

Nurse plants promote taxonomic and functional diversity in an arid Mediterranean annual plant community

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Abstract

Aims: Research in the last decades supports the idea that certain species, namely 'nurse species', can enhance ecosystem function and species diversity in their vicinity through amelioration of the abiotic environment. However, few studies have explored whether nurse plants can promote functional diversity at the microhabitat level. Here, we evaluated the hypothesis that nurse plants can increase functional diversity in the beneficiary annual plant assemblage at the microhabitat level.

Location: Sayeret Shaked Park, the Negev desert (Israel).

Results: The nurse species examined, two shrubs and one large annual, had a negligible or even negative influence on annual above-ground biomass production. Nonetheless, they increased functional diversity in terms of specific leaf area (SLA), maximum plant height (MPH), seed weight (SW), and reproductive ratio (RR) at the microhabitat level.

Conclusions: These findings reinforce the idea that, even if there is not a typical nurse syndrome related to enhanced plant performance, nurse plants might induce a portfolio effect on annual plant assemblages by promoting functional diversity in key functional traits associated to plant survival and reproduction under a set of different microhabitat conditions.

KEYWORDS

annual plant community assemblage, functional diversity, functional portfolio, maximum plant height, plant nurse syndrome, reproductive ratio, seed mass, specific leaf area

1 | INTRODUCTION

Extensive empirical evidence yielded over the last three decades supports the role of nurse plants in arid and semi-arid ecosystems (Filazzola and Lortie, 2014). Nurse shrubs in particular can enhance fitness and productivity in their vicinity through direct and indirect interactions (Segoli et al., 2012) but also local diversity by altering the spatial dynamics of annual plant species (Davies et al., 2007; Soliveres et al., 2012). However, it is still poorly understood whether the

presence of more species under the influence of shrub nurses is indicative of increased functional diversity at the scale of shrub understories. The majority of studies dealing with the influence of nurse plants on beneficiary plant species diversity at the community level usually consider a whole-community scale, pooling species from the different microhabitats up to a local scale. Unveiling this uncertainty may greatly improve our ability to assess vulnerabilities under changing conditions and the potential set of strategies able to adapt and restore ecosystem functions and services in drylands by using shrub nurses.

The nurse plant syndrome, in which adult plants of one species facilitate the establishment of seedlings of another species, has largely been explored at the individual plant level, where performance and fitness of a focal plant species is monitored outside of and under the influence of the nurse plant (Franco and Nobel, 1988). Evaluation of the nurse syndrome at the community level, including direct and indirect interactions among beneficiary species, is much more complex, often leading to contradictory results (Schöb et al., 2013). For instance, while some shrub species ameliorate the physical environment beneath their canopies, others do not, or their effect depends upon the spatial/temporal distribution of resources and conditions (O'Brien et al., 2017). In some cases, the nurse syndrome of a species can be hindered by the resource availability or the environment constraints. Weedon and Facelli (2008) showed how desert shrubs in Australia excluded most annual plants beneath their canopies due to exacerbated water potentials associated with the accumulation of salt on the ground surface. Deep shading also reduces diversity and productivity beneath mature desert shrubs (Forseth et al., 2001), and this effect is contingent on the ontogenetic development of the potential nurse plant (Miriti, 2006). Accordingly, some studies suggest that productivity and diversity under the shrub canopy can be species-specific (Callaway, 1998; Blank and Carmel, 2012) and context-dependent (but see Butterfield and Callaway, 2013). Identification and characterization of potential nurse species able to increase plant performance and functional diversity in beneficiary plant assemblages is therefore critical to evaluate their role as community stabilizers under changing climatic conditions.

The nurse plant syndrome has seldom been explored among functionally similar taxa such as annual–annual plants interactions. This is in part justified by the fact that a positive balance of interaction between two given organisms is commonly assumed to be linked to high functional dissimilarity and thus low niche overlap. Interestingly, previous research in grasslands revealed a particular way by which dead grasses can facilitate seedling survival and recruitment of shrub species (Resco de Dios et al., 2014). This unexplored modality of facilitation might also lead standing dead individuals of an annual species to facilitate others and thus an annual plant could act as a nurse species for other annuals. Although this hypothesis has not been tested before in annual plant assemblages, this could represent an important advance in the knowledge of how positive interactions control diversity maintenance in water-limited environments.

Here, we evaluated the potential role of two shrubs and a large annual plant as nurse species in the annual plant community of a semi-arid Mediterranean region. More specifically, we measured diversity (taxonomic and functional diversity) and productivity (total above-ground biomass) in annual plant assemblages within and outside the influence of the shrubs *Noaea mucronata* (Chenopodiaceae) and *Thymelaea hirsuta* (Thymelaeaceae) and the large annual plant *Carthamus tenuis* (Asteraceae). We hypothesized that these species might affect positively both productivity and diversity of the annual plant community, but through likely

different nurse syndromes. We argue that the nurse syndrome at the community level should be species-specific according to the key role of niche differentiation as a critical process underlying plant–plant interactions (Tilman et al., 2001). Following this idea, we tested the hypothesis that, even though perennial species should be more effective nurses for the annual plant community (in terms of taxonomic and functional diversity) due to a smaller niche overlap among the perennial benefactor and the beneficiary annual species, dead individuals of the large annual *Carthamus tenuis* could also facilitate annual plants diversity, as observed previously in grasslands (Resco de Dios et al., 2014). To this end, we evaluated if the intensity of facilitation is related to the life-form of the nurse plants (annual vs. perennial), and to what extent potential nurse species increase taxonomic and functional diversity in their vicinity. We also analysed the influence of the three above-mentioned nurse species on mean and variability of key functional traits in herb species in dry areas. Specifically, we tested how these nurse species affect the specific leaf area (SLA), maximum plant height (MPH), seed weight (SW) and reproductive ratio (RR) of the associated annual plant assemblies.

2 | MATERIALS AND METHODS

2.1 | Study area

The fieldwork was carried out in Sayeret Shaked Park (Israel; Appendix S1a), in the northern region of the Negev desert (31°17'N, 34°37'E) between the months of March and May 2017. Specifically, the study was conducted in a fenced area of 60 ha, with altitude ranging 75–150 m above sea level (Offer et al., 1998), where grazing has been prevented since 1987 (Boeken and Shachak, 1994). The climate is Mediterranean arid, with an average annual precipitation of 200 mm mostly distributed between November and March. The average minimum temperature in winter is around 6–8°C, while the average maximum temperature in summer is between 32 and 34°C (Stern et al., 1986). The soil consists of loess, composed of 14% clay, 27% silt and 59% sand (Teomin, 1990). Soil surface is covered by a hard biological crust formed by cyanobacteria, bacteria, algae, mosses and lichens (Zaady and Shachak, 1994). The vegetation is a spring flowering annual plant community emerging after the first rains in late autumn (Appendix S1b), where the most abundant species in terms of biomass are *Stipa capensis* (Poaceae) and *Carthamus tenuis* (Asteraceae; Appendix S1c), and sparse shrubs with high dominance of *Thymelaea hirsuta* (Thymelaeaceae; Appendix S1d) and *Noaea mucronata* (Chenopodiaceae; Appendix S1e).

2.2 | Sampling of the annual plant community

We sampled abundance (number of individuals) and biomass production (total above-ground biomass) of each annual plant species in 40 quadrats of 20 cm × 20 cm beneath the canopy of each potential



nurse *Noaea*, *Thymelaea* and *Carthamus*, and in open areas (i.e. 4 microhabitats \times 40 plots = 160 quadrats in total). Species accumulation curves showed that we captured above 90% of species present beneath each nurse species with a confidence interval of 95%, except for bare zones where we captured 80% of species. We measured height and diameter of each nurse plant and solar radiation at soil level with a radiometer (LI-189, LI-COR Inc. Lincoln, NE, USA) in each quadrat (Figure 1).

2.3 | Functional trait measures

Species functional traits were measured for the ten most abundant annual species, i.e. *Stipa capensis*, *Avena barbata*, *Onobrychis crista-galli*, *Anthemis pseudocotula*, *Leontodon laciniatus*, *Crepis aspera*, *Reboudia pinnata*, *Aegilops kotschy*, *Urospermum picroides* and *Sonchus oleraceus*. These species represent 93% of the total abundance and 96% of the total biomass of the annual plant community. Measures of functional traits were based on at least 10 individuals per species, randomly collected from the study area, near the sampled quadrats. We measured four functional traits per species, i.e. MPH, SLA, SW and RR, following the protocols in Cornelissen et al. (2003). Maximum plant height is a good indicator of competitiveness for light and fecundity (Cornelissen et al., 2003). Specific leaf area represents the leaf spectrum economy, namely, low values reveal species with slow resource processing, and tend to occur when environmental conditions are more stressful (Díaz et al., 2004; Wright et al., 2004). The seed weight is related to the probability of a species to successfully disperse and the ability of a seedling to survive under adverse situations (Mark, 1998; Cornelissen et al., 2003). The reproductive ratio (dry biomass of reproductive structures/dry biomass of vegetative aerial structures) informs us about the resource allocation in species. We measured the reproductive ratio after the formation of the first seeds.

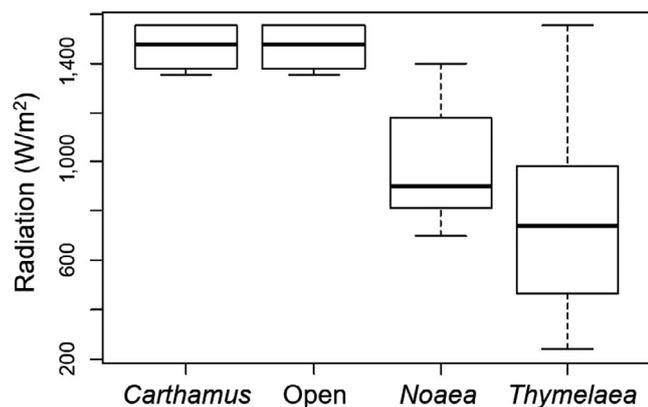


FIGURE 1 Solar radiation at the soil surface level for each of the four microenvironments studied (*Carthamus tenuis*, *Thymelaea hirsuta*, *Noaea mucronata* and open areas). Boxes correspond to the 25th and 75th percentiles; lines inside the boxes show the median; error bars show the minima and maxima

2.4 | Taxonomic and functional diversity of annual plant assemblages

The taxonomic diversity in quadrats was assessed by Simpson's inverse index from plants-per-species counts. We calculated the Community Weighted Mean (CWM) and Rao indices for each functional trait in each quadrat. The CWM shows the weighted average value of a trait in a community. Different studies assume that the CWM reflects the locally "optimal" strategy, that is, species with trait values closer to the CWM will have greater fitness (Muscarella and Uriarte, 2016). The Rao index is an index of functional diversity based on the quadratic entropy of Rao (1982) that takes into account both the relative abundance of species and a measure of the functional differences between species (Botta-Dukát, 2005). High values of Rao's quadratic entropy mean that the species in the assembly have more different values for that specific trait, while low values mean greater similarity of the trait among the species that conform the assembly. We used the "dbFD" function of the "FD" package (Laliberté and Legendre, 2010; Laliberté et al., 2014) in R (R Core Team, 2017).

2.5 | Statistical analyses

We tested for correlations among the explaining variables measured. Since diameter of nurse plants was negatively correlated with solar irradiation reaching the soil beneath each nurse plant ($r = -0.50$; $p < 0.001$), we only considered radiation and microenvironment (three nurse species and open areas) as the explanatory variables in all statistical analyses. We performed Generalized Linear Models (GLM) to evaluate differences in species richness, diversity (inverse of Simpson) and total biomass, and in the CWM and Rao values for each trait per quadrat. Pairwise t tests with Holm's corrections were performed in order to assess differences between microenvironments in pairs.

We constructed PERMANOVA models (Permutational Multivariate Analysis of Variance) to evaluate changes in species composition both in terms of species abundances and biomass in the four microenvironments (three nurse species and open areas), with solar radiation as a covariate (Anderson, 2014). Following McCune and Grace (2002) we removed the species that appeared in less than 5% of the quadrats in order to avoid the disproportionately large influence of rare species on ordination analyses and then the composition matrix was square root-transformed to reduce the weighting of dominant species. We used dissimilarity matrices based on the Bray-Curtis distance (Legendre and Legendre, 1998) and type III sums of squares. The significance of each model was tested using a Monte-Carlo test with 9,999 permutations. We used the "adonis" function (Anderson, 2001) of the "vegan" package (Oksanen et al., 2017). Ordination biplots for the abundance and biomass matrices were represented by means of NMDS (non-metric multidimensional scaling) using the "metaMDS" function of "vegan" (Oksanen et al., 2017) in R version 3.2.

	Distribution	Link	Microenvironment			Radiation		
			ChiSq	df	P	ChiSq	df	P
Richness	Poisson	Log	79.91	3	<0.001	0.13	1	0.714
Diversity	Gamma	Inv.	115.04	3	<0.001	1.32	1	0.251
Total biomass	Gaussian	Id.	49.13	3	<0.001	1.08	1	0.300
CWM SLA	Gaussian	Id.	131.57	3	<0.001	7.74	1	0.005
Rao SLA	Gaussian	Id.	30.05	3	<0.001	0.10	1	0.758
CWM MPH	Gaussian	Id.	31.12	3	<0.001	1.42	1	0.234
Rao MPH	Gaussian	Id.	29.21	3	<0.001	0.45	1	0.500
CWM SW	Gaussian	Id.	5.06	3	0.167	0.36	1	0.549
Rao SW	Gaussian	Id.	12.46	3	0.006	0.07	1	0.785
CWM RR	Gaussian	Id.	138.66	3	<0.001	4.72	1	0.030
Rao RR	Gaussian	Id.	25.62	3	<0.001	1.00	1	0.318

Note: Link functions: Log: logarithmic, inv.: inverse Gaussian, Id.: identity.

Abbreviations: MPH, Maximum plant height; RR, reproductive ratio; SLA, specific leaf area; SW, seed weight.

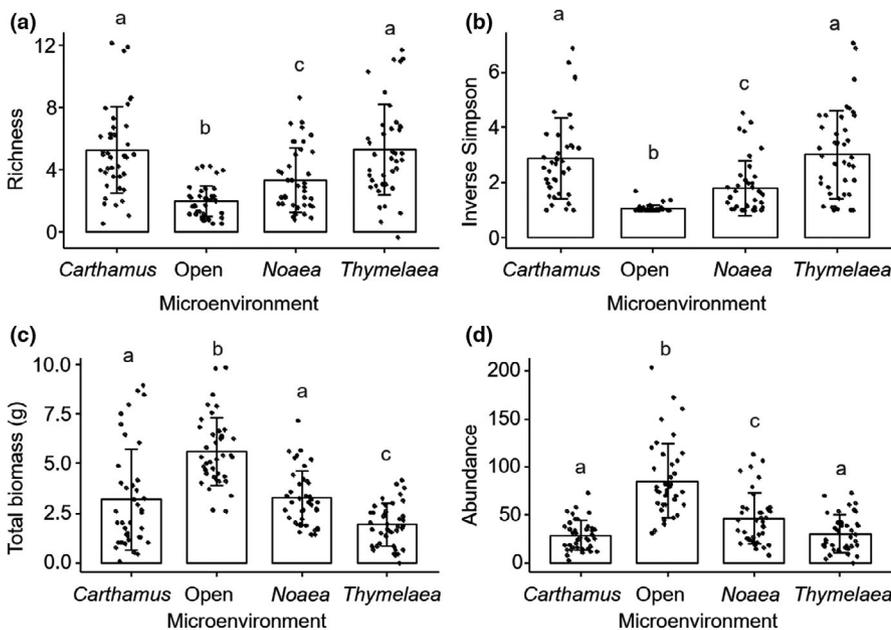


TABLE 1 Results of the Generalized Linear Models (GLM) used to evaluate the effect of the four microenvironments (i.e. open area and the three nurse species *Noaea*, *Thymelaea*, *Carthamus*) and the effect of the incidence of solar radiation at the soil surface on eleven dependent variables of the annual plant communities

FIGURE 2 Mean values (\pm SD) for species richness, inverse Simpson, total biomass and abundance in each microenvironment (*Carthamus tenuis*, *Thymelaea hirsuta*, *Noaea mucronata* and open areas). Different lowercase letter indicate significant differences between microenvironments (post-hoc). Dots represent the observed values and vertical bars standard errors

3 | RESULTS

We identified 30 annual plant species (including *Carthamus tenuis*) distributed through the four microenvironments: 11 species in open areas, 19 beneath *Noaea*, 24 beneath *Thymelaea*, and 28 in *Carthamus* patches (2.0 ± 1.0 species/quadrat, 3.4 ± 2.1 species/quadrat, 5.6 ± 2.9 species/quadrat, and 5.9 ± 2.7 species/quadrat, respectively). Some species like *Aegilops kotschy*, *Brachypodium distachyon*, *Crucianella herbacea* and *Senecio glaucus* appeared associated to either of the three focal species (*Noaea*, *Thymelaea* and *Carthamus*) but never in open areas. Importantly, annual plant assemblies under the three focal species had greater richness and taxonomic diversity than in open areas (Table 1; Figure 2a, b). Therefore, the three focal species can be considered as nurse plants. However, in terms of above-ground biomass, the highest biomass yields occurred in the open space, outside

the nurse canopies (Table 1; Figure 2c). Species composition, both in terms of species biomass and abundances, significantly varied across the microenvironments (Table 2 and Figure 3). Our data showed that *Stipa capensis* was the dominant species in open areas, while under the nurse species, *Crepis aspera*, *Leontodon laciniatus*, *Avena barbata*, *Onobrychis crista-galli* or *Anthemis pseudocotula* occurred more frequently. Interestingly, some plant species such as *Aegilops kotschy* were characteristic of the *Carthamus* patches (Figure 3).

3.1 | Traits at the community level

The species that assembled under the canopy of *Thymelaea* and *Carthamus* had greater SLA values than species under *Noaea*, particularly when compared to those in open areas (Table 1; Figure 4a).

TABLE 2 PERMANOVA analyses to test the species composition of annual plant assemblages in terms of microenvironment (i.e. *Noaea*, *Thymelaea*, *Carthamus* and open areas) and solar radiation

	<i>df</i>	SS	MS	<i>F</i>	<i>R</i> ²	<i>p</i>
Abundance						
Microenvironment	3	8.48	2.83	18.03	0.26	0.0001
Radiation	1	0.19	0.19	1.21	0.01	0.2763
Residuals	155	24.31	0.16		0.73	
Total	159	33.53			1.00	
Biomass						
Microenvironment	3	9.03	3.01	18.24	0.26	0.0001
Radiation	1	0.26	0.26	1.55	0.01	0.1538
Residuals	155	25.57	0.16		0.72	
Total	159	36.27			1.00	

Abbreviations: *df*, degrees of freedom; SS, sum of squares; *F*, *F*-ratio; MS, mean sums; *p*, *p*-value; *R*², proportion of variation explained.

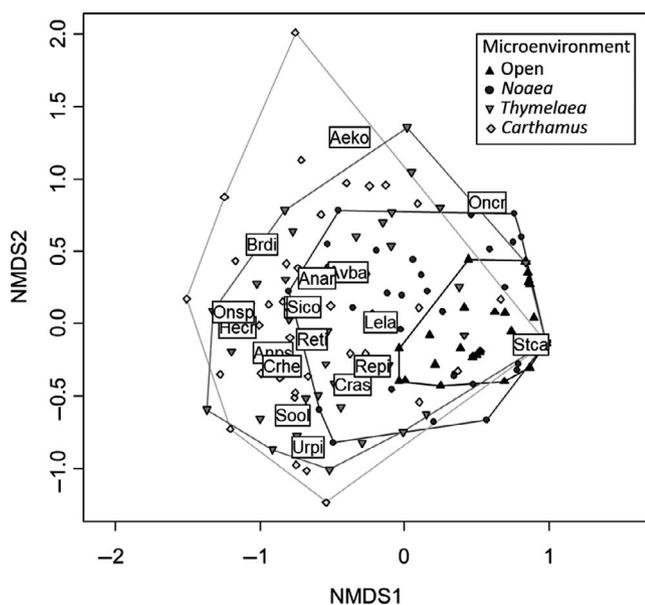


FIGURE 3 Non-metric multidimensional scaling (NMDS) ordination based on the species compositions in quadrats. Stress value for the ordination was 0.221. Species abbreviations: *Aeko*: *Aegilops kotschy*; *Anar*: *Anagallis arvensis*; *Anps*: *Anthemis pseudocotula*; *Avba*: *Avena barbata*; *Brdj*: *Brachypodium distachyon*; *Cras*: *Crepis aspera*; *Crhe*: *Crucianella herbacea*; *Hecr*: *Hedypnois cretica*; *Lela*: *Leontodon laciniatus*; *Oncr*: *Onobrychis crista-galli*; *Onsp*: *Ononis* sp.; *Repi*: *Reboudia pinnata*; *Reti*: *Reichardia tingitana*; *Sico*: *Silene colorata*; *Sool*: *Sonchus oleraceus*; *Stca*: *Stipa capensis*; *Urpi*: *Urospermum picroides*

Furthermore, functional diversity in terms of SLA was also greater beneath nurses than in open areas (Figure 4b), denoting a beneficiary effect of the shrubs favouring coexistence of species with a wider range of SLA values. The species growing in open areas and beneath *Noaea* had smaller and more similar MPH than the species growing beneath *Carthamus* and *Thymelaea* (Figure 4c, d). Mean SW of the species assemblages were not significantly different among the four microenvironments (Table 1; Figure 4e). Species established in open areas and beneath *Noaea* invested more in reproduction,

as denoted by higher RR values, while beneath *Carthamus* and *Thymelaea* species tended to allocate more resources to vegetative parts (Figure 4g). Indeed, species forming the annual plant community beneath the three nurses, showed higher variability of RR than those in open areas (Figure 4h).

4 | DISCUSSION

Our results partially support a nurse syndrome for the shrubs *Noaea* and *Thymelaea* and the large annual *Carthamus*. Even though taxonomic and functional diversity of the annual communities assembled beneath nurses was higher compared to that in open areas, total biomass was drastically reduced. Similar results have been reported in other semi-arid ecosystems for the effect of perennial-herb interaction on biomass production (Forseth et al., 2001; Weedon and Facelli, 2008; Madrigal-González et al., 2016). However, other studies supported a typical nurse syndrome following a classical fertility island model (Flores and Jurado, 2003). These studies observed that shrubs ameliorated the physical environment beneath them (Moro et al., 1997), and thus, increased biomass production and species diversity (Holzapfel and Mahall, 1999; Holzapfel et al., 2006; Luzuriaga et al., 2012, 2015; Espinosa et al., 2014; Lortie et al., 2018).

In our study system, open areas usually have a hard and continuous cyanobacterial crust on the soil surface (Zaady and Shachak, 1994), while beneath shrubs and *Carthamus* soil surface is covered with a mound of loose litter (Boeken and Shachak, 1994). These microenvironmental characteristics usually affect water distribution on the soil surface, water infiltration, and secondary dispersion of seeds (Boeken and Orenstein, 2001). Thus, the hard soil crust may avoid most seeds entering into the soil seed bank (Peralta et al., 2016), being swept along from open areas to vegetation patches, which act as seed traps. Distribution of seeds in the soil may favour the presence of higher species richness beneath *Carthamus* and the shrubs *Noaea* and *Thymelaea*, but only in case environmental conditions are beneficial for seed germination (Sánchez et al., 2014) and seedling establishment (Luzuriaga and Escudero, 2008), will they add to the

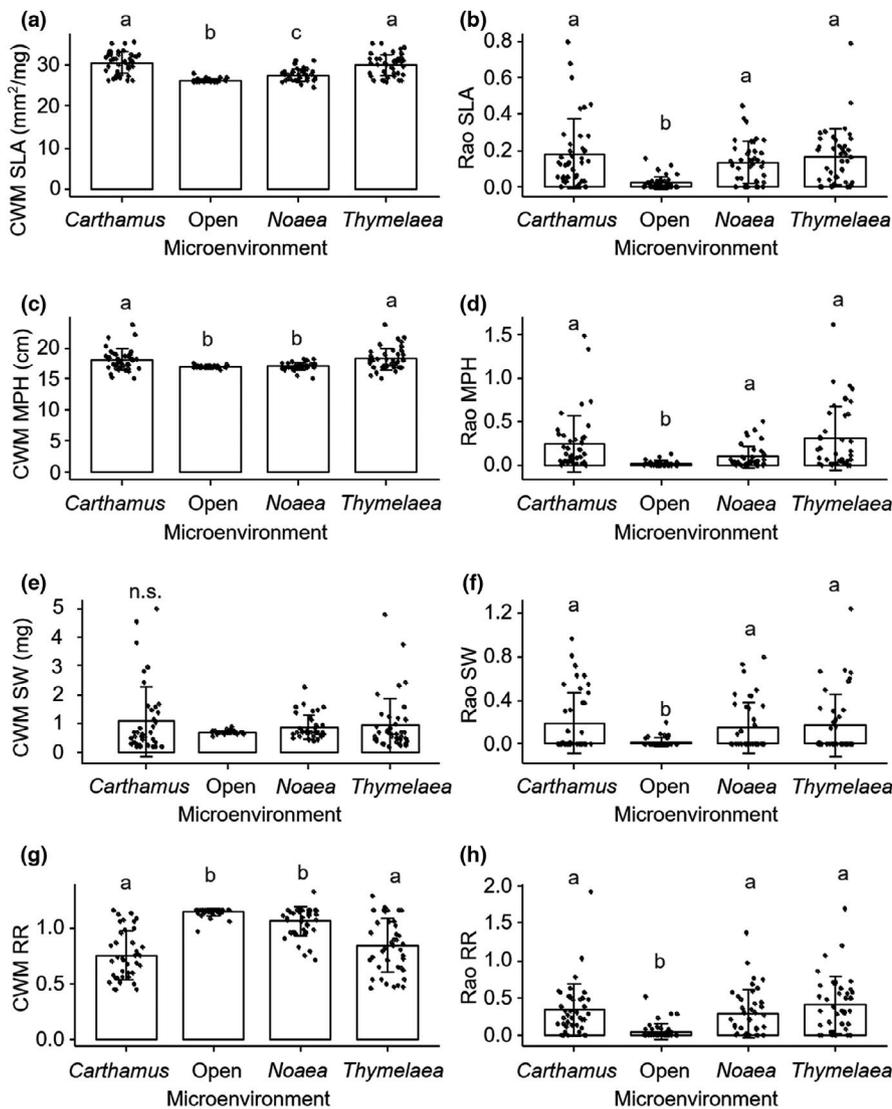


FIGURE 4 Mean values (\pm SD) for Community Weighted Means (CWMs) in the left panels and functional diversity indices (Rao) in the right panels for the significant terms shown in Table 1. SLA: specific leaf area, MPH: maximum plant height, SW: seed weight, RR: reproductive ratio. Different lowercase letters indicate significant differences between microenvironments (post-hoc). Dots represent the observed values and vertical bars standard errors.

realized annual plant assembly. The high production of litter beneath *Carthamus* and both shrubs may improve the water and soil nutrient balance during early seedling stages, thus promoting the higher taxonomic and functional diversity beneath the three nurses.

Shade plays a key role in driving shrub–herb interactions in semi-arid and arid environments (Seifan et al., 2010; García-Camacho et al., 2017). In our study, clear differences in solar radiation beneath and outside *Noaea* and *Thymelaea* canopies indicate that shade is a plausible limiting factor for biomass production in this semi-arid annual plant assembly (see Figure 1). Deep shade is one of the most important limiting factors of plant establishment and growth in dry environments (Forseth et al., 2001). However, studies conducted in arid environments have unveiled a trade-off between water availability and shade beneath nurse plants which determines the intensity of nurse facilitation (Huston and Smith, 1987; Holmgren, 2000). Furthermore, facilitation is common when nurse shrubs can actively take up water from deep soil layers and passively transport and release it into shallow layers (hydraulic lift, Richards and Caldwell, 1987; Prieto et al., 2011), thus making it available for plants under their canopy. In the absence of hydraulic lift, shade beneath nurse

plants can modify the carbon/water balance, reducing the risk of dehydration at the cost of affecting biomass production of understorey plants, compared to open areas. Interestingly, although solar radiation beneath *Carthamus* was similar to that in open areas, we found that plant biomass of the annual assembly growing beneath it was lower than the biomass in open habitats. This implies that not only shading but also strong below-ground competition for water and nutrients between *Carthamus* and the other annual plants may lead to a similar outcome regarding biomass production.

We may attribute the high number of species and functional diversity under the influence of nurse species to the suitable microhabitats created beneath them that facilitate the establishment of annual species, or even because nurse species can exert diffuse influences on the annual plant–plant interactions (Callaway and Pennings, 2000). For instance, nurse plants may protect annuals from the effects of the highly competitive grass *Stipa capensis* (Kadmon and Shmida, 1990; Boeken, 2018), which largely dominates open areas. In addition, biological crusts are known to exert species-specific effects on seed germination (Escudero et al., 2007; Hernandez and Sandquist, 2011) and seedling survival (Serpe et al.,



2008; Langhans et al., 2009; Mendoza-Aguilar et al., 2014). It is also important to note that our results are indicative of conditions during a period of one year only and so potential shifts might occur depending on temporal climatic variability (Tielborger and Kadmon, 2000; O'Brien et al., 2017).

In open areas, the dominant annual species were short species with low SLA values and high reproductive ratios, which indicate more efficient water use (Karlsson and Méndez, 2005; Huxman et al., 2013; Eskelinen and Harrison, 2015). Similar results were found also for the shrub *Noaea*. On the contrary, taller species with high values of SLA, that indicate high growth rates (Reich et al., 1997; Wright et al., 2004; Freschet et al., 2010; Gibert et al., 2016), were more common beneath two of the nurses, namely *Carthamus* and *Thymelaea*. These results agree with those of Peralta et al. (2019) that found that in extremely dry conditions short species with low SLA values are assembled. Therefore, our results provide sound evidence that nurse species relax the environmental filter that selects for the annual plant species constituting the final assemblages. We demonstrated that in open areas environmental filters operate via functionally driven mechanisms (assembly rules sensu Götzenberger et al., 2012), thus inducing shifts in the CWMs of certain functional traits and reducing the functional diversity associated with these traits (Bernard-Verdier et al., 2012). Both shrub species and *Carthamus* favoured the establishment of species with different values of SLA and RR (i.e. high Rao values). This denotes that the milder microenvironmental conditions beneath nurse plants allow for the establishment of a broader range of strategies dealing with the leaf economics spectrum (SLA) and with the investment in reproductive structures (RR). Therefore, we provide evidence that the nurse effect may result in the expansion of species' spatial niches (Espinosa et al., 2014; Luzuriaga et al., 2015). Furthermore, the functional perspective also supports the role of *Carthamus* as a nurse plant for other annual species. *Carthamus* favoured the establishment of species with broader ranges of functional trait values in a similar way as *Thymelaea* and with higher intensity than *Noaea* in some cases. Our results suggest that dead individuals of *Carthamus* and accumulated litter from previous years might improve microenvironmental conditions inside the patch, and thus favour germination and establishment of annual species. Previous findings in this line support the idea that dead neighbours can facilitate passively other late-successional species in a savanna-like ecosystem of North America (Resco de Dios et al., 2014).

The increased nurse-induced functional diversity on beneficiary annual plant assemblages can have implications in terms of a portfolio effect. Experimental evidence in grasslands supports this idea, posing that diverse assemblages maintain productivity within more stable margins than monocultures (Tilman et al., 2006). The scope of our study, nonetheless, is far from providing evidence of annual plant community stability in this arid environment. Rather, the fact that nurse plants increase taxonomic and functional diversity suggests a potential portfolio effect in the long run. In particular, increased aridity due to the ongoing warming conditions might push many species to local extinction or severe constraints, which might

determine the impoverishment in terms of community productivity but also in the set of functional strategies able to cope with the new conditions. If this occurs in the future, we expect that the impact on community functioning beneath the nurse plants could be less drastic than in open areas. For this reason, even if the nurse plants studied do not portray a typical nurse syndrome based on above-ground biomass production, they play a decisive role in preserving diversity and probably ecosystem functioning through facilitation of taxonomic and functional diversity.

AUTHOR CONTRIBUTIONS

JMG, AL and PF conceived the main ideas. CCB and JK designed and conducted field sampling. JMG led the writing of the manuscript. All co-authors contributed to the main text and the statistical analyses.

DATA AVAILABILITY STATEMENT

Data used in this article are available at the URJC public repository under the following link: http://repositories.biodiversos.org/Luzuriaga_A.L/.

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REFERENCES

- Anderson, M. J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46.
- Anderson, M. J. (2014) *Permutational Multivariate Analysis of Variance (PERMANOVA)*. Wiley StatsRef: Statistics Reference Online, 1–15. <https://doi.org/10.1002/9781118445112.stat07841>.
- Bernard-Verdier, M., Navas, M. L., Vellend, M., Violle, C., Fayolle, A. and Garnier, E. (2012) Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology*, 100, 1422–1433.
- Blank, L. and Carmel, Y. (2012) Woody vegetation patch types affect herbaceous species richness and composition in a Mediterranean ecosystem. *Community Ecology*, 13, 72–81.
- Boeken, B. R. (2018) Competition for microsites during recruitment in semiarid annual plant communities. *Ecology*, 99, 2801–2814.
- Boeken, B. and Orenstein, D. (2001) The effect of plant litter on ecosystem properties in a Mediterranean semi-arid shrubland. *Journal of Vegetation Science*, 12, 825–832.
- Boeken, B. and Shachak, M. (1994) Desert plant communities in human-made patches-implications for management. *Ecological Applications*, 4, 702–716.
- Botta-Dukát, Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16, 533–540.
- Butterfield, B. J. and Callaway, R. M. (2013) A functional comparative approach to facilitation and its context dependence. *Functional Ecology*, 27, 907–917.
- Callaway, R. M. (1998) Are positive interactions species-specific? *Oikos*, 82, 202–207.
- Callaway, R. M. and Pennings, S. C. (2000) Facilitation may buffer competitive effects: indirect and diffuse interactions among Salt Marsh plants. *The American Naturalist*, 156, 416–424.

- Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E. *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*, 335.
- Davies, K. W., Bates, J. D. and Miller, R. F. (2007) The influence of *Artemisia tridentata* ssp. *wyomingensis* on microsite and herbaceous vegetation heterogeneity. *Journal of Arid Environments*, *69*, 441–457.
- Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A. *et al.* (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, *15*, 295–304.
- Escudero, A., Martínez, I., de la Cruz, A., Otálora, M. A. G. and Maestre, F. T. (2007) Soil lichens have species-specific effects on the seedling emergence of three gypsophile plant species. *Journal of Arid Environments*, *70*, 18–28.
- Eskelinen, A. and Harrison, S. P. (2015) Resource colimitation governs plant community responses to altered precipitation. *Proceedings of the National Academy of Sciences*, *112*, 13009–13014.
- Espinosa, C. I., Luzuriaga, A. L., De La Cruz, M. and Escudero, A. (2014) Climate and grazing control nurse effects in an Ecuadorian dry shrubby community. *Journal of Tropical Ecology*, *30*, 23–32.
- Filazzola, A. and Lortie, C. J. (2014) A systematic review and conceptual framework for the mechanistic pathways of nurse plants. *Global Ecology and Biogeography*, *23*, 1335–1345.
- Flores, J. and Jurado, E. (2003) Flores 2003 Are nurse-protégé interactions more common among plants from arid environments. *Journal of Vegetation Science*, *14*, 911–916.
- Forseth, I. N., Wait, D. A. and Casper, B. B. (2001) Shading by shrubs in a desert system reduces the physiological and demographic performance of an associated herbaceous perennial. *Journal of Ecology*, *89*, 670–680.
- Franco, A. C. and Nobel, P. S. (1988) Interactions between seedlings of *Agave Deserti* and the Nurse Plant *Hilaria Rigida*. *Ecology*, *69*, 1731–1740.
- Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P. and Aerts, R. (2010) Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? *New Phytologist*, *186*, 879–889.
- García-Camacho, R., Metz, J., Bilton, M. C. and Tielbörger, K. (2017) Phylogenetic structure of annual plant communities along an aridity gradient. Interacting effects of habitat filtering and shifting plant–plant interactions. *Israel Journal of Plant Sciences*, *64*, 122–134. <https://doi.org/10.1080/07929978.2017.1288477>.
- Gibert, A., Gray, E. F., Westoby, M., Wright, I. J. and Falster, D. S. (2016) On the link between functional traits and growth rate: meta-analysis shows effects change with plant size, as predicted. *Journal of Ecology*, *104*, 1488–1503.
- Götzenberger, L., de Bello, F., Bräthen, K. A., Davison, J., Dubuis, A., Guisan, A. *et al.* (2012) Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews*, *87*, 111–127.
- Hernandez, R. R. and Sandquist, D. R. (2011) Disturbance of biological soil crust increases emergence of exotic vascular plants in California sage scrub. *Plant Ecology*, *212*, 1709–1721.
- Holmgren, M. (2000) Combined Effects of Shade and Drought on Tulip Poplar Seedlings : trade-Off in Tolerance or Combined effects of shade and drought on tulip poplar seedlings : in tolerance or facilitation? responses of individual plants to different. *Oikos*, *90*, 67–78.
- Holzapfel, C. and Mahall, B. E. (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology*, *80*, 1747–1761.
- Holzapfel, C., Tielbörger, K., Parag, H. A., Kigel, J. and Sternberg, M. (2006) Annual plant–shrub interactions along an aridity gradient. *Basic and Applied Ecology*, *7*, 268–279.
- Huston, M. and Smith, T. (1987) Plant succession: life history and competition. *The American Naturalist*, *130*, 168–198.
- Huxman, T. E., Kimball, S., Angert, A. L., Gremer, J. R., Barron-Gafford, G. A. and Lawrence Venable, D. (2013) Understanding past, contemporary, and future dynamics of plants, populations, and communities using Sonoran desert winter annuals. *American Journal of Botany*, *100*, 1369–1380.
- Kadmon, R. and Shmida, A. (1990) Competition in a variable environment: an experimental study in a desert annual plant population. *Israel Journal of Botany*, *39*, 403–412.
- Karlsson, P. S. and Méndez, M. (2005) *The Resource Economy of Plant Reproduction*. Cambridge, MA: Academic Press. <https://doi.org/10.1016/B978-012088386-8/50001-6>
- Laliberté, E. and Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.
- Laliberté, E., Legendre, P. and Shipley, B. (2014) *FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology. R Package Version. 1.0-12*. Available at: <http://cran.rproject.org/web/packages/FD>. Accessed November, 2017.
- Langhans, T. M., Storm, C. and Schwabe, A. (2009) Biological soil crusts and their microenvironment: impact on emergence, survival and establishment of seedlings. *Flora: Morphology, Distribution, Functional Ecology of Plants*, *204*, 157–168.
- Legendre, P. and Legendre, L. (1998) *Numerical Ecology*. Amsterdam, Netherlands: Elsevier.
- Lortie, C. J., Gruber, E., Filazzola, A., Noble, T. and Westphal, M. (2018) The groot effect: plant facilitation and desert shrub regrowth following extensive damage. *Ecology and Evolution*, *8*, 706–715.
- Luzuriaga, A. L. and Escudero, A. (2008) What determines emergence and net recruitment in an early succession plant community? Disentangling biotic and abiotic effects. *Journal of Vegetation Science*, *19*, 445–456.
- Luzuriaga, A. L., Sánchez, A. M., Maestre, F. T. and Escudero, A. (2012) Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. *PLoS ONE*, *7*, 1–9.
- Luzuriaga, A. L., González, J. M. and Escudero, A. (2015) Annual plant community assembly in edaphically heterogeneous environments. *Journal of Vegetation Science*, *26*, 866–875.
- Madrigal-González, J., Kelt, D. A., Meserve, P. L., Squeo, F. A. and Gutiérrez, J. R. (2016) Shrub-ephemeral plants interactions in semi-arid north-central Chile: is the nurse plant syndrome manifested at the community level? *Journal of Arid Environments*, *126*, 47–53.
- Mark, W. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227.
- McCune, B. and Grace, J. B. (2002) *Analysis of Ecological Communities*. Gleneden Beach, OR, USA: MJM Software Design.
- Mendoza-Aguilar, D. O., Cortina, J. and Pando-Moreno, M. (2014) Biological soil crust influence on germination and rooting of two key species in a *Stipa tenacissima* steppe. *Plant and Soil*, *375*, 267–274.
- Miriti, M. N. (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology*, *94*, 973–979.
- Moro, M. J., Pugnaire, F. I., Haase, P. and Puigdefábregas, J. (1997) Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semi-arid environment. *Functional Ecology*, *11*, 425–431.
- Muscarella, R. and Uriarte, M. (2016) Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences*, *283*, 1–9.
- O'Brien, M. J., Pugnaire, F. I., Armas, C., Rodríguez-Echeverría, S. and Schöb, C. (2017) The shift from plant–plant facilitation to competition under severe water deficit is spatially explicit. *Ecology and Evolution*, *7*, 2441–2448.
- Offer, Z. Y., Zaady, E. and Shachak, M. (1998) Aeolian particle input to the soil surface at the Northern limit of the Negev desert. *Arid Land Research and Management*, *12*, 55–62.



- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B. et al. (2017) *vegan: Community ecology package, version 2.3-5*. Available at: <http://CRAN.R-project.org/package=vegan>. Accessed November, 2017.
- Peralta, A. M. L., Sánchez, A. M., Luzuriaga, A. L. and Escudero, A. (2016) Factors driving species assemblage in Mediterranean soil seed banks: from the large to the fine scale. *Annals of Botany*, 117, 1221–1228.
- Peralta, A. M. L., Sánchez, A. M., Luzuriaga, A. L., de Bello, F. and Escudero, A. (2019) Evidence of functional species sorting by rainfall and biotic interactions: a community monolith experimental approach. *Journal of Ecology*, 107, 2772–2788.
- Prieto, I., Padilla, F. M., Armas, C. and Pugnaire, F. I. (2011) The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics*, 13, 181–187.
- R Core Team (2017) *R: A language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>. Accessed November, 2017.
- Rao, C. R. (1982) Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology*, 21, 24–43.
- Reich, P. B., Walters, M. B. and Ellsworth, D. S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences*, 94, 13730–13734.
- Resco De Dios, V., Weltzin, J. F., Sun, W., Huxman, T. E. and Williams, D. G. (2014) Transitions from grassland to savanna under drought through passive facilitation by grasses. *Journal of Vegetation Science*, 25, 937–946.
- Richards, J. H. and Caldwell, M. M. (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia*, 73, 486–489.
- Sánchez, A., Luzuriaga, A. L., Peralta, A. L. and Escudero, A. (2014) Environmental control of germination in semiarid Mediterranean systems: the case of annuals on gypsum soils. *Seed Science Research*, 24, 247–256.
- Schöb, C., Armas, C. and Pugnaire, F. I. (2013) Direct and indirect interactions co-determine species composition in nurse plant systems. *Oikos*, 122, 1371–1379.
- Segoli, M., Ungar, E. D., Giladi, I., Arnon, A. and Shachak, M. (2012) Untangling the positive and negative effects of shrubs on herbaceous vegetation in drylands. *Landscape Ecology*, 27, 899–910.
- Seifan, M., Seifan, T., Ariza, C. and Tielbörger, K. (2010) Facilitating an importance index. *Journal of Ecology*, 98, 356–361.
- Serpe, M. D., Zimmerman, S. J., Deines, L. and Rosentreter, R. (2008) Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts. *Plant and Soil*, 303, 191–205.
- Soliveres, S., Eldridge, D. J., Hemmings, F. and Maestre, F. T. (2012) Nurse plant effects on plant species richness in drylands: the role of grazing, rainfall and species specificity. *Perspectives in Plant Ecology, Evolution and Systematics*, 14, 402–410.
- Stern, A., Gradus, Y., Meir, A., Krakover, S. and Tsoar, H. (Eds.) (1986) *Atlas of the Negev*. Beersheva, Israel: Ben-Gurion University of the Negev.
- Teomin, N. (1990) *Soil Survey in the Sayeret Shaked Park*. Gilat, Israel: Jewish National Fund.
- Tielbörger, K. and Kadmon, R. (2000) Temporal environmental variation tips the balance. *Ecology*, 81, 1544–1553.
- Tilman, D., Hill, J. and Lehman, C. (2006) Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, 314, 1598–1600.
- Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T. and Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845.
- Weedon, J. T. and Facelli, J. M. (2008) Desert shrubs have negative or neutral effects on annuals at two levels of water availability in arid lands of South Australia. *Journal of Ecology*, 96, 1230–1237.
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F. et al. (2004) The worldwide leaf economics spectrum. *Nature*, 428, 821–827.
- Zaady, E. and Shachak, M. (1994) Mycophytic soil crust and ecosystem leakage in the Negev desert. *American Journal of Botany*, 81, 109.

SUPPORTING INFORMATION

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

Appendix S1. (a) Location of the study site (Sayeret Shaked Park) in the Negev desert (Israel) (modification from Stern et al. (1986)), with the annual rainfall isohyets represented. Images show (b) a general view of the annual community; (c) a *Carthamus tenuis* patch; (d) an individual of *Thymelaea hirsuta*; and (e) of *Noaea mucronata*

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