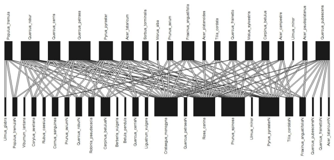

Nurse plants and the regeneration niche of tree seedlings in wood-pastures from Western and North-Western Romania

Ecaterina Fodor✉**, Ovidiu Hâruța, Sorin Dorog**

University of Oradea, Faculty of Environmental Protection, Forestry and Forest Engineering Department, Oradea, Romania

✉ ecaterina.fodor@gmail.com

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Abstract

Facilitation is a positive interaction demonstrated to be one of the important factors shaping the regeneration niche of trees, mostly under stressful conditions which is currently studied in the frame of complex ecological networks. The protection provided by benefactor plants for tree seedlings playing the role of beneficiaries is documented mainly in arid and semi-arid habitats or in situations where herbivores' pressure constitutes the main stressful factor for tree regeneration. One of the iconic Transylvanian landscapes is the wood-pasture, also one of the oldest agro-forestry systems to which recent forest expansion in abandoned agricultural fields or pastures is added. The proposed work represents a preliminary investigation on the association between benefactor plants, mostly spiny shrubs (*Rosa canina, Crataegus monogyna, Prunus spinosa* as the most frequently encountered benefactors) and tree seedlings (*Quercus* spp., *Tilia* spp., *Carpinus betulus*, *Fraxinus angustifolia, Pyrus pyraster* as most frequently encountered beneficiaries), in four different locations from North-Western and Western Romania, wood-pastures, abandoned pastures and abandoned agricultural fields under the consideration that the main stressful factor is represented by livestock grazing. Bipartite, qualitative merged network was generated depicting the interaction between beneficiaries and benefactors. Commonly used metrics were calculated: connectivity, nestedness, modularity, betweenness centrality and centralization compared to similar facilitation networks presented in the literature. Facilitation network is characterized by high nestedness (N=0.896), lack of modularity, relatively high connectance (C=0.233), features encountered in mutualistic networks also. Betweenness centrality scores highlighted the keystone benefactor and beneficiary species, while betweenness centralization score (0.192) indicates the fact that there are several species sharing the dominant position in terms of interactions. The analysis of measurement data (seedlings' and benefactor plants' heights, distance from focal seedlings to nearest benefactor species and orientation) showed that there is common pattern in orientation (most of the benefactor species oriented toward South or South West) also in dimensional variability (MANOVA results).

Keywords

Nurse plants; Bipartite facilitation network; Nestedness; Modularity; Betweennes centrality

Contents

1 Introduction

Species interactions within same trophic level have been in focus during the last decade being considered as key drivers of community assembly and structure (McIntire and Fajardo 2014) and key components of biodiversity, of the richness of ecological functions and services (Jordano 2016). Positive interactions of non-trophic nature, in this context play important roles in structuring communities mostly under stressful conditions (Callaway 2007; Bruno et al. 2003; Tirado and Pugnaire 2005). However, the net balance between competition and facilitation depends on environmental context as Stress Gradient Hypothesis states (Bertness and Callaway 1994).

Facilitation has been highlighted as biotic process with important consequences for the organization of communities, with consistent empirical evidence brought to demonstrate the validity of the concept. It is defined as an interaction wherein one species derives a fitness benefit and the other side is not detrimentally affected (Aslan et al. 2015). Empirical data showed that facilitation is frequent in nature and is encountered within same trophic level but also among organisms situated in different trophic positions. However, facilitative interactions are included in the larger context of interspecific interactions responsible for community assembly and persistence. Facilitation was demonstrated between below ground and above ground phytophagous insects (McKenzie et al. 2013), between frugivorous animals and plants in terms of seed dispersal (Simmons et al. 2018; Marcilio-Silva et al. 2015; Donatti et al. 2011). It was extensively studied in plant communities and systems of protected and protective plants (also metaphorically named nurse plants), interactions considered as favorable to seedlings' development due to spatial proximity and direct/indirect positive effects enhancing the survival of young plants (Sosa and Fleming 2002; Valiente-Banuet et al. 2002; Padilla and Pugnaire 2006; Holland and Mollina-Freaner 2012).

In terms of the growth form, benefactor plants' role can be performed by herbs and forbs, shrubs or other tree species. Facilitation is controlled by biotic and abiotic factors but it is manifested mostly under unfavorable conditions: aridity, grazing, palatable species benefiting from the association with non-palatable species (Pugnaire and Luque 2001), direct light and high temperatures. Nurse plants canopy provide shelter, higher soil and air humidity and shading. However, facilitation is size dependent and as soon as beneficiary plants are overgrowing their benefactors (Soliveres at al. 2010), mostly in close related taxa (Valiente-Banuet and Verdú 2008), competition replaces facilitation. Although nurse syndrome was extensively studied in desert areas and Mediterranean basin, the phenomenon is expected to manifest in temperate zones as well (Gómez-Aparicio et al. 2004). The interaction is modeled by gradients of abiotic factors being expressed on Southern slopes and lower elevations

(Gómez-Aparicio et al. 2004). In this context, nurse species can be seen as founder species (Dayton 1972; Gómez-Aparicio et al. 2004; Lortie et al. 2017).

Facilitation is also a dimension of the regeneration niche hypervolume, enlarging the regeneration niche of the trees which is encompassing the axes of environmental requirements necessary to germination and establishment of woody plant species (Grubb 1977).

In Romania, landscapes harboring thorny shrubs associated to tree seedlings are highly heterogeneous mosaics of wood pastures, agricultural lands, overgrazed pastures, forests, buffer strips with woody vegetation, small patches of trees and shrubs. The main habitat type pertains to Central European sub-continental thickets (EUNIS F 3241). These phytocoenoses develop as secondary successions after deforestation of zonal forests (mixed broadleaved forests with *Quercus petraea, Q. robur, Q. cerris, Q. pubescens, Carpinus betulus, Tilia* spp.). Traditional wood pastures which are semi-natural ecosystems cover over 10,000 ha, largest areas being located in Transylvania, from silvo steppe to colline zone (Hartel et al. 2013) and are considered EMERALD priority habitats. Another largely represented habitat type, the abandoned or postagricultural lands (D'Orangeville et al. 2008) in the proximity of the forest stands contribute to forest expansion with the participation of facilitative interactions.

Recent developments in network science (Barabási 2016), were integrated in ecology as a new sub-domain, network ecology focused on the study of interactions involved in structure, function and evolution of ecological systems at many levels and scales of organization (Borrett et al. 2012; Eklöf et al. 2012; Lau et al. 2017). The network approach using network science formalism, allows the uncovering of hidden properties connected with structure and its irregularities but also dynamics and control of living systems (Kitano 2002) permitting to approach simultaneously mega diverse systems of interacting species (Verdú et al. 2010). Networks are entities composed of nodes (for instance species, genes, proteins, habitats, individuals of a population) and the connection among them, characterized by specific topology and properties. In this context, the study of facilitation networks' properties sheds light on the assembly mechanisms of plant communities (considered not so long ago as being shaped mainly by competition) and biodiversity maintenance mechanisms (Valiente-Banuet et al. 2006). Network metrics help unraveling the latent properties of analyzed interactions, patterns of community organization (Blüthgen et al. 2008), and the functional role of individual species within communities (Simmons et al. 2017).

Many types of ecological interactions, also plant-plant interactions can be depicted by bipartite or two mode networks (Jordano 2016) which contain two sets of nodes where links are possible only between nodes of different sets and not within the sets. The quantitative description of bipartite networks (generally all types of networks) rely on several largely employed metrics. Connectance, one of the first investigated properties of networks in the context of complexity discussions (Pimm 1982) constrains the other derived network properties such as node degree distribution, nestedness and modularity (Poisot and Gravel 2014). *Nestedness* is a statistical property of bipartite networks depicting two entities which interact, but the interpretation depends on the context as long as this is a generic property (Beckett et al. 2014). In general terms, it is described as the tendency of low connected species (specialists) to interact with a subset of highly connected species (generalists). Modularity is a second order network descriptor quantifying the clustering of nodes in groups or modules characterized by higher number of links within a group than between groups, a topology emerging in many real world networks (Danon et al. 2005; Newman and Girvan 2003). Detecting modules, hubs or clusters can be useful since the nodes cluster according to some functional criteria. Both properties are considered to be drivers of network dynamics (Fortuna et al. 2010).

Centrality measures largely employed in social sciences were adopted in the study of bipartite ecological networks (Martín Gonzáles et al. 2010) as alternative metrics for description of local and global properties, evaluating node importance in network context, identifying in this way the keystone species. Centrality associates with different structural patterns characterizing communities (Sazima et al. 2010) and apparently is strongly correlated with the nested structure of the interactions in mutualistic networks (Guimarães et al. 2007) also, with network stability and resilience (Barthélemy 2004; Gómez and Perfectti 2012) or with transmission in pathogen-host networks (Gómez et al. 2013). Betweenness centrality (BC) measures the importance of a node as connector between different parts of a network (Freeman 1977) and contribute to the cohesiveness of mutualistic networks (Martín Gonzáles et al. 2010). In this respect BC is comparable with modularity analysis in the sense of attributing importance roles to nodes. The approach bypasses problems related to small network size, many of empirical ecological networks suffering from this flaw.

The present study aims the establishment of facilitative interactions between benefactor woody plants and tree seedlings in wood pastures which are characteristic for North-Western and Western Romanian landscapes and also in abandoned meadows, pastures or agricultural lands. Establishment of tree seedlings is challenged by higher aridity and grazing pressure. In wood pastures, trees are represented mainly by *Quercus* spp., *Carpinus betulus*, *Tilia* spp., *Populus* spp., *Fagus sylvatica*, *Fraxinus* spp., *Pyrus pyraster* and *Malus sylvatica.*

The study goals:

1. Consider facilitative interaction as an important axis of the regeneration niche.

2. Study of the facilitative interactions between benefactor woody plants and tree seedlings/saplings in wood pastures using network approach.

3. Employ network metrics used for the identification of keystone species contributing to the regeneration niche of trees.

4. Bring arguments for the consideration of facilitation interaction as a potential model to use in reforestation or afforestation programs, in conservation of endangered woody species in harsh environments, also in ecological rehabilitations in Romania since the facilitation model was successfully employed with these specific aims elsewhere (Gómez-Aparicio et al. 2004).

2 Materials and Methods

Site locations: Sampling areas were selected in secondary wood pastures in North Western and Western Romania, in four sites (1 - wooded pasture adjacent to Hoia recreational forest near the city of Cluj-Napoca, 2 - wood pasture near forest stands in the area of Stana commune, degraded pasture near Miersig commune, 3 - adjacent to mixed broadleaved forest dominated by *Quercus cerris* and 4 - a strip of wood pasture adjacent to forest stands near Traian Vuia commune) (Table 1). The main characteristic of the landscapes consists in the vegetation cover mosaic established by forest stands interspersed with secondary wood pastures, abandoned agricultural lands and grasslands, rolling hills of Transylvanian Plain and Western Plain. Transylvanian Plain and the adjacent colline zone harbor remnants of natural forest steppe and secondary meadows with woody vegetation, many of them displaying the reversion to forest vegetation, a common feature for many areas in Romania (Csergö et al. 2013), being characterized also by water deficit. Western Plain and adjacent colline zone are characterized by warm, continental climate. During the last five decades average monthly temperatures have increased, with average annual rainfall between 525-565 mm westwards and between 615-640 mm eastward (Anonymous 2009).

The sampling site 1 placed near Hoia forest (forest stands consist of mixed broadleaved forests dominated by *Quecus petraea, Q. robur, Q. cerris,* and *Q. pubescens*) is placed in Someș Plateau (pertaining to Transylvannian colline zone), on limestone deposits consisting of heterogeneous landscape with forest stands, *Prunus spinosa – Crataegus monogyna* thickets invaded by trees, abandoned agricultural terraces, buffer strips with woody vegetation and traditional wood pastures with *Pyrus pyraster* and *Carpinus betulus*.

Sampling site 2 (Păușa forest, near commune Miersig) is placed in a pasture invaded by *Prunus spinosa- Crataegus monogyna* tickets, adjacent to mixed broadleaved forest stand dominated by *Q. cerris.*

The sampling site 3 is placed near Stana commune, characterized by high landscape fragmentation, with patches of broadleaved forests dominated by *Quercus petraea, Q. cerris* and *Q. robur*, traditional wood pastures (with *Pyrus pyraster, Carpinus betulus, Quercus cerris, Cornus mas*), degraded pastures, buffer strips with woody vegetation and small patches of cultivated land.

The sampling site 4 is placed near the forest edge, in the proximity of Traian Vuia commune, in a hilly zone with broadleaved mixed forests dominated by *Q. cerris* and *Q. frainetto*. Sampling was performed in the open strip placed between a forest stand and the road.

All sites are under intense anthropogenic influence (roads, overgrazing, and proximity of agricultural fields).

Sampling design: benefactor species in the range of approximately 0 to 2 m near 50 randomly chosen seedlings/saplings were considered in areas of average 1000 m^2. The random walk sampling took into consideration tree seedlings associated with protector plants, shrubs and tree saplings. Distance to nearest benefactor plants, azimuth and the height of seedlings and nurse plants were measured. In wood pastures, adult trees were not considered in the sampling process as recruitment in their crowns' projection was determined by limited dispersion.

The presence-absence matrix of nurse plant species and beneficiary species was assembled merging species and interactions from the four locations (supplementary information 1). Apart from several metrics currently used in the analysis of ecological networks such as connectance, nestedness and modularity, we used centrality metrics initially devised for social networks, betweenness centrality and betweenness centralization to gain more information on network architecture under the serious limitation of the relatively small network size. The matrix was employed to generate a merged bipartite, undirected network using the package bipartite in R (R Core Team 2013) and Pajek ver. 5.06 software (Batagelj and Mrvar

2010). Pajek software provided metrics such as connectance, average degree, betweenness centrality, betweenness centralization and Louvain modularity.

Table 1. Data on sampling sites location.

Location	Coordinates of sampling sites	elevation	Relief	Main shrub species	Local Forest type
1.outside Hoia forest, near Cluj Napoca	46°46'26"N 23°29'58"E	438 m	Hills	*Prunus spinosa* *Crataegus monogyna* *Rosa canina*	Broadleaved mixed forests dominated by *Q. petraea* and *Q. cerris*
2.outside Păușa forest near Miersig commune, Bihor County	46°54'27"N 21°50'50"E	140 m	Rolling hills and plain	*Prunus spinosa*	broadleaved mixed forests dominated by *Q. cerris*
3.outside Stana forests, near Stana commune, Sălaj County	46°52'38"N 23°08'50"E	493 m	Hills	*Prunus spinosa* *Crataegus monogyna* *Rosa canina*	Broadleaved mixed forests dominated by *Q. petraea, Q. robur* and *Q. cerris*
4.outside forest stand near Traian Vuia commune, Timiș County	45°43'38.17"N 21°59'37.16"E	233 m	Rolling hills and plain (Lugoj plain, a subdivision of Western Plain)	*Prunus spinosa* *Crataegus monogyna* *Rosa canina*	broadleaved mixed forests dominated by *Q. cerris, and Q. frainetto*

Network analysis. Connectance is a community averaged property predictive for the dynamical properties of the network (Dunne et al. 2002) and one of the first network properties to be analyzed (May 1972). Represents the proportion of realized links among the potential links in a network (May 1972) being a community averaged property (Poisot and Gravel 2014).

Nestedness. The employed algorithm is based on matrix temperature introduced by Atmar and Patterson (1993) and reflects the number of unexpected occurrences and absences in the observed matrix compared to a random or null matrix. It is calculated as N=(100-T)/100, T being the estimated matrix temperature (Bascompte et al. 2003). N is defined within the range [0,1] where 1 corresponds to a perfectly nested network and 0 corresponds to systems where interactions occur completely at random. Nestedness was estimated with Binmatnest, a software devised for the calculation of estimated packed matrix temperature (Rodríguez-Gironés and Santamaría 2006). The software provides three probabilities corresponding to three null models, authors recommending the liberal null model 3 which does not control for row and column totals in the matrix. The software can be run increasing values to tested population size for the generation of GA (greedy algorithm), number of null matrices, number of individuals used for the generation of GA in order to increase the accuracy. We used 20 individuals instead for the recommended 7, the size of populations of 50 instead of the recommended 30 and 2,500 generations instead of the recommended 2,000.

Modularity. Community detection is using a large array of algorithms and indices. We employed two different algorithms: the frequently used in the analysis of ecological networks proposed by Girvan and Newman (2002) incorporated in the

Netcarto software developed by Guimera and Amaral (2005) and the other, Louvain method (Blondel et al. 2008) provided by the software Pajek (Batagelj and Mrvar 2010). Netcarto which is considered as having the best performance in terms of modularity maximization and accurate modules' separation (Danon et al. 2005) uses simulated annealing algorithm recommended for small networks.

However, modularity optimization has a resolution limit decreasing with network size, as community detection is, in fact, an optimization process (Fortunato and Barthélemy 2007); both employed methods do not discriminate overlapping modules assigning nodes exclusively to one module or another. The rationale behind employing two different algorithms was the unbiased estimation of a network latent structural feature, modularity. Community structure in terms of clustering as depicted by modularity can be reliably detected if calculated modularity exceeds expected modularity of random networks constrained by an appropriate null model (Reichardt and Bornholdt 2006). Random Erdős-Renyi bipartite networks were employed as appropriate null models to test whether there was a significant community structure characterizing the network topology.

Accordingly, significance testing of modularity results was performed running 100 simulated random networks with same number of nodes in Netcarto software and 100 random Erdős-Renyi bipartite, undirected networks with same number of nodes and same average node degree in Pajek testing the Louvain algorithm results.

Betweenness centrality and centralization: As centrality measures are not frequently used in interaction networks, we employed betweenness centrality and centralization to the facilitation network depicting the interaction between benefactor plants and their beneficiaries. Betweenness centrality (BC) is measuring the position of a node in relation to the number of geodesic (shortest) paths that pass through the given node weighted by the total number of equivalent paths between the same two nodes including those that do not pass through the given node (Freeman 1977; Borgatti and Everett 1997). It is a good proxy for roles estimated using participation coefficient and z score in modularity analysis. Betweenness centrality is calculated according to the following equation (Freeman 1979):

$$C_B(i) = 2 \cdot \sum \frac{\left[\frac{g_{jk}(i)}{g_{jk}}\right]}{(n-1)(n-2)}$$

Where: $g_{jk}(i)$ stands for number of shortest paths connecting jk nodes and g_{jk} stands for number of shortest path in the network.

The index takes values in the range (0;1). Nodes with BC>0 are considered connectors. Betweenness centrality is considered to be a fine grained measure of the node importance in the context of a network. Another useful category of network structure estimators are centralization indices based on node centralities reflecting the degree of influence of the most central or influential node of the network (Freeman 1979).

We employed betweenness centralization as a group descriptor of the role played by nodes that exert the greatest influence in terms of shared interactions.

All employed algorithms were applied to merged data matrix because local matrices contained few species and small matrices as well as undersampled interactions are prone to flawed results (Jordano 2016).

The merged matrix was also employed for multivariate analysis, such as clustering (UGPMA using Jaccard similarity), and also for niche overlap estimation (Pianka index). Measurement variables (orientation, benefactor plants and seedlings heights, and distances to focal seedling of benefactor species) were used for comparisons among sampling sites (MANOVA and Principal Component Analysis Supplemental information 2) for which Ecosim (Gotelli and Entsminger 2001) and PAST ver. 3.10 software (Hammer et al. 2001) were employed.

3 Results

Merging all four locations, 44 woody species of which 25 performing the role of benefactors, shrubs and also trees were accounted (supplemental information 1). In several instances, saplings performed as benefactors for homospecific and heterospecific tree seedlings. Saplings playing the role of benefactors are depicted in the network with additional N at the end of the name.

The number of benefactor species and number of individuals varied among locations as well as number of beneficiary species (Table 2).

Table 2. Sampling sites (as in Table 1) and the corresponding numbers of benefactor species and individuals, and the numbers of beneficiary species.

Sampling site	Number of beneficiary species	Number of benefactor species	Number of benefactor individuals
1	8	19	208
2	4	19	164
3	9	24	128
4	6	12	120

Roughly 75% of seedlings vegetating in open habitats such as wood pastures and abandoned fields and at the forest margins were associated with benefactor shrubs or saplings.

The bipartite, qualitative network of benefactor shrubs and saplings in one party and beneficiary seedlings in the other party (Figure 1) is characterized by high nestedness (Figure 2), lack of modularity and high betweenness centrality scores of several benefactor shrubs and most frequently recruited tree species (Figure 3). Keystone benefactors are *Crataegus monogyna, Prunus spinosa, Pyrus pyraster* (nurse)*, Rosa canina* and important beneficiaries are *Quercus petraea, Q. robur, Q. cerris, Fraxinus angustifolia*. Low betweenness centralization (table 3) suggest that the role of most influential nodes is played by several dominant beneficiary and benefactor species which can be considered foundation species (*sensu* Dayton 1972).

At the other end of the importance gradient are placed conspecifics acting occasionally as nurses under the harsh conditions of the open space of pastures or abandoned agricultural lands. High betweenness scores show the degree of connectedness of a node in a network (Freeman 1977; Martin Gonzáles et al. 2010) and highlight keystone species, those establishing transitional communities toward forests or stable, semi natural wood pastures. 39 species displayed BC scores greater than 0 meaning that they play the role of connectors in the network.

Niche overlap quantifying the share of nurse plants among seedlings of different species showed that there was a considerable and significant overlap (Table 3) matching the extended nestedness induced by the generalist benefactor shrubs.

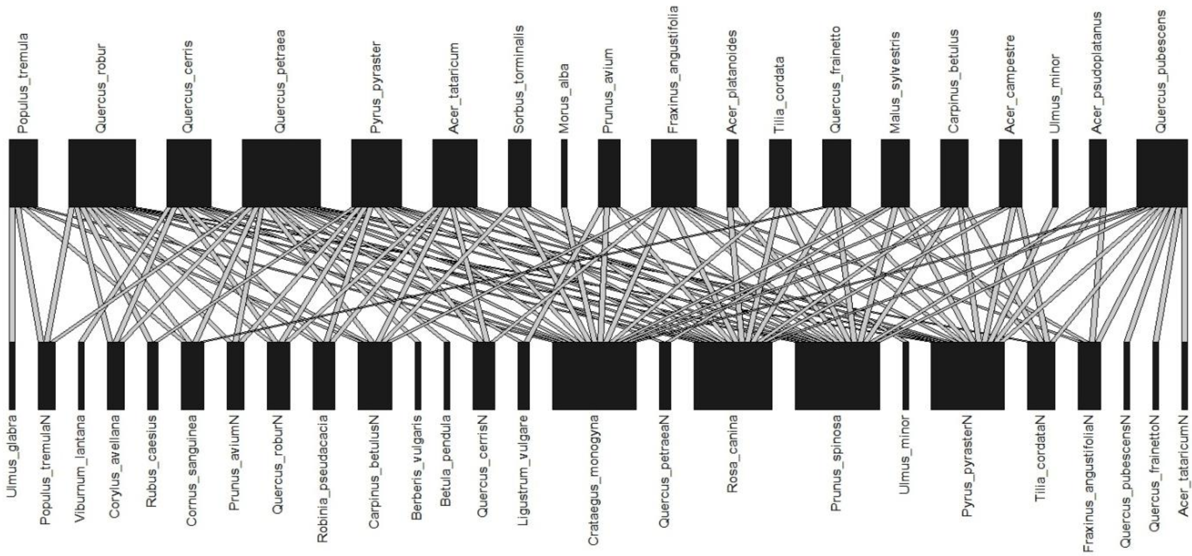

Figure 1. Facilitation bipartite network depicting the facilitation interaction of tree seedlings and benefactor species (shrubs and adult trees) established in wood pastures and forest edges.

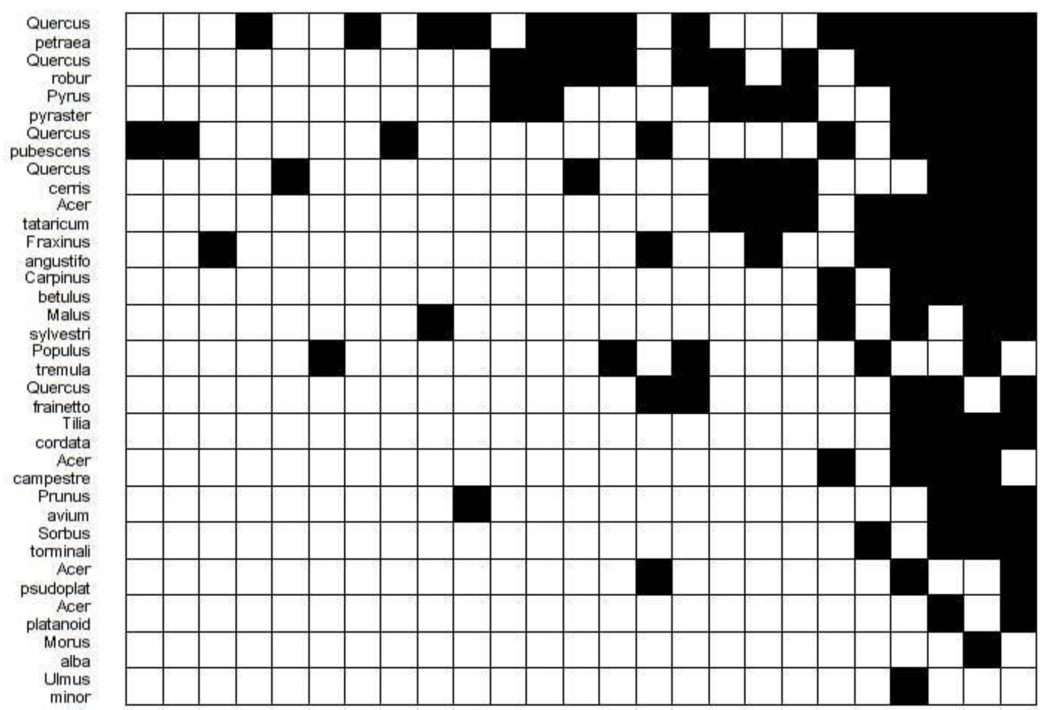

Figure 2. Re-ordered packed matrix illustrating high nestedness of the benefactor-beneficiary plants' facilitation matrix (nurse plants and tree seedlings in wood pastures and forest edges).

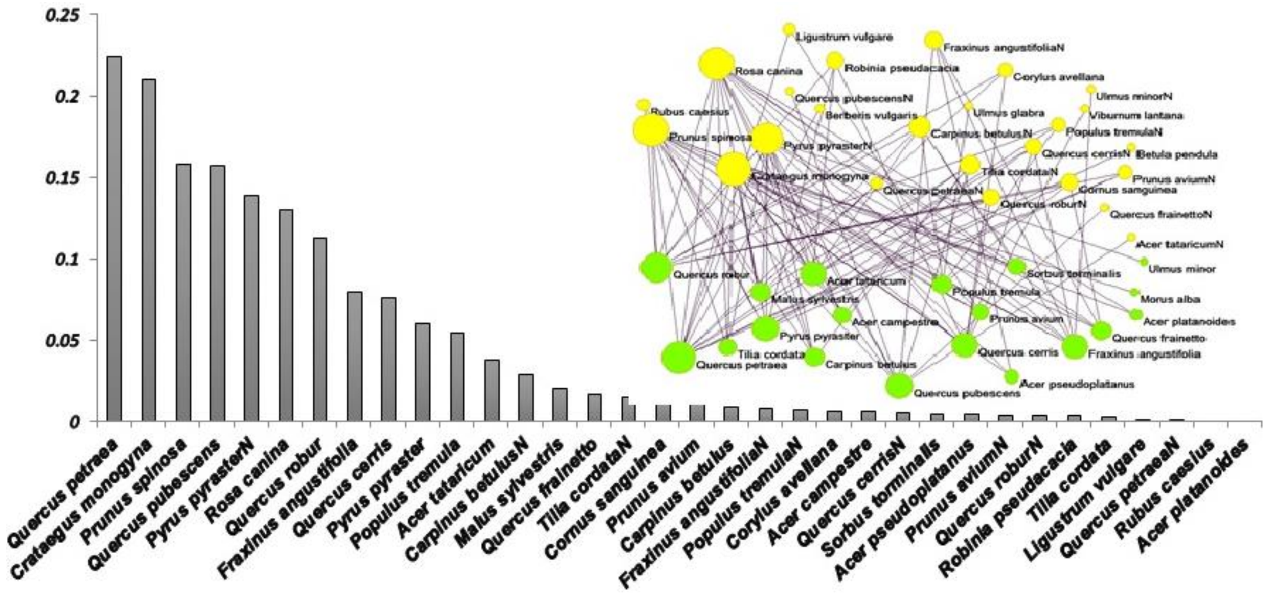

Figure 3. Species participating in the facilitation network ordered according to their betweenness centrality ranking. The network depicts the interacting species with dimension of nodes proportional to betweenness centrality ranking (green nodes – beneficiary seedlings, yellow nodes – benefactor species).

Table 3. Network metrics corresponding to merged data (benefactor and beneficiary species) from four sampling sites.

Metrics	Merged network
Connectance	0.233
nestedness	0.896***
Modularity(both algorithms)	NS
Number of links	111
Number of nodes	44 (25 nurse species)
Average degree	5.045
Niche overlap (Pianka index)	0.532*** (SES=22.96)
Betweenness centralization	0.192

***P<0.001

Modularity was not significant under both algorithms, taking values below the average calculated for Erdős-Renyi random networks. This is an intrinsic property of random graphs that can be differentiated from functional modularity of real world networks (Reichardt and Bornholdt 2006) as taking values below those calculated for observed networks. Same situation was reported for liana-phorophyte networks displaying high nestedness but no significant compartmentalization (Sfair et al. 2010). An alternative explanation for lack of modularity stays in the resolution limit which is set by the size of the network.

The analysis of benefactor species relative frequency in the four sampling sites (Figure 4) shows that most abundant species are also the most highly connected and influential (*Prunus spinosa, Crataegus monogyna, Rosa canina* and *Pyrus pyraster*). In terms of similarity (Figure 4), sampling sites 2 and 4 (located in North Western and Western Romania, at lower altitudes and warmer climate) have in common more species than sites located at higher altitudes (sites 1 and 3).

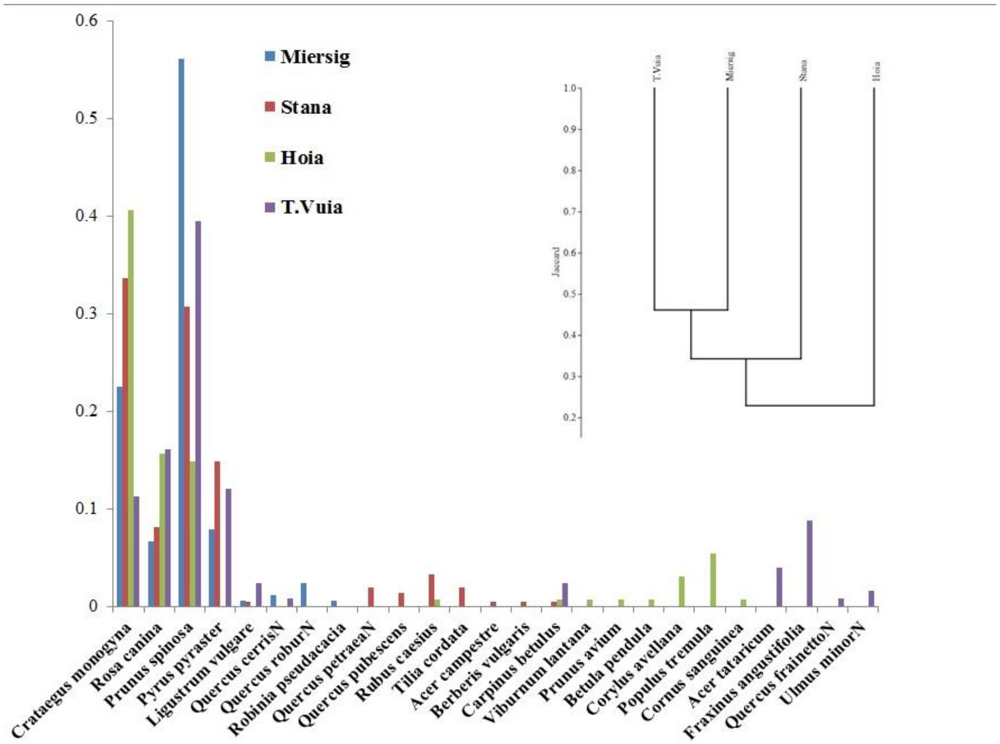

Figure 4. Relative frequency of benefactor species in four sampling sites and the dendrogram depicting similarities in terms of shared benefactor species (UPGMA algorithm, Jaccard similarity index) among the four sampling sites (North-Western and Western Romania).

Principal Component Analysis (supplemental information 2), results show that 43.01% of variance is accounted to PC1 and 33.65% to PC2. Distance and height display high level of correlation with PC1 (0.81 and 0.8) while orientation is highly correlated with PC2 (0.98). However, the pattern of dimensional variation, the distance from focal seedlings to nearest shrubs playing the role of benefactors and the orientation pattern vary among sampling sites (Figure 5 and Figure 6). Box plot representations (Figure 6) illustrate the skewness of data toward high values but median is varying within a narrow range: distances between 20 and 40 cm, seedlings/saplings' heights between 40 and 100 cm and benefactor plants' height between 40 and 130 cm. However, a trend toward Southern and South-Western orientations of shrubs with relation to seedlings is visible (Figure 5).

Multiple comparison among sampling sites in terms of dimensional variables, MANOVA results (supplemental information 2) have shown significant differences yet characterized by high amount of unexplained variance (Wilk's lambda = 0.788, $F_{(9,1507)}$= 17.21, p<0.0005; Pillai's trace = 0.022, $F_{(9, 1507)}$= 16.4, p<0.0005). Convex hulls depicting the variability space show high level of superimposition among locations, with smaller variability areas corresponding to sampling sites 3 and 4, apparently more similar.

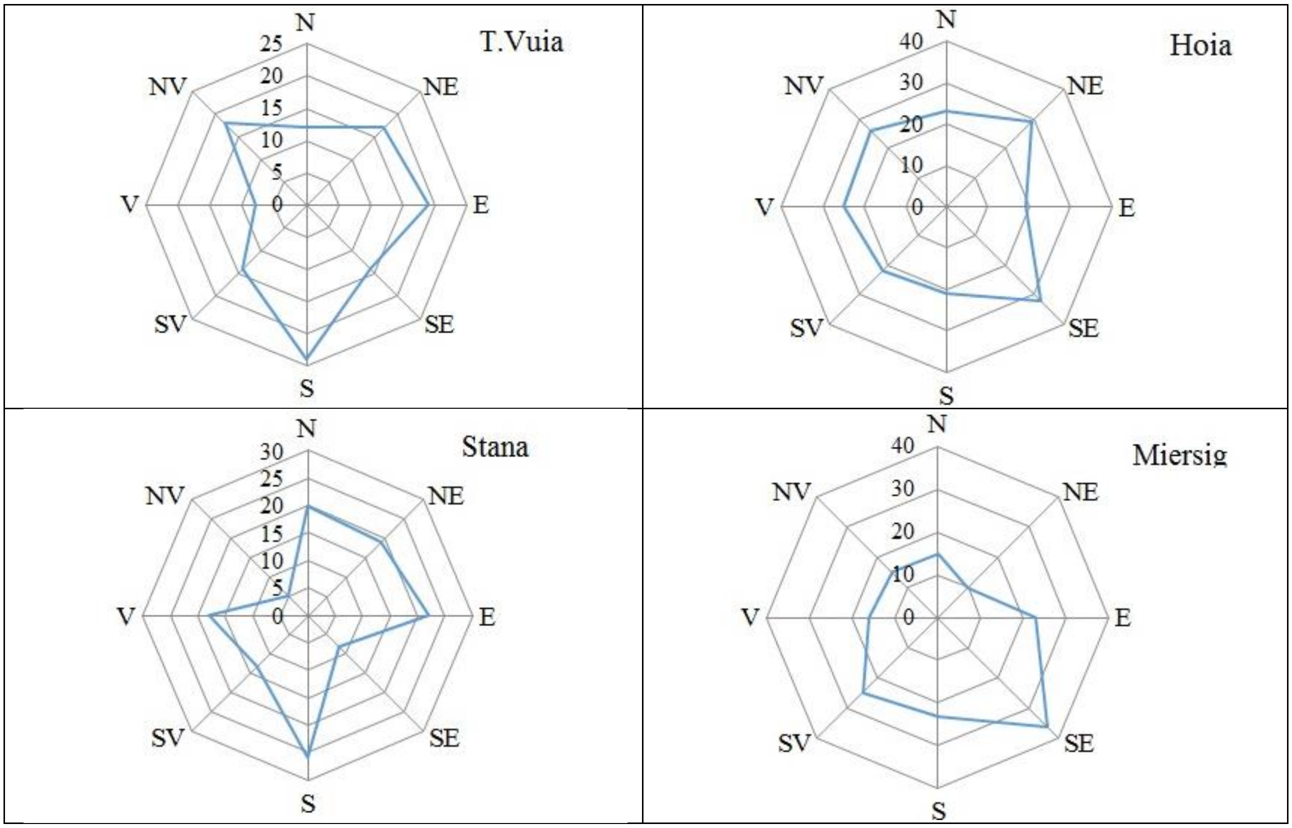

Figure 5. The orientation of benefactor plants (beneficiary seedlings in focus) (four sampling sites in North-Western and Western Romania).

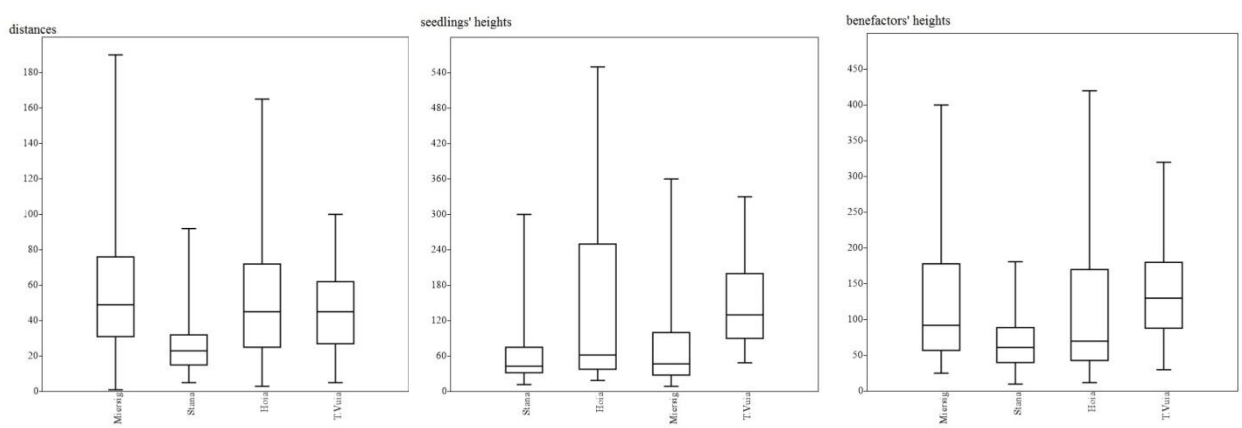

Figure 6. Box plot representations of distances among benefactor and beneficiary plants, heights of benefactor and beneficiary plants (four sampling sites in North-Western and Western Romania).

4 Discussion

Regeneration is one of the problems species must solve during its evolution adopting a regeneration strategy. For instance, frequently oaks fail to recruit due to poor acorn production, acorn predatorism, pests and pathogens (Shaw 1968). However, oaks rely on seedlings and sprouting for regeneration (Johnston et al. 2009).

Our preliminary results show that recruitment of *Quercus* spp. in open habitats is a frequent event and is assisted by benefactor thorny shrubs.

This fact is correlated with one characteristic feature of the regeneration niche for of the most frequently recruited *Quercus* species, light demands of *Q. petraea* and *Q. robur* are increasing at the transition from seedling to sapling stage and later (Annighöfer et al. 2015).

In this context, seedlings' survival in open grassland or wooded pastures is enhanced by facilitation interaction and the distance from parent trees with whom they can share pathogens and consumers, limiting their chances to survival in the light of Janzen-Connell Hypothesis (Janzen 1970; Connell 1971). Benefactor shrubs can be considered as foundation species for semi-natural ecosystems where secondary succession occurs reversing to forests as site specific and fundamental type of ecosystem.

Western and North-Western Romania harbor semi-natural traditional wood pastures and various types of open habitats (former agricultural fields, degraded meadows and pastures, forest edges) where thorny shrubs develop and serve as shelter for tree seedlings, establishing this way facilitation networks with specific topological properties.

Facilitation provides the background for trees' regeneration niche (Valiente-Banuet et al. 2006) under harsh conditions such as open field for shadow demanding seedlings and protection against grazing in overgrazed wood pastures. If in many reported examples nurse-beneficiary system is species specific (Puerta-Piñero et al. 2006; Valiente-Banuet and Verdu 2008), there are generalist benefactor shrubs, in our case, the most connected and also most frequent to different species of beneficiaries, *Prunus spinosa, Rosa canina* and *Crataegus monogyna,* sharing a common characteristic, the presence of thorns. The presence of woody plants in the investigated sampling sites, as parts of open landscapes was determined by dispersion which, in the case of nurse shrubs, previous studies have shown, was relying on frugivorous consumers (Herrera et al. 2011). Trees on the other hand are dispersed from adjacent forest stands by birds or small mammals (Kollmann 2000; Kollmann and Schill 1996). In several cases, we observed congeneric facilitation, even among conspecific individuals, a type of facilitation considered as being infrequent and determined by the share of the mycorrhizal symbionts (Dickie et al. 2002; Beltrán et al. 2012), low densities of benefactor individuals or modifications of the microenvironment (Dickie et al. 2005). The observed self-facilitation cannot be confounded with limited seed dispersal especially in the case of oaks since the inception of fruiting is linked with mature stage and in all sampling sites older trees are saplings.

The topological properties demonstrate that the assembly of the facilitation network is non-random (Valiente-Banuet et al. 2014) with several keystone, generalist benefactor species, mainly thorny shrubs. Important characteristics of the described facilitation network are high nestedness and lack of modularity.

High nestedness displayed by merged network combined with lack of modularity conform to the properties of similar networks described in the literature (Marcilio-Silva et al. 2015). High nestedness reported for other facilitation plant-plant interactions (Valiente-Banuet and Verdu 2008) is similar with other types of facilitative and mutualistic networks such as pollinators' networks or seed dispersal networks (Donatti et al. 2011) being a topological characteristic responsible for extinction prevention (Memmott et al. 2004; Verdu and Valiente-Banuet 2008). Apparently, high connectance determines high nestedness but is negatively correlated with compartmentalization (Fortuna et al. 2010) a feature characterizing the networks analyzed in the present paper. The higher connectance of bipartite networks (Poisot and Gravel 2014) is no doubt, an important feature partly dictated by innate constraints, the lack of links among the nodes of the same set; this type of constraint is lacking in food webs which are unipartite and display low connectance. Nestedness is an important topological feature since it reflects functional redundancy which increases the stability of the system in the case of disappearance of some interactions (Bascompte and Jordano 2007; Rumeu et al. 2018) However, it is still under debate whether nestedness is a consequence or a causative agent of structural characteristics of communities (Valverde et al. 2017).

As a general observation, network properties depend on interaction type (Thébault and Fontaine 2010). Important for network properties, modularity was not found to characterize the seedlings-benefactor plants network, a fact consistent with previous observations on facilitation networks (Sfair et al. 2010).

The use of centrality metrics (betweenness centrality) facilitated the identification of keystone or foundation species which functioned as connectors within the network: most important beneficiary species which were late successional trees (*Quercus* spp.) and keystone nurse shrubs. Highest ranking species in wood pastures and thorny shrubs thickets (*Crataegus monogyna, Prunus spinosa*, *Rosa canina*) displayed highest betweenness centrality scores, showing that most of the recruited tree species were taking benefit of those. Apparently, *Quercus* spp. have higher advantage in surviving in open spaces with the help of nurse plants compared to other species such as *Fagus sylvatica* (Kunstler et al. 2011) an observation supported by high betweenness centrality scores. Other species taking advantage of thorny shrubs are pioneer tree seedlings (*Populus tremula*) or characteristic, light demanding species from wood pastures and forest edges such as *Malus sylvestris* and *Pyrus pyraster*. *Fraxinus angustifolia*, an intermediate species in ecological successions, presented high scores in terms of frequency and BC. It seems that ash regeneration in open habitats is facilitated by benefactor plants providing shade for seedlings and juveniles. These stages which tolerate shading evolve later toward light demanding (Garbarino and Bergmeier 2014), probably changing the status from facilitated to competitor.

The cohesion of the seedlings-benefactor plants facilitation network is provided by the connector species characterized by highest BC scores. Extraction from a network of the most influential nodes (thorny shrubs in our case) may compromise tree recruitment in open habitats.

Multivariate analysis have shown that there is a common pattern in the distribution of distances among seedlings and benefactor plants, the heights and orientation of benefactors.

Our preliminary results (the study needs to be extended to capture the diversity of open habitats with woody vegetation in Romania) stress the importance of facilitation interactions from with some practical consequences for the management of semi-natural and natural ecosystems in the future. Major climatic changes occurring during the last decades in Transylvania (Rusu et al. 2014) will increase the pressure on tree regeneration and lower the chances for successful reforestations, likewise facilitation included in management plans would make a good alternative for classical approaches.

Best choice in artificial regeneration would be the use of most connected, with most strategic positions within the network nurse plants, with best performance in terms of protection of the largest number of seedlings: *Crataegus monogyna, Prunus spinosa, Rosa canina, Pyrus pyraster.*

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