Cohen's ω = 0.61 and X^2 (1, N = 53) = 21.701, p < 0.0001, Cohen's ω = 0.64 respectively).

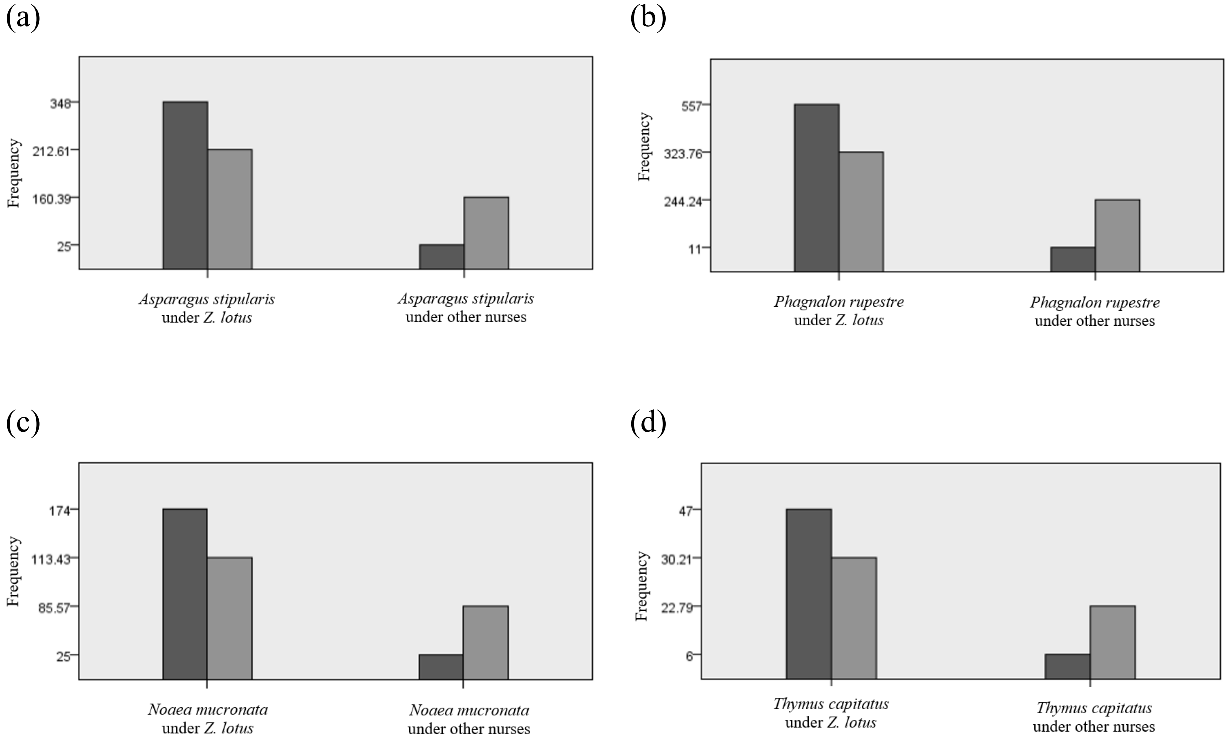

Figure 3. 9 The observed frequencies of *Asparagus stipularis* (a), *Phagnalon rupestre* (b), *Noaea mucronata* (c), and *Thymus capitatus* (d) recruits under *Z. lotus* or other canopies Vs the expected frequencies (light grey). The boxes' range represents the recruits' frequencies at p < 0.0001.

Sarcopoterium spinosum showed a statistically higher dependency on its species as a nurse plant, followed by *Z. lotus* than on any other nurse plants in the community (Fig. 3.10). The observed number of recruits under *Sarcopoterium spinosum* was 42 versus the expected 2.4, the observed number of recruits under *Z. lotus* was 23 versus 38 and the observed number of recruits under all the other nurses was 4 versus 28.6. Thus, the null hypothesis that *Sarcopoterium spinosum* recruits occur with specified probabilities (percentage of the transect) under the nurses was rejected (X^2 (1, $N = 69$) = 675.933, $p < 0.0001$, Cohen's ω = 3.13).

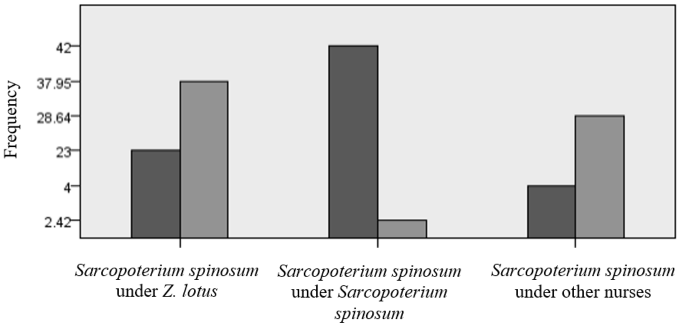

Figure 3. 10 The observed frequencies of *Sarcopoterium spinosum* recruits under *Z. lotus*, *Sarcopoterium spinosum,* and other nurses (dark grey) Vs the expected frequencies (light grey). The boxes' range represents the recruits' frequencies at $p < 0.0001$.

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 inside the nurses and in open ground are presented in Table 3.5.

Table 3. 5 The number of recruits per plant species, in alphabetical order, under a nurse, and in open ground.

Recruited species	Number of recruits under a nurse	Number of recruits in open ground
Anthemis tricolor	0	2
Asparagus stipularis	373	13
Crataegus azarolus var. *aronia*	2	0
Helianthemum obtusifolium	6	8
Noaea mucronata	199	86
Phagnalon rupestre	557	11
Rhamnus oleoides subsp. *graecus*	11	9
Sarcopoterium spinosum	69	2
Teucrium micropodioides	15	20
Thymus capitatus	53	80
Ziziphus lotus	0	0

3.5 Discussion

The network-like structure has been documented as the way in which plants coexist in many communities. These networks have specific characteristics, and their presence has been documented by studies in various ecosystems, such as creosote bush scrub communities in North American deserts (Verdú and Valiente-Banuet, 2008), forest communities, and anthropogenic micro-deserts of high salinity in south-eastern Spain (Alcántara and Rey, 2012, Navarro-Cano et al., 2021) to tropical alpine and alpine plant communities (Anthelme and Dangles, 2012, Losapio et al., 2019, Pescador et al., 2020). Here, we examined the possibility of forming a similar network of plants in a phryganic community of the Eastern Mediterranean by sampling a 0.136 km^2 arid phryganic plant community with *Ziziphus lotus* (Fig. 3.2; Fig. 3.3). We quantified the spatial patterns and found that it was characterized by a non-random, nested pattern exhibiting a highly nested structure. In particular, the community exhibited high NODF values, significantly different ($p<0.001$) relative to the simulated values created by two null models (Table 3.1), and a relatively high connectance value (26% of the potential links). Eleven species were found in the community, which may be one of the reasons behind its high nestedness. 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., 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 phryganic communities.

Although nestedness studies in a post-community context are conducted on large spatial scales, spatial community-scale study can help us identify biotic interactions that play a dominant role in the construction of a plant community (Burns, 2007). A combination of biotic processes, such as species interactions and mass effect (Bascompte and Jordano, 2007; Vázquez et al., 2009), could be the underlying force behind the common hemispherical cluster vegetation structure, present in Mediterranean phryganic communities. The presence of species-specific interactions was reflected by the high connectance between cluster facilitators and their facilitated plant species, which was confirmed by significantly higher (about twice as many) numbers of recruits under the canopies of facilitators versus open ground (Table 3.2; Fig. 3.4). A cluster-form network was described in the Mediterranean alpine grasslands (plant–patch network nestedness) by Pescador et al. (2020) and was positively correlated with the size of the patch area. *Z. lotus*, an established facilitator in the community and at the same time the species with the largest crown in diameter, demonstrated the highest facilitation capacity (ca. 1.4 times higher than expected) followed by facilitators with smaller crowns such as *Thymus capitatus* and *Noaea mucronata* (Fig. 3.7). These findings are consistent with the proposed species-area relationship (Arrhenius, 1921; McGuinness, 1984) according to which larger facilitating areas (i.e., canopies) can accommodate more species that coexist compared to smaller patches, as nested structures are formed. They also confirm the "Facilitator size" hypothesis (Callaway and Walker, 1997) by which the facilitator's size is expected to increase the frequency of facilitative interactions (Anthelme and Dangles, 2012). This increased ability of *Z. lotus* to facilitate plants, compared to the other facilitating species in the community, is probably related to an improved ability to concentrate resources (Connor and McCoy, 2001, Constantinou et al., 2021) since resource limitation may be more critical under the influence of smaller facilitators, thus limiting the emergence of rare species such as *Teucrium micropodioides* and *Crataegus azarolus var. aronia*. The different requirements of species concerning their ability to be established on a certain site (Wright et al., 1997), could be another additional parameter contributing to the different facilitation capacities among the three main nurses. Therefore, species with large area requirements, such as *Rhamnus oleoides subsp. graecus* and *Crataegus azarolus var. aronia*, were more able to be established under larger nurses such as *Z. lotus*.

Whereas biotic interactions play a dominant role in structuring a plant community (Olesen and Jordano, 2002; Verdú and Valiente-Banuet, 2008) and following the theory of mutualistic networks (Bastolla et al., 2009), we hypothesized that the observed nested patterns may be driven by positive associations among the facilitators and their recruits that promote the patched distribution as subsets of a common species pool, rather than supporting an organization defined by chance (Fortuna et al., 2010). Thus, we identified the extent of each species recruit's dependence on facilitators within the community. Examining all facilitated species (Table 3.5) it became clear that *Asparagus stipularis*, *Phagnalon rupestre*, *Noaea mucronata,* and *Sarcopoterium spinosum* showed high dependence on facilitative canopies as the numbers of recruits recorded under other plants' canopies were almost three times higher than expected by chance (Table 3.4; Fig. 3.8a, b, c, and d). This dependence proved to be higher towards *Z. lotus* regarding *Asparagus stipularis*, *Phagnalon rupestre*, and *Noaea mucronata* (approximately two times more recruits were found under *Z. lotus*) (Fig. 3.9). *Sarcopoterium spinosum* although proved to be highly dependent on facilitation (Fig. 3.8d), it was mostly facilitated by adult plants of its own species (Fig. 3.10). Out of the ten perennial species present at the site, *Ziziphus lotus* was the only species that did not have any dependence on nurses for its existence (Table 3.3). *Thymus capitatus* although present as a recruit under nurses, mainly under *Z. lotus* (Fig. 3.9d), did not show any statistically significant dependence on them (Fig. 3.8e).

Several studies (Verdú and Valiente-Banuet, 2008; Alcántara and Rey, 2012; Pulgar et al., 2017) have demonstrated that a plant community's resistance to the removal of species is highly related to the structure of plant-to-plant interaction networks. Thus, the high nestedness and connectance detected herein suggest that this phryganic community could be robust to species extinction (Verdú and Valiente-Banuet, 2008). Then again, the community may be endangered if extinction hits the most connected species (Verdú and Valiente-Banuet, 2008). Simulations done by Verdú and Valiente-Banuet (2008) showed that the species diversity in a nested community is not significantly altered, provided that the sequence of extinction occurs from the least (i.e., *A. stipularis, R. oleoides* subsp. *graecus*, and *S. spinosum*) to the most connected nurse species (i.e., *Z. lotus*, *T. capitatus*, and *N. mucronata).* The detected species-specific relations among the plants of the community could impact the risk of local extinctions since the extinction of the highly connected species (i.e., *Z. lotus*, *T. capitatus*, and *N. mucronata*) could be fatal for many other species (Table 4) (Valiente-Banuet & Verdú, 2013). This is based on the simple assumption that since nurse extinction causes a facilitated plant to lose its regeneration niche, this plant could also become extinct (Dunne, 2006). Consequently, in communities governed by facilitation through multiple benefactor species, conservation efforts must be allocated to the benefactor species assembling the community (Altieri et al., 2007). Since *Z. lotus*, *T. capitatus*, and *N. mucronata* are the community's main facilitators, these should be the keystones of any conservation attempt to protect the community's biodiversity. Especially *Z. lotus*, which is 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*), is the benefactor species that when protected may provide even more resistance to extinction.

Most plant-to-plant interaction networks studied to date show connectance below 30%, a fact that implies the potential existence of more than 70% of unobserved interactions (Alcántara et al., 2019). In consistency with the conclusions of Alcántara et al. (2019), the community's connectance was 26% and among the realized interactions, neutral or enhancing interspecific interactions were more frequent while intraspecific interactions, although present were much less frequent (Table 3.3). The presence of many weak and few strong interactions in the network (Fig. 3.5), along with high connectance and the frequency of intraspecific interactions shields the community with great stability even more (McCann, Hastings, & Huxel, 1998; Wootton & Stouffer, 2016). Although 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; and Alcántara, Pulgar, Trøjelsgaard, Garrido, and Rey 2018), the Chi-square test of goodness-of-fit performed to test whether the interactions between the plants of the community occurred with specified probabilities (percentage of the transect covered by a plant species) revealed that in this community canopy-recruit observed interaction were not only explained by the species abundance and there should be other ecological processes beyond species abundance that shape these species-specific interactions. (Fig. 3.6, 3.7, 3.9, and 3.10). Alcántara et al. (2018) suggested that an important part of the potential interactions is impeded for some ecological reason and that the frequency of any individual canopy–recruit interaction is the result of the balance between multiple positive and negative interactions which can be determined by multiple factors. Water availability is by far the most limiting factor for plant productivity in dryland ecosystems such as phryganic communities (Sarris et al., 2007; Nolan et al., 2018;). Constantinou et al. (2021) have demonstrated that *Z. lotus* can improve soil moisture availability not only under its canopy but up to 5 meters around it, a fact that justifies the emergence of *Z. lotus* as the most statistically significant facilitator (Fig. 3.6).

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. 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 (Tielbörger 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. 2016 a, b, 2017) as well as the traits forming these interactions. Identifying these traits will allow us to understand how biodiversity in the phryganic communities is shaped and apply this knowledge to restore species (Navarro-Cano et al., 2021) and ecosystem functions (Montoya et al., 2012; Navarro-Cano et al., 2018).

Chapter 4

The possible role of *Ziziphus lotus* as an ecosystem engineer in semiarid landscapes [2]

4.1 Abstract

Positive interactions between nurse plants and their facilitated species are most notable in dry/high-elevation habitats. Plants that modify limiting resources or constraining variables creating an even stronger positive impact on the community are considered ecosystem engineers. *Ziziphus lotus*, a dominant deep-rooted shrub of arid/semi-arid Mediterranean habitats, can create fertile islets; most likely acting as a nurse plant. To further investigate its role as an ecosystem engineer, we assessed the density of 1377 individual *Thymbra capitata* plants and the night-time dehydration of 66 individuals, growing around 11 *Z. lotus* plants for three successive zones (0–5 m, 5–10 m, and 10–15 m) in wetter and drier habitats created by topography in Cyprus. We discovered that *T. capitata* significantly increases in density (by c. 2.5 times) and can improve its night-time rehydration in mid-summer (by c. 60 times) when growing up to 5m around *Z. lotus* compared to thymes growing 10–15m away. Density and stem moisture for thymes growing near *Z. lotus* do not seem to be significantly affected by topography. Hence, *Z. lotus* may have properties to be classified as an ecosystem engineer and the potential to boost semiarid ecosystem productivity in the battle against desertification under global climatic change.

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[2] Constantinou, E., Sarris, D., Vogiatzakis, I.N. (2021) The possible role of *Ziziphus lotus* as an ecosystem engineer in semiarid landscapes. *Journal of Arid Environments*, 195. https://doi.org/10.1016/j.jaridenv.2021.104614

4.2 Introduction

Interactions between individuals of different species regulate the spatial arrangement of plants in a community shaping its structure and dynamics (Tirado and Pugnaire, 2005; Padilla and Pugnaire, 2006). The net balance of positive and negative effects among individuals characterizes the interaction either as competition or facilitation (Callaway and Walker, 1997; Holmgren et al., 1997). Such interactions can be dynamic in space and time (Armas and Pugnaire, 2005). Competition or interference characterizes a community dominated by negative effects between neighboring plants, due to limited resources or allelopathy. On the other hand, when plants exercise a positive influence on their neighboring species, improving survival, reproduction, growth, or fitness, the interaction results in facilitation (Callaway, 2007).

The use of positive interactions between neighboring plants has received substantial attention during the past two decades (Maestre et al., 2001, 2002, 2003a, 2004; Padilla and Pugnaire, 2006; Valiente-Banuet et al., 2015; Losapio and Schöb, 2017). Positive interactions have been increasingly proposed as ubiquitous forces driving community structure and function, especially under harsh conditions such as thermal, water, or nutrient stress (Bertness and Callaway, 1994; Callaway, 1995; Stachowicz, 2001; Callaway et al., 2002). There are many examples of positive effects from the interaction among plants, starting from improving microclimatic conditions and soil properties (Bonanomi et al., 2011; Brooker et al., 2008; Maestre et al., 2010) to nurse plant effects and enhanced growth as well as survival rates of seedlings and plants under trees and shrubs (Egerton et al., 2000; Tewksbury and Lloyd, 2001; Pugnaire et al., 1996a, 1996b; Holzapfel and Mahall, 1999).

However, indicating a positive effect of one species on another is a much clearer undertaking compared to demonstrating the ability of one species to act as an ecosystem engineer. Ecosystem engineers change their environment by altering habitat suitability or community composition (Wright and Jones, 2006; Matsuzaki et al., 2009). Their influence is exerted by directly or indirectly modulating the availability of resources to other species, by causing physical state changes in biotic or abiotic materials, and by doing so modify, maintain, and create habitats. Many keystone species can exert such impacts and can be classified as ecosystem engineers based on six suggested criteria among which are: (a) the type and formation rate of the impacts, and their durability in the absence of the engineers; and (b) the number and types of resources that are directly or indirectly controlled, the ways these resources are controlled, and the number of other organisms that depend on these resources (Jones et al., 1994).

Ziziphus lotus (L.) is the keystone species of priority habitat ‘Arborescent matorral with Ziziphus’ (code *5220; Annex I; European Commission, 2013) occurring in Spain (south-eastern Iberian Peninsula), Greece, Sicily, and Cyprus under a xerophytic thermo-Mediterranean bio-climate and corresponds to the mature phase or climax of climatophile and edapho-xero-psammophile vegetation (European Commission, 2013). Despite its importance, the habitat is severely fragmented and of poor conservation status. In addition to Europe, the habitat is found in semi-arid and arid zones of North Africa (Algeria, Morocco, Tunisia, and Libya; Pottier, 1981). *Z. lotus* is a facultative or partial phreatophyte with extreme anisohydric stomatal regulation able to obtain water from lower soil horizons and possibly from a free water table (Le Houérou, 1972; Drew, 1979; Evenari et al., 1982; Torres-Garcia et al., 2021a). It maintains its vegetative growth throughout the summer and behaves as an aridoactive species (Evenari et al., 1982; Gorai et al., 2010). It reaches 2–5 m in height, with mounds composed of wind-borne sediment that accumulates around it (Tengberg and Chen et al., 1998), and has a notable ability as a resprouter, with individual stands reaching up to 30 m in diameter and living above 100 years (Rey et al., 2016). *Z. lotus* is indigenous to Cyprus, abundant mostly in the semi-arid areas of the central Mesaoria plain, and in the western part of the Island (Georgiou et al., 2008). However, due to intensive agriculture and grazing practices, the species is restricted to isolated clusters, usually at the edges of cultivated fields (Delipetrou, 2005).

Cyprus is part of the East Mediterranean where areas particularly susceptible to desertification are likely to increase significantly due to climate change. The Island is mainly characterized by critical and fragile to desertification areas covering 42.9% and 44.6% of the total land, whereas potentially non-threatened areas to desertification cover only 3.9% and 0.8% of the land, respectively (CCRA, 2016). Therefore, drought-resistant plant species capable of facilitative interactions with other plants may prove very useful in combating both desertification and mitigating climate change. Such interactions are broadly documented in many plant communities (Brooker et al., 2008; Maestre et al., 2009) and particularly in arid and semi-arid environments, where vegetation is often arranged in a two-phase mosaic composed of high plant cover patches in a low-cover matrix (Montana, 1992; Aguiar and Sala, 1999). This clumped distribution pattern is often considered evidence for positive plant interactions (Cavieres et al., 2014; Losapio et al., 2018; Thomsen et al., 2018; Ellison, 2019).

Thymbra capitata [(L.) Cav.] is a very drought-resistant plant found in the thermo-Mediterranean vegetation belt of the Mediterranean, typical of garrigue or phrygana vegetation, and is abundant within the *5220 habitat type in Cyprus. Because of such properties, it can also be considered as a candidate plant for combating desertification. Although *T. capitata* grows within the habitats of *Z. lotus* in Cyprus, the possible facilitation between these two species has never been investigated and could be used to elucidate the potential role of *Z. lotus* as an ecosystem engineer. There has been limited evidence that Ziziphus can influence the distribution of other plants (Tirado and Pugnaire, 2003; as well as support numerous pollinators; González-Robles et al., 2020). For example, *Asparagus albus* has been found to produce a significant trend toward spatial aggregation in the presence of *Z. lotus*, but this has never been assessed with respect to *Thymbra capitata*.

Hence, it seems that *Z. lotus* is a keystone species with a wide distribution range around the Mediterranean capable of maintaining the presence of its stands for centuries as the climax vegetation in arid and semiarid conditions with some known facilitating properties. Further investigation of the facilitation potential of *Z. lotus* could play a prominent role in restoring the dynamics of plant communities in degraded arid and semiarid ecosystems while helping to halt desertification.

This paper aims to assess the potential role of *Z. lotus* in combating desertification and identify whether it behaves as an eco-engineer at the habitat level by testing for the first time: (i) the impact it may exert on the population dynamics of *T. capitata*, and the durability of such impacts in the absence of the *Z. lotus*, (ii) whether moisture availability is one of the key resources that is directly or indirectly controlled by the potential ecoengineer within the habitat. To address these goals, we explored whether the (i) density and the (ii) moisture content of *T. capitata* increase based on its proximity to *Z. lotus*, and whether this occurs (iii) against expected moisture gradients shaped by topography.

4.3 Materials and methods

The study was conducted in Cyprus, in a lowland semi-arid arborescent matorral with *Ziziphus lotus* (L.) (priority habitat type *5220) within the National Forest Park of Rizoelia (34o56′ 10.28″N, 33o34′ 23.57″E; Fig. 4.1). The selected total study area within the park was 9692 m^2, divided into three subareas (classes) based on topographic aspect, namely East, Ridge and South. The soil within the sampling area is sandy with poor organic content at the top 10 cm and is of gypsiric formation (Regosols-leptic Gypsisols). The altitude of the study area ranges from 69 to 83 m. It has a thermo - Mediterranean climate with hot, dry summers from May to mid-October and mild winters from November to March. The mean annual temperature is c. 19.5˚C and the mean annual precipitation is c. 325 mm (Department of Meteorology, 2020).

Hosting important biodiversity elements (Manolaki and Vogiatzakis, 2017) the Park is part of the European Natura 2000 network (CY6000006). It includes four natural habitat types which are home to 44 bird species, including two Cyprus endemic species (*Oenanthe cypriaca*, *Sylvia melanothorax*); 8 mammal species, and 16 reptile species. The contribution of the site to Cyprus' biodiversity is high with 180 indigenous plant species (11% of the indigenous flora of Cyprus), of which 11 are endemic (7.9% of the endemic flora) while 6 species are endangered and listed in the Red Book of the Flora of Cyprus (Tsintides et al., 2007).

4.3.1 *T. capitata* density measurements around *Z. lotus*

Within the study area 11 *Z. lotus* plants, between 1.5 m and 2 m in height and between 3 m and 6 m in diameter were selected. However, since 3 out of the 11 Ziziphus plants were growing very close together they were considered as one cluster (Fig. 4.2). Thus, nine *Z. lotus* clusters were further evaluated. The experimental area was selected as having no signs of human disturbance in between the *Z. lotus* plants and no influence of any other deep-rooted plant species for more than 15 m from the selected *Z. lotus* individuals.

Figure 4. 1 (a) Location of the National Forest Park of Rizoelia in Cyprus, and (b) caption of *Z. lotus* (Z) and *T. capitata* (T) within the study area in mid-July 2015 (Photo Sarris D).

Starting from each *Z. lotus* crown's center, 3 successive zones (Zone 1: 0–5 m, Zone 2: 5–10 m, and Zone 3: 10–15 m) were delimited (Fig. 4.2). The sampling area of zone 1 was calculated per *Z. lotus* as a circular sector (R = 5 m radius) minus the plant's crown. For the next two successive zones, the sampling area was calculated as a circular sector (R = 10 m and 15 m respectively) minus the previous zone's sampling area. In the case of neighboring *Z. lotus* plants, each *T. capitata* was considered as part of the population of the nearest *Z. lotus*. Within each of the three successive zones, the number of *T. capitata* individuals per m^2 was calculated by counting the number of *T. capitata* plants per *Z. lotus* in each zone. Measurements covered an area of 5524 m^2 (311 m^2 in Zone 1; 817 m^2 in Zone 2; 937 m^2 in Zone 3), with a total of 1377 *T. capitata* individuals present.

Topographically, 3 out of 9 *Z. lotus* clusters (Z4, Z7, and Z8; Fig. 4.2) were located within the South-facing slope, 3 clusters (Z2, Z5, and Z6; Fig. 4.2) grew within the East-facing slope and

3 clusters (Z1, Z3, and Z9; Fig. 4.2) were located at the Ridge. The South facing area was also found to be by c. 5% steeper than the area to the East, adding up to its higher water loss due to runoff. We expect that the South aspect's warmer and drier soil conditions would affect the moisture content and density of thyme plants.

To confirm the expected soil moisture differences, 91 volumetric soil water content measurements were performed with the Delta-T Devises SM150 kit at midday and at mid-summer, in the soil of the three subareas (c. 30 recordings per aspect; Table 4.1). Measurements were made at the topsoil (covering 5 cm in depth) on bare ground, at similar altitudes, with c. half a meter distance in between each measurement and at c. 10 m away from the nearest *Z. lotus* plant.

Figure 4. 2 Aerial photo of the study area with the location of the 11 *Z. lotus* plants and the 3 radii used to identify the three zones (Zone 1 = 0–5 m, Zone 2 = 5–10 m, Zone 3 = 10–15 m) within which the density of all growing *T. capitata* plants (n = 1377) was evaluated. The three plants in closer proximity (Z1a, Z1b, and Z1c) were considered as one *Z. lotus* cluster (center-right of photo).

Table 4. 1 Volumetric Water Content (VWC) in soil (%) for the three aspects investigated.

Aspect	N	VWC	Std. Error
East	***30***	***2.43***	***0.16***
Ridge	31	2,13	0.12
South	***30***	***1.84***	***0.12***
Total	91	2.13	0.08

Statistically significant differences in bold italics at $p = 0.006$

4.3.2 Assessment of moisture content in *T. capitata* based on its proximity to *Z. lotus*

Out of the 1377 *T. capitata* plants used to calculate density, we selected 66 *T. capitata* plants, between 40 and 50 cm in height and 0.5–1 m in diameter (32 in the 0–5 m zone, 23 in the 5–10 m zone and 14 in the 10–15 m zone). Sampling took place in mid-summer (July 2015) to represent the conditions where drought is expected to exercise a strong effect on the moisture content of plant tissues. In July, topsoil can dry out, but significant moisture may still be retained in the deeper ground creating a horizontal soil moisture gradient. Sampling was conducted in two phases during two consecutive days: the first phase immediately after sunset and the second before dawn of the following day. At each sampling, a 10 cm length tissue, containing stem, leaves, and flowers, was obtained from each individual *T. capitata*. The samples were placed directly into pre-weighed bags closed tightly and remained stored in an insulated cool box until weighing. The sealed bags with the samples were weighed in the laboratory, not more than 1 h after collection, with a two-decimal precision scale. After having been opened, the bags were placed in a furnace at 60 ˚C, and 72 h later they were resealed and reweighed. By subtracting dried from fresh stem biomass and dividing by fresh stem biomass we determined the moisture content of each fresh stem in % at the time of sampling (i.e., g of water per 100 g of stem). Further on, the Moisture Content Difference index (MCD) was calculated. This index estimates in percentage the stem moisture difference when subtracting nightfall from morning (predawn) stem moisture content as calculated above. Thus, as plants experience daytime transpiration losses, MCD indicates the percentage of moisture thymus stems gained during their night-time rehydration.

4.4 Data analysis

T. capitata density and MCD measurements around *Z. lotus* were analyzed per zone (Zone 1, Zone 2, Zone 3) and per topographic class (East, South, Ridge). Following a Kolmogorov – Smirnov test, data were not found to be normally distributed. Thus, we applied the Kruskal-Wallis non-parametric Test to test for differences among data groups and performed the Dunn-Bonferroni post hoc test following a significant Kruskal-Wallis test. To report the data means the standard errors were estimated, while to visualize the data, medians with 5, 25, 75, and 95 percentiles were also plotted. For statistical analysis, the IBM SPSS program v. 25.0 was used.

4.5 Results

Volumetric Water Content (VWC) in topsoil was the highest in the East-facing slope (Table 4.1) and statistically significant compared to the South-facing slope (distribution not normal; medians for VWC 2.4% for East, 2.2% for Ridge, 1.6% for South) at p = 0.006 ($p = 0.019$ when adjusted by the Bonferroni correction; Dunn-Bonferroni post hoc test following a significant Kruskal-Wallis test at $p = 0.024$). It confirmed that thymes on the South facing slope experience reduced soil moisture availability compared to those on the East-facing slope.

4.5.1 *T. capitata* density variability

Zone 1 provided the highest density of *T. capitata* with 0.44 plants per m^2 (Standard Error; SE=0.08) followed by Zone 2 (0.25 plants per m^2; SE = 0.08) and Zone 3 (0.17 plants per m^2; SE=0.03). The medians were 0.36, 0.23, and 0.18 per zone respectively (Fig. 4.3a). The Kruskal - Wallis test identified that statistically significant differences exist between the thyme distribution of Zones 1 and 3 ($p = 0.008$).

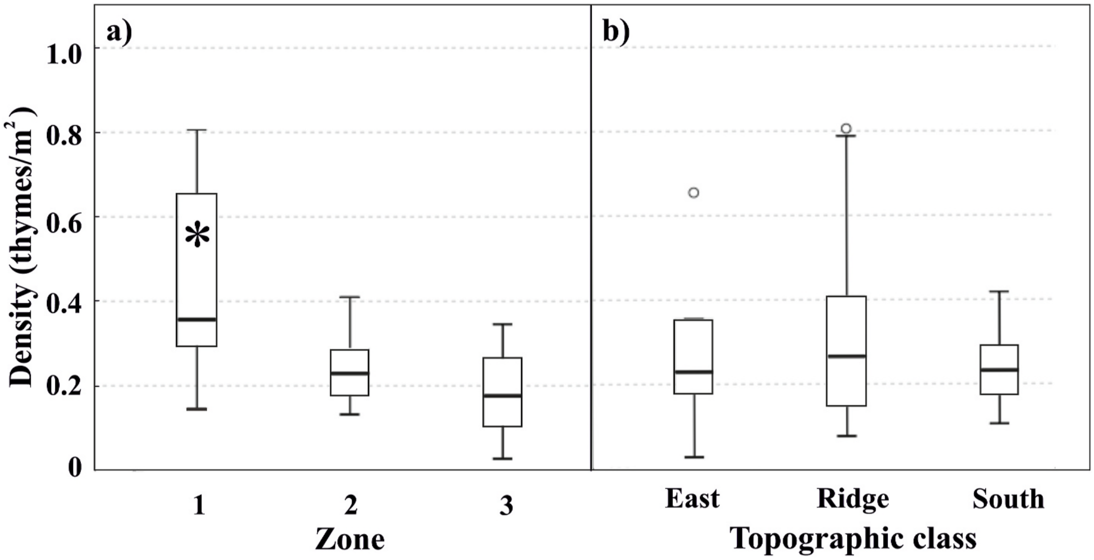

Figure 4. 3 The density (plants/m^2) of *T. capitata* per zone (a) and topographic class (b). The boxes' range represents the interquartile range (IQR) and the line within the IQR is each zone's median (n = 9). The bars on either side of the IQR represent its upper and lower whiskers. Mild outliers are marked with an open circle. Significant differences at $p = 0.008$ are indicated by an asterisk (*).

The mean density per topographic class was 0.27 plants per m^2 in the East (SE = 0.06), 0.36 plants per m^2 at the Ridge (SE = 0.09), and 0.24 plants per m^2 for South-facing thymes (SE=0.03). The medians were 0.23, 0.27, and 0.23 per class respectively (Fig. 4.3b). Though there is a slightly higher density of *T. capitata* on the Ridge of the experimental site, the Kruskal-Wallis test suggests that the thyme plant densities were not statistically significant based on topography (p = 0.741).

4.5.2 *T. capitata* Moisture Content Difference index

The mean MCD score of *T. capitata* was 8.27% for Zone 1 (SE = 0.54), 4.97% for Zone 2 (SE=1.49) and 0.14% for Zone 3 (SE=0.54). The medians were 8.01%, 3.69% and 0.17% per zone respectively (Fig. 4.4a). A pairwise comparison of MCD per zone (Dunn-Bonferroni post hoc test following a significant KruskalWallis test) revealed a statistically significant difference between Zone 1 and 2 and between Zones 1 and 3 at $p < 0.0001$, while Zones 2 and 3 were found significantly different at $p = 0.037$.

The MCD averages for thyme per topographic class were 5.89% for East (SE = 1.3), 5.55% for Ridge (SE = 1.48) and 5.61% for South-facing thymes (SE = 0.5). The medians were 6.54%, 3.35% and 4.72% per class respectively (Fig. 4.4b). Based on the Kruskal-Wallis Test, the distribution of MCD does not appear to be statistically different across the topographic classes ($p = 0.186$).

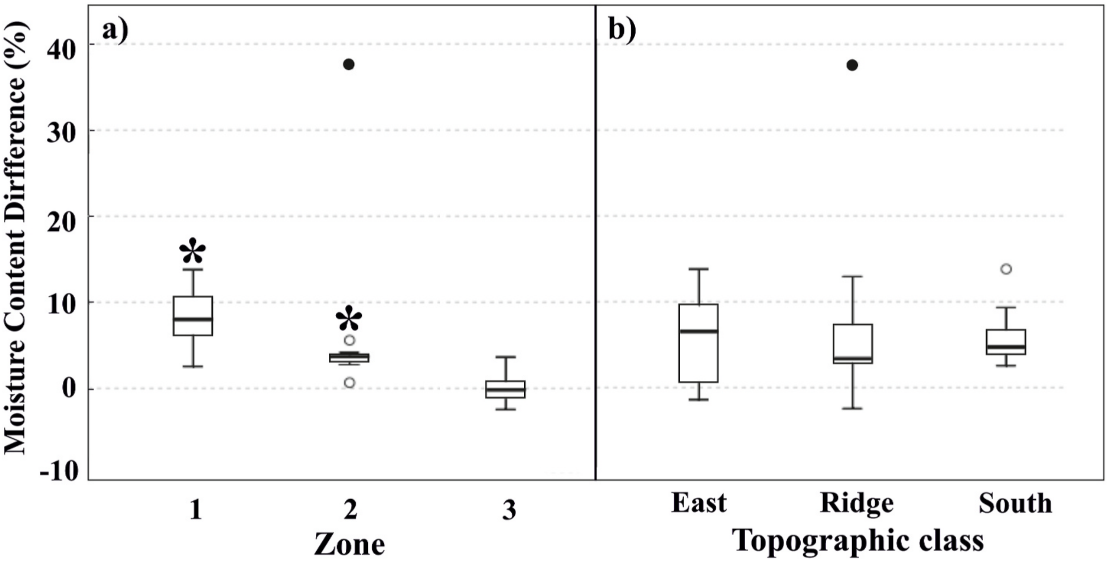

Figure 4. 4 Moisture Content Difference (MCD) of *T. capitata* per zone (a) and topographic class (b). The boxes' range represents the interquartile range (IQR) and the line within the IQR is each zone's median. The bars on either side of the IQR represent its upper and lower whiskers. Mild outliers are marked with an open circle, an extreme outlier is marked with a closed circle. Significant Differences at $p < 0.0001$ are indicated by an asterisk (*). N = 31, 23 and 12 for Zones 1, 2 and 3. N = 14, 27, 25 for East, Ridge and South facing thymes.

4.6 Discussion

The classification of a species as an ecosystem engineer requires significant evidence of its impacts on community structure and functions, with the impacts diminishing in its absence (Jones et al., 1994). Our findings indicate that the population density of *T. capitata* can significantly increase c. 2.5 times when located up to 5 m away from *Z. lotus* (Fig. 4.3) compared to thymes growing 10–15m away, where the impact of *Z. lotus* roots and canopy is not expected to exert any strong influence. The density of thymes 10–15m away from Ziziphus was found at 0.17 plants per m^2 and reached 0.44 plants per m^2 moving within a 5m radius from the keystone species.

The first evidence of the ability of *Ziziphus lotus* to facilitate other plants was reported from a sand dune-strip on the Almería coast, SE Spain (Tirado and Pugnaire, 2003). *Asparagus albus* showed a significant trend towards spatial aggregation in the presence of *Z. lotus*. Asparagus plants were more frequent within Ziziphus patches than in gaps or when associated with other shrub species. Seedlings mainly survived when growing within the Ziziphus canopy, suggesting a nurse-plant effect in the early growth stages of Asparagus (Tirado and Pugnaire, 2003). More recent findings suggest that the productivity of Avena sp. in Cyprus also greatly benefits when growing within the canopy of *Z. lotus* (Michael, unpublished). However, our results demonstrate that *Z. lotus*, when acting as a host plant, may also have the capacity to create favorable conditions for *T. capitata* as far as 5 m around the host plant. Thus, it is likely that *Z. lotus* can have a positive influence on plant life not only within its canopy, but also up to 5 m around it. As this is the first documentation of the phenomenon, further investigation is required on whether it can be observed in other locations as well or whether other species can also improve their productivity, not only within, but also around *Z. lotus*. Moreover, insects belonging to 82 different taxa including diptera, wild bees, ants, wasps, honeybees, beetles, butterflies, hoverflies, bee-flies, and bugs, have been recorded on *Z. lotus* flowers (González-Robles et al., 2020). Thus, not only thymes but also other plants and animals may be positively influenced suggesting a broader positive effect of *Z. lotus* at the community level than previously considered.

4.6.1 Control over key ecosystem resources

Evidence based on the variation of the moisture content in *T. capitata* stems in relation to the distance the plants grow from *Z. lotus* supports that *T. capitata* rehydrate their stems much more efficiently at nighttime the closer they grow to *Z. lotus* and up to 10 m away (Fig. 4.4); improving stem moisture content by c. 60 times in mid-summer (from 0.14% at 10–15 m to 8.27% at 0–5 m). Therefore, improved moisture availability may be the key, in the semi-arid conditions investigated, for the higher density of thymus plants when growing close to *Z. lotus*, and appears to be one of the primaries, if not the primary resource that is directly or indirectly controlled by the potential eco-engineer within the habitat.

Other factors and resources may also be regulated by *Z. lotus*. Higher values of soil moisture underneath the canopy of specific plants, compared to bare ground areas, have been reported for species such as Stipa (Maestre et al., 2003; Maestre and Cortina, 2003) and Retama (Pugnaire and Luque, 2001; Pugnaire et al., 2004), but other studies indicate that these may not be general effects (Maestre et al., 2002; Cuesta et al., 2010). Nonetheless, the investigated thymes were not under the influence of the canopy of *Z. lotus*. Thus, extra factors need to be considered. For instance, deeper soil with better moisture holding capacity may occur when moving closer to *Z. lotus*, out of which other species in addition to thyme can benefit from. The microclimate can also be affected by plant litter, changing the physical and chemical environment. Litter reduces the thermal amplitude of soils by its ability to intercept sunlight, reduces evaporation and affects seed germination and growth (Facelli and Pickett, 1991; Petrone et al., 2001). Plant facilitated water redistribution could also come into practice.

The phenomenon of higher MCD in *T. capitata* when located closer to *Z. lotus* was observed in July, during the dry season, when the moisture contrast between topsoil and deeper ground is expected to be the highest within the year. Such conditions might favor hydraulic lift during nighttime (Caldwell and Richards, 1989; Dawson, 1993; Torres-Garcia et al., 2021a). If this can occur, then deeper water could be utilized by *Z. lotus* and become available to the shallower rooted *T. capitata* plants (and to perhaps other plants) growing in close proximity to *Z. lotus*. Many woody species have deep roots to access deep soil water sources (Canadell et al., 1996; Sarris and Mazza, 2021). Species with deep roots play a key role both in deep water utilization (Sarris et al., 2013) and in redistributing it within the soil profile via hydraulic lift, subsequently also improving the survival of shallow-rooted plants (Burgess et al., 1998, 2000; Prieto et al., 2012; Wang et al., 2018).

A strong control exerted by *Z. lotus* within the habitat would mean that it can overcome expected moisture gradients shaped by topography. Differences in topographic exposure may cause heterogeneity of re- sources that could influence the spatial pattern in plant communities (Chapin et al., 2002; Yasuhiro et al., 2004). Since our findings showed no significant difference in the density for the three experimental conditions (East, South, Ridge; Fig. 4.3) we assume that the spatial heterogeneity of resources leading to the aggregation of *T. capitata* is most likely caused by the ability of Ziziphus to modify its surrounding environment and improve habitat suitability, which is one of the key characteristics for it to be classified as an ecosystem engineer.

This assumption is reinforced by our MCD index data which revealed no differences in predawn moisture content improvement in *T. capitata* the shortest the distance *T. capitata* grew from *Z.*

lotus, when comparing East to South growing thymes. Plants growing on south slopes are more exposed to solar radiation, receive higher heat stress, hold less soil moisture, and thus are expected to have reduced population densities (Príncipe et al., 2019). Thus, *Z. lotus* seems to act in a way that may counterbalance any negative effects of south facing aspects on thyme plant distribution. This may also be expected if facilitation is the main force driving community structure and function (Bertness and Callaway, 1994; Callaway, 1995; Stachowicz, 2001; Callaway et al., 2002). Hence, our findings go beyond documenting the ecological role of *Z. lotus* as a late successional species (Padilla et al., 2009), to suggesting that it is valid to consider it as an ecosystem engineer within the habitat type *5220.

4.6.2 The potential of *Z. lotus* for ecosystem restoration and combating desertification

In climatically harsh environments such as arid and semi-arid habitats, slight alterations in physical parameters could create favorable habitats for organisms that would otherwise be unable to tolerate limiting physical conditions. Maintaining ecosystem functions is a top conservation priority (Balvanera et al., 2001) particularly in such environments. Therefore, identifying species that maintain, or influence ecosystem functions is a wise conservation approach. *Z. lotus* appears to possess properties of a successful ecosystem engineer. It seems capable of a significant positive impact on the community, and capable of modifying limiting resources or constraining variables in the system i.e., moisture availability.

Moreover, in extreme environments, the most suitable options for terrestrial ecosystem management are native species that can improve environmental conditions and minimize the risk of biological invasions (Padilla and Pugnaire, 2006). Ziziphus sp. is native to arid and semiarid ecosystems, intrinsically adapted to dry and hot climates and thus has excellent potential for dryland reforestation (Mizrahi and Nerd, 1996). Ziziphus species, including *Z. lotus*, have been successfully used in dryland reforestation as multifunctional tree species, which meet the criteria of drought resistance, minimal distraction of ecosystem integrity and maximization of ecosystem services, including supporting community livelihoods (Reisman-Berman et al., 2019).

Tirado and Pugnaire (2005) exhibited that *Ziziphus lotus* shrubland patches can gather more species in a patch, compared to six other scrub communities. Given the fact that *Z. lotus* is the dominant species of the priority habitat *5220, highlighting its role as an ecosystem engineer may improve the outcomes of future restoration efforts, and assist in the expansion of the habitat's range, which is now severely districted in Europe and of poor conservation status. Improving the biomass of neighboring plants *Z. lotus* may also prove beneficial for agroforestry systems in creating resilient hedgerows to combat desertification or for providing pollinator, fodder, fruits, and other services where tree life forms fail because of climatic stress. Thus, a change in attitude is required from both farmers and policy makers (who currently see *Z. lotus* as an agricultural pest) in reevaluating its potential to promote arid and semiarid agroecosystem sustainability (Abdallah et al., 1999; Boussaid et al., 2018) particularly under climatic change.

4.7 Conclusions

Z. lotus seems to exert a significant positive impact on the investigated community of habitat type *5220, and can modify population densities, together with limiting resources or constraining variables in the system i.e., moisture availability, improving habitat suitability. It thus appears to possess key properties of an ecosystem engineer, as it has been reported for other shrub species (Cushman et al., 2010). However, the mechanisms with which Ziziphus improves the moisture availability of neighboring *T. capitata* remain open to further investigation. Not only thymes but also other plants and animals may be positively influenced by *Z. lotus* suggesting a broader positive effect at the community level than previously considered. If our findings can be confirmed at a wider scale, from other sites around the Mediterranean, then *Z. lotus* may be one of the plants with a potential to significantly improve semiarid ecosystem productivity and be used against desertification, in light of the expected aridity increase that the Mediterranean will experience under global climatic change.

Chapter 5

How can ecosystem engineer plants boost productivity in east Mediterranean drylands[3]

5.1 Abstract

Background: Water availability is the key limiting factor for plant productivity in drylands covering ca. 40% of Earth's land surface. For such ecosystems to retain productivity and biodiversity under climatic change, it would be valuable to identify/promote keystone plant species that (i) have developed strategies to more efficiently utilize moisture resources not easily accessible and (ii) improve moisture conditions for neighboring plants. The very deep-rooted *Ziziphus lotus,* considered an ecosystem engineer*,* is one such example. However, it is not known which biotic traits: (a) canopy interception of moisture/rainfall, (b) hydraulic redistribution of deep ground moisture by roots, or non-biotic factors: (c) soil's volume, and (d) organic matter content, *Z. lotus* activates/modulates to play such a role. We, thus, selected dryland ecosystems where the plant dominates and measured for potential effects on the less deep-rooted *Thymbra capitata*. For assessing impacts on ecosystem productivity, we measured the spatial aggregation of ca. 3600 *T. capitata* plants. As a proxy for soil moisture availability (SMA) and its spatial variability, we conducted a seven-year-long study using thymes' nighttime rehydration. Sampling extended up to 15m away from *Z. lotus.*

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[3] Constantinou, E., Sarris, D., Psichoudaki, M., Cabello, J., Vogiatzakis, I.N. (2023) How can ecosystem engineer plants boost productivity in east Mediterranean drylands. *Ecological Processes*. doi: 10.1186/s13717-023-00437-w

Results: The density of *T. capitata* plants growing up to 5m around *Z. lotus* vs. thymes growing 10–15m away was found significantly increased (2.5 to 4.5 times), while their stem/leaf moisture was ca. 10% higher at predawn compared to nightfall during the dry season. This suggests that ecosystem productivity is driven by a greater SMA around *Z. lotus* permitting more thyme daytime transpiration, in contrast to thymes growing further away. The phenomenon appeared only under dry topsoil (during the dry season; becoming stronger during dry climatic years). Nor did morning dew/rainfall interception from the canopy or soil depth/organic matter show significant effects, leaving only the hydraulic lift (HL) properties of *Z. lotus* as the most likely driver for SMA.

Conclusions: The deep-rooting properties and HL potential of *Z. lotus* may be the key, in permitting it to boost ecosystem productivity. Such hydraulic plant traits require more attention as they may prove valuable in combating desertification and restoring ecosystems in arid/semiarid regions threatened by climate change.

5.2 Background

Water availability is the most important limiting factor for plant productivity in drylands, which cover arid and semi-arid regions, ca. 40% of Earth’s land surface. Drylands are particularly affected by climate change through changing rainfall patterns and land degradation, which reduces the ability of species and people to cope with dryland conditions (Millennium Ecosystem Assessment, 2005; Sarris et al., 2011; IUCN, 2019). Thus, for ecosystems in such regions to retain productivity/biodiversity under climatic change, it would be valuable to identify/promote keystone plant species that (i) have developed strategies to more efficiently utilize moisture resources not easily accessible and (ii) improve moisture conditions for neighboring plants. Nonetheless, identifying such plants and understanding how they function is a promising but still little-explored field.

Arid and semi-arid perennial plants may develop deep root systems to reach moist soil layers and groundwater sources, and essentially function as phreatophytes (Gorai et al., 2010; Sarris et al., 2013; Fan et al., 2017). Such functioning may involve hydraulic redistribution (HR), a process where roots serve as preferential low-resistance pathways for water along soil-water potential gradients between wet and dry soil zones, and between roots and the soil matrix (Schulze et al., 1998, Hultine et al., 2004). This trait permits temporary water storage external to the plant, in the upper dry soil layers, as a way for the plant to obtain additional moisture when transpiration restarts during the daytime. In some cases, water can move both downward from the moist upper layers during wet periods (hydraulic descent) and upward from the deeper zones with access to groundwater into the middle layers (hydraulic lift; HL), if the prevailing soil water potential gradient so dictates (Lee et al., 2021). During HR, the movement of water could take place typically at nighttime or when the canopy is inactive, depending on the plant's water stress levels (Hultine et al., 2004; Scott et al., 2008).

Especially during long periods of drought, the hydraulically lifted water can be used by the neighboring plants effectively, ameliorating their performance and growth (Caldwell and Richards, 1989; Dawson, 1993; Horton and Hart, 1998; Filella and Peñuelas, 2003; Barron - Gafford et al., 2017). The uplifted water by deep-rooted species can particularly benefit shallow-rooted species (Burgess, 2011), thus enhancing the survival not only of the lifting but also of the neighboring plants (Liste and White, 2008; Katul and Siqueira, 2010; Prieto et al., 2011; Cardon et al., 2013; Matimati et al., 2014; Sun et al., 2014). Plants growing under the hydraulic lifting plants may use such water (Prieto et al., 2010) to improve their moisture content and growth rates compared to those that do not have access to this source of water (Filella and Peñuelas, 2003; Zou et al., 2005; Bogie et al., 2018). Thus, the important consequence of hydraulic lift is that a significant part of water lifted (3–60%) can be also used by other species, normally growing in the lifting trees' understory (Dawson, 1993; Schoonmaker et al., 2007). This function has been found to disappear during the wet spring season and to depend on the size of the tree (and the corresponding root depth; Filella and Peñuelas, 2003). Hence dry topsoil coupled with root access to deep moisture availability would be a prerequisite for HL to function. HL favors biogeochemical conditions that enhance, the otherwise poor soil organic matter decomposition process, by providing topsoil with additional moisture (Armas et al., 2012; Torres-García et al., 2022) and facilitating plant nutrient uptake (Cardon et al., 2013). These indirect benefits of HL could have been the primary selective force in the evolution of this process, or it may simply be the result of roots not having true rectifying properties (i.e., roots are leaky to water) (Caldwell et al., 1998).

In addition to improving soil properties, some facilitating plants also influence soil aggregation, mediated by environmental variables such as soil temperature and soil moisture, but also by factors such as soil organic carbon, soil fauna, soil microorganisms, roots, and inorganic binding agents (Bronick and Lal, 2005; Lehmann et al., 2017). These positive effects on soil processes may influence neighboring plant survival, establishment, and growth, determining the structure of plant communities in nurse plant systems (Bronick and Lal, 2005; Lozano et al., 2020).

The difference between water uptake and water loss is known as the water balance. A negative water balance results when transpiration exceeds water uptake, the reverse corresponding to a positive water balance. During the day, intense transpiration may lead to a negative balance, whereas during the night, the deficit is fully compensated (Sonnewald, 2013). However, when soils are dry, the daytime deficit is not expected to be high for isohydric plants, i.e., plants that have evolved to maintain cell turgor via the closing of stomata. In these plants, daytime moisture deficits in the immediate surroundings of fine roots are related to transpiration (Körner, 2018). Therefore, plants such as thymes that respond to drought stress by stomatal closure to reduce such water loss (Tátrai et al., 2016) are not expected to experience a too-negative water balance in the daytime and thus would be found to rehydrate less from soil water at night-time.

Ziziphus lotus (L.) is an anisohydric phreatophyte (Guirado et al., 2018; Torres-García et al., 2021a,b,c), its dimorphic deep root may reach tens of meters in depth (Gorai et al., 2010), being able to obtain water from lower soil horizons and possibly from a free water table. Anisohydric species exhibit plasticity in their hydraulic behavior, exhibiting seasonal patterns due to the predominant role of environmental conditions in regulating soil water potential gradients (Guo et al., 2020). Their anisohydric behavior suggests great physiological plasticity, in terms of rooting depth and stomata regulation, enabling them to adapt to different water table depths (Hultine et al., 2020). *Z. lotus* could be carrying out HR by its deep roots to facilitate nutrient uptake from dry upper soil layers (Torres-García et al., 2021a,b,c). *Z. lotus* is found in the thermo-Mediterranean bio-climatic zone and even drier areas, in Spain, Italy, Cyprus, and North Africa (European Commission, 2013).

Thymbra capitata [(L.) Cav.] is a very drought-resistant plant found in the thermo-Mediterranean vegetation belt typical of garrigue or phrygana vegetation. Thymes generally are not considered very shallow-rooted shrubs (ca. 1m rooting depth; Nielsen et al., 2014) but cannot be compared to *Z. lotus*, since Ziziphus roots may reach 60 m in depth (Gorai et al., 2010).

Nevertheless, these two species, as part of a positive association, may play an important role in retaining dryland ecosystem productivity. Constantinou et al. (2021) discovered that *T. capitata* may significantly increase in density and can improve its night-time rehydration in mid-summer when growing up to 5 m around *Z. lotus* compared to thymes growing 10–15 m away. Moreover, density and stem moisture for thymes growing near *Z. lotus* do not seem to be significantly affected by topography, suggesting that *Z. lotus* may have traits that act against natural drought gradients; a property that resembles that of an ecosystem engineer.

To provide insight into the functioning of *Z. lotus* as an ecosystem engineer plant and its potential role in combating desertification for dryland ecosystems this study addresses the following questions:

1. Does *Z. lotus* improve ecosystem productivity? To investigate such effects, we measured the spatial aggregation of ca. 3600 *T. capitata* plants, the less deep-rooted perennial plant with the highest population around *Z. lotus* in Cyprus (southeast Mediterranean). Our hypothesis being that the density of thymes would increase the closest to *Z. lotus* clusters.
2. Does *Z. lotus* improve neighboring plants' soil moisture availability? To address this question, we conducted a seven-year study using the difference between predawn and nightfall moisture content of thymes as a proxy for soil moisture availability (SMA) and assessed its spatial variability up to 15 m away from *Z. lotus* covering wet and dry seasons. We hypothesize that SMA would increase as thymes get closer to *Z. lotus* clusters.

The biotic factors (a) canopy interception of moisture/rainfall and (b) hydraulic lift, as well as the non-biotic factors (c) soil's volume, and (d) soil organic matter content, have been known as key features influencing SMA. Our third question is:

3. Which of the above does Z. lotus activate/modulate to effect neighboring plants' SMA? If factors (a), (c), and (d) do not appear to be significant, but still (i) SMA increases for thymes close to *Z. lotus* and (ii) this appears only during the seasons when topsoil is expected to be dry, we hypothesize that hydraulic lift could be the determining trait for the functioning of *Z. lotus* in effecting SMA and in turn ecosystem productivity.

5.3 Materials and methods

5.3.1 Study area

The study was conducted in Cyprus, on semi-arid arborescent matorral with *Ziziphus lotus* (L.) (priority habitat type *5220) within two Natura 2000 sites; the National Forest Park of Rizoelia site (R; 34º56΄10.28΄΄ N, 33º34΄23.57΄΄ E; Fig. 5.1) and the Alykos potamos – Agios Sozomenos site (S; 35º03΄33΄΄ N, 33º25΄23΄΄ E; Fig. 5.1). Their climate is semiarid (annual rainfall <400mm; $0.2 < P/ET_o < 0.5$) with hot, dry summers from May to mid-October and mild winters from November to March (Pantelas et al., 1995).

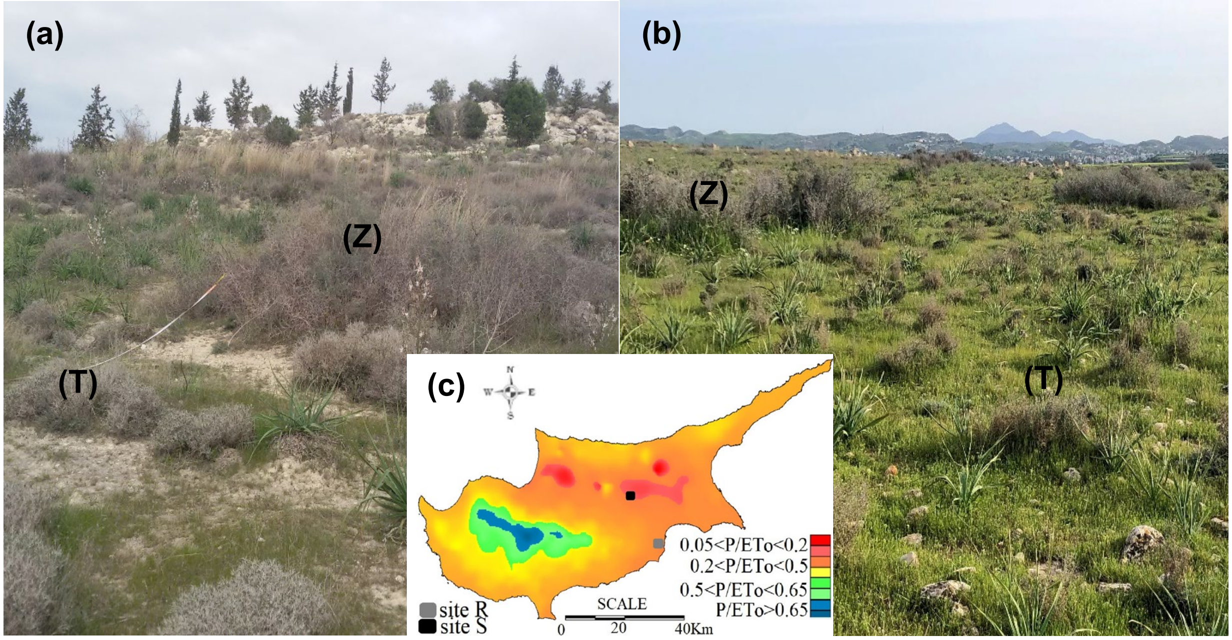

Figure 5. 1 (a) *Ziziphus lotus* (Z) and *Thymbra capitata* (T) within site R (National Forest Park of Rizoelia) (in mid-February 2015), (b) within site S (Alykos potamos – Agios Sozomenos) (in mid-March 2020), and (c) Location of sites R and S situated within the semiarid climatic zone of Cyprus ($0.2 < P/ETo < 0.5$; P= precipitation; ETo = reference evapotranspiration). Photos Constantinou E.

The experimental areas were selected as having no signs of human disturbance between the *Z. lotus* plants and no influence of any other deep-rooted plant species for more than 15 meters from the selected *Z. lotus* plants. The total study area within site R was 3650 m^2 and included 9 *Z. lotus* clusters. The altitude ranges from 71 to 80 m with sandy soil of gypsiric formation (Regosols-leptic Gypsisols). In site S the study area was 9800 m^2 and included 13 *Z. lotus* clusters. All clusters were randomly selected. The altitude ranges from 235 to 244 m with sandy

Calcaric Regosols. Both sites are of poor organic content (<1.4 %) at the top 10 cm (de Brogniez et al., 2014).

5.3.2 Experimental sampling design

5.3.2.1 T. capitata density variability

Starting from each *Z. lotus* cluster's crown center, 3 successive zones (Zone 1: 0 – 5 m, Zone 2: 5 – 10 m, and Zone 3: 10 – 15 m) were delimited to identify any possible effects of *Z. lotus* on *T. capitata* density and moisture content (MC; see below), (Fig. 5.2). The sampling area of Zone 1 was calculated per cluster as a circular sector (r=5 m radius). For the next two successive zones, the sampling area was calculated as a circular sector (r = 10 m and 15 m respectively) minus the previous zone's sampling area. In the case of neighboring *Z. lotus* clusters, each *T. capitata* was considered as part of the population affected by the nearest *Z. lotus*. Within each of the three successive zones, the number of *T. capitata* individuals per m^2 was calculated by counting the number of *T. capitata* plants per *Z. lotus* zone and dividing by the surface of each zone.

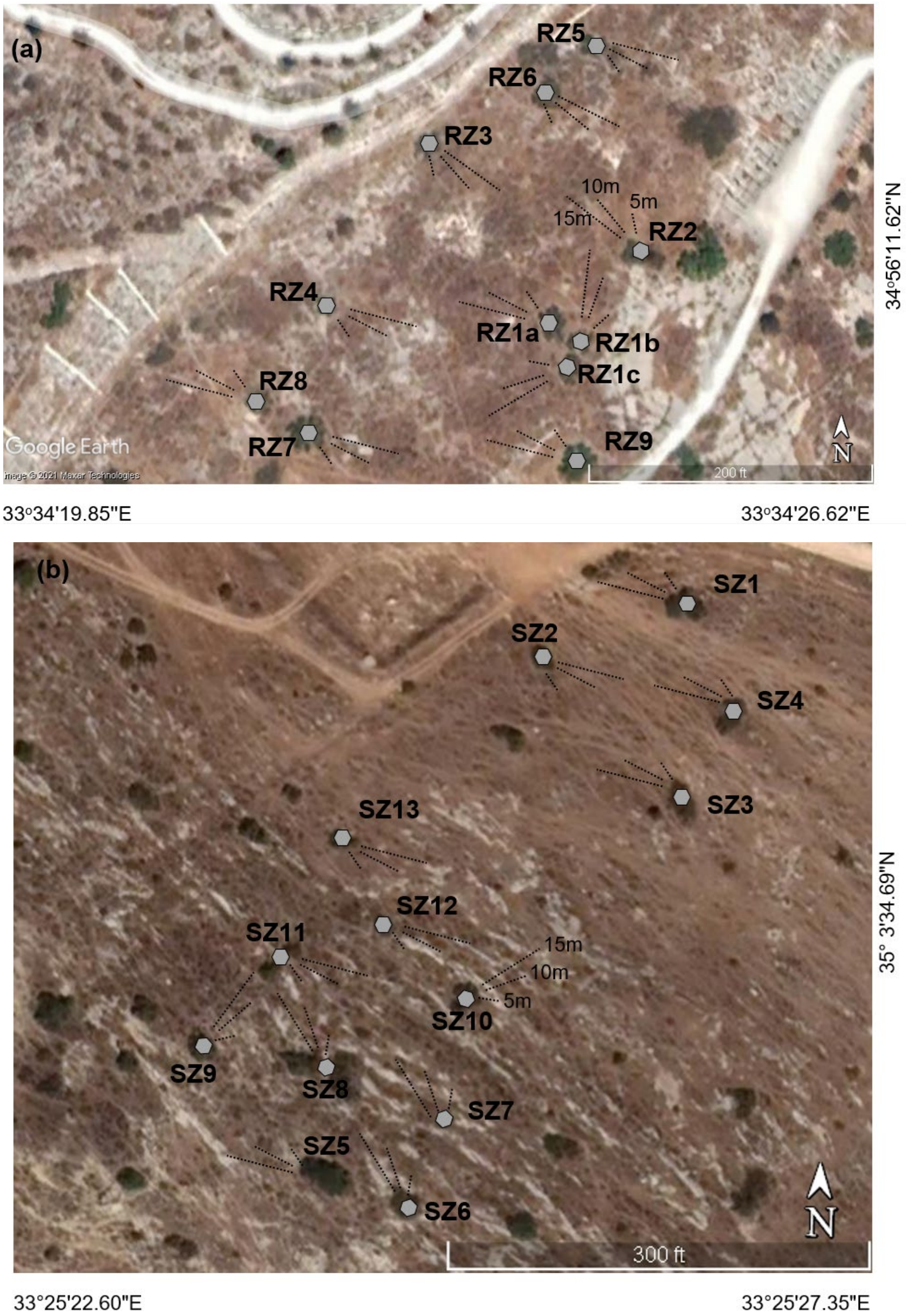

Figure 5. 2 Aerial photos of study areas (a) R, and (b) S with the location of the *Z. lotus* clusters and the 3 radii used to identify the three zones (Zone 1 = 0-5 m, Zone 2 = 5-10 m, Zone 3 = 10-15 m) for measuring within them the density and MC of *T. capitata*.

5.3.2.2 Moisture content estimation in *T. capitata*

Since thymes (isohydric plants) respond to drought stress by stomatal closure to reduce water loss through transpiration (Tátrai et al., 2016), they are not expected to experience a too-negative water balance in the daytime and thus would be found to rehydrate less from soil water at night-time. Thus, the level of rehydration of thyme stems and leaves from soil water at night-time, i.e., the difference in predawn vs. nightfall MC, could act as a proxy for the nocturnal availability of soil moisture. For measuring stem/leaf MC in *T. capitata* within the three zones around *Z. lotus*, we collected ca. 1900 samples in total, of stems with leaves, from up to 180 thymes in eight fieldwork campaigns from 2015 to 2021 that covered wet and dry seasons and years. Five campaigns were within the dry season (May, July, and September) and three were during the wet season (February and March; Table 5.1). Sampling in wet and dry seasons permitted testing whether moisture gradients between topsoil and deeper soil moisture conditions could have had a different impact on the MC of *T. capitata* populations based on their proximity to *Z. lotus*. However, some years are drier than others. Comparing similar seasons between years provides another opportunity to test such effects. HL is expected to maximize when the topsoil is at its driest, but still, water accessed by deep roots is available. Thus, improved thyme night-time rehydration only close to *Z. lotus* during the dry seasons could indicate HL functioning. In turn, during wetter climatic seasons/years, when the soil would be closer to moisture saturation, such effects could be canceled out.

The effects of air temperature and rainfall and their subsequent influence on soil moisture were also assessed. For this goal, the De Martonne Aridity Index (Pellicone et al., 2019) was calculated for the month of sampling (IDM_1) and the previous period of 3 and 6 months, including the month of sampling (IDM_3 and IDM_6). The index follows the equation: $IDM_{Nmonths} = P/(T_a + 10)$, where P is the amount of rainfall for the specific period (in millimeters) and T_α is the mean air temperature for the corresponding period (in degrees Celsius). Climatic data were provided by the Cyprus Department of Meteorology from the closest meteorological station (Larnaka International Airport for site R and Athalassa National Forest for site S). Sampling corresponded to IDM_3 <2.5 for the dry season and >4 for the wet season (Fig. 5.4).

Starting from the crown of each *Z. lotus* cluster and up to the distance of 15 m, we selected 62 *T. capitata* plants, for site R and 180 for site S (Table 5.1), between 40 – 50 cm in height and 0.5 – 1 m in diameter. Each sampling was conducted in two phases on two consecutive days: the first phase immediately after sunset and the second before the dawn of the following day. From each *T. capitata* plant, a 10 cm length tissue containing stem and leaves was collected and its moisture content (MC) at nightfall was measured. The same approach was repeated at predawn, leading to a total of 1894 MC measurements from 2015 to 2021. The airtight bags containing the samples were placed in insulated boxes with ice packs until weighed. Sealed sample bags were weighed no later than one hour after collection, using a two-decimal scale. After opening, they were placed in a furnace at 60 °C for 72 h and reweighed. MC, one for nightfall (MC_{nf}) and one for predawn (MC_{pd}) per thyme, was produced by subtracting the net weight of the dry sample from the net weight of the fresh sample. These were expressed as a percentage by dividing MC by the net weight of the fresh field sample. However, these values were not used independently but in relative terms to avoid limitations as noted by Turner (1981) and Jones (2007).

Table 5. 1 Spearman's Rho (r_s) from correlations between MCD of *T. capitata* and their distance from *Z. lotus* clusters ranked from the lowest to the highest p_{MCD}; n=number of *T. capitata* plants. Sampling during the dry season is in bold.

Sampling month	r_s	p_{MCD}	n	Study area
JUL 2021	-0.679	<0.0001	180	S
SEP 2020	-0.618	<0.0001	175	S
JUL 2015	-0.813	<0.0001	62	R
JUL 2020	-0.624	<0.0001	109	S
MAY 2020	-0.609	<0.0001	90	S
FEB 2016	-0.349	0.037	36	R
MAR 2020	-0.183	0.045	120	S
FEB 2021	-0.117	0.125	175	S

Instead, the moisture content difference (MCD) of each thyme, was calculated using the equation: $MCD = (MC_{pd}) - (MC_{nf})$. Under lack of nighttime transpiration plant tissues are typically rehydrated during night-time (Dawson, 2007). This new index represents the degree by which night-time rehydration occurs for thyme tissues. A positive MCD value would suggest that transpiration is active during daytime and that plant tissue MC losses, due to stomata transpiration, are replenished during night-time. This indicates adequate soil moisture availability. An MCD of close to zero would suggest that stomata remain closed during daytime to minimize transpiration losses, which in turn suggests low soil moisture availability.

5.3.3 Soil depth, organic carbon, and atmospheric moisture impacts on soil

Improved soil moisture around *Z. lotus* may be the result of deeper soil, higher soil organic matter, or/and more rainfall and morning dew interception from the plant's canopy. To determine any differences in soil depth between zones that could influence soil moisture availability, the soil depth for 90 *T. capitata* was measured (ca. 30 recordings per zone) in site S using an Edelman soil sampler.

As a proxy for differences in soil organic matter between zones, the dissolvable organic carbon (DOC; mg/L) content in zones 1 and 3 in area S was measured using a Total Organic Carbon (TOC) analyzer (TOC analyzer Aurora Model 1030, OI Analytical, Inc.) for 100 thymes included in the MC estimation methodology (1 soil sample per thyme; 50 samples per zone). Before TOC analysis every 5 samples were pooled together producing 10 TOC measurements per zone (20 TOC samples in total). Each soil sample contained 10 cm of topsoil, collected with a metallic tube, from 5 different locations in each zone. The pooled samples were homogenized using a shaker for 30 min. Then 10 g from the homogenized sample was dissolved in 40 ml of $CaCl_2.2H_2O$ (2.94 g in 2 L) and filtered through Whatman 42 filter paper. Samples were stored in the freezer until they were processed.

For monitoring surface soil moisture input from rainfall and morning dew, nine EC5 Soil Moisture Smart Sensors connected to two H21-002 HOBO Micro Station Data Loggers (ONSET) were installed in site S under two thymes and a *Z. lotus* plant (RZ4; Fig. 5.2a). The first thyme was in Zone 1 about 2 m away from the canopy of RZ4 and the second in Zone 3 about 15 m away from the nearest *Z. lotus*. At each *T. capitata,* two sensors were placed at a depth of 10 cm and two at a depth of 50 cm next to the canopy and within the thyme rhizosphere. An additional sensor was placed 5 cm deep under the canopy of RZ4. Soil moisture (in m^3/m^3) was recorded every hour beginning from the 25th of January 2020 for one year.

5.4 Statistical analysis

Statistical analysis was carried out using the IBM SPSS program v. 25.0. All data were analyzed for normal distribution with the Kolmogorov – Smirnov test. For data not found to be normally distributed either the Kruskal-Wallis non-parametric Test was applied for differences among data groups (followed by the Dunn-Bonferroni post hoc test) or the non-parametric Spearman's Rho when correlation analysis was performed. For data found to be normally distributed the one-way ANOVA test was performed.

5.5 Results

5.5.1 *T. capitata* density variability

In a total of 1377 *T. capitata* plants, Zone 1 produced the highest density for *T. capitata* with 0.44 plants per m^2 (Standard Error; SE = 0.08), in the experimental area of site R, followed by Zone 2 (0.25 plants per m^2; SE = 0.03) and Zone 3 (0.17 plants per m^2; SE = 0.03). The corresponding medians were 0.36, 0.23, and 0.18 (Fig. 5.3a). In the study area of site S, in a total of 2186 *T. capitata* plants, the highest density of T. *capitata* was recorded in Zone 1, with 0.57 plants per m^2 (SE=0.09), followed by Zone 2 (0.23 plants per m^2; SE=0.03) and Zone 3 (0.13 plants per m^2; S.E.=0.04). The medians were 0.63, 0.26, and 0.09 per zone respectively (Fig. 5.3b). The Kruskal-Wallis test identified statistically significant differences between the thyme densities of Zones 1 and 3 in both sites ($p< 0.01$ for R and $p<0.0001$ for S).

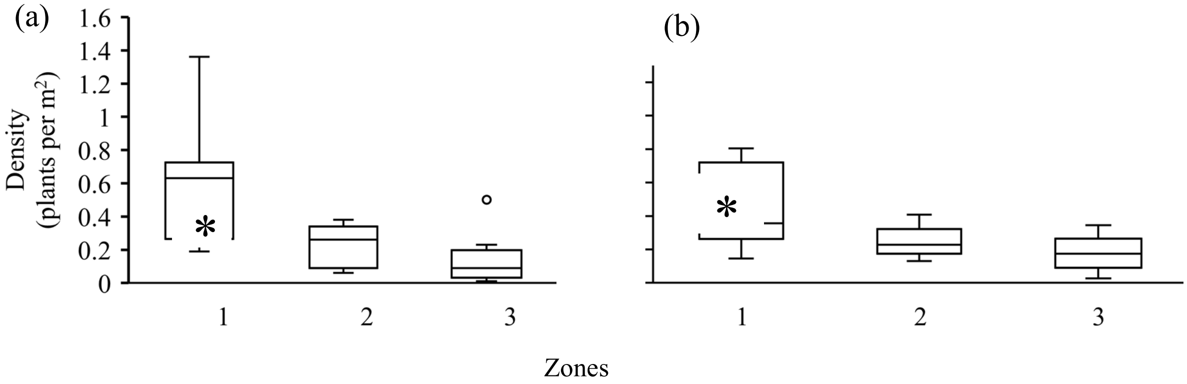

Figure 5. 3 The density (plants/m^2) of *T. capitata* around *Z. lotus* per zone in sites (a) R and (b) S. The horizontal line within each box represents the median. Mild outliers are marked with an open circle. Statistically significant differences, indicated by an asterisk (*), exist between Zones 1 and Zone 3 in both sites at $p < 0.01$ for R and $p < 0.0001$ for S.

5.5.2 Moisture content differences in *T. capitata*

The Spearman's rank correlation between thymes' MCD and their distance from *Z. lotus* in each sampling period produced a strong negative correlation ($p_{\mathrm{MCD}} < 0.0001$) for thymes sampled during the dry season months, in both study areas (Fig. 5.4). Regression analysis produced similar results. For the wet season months, correlations were much weaker $p_{\mathrm{MCD}} > 0.01$ or not significant at all in both sites (Table 5.1). Note, that mild winters in Cyprus (as also in neighboring Israel) do not produce full *Z. lotus* canopy defoliation. The full p_{MCD} values, from all months of sampling that are shown in Table 5.1, were found to be significantly correlated with IDM_1, $\mathrm{IDM}_{3,}$ or even better with IDM_6 (Table 5.2). This suggests that the driest the months prior to sampling, the higher was the MCD for the thymes closer to *Z. lotus* clusters and that differences in climatic dryness not only within a year but also between years appear to influence MCD. Furthermore, these results suggest that the more MCD departs from zero the more stomata remain open during the daytime as a result of more soil moisture being available, based on our original hypothesis.

The statistical analysis for possible soil depth differences in site S illustrated that soil depth did not differ across the three zones ($p = 0.462$). The mean soil depths for Zones 1 to 3 were 15.03 cm (SE = 0.68), 14.30 cm (SE = 0.72), and 15.5 cm (SE = 0.62) respectively. The one-way ANOVA revealed that there were no statistically significant differences in DOC content between Zones 1 and 3 [F (1,18) = 3.134, $p = 0.094$]. The mean DOC content for Zone 1 was 7.56 mg/L (SE = 2.39) and for Zone 3 was 17.75 mg/L (SE = 1.39).

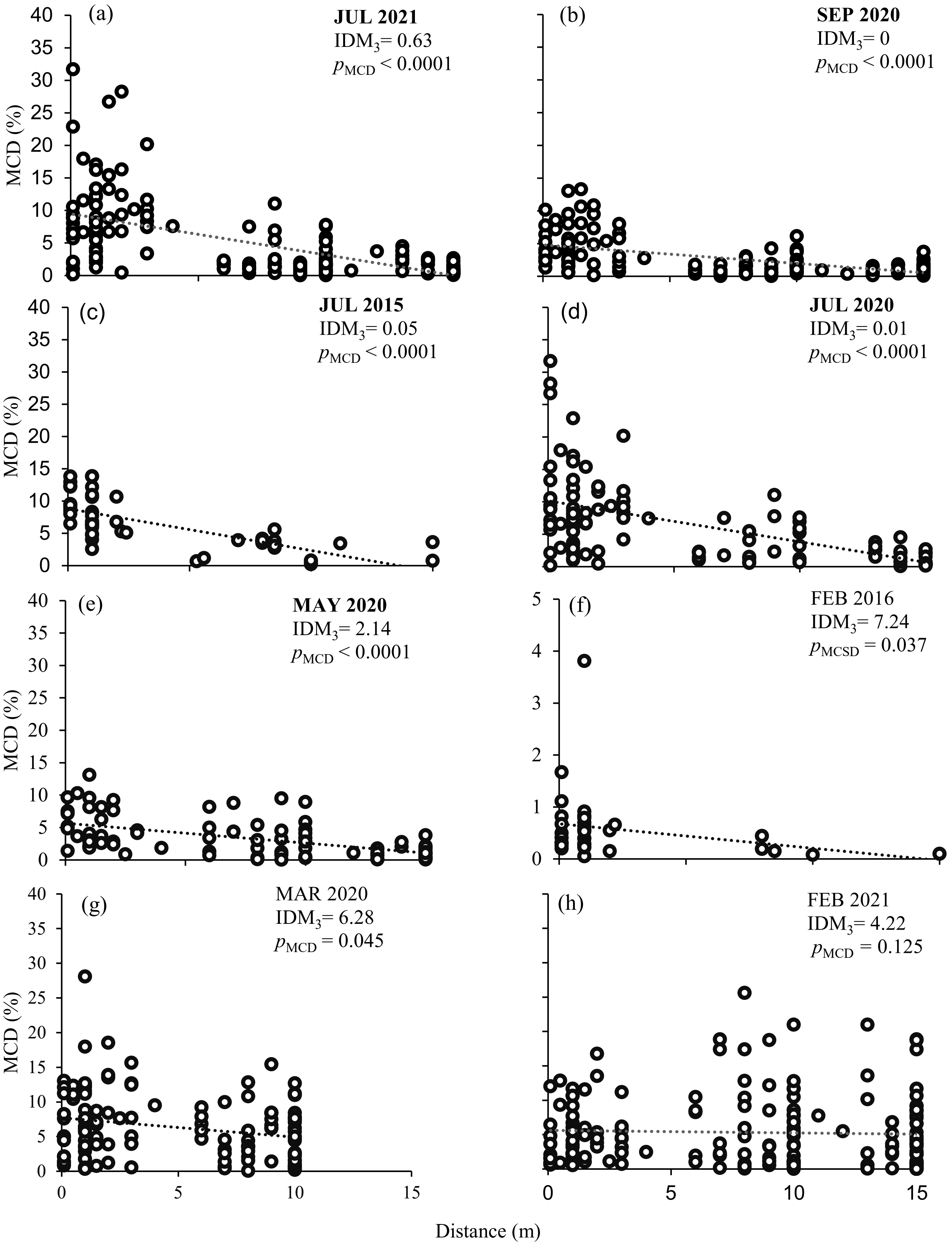

Figure 5. 4 Linear regression between moisture content differences (MCD) in stems of *T. capitata* and their distance from the closest *Z. lotus* ranked from the lowest to the highest p_{MCD}. IDM_3= the De Martone Aridity Index for the previous period of 3 months, including the month of sampling. Dry

season months of sampling are in bold. For full statistics see Table 5.1. Note that the scale for MCD in figure (f) differs and the Zone 3 data for March 2020 are missing.

Table 5. 2 The Spearman's Rho (rs) from the correlation between p_{MCD} of Table 5.1 and the IDM of the month of sampling (IDM1) as well as of the previous period of 3 and 6 months (including the month of sampling, IDM3, and IDM6).

	IDM_1	IDM_3	IDM_6
r_s	0.736	0.738	0.786
p	0.038	0.037	0.021
n	8	8	8

The comparison of the soil moisture sensors recordings of site R to Larnaka Airport Station confirmed that rainfall events produced an increase in soil moisture under the RZ4 canopy, and within 2 hours the increase was recorded by all four sensors placed at 10 cm, without soil moisture recordings being higher for the closer to *Z. lotus* sensors. The increase was also recorded by the four sensors at 50 cm but after several hours. On the other hand, morning dew events recorded at the Meteorological station did not produce any soil moisture increase under the *Z. lotus* canopy nor in any of the sensors placed on the thymes.

5.6 Discussion

Our findings clearly document that thyme population densities are significantly greater up to 5 m away from dominant *Z. lotus* plants under the natural spatial distribution established within the semiarid plant communities investigated in Cyprus (Fig. 5.3). The *Z. lotus* habitat (Priority habitat type *5220) is considered the climax vegetation stage in these low productivity systems, suggesting that it may have taken even centuries for natural vegetation succession to produce such an aggregation.

Constantinou et al. (2021) proposed that *Z. lotus* may be classified as an ecosystem engineer and that the plant may possess traits that act against natural drought gradients. Our seven-year long study has identified that *Z. lotus* has a positive impact on thyme stem/leaf moisture content availability, which in turn may be the key to explaining the increased densities of thymes around dominant *Ziziphus* plants (Fig. 5.4). Additionally, the shortest the distance *T. capitata* grew from

Z. lotus, the higher was the moisture content difference (MCD) in *T. capitata*, in the dry season in both study areas (Table 5.1). In fact, the driest the climatic year, the more pronounced the phenomenon appeared (Table 5.2). Considering that MCD measurements can act as a proxy for soil moisture availability, we identified more water in the soil exploited by the rhizosphere of *T. capitata* close to *Z. lotus* during the dry season and in dry years not more than 5 meters away from dominant Ziziphus plants. Thymes that are better watered can open stomata and transpire in the daytime, reduce moisture content by nightfall and replenish their cell turgor pressure (rehydrate tissues) by dawn. Thus, their MCD is expected to increase. Thymes that do not have such moisture pools available retain stomata closed for longer periods in the daytime and keep transpiration to minimum levels. Accordingly, no significant differences occur between nightfall and predawn stem/leaf moisture content (MCD close to zero).

Z. lotus may possess multiple ecological functions leading to improved soil moisture in its proximity. Our findings permit us to determine the most probable ones.
(A) Soil was not found to be deeper in 5-meter proximity from *Z. lotus* compared to 15-meter away. Thus, it is not likely that the plant creates deeper soils around it by capturing, wind-swept soil particles through its canopy as has been found for other species (Flores and Jurado 2003).
(B) The potential impact of rainfall and morning dew intercepted by the canopy on soil moisture availability of *Ziziphus* was investigated using nine soil moisture sensors over a year. Every recorded rainfall event from the closest Meteorological Station (distance of 8.5 km), produced a soil moisture increase as recorded by all nine sensors. Following rainfall events, soil moisture levels were not recorded to be the highest by the sensors closer to *Z. lotus*, nor did meteorologically documented incidents of morning dew produce noticeable soil moisture recordings in any of the sensors. Thus, it is not likely that the plant's canopy, as the dominant plant structure within its ecosystem, intercepts more rainfall and morning dew compared to bare soil further away, which then becomes available to neighboring thymes. Soil moisture has been reported to be higher under some plant species' canopy compared to bare ground areas (Maestre and Cortina, 2003). However, other studies showed that these effects are not general (Maestre et al., 2002; Cuesta et al., 2010). Note that thymes, in this study, were not under the immediate influence of *Z. lotus* canopy, which makes any impact of rainfall interception of *Ziziphus* on thymes less likely. Future analysis could also cover any torrential rainfall effects (Dorman et al., 2015a,b).

(C) It has been shown that plant litter carbon and carbon extracts from *Z. lotus* roots into soil biota and from there into the soil may increase soil organic matter, which in turn may improve its water-holding capacity (Minasny and Mcbratney, 2018). Although this function cannot be ruled out from influencing our systems, the DOC analysis did not indicate that dissolvable soil carbon was higher for thymes closer to *Ziziphus*. However, a more in-depth soil analysis that may include measuring among others, soils' water holding capacity, would be useful for future verification.

(D) Thyme MCD measurements vs. plant distance from *Z. lotus* (Fig. 5.4) revealed that the closest thymes grew to *Z. lotus* the highest was their ability to rehydrate at nighttime (p_{MCD} <0.0001), particularly during the dry season in both study areas. For the wet season months, correlations were much weaker $p_{MCD} > 0.01$ or not significant at all (Table 5.1). Furthermore, the driest the year ($IDM_3<2.5$), the strongest the effect that the above phenomenon exercised (Table 5.2). Thus, it is when the moisture contrast between topsoil vs. deeper ground is expected to be the highest within the year or in-between years, (i.e., conditions that favor HL) that thymes close to *Z. lotus* benefit from improved moisture content. This, in turn, may explain the significantly higher thyme population densities around the facilitating plant as HL water would reduce plant moisture stress, sustain more vigorous microbial populations, and improve nutrient availability. Stable isotope analysis could further shed light on the phenomenon as has been the case with other species performing "bio-irrigation" through hydraulic redistribution (HR; Bogie et al., 2018).

Hydraulically lifted water during the dry season and particularly in dry years is a phenomenon from which neighboring plants benefit (McMichael and Lascano, 2010). In the long Mediterranean dry season, topsoil becomes dry but still, moisture from the wet season may exist in the deeper ground, a condition which favors the occurrence of hydraulic lift (Richards and Caldwell, 1987). In dry years where still deeper ground moisture is available, we would again expect the soil moisture difference between topsoil and deeper ground to be strong, with very low water potentials to occur in soil layers outside the upper rhizosphere. Such conditions favor hydraulically lifted water to move osmotically from the deeper ground towards the outside of the fine roots and into the upper soil layers. Neighboring plants with roots exploiting these soils may make use of such water likely with assistance from mycorrhiza networks (Egerton-Warburton, 2007; Pickles and Simard, 2017). Thymes further away from the plant performing hydraulic lift (HL) would not be able to exploit such a resource. HL has been indirectly (Tewksbury and Lloyd, 2001), as well as directly (Liste and White, 2008) linked to the ability of plants to increase ecosystem productivity. Such examples are *Quercus suber* L. (Kurz-Besson et al., 2006), *Acacia tortilis* (Ludwig et al., 2003), four woody species of the Brazilian Cerrado (Scholz et al., 2002), three Amazonian trees (Oliveira et al., 2005) as well as the Sahel native shrub pearl millet (*Pennisetum glaucum*) in drought years (Bogie et al., 2018). Thus, the role of *Z. lotus* as an ecosystem engineer could very well involve such functioning.

Anisohydric phreatophytic species, such as *Z. lotus,* are known for their plasticity in their hydraulic behavior (Sun et al., 2014; Guo et al., 2020). *Z. lotus* has a very deep rooting potential (Gorai et al., 2010) and has been suggested to conduct HR by its deep roots to facilitate nutrient uptake from dry upper soil layers (Torres-García et al., 2021a). Therefore, improved moisture availability may be the key, in the semi-arid conditions investigated, to the higher density of thyme plants when growing close to *Z. lotus*. This may explain how the plant counterbalances the negative effects of south-facing aspects on thyme plant distribution (Constantinou et al., 2021) and is in support of facilitation being the main force driving community structure and function (Callaway et al., 2002).

The ecological role of late-successional species has been demonstrated in arid environments (Padilla et al., 2009) since the maintenance of ecosystem functions is a top conservation priority (Balvanera et al., 2001). HR is a key process in drylands that not only provides moisture to generally dry soil but also facilitates the acquisition of nutrients by plants (Cardon et al., 2013). Therefore, identifying species, such as *Z. lotus,* which maintain or influence such ecosystem functions is a wise conservation approach and provides an excellent potential for dryland reforestation within their native range, minimizing the risk of biological invasions (Mizrahi and Nerd, 1996; Padilla and Pugnaire, 2006). Thus, our findings can support future restoration efforts, to expand habitat type *5220, which is now severely districted in Europe and of poor conservation status and contribute towards changing the attitude of farmers and policymakers that see *Z. lotus* as an agricultural pest.

It is a question of how *Z. lotus* benefits from higher thyme densities in its proximity as having this could increase competition for resources. However, in conditions where soil evaporation pressure is high because of high solar radiation, denser thyme communities may favor *Z. lotus* as well, by reducing topsoil temperatures that can exceed 60ºC in the summertime at 34º latitude. Thyme canopies can reduce these temperatures by even ca. 20ºC, improving moisture conditions (Matsi and Sarris, under review), while making very conservative use of soil moisture (Moradi et al., 2014). This minimizes the risk of losing water to evaporation for the HL species as well. Sheltering from the detrimental effects of high solar radiation also permits higher seedling establishment rates (Príncipe et al., 2019). Therefore, these two species, as part of a positive association, appear to play an important role in maintaining key ecosystem functions of their habitat as may be the case for other ecosystem engineering species and their facilitating plant communities. Thus, this paper provides an excellent example and the methodological tools to expand such research. The MCD method we applied would benefit from further evaluation by comparison with the standard instrumental moisture content assessment approaches (Turner, 1981; Jones, 2007); although this could produce limitations in large-scale field sampling campaigns at night-time due to the more time-consuming requirement of the latter. Nonetheless, it is important to advance our understanding of hydraulic plant traits for improving dryland ecosystem productivity to the benefit of rural human populations that depend on their services. This may be key in the battle against desertification since drylands are home to more than two billion people and are the source of a large proportion of the food and fibre used around the world (IUCN, 2019).

5.7 Conclusions

In conclusion, our findings provide evidence that the moisture content of *T. capitata* and its density significantly increase around *Z. lotus*, as a most likely result of the HL properties of the latter. HL may be one of the key plant functions in explaining the spatial aggregation of shrubs around ecosystem engineering plants in drylands requiring, however, not only direct but also novel indirect methodological designs, as provided in this paper, for its large-scale investigation. Such hydraulic plant traits require more attention as they may prove valuable in combating desertification and restoring ecosystems in arid/semiarid regions threatened by climate change to the benefit of rural human populations that depend on dryland ecosystem services.

Chapter 6

Conclusions

6.1 Summary of findings

Phryganic communities are governed by facilitation, exhibiting an ecological network's highly nested structure and specific characteristics. *Ziziphus lotus*, a dominant plant in arid and semiarid environments, is proven to act not only as a facilitator in the community but also has the properties of an ecosystem engineer boosting productivity.

A) We quantified the spatial patterns of a 135.550 m^2 arid phryganic plant community with *Ziziphus lotus*, on the island of Cyprus in the Eastern Mediterranean, and found that it is characterized by a non-random, nested pattern exhibiting a high nested structure. Thus, forming a network with the same specific characteristics as the networks presented and documented by studies in various other ecosystems (Verdú and Valiente-Banuet, 2008), forest communities, and anthropogenic micro-deserts of high salinity in south-eastern Spain (Alcántara and Rey, 2012; Navarro-Cano et al., 2021) and tropical alpine and alpine plant communities (Anthelme and Dangles, 2012; Losapio et al., 2019; Pescador et al., 2020). In particular, the community exhibits high NODF values, significantly different (p<0.001) relative to the simulated values created by two null models (Table 3.1), and a relatively high connectance value (26% of the potential links). The Chi-square test of goodness-of-fit performed to test whether the interactions between the plants of the community occurred with specified probabilities (percentage of the transect covered by a plant species) revealed that in this community canopy-recruit observed interaction were not only explained by the species abundance and there should be other ecological processes beyond species abundance that shape these species-specific interactions. (Fig. 3.6, 3.7, 3.9, and 3.10). The 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 phryganic communities. The presence of species-specific interactions was reflected by the high connectance between cluster facilitators and their facilitated plant species, which was confirmed by a significantly higher (about twice as many) number of recruits under the canopies of facilitators versus open ground (Table 3.2; Fig. 3.4). *Z. lotus*, an established facilitator in the community, demonstrated the highest facilitation capacity (ca. 1.4 times higher than expected) followed by facilitators with smaller crowns such as *Thymus capitatus and Noaea mucronata* (Fig. 3.7). *Asparagus stipularis*, *Phagnalon rupestre*, *Noaea mucronata*, and *Sarcopoterium spinosum* showed high dependence on facilitative canopies as the numbers of recruits recorded under other plants' canopies were almost three times higher than expected by chance (Table 3.4; Fig. 3.8a, b, c, and d). Approximately two times more recruits of *Asparagus stipularis*, *Phagnalon rupestre*, and *Noaea mucronata* were found under *Z. lotus* proving their dependence to be higher on *Z. lotus* than on other facilitators (Fig. 3.9). *Sarcopoterium spinosum,* although proved to be highly dependent on facilitation (Fig. 3.9), was mostly facilitated by adult plants of its own species. Out of the ten perennial species present at the site, *Ziziphus lotus* was the only species that did not have any dependence on nurses for its establishment (Table 3.3). *Thymus capitata,* although present as a recruit under nurses, mainly under *Z. lotus*, did now show any statistically significant dependence on them (Fig. 3.8e).

B) Our findings indicate that the population density of *T. capitata* can significantly increase c. 2.5 times when located up to 5 m away from *Z. lotus* (Fig. 4.3) compared to thymes growing 10–15m away, where the impact of *Z. lotus* roots and canopy is not expected to exert any strong influence. The density of thymes 10–15m away from *Ziziphus* was found at 0.17 plants per m^2 and reached 0.44 plants per m^2 moving within a 5m radius from the keystone species. Furthermore, our findings showed no significant difference in the density for the three experimental conditions (East, South, Ridge; Fig. 4.3). Thus, the spatial heterogeneity of resources leading to the aggregation of *T. capitata* is most likely caused by *Z.* lotus. The ability to modify the surrounding environment and improve habitat suitability is one of the key characteristics for *Z. lotus* to be classified as an ecosystem engineer. Evidence, based on the variation of the moisture content in *T. capitata* stems in relation to the distance the plants grow from *Z. lotus* supports that *T. capitata* rehydrates their stems much more efficiently at nighttime the closer they grow to *Z. lotus* and up to 10 m away (Fig. 4.4), improving stem moisture content by c. 60 times in mid-summer (from 0.14% at 10–15 m to 8.27% at 0–5 m). This strong control exerted by *Z. lotus* within the habitat would mean that it can overcome expected moisture gradients shaped by topography.

C) Our findings clearly document that thyme population densities are significantly greater up to 5 m away from dominant *Z. lotus* plants under the natural spatial distribution established within the semiarid plant communities investigated in Cyprus (Fig. 5.3). Our seven-year-long study identified that *Z. lotus* has a positive impact on thyme stem/leaf moisture content availability, which in turn may be the key to explaining the increased densities of thymes around Ziziphus plants (Fig. 5.4). The shortest the distance *T. capitata* grew from *Z. lotus*, the higher the moisture content difference (MCD) in *T. capitata*, in the dry season in both study areas (Table 5.1). In fact, the driest the climatic year, the more pronounced the phenomenon appeared (Table 5.2). Considering that MCD measurements can act as a proxy for soil moisture availability, we identified more water in the soil exploited by the rhizosphere of *T. capitata* close to *Z. lotus* during the dry season and in dry years not more than 5 meters away from dominant *Ziziphus plants*. When investigating probable ecological functions *Z. lotus* may possess leading to improved soil moisture in its proximity our findings were as follows:

- The soil was not significantly deeper in its 5-meter proximity to *Z. lotus* compared to 15-meter away.
- Every recorded rainfall event from the closest Meteorological Station (distance of 8.5 km), over a year, produced a soil moisture increase recorded by all nine sensors. However, following rainfall events, soil moisture levels were not recorded to be significantly higher by the sensors closer to *Z. lotus* compared to the sensors placed 15 meters away, nor did meteorologically documented incidents of morning dew produce any noticeable soil moisture recordings in any of the sensors.
- The DOC analysis did not indicate that dissolvable soil carbon was higher for thymes closer to *Ziziphus*.
- Thyme MCD measurements vs. plant distance from *Z. lotus* (Fig. 5.4) revealed that the closest thymes grew to *Z. lotus* the highest was their ability to rehydrate at nighttime ($p_{MCD} < 0.0001$), particularly during the dry season in both study areas. For the wet season months, correlations were much weaker $p_{MCD} > 0.01$ or not significant at all (Table 5.1). Furthermore, the driest the year ($IDM_3 < 2.5$), the strongest the effect that the above phenomenon exercised (Table 5.2).

6.2 Implications of the findings

The network-like structure has been documented as the way in which plants coexist in many communities. These networks have specific characteristics, and their presence has been documented by studies in various ecosystems (Verdú and Valiente-Banuet, 2008; Alcántara and Rey, 2012; Navarro-Cano et al., 2021; Anthelme and Dangles, 2012; Losapio et al., 2019; Pescador et al., 2020). Phryganic communities of Cyprus in the Eastern Mediterranean form such a network, characterized by a non-random, nested pattern exhibiting a high nested structure with significantly high NODF values, and a relatively high connectance value (26% of the potential links). The high nestedness is a characteristic of communities with low species richness (Pescador et al., 2020). Eleven species were found in the community, in which the meta-community follows a dynamic process with a dominant species (i.e., plant-nursery 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 phryganic communities.

Although nestedness studies in a post-community context are conducted on large spatial scales, a spatial community-scale study can help us identify biotic interactions that play a dominant role in the construction of a plant community (Burns, 2007). A combination of biotic processes, such as species interactions and mass effect (Bascompte and Jordano, 2007; Vázquez et al., 2009), could be the underlying force behind the common hemispherical cluster vegetation structure, present in Mediterranean phryganic communities. The presence of species-specific interactions, reflected by the high connectance between cluster facilitators and their facilitated plant species, is confirmed by the significantly higher number of recruits under the canopies of facilitators versus open ground. A cluster-form network was described in the Mediterranean alpine grasslands (plant–patch network nestedness) by Pescador et al. (2020) and was positively correlated with the size of the patch area. *Z. lotus*, an established facilitator in the community and at the same time the species with the largest crown in diameter, demonstrated the highest facilitation capacity (ca. 1.4 times higher than expected) followed by facilitators with smaller crowns such as *Thymus capitatus* and *Noaea mucronata*. These findings are consistent with the proposed species-area relationship (Arrhenius, 1921; McGuinness, 1984) according to which larger facilitating areas (i.e., canopies) can accommodate more species that coexist compared to smaller patches, as nested structures are formed and confirm the "Facilitator size" hypothesis (Callaway and Walker, 1997) by which the facilitator's size is expected to increase the frequency of facilitative interactions (Anthelme and Dangles, 2012). This increased ability of *Z. lotus* to facilitate plants, compared to the other facilitating species in the community, is probably related to an improved ability to concentrate resources (Connor and McCoy, 2001; Constantinou et al., 2021) since resource limitation may be more critical under the influence of smaller facilitators, thus limiting the emergence of rare species. The different requirements of species concerning their ability to be established on a certain site (Wright et al., 1997), could be another additional parameter contributing to the different facilitation capacities among the three main nurses.

Several studies (Verdú and Valiente-Banuet, 2008; Alcántara and Rey, 2012; Pulgar et al., 2017) have demonstrated that a plant community's resistance to the removal of species is highly related to the structure of plant-to-plant interaction networks. Thus, the high nestedness and connectance detected herein suggest that this phryganic community could be robust to species extinction (Verdú and Valiente-Banuet, 2008). Then again, the community may be endangered if extinction hits the most connected species (Verdú and Valiente-Banuet, 2008). Simulations done by Verdú, and Valiente-Banuet (2008) showed that the species diversity in a nested community is not significantly altered, provided that the sequence of extinction occurs from the least (i.e., *A. stipularis*, *R. oleoides subsp. graecus*, and *S. spinosum*) to the most connected nurse species (i.e., *Z. lotus*, *T. capitatus*, and *N. mucronata*). The detected species-specific relations among the plants of the community could impact the risk of local extinctions since the extinction of the highly connected species (i.e., *Z. lotus*, *T. capitatus*, and *N. mucronata*) could be fatal for many other species (Valiente-Banuet & Verdú, 2013). This is based on the simple assumption that since nurse extinction causes a facilitated plant to lose its regeneration niche, this plant could also become extinct (Dunne, 2006). Consequently, in communities governed by facilitation through multiple benefactor species, conservation efforts must be allocated to the benefactor species assembling the community (Altieri et al., 2007). Since *Z. lotus*, *T. capitatus*, and *N. mucronata* are the community's main facilitators, these should be the keystones of any conservation attempt to protect the community's biodiversity. Especially *Z. lotus*, which is 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*), is the benefactor species that when protected may provide even more resistance to extinction.

Most plant-to-plant interaction networks studied to date show connectance below 30%, a fact that implies the potential existence of more than 70% of unobserved interactions (Alcántara et al., 2019). In consistency with the conclusions of Alcántara et al. (2019), the community's connectance was 26% and among the realized interactions, neutral or enhancing interspecific interactions were more frequent while intraspecific interactions, although present were much less frequent (Table 3.3). The presence of many weak and few strong interactions in the network (Fig. 3.5), along with high connectance and the frequency of intraspecific interactions shields the community with great stability even more (McCann, Hastings & Huxel, 1998; Wootton & Stouffer, 2016). The Chi-square test of goodness-of-fit revealed that in this community canopy-recruit observed interactions were not explained by the species abundance but there should be other ecological processes beyond species abundance that shape these species-specific interactions. (Fig. 6, 7, 9, and 10). Alcántara et al. (2018) suggested that an important part of the potential interactions is impeded for some ecological reason and that the frequency of any individual canopy–recruit interaction is the result of the balance between multiple positive and negative interactions which can be determined by multiple factors.

In climatically harsh environments such as arid and semi-arid ecosystems of the Mediterranean, slight alterations in physical parameters could create favorable habitats for organisms that would otherwise be unable to tolerate limiting physical conditions. In these environments maintaining ecosystem functions is a top conservation priority (Balvanera et al., 2001). Therefore, identifying species that maintain, or influence ecosystem functions is a wise conservation approach. *Z. lotus* appears to possess the properties of a successful ecosystem engineer. It seems capable of a significant positive impact on the community, and capable of modifying limiting resources or constraining variables in the system i.e., moisture availability, especially in dryland ecosystems where water availability is by far the most limiting factor for plant productivity (Nolan et al., 2018; Sarris et al., 2007).

Moreover, in extreme environments, the most suitable options for terrestrial ecosystem management are native species that can improve environmental conditions and minimize the risk of biological invasions (Padilla and Pugnaire, 2006). *Ziziphus* sp. is native to arid and semiarid ecosystems, intrinsically adapted to dry and hot climates, and thus has excellent potential for dryland reforestation (Mizrahi and Nerd, 1996). Species of the genus *Ziziphus* have been successfully used in dryland reforestation as multifunctional tree species, which meet the criteria of drought resistance, the minimal distraction of ecosystem integrity, and maximization of ecosystem services, including supporting community livelihoods (Reisman-Berman et al., 2019).

Ziziphus lotus is a dominante plant of the Thermomediterranean scrub habitat, that has been assessed as a vulnerable habitat in the European Red List of Habitats (2016). This habitat constitutes a mature stage of succession in the most arid areas of southern Europe, the Near East, and Mediterranean North Africa. Nowadays, it is declining in its main area in Spain and also in Sicily. Although in Cyprus the habitat accounts for a more stable trend, there a need for its protection against intensive agriculture and urbanisation. In the past, firewood harvesting, and goat grazing were also among the main causes of its retreat. This habitat includes Annex 1 types 5220 and 5330, and thus deserves a clear conservation effort in the sense of implementing a sound conservation policy in order to preserve its biodiversity. Tirado and Pugnaire (2005) exhibited that *Ziziphus lotus* shrubland patches can gather more species in a patch, compared to six other scrub communities. Given the fact that *Z. lotus* is the dominant species of the priority habitat *5220 and many phryganic communities in Cyprus, highlighting its role as an ecosystem engineer may improve the outcomes of future restoration efforts, and assist in the expansion of the habitat's range, which is now severely districted in Europe and of poor conservation status.

Improving the biomass of neighboring plants *Z. lotus* may also prove beneficial for agroforestry systems in creating resilient hedgerows to combat desertification or for providing pollinators, fodder, fruits, and other services where tree life forms fail because of climatic stress. Thus, a change in attitude is required from both farmers and policymakers (who currently see *Z. lotus* as an agricultural pest) in reevaluating its potential to promote arid and semiarid agroecosystem sustainability (Abdallah et al., 1999; Boussaid et al., 2018), particularly under climatic change.

At the same time, a native species such as *Z. lotus*, which maintains or influences ecosystem functions is a wise conservation approach and provides an excellent potential for dryland reforestation within their native range, minimizing the risk of biological invasions (Mizrahi and Nerd, 1996; Padilla and Pugnaire, 2006).

6.3 Methodology evaluation and study limitations

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. Although there is increasing evidence of the permanence of the nature of the interactions between functionally different species exists (Navarro-Cano et al., 2019), 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 (Tielbörger and Kadmon, 2000). The results of our study regarding the relationship between *Z. lotus* and adult *T. capitata* prove that, at least in this case, the relationship remains beneficial throughout the life stages of *T. capitata* our study did not include any other plants in their adult form.

The phryganic community used in the study was chosen as being a community with high representation in the island of Cyprus. Thus, the particular nodes and links in the ecological network, the extent and form of facilitative interactions among species that are not present in the phryganic communities of Cyprus have yet to be explored.

This study is also the very first attempt to investigate the multiple ecological functions *Z. lotus* may possess leading to improved soil moisture in its proximity. Our findings allowed us to determine the effects of canopy interception of moisture/rainfall, soil volume, air temperature, shade, topography, and organic matter content in soil moisture availability. The possible effect of shade was not estimated through an experiment but ruled out as a possible factor since improved soil moisture availability was achieved overnight. Also, the improvement of soil's water-holding capacity by the possible increase in soil organic matter from plant litter carbon and carbon extracts from *Z. lotus* roots into soil biota and from there into the soil (Minasny and Mcbratney, 2018), should not be adequately ruled out from influencing our systems. Although the DOC analysis did not indicate that dissolvable soil carbon was higher for thymes closer to *Ziziphus*, a more in-depth soil analysis that may include measuring among others, soils' water-holding capacity, would be useful for future verification. The conclusion that HR was the only possible factor responsible for the improved soil moisture availability, was made exclusively following the exclusion principle i.e., excluding the influence of the other possible factors, and was not confirmed through an experimental procedure that proves the presence of hydraulically lifted water in thymes.

6.4 Future research directions

The data collected from the phryganic communities to assess the extent of facilitation interactions and the existence of an ecological network, can be viewed as a snapshot of the status of the community. Although only facilitation at a recruit stage was evaluated, there is increasing evidence that the nature of the interactions between functionally different species could be permanent (Navarro-Cano et al., 2019). Nevertheless, this evaluation of the interaction on a recruit stage represents an outstanding opportunity to resample the network in the future and monitor changes in the structure of the plant community. Thus, adding a temporal dimension to the recruit facilitation stage of the network would provide invaluable information about successional dynamics (Verdú et al., 2023; Sortibrán et al., 2014, 2019; Montesinos-Navarro et al., 2016a, 2017). Aspects related to the water-use strategy of *Ziziphus lotus* regarding the origin of water it uses and how it regulates its use, and the spatiotemporal variability in the ecophysiology of the plant are already known (Torres-García et al., 2021a, 2021c). The modular growth and functional heterophylly traits of the plant are also investigated in its southeast of Spain populations (Torres-García et al., 2021b). Further identification of the traits behind all the interactions, regarding all the main facilitators, will allow us to understand how biodiversity in the phryganic communities is shaped and apply this knowledge to restore species (Navarro-Cano et al., 2021) and ecosystem functions (Montoya et al., 2012; Navarro-Cano et al., 2018).

The phryganic communities of the Mediterranean are communities with a high biodiversity index. For this reason, a similar work that will include species that are not found in Cyprus would be necessary for a more complete understanding of the phryganic ecological networks. Also, by intensifying the traits of the main facilitators and recruits in various sites the goal of protecting and conserving these ecosystems will become more effective.

Since the improvement of soil's water-holding capacity by the possible increase in soil organic matter from plant litter carbon and carbon extracts from *Z. lotus* roots into soil biota and from there into the soil (Minasny and McBratney, 2018), could not be sufficiently ruled out from influencing our systems by solely the DOC analysis as a technique, a more in-depth soil analysis that may include measuring among others, soils' water-holding capacity, would be useful for future verification. A confirmation of the assumption that HR may be the only possible factor responsible for the improved soil moisture availability could be further investigated by an experiment using the abundance of deuterium in *T. capitata* xylem water. One such experiment revealing the magnitude of hydraulically lifted water utilization by neighbors was demonstrated in the field by Dawson (1993). Dawson proposed the use of the known isotope ratios (signatures) of xylem, soil, and groundwater and a mixing model to determine the proportion of hydraulically lifted water used by neighboring plants.

If our findings can be confirmed at a wider scale, from other sites around the Mediterranean, then *Z. lotus* may be one of the plants with the potential to significantly improve semiarid ecosystem productivity and be used against desertification, considering the expected aridity increase that the Mediterranean will experience under global climatic change.

6.5 Concluding Statement

Phryganic communities are a very widespread form of vegetation in the Eastern Mediterranean. Their presence under great environmental and anthropogenic pressures seems to be justified by the high rate of connectance and facilitative interactions they present. The knowledge offered by the study of their ecological networks, as well as the identification of the main facilitators and their network characteristics, ensures their continued existence. *Ziziphus lotus*, as one of the most important facilitators in many of the Mediterranean's phryganic ecosystems, ensures the community plants ability to survive despite severe water scarcity. Furthermore, since *Ziziphus lotus* has the properties of an ecosystem engineer ensures, in addition to higher productivity, the persistence and further expansion of the habitat.

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Appendix

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